Recurrent Selection for Partial Resistance to Crown Rust in Oat

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ABSTRACT

Crown rust (caused by the fungus *Puccinia coronata* Cda. f. sp. *avenae* Eriks.) is a major disease of cultivated oat (*Avena sativa* L.). Partial resistance is a form of incomplete resistance characterized by a reduced rate of epidemic development and is potentially more durable than complete race-specific resistance. Four rapid cycles of selection for partial crown rust resistance were conducted in an oat recurrent selection population after the completion of the seventh cycle of selection for grain yield. The objectives of this research were to: (i) determine the effectiveness of rapid cycle recurrent selection for partial crown rust resistance; (ii) assess the indirect effect on grain yield, flowering date, and plant height; and (iii) estimate phenotypic and genetic correlations between traits and broad-sense heritabilities. Recurrent selection parents and check cultivars were evaluated in six environments. Four cycles of selection for partial resistance reduced the area under the disease progress curve (AUDPC) 42%. This increased resistance was not reflected in higher grain yields under moderate crown rust epidemics, but it produced a 4.7% grain yield gain per cycle in an environment with a severe rust infection. Selection for partial resistance indirectly delayed the flowering date by 2 d. Entry mean broad-sense heritability estimates were intermediate (41–64%) for AUDPC. Our results show the usefulness of rapid cycle recurrent selection as a population improvement procedure capable of effectively increasing the level of partial resistance to crown rust in a high-yielding oat population.

Crown rust is a major fungal disease of cultivated oat, producing both grain yield and grain quality losses (Simons et al., 1979; Simons, 1985). Breeding for complete race-specific resistance has been the primary control measure for this disease (Simons, 1985). However, this strategy usually provides protection for limited periods of time. For example, the cultivar Woodstock was highly resistant when it was released in Ontario in 1982 and after 5 yr of commercial production more than half of the pathogen isolates collected in this region were virulent on it (Chong and Seaman, 1989). Alternative types of resistance, capable of providing longer lasting cultivars, are necessary, and partial resistance is currently being explored as one.

Partial resistance is a form of incomplete resistance, characterized by a reduced rate of epidemic development despite a susceptible or high infection type (Parlevliet, 1978). This resistance is assumed to be largely race nonspecific and inherited polygenically (Parlevliet, 1985). Since race nonspecific resistance is expressed by the absence of significant genetic interactions between host and pathogen genotypes (Parlevliet, 1985), the use of this type of resistance in crop cultivars should prevent major shifts in the composition of the pathogen population increasing the durability of the disease resistance (Geiger and Heun, 1989).

Recurrent selection is a population improvement procedure that increases the frequency of desirable alleles through repeated cycles of selection and systematic recombination. This breeding method has been widely used for improving quantitative traits in cross-pollinated crops. The expression of partial resistance to fungal pathogens is usually controlled by several genes with additive gene action (Veillet et al., 1996; Geiger and Heun, 1989; Parlevliet, 1978). Although these attributes suggest that recurrent selection could be an appropriate and effective breeding method for improving disease resistance in plants, it has received only limited attention in self-pollinated crops. Recurrent selection has been used successfully to increase the resistance in soybean [*Glycine max* (L.) Merr.] to Phytophthora rot (caused by *Phytophthora megasperma* Drechs. f. sp. *glycinea* Kuan and Erwin) (Walker and Schmitthenner, 1984), in barley (*Hordeum vulgare* L.) to leaf rust (caused by *Puccinia hordei* Otth.) (Parlevliet and Van Ommeren, 1988; Reinhold et al., 1993), and powdery mildew (caused by *Erysiphe graminis* DC. f. sp. *hordei* Em. Marchal) (Parlevliet and Van Ommeren, 1988), in wheat (*Triticum aestivum* L.) to powdery mildew (caused by *Erysiphe graminis* f. sp. *tritici*) (Abdalla et al., 1989), and scab (caused by *Gibberella zeae* Petch.) (Jiang et al., 1994), and in oat to barley yellow dwarf virus (Baltenberger et al., 1988).

A recurrent selection program to improve oat grain yield was initiated at the University of Minnesota in 1968 (Stuthman and Stucker, 1975). Payne et al. (1986) and Bregitzer et al. (1987) studied this population after three cycles of selection and reported an average grain yield gain of 3.8 and 4.5% per cycle, respectively. Reysack et al. (1993) estimated an average response per cycle of 7.1% after four cycles and Pomeranke and Stuthman (1992) reported average gains of 7.9% after five cycles of recurrent selection for grain yield. De Koeyer and Stuthman (1998) evaluated the response to seven cycles of selection and estimated a realized gain per cycle of 3.1%. After the completion of the seventh cycle of recurrent selection for grain yield, this adapted and high-yielding oat population was subjected to four rapid recurrent selection cycles (Walker and Schmitthenner, 1984; Frey et al., 1988) for partial resistance to crown rust.

The objectives of this research were to: (i) determine the effectiveness of rapid cycle recurrent selection as a method for improving partial resistance to oat crown rust in a high-yielding breeding population; (ii) assess

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the indirect effect of selecting for disease resistance on three other plant traits: grain yield, maturity, and plant height; and (iii) estimate phenotypic and genetic correlations among traits and broad-sense heritabilities.

MATERIALS AND METHODS

Population Development and Improvement Schemes

Five oat cultivars and seven elite experimental lines were selected on the basis of grain yield and diversity in phenotype and pedigree, to initiate a recurrent selection program. Stuthman and Stucker (1975) described the development of the base population in detail. This closed recurrent selection population was first selected for increased grain yield (Phase I) for seven cycles, and then it was improved for partial crown rust resistance (Phase II) for an additional four cycles. In both breeding phases, 21 future parental lines were selected by means of replicated single-year hill plot field trials sown at one or two locations. These parents were then intercrossed in the greenhouse following a circulant partial diallel ($s = 6$ and $k = 8$) without reciprocals crossing scheme. During Phase I of the population improvement program, lines were advanced by single-seed descent to the S0:3 generation before selection and each recurrent selection cycle lasted 3 yr. These selection experiments were never affected by severe or moderate crown rust epidemics. The systemic fungicide tebuconazole [alpha-tert-butyl-alpha-(*p*-chlorophenethyl)-1*H*-1,2,4-triazole-1-ethanol] was applied in two occasions to protect oat plots from crown rust. Payne et al. (1986) provide additional information regarding the selection procedures used during Phase I. To prevent additional undesirable changes in flowering date, the number of days to flowering was included as a secondary selection trait after the completion of the third cycle of selection for grain yield.

A rapid cycle improvement scheme, similar to the one proposed by Walker and Schmitthenner (1984) and Frey et al. (1988), was followed in Phase II. The duration of a complete recurrent selection cycle was 1 yr. The S0:2 progenies of the 21 selected plants were crossed in the fall and the S0 plants were grown during winter to produce S0:1 seed for the following field selection trials. The 63 S0:1 full-sib families were evaluated in replicated hill plot field experiments grown at one or two locations. In years with two selection experiments, one location was artificially inoculated with a mixture of crown rust races collected the previous year at the Minnesota buckthorn (*Rhamnus cathartica* L.) nursery. A detailed description of this nursery can be found in Al-Kherb et al. (1987). After flag leaves were fully expanded, the upper portion of the experiment's canopy was inoculated on three consecutive evenings with a gas powered backpack mist blower. Fresh crown rust urediniospores were applied at a rate of 15 g ha^{-1} suspended on lightweight mineral oil (Soltrol 170, 4 L ha^{-1}). All selection experiments had two complete replicates. The level of partial resistance to crown rust was assessed by visually rating the proportion of diseased flag leaf area using the modified Cobb's scale (Peterson et al., 1948). Ten leaves were assessed per plot to estimate the average disease severity. Crown rust was assessed two, three, or four times after the appearance of the first symptoms on the flag leaves of the susceptible check. The multiple crown rust readings were then used to calculate the AUDPC as described by Shaner and Finney (1977). The 21 parents for the next recurrent selection cycle were selected by choosing the plants with lowest disease severity from each of the 21 families with the lowest AUDPC values.

The presence of race-specific resistance genes effective against part of the pathogen population can be confounded with partial resistance, especially when field experiments are artificially inoculated with a mixture of races or preformed under natural infection (Parlevliet, 1985). To test for the presence of effective race-specific resistance genes, 7-d-old plants of the 12 genotypes that compose the base population and a random subset of 40 recurrent selection parents were inoculated with 10 single pustule isolates of variable virulence. Inoculated plants were placed in a dew chamber overnight at 18°C, and then transferred to a greenhouse where temperature varied from 18 to 28°C. The infection types were read 12 to 15 d after inoculation. Susceptible or high infection types were observed for 85% of all oat-genotype × crown-rust-isolate combinations.

Evaluation Experiments

Six evaluation experiments were conducted to determine the direct and indirect response to 11 cycles of recurrent selection. Table 1 presents information on year, location, number of replications, planting and harvest dates, pesticide applications, and artificial inoculation dates, for each of the six trials. Experiments were conducted at two locations: Rosemount and St. Paul, MN. Soil type at both locations was a Waukegan silt loam (fine-silty over sandy or sandy-skeletal, mixed, mesic Typic Hapludoll). The experimental design used was a randomized complete block design with a maximum of three or five replications (Table 1). The experimental unit was a hill plot planted with 30 seeds and spaced in a 30-cm grid. Each replication was surrounded by two rows of hills to control border effects. All experiments were hand weeded and one was protected from fungal foliar diseases with one application of 220 g ha^{-1} of the systemic fungicide tebuconazole (Table 1). The systemic insecticide Imidacloprid (1-[(6-Chloro-3-pyridinyl)methyl]-*N*-nitro-2-imidazolidinimine) was used in 2000

Table 1. Description of the evaluation experiments used to study the effects of seven cycles of recurrent selection for grain yield followed by four cycles of selection for partial resistance to crown rust in an oat population.

	Experiment					
	1	2	3	4	5	6
Year	1999	1999	1999	2000	2000	2000
Location	St. Paul, MN	St. Paul, MN	Rosemount, MN	St. Paul, MN	St. Paul, MN	Rosemount, MN
Number of replications						
Crown rust severity	–	2	3	3	3	3
Grain yield	5	5	3	3	3	3
Flowering date	2	2	–	3	3	–
Plant height	2	2	–	3	–	3
Planting date	30 April	4 May	25 May	23 April	15 May	1 May
Harvest date	31 July	1 August	11 August	28 July	8 August	3 August
Insecticide application	–	–	–	4 May	3 June	24 May
Fungicide application	17 June	–	–	–	–	–
Crown rust inoculation	–	28–30 June	–	13–15 June	22–24 June	–

to protect plants from aphids. Half of the evaluation experiments were artificially inoculated with a mixture of crown rust races collected the previous year at the Minnesota buckthorn nursery and following the inoculation procedure previously described.

One hundred seventeen parents (12 original parents, and 21 from each of Cycles I-4, I-7, II-1, II-2 and II-3) and four check entries ('Starter', 'Portage', 'Belle', and MN 841801) were evaluated in the six experiments. The 21 Cycle II-4 parents were present only in the three field trials of the year 2000. Starter is an early maturing variety susceptible to oat crown rust. Portage is a local variety with an intermediate level of partial resistance to crown rust. Belle is a high yielding late maturing variety with effective complete resistance. MN 841801 is an experimental line with a high level of partial resistance to crown rust. The four traits measured were crown rust disease severity, grain yield, flowering date, and plant height. The assessment procedure for crown rust severity and AUDPC was described in the previous subsection. Grain yield was measured as the grams of grain harvested from a hill plot (g hill^{-1}). Flowering date was determined as the number of days from planting to 50% panicle emergence, and plant height as the average length of mature plants. Table 1 presents the locations and the number of replications within locations in which each trait was measured.

Statistical Analyses

The homogeneity of error variances across experiments was evaluated using Hartley's F_α-max test (Hartley, 1950). AUDPC and grain yield obtained F_α-max values above the critical F-max ($\alpha = 0.05$), while no error variance heterogeneity was detected in flowering date and plant height. Scatterplots of error variances against trial means were visually inspected to discover possible associations between mean and variance. This type of association was found only for the AUDPC data. The Shapiro-Wilks' W, the kurtosis, and the skewness were estimated, by means of SAS Proc Univariate (SAS Institute, 2000), to detect deviations from the normal distribution. The Shapiro-Wilks' W test indicated that all distributions departed slightly from normality. The kurtosis and the skewness showed that distribution of AUDPC data was clearly not normal. The Box-Cox power transformation series (Box and Cox, 1964) was tested on the AUDPC data as a possible solution to achieve error variance homogeneity, to break the association between mean and variance, and to attain normality. The square root transformation had the lowest mean square error, reduced the F-max value by half (4.5 vs. 2.3), and eliminated the association between mean and variance. This transformation also reduced the kurtosis from 2.3 to 0.25 and the skewness from 1.2 to 0.2. No power transformation improved error variance homogeneity of the grain yield data (F-max = 4.0).

Combined analyses of variance of the square root transformed AUDPC, and nontransformed grain yield, flowering date, and plant height data for the six evaluation experiments were conducted by SAS Proc GLM (SAS Institute, 2000). Environments and replicates within environments were considered random effects and recurrent selection cycles and checks were considered fixed effects. The significance of main effects and interactions was evaluated by appropriate F tests. All main effects and interactions were found significant at the 0.01 level. The Azzalini-Cox test, described by Baker (1988), was used to evaluate the presence of crossover interactions. The critical value for this test was calculated following the modifications suggested by Cornelius et al. (1992). The number of significant crossover interactions detected, using a 0.05 interaction-wise α, were 8 for squared root transformed AUDPC, 33 for grain yield, 10 for flowering date, and 8 for plant height, out of 450, 675, 270, and 270 total interaction contrasts, respectively. These numbers are below the expected values under the null hypothesis, indicating absence of significant genotype × environment crossover interaction in the four dependent variables studied.

Generalized least-squares means across environments and corresponding standard errors for the seven recurrent selection cycles and four check cultivars were estimated by the restricted maximum likelihood procedure of SAS Proc Mixed (SAS Institute, 2000). Means were compared by two-tailed t-tests of pairwise differences with no adjustment for multiple comparisons and a 0.05 comparisonwise α. Removal of check cultivars from the data set before analysis reduced the transformed AUDPC treatment × environment interaction variance by 87% and the average standard error of a difference between two transformed AUDPC means by 60%. Consequently, to increase the power of detecting significant differences among recurrent selection cycle AUDPC means, only the seven recurrent selection parental cycle means were compared. The direct and indirect responses to recurrent selection for the two population improvement phases were estimated by SAS Proc Mixed (SAS Institute, 2000). Checks were excluded from the data set and regression coefficient estimates and standard errors for the four response variables were computed by considering the recurrent selection cycle number as the only fixed effect in the mixed model. The statistical significance of the linear regression coefficients was evaluated with a t-test and the average change per cycle was calculated as the regression coefficient divided by the corresponding cycle zero mean. When the quadratic regression coefficient was significant, the average response per cycle was estimated as the difference between the mean of the last cycle minus the cycle zero mean divided by the number of recurrent selection cycles.

Phenotypic and genetic correlation coefficients among response variables were estimated for each recurrent selection cycle. Phenotypic correlations were determined using genotype means across environments. Genetic correlations were calculated by means of genetic variance and covariance estimates obtained from the analysis of the multienvironment trial by Proc Mixed (SAS Institute, 2000) considering all effects random. Genetic covariances between traits were estimated as $\mathrm{Cov}_{Gab} = [S^2_{G(a+b)} - S^2_{Ga} - S^2_{Gb}]/2$, where $S^2_{G(a+b)}$ is the genetic variance of the compound observation $a + b$ (Kempthorne, 1957). The statistical significance of the correlation coefficients was tested as $t_{(n-2)} = r/\sqrt{[(1 - r^2)/(n - 2)]}$ (Kearsey and Pooni, 1996). Broad sense heritability estimates were computed on an entry mean basis for each recurrent selection cycle as $H = S^2_G/(S^2_G + S^2_{GE}/e + S^2/re)$. The numbers of replicates (r) and environments (e) used to estimate H are presented in Table 1. Exact 90% confidence intervals for H were calculated by the method of Knapp et al. (1985). Approximate values for the numerator and denominator of the F-statistic (M_1/M_2) were obtained from the estimated components of variance as $M_1 = re\,(S^2_G + S^2_{GE}/e + S^2/re)$ and $M_2 = M_1 - re\,S^2_G$.

RESULTS AND DISCUSSION

Response to Selection

The Phase I recurrent selection for grain yield did not indirectly alter the level of resistance to oat crown rust, but four rapid cycles of recurrent selection for partial resistance (Phase II) reduced the AUDPC from 84.4 to 43.9 (Table 2). The average AUDPC reduction

Table 2. Area under disease progress curve (AUDPC), grain yield, flowering date and plant height of recurrent selection cycle parents and checks evaluated in four (flowering date and plant height), five (AUDPC), or six (grain yield) hill plot experiments.

	AUDPC		Grain yield		Flowering date		Plant height	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
			g hill^{-1}		d		cm	
Phase I†								
Cycle 0	90.6a§	19.6	20.5ab	5.1	61.9b	2.2	105.8bc	8.0
Cycle 4	89.2a	19.5	24.0bc	5.1	59.9d	2.2	108.6ab	8.0
Cycle 7	84.4a	19.5	31.7de	5.1	57.8e	2.2	110.4a	8.0
Phase II‡								
Cycle 1	70.2b	19.5	30.0d	5.1	58.6e	2.2	110.6a	8.0
Cycle 2	59.1bc	19.5	30.6d	5.1	59.9d	2.2	110.1a	8.0
Cycle 3	50.6cd	19.5	31.7de	5.1	60.4d	2.2	112.0a	8.0
Cycle 4	43.9d	22.1	36.7e	5.4	60.5cd	2.2	111.6a	8.1
Checks								
Starter	175.2	19.9	19.0a	5.2	54.3f	2.2	90.6e	8.0
Portage	64.5	20.2	19.4ab	5.2	60.4d	2.2	111.0a	8.0
MN 841801	20.7	20.0	20.7b	5.2	61.9bc	2.2	103.6c	8.0
Belle	3.4	20.6	27.3cd	5.2	66.8a	2.3	96.4d	8.1

† Phase I: Recurrent selection for grain yield.
‡ Phase II: Recurrent selection for partial resistance to crown rust.
§ Within columns, means followed by the same letter are not significantly different according to two-tailed tests of pairwise differences with no adjustment for multiple comparisons. Comparisonwise α: 0.05.

per cycle for Phase II was 11%. A similar intermediate response was obtained by Baltenberger et al. (1988) after two cycles of recurrent selection for tolerance to barley yellow dwarf virus in an adapted oat population (−10%). Lower absolute responses (−3%) were found by Reinhold et al. (1993) and Walker and Schmitthenner (1984) after eight cycles of recurrent selection for adult plant resistance to leaf rust in barley and three cycles of recurrent selection for tolerance to Phytophthora rot in soybean, respectively. Higher absolute gains per cycle have been reported for resistance to scab (−18%; Jiang et al., 1994) and powdery mildew (−18%; Abdalla et al., 1989) in wheat and leaf rust and powdery mildew in barley (−32 and −19%, respectively; Parlevliet and Van Ommeren, 1988). The four rapid recurrent selection cycles for partial resistance to oat crown rust of Phase II produced an average reduction in AUDPC of −8.87 cycle^{-1} (Fig. 1). At this rate of progress three additional recurrent selection cycles would be required to attain the level of partial resistance of the experimental line MN 841801 (Table 2).

The experimental unit used in the six evaluation experiments was a hill plot. With this plot type a complete repetition, with 142 treatments, occupied 30 m^2 of field space, and each plot required only 30 seeds. These features allowed us to use multiple environments and numerous repetitions per environment. More evaluation sites provided a better sample of the target population of environments, while increased replication improved the control of the experimental error. Conversely, small plots may have reduced the precision of the disease resistance assessment through an increase in the interplot interference (Parlevliet and Van Ommeren, 1984). Genotypes susceptible to oat crown rust produce large amounts of inoculum that artificially increase the level of disease of more resistant neighbors, reducing the expected differences between treatments. Although the corresponding experiments with isolated plots have not been conducted, interplot interference may have caused the level of partial resistance of the recurrent selection parents and resistant checks to be underestimated by the hill plot evaluation experiments.

A continuous positive response in grain yield was observed during Phase I. The grain yield of Cycle I-0 parents is comparable with the yield of Starter, Portage, and MN 841801, and Cycle I-4 has a grain yield similar to Belle and significantly lower ($P < 0.05$) than Cycle I-7 and Phase II Cycle parents (Table 2). The Phase I average gain in grain yield per cycle was 8.1%. This direct response estimate is similar to the average gains reported by Reysack et al. (1993), Pomeranke and Stuthman (1992), and De Koeyer et al. (1993) for the same oat population after four, five, and five cycles of recurrent selection for grain yield, respectively. Payne et al. (1986) and Bregitzer et al. (1987) studied this population after three cycles of selection and reported smaller realized gains (3.8 and 4.5%), comparable to the 3.1% average response per cycle estimated after seven cycles of selection by De Koeyer and Stuthman (1998). All seven selection response estimates were obtained from combined hill plot experiments. Pomeranke and Stuthman (1992) and De Koeyer et al. (1993) also studied the response to recurrent selection for grain yield using two-row plots. Pomeranke and Stuthman (1992) found similar gains for hill and row plots (7.9 and 7.5%, respectively), while De Koeyer et al. (1993) estimated a higher selection response for hill plots (11.1 vs. 5.4%). The phenotypic correlations between hill and row plot means estimated by Pomeranke and Stuthman (1992) and De Koeyer et al. (1993) were 0.85 and 0.68, respectively.

In Phase II of this study, recurrent selection parents were selected for partial resistance to oat crown rust. The indirect response in grain yield to four cycles of recurrent selection for partial resistance was not significant (Fig. 1b). When the six evaluation experiments were separated into two groups on the basis of the presence or absence of crown rust disease, the estimated grain yield responses for Phase I and Phase II did not differ from the general averages presented previously

(Table 3). The lack of response in grain yield during Phase II could be attributed to moderate crown rust epidemics in all but one of the six evaluation experiments. 40% was the average final disease severity of the susceptible check (Starter) in the experiments with moderate epidemics. In Exp. 5 (Table 1), the average final crown rust severity was 89%, and the Phase II progress in resistance to crown rust was reflected in an average grain yield gain of 4.7% cycle^{-1}. The positive association between partial resistance to crown rust and grain yield under high disease pressure has been documented previously. Holland and Munkvold (2001) studied this association in artificially inoculated field experiments, and report a genotypic correlation between AUDPC and grain yield of −0.63.

The flowering date of the recurrent selection population is halfway between the early (Starter) and late (Belle) maturity checks (Table 2). After seven cycles of recurrent selection for grain yield (Phase I) with selection for earlier flowering date as a secondary selection criterion between Cycles I-4 and I-7, the number of days to anthesis was reduced by 4 d (Table 2). Two previous studies of this oat population have reported positive indirect responses in the number of days to flowering. Reysack et al. (1993) reported an increase in flowering date of 1.3 d after four cycles of recurrent selection, and Payne et al. (1986) found a positive tendency in the number of days to flowering after three cycles. De Koeyer and Stuthman (1998), on the other hand, report a 1-d reduction in the flowering date after seven cycles of selection. This study confirms that including flowering date as a secondary selection criterion, effectively controlled the potential positive indirect response in flowering date between Cycles I-4 and I-7. This data set also shows that four cycles of recurrent selection for partial resistance to crown rust (Phase II) indirectly delayed the flowering date by 2 d (Table 2). The positive association between crown rust resistance and the number of days to 50% flowering is reflected in the genetic and phenotypic correlations presented in Table 4. The within cycle correlations between AUDPC (AU) and flowering date (FD) are the only consistent ones in sign and significance. AU-FD phenotypic correlations ranged from −0.16 to −0.67 with a mean of −0.46 and a median of −0.49, while the genetic correlations varied between −0.40 and −0.81 with a mean of −0.66 and a median −0.71. These genetic correlation values indicate that almost half of the variation in partial resistance to crown rust could be accounted by the variation in flowering date. Although most of the covariation observed in small populations is due to transient loose linkages, this oat population has been subjected to 11 random recombination events and the association between AUDPC and flowering date has not changed substantially. Therefore, it is likely that tight linkages and/or pleiotropy are responsible for the observed association. Our study confirms a previous report by Luke et al. (1972) indicating a positive relationship between plant maturity and partial resistance to oat crown rust. Positive associations between disease resistance and delayed maturity have also been found in other self-pollinated small-grain crops (Tavella, 1978;

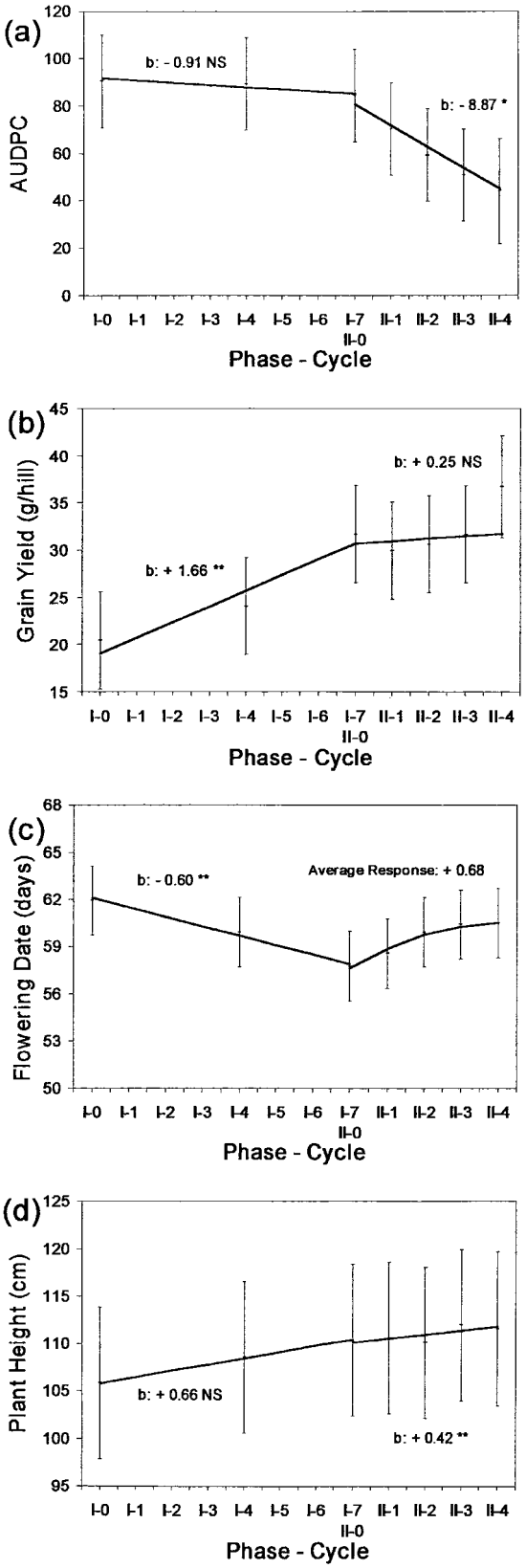

Fig. 1. Direct and indirect responses in area under the disease progress curve (AUDPC), grain yield, flowering date, and plant height to seven cycles of recurrent selection for grain yield (Phase I) followed by four cycles of recurrent selection for partial resistance to crown rust (Phase II) in and oat population.

Table 3. Direct and indirect responses in grain yield to seven cycles of recurrent selection for grain yield (Phase I) followed by three cycles of recurrent selection for partial resistance to crown rust (Phase II) in an oat population.

	Grain Yield								
	All Experiments			Five unprotected Exp.†			One protected Exp.†		
	b	SE	%‡	*b*	SE	%	*b*	SE	%
	g hill^{-1}			g hill^{-1}			g hill^{-1}		
Phase I	1.66**	0.21	8.1	1.58**	0.18	7.3	2.05**	0.24	14.7
Phase II§	0.04	0.28	0.1	0.24	0.25	0.7	−0.83	0.43	−3.0

** *b* greater than 0 at the 0.01 probability level.
† Protection from crown rust disease with a fungicide application.
‡ % change cycle^{-1} calculated as (b/mean of the corresponding Cycle 0) × 100.
§ Estimates calculated excluding Cycle II-4.

Rosielle and Brown, 1980; Qi et al., 1998; de la Pena et al., 1999).

Cycle I-0 parents are significantly taller ($P > 0.05$) than Belle and Starter and seven cycles of recurrent selection for grain yield increased plant height an additional 4.3% (Table 2). This accumulated indirect response estimate is comparable to the 3.6% gain in plant height reported by De Koeyer and Stuthman (1998) for the same oat population. These authors suggest that the use of hill plots in the selection experiments might cause high interplot competition and indirectly benefit taller genotypes. Cycle I-7 and Phase II parents have a similar plant height (Table 2). Taller oat genotypes usually have a higher risk of lodging. Reysack et al. (1993) studied this population after four cycles of recurrent selection for grain yield and not only observed the indirect response in plant height but also reported a significant increase in lodging. Phase II parents have similar heights to those of Cycle I-7 (Table 2).

Broad-Sense Heritability Estimates

Hanson (1963) defined heritability as the fraction of the selection differential expected to be gained when selection is practiced on the declared reference unit. This definition emphasizes the importance of describing the basis (plant, plot, or replicated plot) used in the estimation. Table 5 presents broad-sense heritability estimates computed on an entry-mean basis for each recurrent selection cycle, and the corresponding reference units are presented in Table 1.

The broad-sense heritability estimates for AUDPC ranged from 58 to 80%, with the exception of one particularly low value (Cycle II-1: 45%) (Table 5). These estimates are based on a total of 14 replicates and five environments. Recurrent selection for partial crown rust resistance was practiced using four replicates in each of two environments, and with this reference unit the previous heritability range would become 41 to 64%. Placing the eight replicates in a single environment would reduce the heritability range to 29 to 51%; while doubling the total number of replicates to sixteen would only increase it to 46 to 67%. According to these heritability estimates the current selection procedure (four replicates at two environments) allocates resources adequately. An interesting alternative would require the addition of one environment. With four replicates at three environments the previous heritability range would increase to 51 to 73%.

Luke et al. (1975) and Holland and Munkvold (2001) reported the only other heritability estimates for partial resistance to oat crown rust of which we are aware. Luke et al. (1975) evaluated crown rust resistance on the progeny of a resistant by susceptible cultivar cross and found a single-plant broad-sense heritability value of 87% using indirect estimates of environmental variation. Holland and Munkvold (2001) studied partial resistance in a random-mated population derived from crossing 10 partial resistance donor lines and 10 grain yield donor parents, and report an entry-mean broad-sense heritability estimate of 89% based on three environments. High heritability values for partial resistance to plant diseases are frequently observed in resistant by suscepti-

Table 4. Phenotypic and genetic correlation coefficients between area under disease progress curve (AU), grain yield (GY), flowering date (FD), and plant height (PH) in a recurrent selection oat population evaluated in a multienvironment trial.

	AU-FD		AU-GY		AU-PH		GY-PH		GY-FD		FD-PH	
	r_P†	r_G‡	r_P	r_G	r_P	r_G	r_P	r_G	r_P	r_G	r_P	r_G
Phase I§												
Cycle 4	−0.16	−0.53*	−0.04	−0.33	−0.17	−0.22	0.33	0.42	−0.57**	−0.54*	0.04	−0.03
Cycle 7	−0.46*	−0.78***	−0.18	−1.66	−0.13	−0.24	0.54*	1.02	0.09		0.30	0.29
Phase II#												
Cycle 1	−0.41	−0.40*	−0.20	−0.50*	−0.03		0.57**	1.05	0.27	0.74***	0.51*	0.62**
Cycle 2	−0.51*	−0.67**	−0.14		−0.48*	−0.71***	0.29	3.13	0.01		0.37	0.28
Cycle 3	−0.54*	−0.81***	−0.07	−1.17	−0.25	−0.33	0.59**	0.72***	0.12	−0.33	0.57**	0.60**
Cycle 4	−0.67**	−0.75***	−0.03	−0.33	−0.40	−0.22	0.43	−0.57**	−0.03	−0.22	0.44*	0.34

* Indicates significance at $P = 0.05$.
** Indicates significance at $P = 0.01$.
*** Indicates significance at $P = 0.001$.
† r_P: phenotypic correlation, estimated using genotype means across environments.
‡ r_G: genetic correlation, calculated using genetic variance and covariance estimates from a multienvironment trial.
§ Phase I: Recurrent selection for grain yield.
# Phase II: Recurrent selection for partial resistance to crown rust.

Table 5. Broad-sense heritabilities (H) for area under the disease progress curve (AUDPC), grain yield, flowering date, and plant height in a recurrent selection oat population evaluated in a multienvironment trial.

	AUDPC	Grain yield	Flowering date	Plant height
	H† (90% C.I.)‡	H (90% C.I.)	H (90% C.I.)	H (90% C.I.)
	%			
Phase I§				
Cycle 0	80 (60–92)	8 (−74–62)	92 (83–97)	73 (47–89)
Cycle 4	62 (35–80)	79 (66–89)	96 (94–98)	91 (84–95)
Cycle 7	58 (29–78)	12 (−48–54)	92 (86–96)	82 (69–91)
Phase II#				
Cycle 1	45 (6–71)	57 (27–77)	96 (94–98)	87 (77–93)
Cycle 2	72 (52–85)		95 (91–97)	77 (60–88)
Cycle 3	60 (32–79)	45 (8–71)	95 (91–97)	78 (62–89)
Cycle 4	62 (30–81)	52 (12–76)	94 (87–97)	69 (34–85)

† Broad sense heritability, estimated on an entry mean basis by the variance component method.
‡ Values in parentheses represent lower and upper limits for a 90% confidence interval.
§ Phase I: Recurrent selection for grain yield.
# Phase II: Recurrent selection for partial resistance to crown rust.

ble crosses. Qi et al. (1998) studied partial resistance to leaf rust in 103 recombinant inbred lines from a partially resistant by susceptible barley cross and reported a broad-sense heritability of 82% based on three replications at one environment. Bjarko and Line (1988) estimated broad-sense heritabilities for resistance to wheat leaf rust (caused by *Puccinia triticina* Eriks.) using data from one experiment with three replications. The highest heritability (92%) was obtained for the cross of the highly resistant by the susceptible cultivar, while the cross between the two slow-rusting varieties had the lowest heritability estimate (44%).

Grain yield heritabilities varied greatly between recurrent selection cycles and this fluctuation did not follow any apparent tendency (Table 5). Our evaluation experiments failed to produce precise estimates of the genetic variances for grain yield, and the poor quality of these estimates was reflected in the variability of the broad-sense heritabilities and genetic correlations between grain yield and other traits. Frey and Holland (1999) also estimated broad-sense heritabilities for oat grain yield after nine cycles of recurrent selection for increased groat-oil content, and their combined analysis of three replicated hill plot field trials produced similar and equally variable grain yield heritability estimates.

The flowering date and plant height broad-sense heritabilities presented in Table 5 are based on four environments and 10 replicates. Heritability estimates for flowering date ranged from 92 to 96% and from 69 to 91% for plant height. Our data set suggests that two replicates at two environments could provide a satisfactory assessment of the flowering date, while plant height would require four replicates at two environments. With these reference units the broad-sense heritability estimates would range from 83 to 92% for flowering date and from 66 to 87% for plant height.

This study demonstrated the usefulness of rapid cycle recurrent selection as a population improvement procedure capable of effectively increasing the level of partial resistance to crown rust in an adapted and high-yielding oat population. Although higher heritability estimates and greater gains per cycle could be obtained if the evaluation and selection were conducted on inbred lines, our results indicate that selection for partial crown rust resistance in early generations can produce adequate gains per recurrent selection cycle with a minimum cycle length. The use of hill plots as the experimental unit in the selection field trials did not hinder the ability of accurately assessing crown rust resistance. The benefit of additional replication more than compensated for the potential interplot interference effect caused by the plot type. In addition, our results confirm that the previous seven cycles of recurrent selection for grain yield produced a continuous positive response for grain yield. Single-trait recurrent selection induced correlated changes in other agronomically important variables during the two breeding phases. Therefore, proper correction measures should be implemented to prevent undesirable indirect responses in flowering date and plant height while selecting for grain yield or partial resistance to oat crown rust. Finally, broad-sense heritability estimates indicate that four replicates at two or three environments are required to assess properly partial resistance to crown rust, while satisfactory assessment of flowering date and plant height would demand two and four replicates at two environments, respectively.

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