Inheritance of Slow Rusting of Barley Infected with Puccinia hordei and Selection of Latent Period and Number of Uredia

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ABSTRACT

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The inheritance of slow rusting was studied using nine crosses among fast- and slow-rusting barley cultivars or lines infected with *Puccinia hordei*. Progenies from the crosses were advanced by single seed descent, and 100 F_5 families and parents of each cross were planted in replicated hill plots at St. Paul and Rosemount, MN. The area under the disease progress curve was used to indicate the degree of slow rusting. The slow-rusting character behaved as a quantitatively inherited trait in that the progenies were distributed continuously from slow to fast rusting and transgressive segregation occurred in most of the crosses. Estimates of heritability for slow rusting ranged from 53 to 89% among the various crosses tested at Rosemount, indicating that selection for the slow-rusting character should be effective. Selection experiments with F_3 plants from three crosses among fast- and slow-rusting barleys indicated that selection for latent period was effective but selection for relative numbers of uredia per square centimeter of leaf surface was not, probably because the plants could not be inoculated uniformly.

Leaf rust of barley (*Hordeum vulgare* L.) caused by *Puccinia hordei* Otth has not been a significant factor in barley production in the United States during the past 25 years, but this favorable situation may not continue because the disease is now commonly observed throughout the upper Mississippi Valley. In some yield trials in Minnesota, leaf rust has reduced yield. During 1970–1972 several hundred barley lines and cultivars were rated susceptible to leaf rust in natural epidemics at Crookston, MN, but some rusted more slowly than others. Therefore, the inheritance of the slow-rusting type of resistance was studied, using the area under the disease progress curve to indicate the degree of slow rusting. Selection for two components of slow rusting—latent period and number of uredia per square centimeter of leaf surface—also was attempted.

MATERIALS AND METHODS

Inheritance of slow rusting. Nine barley populations were derived from several fast- or slow-rusting cultivars and lines that were crossed in the following combination: fast ruster × fast ruster (Larker × Cree), fast ruster × slow ruster (Larker × Rogers, Cree × MN7572, MN7544 × Cree, M25 × MN7572, and MN9062 × Cree), and slow ruster × slow ruster (Rogers × MN7572, Rogers × MN7544, and MN9062 × MN7544).

The slow- and fast-rusting characteristics of the parents had been determined in a natural epidemic in 1975. After 100 familes in each of the crosses were advanced to the F_4 generation by single seed descent, the parents and F_5 families were planted in hill plots in a randomized complete block with three replications at St. Paul and Rosemount, MN. The hills were planted 30.5 cm apart with 10–15 seeds per hill, and each population was arranged in two parallel rows 15.6 m long bordered by hills of Manker, a cultivar susceptible to leaf rust. Border hills were inoculated with oil (Mobilsol 106) suspensions of urediospores of races 9 and 23 of *P. hordei* that were frequently isolated in the Midwest.

Rust severity, based on the modified Cobb's scale (9), was estimated three times at Rosemount and twice at St. Paul at weekly intervals during the course of the epidemic. Evaluation of rust severity ended when the plants were ripe. The area under the disease progress curve (AUDPC), computed with the Fortran IV subroutine AREA and the associated subroutine INTEG (1), was the statistic used to indicate the slow-rusting character of the lines. AUDPC data for each cross were used to obtain an analysis of variance with the computer program BMD 08V. Heritability estimates were calculated on a line basis, using the ratio of genetic variance to total variance (13).

Negative estimates of variance components were not encountered in calculating the total of phenotypic variance. Standard error for heritability estimates were computed with the formula:

$$\text{std} = \sqrt{\frac{\text{var.}\hat{\sigma}^2_G}{\hat{\sigma}^2_p}}$$

where: $\hat{\sigma}^2_G$ = genetic variance and $\hat{\sigma}^2_p$ = phenotypic variance.

$$\text{The variance of } \hat{\sigma}^2_G = \frac{2}{c^2}\left[\frac{(MS_l)^2}{\text{d.f.}} + \frac{(MS_{lp})^2}{\text{d.f.}}\right]$$

where: c = locations × replications, MS_l = mean square for lines, MS_{lp} = mean square for lines × locations, and d.f. = degree of freedom for respective mean square.

The normality of the population distributions, according to the AUDPC for the F_5 lines, was tested using the chi-square test for goodness of fit (14).

Selection for components of slow rusting. The latent period and the relative number of uredia on the upper surface of the leaves were studied in a selection experiment in the greenhouse with populations of plants from the following crosses: fast ruster × fast ruster (Larker × Cree), slow ruster × fast ruster (MN7544 × Cree), and slow ruster × slow ruster (Rogers × MN 7544). These three combinations are referred to hereafter as FF, SF, and SS, respectively.

Six F_3 plants from the FF and SF crosses and each parent and five F_3 plants from the SS cross and each parent and Larker, a fast-

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rusting cultivar, were inoculated as uniformly as possible in a settling tower. The base of the tower had a platform that revolved as eight disks on the platform were rotated. Plants in the boot stage of growth, in 10-cm diameter pots, were placed on the rotating disks, and a cloud of urediospores of *P. hordei*, race 23, was created above the plants by shooting 5 mg of spores with a carbon dioxide blast into the air in the top of the tower. The plants were left in the settling tower for 5 min after the cloud had been created, placed in a moist chamber for 16 hr, and then moved to a greenhouse at 21 ± 4 C. These experiments were repeated 9, 10, and 11 times for the FF, SF, and SS crosses, respectively. Each F_3 plant tested was derived from a different F_2 plant.

In the greenhouse, natural light supplemented with fluorescent light provided a photoperiod of 16 hr. Plants were fed a 10-10-10 (NPK) fertilizer 3 wk after planting and at the time of inoculation.

The latent period and the number of uredia per square centimeter of the upper surfaces of both the flag and the second leaves were observed. The latent period was the time between inoculation and appearance of 50% of the uredia; uredia were counted each day after inoculation until no more developed.

Families in the F_4 generation were derived from various F_3 plants that had been selected for long or short latent periods or for high or low numbers of uredia per square centimeter of leaf area. From cross FF, six plants were selected with a long and five with a short latent period and four plants were selected with a high and five with a low number of uredia per square centimeter of leaf area. From cross SF, five plants were selected with a long and four with a short latent period and six plants were selected with a high and three with a low number of uredia per square centimeter of leaf area. From cross SS, five plants were selected with a long and four with a short latent period and four plants were selected with a high and four with a low number of uredia per square centimeter of leaf area.

The families of the F_4 generation and the parents were tested for latent period and uredia per square centimeter of leaf area. Four to seven plants per family and a parent were inoculated in the settling tower. Plants from different families but within the same population were inoculated together. The mean and standard errors for latent period and uredia per square centimeter of leaf surface for each F_4 family were determined.

Realized heritability values were calculated for latent period with the formula:

$$h_R^2 = (\bar{x}\ F_4\ \text{family}) - (\bar{x}_{Pa})\ /\ (F_3\ \text{selected plant}) - (\bar{x}_{Pb})$$

where $\bar{x}_{Pa}$ is the mean for parents tested with F_4 plants, $\bar{x}_{Pb}$ is the mean for parents tested with F_3 plants, and h_R^2 is the realized heritability value. Mean and standard errors for the long and short latent period selections in each population were computed from realized heritability values from the F_3 plant selections.

Realized heritability values were not calculated for uredia per square centimeter of leaf surface because a large amount of variation was associated with urediospore deposition.

The effectiveness of selecting latent period or number of uredia per square centimeter of leaf surface was determined when divergent selections were made from the same F_3 subpopulation. Student's *t* test was used to determine whether the divergent selections were significantly different.

RESULTS

Inheritance of slow rusting. At Rosemount, the epidemic started when most lines were heading and developed rapidly for 4 wk, until the plants were ripe. The mean initial rust severities ranged from 0 to 10%, and the terminal severities ranged from 30 to 100%.

At St. Paul, the epidemic started when most lines were in the soft-dough stage of growth and terminated 1–2 wk later. It did not develop uniformly throughout the nursery. The mean initial rust severities ranged from 0 to 10%, and the terminal severities ranged from 1 to 80%. The AUDPC of parental cultivars and lines infected at Rosemount and St. Paul is shown in Table 1.

At Rosemount, the F_5 progenies of all the crosses were continuously distributed (Fig. 1). The progenies from five crosses, namely, Larker × Cree (fast rusting × fast rusting), M25 × MN7572 and MN7544 × Cree (slow rusting × fast rusting), and MN9062 × MN7544 and Rogers × MN7572 (slow rusting × slow rusting), were normally distributed. The progenies from four crosses, namely, Cree × MN7572, Larker × Rogers, and MN9062 × Cree (slow rusting × fast rusting) and Rogers × MN7544 (slow rusting × slow rusting), were not noramlly distributed.

The estimate of heritability for AUDPC at Rosemount from the cross between Larker and Cree (two fast-rusting cultivars) was 53% (Table 2). The range of estimates of heritability for crosses of fast-rusting with slow-rusting parents was 64–89%, with a mean of 75%, and the range for crosses between two slow-rusting parents was 55–80%, with a mean of 70% (Table 2).

The AUDPC for most of the progenies from crosses between fast- and slow-rusting parents was intermediate to the parents. Parents of crosses between two fast- or two slow-rusting parents were near the center of the array of progenies, except for the cross Rogers × MN7572, in which the parents were located toward the slow-rusting end of the distribution (Fig. 1).

Lines that rusted significantly faster than the fast-rusting parents Larker and Cree and slower than the slow-rusting parents MN9062, Rogers, and MN7544 were observed in five crosses. The five crosses were Larker × Cree, MN9062 × Cree, Larker × Rogers, Rogers × MN7544, and MN9062 × MN7544. Lines that rusted significantly faster than the fast-rusting parents M25 and Cree but not as slowly as MN7572 were observed in the crosses M25 ×

TABLE 1. Mean area under disease progress curve (AUDPC) of parental barley cultivars and lines when tested with F_5 progeny at Rosemount and St. Paul, MN, for reaction to *Puccinia hordei*

Cultivar or line	Mean area under curve per location[a]	
	Rosemount	St. Paul
Fast rusting		
Larker	512	203
Cree	546	191
M25[b]	678	250
Slow rusting		
Rogers	250	25
MN7572	287	59
MN7544	222	30
MN9062	275	26

[a] Mean of 3–12 replicates.
[b] M = Minnesota advanced line now named Morex. The other MN lines are Minnesota breeding lines.

TABLE 2. Estimates of heritability for slow development of leaf rust from nine crosses among various fast- and slow-rusting barleys infected with *Puccinia hordei* at Rosemount and St. Paul, MN

Cultivar or line	Heritability estimates per location		
	Rosemount (%)	St. Paul (%)	Combined (%)
Fast × fast			
Larker × Cree	53 ± 16	31 ± 17	42 ± 16
Fast × slow			
Larker × Rogers	89 ± 14	71 ± 15	44 ± 16
MN9062 × Cree	79 ± 14	73 ± 15	62 ± 15
MN7544 × Cree	71 ± 15	62 ± 15	61 ± 15
M25 × MN7572	64 ± 15	54 ± 16	65 ± 15
Cree × MN7572	73 ± 15	25 ± 18	35 ± 17
Mean	75	57	53
Slow × slow			
Rogers × MN7572	55 ± 16	58 ± 16	35 ± 17
Rogers × MN7544	80 ± 15	0	13 ± 19
MN9062 × MN7544	76 ± 15	29 ± 18	24 ± 18
Mean	70	29	24

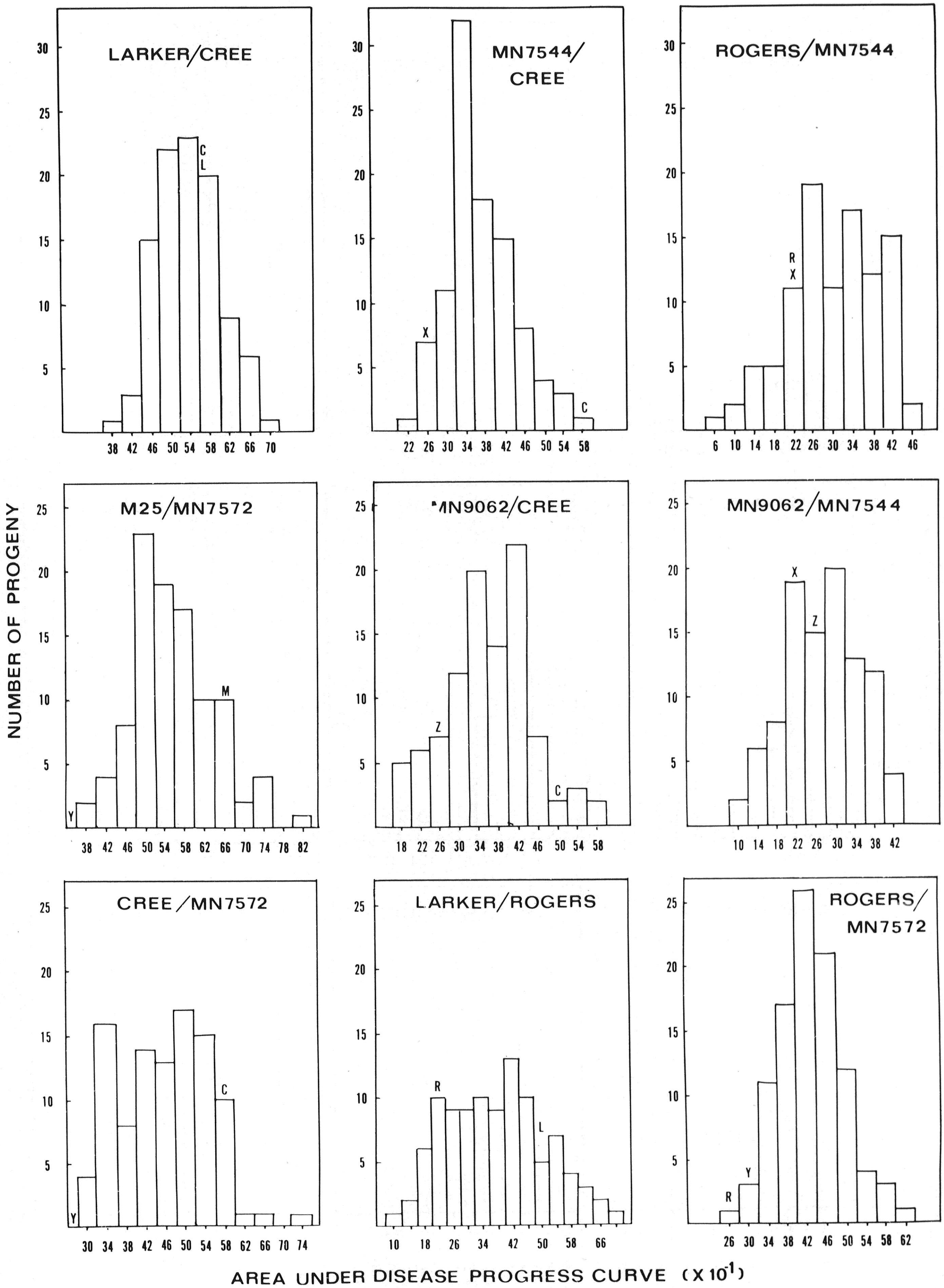

Fig. 1. Frequency distributions for the area under the disease progress curve of F_5 lines of nine barley crosses infected with *Puccinia hordei* at Rosemount, MN. The first letter of the parent cultivars indicates the class in which they fall. The letters M, X, Y, and Z, respectively, indicate the classes in which the parent lines M25, MN7544, MN7572, and MN9062 fall.

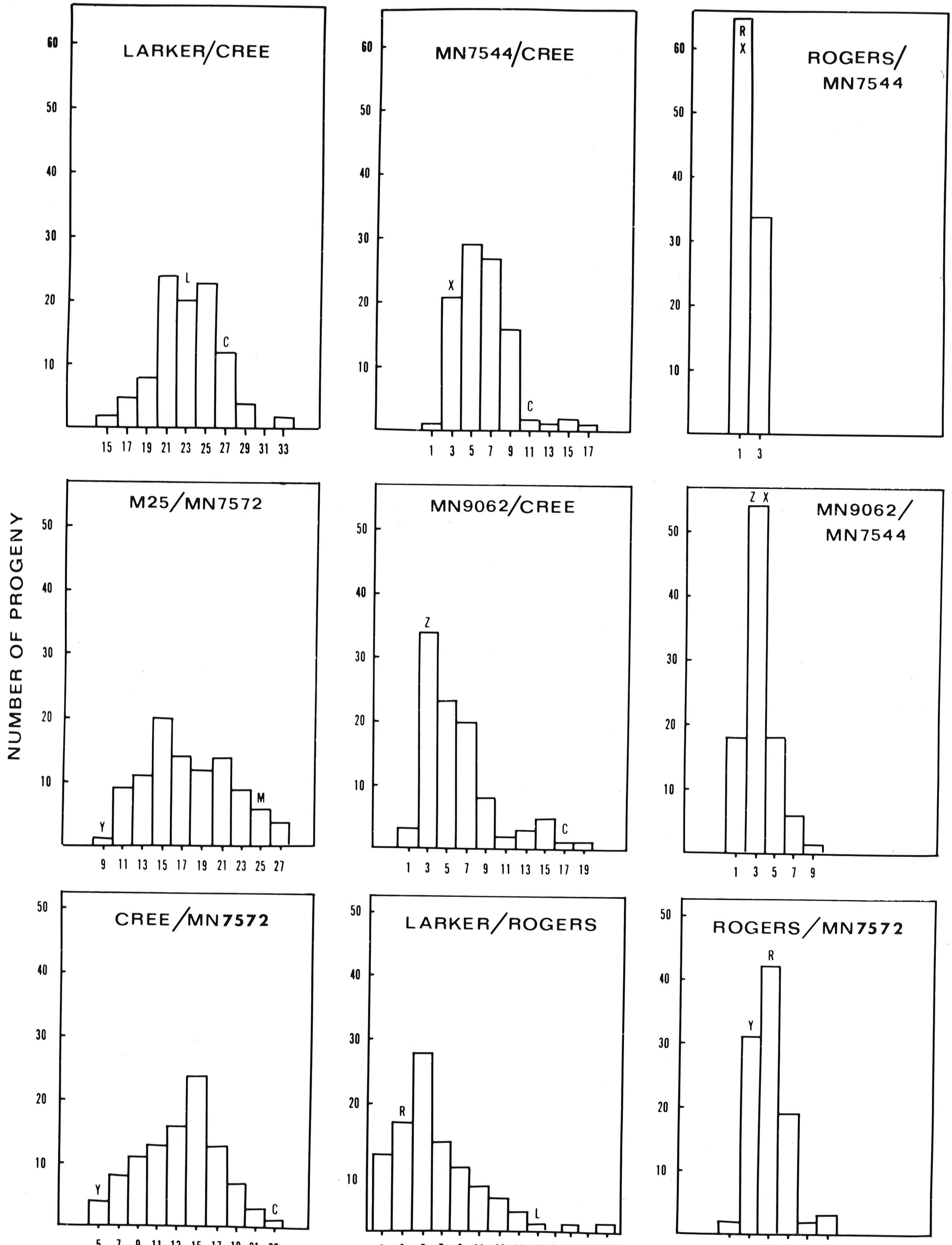

Fig. 2. Frequency distributions for the area under the disease progress curve of F_5 lines of nine barley crosses infected with *Puccinia hordei* at St. Paul, MN. The first letter of the parent cultivars indicates the class in which they fall. The letters M, X, Y, and Z, respectively, indicate the classes in which the parent lines M25, MN7544, MN7572, and MN9062 fall.

TABLE 3. Mean latent period for appearance of uredia of *Puccinia hordei* and mean number of uredia per square centimeter of leaf area for the parents in three crosses of barley that rusted slowly and rapidly; tests were with the F_3 populations and the F_4 families shown in Tables 5 and 6

Cross and parents	Latent period		Uredia per square centimeter	
	Tested with F_3[a] populations (days)	Tested with F_4[b] families (days)	Tested with F_3[a] populations (no.)	Tested with F_4[b] families (no.)
Cross FF (Larker × Cree)				
Larker	7.8 ± 0.3	7.7 ± 0.2	0.90 ± 0.28	1.94 ± 0.43
Cree	8.6 ± 0.3	8.3 ± 0.2	0.60 ± 0.15	1.40 ± 0.35
Cross SF (MN7544 × Cree)				
MN7544	11.1 ± 0.5	13.4 ± 0.4	0.28 ± 0.08	0.10 ± 0.04
Cree	8.4 ± 0.2	8.5 ± 0.2	0.53 ± 0.24	0.90 ± 0.22
Cross SS (Rogers × MN7544)				
Rogers	11.2 ± 0.5	13.2 ± 0.5	0.47 ± 0.21	1.38 ± 0.24
MN7544	11.4 ± 0.9	12.8 ± 0.4	0.42 ± 0.19	0.94 ± 0.42

[a]Values based on 9–11 observations.
[b]Values based on 7–8 observations.

TABLE 4. Realized heritability values when F_3 plants were selected for long or short latent periods using three barley crosses in which the parents rusted slowly or rapidly after infection with *Puccinia hordei*

Cross	Heritability value per latent period[a]	
	Long	Short
Cross FF (Larker × Cree)	0.54 ± 0.13	0.27 ± 0.22
Cross SF (MN7544 × Cree)	0.59 ± 0.14	0.75 ± 0.15
Cross SS (Rogers × MN7544)	0.13 ± 0.17	0.72 ± 0.26

[a]Number of F_4 families selected: for long latent periods, six in cross FF and five in crosses SF and SS; for short latent periods, five in cross FF and four in crosses SF and SS.

MN7572 and Cree × MN7572. Lines that rusted as slowly as but not slower than MN7544 (a slow-rusting line) and as fast as but not faster than Cree were observed in the progeny from the cross MN7544 × Cree. Lines that rusted as slowly as MN7572 and Rogers were observed in the cross Rogers × MN7572.

The F_5 progenies of most of the crosses at St. Paul were continuously distributed (Fig. 2). The progenies from crosses M25 × MN7572, MN7544 × Cree, and Larker × Rogers were normally distributed, whereas the progenies from the other six crosses were not.

The estimate of heritability for AUDPC at St. Paul from the cross between Larker and Cree (two fast-rusting parents) was 31% (Table 2). The range of estimates of heritability for crosses of fast-rusting with slow-rusting parents was 25–73%, with a mean of 57%. The range for crosses between two slow-rusting parents was 0–58%, with a mean of 29%.

At St. Paul, lines that rusted significantly faster than the fast-rusting parents Larker and Cree were observed in the crosses Larker × Cree, MN7544 × Cree, and Larker × Rogers. Lines with values equal to the slow-rusting parents were recovered, but lines that rusted significantly slower than the slow-rusting parents were not observed in any of the crosses.

When data from St. Paul and Rosemount were combined, the progenies of the crosses were continuously distributed and the frequency distributions resembled those from Rosemount (Fig. 1). The estimates of heritability for lines grown at both locations for each of the nine populations are shown in Table 2.

Selection for latent period. The mean latent periods, that is, the time required for 50% of the uredia to form, of MN7544 and Rogers (slow-rusting parents) were significantly ($P = 0.01$) longer than those of Larker and Cree (fast-rusting parents) (Table 3).

The FF cross had a mean realized heritability of 54 ± 13% when selection was for long latent period and 27 ± 22% when it was for short latent period (Table 4). The SF cross had a mean realized heritability of 59 ± 14% when selection was for a long latent period and 75 ± 15% when it was for a short latent period. The SS cross had a mean realized heritability of 13 ± 17% when selection was for a long latent period and 72 ± 26% when it was for a short latent period.

Divergent selections for long and short latent periods in F_3 plants were effective when tested with F_4 plants in each of the populations from the three crosses (Table 5). The selections were considered to be effective when the F_4 lines differed significantly from each other, according to Student's *t* test.

Selection for relative numbers of uredia. The method of inoculating adult barley plants did not produce uniform infection, as indicated by the variation in the numbers of uredia obtained in the F_3 populations (Table 6). For this reason it was not possible to estimate heritabilities for uredia per square centimeter of leaf surface, and the conclusions on the effectiveness of selection should be considered tentative. However, the information is presented in Table 6 because the data suggest that progress could be made with selection, especially with slow × fast and slow × slow crosses. The infection of the parents when tested with F_3 populations and F_4 families is shown in Table 3.

DISCUSSION

Slow rusting in barley infected with *P. hordei* behaved genetically as a quantitatively inherited trait in that the progenies were continuously distributed from slow to fast rusting and transgressive segregation occurred in most of the crosses. Because the heritability values were moderately high, significant progress in cultivar improvement programs should be possible. The heritability values were greatest in the crosses of slow- with fast-rusting parents, as might be expected. Nevertheless, progress in selecting for slow rusting would have been possible in all three types of crosses.

Our work indicates the importance of making tests in severe epidemics when evaluating slow rusting. Estimates of heritability were higher and standard errors were lower from data collected at Rosemount than from those collected at St. Paul, probably because the epidemic at Rosemount was more severe than that at St. Paul.

The transgressive segregation found in most crosses indicated that degrees of slow rusting lower than those found in the slow-rusting parents might be obtained. Furthermore, the fast-rusting transgressive segregates rusted faster than the fast-rusting cultivars Larker and Cree and the line M25.

Our conclusions on the inheritance of slow development of leaf rust in barley are in harmony with those of other workers. Slow rusting has been found to be inherited quantitatively in wheat infected with the stem rust fungus (12) and the leaf rust fungus (3) and in oats infected with the crown rust fungus (6). Heritability estimates for the slow development of rust in small grains have ranged from 46 to 92% (3,6,11,12), and transgressive segregation usually was observed (3,12).

TABLE 5. The mean and range for latent periods of F_3 populations and means of F_4 families derived from F_3 plants with long or short latent periods, from three barley crosses infected with *Puccinia hordei*

F_3 populations		Value of selected F_3 plant (days)	F_4 family mean[b] ± standard error (days)	Effectiveness of selection procedure[c]
Mean[a] (days)	Range[a] (days)			
Cross FF[d] (Larker × Cree)				
9.0	8–12	12	8.5 ± 0.2	Effective*
		8	7.8 ± 0.3	
8.0	7–9	9	8.5 ± 0.5	Effective†
		7	7.4 ± 0.3	
9.3	7–13	13	10.3 ± 0.6	Effective*
		7	7.8 ± 0.4	
Cross SF (MN7544 × Cree)				
11.7	9–15	15	15.1 ± 0.6	Effective**
		9	9.8 ± 0.1	
9.5	7–17	17	10.2 ± 0.1	Effective†
		7	9.1 ± 0.5	
Cross SS[e] (Rogers × MN7544)				
9.9	8–13	13	12.8 ± 1.3	Effective**
		8	8.9 ± 0.8	
9.0	7–13	13	14.1 ± 1.1	Effective**
		8	9.7 ± 0.5	
11.4	8–16	16	14.6 ± 0.7	Effective†
		13	12.5 ± 1.1	

[a]Based on six plants.
[b]Based on four to seven plants per family.
[c]Selection was effective, as judged by Student's *t* test, when the latent period of the F_4 family derived from an F_3 plant with a long latent period was significantly longer than the latent period of the F_4 family derived from an F_3 plant with a short latent period. † *, **, significant $P = 0.10$, 0.05, 0.01, respectively.
[d]FF = both parents rusted rapidly.
[e]SS = both parents rusted slowly.

TABLE 6. The mean and range for numbers of uredia per square centimeter of leaf area for F_3 populations and means of F_4 families derived from F_3 plants with low or high numbers of uredia per square centimeter of leaf area, from three barley crosses infected with *Puccinia hordei*

F_3 populations		Value of selected F_3 plant (no.)	F_4 family mean[b] ± standard error (no.)	Effectiveness of selection procedure[c]
Mean[a] (no.)	Range[a] (no.)			
Cross FF[d] (Larker × Cree)				
0.37	0.09–0.81	0.09	1.74 ± 0.26	Ineffective
		0.81	2.59 ± 0.60	
0.73	0.12–2.34	0.12	1.27 ± 0.54	Ineffective
		2.34	1.01 ± 0.35	
0.09	0.03–0.18	0.03	0.71 ± 0.26	Ineffective
		0.17	0.75 ± 0.13	
1.51	0.60–4.08	0.60	2.61 ± 1.37	Ineffective
		1.06	2.10 ± 0.89	
Cross SF (MN7544 × Cree)				
0.39	0.22–0.61	0.22	0.08 ± 0.03	Effective†
		0.61	1.60 ± 0.81	
0.12	0.03–0.32	0.04	0.21 ± 0.09	Effective**
		0.18	1.42 ± 0.20	
Cross SS[e] (Rogers × MN7544)				
0.64	0.19–0.90	0.19	0.21 ± 0.07	Effective**
		0.90	1.62 ± 0.18	
0.96	0.42–1.77	0.42	0.29 ± 0.12	Effective**
		0.86	1.34 ± 0.41	
3.15	0.54–6.53	0.54	0.78 ± 0.33	Ineffective
		4.74	0.54 ± 0.22	

[a]Based on six plants.
[b]Based on four to seven plants per family.
[c]Selection was effective, as judged by Student's *t* test, when the number of uredia of the F_4 family derived from an F_3 plant with a high number of uredia was significantly greater than the number of uredia of the F_4 family derived from an F_3 plant with a low number of uredia. †, **, significant $P = 0.10$, 0.01, respectively.
[d]FF = both parents rusted rapidly.
[e]SS = both parents rusted slowly.

There is little information on the inheritance of components of slow rusting. Latent period was found to be quantitatively inherited in barley infected with leaf rust (7). In our study, selection for latent period was effective in three crosses (Table 5). However, the mean realized heritabilities for a long latent period were low or moderately low (Table 4), and, as seen by the magnitude of the standard errors, a large amount of unaccountable variation existed (Table 4). Moreover, the realized heritabilities probably could have been higher and the variation probably could have been reduced if selection had been on a family basis.

Information on selecting for latent period in this study and information showing a high and significant correlation between latent period and AUDPC from a previous study (5) suggest that two or more selections for slow rusting each year may be effective in a breeding program. Selection could be practiced in the field with the use of the area under the disease progress curve and then in the greenhouse with the use of the latent period.

Even though the fact that different cultivars produce different numbers of uredia under the same conditions has been reported for several cereals infected with various rust fungi (2,4,8), there is little information on the heritability of this trait (10). Selection for uredia per square centimeter of leaf surface was ineffective in the cross between two fast-rusting parents but effective in the cross between a fast- and slow-rusting parent and in the cross between two slow-rusting parents (Table 6). However, the number of divergent selection from the three crosses was small, and more studies should be made before definite conclusions on the selection for uredia per square centimeter of leaf surface are made.

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