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Predicting the relative effectiveness of direct versus indirect selection for oat yield in three types of stress environments

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Summary

In breeding crop varieties for stress environments, it must be decided whether to select directly, in the presence of stress, or indirectly, in a nonstress environment. The relative effectiveness of these two strategies depends upon the genetic correlation (r_G) between yield in stress and nonstress environments and upon heritability in each. These parameters were estimated for grain yield of 116 random oat lines grown in nonstress, P-deficient, N-deficient, and late-planted environments. Estimates of r_G between yield in nonstress and yield in P-deficient, N-deficient, and late-planted environments were 0.52 ± 0.24, 1.08 ± 0.16, and 0.06 ± 0.24, respectively. No consistent relationship between heritability and environment mean yield was observed. Direct selection in the presence of stress was predicted to be superior for yield in low-P and late-planted environments, but indirect selection in high-N environments was predicted to be as effective as direct selection in producing yield gain in low-N environments. These results confirm that neither high-yield environments nor environments in which the heritability of yield is maximized are necessarily optimum when the goal is to maximize yield gain in stress environments.

Introduction

When breeding crop varieties for yield in stress environments, it must decided whether genotypes should be selected directly, in the presence of stress, or indirectly, in its absence. Whether direct or indirect selection is superior depends upon the heritabilities of yield in stress and nonstress conditions (h^2_s and h^2_{ns}, respectively) and the genetic correlation between yields in stress and nonstress environments (r_G) (Falconer, 1952; Allen et al., 1978; Rosielle & Hamblin, 1981; Atlin & Frey, 1989). The relative effectiveness of indirect versus direct selection for a trait such as yield in stress environments can be predicted (Falconer, 1981) as:

$$CR_s/R_s = r_G\, h_{ns}/h_s \qquad (1)$$

where CR_s is correlated response in stress environments to selection in nonstress environments, R_s is response to direct selection in stress environments, and h_{ns} and h_s are the square roots of h^2_{ns} and h^2_s, respectively. Estimates of h^2_s and h^2_{ns} have been reported (Gotoh & Osanai, 1959; Frey, 1964; Johnson & Frey, 1967; McNeill & Frey, 1974; Allen et al., 1978; Rumbaugh et al., 1984), but few estimates of r_G exist in the plant breeding literature. The magnitude of r_G is inversely related to genotype × environment interaction (with 'environment' meaning 'stress level' in this report) and can, under restricted conditions, be calculated as:

$$r_G = \sigma^2_G/(\sigma^2_G + \sigma^2_{GE}) \quad (2)$$

where σ^2_G and σ^2_{GE} are genetic and genotype × environment variances, respectively (Robertson, 1959; Dickerson, 1962; Yamada, 1962; Fernando et al., 1984). When only two environments or stress levels are considered, r_G can also be estimated as a product-moment correlation (Via, 1984; Atlin & Frey, 1989).

Atlin & Frey (1989) demonstrated in a population of random oat lines that grain yield in stress, or low-productivity, environments (LPE) and grain yield in high-productivity environments (HPE) were not controlled by identical sets of alleles. The genetic correlation between yield in HPE and LPE was only 0.59, with the result that yield gain was greater for direct selection in LPE than for indirect selection in HPE, even though h^2 was greater in HPE.

In their experiments, Atlin & Frey (1989) grouped low-N, low-P, and later-planted environments together as LPE. They did not determine the relative degree of responsibility of these different causes of stress for the overall r_G between yields in LPE and HPE. Knowledge of the extent to which individual stress factors caused the low overall r_G would permit direct selection for yield in LPE to be more precise by permitting testing and selection to be concentrated in stress environments requiring the greatest degree of specific adaptation. Therefore, the main objective of this research was to estimate r_G between yields in nonstress environments and yields in low-N, low-P, and late-planted environments in the same population of oat lines used by Atlin & Frey (1989). These r_G values were used to predict whether response to direct selection for yield in any stress environment would exceed response to indirect selection in the absence of stress.

Materials and methods

The homozygous oat lines for this study were extracted from a bulk population made by mixing F_2 seeds from approximately 75 matings. The bulk was mass-selected from F_2 through F_8 for earliness, shortness, and crown rust resistance. In the F_9, a large number of plants were space-sown and harvested individually. The seed from a plant was used to establish an F_9-derived line; 116 such random lines were included in this study.

To estimate r_G between yields in low-P and high-P environments, the lines were planted in paired, randomized complete-block experiments, each with two replications, in P-deficient soil at Castana, Iowa, in 1972, 1973, and 1986. The field in which the experiments were planted had received no supplemental P for several years before 1972. In each year of the study, one experiment (low-P) received no supplemental P, and the other (high-P) was fertilized to recommended levels. In 1972 and 1973, one replicate of the high-P experiment received 59 kg ha^{-1} P, and the other received 88 kg ha^{-1}, both broadcast preplanting. In 1986, the high-P experiment received a preplanting broadcast application of 87 kg ha^{-1} P. Each plot was a hill sown with 30 seeds (approximately 105 kg ha^{-1}). Hills were spaced 30 cm apart in perpendicular directions. Each experiment was bordered on all sides by two rows of hills. Plot areas were hand-weeded, and the plants were sprayed with the fungicide Maneb (manganese ethylene bisdithiocarbamate) in 1972 and 1973 and the fungicide Bayleton [1-(4-chlorophenoxy)-3.3-dimethyl-1-(1H-1,2,4-triazol-1-yl)-2-butanone] in 1986 to control foliar diseases. Grain yield was the weight of threshed grain from a plot expressed in kg ha^{-1}.

Analyses of variance within P levels were computed according to the model

$$Y_{ijk} = \mu + G_i + E_j + (GE)_{ij} + R/E_{k/j} + \varepsilon_{ijk} \quad (3)$$

where Y_{ijk} is the grain yield of a plot, μ is the experiment mean, G_i is the effect of the ith genotype, E_j is the effect of the jth year, $(GE)_{ij}$ is the interaction of the ith genotype and jth year, $R/E_{k/j}$ is the effect of the kth replicate in the jth year, and ε_{ijk} is the residual.

Analyses of variance were computed from data that had been standardized within trials. Standardized values for plot grain yield were calculated as:

$$Z_{ijk} = (Y_{ijk} - Y_{.j.})/S_j \qquad (4)$$

where Z_{ijk} is the standardized value for grain yield of a plot, Y_{ijk} is the value on the original scale, and $Y_{.j.}$ and S_j are the mean and standard deviation in the jth year, respectively.

All factors were considered random. Variance components were estimated from appropriate linear functions of mean squares, and standard errors for components were calculated according to the method of Anderson & Bancroft (1952). Heritabilities within P levels, expressed on an entry-mean basis for a reference unit of mean yield from three 2-replicate trials (thus referring to genotype means of six hill plots), were computed as:

$$h^2 = \sigma^2_G/\sigma^2_P \qquad (5)$$

where σ^2_G and σ^2_P are the genotypic and phenotypic variances, respectively. Confidence intervals ($\alpha = 0.10$) for h^2 were calculated according to the method of Knapp et al. (1985).

The genetic covariance between yield in high-P and low-P environments was computed from line means within experiments according to the analysis of covariance presented in Table 1. This analysis permitted the estimation of the genetic covariance without bias from year and genotype × year covariances. The genetic correlation (r_G) between yield in high-P and low-P environments was calculated as:

Table 1. Analysis of covariance for mean grain yield in oat lines in high-P and low-P environments

Source	df	Expected mean cross-products
Years (Y)	2	
Genotypes (G)	115	$\sigma_{GY} + 3\sigma_G$
G × Y	230	σ_{GY}

$$r_G = \sigma_{G_{LH}}/(\sigma_{G_L}\,\sigma_{G_H}) \qquad (6)$$

where $\sigma_{G_{LH}}$ is the genetic covariance of line means in low-P environments with line means in high-P environments, and σ_{G_L} and σ_{G_H} are the square roots of genetic variance estimated in low-P and high-P environments, respectively. The standard error of r_G was calculated according to Scheinberg (1966). Estimates of r_G and h^2 were combined according to equation 1 to predict the relative effectiveness of direct selection in low-P versus indirect selection in high-P environments.

A similar protocol was used to estimate r_G between yield in low-N and high-N environments. Paired low-N and high-N trials were conducted at Kanawha in 1972, 1973, and 1986. High-N trials received 40 kg ha^{-1} supplemental N in 1972 and 1973 and 51.5 kg ha^{-1} in 1986. Low-N trials received no supplemental N and were situated in an area that had received no N for several years before 1972. Experimental design, plot management, and statistical analyses were the same as described for the paired P experiments.

The genetic correlation between yields from heat-stressed and nonstressed environments was estimated by pairing, within locations, early- and late-planted experiments in Ames, Kanawha, and Sutherland, Iowa. Late-planted experiments were considered to be heat-stressed environments and early-planted experiments were considered nonstress environments. Within a location, early- and late-planted experiments were conducted in different years. The early trials were sown on 20 March 1968, 19 April 1972, and 5 April 1973 at Ames, Kanawha, and Sutherland, respectively, and late trials were sown on 16 May 1973, 10 May 1986, and 12 May 1986 at Ames, Sutherland, and Kanawha, respectively. Experimental design, plot management, and statistical analyses were as decribed for the P and N experiments, except that locations instead of years were considered to be environments in the analyses of variance. As a result, estimates of σ^2_G also contained a portion of the genotype × year interaction variance ($\sigma^2_{GY}/3$), which may have resulted in deflation of estimates of r_G. The extent of this bias is unknown, since estimates of σ^2_{GY} could not be obtained from this experiment.

oat genotypes produce high yields because they are early maturing and, thus, can avoid the onset of high temperatures, whereas other seem to resist heat stress (Colville-Baltenberger & Frey, 1987; Wych et al., 1982). To clarify whether differential maturities were responsible for yield differences among lines tested in late-planted (heat-stressed) environments, r_G was computed between yield in late-sown experiments and maturity. The measure of maturity used was heading date (number of days from planting until 50% of panicles had emerged from the leaf sheath) in early-sown experiments. Heading dates from late-sown experiments were unavailable, but the trait is highly heritable, so the substitution of values from early-sown trials can still be expected to result in an accurate estimate of r_G between late-sown yield and maturity. Heading dates from Ames in 1967 and 1972 and grain yields in Ames in 1973, Kanawha in 1986, and Sutherland in 1986 were used for these computations. Because heading dates and grain yields were measured in experiments grown in different years, the covariance of line means for the two traits was genetic in origin. Therefore, r_G between heading date in early-sown and yield in late-sown environments was estimated as:

$$r_G = \sigma_{G_{HG}} / (\sigma_{G_H} \times \sigma_{G_G}) \qquad (7)$$

where $\sigma_{G_{HG}}$ is the covariance of line means for heading data at Ames with line means for grain yield in the late-planted environments, and σ_{G_H} and σ_{G_G} are square roots of genotypic variances of heading dates from the early-sown and yield from the late-sown experiments, respectively.

For all three comparisons between stress and nonstress environments, the predicted relative efficiency of direct and indirect selection was computed as defined in equation 1.

Results and discussion

Mean yields, heritabilities, r_G between yields in stress and nonstress environments, and predicted ratios of correlated versus direct response are presented in Table 2 for the comparison of low-P, low-N, and heat-stressed with nonstress environments. Each stress environment reduced grain yield by more than 50% when compared with the appropriate nonstress environment.

The genetic correlation between grain yield in low- and high-P environments was 0.52 (Table 2), indicating that only 27% of the genetic variation at either P level resulted from causal factors common to both levels. The estimate of heritability of yield at the low-P level was somewhat greater than at the high level; although the difference was not statistically significant, low P would be judged superior if point estimates of h^2 were the only criteria available for use in deciding which environment was best for selection. However, the low r_G resulted in a large predicted advantage for direct selection at each level of P. In low-P environments, response to direct selection was predicted to be more than twice as great as correlated response to selection in high-P environments.

Table 2. Heritability[a] (h^2) of oat grain yields in stress and non-stress environments, the genetic correlations (r_G) between yields in stress and non-stress environments, and the predicted ratio of correlated and direct response to selection (CR/R) at each stress level for three types of stress environments

Type of Environment	Mean yield (kg ha^{-1})	h^2	r_G	CR/R
Low P	1140	0.40 (0.22, 0.54)		0.38
High P	2471	0.21 (−0.02, 0.40)	0.52 + 0.24	0.71
Low N	1240	0.32 (0.12, 0.48)		1.09
High N	2850	0.38 (0.19, 0.53)	1.08 + 0.16	0.92
Late-planted	1500	0.15 (−0.10, 0.36)		0.12
Early-planted	3970	0.63 (0.52, 0.72)	0.06 + 0.24	0.03

[a] Reference unit for h^2 is mean yield in three 2-replicate yield trials. Upper and lower bounds of the 90% confidence interval in parentheses.

In contrast to the results from the comparison over P levels, r_G between yield in low-N and high-N environments was not significantly different from 1. This suggests that an identical complement of alleles controlled yield at both N levels. H^2 was slightly greater in high-N than in low-N environments, so selection at high N was predicted to give at least as great a response in the low-N environment as direct selection in the low-N environment itself.

The r_G between yield in early- and late-planted environments did not differ significantly from 0, so almost none of the gain from selection in nonstress environments was predicted to be expressed under heat-stressed conditions and vice versa. The genetic correlation between maturity and yield in late-sown environments was -0.74, indicating that approximately 55% of the genetic variation for yield in late-planted environments was due to variation in maturity. The remainder probably was due to differences among lines in ability to set and fill seeds under high-temperature conditions.

Our results can be interpreted to show that oat genotypes with specific adaptation to heat and P stress, but not to N deficiency, can be selected from the population used in this study and that selection for yield in heat- and P-stressed environments should be done directly in those environments. Also, they demonstrate that low-P and late-planted environments were responsible for the low r_G between yield in low-productivity environments and high-productivity environments reported by Atlin & Frey (1989). In general, the results indicate that HPE are not necessarily optimum for selecting oat varieties for all environments in which oats are grown in Iowa. A similar result for wheat was reported by Pederson & Rathjen (1981) in South Australia. They observed that variety trials conducted under high-yield conditions at experiment stations were poorer predictors of on-farm performance than were lower-yielding on-farm trials.

Interactions between genotypes and degree of heat stress have been reported in small grains (Wych et al., 1982; Colville-Baltenberger & Frey, 1987), and instances of specific adaptation of certain genotypes to low-P environments have been observed in a number of species (Gabelman & Gerloff, 1983; Caradus, 1982; Brown et al., 1977). Reports such as these show that genotype × stress-level interaction is common. However, little use has been made of estimates of this interaction in the development of breeding strategies for stress environments, both because experiments designed to estimate genotype × environment interaction rarely include enough genotypes to obtain reliable estimates of genetic parameters and because few plant breeders seem to be aware of the nature of the relationship between r_G and σ^2_{GE}. This relationship is the basis for the quantitative approach described in this report to the choice of the optimum selection environment for a particular type of target environment. This approach is especially well suited to the identification of classes of production environments within a geographical region for which separate breeding programs are warranted and may be particularly useful in developing countries, where a given crop species is often grown in diverse production environments.

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