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Responses to Selection for Partial Resistance to Crown Rust in Oat

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Crown rust, caused by the fungal pathogen, *Puccinia coronata* Corda var. *avenae* W.P. Fraser Ledingham, reduces kernel quality and grain yield in oat (*Avena sativa* L.). Partial resistance is considered to be a durable form of rust resistance. This study sought to evaluate the feasibility of simultaneously improving partial resistance to crown rust, grain yield, and seed weight in an oat population, and to estimate predicted and realized heritabilities for area under disease progress curve (AUDPC) and genetic correlations between AUDPC and agronomic traits in both crown rust-inoculated and fungicide-treated plots. A single cycle of selection for partial resistance to crown rust was performed. The initial (C_0) and selected (C_1) generations were evaluated in a field experiment in 2001 and 2002 at two Iowa locations. Selection on an index increased the levels of crown rust resistance, grain yield, and seed weight in crown rust–inoculated plots, and seed weight in fungicide-treated plots. However, the change for the grain yield in fungicide-treated plots was not significant. In both C_0 and C_1 populations, AUDPC was highly heritable ($H = 0.77$ and 0.78 respectively), and was favorably correlated with grain yield, seed weight, and test weight measured in inoculated plots. Realized heritabilities for all traits except grain yield under fungicide treatment were consistent with predicted heritabilities. Our results suggested that index selection could increase levels of crown rust resistance, grain yield, and seed weight simultaneously.

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ABSTRACT

Crown rust, caused by the fungal pathogen, *Puccinia coronata* Corda var. *avenae* W.P. Fraser Ledingham, reduces kernel quality and grain yield in oat (*Avena sativa* L.). Partial resistance is considered to be a durable form of rust resistance. This study sought to evaluate the feasibility of simultaneously improving partial resistance to crown rust, grain yield, and seed weight in an oat population, and to estimate predicted and realized heritabilities for area under disease progress curve (AUDPC) and genetic correlations between AUDPC and agronomic traits in both crown rust-inoculated and fungicide-treated plots. A single cycle of selection for partial resistance to crown rust was performed. The initial (C_0) and selected (C_1) generations were evaluated in a field experiment in 2001 and 2002 at two Iowa locations. Selection on an index increased the levels of crown rust resistance, grain yield, and seed weight in crown rust−inoculated plots, and seed weight in fungicide-treated plots. However, the change for the grain yield in fungicide-treated plots was not significant. In both C_0 and C_1 populations, AUDPC was highly heritable (H = 0.77 and 0.78 respectively), and was favorably correlated with grain yield, seed weight, and test weight measured in inoculated plots. Realized heritabilities for all traits except grain yield under fungicide treatment were consistent with predicted heritabilities. Our results suggested that index selection could increase levels of crown rust resistance, grain yield, and seed weight simultaneously.

Crown rust is one of the most widespread and destructive diseases of cultivated oat. In susceptible oat cultivars, this disease can cause grain yield losses of up to 30% (Endo and Boewe, 1958; Frey et al., 1973). The disease can be controlled with fungicides or genetic resistance. Historically, resistance has been based on single major genes that confer complete resistance to specific pathotypes of *P. coronata*. However, new pathotypes with virulence to these genes have developed rapidly after the introduction of cultivars possessing them, rendering the resistance ineffective. A form of resistance that does not confer complete resistance but that is presumed to act against all pathotypes has been dubbed partial resistance (Parlevliet, 1978). Partial resistance is thought to be polygenic. Both because all pathotypes have some virulence against it and because it acts more broadly than single-gene resistance, partial resistance is hypothesized to cause smaller selection differentials between pathotypes and therefore slow the evolution of virulence relative to single-gene resistance (Simons, 1972). Thus, increasing partial resistance may provide genotypes capable of economically useful disease control for long periods of time.

Selection for partial resistance may provide an effective means to control crown rust resistance in oat. However, the value of a cultivar will generally not depend on the single trait of disease resistance. Agronomic and grain quality traits also strongly affect the value of a cultivar. Selection on one trait often affects other traits because of genetic correlation between traits. Genetic correlations between traits may be due to gene pleiotropy or linkage disequilibrium between loci (Falconer and Mackay, 1996). Therefore, selection on one trait is insufficient to generate genotypes useful as commercial varieties. For example, selection for greater β-glucan content in oat caused unfavorable correlated responses for agronomic performance in one population because β-glucan content was negatively genetically correlated with grain yield, biomass, and test weight (Cervantes-Martinez et al., 2002). Holland and Munkvold (2001) found that partial resistance to crown rust was favorably genetically correlated with grain yield and seed weight measured in pathogen-inoculated plots, but not significantly genetically correlated with grain yield and seed weight measured in fungicide-treated plots. These results suggested that selection combining partial resistance to crown rust with grain yield and seed weight would be possible for oat.

Index selection is the method of choice to simultaneously select for multiple traits (Baker, 1986). It allows appropriate consideration of economic value and genetic and phenotypic parameters. Sharma and Duveiller (2003) applied index selection to improve resistance to *Cochliobolus sativus* (Ito & Kurib.) Drechs. and *Pyrenophora tritici-repentis* (Died.) Drechs., maturity, and kernel weight in spring wheat. Area under disease progress curve was used as the measurement of disease severity. Their results from replicated field tests showed the reduction of AUDPC was associated with increased grain yield and kernel weight, without significant change for maturity.

The objectives of this research were to: (i) test the feasibility of improving partial resistance to crown rust, grain yield, and seed weight in an oat population simultaneously using index selection; (ii) estimate broad-sense heritabilities, realized heritabilities, and genetic and phenotypic correlations of AUDPC; grain yield, seed weight, and test weight in diseased plots; and grain yield, seed weight, and test weight in disease-free plots. The results of this experiment will guide further experiments to develop durably resistant oat lines with good agronomic performance.

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Abbreviations: AUDPC, area under disease progress curve.

MATERIAL AND METHODS

Population Development

The base population used in this study was developed by Holland and Munkvold (2001) who described it in detail. Briefly, nine cultivars and lines were selected based on field evaluations to serve as donors of putative partial resistance genes ("rust resistance donor parents," Table 1). Another 10 cultivars and lines with excellent grain yield and agronomic performance were selected to serve as donors of favorable alleles for grain yield and quality traits ("yield donor parents," Table 1). Effective selection for polygenic partial rust resistance requires that the population lack major-gene complete resistance to the inoculum used for artificial infection (Parlevliet, 1985; Cox, 1995). The cultivars and lines used fulfilled this requirement (Holland and Munkvold, 2001).

Unrelated F_1s from a Design II mating between the yield and crown rust donor parents were intermated to produce 83 full-sib families. A total of 162 S_0 seeds were developed from these four-way crosses, from which $S_{1:3}$ families were obtained. In addition, 36 $F_{3:5}$ families from biparental crosses were included to make approximately equal the allelic contributions from each original parent of the population. The $S_{1:3}$ and $F_{3:5}$ families together constituted 198 lines which comprised the C_0 base population.

Trait Evaluation

Experimental units and trait measurements were similar in both selection and evaluation experiments, as follows. The experimental unit was a hill plot planted with 30 seeds and spaced 0.3 m in perpendicular directions. Experiments were surrounded by two rows of border hills of the crown rust susceptible cultivar Markton. The experiment was conducted with two treatments: inoculated (by injecting about 0.2 mL of 10^5 urediniospore mL^{-1} suspension of isolate 345 of *P. coronata* into three stems at the three- to four-leaf development stage, in both data and border plots) and sprayed (using the systemic fungicide triadimefon [Bayleton], 1-(4-chlorophenoxy)-3,3-dimethyl-1-(1*H*-1,2,4-triazol-1-yl)-2-butanone at the four- to five-leaf stage, with a concentration of 500 g a.i. in 815 L of H_2O per hectare). The four traits measured were crown rust disease severity, grain yield, 100-seed weight, and test weight. The assessment for crown rust severity was conducted by visually scoring the percentage of leaf area infected (Peterson et al., 1948) on the flag leaf and second leaf of four tillers in every plot in the inoculated treatment. Scores from the eight readings in each plot were averaged. The measurements were made on three dates, each separated by about 1 wk, from the beginning to close to the end of the epidemic, which corresponded to the end of the third week of June to the beginning of the first week in July. On each rating date, the average percentage of leaf area infected from both flag and second leaves was computed for each plot. AUDPC was then computed for each plot according to the formula given by Bjarko and Line (1988):

$$\text{AUDPC} = 1/2 \sum_{i=1}^{N} [(Y_{i+1} + Y_i)(T_{i+1} - T_i)],$$

where Y_i = rust severity at the ith observation; T_i = time (day) at the ith observation; and N = total number of observation (N = 3 in our case). This approach was also used by Holland and Munkvold (2001), who illustrate typical disease progress curves.

Plots were harvested by manually cutting, bagging, and tying the plots, allowing the bundles to dry in the open for at least 5 d, then threshing. After weighing seed on a plot basis, yields were converted to grams per square meter. Seed weight was measured on each plot by averaging the weights of two samples of 100 randomly selected seeds. Test weight

Table 1. Area under disease progress curve (AUDPC) and agronomic traits of yield donor and resistance donor parents and checks measured under crown rust inoculation and fungicide treatment, estimated from two locations in 2001 and 2002.

	Traits measured in crown rust–inoculated plots				Traits measured in fungicide-treated plots		
Line	AUDPC	Grain yield	100-seed weight	Test weight	Grain yield	100-seed weight	Test weight
		g m^{-2}	g	kg m^{-3}	g m^{-2}	g	kg m^{-3}
Yield donor parents							
Armor	295	415	2.41	369	566	2.76	406
Brawn	91	435	3.39	371	602	3.59	386
Don	72	533	2.97	384	644	3.04	391
Hazel	132	481	2.78	406	569	2.99	423
IAR30–20	138	553	2.90	404	553	3.05	413
Ogle	186	490	2.84	380	604	3.04	395
Prairie	107	566	2.87	382	616	2.97	389
Premier	231	469	2.61	423	609	2.74	443
Sheldon	281	466	2.62	380	574	2.95	439
Starter	235	431	2.53	360	557	2.77	393
Group mean	177	484	2.79	386	589	2.99	408
Rust resistance donor parents							
Calibre	140	311	2.45	326	505	2.95	373
H632–518	131	388	2.81	404	438	2.94	419
Milton	188	444	2.61	380	555	2.79	417
Moore	142	503	2.86	421	536	3.02	430
MN841810	113	440	2.82	386	498	2.99	413
MN841823	167	440	2.65	350	476	2.73	358
Pan4/Pan5 F3–6	230	383	2.55	386	472	2.81	402
Pan5/Asc F2 3–14	176	401	2.75	386	462	2.84	393
Portage	122	458	2.71	415	543	2.81	423
Group mean	157	419	2.69	384	498	2.87	403
LSD(0.05)†	69	79	0.20	23	81	0.19	12
Resistance vs. yield parents‡	NS	*	*	NS	*	*	*

* Difference between mean of rust resistance and yield donor parents significant at P = 0.05.
† For parents that differ by the LSD or more, the null hypothesis that their means are equal can be rejected with a type I error rate of 0.05.
‡ NS, no significant difference between mean of rust resistance and yield donor parents.

was measured in a container with a volume of 46 mL (Klein et al., 1993).

Selection Experiment

In 1998, 198 lines of the C_0 population were evaluated at three locations: the Agronomy and Agricultural Research Farm, Boone Co., IA; the Hinds Research Farm, north of Ames, Story Co., IA; and the Iowa State University Northern Research Farm, near Kanawha, Hancock Co., IA. Soil types were Nicollet loam (fine-loamy, mixed, superactive, mesic Aquic Hapludoll) in Boone Co., Coland clay (fine-loamy, mixed, superactive, mesic Cumulic Endoaquoll) in Story Co., and Canisteo loam (fine-loamy, mixed, calcareous, mesic Typic Endoaquoll) in Hancock Co. In each location, the inoculated versus sprayed treatments were applied to whole plots. Within whole plots, lines were replicated three times, with each replication designed as an 11 by 11 square lattice.

A Smith–Hazel selection index (Baker, 1986) was calculated such that equal economic weight was given to one phenotypic standard deviation in each of five traits: AUDPC, grain yield, and 100 seed weight under inoculation, and grain yield and 100 seed weight under sprayed treatments. Selection was performed on the index value which combined high yield, high 100-seed weight, and low AUDPC. The 15 families with the highest index values were intermated in a full diallel to generate 210 F_1 seed from which $F_{3:5}$ families were obtained to form the C_1 population.

Evaluation Experiment

In 2001 and 2002, an evaluation experiment was conducted at the Boone Co. and Story Co. locations to determine the efficacy of one cycle of selection for AUDPC and other agronomic traits in the index. The experiment contained: (i) nine crown rust resistance donor parents, (ii) 10 yield donor parents, (iii) two resistant checks ('Jim' and 'Gem') and one susceptible check (Markton), (iv) 79 random $S_{1:5}$ or $F_{3:7}$ lines from the C_0 population, and (v) 79 random $F_{3:6}$ lines from the C_1 population. This gave a total of 180 entries. The entries were randomized into 18 blocks of ten plots using an α (0, 1) design such that one or two plots in each block were a parent or check cultivar. Three replications of the 180 entries were planted in each whole plot, which consisted of either inoculated or sprayed treatments.

Statistical Analysis

Variance components for all traits were evaluated on the random lines from the C_0 and C_1 cycle entries only. To take advantage of all data to estimate replication and block effects, a first analysis was peformed using Proc Mixed of SAS (SAS Institute Inc., 1999) with all data. Whole plot treatments and environments were considered fixed effects, and replications, blocks, and lines were considered random effects; interactions between lines and treatments or environments were also considered random. Measured phenotypes were then adjusted for replication and block effects by subtracting the effect estimates. Adjusted phenotypes of the random lines were then analyzed by cycle, considering whole plot treatments and environments as fixed effects, and lines and their interactions with treatment and environment as random effects. Replication and block effects were not included in this second analysis. Significance of response to selection was tested using contrasts between the C_0 and C_1 population means.

Genotypic variance components were estimated as the line variance component for a given cycle population. The phenotypic variance on a plot basis for each trait was estimated as a linear combination of the variance components due to the main and interaction variance components for the following factors: line, location, year, and experimental error. In this study, the same trait measured under different treatments was considered as a different trait. Thus, the phenotypic variance on a plot basis was estimated for yield, 100-seed weight, and test weight under either inoculated treatment or sprayed treatment and for AUDPC as $\hat{\sigma}^2_{P(\text{plot})} = \hat{\sigma}^2_{\text{line}} + \hat{\sigma}^2_{\text{line}\times\text{location}} + \hat{\sigma}^2_{\text{line}\times\text{year}} + \hat{\sigma}^2_{\text{line}\times\text{location}\times\text{year}} + \hat{\sigma}^2_{\text{error}}$ and the phenotypic variance on a line mean basis for these traits was estimated as $\hat{\sigma}^2_{P(\text{line})} = \hat{\sigma}^2_{\text{line}} + \frac{\hat{\sigma}^2_{\text{line}\times\text{location}}}{l} + \frac{\hat{\sigma}^2_{\text{line}\times\text{year}}}{y} + \frac{\hat{\sigma}^2_{\text{line}\times\text{location}\times\text{year}}}{ly} + \frac{\hat{\sigma}^2_{\text{error}}}{lyr}$ where, l, y, and r are the number of locations (2), years (2), and replications within location, year, and treatment combination (3).

Heritabilities on a plot basis and on a line mean basis were estimated as

$$h^2_{(\text{plot})} = \frac{\sigma^2_G}{\sigma^2_{P(\text{plot})}} \text{ and } h^2_{(\text{line})} = \frac{\sigma^2_G}{\sigma^2_{P(\text{line})}}, \text{ respectively.}$$

Genetic and phenotypic correlations between traits were estimated using data adjusted to remove replication and block effects as described above. Variance components needed to compute the correlations were estimated using SAS Proc Mixed (SAS Institute Inc., 1999). Because Proc Mixed allows only a single dependent variable, data for two traits at a time were read into a single variable, which was analyzed as follows. Effects of environment within trait were considered fixed. For both line and line × environment effects, trait was specified as a random effect. The subject and type options of the procedure were used to define line or line × environment as subjects and to specify an unstructured covariance matrix between traits. For traits that were measured in the same treatment (e.g., AUDPC and inoculated yield), trait was also specified as the repeated effect using the repeated statement; plot was then considered the subject and again an unstructured covariance matrix was specified. For traits that were measured in different treatments (e.g., inoculated yield and sprayed yield), separate error variances were estimated using the group option of the repeated statement. No error covariance could then be estimated. Together, these statements generated the correct overall variance–covariance matrix among all observations and allowed for the estimation of nine or eight variance components for pairs of traits measured in the same or different treatments: two variances at the line, line × environment, and plot levels and a covariance at the line and line × environment levels, as well as an error covariance for traits measured in the same treatment. Genetic correlations were calculated in the usual way from variances and covariances at the line level. Phenotypic correlations were calculated by dividing the summed covariances by the square root of the product of the variances, summed within each trait. Standard errors for these correlations were obtained using the asymptotic variances and covariances of the estimated variance components. Formulae for the standard errors were developed using the delta method (Lynch and Walsh, 1998, equation A1.7c).

Realized heritabilities were calculated as

$$\hat{h}^2_{\text{Realized}} = \frac{\overline{C}_{1\text{E}} - \overline{C}_{0\text{E}}}{\overline{S}_{0\text{S}} - \overline{C}_{0\text{S}}},$$

where $C_{0\text{E}}$ and $C_{1\text{E}}$ were the average phenotype of lines in the evaluation experiment for cycle 0 and cycle 1, respectively, $C_{0\text{S}}$ was the average phenotype of all lines in the selection experiment, and $S_{0\text{S}}$ was the average phenotype of selected lines in

the selection experiment. Following Walsh and Lynch (2005), variances of the realized heritabilities were calculated as

$$\mathrm{var}(\hat{h}^2_{\mathrm{Realized}}) = \frac{\mathrm{var}(\overline{C}_{1E} - \overline{C}_{0E})}{(\overline{S}_{0S} - \overline{C}_{0S})^2} = \frac{\mathrm{var}(\overline{C}_{1E}) + \mathrm{var}(\overline{C}_{0E}) - 2\mathrm{cov}(\overline{C}_{1E},\overline{C}_{0E})}{(\overline{S}_{0S} - \overline{C}_{0S})^2}$$

The variances and covariance of the C_{iE} accounting for drift are given by Walsh and Lynch (2005) as

$$\mathrm{var}(\overline{C}_{0E}) = \frac{\sigma_z^2}{M_{0E}},$$

$$\mathrm{var}(\overline{C}_{1E}) = \left[\left(\frac{1}{M_{0S}} + 2f_1\right)h^2 + \frac{1}{M_{1E}}\right]\sigma_z^2, \text{ and}$$

$$\mathrm{cov}(\overline{C}_{1E},\overline{C}_{0E}) = \frac{h^2\sigma_z^2}{M_{0S}},$$

where σ_z^2 is the phenotypic variance among evaluated lines, M_{iX} is the number of lines observed in cycle i in the selection (S) or evaluation (E) experiment, and f_1 is the inbreeding coefficient of C_1. To calculate σ_z^2, best linear unbiased estimators of the line effects were obtained by analyzing the data treating lines as fixed effects and all year, location, replication, and block as random effects using SAS Proc Mixed. The variance of these estimators was then calculated. To calculate f_1, we accounted for the fact that 15 S_1–derived lines were used as parents and that the family size of each parent was fixed at 28. Furthermore, each progeny was selfed once before seed was increased for evaluation. These considerations allowed us to obtain the expected founder allele frequency and its variance in the cycle 1 population. With these parameters we calculated $E(f_1) \cong 0.049$.

RESULTS AND DISCUSSION

Response to Selection

From cycle C_0 to C_1, selection for partial resistance reduced the mean AUDPC from 162 to 143 (Table 2), a reduction of 12%. Because the duration of the selection cycle was 2 yr, the reduction of AUDPC was 6% per year. This response is less than that obtained by Diaz-Lago et al. (2002). After four cycles of rapid recurrent selection for partial resistance, they found an average reduction of 11% in AUDPC per year. One might expect the response to selection in AUDPC to be greater in the experiment by Diaz-Lago et al. (2002) than in this experiment because they selected solely on the basis of AUDPC, whereas this experiment involved multiple-trait index selection. Another difference between their procedure and the one used here is that they inoculated with a mixed-race rust population whereas we used a single rust isolate. In the presence of a mixed-race population, partial resistance can be confounded with the presence of major genes conferring complete resistance against part of the pathogen population (Parlevliet, 1985). Diaz-Lago et al. (2002) tested for the presence of major genes in their oat population and found that about 15% of all oat genotype by crown rust race reactions were of the complete resistance type. Thus, major genes were segregating in their population, and it is possible that through the use of a mixed-race inoculum they selected for increased population frequencies of the major genes as well as for increased partial rust resistance. Selection for major genes might have increased the rate of response that they observed relative to our observation. Note that, in our case, we cannot guarantee that natural inoculum with other virulence specificities than the artificial inoculum was absent from the trial. Our methods and some anecdotal observations, however, suggest that the artificial inoculum dominated. First, we inoculated before natural infection was observed on surrounding plots, giving the artificial inoculum a head start. Second, in our plots, we often observed initial pustules close to punctures in the leaves made by the syringe inoculation.

After one cycle of selection, the average AUDPC for the population was 143, the level of partial resistance of the disease resistance donor parental line Moore (Table 1). If this rate of progress were maintained, two more cycles would be required to attain the level of resistance of parental line MN841810 which showed the highest partial resistance level (AUDPC = 113) among all resistance donor parents. Grain yield increased significantly from C_0 to C_1 under crown rust inoculation ($P < 0.05$) (Table 2). However, there was no significant change for grain yield under fungicide treatment. One possible reason might be a weak correlation between the selection index and grain yield under fungicide treatment. However, we calculated the correlation between the selection index and grain yield for the C_0 population in the evaluation experiment under both fungicide and inoculated treatments, and they were similar. It therefore seems unlikely that a lack of correlation can explain the poor response of grain yield

Table 2. Area under disease progress curve (AUDPC), grain yield, 100-seed weight, and test weight, estimated from two cycles (C_0 and C_1) in two treatments in 2001 and 2002.

	Traits measured in crown rust–inoculated plots				Traits measured in fungicide-treated plots		
	AUDPC	Grain yield	100-seed weight	Test weight	Grain yield	100-seed weight	Test weight
		g m^{-2}	g	kg m^{-3}	g m^{-2}	g	kg m^{-3}
Cycle C_0							
Lowest line	**77**	**315**	**2.20**	**309**	**382**	**2.37**	**340**
Highest line	**261**	**599**	**3.24**	**454**	**642**	**3.72**	**455**
Average	**162**	**445**	**2.75**	**383**	**534**	**2.92**	**399**
Cycle C_1							
Lowest line	**49**	**278**	**2.34**	**306**	**363**	**2.52**	**322**
Highest line	**232**	**606**	**3.74**	**427**	**657**	**3.90**	**442**
Average	**143**	**470**	**3.00**	**385**	**546**	**3.13**	**398**
C_0 vs. C_1	*	*	*	**NS†**	**NS**	*	**NS**

* $P = 0.05$.
† NS, no significant difference.

Table 3. Variance component estimates of grain yield, 100-seed weight, test weight, and area under the disease progress curve (AUDPC) measured in inoculated plots, and grain yield, 100-seed weight, test weight measured in plots treated with fungicide. Estimates were based on lines from two cycles evaluated in two Iowa locations in 2001 and 2002. Location and treatment are abbreviated loc and trt.

	Traits measured in inoculated plots						Traits measured in sprayed plots			
			Grain yield		100-seed weight		Grain yield		100-seed weight	
	AUDPC		g m^{-2}		g		g m^{-2}		g	
	Variance†	SE†	Variance†	SE†	Variance‡	SE‡	Variance†	SE†	Variance‡	SE‡
C_0 population										
line	**2.96**	**0.63**	**3.19**	**0.81**	**6.39**	**1.14**	**3.16**	**0.76**	**7.14**	**1.21**
loc × line	**0.00**	**0.00**	**0.00**	**0.00**	**0.24**	**0.11**	**0.37**	**0.44**	**0.00**	**0.00**
year × line	**1.02**	**0.30**	**2.07**	**0.51**	**0.67**	**0.18**	**0.40**	**0.44**	**0.32**	**0.14**
loc × year × line	**0.56**	**0.18**	**0.00**	**0.00**	**0.00**	**0.00**	**0.62**	**0.58**	**0.08**	**0.12**
Error	**2.91**	**0.16**	**6.54**	**0.33**	**2.69**	**0.14**	**8.55**	**0.48**	**2.66**	**0.15**
C_1 population										
line	**2.33**	**0.50**	**2.76**	**0.69**	**9.99**	**1.69**	**4.90**	**0.97**	**8.19**	**1.41**
loc × line	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.05**	**0.42**	**0.06**	**0.14**
year × line	**0.47**	**0.24**	**1.47**	**0.46**	**0.78**	**0.23**	**0.04**	**0.42**	**0.76**	**0.23**
loc × year × line	**0.70**	**0.21**	**0.09**	**0.31**	**0.26**	**0.15**	**0.81**	**0.60**	**0.23**	**0.19**
Error	**3.01**	**0.17**	**7.23**	**0.41**	**2.80**	**0.16**	**8.46**	**0.48**	**2.68**	**0.15**

† Divided by 1000.
‡ Multiplied by 100.

under fungicide treatment. Continued selection would be required to test if index selection will also increase grain yield under fungicide treatment.

Heritability

Broad-sense heritabilities were estimated by means of variance components from evaluation experiments in 2001 and 2002 (Table 3 and Table 4). The high line-mean heritabilities for all traits measured (from 0.67 for grain yield under crown rust inoculation to 0.94 test weight under the sprayed treatment) suggest that all traits should respond well to selection on the basis of line means among C_0 and C_1 populations (Table 4). Heritabilities on a plot basis were lower, especially for AUDPC and grain yield in inoculated plots (Table 4), suggesting that replication and multiple-environment testing are needed for evaluating these traits. There was no evidence for decreased genotypic variances or heritabilities for any trait following selection, suggesting that further genetic progress from selection can be made in this population.

Realized heritability is based on the selection effects that are actually transmitted to the next generation or cycle. Realized heritabilities for the selection from C_0 to C_1 population were calculated for grain yield, and 100 seed weight under inoculation and fungicide treatments and for AUDPC (Table 4), because these five traits contributed to the selection index for the C_0 population.

Based on variance components estimated during the evaluation experiment, we also calculated the broad-sense line-mean heritability predicted for the selection experiment that was conducted in three locations but only 1 yr (Table 4). For all traits except grain yield under disease-free treatment, realized heritabilities were greater than half of line-mean heritabilities during selection, indicating that more than half of genetic variance was additive. Note, however, that the realized heritability standard errors are quite high, which results from accounting for genetic drift in their calculation.

Correlation

AUDPC was genetically and phenotypically negatively correlated with grain yield, 100-seed weight, and test weight under crown rust inoculation in both cycles (Table 5). This result is consistent with Holland and Munkvold's (2001) results, indicating that higher levels of crown rust resistance contribute to increased grain yield and grain weight under inoculation. Under fungicide treatment, AUDPC was genetically positively correlated with test weight and 100-seed test weight, but negatively correlated with grain yield in the C_0 and positively in the C_1 cycles. These data support Holland and Munkvold's (2001) suggestion that there may be different sets of genes affecting grain yield under disease-stress and disease-free environments.

Table 4. Heritability estimates and standard errors (in parentheses) of oat grain yield, 100-seed weight, test weight, and area under the disease progress curve AUDPC measured in inoculated plots, and grain yield, 100-seed weight, and test weight measured in plots treated with fungicide. Estimates were based on lines from two cycles evaluated in two Iowa locations in 2001 and 2002.

	Traits measured in crown rust–inoculated plots				Traits measured in fungicide-treated plots		
	AUDPC	Grain yield	100-seed weight	Test weight	Grain yield	100-seed weight	Test weight
C_0 population							
Plot heritability	**0.40 (0.06)**	**0.27 (0.05)**	**0.64 (0.04)**	**0.62 (0.05)**	**0.24 (0.05)**	**0.70 (0.04)**	**0.65 (0.04)**
Line mean heritability	**0.77 (0.05)**	**0.67 (0.08)**	**0.90 (0.02)**	**0.88 (0.03)**	**0.72 (0.08)**	**0.95 (0.01)**	**0.93 (0.02)**
C_1 population							
Plot heritability	**0.36 (0.05)**	**0.24 (0.05)**	**0.72 (0.04)**	**0.66 (0.05)**	**0.34 (0.05)**	**0.69 (0.04)**	**0.67 (0.04)**
Line mean heritability	**0.78 (0.05)**	**0.67 (0.07)**	**0.94 (0.01)**	**0.89 (0.02)**	**0.84 (0.05)**	**0.92 (0.02)**	**0.94 (0.02)**
C_0 selection heritability†	**0.66 (0.06)**	**0.55 (0.08)**	**0.78 (0.04)**		**0.72 (0.06)**	**0.91 (0.02)**	
Realized heritability	**0.35 (0.21)**	**0.47 (0.45)**	**0.50 (0.14)**		**0.27 (0.56)**	**0.58 (0.23)**	

† C_0 selection heritability was calculated on a line mean-basis assuming the selection experiment design which was conducted in three locations and 1 yr.

Table 5. Genotypic and phenotypic correlation estimates and standard errors (in parentheses) among grain yield, test weight, 100-seed weight, and area under the disease progress curve AUDPC measured in inoculated plots and among grain yield, test weight, and 100-seed weight measured in plots treated with fungicide. Genetic correlations are given in the upper right half of the table, phenotypic correlations are given in the lower left.

	Traits measured in crown rust-inoculated plots				Traits measured in fungicide-treated plots		
C_0 population	AUDPC	Grain yield	100-seed weight	Test weight	Grain yield	100-seed weight	Test weight
Inoculated plots							
AUDPC	–	−0.38 (0.11)	−0.14 (0.12)	−0.10 (0.13)	−0.13 (0.14)	0.02 (0.12)	0.16 (0.12)
Grain yield	−0.30 (0.13)	–	0.34 (0.11)	0.45 (0.11)	0.81 (0.07)	0.22 (0.12)	0.30 (0.12)
100-seed weight	−0.16 (0.10)	0.37 (0.12)	–	0.42 (0.10)	0.06 (0.13)	0.95 (0.02)	0.37 (0.10)
Test weight	−0.05 (0.11)	0.40 (0.11)	0.46 (0.08)	–	0.04 (0.03)	0.26 (0.11)	0.94 (0.02)
Fungicide plots							
Grain yield	0.03 (0.05)	0.31 (0.05)	0.04 (0.06)	0.05 (0.01)	–	0.12 (0.13)	0.08 (0.13)
100-seed weight	0.10 (0.07)	0.11 (0.06)	0.67 (0.04)	0.19 (0.08)	−0.06 (0.11)	–	0.27 (0.11)
Test weight	0.04 (0.09)	0.18 (0.06)	0.26 (0.07)	0.67 (0.04)	−0.03 (0.15)	0.37 (0.09)	–
C_1 population							
Inoculated plots							
AUDPC	–	−0.08 (0.14)	−0.19 (0.12)	−0.04 (0.13)	0.11 (0.14)	0.01 (0.13)	0.14 (0.13)
Grain yield	−0.45 (0.08)	–	0.23 (0.12)	0.48 (0.10)	0.93 (0.04)	0.19 (0.13)	0.45 (0.11)
100-seed weight	−0.19 (0.09)	0.22 (0.06)	–	0.51 (0.09)	−0.11 (0.03)	0.96 (0.01)	0.42 (0.10)
Test weight	−0.18 (0.09)	0.47 (0.08)	0.51 (0.06)	–	0.18 (0.12)	0.45 (0.10)	0.97 (0.01)
Fungicide plots							
Grain yield	0.01 (0.05)	0.37 (0.05)	−0.06 (0.01)	0.11 (0.06)	–	−0.08 (0.12)	0.24 (0.12)
100-seed weight	0.03 (0.09)	0.11 (0.06)	0.32 (0.07)	0.72 (0.04)	0.12 (0.09)	–	0.42 (0.10)
Test weight	0.10 (0.07)	0.22 (0.05)	0.72 (0.04)	0.32 (0.07)	0.18 (0.11)	0.31 (0.09)	–

After one cycle of selection, the genetic correlations between AUDPC and most other agronomic traits shifted in an unfavorable direction from the perspective of selection (Table 5). For example, a strong negative correlation between AUDPC and grain yield would be desirable for selection, since we seek to decrease AUDPC but increase yield. The genetic correlation between AUDPC and grain yield under inoculation, however, shifted in a positive direction, from −0.38 to −0.08. This effect is undesirable for selection in subsequent generations. This result is consistent with the prediction that the genetic correlations could easily change in the undesirable direction as a result of index selection (Itoh, 1991).

In this study, we used index selection for improving crown rust resistance, grain yield, and 100-seed weight in oats. The results showed that there was a significant decrease in AUDPC and significant increases in grain yield, seed weight under crown rust inoculation, and seed weight measured in the disease-free environment, but no significant increase in grain yield in the disease-free environment (Table 2). High heritabilities and desired trait correlations indicate that further selection should be effective (Table 4 and Table 5).

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