Heritability of Field Resistance to the Oat Crown Rust Fungus

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ABSTRACT

Four unadapted strains of oats *(Avena sativa)* with field resistance to crown rust *(Puccinia coronata)* were crossed with an adapted, but susceptible, cultivar. Lines from these crosses previously selected for adapted plant type were tested in two generations for resistance to crown rust, as measured by relative reduction in yield and kernel weight caused by crown rust infection. Lines from each of the four crosses showed the continuous variation from susceptibility to resistance characteristic of polygenic inheritance. Heritability values estimated from components of variance for resistance, measured in terms of yield reduction, ranged from 46 to 86%; and, in terms of reduction in kernel weight, from 65 to 92%. The relationship of yield to resistance in the absence of rust was generally negative, with correlation coefficients ranging from 0 to −0.69. None of the lines tested combined maximum yield with maximum resistance.

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Currently, there is much interest in the type of host disease resistance that is expressed under natural field conditions, as opposed to "seedling resistance." Field resistance (also commonly called "mature" or "adult plant" resistance) often is lower in degree than seedling resistance, but at the same time usually affords protection from a wider spectrum of races than does seedling resistance. Field resistance usually is polygenic in inheritance, and we hope, usually corresponds to the "horizontal" resistance of van der Plank (12). General aspects of the heritability (ratio of genetic to total variability) of field resistance and its possible use in plant breeding were reviewed recently (10).

There are many studies of the inheritance of oligogenically inherited reaction to the cereal rusts, and the subject has been covered in a review by Hooker (6). Heritability of polygenically controlled resistance to these rusts has been studied in detail for only a short time. The heritability of polygenic resistance to rust *(Puccinia sorghi)* of corn *(Zea mays)* was shown to be more than 85% in 45 of 65 different crosses (5). Heritability of tolerance to crown rust *(Puccinia coronata* Cda. var. *avenae* Fraser & Led.) of oats *(Avena sativa* L.), as measured by the response of grain yield to infection, was estimated to be about 50% in two crosses and 48% in a group of pure lines (9).

The purpose of the study reported here was to determine the heritability of the field resistance of four strains of oats, with the idea that such information might be useful in transferring field resistance from unadapted strains to adapted cultivars.

MATERIALS AND METHODS.—The basic experimental material consisted of four strains of oats (P.I. 174544, 197279, 174545, and 185783) shown previously to have a relatively high degree of field resistance to certain races of the crown rust fungus (7). Except for P.I. 174544, these were very poorly adapted to growing conditions in the mid-western United States. The four strains were crossed with the well-adapted, but highly susceptible, cultivar Clinton. Segregating lines were selected for adaptation with emphasis on maturity, in the F_2, F_3, and F_4 generations (11). About 100 adapted lines from each cross were then grown in the F_5 and F_6 and sometimes in the F_7 in hill plots (2) replicated eight times. Common, suitable races of the crown rust fungus were used to initiate epiphytotics artificially. A duplicate planting was maintained free of rust damage with a fungicide to show differences among the lines in the absence of rust. Responses to infection were then expressed as ratios of rusted to unrusted values to eliminate inherent differences among the lines that were not associated with infection. Data on grain yield and kernel weight (g), the latter based on a sample of 200 kernels, were recorded for all plots. Data on heading date were taken from three replications of unrusted plots each generation.

Statistical methods used to estimate heritability were similar to those found most useful in a previous study of the heritability of tolerance to crown rust infection (9). The analysis of variance and general formulas used to estimate genetic and phenotypic variances and heritability by the components of variance method (1, 4) are shown below (L = lines; Y = years; and R = replications):

Source	d.f.	m.s.	Expectation of m.s.
Lines	L-1	M1	$\sigma_e^2 + R\sigma_{LY}^2 + YR\sigma_L^2$
Lines × years	(L-1)(Y-1)	M2	$\sigma_e^2 + R\sigma_{LY}^2$
Error	Y(R-1)(L-1)	M3	σ_e^2

Genotypic component of variance $(\hat{\sigma}_g^2) = (M1 - M2)/YR$

Lines × years component $(\hat{\sigma}_{LY}^2) = (M2 - M3)/R$

Error component $(\hat{\sigma}_e^2) = M3$

Phenotypic variance $(\hat{\sigma}_{ph}^2) = \hat{\sigma}_g^2 + \hat{\sigma}_{LY}^2/Y + \hat{\sigma}_e^2/YR$

Heritability $(H) = \hat{\sigma}_g^2/\hat{\sigma}_{ph}^2 \times 100$.

The standard-units method of estimating heritability developed by Frey and Horner (3), in which regression values are obtained by use of data coded in terms of standard deviation units, was used also to estimate heritability in some analyses.

RESULTS.—*Growth conditions and severity of infection.*—Growing conditions were generally favorable, except that yield data from the F_6 of the crosses with P.I. 174544 and 197279 were lost because of hail. Kernel-weight data were obtained for this material.

In most instances, rust developed heavily, with yields of the susceptible Clinton parent reduced to less than half of those of the unrusted controls. Kernel weights of Clinton were reduced by about 40%. Unfortunately, conditions for development of the rust were not favorable when the F_6 lines from crosses with P.I. 174545 and 185783 were grown. The rust did significantly reduce yield and kernel weight, but not nearly as much as had been anticipated.

Mode of inheritance.—Previous work (M. D. Simons, *unpublished)* with these field-resistant lines had been designed and carried out to test the hypothesis that the resistance was under some kind of relatively simple oligogenic control. With the possible partial exception of P.I. 174544 (8), no such oligogenic resistance was ever shown.

The data shown graphically in Figs. 1 and 2 strongly suggest that a large number of unselected lines derived from such crosses would form smooth curves for response of both yield and kernel weight to infection. Such curves would be expected if the resistant parents carried many independent genes for resistance. Therefore, it is reasonable to conclude that the rust resistance of these four lines is determined polygenically.

Heritability.—Because of loss of F_6 yield data for the P.I. 174544 and P.I. 197279 progenies, the F_7 was grown so that data for 2 years would be available for estimating possible year × line interactions. Heritabilities calculated from components of variance for response of yield to infection in the F_5 and F_7 were 63% and 84% for P.I. 174544 and 197279, respectively (Table 1). Corresponding heritability values calculated by regression in standard units were 48% and 74%.

Because the hail damage did not result in loss of all the grain, it was possible to take kernel-weight data on the F_6 for these two crosses. Therefore, components of variance for response of kernel weight to infection were calculated from analysis of variance of data from three generations. The heritability values of 89% for P.I. 174544, and 92% for P.I. 197279, were appreciably higher than corresponding figures for yield response. Because data for three generations were available, it was possible to make three estimates of heritability based on the regression of one generation on another. These estimates were high, ranging from 67% to 85%, but not quite as high as the estimates made from components of variance.

The light rust infection in progenies from P.I. 174545 and 185783 in the F_6 raised questions about the desirability of combining the F_5 and F_6 data. Hence, heritability values were calculated with combined data from the two generations, and also with data from only the F_5, which had been heavily infected. Heritability values for response of yield in the F_5 were 76% and 86% for P.I. 174545 and P.I. 185783, respectively. Corresponding values based on the combined F_5 and F_6 were appreciably lower, especially for P.I. 174545.

Estimates of heritability, in terms of kernel-weight response to infection in the F_5, were a little higher than those estimates for yield response. Data for kernel-weight response from combined F_5 and F_6 gave estimates that were appreciably lower than those from the F_5 alone. These values, however, were still relatively higher than the corresponding estimates based on response of yield to infection.

Heritabilities of yield and kernel-weight response for P.I. 174545 and 185783, estimated by regression of F_6 on F_5, in standard units, were disappointingly low (Table 1). The disparity between these estimates and those obtained from components of variance probably was related to the paucity of infection in the F_6.

Relationship of resistance to plant type and performance.—Relative maturity, as measured by date of heading, was one of the principal traits considered in the process of selecting lines to be used in this heritability study. An attempt was made to select lines that were similar in maturity to Clinton, mainly because maturity must be within a certain range for meaningful results. However, maturity was not deemed to be as important in heritability studies in which the principal objective was not to compare different lines. Therefore, the data were not corrected for the small differences in heading dates that existed (11). These small differences were of some importance, because most simple correlation coefficients of yield and kernel-weight responses with maturity were statistically significant, even though generally not large (Table 2).

Practically, the relationships between yield and response to rust are of the utmost importance. An indication of the degree of such possible relationships is furnished by the simple correlation coefficients of yield responses and kernel-weight responses with yields in the unrusted control plots (Table 2). These coefficients for progenies from P.I. 174544 and 197279 in the F_6 ranged from −0.451 to −0.692. All were negative, and all were statistically significant. The corresponding coefficients in F_5 were not as high, but three of the four were significant, and all were again negative. Thus a real tendency appeared for greater resistance to be associated with lower yield in these two crosses.

The negative relationship between response to infection and yield in progenies from P.I. 174545 and

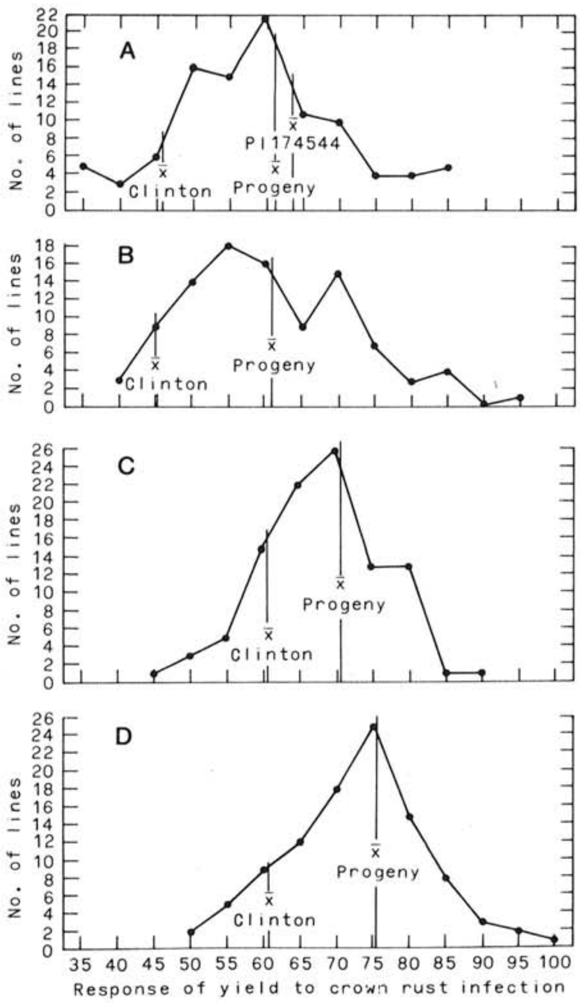

Fig. 1-(A to D). Distribution of progeny lines from oat crosses according to the responses of their yields to crown rust infection (response expressed as a ratio of yields of rusted plots to yields of unrusted control plots, obtained by dividing the rusted value by the unrusted value). **A)** Progeny lines from Clinton (susceptible) × P.I. 174544 (resistant). **B)** Lines from Clinton × P.I. 197279. **C)** Lines from Clinton × P.I. 174545. **D)** Lines from Clinton × P.I. 185783.

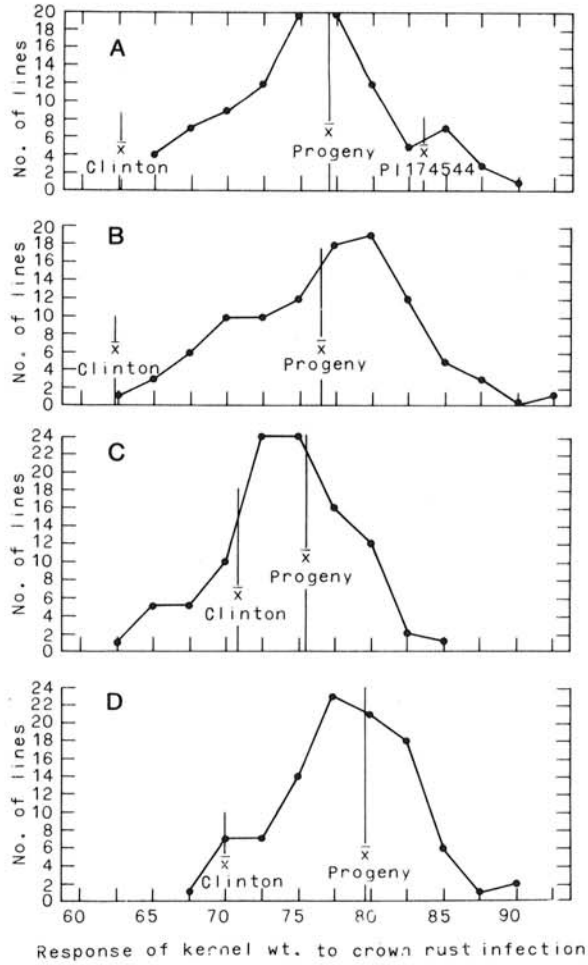

Fig. 2-(A to D). Distribution of progeny lines from oat crosses according to the responses of their kernel weights to crown rust infection (response expressed as a ratio of kernel weights of rusted plots to kernel weights of unrusted control plots, obtained by dividing the rusted value by the unrusted value). **A)** Progeny lines from Clinton (susceptible) × P.I. 174544 (resistant). **B)** Lines from Clinton × P.I. 197279. **C)** Lines from Clinton × P.I. 174545. **D)** Lines from Clinton × P.I. 185783.

185783 was not as pronounced as in progenies from P.I. 174544 and 197279. For progenies from P.I. 174545, there seemed to be little, if any, relationship. The correlation coefficients for progenies from P.I. 185783 were statistically significant, but were low in absolute terms. For practical purposes, it could be assumed that there was little relationship between yield and resistance in these two crosses.

From another perspective, the lines with the highest inherent yielding ability were compared individually with the susceptible Clinton parent for both yield in the absence of rust and response to infection. With progenies from P.I. 174544, data on the resistant parent were also available. The 10 highest-yielding lines from this parent varied considerably in response to crown rust. Three of the 10 showed greater yield reductions than Clinton, but four were significantly better than Clinton. None was as resistant as P.I. 174544. In kernel-weight response, all were better than Clinton, as were most of the other lines, but they also were all significantly inferior to P.I. 174544.

Because P.I. 197279 is so poorly adapted to midwestern conditions, it could not be included in these experiments. Interestingly, none of the lines, in the absence of rust, yielded as well as Clinton, even though they were superficially similar in plant type and maturity. Six of the 10 highest-yielding lines showed significantly less response to crown rust in terms of yield reduction than did Clinton. Because the resistant parent was not included, there was no direct estimate of the maximum amount of rust protection that might be expected. However, several lines had significantly higher resistance than the most resistant of the high-yielding lines. In terms

TABLE 1. Heritability of field resistance to the crown rust fungus (in terms of yield and kernel-weight responses to infection) based on data from F_5, F_6, and F_7 generations of four resistant lines crossed with the susceptible cultivar Clinton

Resistant parent	Generation	Method of calculation	Heritability (%) Yield	Heritability (%) Kernel weight (g/200 kernels)
P.I. 174544	F_5, F_7	Components of variance	63	. . .
	F_5, F_6, F_7		. . .	89
	F_5, F_7	Regression in standard units	48	67
	F_5, F_6		. . .	85
	F_6, F_7		. . .	70
P.I. 197279	F_5, F_7	Components of variance	84	. . .
	F_5, F_6, F_7		. . .	92
	F_5, F_7	Regression in standard units	74	87
	F_5, F_6		. . .	85
	F_6, F_7		. . .	86
P.I. 174545	F_5	Components of variance	76	79
	F_5, F_6		46	65
	F_5, F_6	Regression in standard units	18	22
P.I. 185783	F_5	Components of variance	86	90
	F_5, F_6		69	80
	F_5, F_6	Regression in standard units	23	36

TABLE 2. Correlation coefficients between certain traits in progeny of crosses involving four crown rust-resistant parents and the susceptible cultivar Clinton

Resistant parent	Traits	Generation F_5	Generation F_6 or F_7
P.I. 174544	Yield index and heading date	−0.307**[a]	−0.665**
	Kernel wt index and heading date	−0.158	−0.559**
	Yield index and unrusted yield	−0.421**	−0.692**
	Kernel wt index and unrusted yield	−0.119	−0.451**
P.I. 197279	Yield index and heading date	−0.418**	−0.436**
	Kernel wt index and heading date	−0.283**	−0.389**
	Yield index and unrusted yield	−0.474**	−0.635**
	Kernel wt index and unrusted yield	−0.516**	−0.535**
P.I. 174545	Yield index and heading date	−0.273**	0.015
	Kernel wt index and heading date	−0.256**	−0.243**
	Yield index and unrusted yield	0.053	−0.080*
	Kernel wt index and unrusted yield	0.047	0.173**
P.I. 185783	Yield index and heading date	−0.190**	−0.211**
	Kernel wt index and heading date	−0.126*	−0.128*
	Yield index and unrusted yield	−0.266**	−0.078*
	Kernel wt index and unrusted yield	−0.232**	−0.155**

[a] Correlation coefficient significant $P = 0.05$ (*) and $P = 0.01$ (**), respectively.

of reduction in kernel weight, all the lines were superior to the susceptible Clinton parent. All of the 10 highest-yielding lines, however, were significantly inferior in kernel-weight response to the lines shown to be most resistant by this criterion.

Lines derived from P.I. 174545 yielded differently than lines from P.I. 197279, with many yielding more grain than the Clinton parent. In fact, all of the 10 highest yielding lines were well above Clinton. Only two of these high yielders were significantly more resistant than Clinton, as measured by response of yield to infection, and both obviously were far less resistant than the most resistant of the derived lines. Five of the high-yielding lines were significantly more resistant than Clinton, with response of kernel weight as the criterion of resistance. Again, several lower-yielding lines showed better resistance.

The 10 highest-yielding lines from P.I. 185783 were about equal to Clinton for yield. Most were significantly superior to Clinton for rust resistance, as measured by either yield or kernel-weight response. The most resistant lines, however, were not among this group of high yielders.

DISCUSSION.—If the polygenic field resistance to crown rust that was the subject of this study is to be practical, it must be transferred to adapted cultivars without resulting in any appreciable loss of yield. The overall correlations between resistance and yield among lines from the four crosses suggested that, although there probably was a trend toward a negative relationship between these traits, lines combining high yield and high resistance would not be too difficult to select. In fact, many of the highest-yielding lines had more resistance than the Clinton parent. Disappointingly, none of the lines from any of the crosses combined the highest yielding ability with maximum resistance.

One explanation is that the number of genes for resistance is so large that very large populations must be grown and tested for a reasonable chance of finding a line that combines all or most of these resistance genes with whatever genes are needed for high yielding potential. Alternatively, linkage of resistance genes and undesirable genes in the resistant parents may possibly account for the lack of lines combining high yield and high resistance. If only part of the resistance genes are tightly linked in this way, it might be very difficult to locate lines combining maximum resistance and yield.

A third possibility is suggested by a hypothesis developed by van der Plank (12). He theorized that polygenic horizontal resistance is governed by genes that are not special resistance genes, but are simply genes that regulate ordinary processes in plants. Thus, if these "processes", whether physiological or anatomical, that actually account for the resistance are inimical to maximum yield, it would, in theory, be impossible ever to combine maximum yield and maximum resistance.

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