Transfer of Field Resistance to *Puccinia coronata* from *Avena sterilis* to Cultivated Oats by Backcrossing

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ABSTRACT

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Fourteen strains of *Avena sterilis*, all lacking seedling resistance to the crown rust fungus (*Puccinia coronata*), were selected to represent a wide range of field resistance to this pathogen. They were crossed and backcrossed once and twice with the susceptible oat cultivar Clinton. Lines derived from F_1, BC_1, and BC_2 plants were selected for cultivated plant type and exposed to *P. coronata* in the F_6 and F_7 generations in replicated hill-planted plot trials. The effect of *P. coronata* was measured by dividing grain yield and mean seed weight values of rusted plots by corresponding values for the same lines in rust-free control plots. Yields in the rust-free plots showed a uniform, significant progression of improvement as degree of backcrossing to Clinton increased. Resistance to *P. coronata*, as measured by depression of grain yield and seed weight, decreased with degree of backcrossing. Averaged over the 14 parents, 80% of the lines from F_1, 58% from BC_1, and 30% from BC_2 plants were significantly more resistant than Clinton in terms of reduction in seed weight. Lines combining the yield of Clinton with a significant improvement in resistance appeared in progeny from all parents of *A. sterilis*. Mean heritability values for resistance measured by reduction in grain yield and seed weight were 41 and 58%, respectively. There was only a weak relationship between grain yield and resistance.

Additional key words: disease resistance, germ plasm enhancement, wild germ plasm.

During the last two decades, the crown rust fungus (*Puccinia coronata* Cda.) has not damaged oats (*Avena sativa* L.) grown in the United States as extensively as it did previously. Nevertheless, it remains a threat in much of the United States, causing economically significant losses in some areas almost every year (David L. Long, Plant Pathologist, USDA-ARS, University of Minnesota, St. Paul; *unpublished*). One reason that damage has been reduced in recent years is that current oat cultivars are more resistant than older cultivars. It is amply documented (6), however, that such resistance is not necessarily permanent. If oat cultivars are bred and grown without regard to possible losses from *P. coronata*, more frequent and severe damage might again be experienced by oat producers.

Browning and Frey (1) reviewed the recent history of resistance in oat cultivars to *P. coronata* and emphasized the importance of the wild oat, *Avena sterilis* L., which is indigenous to the Mediterranean and the Near East, as a source of resistance genes for new cultivars, particularly multilines. There are many genes in *A. sterilis* that confer specific resistance (defined here as resistance that is conferred by one or a few genes and is expressed in the seedling stage) to *P. coronata* (2,5). Some of these genes have been used in the development of commercially important pure-line as well as multiline oat cultivars.

Resistance to *P. coronata* other than specific resistance takes many forms and goes by many names, including general, field, adult-plant, slow-rusting, etc. It has been recognized (10,13,16,18,19) and studied (9,15,17,25) by a number of investigators. There is a general consensus that such resistance will probably be less subject to breakdown caused by the appearance and spread of new forms of the fungus than is specific seedling resistance.

Browning et al (2) emphasized that a program of disease resistance breeding should not depend entirely on genes for specific resistance regardless of how abundant or well deployed they might be. Resistance of cultivars with these genes would persist longer if the cultivars also had general resistance. General and specific resistance are miscible in all proportions in either pure-line or multiline cultivars. The availability of general resistance in strains of *A. sterilis* has been recognized since Wahl (26) showed that 16% of the adult plants growing from seed collected in Israel had field resistance to virulent races of *P. coronata*.

Field- or general resistance to *P. coronata* is sometimes controlled by one or a few genes (8,14), but is usually conditioned polygenically (21,23), which means that general resistance should be more difficult to transfer from *A. sterilis* to cultivated oats than specific resistance. Traits conditioned by polygenes, however, have been successfully transferred from *A. sterilis* to *A. sativa*. Lawrence and Frey (11,12) transferred agronomic traits, which were presumably under polygenic control, from *A. sterilis* to *A. sativa*. Simons (20,22) showed that polygenically inherited tolerance to infection by *P. coronata* in *A. sterilis* could be transferred to cultivated oats. Minor genes as well as major genes for resistance to *P. coronata* have also been transferred to cultivated oats (24).

Dudley (3) reviewed recent literature on the use of backcrossing in transferring desirable quantitative traits from exotic germ plasm into adapted populations. Results of his computer simulation studies suggested that if one parent has more loci containing favorable alleles than the other, at least one generation of backcrossing will be beneficial, and that the more diverse the parents, the more useful one or more generations of backcrossing becomes.

The purpose of this study was to determine experimentally if the protection from *P. coronata* that is presumably associated with visual evidence of different degrees of field resistance in strains of *A. sterilis* could be transferred to cultivated oats, and, if so, what would be the optimum proportion of germ plasm of *A. sterilis* in test populations.

MATERIALS AND METHODS

During the 1960s and 1970s many strains of *A. sterilis* from the Mediterranean and Near East that were shown to be susceptible to *P. coronata* as greenhouse-grown seedlings exhibited various degrees of resistance when grown as older plants in the field. For

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purposes of this study, this pattern of reaction is defined as field resistance. It was necessary to limit the study to strains that were susceptible as seedlings because seedling resistance would mask field resistance. The 14 strains selected for this study were all from Israel (26), and they represented a wide range of field resistance, from barely detectable to highly resistant in which little sporulation occurred.

The 14 strains were crossed and backcrossed with the highly susceptible oat cultivar Clinton. Three populations were derived by making selections among progeny segregating from F_1, BC_1, and BC_2 plants. Single-plant selection was practiced in F_2, F_3, and F_4 generations from the F_1 or backcross plants. Only plants with a range of maturity adapted to the upper midwestern United States, and which lacked the undesirable traits of the wild parents such as heavy awns, wild-type disarticulation of the florets, etc., were chosen. Such selection was necessary because of the difficulty of testing *A. sterilis* and segregates morphologically similar to it for reaction to infection expressed in quantitative characters such as yield. Plants were not selected for reaction to *P. coronata*. Plants from the F_4, BC_1F_4, and BC_2F_4 generations were further selected and increased as F_5 lines.

The F_6 and F_7 generations were tested near Ames, IA, in hill plots (4), with hills spaced 0.3 m apart, in rows 0.3 m apart, and 30 seeds per hill. A randomized block design with five replications was used to evaluate the F_6 populations, with seven of the original parental *A. sterilis* tested in 1978 and the other seven in 1979. To confirm results, F_7 populations from three of the parents tested in 1978 and three in 1979 were retested in 1980. Epidemics of *P. coronata* were initiated by hypodermically injecting an aqueous suspension of urediniospores into the culm of one plant per hill as soon as the culms had started to elongate. Trickle irrigation was applied as necessary to prevent drought damage and to ensure spread of the fungus.

It was anticipated that these lines would vary greatly in inherent yielding ability, seed weight, and other quantitative traits. Therefore, duplicate plantings, separated from the diseased plots by a 2-m-wide alley, were maintained free of disease by application of maneb fungicide (manganese ethylene bisdithiocarbamate) applied four to six times per season at a rate of 1 kg of active ingredient per hectare per application to provide comparisons of responses to *P. coronata*. Resistance data were expressed as indexes, obtained by dividing the value of each diseased plot by the corresponding value of the mean of the five replications of its rust-free control. Seed weight was estimated from samples of 200 seeds.

Heritability values for populations from the six parental *A. sterilis* that were grown in 2 yr were calculated by using the standard unit method described by Frey and Horner (7). This consisted of correlating the mean values of the five replications grown in 1 yr with corresponding values from the second year.

RESULTS

Performance in rust-free plots. The performance of Clinton in rust-free plots showed that growing conditions varied greatly in the 3 yr of the study. Mean yields of Clinton in 1978, 1979, and 1980 reflected poor, average, and good growing conditions, respectively (Table 1). Because of these large differences among years, the data will be presented and discussed on a yearly basis.

When averaged over all 14 parental *A. sterilis*, the mean yield of rust-free lines from BC_2 plants was significantly lower than the yield of Clinton, but exceeded that of lines from BC_1 and F_1 plants (Table 1). The mean yield of lines from BC_1 plants exceeded that of lines from F_1 plants. Within progeny from a given parental *A. sterilis*, there were a few cases in which the means of lines from F_1 and BC_1 plants did not differ significantly (data not shown to conserve space), but mean yields of lines from BC_2 plants were always at least as good as those from F_1 or BC_1 plants.

A comparison of mean yields of all lines from each of the 14 parental *A. sterilis* suggests that some of these parents might confer higher yielding ability than others. For example, in 1978 the mean of all progeny from PI 309560 was 17.5 g per plot, while the mean of lines derived from PI 309578 was 22.5 g per plot, a difference of almost 30%. Similarly in 1979, the mean difference in yield between the lowest and highest population was 24%.

A comparison of individual lines within types of populations (Table 2) revealed some relationships not evident in the means. In all 3 yr, the BC_2 populations contained the highest yielding line. Differences in this regard between F_1 and BC_1 populations were not consistent. Distribution of the lowest-yielding lines showed a different pattern, with the lowest-yielding lines being as likely to occur in populations from BC_2 plants as in populations from F_1 plants. When all lines within each type of population that were significantly higher ($P = 0.05$) in yield than Clinton were considered, a strong progression of improved yield with more backcrossing was evident (Table 2). Most of the lines derived from F_1 plants were lower yielding than Clinton, while over half of the lines from BC_2 plants yielded as well as Clinton. Lines significantly higher in yield than Clinton were not uncommon, especially in populations derived from BC_2 plants.

Response to infection. Occurrence of fungal diseases other than crown rust was negligible in all 3 yr. Crown rust was extremely severe in 1978 and 1980, with grain yields of Clinton reduced to one-third of the rust-free controls. Seed weight of Clinton was reduced by almost half in those 2 yr (Table 1). Disease development was less severe in 1979, with grain yield and seed weight of Clinton reduced to about two-thirds that of the control.

The mean yield index data (yield of the diseased line as a proportion of the yield of its rust-free control) showed that the three types of populations decreased in resistance as the percentage of recurrent parent in the population increased (Table 1). The mean yield index of lines from BC_2 plants was higher than the mean of Clinton in all 3 yr, but significantly so only in 1980. The individual means of F_1-derived populations from all 14 parental *A. sterilis* were significantly higher than Clinton, indicating that significant amounts of resistance were transferred from all of the wild parents. The mean yield indexes of all progeny from the parental *A. sterilis* having the greatest resistance were 24 and 16% higher than indexes of progeny from the parent transmitting the least resistance in 1978 and 1979, respectively. This suggests that more resistance was transferred from some parental *A. sterilis* than from others.

The seed weight index results (Table 1) follow the same general pattern as the yield index results. In all 3 yr, population means for seed weight indexes from BC_2 plants were lower than population means from F_1 or BC_1 plants. There were a few instances in which

TABLE 1. Means[y] of three traits in lines derived from F_1, BC_1, and BC_2 plants from crosses between 14 strains of *Avena sterilis* and the cultivar Clinton

Origin	Rust-free yield (g/plot)			Yield index[z]			Seed weight index[z]		
	1978	1979	1980	1978	1979	1980	1978	1979	1980
F_1	16.6 a	22.6 a	28.7 a	0.52 a	0.69 a	0.61 a	0.66 a	0.77 a	0.73 a
BC_1	19.3 b	26.4 b	32.2 b	0.46 b	0.65 bd	0.53 b	0.59 b	0.74 b	0.66b
BC_2	21.8 c	30.7 c	34.6 c	0.42 c	0.63 c	0.44 c	0.54 c	0.71 c	0.59 c
Clinton	25.0 d	32.7 d	40.9 d	0.38 c	0.60 cd	0.34 d	0.55 c	0.66 d	0.56 d

[y]Totals of 280, 560, and 1,120 lines derived from F_1, BC_1, and BC_2 plants, respectively, were tested (see Table 4). Means in the same column not having a letter in common differ significantly (Fisher's protected LSD test, $P = 0.05$).

[z]Measures of damage from *P. coronata* obtained by dividing respective values of rusted plots by corresponding values of the mean of rust-free control plots.

the means of BC_1 populations of individual parental *A. sterilis* were higher than means of populations from F_1 plants (*unpublished*). However, overall means of populations from all parental *A. sterilis* exceeded those of Clinton, another indication that field resistance was transferred from all the wild parents to cultivated-type progeny.

When the mean seed weight indexes among populations from the 14 parental *A. sterilis* were compared, large differences were not apparent. Nevertheless, the population with the highest mean exceeded the lowest by 20% in 1978 and by 11% in 1979 (*unpublished*).

The ranges of yield indexes of individual lines within each of the three types of populations showed little pattern. Lines with both very low and very high yield indexes appeared in all three types of populations (Table 2). The very low-seed-weight indexes also seemed to occur at random; but, in all 3 yr, lines with the highest seed-weight indexes occurred in F_1 or BC_1-derived populations. This suggests that some resistance was lost in the BC_2. The percentage of lines in the different types of populations that were significantly higher than Clinton for both yield and seed weight indexes decreased regularly and substantially with backcrossing (Table 2). In the different years there were only about one-third to one-half as many lines in the BC_2-derived populations as in the F_1-derived populations that were significantly more resistant than Clinton.

Relationship of yield potential to disease resistance. Possible linkages in wild parental *A. sterilis* between an undesirable trait, such as low grain yielding capacity and resistance to *P. coronata*, are vitally important when transferring crown rust resistance to cultivated-type oats. Although the correlation coefficients between rust-free yield and both yield and seed weight indexes in 1978 and 1979 were statistically significant, their values were low, which indicates that only a small proportion of the resistance is associated with low yielding ability (Table 3). This relationship should not be a serious problem in practical plant breeding.

TABLE 2. Ranges of three traits in lines derived from F_1, BC_1, and BC_2 crosses between 14 strains of *Avena sterilis* and the cultivar Clinton

			Percentage of lines:	
Trait and year	Lines from:	Range	similar to Clinton[b]	higher than Clinton[b]
Rust-free yield (g/plot)				
1978	F_1	4.6–32.2	18	1
	BC_1	3.4–32.8	45	2
	BC_2	4.8–35.0	65	4
1979	F_1	11.8–40.2	19	1
	BC_1	10.4–39.6	44	0
	BC_2	14.2–43.4	65	6
1980	F_1	18.8–43.8	17	0
	BC_1	15.8–49.2	44	0
	BC_2	15.2–54.4	54	1
Yield index[a]				
1978	F_1	0.14–0.92	44	54
	BC_1	0.10–0.99	62	33
	BC_2	0.09–0.98	70	25
1979	F_1	0.31–1.28	57	36
	BC_1	0.11–0.91	75	21
	BC_2	0.22–0.94	81	12
1980	F_1	0.24–0.96	22	78
	BC_1	0.07–1.00	42	57
	BC_2	0.12–1.23	65	34
Seed wt index[a]				
1978	F_1	0.06–0.82	25	67
	BC_1	0.01–0.87	51	41
	BC_2	0.08–0.76	78	12
1979	F_1	0.58–0.92	24	75
	BC_1	0.40–0.93	36	62
	BC_2	0.52–0.86	56	42
1980	F_1	0.55–0.88	3	97
	BC_1	0.17–0.90	27	72
	BC_2	0.41–0.85	55	37

[a] Measures of damage from *P. coronata* obtained by dividing respective values of rusted plots by corresponding values of the mean of the rust-free control plots.

[b] Based on Fisher's protected LSD test, $P = 0.05$.

Heritability. Heritability values for three traits, calculated from two year's data, are shown in Table 4. For rust-free grain yield, only two of the heritability values for the 18 populations failed to reach significance at $P = 0.05$. Heritability of resistance, measured by yield index, was more erratic, with values for individual populations ranging from 8 to 58%. All six of the values for populations from BC_2 plants, where each population consisted of 80 lines, were significant. Heritability values for seed weight index averaged a little higher and were more consistent than those for yield index. Only three of the 18 values failed to reach significance. Average values for both yield and seed weight indexes tended to increase with increased backcrossing.

DISCUSSION

The experimental results reported here generally substantiate Dudley's (3) computer simulation studies on the use of backcrossing to transfer desirable traits from exotic germ plasm. This is particularly true with regard to the suggestion that one or more generations of backcrossing will be useful when the parents are relatively diverse. The parents involved in my study differed greatly in agronomic traits, and it was clearly much easier to select for plant type, as it is expressed in yield potential, in backcross than in nonbackcross progenies.

The data also show, however, that as the percentage of germ plasm of *A. sterilis* decreased, the amount of resistance to *P. coronata* also decreased. The most highly resistant line from a given wild parent usually was found among lines derived from F_1 plants rather than from backcross plants. This suggests that progeny derived from F_1 plants should be used if the objective is to transfer the maximum amount of resistance from the parental *A. sterilis*. It should be noted, though, that lines combining the yield of Clinton with a significant improvement in resistance appeared in all three types of populations. Thus, reasonable progress could be expected in a breeding program that started with material derived from BC_2 plants.

The 14 parental *A. sterilis* were originally chosen to represent a wide range of reaction to *P. coronata*, from highly resistant to a degree of resistance that could barely be distinguished visually from susceptibility. Cultivated-type progeny did not have nearly so wide a range of reaction. The data, in fact, suggest that it makes relatively little difference which parental *A. sterilis* is chosen. All of them, regardless of whether they appeared to be only slightly resistant or highly resistant, seemed capable of transmitting significant amounts of protection to progenies with a cultivated plant type. The magnitude of the heritability values calculated for this resistance suggested that it could be manipulated in practical breeding programs even when field conditions are less than ideal.

The extreme susceptibility of some of the derived lines raises an interesting question concerning the concept of relative susceptibility. The cultivar Clinton was chosen as the parent

TABLE 3. Mean phenotypic correlation coefficients[a] between traits of oat lines derived from crosses between 14 strains of *Avena sterilis* and oat cultivar Clinton

Traits	Rust-free yield	Yield index	Seed wt. index
Rust-free yield	···	−0.084**	0.104**
Yield index	−0.285**	···	0.755**
Seed wt. index	−0.280**	0.678**	···

[a] Coefficients above dotted lines are for populations derived from crosses between each of seven parental *A. sterilis* and Clinton and grown in 1978; below, for populations derived from seven parents and that were grown in 1979. Asterisks (**) indicate statistical significance, $P = 0.01$.

TABLE 4. Field reactions of 14 strains of *Avena sterilis* to *Puccinia coronata*, and heritability values for three traits in populations of lines derived from F_1, BC_1, and BC_2 crosses between Clinton and six strains of *A. sterilis*

A. sterilis strain (PI)	Reaction to *P. coronata*[a]	Years grown	Heritability (%) Rust-free yield F_1	BC_1	BC_2	Yield index[b] F_1	BC_1	BC_2	Seed wt index[b] F_1	BC_1	BC_2
295910	MR	1978									
296241	MR	1978									
296245	MS	1978,1980	25	50*	38*	35	23	57*	63*	48*	74*
298129	S	1978,1980	73*	68*	36*	34	62*	53*	50*	75*	78*
298201	HR	1978									
309560	R	1978, 1980	38	68*	50*	46*	8	58*	39	22	51*
309578	MS	1978									
309193	MS	1979, 1980	64*	32*	48*	12	60*	30*	39	80*	55*
309302	MS	1979									
309432	S	1979									
309527	MS	1979									
309561	R	1979, 1980	86*	60*	48*	40	44*	44*	61*	72*	59*
309613	MS	1979									
309617	R	1979, 1980	61*	61*	25*	47*	39*	49*	50*	71*	55*
Mean heritability (%)			58	56	41	36	39	48	50	61	62

[a] HR (highly resistant) = numerous chlorotic areas on leaves, some containing small uredinia; R (resistant) = small uredinia in chlorotic areas; MR (moderately resistant) = mid-sized uredinia in chlorotic areas; MS (moderately susceptible) = full-sized uredinia mostly in chlorotic areas; and S (susceptible) = full-sized uredinia surrounded by only faintly discolored leaf tissue. There was a tendency for the relative number of uredinia per unit of leaf area to increase as the size of the uredinia increased.

[b] Measures of damage from *P. coronata* obtained by dividing respective values of rusted plots by corresponding values of the mean of the rust-free control plots. Asterisks (*) indicate statistical significance of the corresponding correlation coefficient, $P = 0.05$.

because it was regarded as "highly susceptible," and its performance in this study clearly confirmed this assumption. Many of the derived lines, however, were damaged far more severely than Clinton, indicating that even Clinton has a significant degree of resistance on an absolute scale. Such "resistance" undoubtedly protects most oat cultivars from severe losses due to *P. coronata*, and it could be lost if future breeding efforts fail to include attention to resistance.

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