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Selection of oat lines for use in low-productivity environments

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Iowa State University, 1988

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Selection of oat lines for use in low-productivity environments

by

Gary Neil Atlin

**A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
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DOCTOR OF PHILOSOPHY**

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INTRODUCTION

Crop cultivars must frequently be grown in environments that limit yields to a fraction of what can be produced under optimum conditions. Should genotypes destined for use in such low productivity environments (LPE) be screened in nurseries that are themselves low in productivity and thus representative of conditions encountered in commercial production, or should they be evaluated under highly productive conditions, permitting each genotype to express its full yield potential? When a single constraint to yield occurs over a very large region and cannot practically be overcome through environmental manipulations such as application of inorganic fertilizer or irrigation, and when genetic variation for productivity in the presence of the constraint exists, then it is clear that selection should be done in the presence of the yield-constraining factor (Devine, 1982). Such conditions exist, for example, in large areas of acid soil in the humid tropics, where selection of acid-tolerant germplasm is the most effective means of increasing productivity (Plucknett and Smith, 1982; Sanchez and Benites, 1987). The situation is less clear-cut, however, when the degree of yield constraint imposed by a particular stress is continuous rather than discrete within the region, and when the factor is easily (if not necessarily economically) eliminated in the breeding nursery. Examples of such factors include the presence of weeds and deficiencies of N, P, K, and moisture. How does a breeder decide whether to select in the presence of such stress factors or to eliminate them from the nursery, although they may frequently occur in farmers' fields?

This is a question of some concern in North America where, in the face of low commodity prices, farmers are increasingly interested in reducing production costs by minimizing purchased inputs, but the issue is particularly important in developing countries where, because of credit constraints, commodity prices, or other reasons, some small farmers cannot make cash investments for inputs that alleviate yield constraints. Such farmers apply little or no inorganic fertilizer, use low seeding rates, and achieve incomplete weed control. Even farmers who have adopted nitrogen-responsive cultivars selected under high fertility conditions may face severe constraints on use of purchased inputs (IRRI, 1984).

Even though much crop production in developing countries takes place in "low-input" environments, new crop varieties usually are selected, at least in early stages of testing, in highly fertile, well-watered, weed-free nurseries. The validity of this practice can be questioned (Jennings, 1974) in light of frequent reports of significant interactions of genotypes with soil fertility level and moisture availability (e.g., Ohm, 1976; Gardener and Rathjen, 1975; Gabelman and Gerloff, 1983; Caradus, 1982; Brown et al., 1977; Laing and Fischer, 1977). Although experiments comparing yields of modern and unimproved cultivars in both high productivity environments (HPE) and LPE have demonstrated that modern cultivars, selected primarily in HPE, are higher yielding under both conditions (Carlone and Russell, 1986; Castleberry et al., 1984), such experiments do not constitute tests of the hypothesis that selection for performance in LPE is best done in HPE. A test of this hypothesis requires

that cultivars selected in LPE be compared in LPE with cultivars selected in HPE. Few such experiments have been reported.

The present study was undertaken to adapt a theoretical model for predicting response to selection in LPE and HPE (Falconer, 1952) to the problem of choosing an appropriate productivity level in which to select for increased oat grain yield in LPE. Specific objectives were:

1. To develop a method for predicting correlated response in LPE to selection for yield in HPE, and to compare predictions made by this method with predictions of response to direct selection in LPE;
2. To test the accuracy of predictions made in 1 through empirical selection experiments; and
3. To compare predicted gains from direct selection in P-deficient, N-deficient, and heat-stressed environments with predicted gains, in each of the stress environments, from indirect selection in nonstress environments.

LITERATURE REVIEW

Selecting for Broad Adaptation

The problem of choosing the best productivity level for selecting genotypes adapted to a range of environments has been studied extensively. The consensus among breeders is that greater mean yield gains over the range of productivity levels encountered in production of a crop species result from selection in high-productivity environments (HPE) than from stress, or low-productivity, environments (LPE), but empirical evidence favoring selection in either HPE or LPE for broad adaptation has been reported. Frey (1964) reported that equal gains in grain yield of oat (Avena sativa L.) lines resulted from selection under stress and non-stress conditions when selected lines were evaluated in three environments that differed greatly in productivity. He concluded, however, that HPE were superior to LPE for selection because (a) heritability of grain yield was greater in HPE and (b) lines selected in LPE exhibited a larger genotype x environment interaction. In subsequent experiments in oats, selection in HPE has frequently been demonstrated to produce the greatest gains in yield averaged over all productivity levels (Barrales, 1985; Shabana et al., 1980; Vega and Frey, 1981). Similar results have been reported with cotton (Gossypium hirsutum L.) by Quisenberry et al. (1980), with alfalfa (Medicago sativa L.) by Salter et al. (1984), and with wheat (Triticum aestivum L.) by Roy and Murty (1970). On the other hand Byth et al. (1969) reported that selection in HPE resulted in no greater yield gains in two soybean [Glycine max L. (Merrill)] populations than

did selection in LPE. Similarly, McNeill and Frey (1974) reported that the magnitude of gain from selection in a population of 1200 oat lines was not related to the productivity level of the environment in which selection was carried out. Several authors have reported cases in which genotypes selected in stress environments were more productive over a range of environments than genotypes selected in HPE (Gotoh and Osanai, 1959; St. Pierre et al., 1967).

Selecting for Adaptation to Stress Environments

In contrast to the problem of choosing the most effective selection environment for increasing mean yield over a range of productivity levels, little attention has been paid to the question of maximizing gains in LPE. Opinion is divided over whether selection should be direct, i.e., conducted in LPE, or indirect, in HPE.

Supporting the hypothesis that selection for performance in LPE should be conducted indirectly in HPE, Pfeiffer (1987) reported that soybean lines selected in early planted environments outyielded those selected in lower-yielding late plantings, regardless of whether they were evaluated in early or late plantings. Similarly, Van Sanford and Matzinger (1983), in a study comparing recurrent selection on low- and high-nutrient media for increased seedling weight in tobacco (Nicotiana tabacum L.), observed that the greatest gains resulted from selection on high-nutrient medium, irrespective of the level at which response was evaluated. An advantage for selection in the absence of stress for performance under conditions of stress has also been reported in cotton

(Quisenberry et al., 1980), oats (Shabana et al., 1980), and alfalfa (Salter et al., 1984). On the other hand, Arboleda-Rivera and Compton (1974) reported that direct selection in drought-stress environments was superior to indirect selection in the absence of drought for producing a drought-hardy maize (Zea mays L.) synthetic, and both Falconer and Latyszewski (1952) and Bateman (1974) observed that direct selection on a poor diet for increased body size in mice was superior to indirect selection at an optimum nutritional level.

The main argument made in favor of the practice of selecting in HPE, regardless of the productivity level of the target environment, is that the value of a genotype attains its fullest expression, and differences among phenotypes are maximized, under optimum conditions for growth. This increased differentiation among phenotypes permits superior genotypes to be identified with greater ease than in poor environments (Frey, 1964; Castleberry et al., 1984). According to this view, originally stated by Hammond (1947, in Falconer and Latyszewski, 1952) and subsequently by Daday et al. (1973) and Mederski and Jeffers (1973) among others, gains from selection in good environments are also expressed in poor environments and are likely to exceed gains resulting from direct selection in the poor environments. Falconer and Latyszewski (1952), however, pointed out that for this to be generally true, heritability must always be greater in good than in poor environments, and

The genes determining the expression of the character selected (must be) mainly the same in both good and bad environments. In other words, there must be an absence of genotype-environment interaction of the generally recognized sort, where the superior phenotypes rely on different genotypes for their expression in the two environments.

Neither of these conditions is generally true. Genotype x environment (GE) interaction has long been recognized as a cause of low correlation between genotypic and phenotypic values of quantitatively inherited characters (Comstock and Moll, 1963), and although there appears to be a tendency for heritability to be greater in high-yield environments (Frey, 1964; Byth et al., 1969; Roy and Murty, 1970; Vela-Cardenas and Frey, 1972; Quisenberry et al., 1980; Vega and Frey, 1981; Rumbaugh et al., 1984; Barrales, 1985), this is by no means invariably true (Falconer and Latyszewski, 1952; Johnson and Frey, 1967; McNeill and Frey, 1974; Allen et al., 1978; Pederson and Rathjen, 1981).

Although several authors (Falconer, 1952; Johnson and Frey, 1967; McNeill and Frey, 1974; Allen et al., 1978) have emphasized the need to account for both GE interaction and heritabilities in order to predict the best selection environment for a given target environment, the conventional analysis of GE interaction does not, in itself, lead to such a prediction (Comstock, 1977). In this analysis, the value of a phenotype is expressed as a linear function of genotype, year, and location effects and their first- and second-order interactions. These effects and their variances can be estimated from factorial experiments in which a sample of genotypes from a reference population is grown in several years at several locations, with replication of genotypes within locations. Variance component estimates derived via this model have several applications in the design of breeding programs. These include (a) determining the best allocation of experimental resources among locations, years, and replications (Sprague and Federer, 1951; Comstock and Moll, 1963),

(b) division of a geographical region into homogeneous subregions within which GE interaction is minimized (Horner and Frey, 1957; Abou El-Fittouh et al., 1969), and (c) predicting the increase in gains from selection resulting from such division (Comstock and Moll, 1963). However, the relative magnitudes of variance components do not directly predict the extent to which gains from selection in one environment are expressed in another.

Predicting the Best Selection Environment

Falconer's model

A useful approach to the integration of information on heritability and GE interaction in a prediction of the best selection environment for a given target environment was proposed by Falconer (1952). Performance in selection and target environments, in this case HPE and LPE, can be considered separate genetic traits, and their genetic correlation can be measured. This method of analyzing genotype x environment interaction, more recently discussed by Allen et al. (1978) and Rosielle and Hamblin (1981), permits application of the theory of selection for correlated characters in deciding whether to select genotypes for stress environments directly, in LPE, or indirectly, in HPE. Response to direct selection in LPE (R_L), and correlated response in LPE to indirect selection in HPE (CR_L), can be predicted (after Falconer, 1981, p. 291), as:

$$R_L = i H_L \sigma_{GL} \quad (1)$$

$$CR_L = i H_L H_H r_G \sigma_{PL} \quad (2)$$

where i is selection intensity in standard units, r_G is the genetic correlation between yields in LPE and HPE, σ_{GL} and σ_{PL} are the genetic and phenotypic standard deviations, respectively, in LPE, and H_L and H_H are the square roots of heritability in LPE and HPE, respectively. Choice of the selection environment that gives maximum gain in LPE is reduced to a comparison of R_L with CR_L . This approach can be adapted to many plant breeding problems, including choice of optimum location, type of plot, productivity level, and agronomic management for yield testing.

Estimating r_G

The above equations show that in order to choose the selection environment that maximizes yield gain in LPE, estimates are required not only for heritability within productivity levels but also for r_G . Methods for estimating heritability are well documented and will not be discussed here, but methods for estimating the genetic correlation between expressions of a trait in different environments are less widely known. Brascamp et al. (1985) describe two classes of estimation procedure for r_G : those which can be used only when a single pair of environments is considered and those which can be used to estimate the average value of r_G over several environments. In the analysis of a pair of environments, say A and B, r_G is computed as the product-moment correlation of genotypic values estimated within A and B. The numerator of this correlation is the covariance of the genotypic value of a trait in A with that of the same trait in B; this covariance can be estimated as the

covariance of the means of genetic groups in A and B. If environments A and B are not correlated, i.e., if they are different locations or different seasons, and if measurements for a given genetic group are made on different individuals in environments A and B (as is normally the case in experiments with plants, this covariance ($\sigma_{G_{AB}}$) is entirely genetic in origin (Eisen and Saxton, 1983). Genetic variances estimated within environments, $\sigma_{G_A}^2$ and $\sigma_{G_B}^2$, are used in the denominator, and r_G is computed (after Via, 1984) as:

$$r_G = \sigma_{G_{AB}} / (\sigma_{G_A}^2 \sigma_{G_B}^2)^{1/2} \quad (3)$$

The contrasting environments of interest may be agronomic treatments, such as fertility levels or plant densities, rather than seasons or locations. In this case, the covariance of genetic-group means between treatments is not purely genetic in origin if treatments are applied within the same year or location, but $\sigma_{G_{AB}}$ can be partitioned from environmental covariances if there is replication over locations and/or seasons (e.g., Weaver and Wilcox, 1982; Atlin and Frey, 1988b).

The value of r_G among more than two environments can be obtained by pooling all possible pair-wise estimates of r_G , each computed as outlined above. Alternatively, r_G can be computed as an intraclass correlation coefficient from components of variance estimated in the standard two-way model for the phenotype:

$$Y_{ijk} = \mu + G_i + E_j + (GE)_{ij} + \epsilon_{ijk} \quad (4)$$

where Y_{ijk} is the phenotypic value of the k th individual of the i th genetic group in the j th environment, μ is the population mean, G_i is

the effect of the i th genetic group, E_j is the effect of the j th environment, $(GE)_{ij}$ is the interaction of genetic group and environment, and ϵ_{ijk} is residual error. Robertson (1959) showed that r_G , under highly restricted conditions, can be estimated as:

$$r_G = \sigma_G^2 / (\sigma_G^2 + \sigma_{GE}^2) \quad (5)$$

Dickerson (1962) and Yamada (1962) showed that estimates of r_G obtained in this way are subject to bias when there is heterogeneity of genetic variances among environments, and Fernando et al. (1984) demonstrated additional bias resulting when data are unbalanced or when heritabilities in each of the environments under consideration are not equal. Robertson's technique is thus of limited practical utility, but is conceptually useful in making clear the inverse relationship between r_G and σ_{GE}^2 .

Applications in animal breeding

Animal breeders have made more extensive use of Falconer's (1952) approach to predicting the relative effectiveness of direct and indirect selection in different environments than have plant breeders. A brief survey of the animal breeding literature serves to illustrate the range of problems to which the model has fruitfully been applied; the concept of "environment" has been extended to include (a) sex, when selection among males is practiced for traits that are of economic importance only in females; (b) genetic background, when selection among sires of a single breed is practiced for traits which are measured in progeny of matings to dams of several different breeds; (c) test environment; and (d) productivity level.

Massey and Benyshek (1981) measured values of r_G of 0.57 to 0.85 for expressions of beef production traits between progenies of Limousin sires resulting from matings to dams of several different breeds. In a similar application involving progenies of purebred boars, McLaren et al. (1985) obtained estimates of r_G ranging from 0.26 to 0.88 for expressions of production traits in purebred versus crossbred offspring, and concluded that selection for specific combining ability might be superior to mass selection. MacNeil et al. (1984) observed large genetic correlations between growth and composition traits measured on male beef cattle and reproductive traits measured on their female half sibs and, therefore, predicted correlated changes in maternal fertility and calving difficulty in response to selection among males for increased postweaning daily gain.

Several authors have discussed the genetic correlation between swine production traits measured at pig breeding stations and on commercial farms. They reported moderate values of r_G (0.23 to 0.45) for average daily gain, but a negligible correlation between feed conversion ratio measured at breeding stations and average daily gain on farms (Bampton et al., 1977; Standal, 1977). This led Standal (1977) to question the widespread use of feed conversion ratio as a selection criterion.

Hill et al. (1983) classified dairy herds according to mean production level and estimated values of r_G for milk, fat, and protein production between low- and high-productivity herds. Correlations approached 1.0, and heritabilities were higher in high-productivity herds, which led the authors to conclude that progeny testing of bulls is most

efficiently done in highly productive herds.

Applications in plant breeding

The most frequently reported application of Falconer's (1952) method in plant breeding has been in comparing different plot types for yield testing. Comparisons of microplots and two- or four-row plots have been made in oats by Frey (1965), in wheat by Baker and Leisle (1970), in barley by Walsh et al. (1976), and in soybeans by Garland and Fehr (1981). All reported high estimates of r_G for the two types of plot and concluded, on the basis of seed increase considerations and predictions from equations 1 and 2, that microplots were more efficient than larger plots for preliminary yield trials.

Plant breeders also have applied the method in choosing the best selection environment when the target environment is a particular cropping system, management regime, or fertility level. In order to decide whether separate breeding programs were needed for soybeans grown in wide and narrow rows, Weaver and Wilcox (1982) compared predicted response to direct selection in 30-cm rows with correlated response in 30-cm rows to indirect selection in 76-cm rows. For yield, r_G between row spacings was approximately 1.0 and heritability was slightly greater in narrow rows, leading the authors to conclude that selection for yield in both row spacings was more efficiently done in narrow than in wide rows.

In a similar application, Pfeiffer (1987) compared direct selection for soybean yield in late planted environments with indirect selection in early planted environments for yield in late plantings to determine

whether separate breeding programs were required for full-season cultivars and cultivars adapted to double cropping. The heritability of yield was greatest in early plantings, and r_G between yields in the two environments did not differ significantly from 1. Consequently, selection in early sown trials was predicted to be most efficient in increasing yield in both full-season and double-cropping regimes.

To determine whether recurrent selection in maize should be conducted under conditions of moderate or high productivity, Lambert (1984) estimated r_G between maize yields in highly fertile, irrigated environments and environments in which normal agronomic practices for Illinois were followed. All estimates were positive, ranging from 0.02 to 0.87 in five years of testing, and thus, Lambert concluded that selection under conditions of high productivity resulted in gains for both moderate and high productivity environments. Because he reported neither heritability estimates nor predictions of correlated and direct response to selection, his results do not indicate which of the levels is superior for selecting genotypes for moderately fertile environments.

Explanation of Dissertation Format

This dissertation contains three sections. Section 1 concerns the genetic correlations between oat grain yields in LPE, medium productivity environments (MPE), and HPE, and presents predictions of the relative effectiveness of direct and indirect selection for yield in LPE. Section 2 describes an empirical selection experiment comparing the effectiveness of direct and indirect selection in LPE, MPE, and HPE. In Section 3,

predictions of the relative effectiveness of indirect and direct selection for oat grain yield in low-nitrogen, low-phosphorus, and heat-stressed environments are presented. Each section is in the form of a complete manuscript, minus a separate list of references, and is suitable for publication with little or no modification. All references cited are listed following the general conclusions.

**SECTION I. PREDICTING OAT YIELD GAINS IN LOW-PRODUCTIVITY
ENVIRONMENTS FROM SELECTION UNDER LOW-, MEDIUM-,
AND HIGH-PRODUCTIVITY CONDITIONS**

ABSTRACT

Cultivars for use in low-productivity environments (LPE) can be selected directly in LPE or indirectly in medium- or high-productivity environments (MPE or HPE, respectively). The best productivity level at which to select oat genotypes for use in LPE was predicted for a population of 116 random oat lines tested in replicated yield trials in 36 Iowa environments. The 36 trials were classified as LPE, MPE, or HPE, and grain yield at each productivity level was considered a separate character. Heritabilities (H^2) of grain yield within and genetic correlations (r_G) among productivity levels were used to predict expected response in LPE to selection in LPE, MPE, and HPE. H^2 was highest in HPE, but r_G between yield in LPE and HPE was only 0.59. For 10% selection based on genotype means in 2 or 4 two-replicate yield trials, the greatest yield gain in LPE was predicted to result from selection in MPE. For selection in 12 six-replicate trials, the greatest yield gain in LPE was predicted to result from direct selection in LPE. These results show that selection in HPE is not necessarily optimum when genotypes are destined for use in LPE.

Additional index words: Avena sativa L., genotype by environment interaction, genetic correlation, stress environments, selection, effect of replication.

INTRODUCTION

Should crop varieties destined for use in stress, or low-productivity, environments (LPE) be selected directly in LPE or indirectly in high-productivity environments (HPE)? Most efforts to predict the best productivity level for selection have used criteria specific to the candidate selection environments, such as heritability or expected genetic gain, as bases for comparisons among them (Johnson and Frey, 1967; Byth et al., 1969; Vega and Frey, 1981; Rumbaugh et al., 1984). These measures, however, may be unreliable in the presence of genotype x productivity level (GP) interaction (Comstock and Moll, 1963; Allen et al., 1978; Johnson and Frey, 1967). GP interaction is a class of genotype x environment interaction and, if present, reduces the extent to which selection gain made at one productivity level is expressed at another.

In choosing the best productivity level for selection, the existence of GP interaction may be accommodated by considering yields in HPE and LPE to be separate genetic traits (Falconer, 1952; Allen et al., 1978; Rosielle and Hamblin, 1981). The genetic correlation between these traits (r_G) can be measured and, with estimates of heritability (H^2) from both LPE and HPE, used to predict yield gains in LPE resulting from direct selection and from indirect selection in HPE.

R_G may be expressed as a function of the genetic (σ_G^2) and genotype x productivity level (σ_{GP}^2) variances, and can be calculated (after Robertson, 1959; Dickerson, 1962; Yamada, 1962) as:

$$r_G = \sigma_G^2 / (\sigma_G^2 + \sigma_{GP}^2) \quad (1)$$

This method of estimating r_G , i.e., as an intraclass correlation coefficient, makes obvious r_G 's inverse relationship with genotype x environment interaction, and is useful for measuring the average correlation among expressions of a trait across many environments. However, intraclass estimates of r_G are unbiased only when heritabilities are equal in the environments under comparison and when error variances within environments are homogeneous (Fernando et al., 1984). The latter condition can be achieved by transformation, but the requirement that heritabilities be equal can rarely be met. Both types of bias can cause underestimation of r_G . When only two environments (productivity levels) are under consideration, product-moment estimates of r_G are easily obtained and are not subject to bias due to heterogeneity of error variances or heritabilities among environments.

Few direct estimates of r_G between yields measured in different production environments have been published. In a study designed to determine whether separate breeding programs were required for soybean (Glycine max L.) varieties adapted to double cropping after winter wheat (Triticum aestivum L.), Pfeiffer (1987) reported that r_G between soybeans yields in early and late plantings did not differ significantly from 1.0. He concluded that the same varieties could be used in both full-season and double-crop production and that these varieties were selected most efficiently in early plantings, wherein the heritability of yield was highest. Also with soybeans, Weaver and Wilcox (1982) found that r_G equalled 1.0 between yields in 30-cm and 76-cm row spacings. Lower estimates of r_G

between maize (Zea mays L.) yields in high- and low-fertility environments, ranging from 0.02 to 0.87, have been reported by Lambert (1984).

Few previous oat (Avena sativa L.) studies have attempted to identify the best productivity level for selection when the goal is to make yield gains in LPE, and none have made use of estimates of r_G . Therefore, the objectives of this paper are (a) to estimate genetic correlations among grain yields of oat lines tested in LPE, MPE, and HPE, (b) to examine the effect of heterogeneity of variances among yield levels on these estimates, and (c) to use estimates of genetic correlation and heritability to predict the relative effectiveness of selection in LPE, MPE, and HPE for improving grain yields in stress environments.

MATERIALS AND METHODS

Genotypes

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. A random sample of 116 such lines was used.

Environments

The lines were tested in 36 yield trials conducted in Iowa in 1967, 1968, 1972, 1973, and 1986. Yield variation among trials resulted from natural environmental variation and from differences in agronomic treatments such as planting date, seeding rate, rotation, and amount of N and P applied. Locations, mean yields, and agronomic treatments of the 36 trials are presented in Table 1. Each trial was conducted in a randomized complete-block design with two replicates. Plots were hills spaced 30 cm apart in perpendicular directions. In all experiments except nos. 24 and 30, the seeding rates was 30 or 32 seeds per plot, which corresponds to approximately 105 kg ha^{-1} . Each trial was bordered on all sides by two rows of hills. Plot areas were hand weeded and the plants were sprayed with a fungicide (Maneb, or manganese ethylene bisdithiocarbamate, in 1967-1973, and the systemic fungicide Bayleton, or 1-(4-chlorophenoxy)-3,3-dimethyl-1-(1H-1,2,4-triazol-1-yl)-2-

Table 1. Mean yields, locations, years, and agronomic treatments of 36 oat yield trials

| Trial | Mean yield (kg/ha) | Location | Year | Seeds/plot | Rotation ^{a,c} | Fertilizer ^{a,b} (kg/ha) | Planting date |
|-------|--------------------|------------|------|------------|--|-----------------------------------|---------------|
| 1 | 900 | Castana | 1973 | 30 | CCOM ^d COMM ^e | 0 P 0 P | 4/7 |
| 2 | 920 | Kanawha | 1972 | 30 | CCCO | 0 N | 4/18 |
| 3 | 980 | Castana | 1972 | 30 | CCOM ^d COMM ^e | 0 P 0 P | 4/17 |
| 4 | 1200 | Castana | 1986 | 30 | CCOM | 0 P | 4/2 |
| 5 | 1260 | Sutherland | 1986 | 30 | | 17 N, 29 P, 18 K | 5/12 |
| 6 | 1370 | Kanawha | 1973 | 30 | 0000 | 0 N | 4/24 |
| 7 | 1390 | Kanawha | 1986 | 30 | | 52 N, 3 P, 4 K | 5/10 |
| 8 | 1410 | Kanawha | 1986 | 30 | 0000 | 0 N | 4/23 |
| 9 | 1460 | Kanawha | 1972 | 30 | CCCO | 67 N ^f | 4/18 |
| 10 | 1590 | Hinds | 1986 | 30 | | | 5/2 |
| 11 | 1750 | Kanawha | 1986 | 30 | | 52 N, 3 P, 4 K | 4/23 |
| 12 | 1840 | Ames | 1973 | 30 | | 10 N, 40 P, 20 K | 5/16 |
| 13 | 1950 | Sutherland | 1986 | 30 | CCOM ^d SCOM ^e | 0 N 0 N | 4/22 |
| 14 | 2150 | Kanawha | 1972 | 30 | CCCO | 134 N ^f | 4/18 |
| 15 | 2160 | Kanawha | 1972 | 30 | CCOM | 0 N | 4/18 |
| 16 | 2210 | Sutherland | 1986 | 30 | CBOM | 18 N, 27 P, 20 K | 4/? |
| 17 | 2350 | Castana | 1972 | 30 | CCOM ^d COMM ^e | 59 P | 4/17 |
| 18 | 2370 | Ames | 1986 | 40 | | 34 N, 22 P, 28 K | 5/2 |
| 19 | 2430 | Castana | 1973 | 30 | CCOM ^d COMM ^e | 59 P 88 P | 4/7 |

^aBlanks indicate that treatment is unknown.

^bWhen only one element is listed, it is the primary yield-limiting element at the location. Records concerning applications of other elements were unavailable.

^cC represents corn, B soybeans, M meadow, O oats, S sorghum.

^dReplicate 1.

^eReplicate 2.

^fApplied to previous corn crop.

Table 1. (Continued)

| Trial | Mean yield (kg/ha) | Location | Year | Seeds/plot | Rotation | Fertilizer (kg/ha) | Planting date |
|-------|--------------------|------------|------|------------|----------|--------------------|---------------|
| 20 | 2510 | Kanawha | 1972 | 30 | 0000 | 0 N | 4/18 |
| 21 | 2610 | Kanawha | 1973 | 30 | | 34 N, 34 P, 34 K | 4/24 |
| 22 | 2790 | Cresco | 1968 | 32 | | 0 N | 4/? |
| 23 | 3110 | Cresco | 1967 | 32 | | 0 N | 4/? |
| 24 | 3160 | Ames | 1973 | 8 | | 10 N, 40 P, 20 K | 4/22 |
| 25 | 3370 | Ames | 1973 | 30 | | 10 N, 40 P, 20 K | 5/5 |
| 26 | 3470 | Ames | 1986 | 30 | | 34 N, 22 P, 28 K | 3/28 |
| 27 | 3500 | Kanawha | 1972 | 30 | CCOM | 67 N ^F | 4/18 |
| 28 | 3540 | Ames | 1967 | 32 | | 18 N, 27 P, 27 K | 3/? |
| 29 | 3570 | Sutherland | 1972 | 30 | | | 4/11 |
| 30 | 3590 | Ames | 1973 | 64 | | 10 N, 40 P, 20 K | 4/22 |
| 31 | 3630 | Ames | 1973 | 30 | | 10 N, 40 P, 20 K | 4/21 |
| 32 | 3720 | Ames | 1973 | 32 | | 10 N, 40 P, 20 K | 4/22 |
| 33 | 3750 | Ames | 1972 | 30 | | 10 N, 40 P, 20 K | 4/8 |
| 34 | 3830 | Ames | 1968 | 32 | | 10 N, 40 P, 20 K | 3/? |
| 35 | 3890 | Sutherland | 1973 | 30 | | | 4/5 |
| 36 | 4180 | Kanawha | 1972 | 30 | | 50 N, 50 P, 50 K | 4/19 |

butanone in 1986) as needed to control foliar diseases. Grain yield of a plot was the weight of threshed grain expressed in kg ha⁻¹.

Statistical Analyses

Heritabilities within productivity levels

The 36 trials were divided into three yield groups (low, medium, and high) of 12. Analyses of variance within yield levels were conducted according to the model:

$$Y_{ijk} = \mu + G_i + E_j + (GE)_{ij} + R/E_{k/j} + e_{ijk} \quad (2)$$

where Y_{ijk} is the grain yield of a plot, μ is the population mean, G_i is the effect of the i th genotype, E_j is the effect of the j th environment, $(GE)_{ij}$ is the interaction of the i th genotype and j th environment, $R/E_{k/j}$ is the effect of the k th replicate in the j th environment, and e_{ijk} is the residual. Variance components were estimated from appropriate linear functions of mean squares, and their standard errors were calculated according to the method of Anderson and Bancroft (1952).

Heritabilities within yield levels, expressed on a per-line basis for a reference unit of four 2-replicate trials, were computed as:

$$\begin{aligned} H^2 &= \sigma_G^2 / \sigma_P^2 \\ &= \sigma_G^2 / (\sigma_G^2 + \sigma_{GE}^2/e + \sigma^2/re) \end{aligned} \quad (3)$$

where σ_G^2 and σ_P^2 are the genotypic and phenotypic variances, respectively, σ_{GE}^2 is the genotype x environment variance, σ^2 is the error variance, r is the number of replicates per environment, and e is the number of environments. Standard errors of H^2 were calculated according to Dickerson's (1969) approximate method.

Genetic correlations between environments

Analyses of variance for the three possible pairings of yield levels (low-high, low-medium, and high-medium) were computed according to the model:

$$\begin{aligned} Y_{ijkl} &= \mu + G_i + P_j + GP_{ij} + E/P_{k/j} + GE/P_{ik/j} + R/E/P_{l/k/j} \\ &\quad + e_{ijkl} \end{aligned} \quad (4)$$

where Y_{ijk1} is the yield of a plot, μ is the population mean, G_i is the effect of the i th genotype, P_j is the effect of the j th productivity level, GP_{ij} is the interaction of the i th genotype with the j th productivity level, $E/P_{k/j}$ is the effect of the k th environment within the j th productivity level, $GE/P_{ik/j}$ is the interaction of the i th genotype with the k th environment within the j th productivity level, $R/E/P_{1/k/j}$ is the l th replicate within the k th environment within the j th productivity level, and e_{ijk1} is the residual. All effects except productivity levels were considered to be random. Because there was a tenfold range in magnitude of error variances for individual trials, and because the correlation between mean yield and error variance was highly significant ($r = 0.69$), analyses of variance were computed for transformed as well as raw data. The appropriate power transformation was identified by the method of Hinz and Eagles (1976) to be the square-root transformation. Analyses of variance were also computed from data which had been standardized within trials. Standardized values for plot grain yield were calculated as:

$$Z_{ijk1} = (Y_{ijk1} - Y_{.jk.})/s_{jk} \quad (5)$$

where Z_{ijk1} is the standardized value for grain yield of a plot, Y_{ijk1} is the value on the original scale, and $Y_{.jk.}$ and s_{jk} are the mean and standard deviation of the k th environment in the i th productivity level, respectively. Expectations of mean squares from the analyses of variance are presented in Table 2. Variance components and their standard errors were calculated in the same way as for the within-productivity-levels analyses.

Table 2. Expected mean squares from analysis of variance of grain yields of 116 oat lines tested at two productivity levels

| Source of variation | df | Expected mean square |
|-------------------------|------|---|
| Productivity levels (P) | 1 | |
| Environments (E)/P | 22 | |
| Replicates (R)/E/P | 24 | |
| Genotypes (G) | 115 | $\sigma^2 + r\sigma_{GE/P}^2 + rpe\sigma_G^2$ |
| G x P | 115 | $\sigma^2 + r\sigma_{GE/P}^2 + re\sigma_{GP}^2$ |
| G x E/P | 2530 | $\sigma^2 + r\sigma_{GE/P}^2$ |
| Error | 2760 | σ^2 |

Estimates of σ_G^2 and σ_{GP}^2 were used to calculate the genetic correlation between grain yields in different productivity levels by Robertson's (1959) method:

$$r_{G_{ij}} = \sigma_G^2 / (\sigma_G^2 + \sigma_{GP}^2) \quad (6)$$

where $r_{G_{ij}}$ is the genetic correlation of yields from the *i*th and *j*th productivity levels, σ_G^2 is the genotypic component of variance estimated over the *i*th and *j*th productivity levels, and σ_{GP}^2 is the genotype x productivity level interaction variance. An approximate standard error for r_G was obtained by using Kempthorne's (1957, p. 246) method for computing the standard error of an intraclass correlation coefficient.

A second estimate of r_G was calculated according to Via's (1984) method 2 as:

$$r_{G_{ij}} = \sigma_{G_{ij}} / (\sigma_{G_i} \sigma_{G_j}) \quad (7)$$

where $r_{G_{ij}}$ is defined as in 6, $\sigma_{G_{ij}}$ is the covariance of genotype means in productivity levels i and j , and σ_{G_i} and σ_{G_j} are the genotypic standard deviations within productivity levels i and j , respectively. The covariance of the mean of a genotype in i with its mean in j is entirely genetic in origin; thus, $r_{G_{ij}}$ in this case gives an estimate of genetic correlation over productivity levels, unbiased by environmental or genotype x environment covariances. An approximate standard error for this r_G was calculated according to Falconer (1981, p. 285).

Predicted gains from selection

Estimates of H^2 and r_G were used to predict response to direct and indirect selection for grain yield in LPE according to equations 8 and 9.

$$R_L = i H_L \sigma_{GL} \quad (8)$$

$$CR_L = i H_L H_H r_G \sigma_{PL} \quad (9)$$

where r_G is the genetic correlation between yields in LPE and HPE, σ_{GL} and σ_{PL} are the genetic and phenotypic standard deviations in LPE, and H_L and H_H are the square roots of heritability in LPE and HPE, respectively. Rearrangement of these equations gives the ratio CR_L/R_L

(after Falconer, 1981, p. 291):

$$CR_L/R_L = r_G H_H/H_L \quad (10)$$

RESULTS AND DISCUSSION

Mean grain yields in the 36 oat experiments ranged from 900 to 4180 kg ha⁻¹ (Table 1). There was a tenfold range in magnitude among error variances of the individual experiments, and experiment means and variances were highly correlated ($r = 0.69^{**}$). Both the square root and standard unit transformations eliminated the correlation between means and error variances, but the standard unit method was more effective in reducing heterogeneity of variances. The importance of transformation in obtaining accurate estimates of the relative magnitudes of σ_G^2 and σ_{GP}^2 can be seen from Tables 3, 4, and 5, which contain variance component estimates from combined analyses over LPE and MPE, LPE and HPE, and MPE and HPE, respectively. Estimates of σ_{GP}^2 were always greater, relative to σ_G^2 , on the original and square root than on the standard unit scale, probably due to error heterogeneity among trials. Use of variance components estimated on the original and square root scales to compute r_G thus would result in significant downward bias. Even though they were reduced relative to estimates obtained on the other scales, all three standard unit estimates of σ_{GP}^2 were significantly greater than 0 ($\alpha = 0.05$).

Intraclass (above diagonal) and product moment (below diagonal) estimates of r_G among yields from LPE, MPE, and HPE are presented in Table 6. Estimates from the two methods were similar. Values of r_G between yields from LPE and MPE, and between yields from MPE and HPE were high, but the lower r_G between yields from LPE and HPE indicates that performances in these two contrasting environments were conditioned

Table 3. Variance components, with standard errors in parentheses, for grain yields of oat lines on original, square root, and standardized scales, estimated from a combined analysis of low- and medium-productivity environments

| Component | Scale | | |
|----------------------------|--------------|----------------------------------|-----------------------------------|
| | Direct | Square root ($\times 10^2$) | Standardized ($\times 10^2$) |
| σ^2_G | 2.54 (0.40) | 3.44 (0.56) | 9.85 (1.51) |
| σ^2_{GP} | 1.00 (0.27) | 0.71 (0.31) | 1.63 (0.73) |
| $\sigma^2_{GE/P}$ | 3.92 (0.43) | 5.88 (0.66) | 13.39 (1.60) |
| σ^2 | 17.72 (0.48) | 27.02 (0.73) | 67.41 (0.18) |
| σ^2_{GP}/σ^2_G | 0.39 | 0.21 | 0.17 |

Table 4. Variance components, with standard errors in parentheses, for grain yields of oat lines on original, square root, and standardized scales, estimated from a combined analysis of low- and high-productivity environments

| Component | Scale | | |
|----------------------------|--------------|----------------------------------|-----------------------------------|
| | Direct | Square root ($\times 10^2$) | Standardized ($\times 10^2$) |
| σ^2_G | 3.72 (0.57) | 3.70 (0.58) | 11.20 (1.71) |
| σ^2_{GP} | 3.43 (0.61) | 2.20 (0.49) | 5.60 (1.23) |
| $\sigma^2_{GE/P}$ | 3.70 (0.51) | 5.00 (0.61) | 10.40 (1.59) |
| σ^2 | 22.31 (0.61) | 26.00 (0.70) | 70.30 (1.89) |
| σ^2_{GP}/σ^2_G | 0.93 | 0.59 | 0.50 |

Table 5. Variance components, with standard errors in parentheses, for grain yields of oat lines on original, square root, and standardized scales, estimated from a combined analysis of medium- and high-productivity environments

| Component | Scale | | |
|----------------------------|--------------|----------------------------------|-----------------------------------|
| | Direct | Square root ($\times 10^2$) | Standardized ($\times 10^2$) |
| σ^2_G | 6.90 (1.00) | 6.07 (0.88) | 18.10 (2.60) |
| σ^2_{GP} | 0.73 (0.28) | 0.44 (0.23) | 1.00 (0.60) |
| $\sigma^2_{GE/P}$ | 3.84 (0.60) | 3.87 (0.55) | 9.30 (1.50) |
| σ^2 | 26.59 (0.72) | 24.10 (0.65) | 67.00 (1.80) |
| σ^2_{GP}/σ^2_G | 0.11 | 0.07 | 0.06 |

Table 6. Intraclass (above diagonal) and product moment (below diagonal) estimates of genetic correlations and standard errors (in parentheses) among grain yield of oat lines in low-productivity environments (LPE), medium-productivity environments (MPE), and high-productivity environments (HPE)

| Productivity level | LPE | MPE | HPE |
|--------------------|-------------|-------------|-------------|
| LPE | 1 | 0.86 (0.06) | 0.66 (0.06) |
| MPE | 0.84 (0.04) | 1 | 0.95 (0.06) |
| HPE | 0.59 (0.08) | 0.95 (0.01) | 1 |

by substantially different sets of alleles.

Variance component and heritability estimates for yield in each productivity level are presented in Table 7. Heritability of yield, based on a reference unit of four trials, each with two replicates, was more than twice as large in HPE as in LPE. Nevertheless, because of the low r_G between yields in LPE and HPE, the largest predicted gain in LPE did not result from selection in HPE (Table 8). (Because predicted gains based on intraclass and product moment estimates of r_G were very similar, only the latter are presented in Table 8.) The greatest predicted gain, averaged over all productivity levels, resulted from selection in MPE or HPE. However, the greatest predicted gains for yield in LPE resulted from selection in MPE when selection was based on two or four trials, and from direct selection in LPE when 12 six-replicate trials were used. Direct selection in LPE, in the latter instance, produced predicted gains that were 8 and 47% greater than those from MPE and HPE, respectively. A similar advantage for direct selection in HPE was also observed at the highest level of replication, where predicted gains from indirect selection in MPE and LPE were only 93 and 52% as great as those resulting from direct selection. That the relative effectiveness of direct and indirect selection, for any value of r_G , should be dependent on the degree of replication of the selection unit can be seen by considering equation 10. As replication increases, the value of H_H/H_L tends towards 1. If $r_G < 1$, CR_L/R_L also must be reduced to < 1 at some level of replication. The dependence of the value of CR_L/R_L on replication probably explains why Shabana et al. (1980), who used a similar

Table 7. Estimates (standard errors in parentheses), on original scale, of genotype (σ^2_G), genotype x environment (σ^2_{GE}), and error (σ^2) variance components, and heritability^a (H^2) for grain yields of oat lines in low-, medium-, and high-productivity environments

| Productivity level | σ^2_G | σ^2_{GE} | σ^2 | H^2 |
|--------------------|--------------|-----------------|--------------|-------------|
| Low | 1.21 (0.28) | 3.78 (0.49) | 13.44 (0.51) | 0.32 (0.07) |
| Medium | 4.87 (0.56) | 4.06 (0.81) | 22.00 (0.84) | 0.56 (0.09) |
| High | 9.67 (0.67) | 3.62 (1.49) | 31.17 (1.19) | 0.67 (0.10) |

^aReference unit: line means in four trials, each with two replicates.

Table 8. Predicted gains (% of population mean within evaluation environment) in grain yield resulting from direct and indirect selection at three levels of productivity, for three levels of replication of the selection unit

| Selection environment | | | Evaluation environment | | | |
|-----------------------|----------------------|--------------------|------------------------|--------|------|------|
| No. of trials | Replicates per trial | Productivity level | Low | Medium | High | Mean |
| 2 | 2 | Low | 6.6 | 6.0 | 4.0 | 5.1 |
| | | Medium | 8.0 | 10.3 | 9.3 | 9.4 |
| | | High | 6.3 | 11.1 | 11.1 | 10.2 |
| 4 | 2 | Low | 8.5 | 7.8 | 5.2 | 6.6 |
| | | Medium | 9.6 | 12.3 | 11.2 | 11.3 |
| | | High | 7.3 | 12.8 | 12.8 | 11.8 |
| 12 | 6 | Low | 12.8 | 11.6 | 7.8 | 9.9 |
| | | Medium | 11.9 | 15.5 | 14.0 | 14.1 |
| | | High | 8.7 | 15.1 | 15.1 | 13.9 |

group of oat lines but based selection on only two or three replicates, found no advantage for direct selection at the low productivity level. If their estimates of H_H , H_L , and r_G were similar to those in this study, direct selection in LPE would only have been advantageous for selection based on many more replications than the two or three they used.

Our results demonstrate that the choice of the best productivity level for selecting oat genotypes depends not only upon heritability within a productivity level but also upon r_G between levels. Genotype x productivity level interactions were large and significant, with the result that HPE did not maximize predicted yield gains for low productivity conditions. These results also illustrate the fact that maximizing gains in LPE and maximizing mean gains over productivity levels can be mutually exclusive goals. This is likely to occur whenever $r_G < 1$, $H_H > H_L$, and LPE and HPE occur with equal frequency, as was the case in this study. It should be noted, however, that if LPE are much more frequent than HPE and thus contribute more to total production, selection in LPE might result in larger mean gains.

In general, the assumption that selection in HPE will produce the greatest yield gains in all target environments, regardless of their productivity level, must be tested on a case-by-case basis. It is particularly important that this assumption be tested in breeding programs operating in developing countries where, because of lack of credit, low commodity prices, or other reasons, many small farmers use low plant densities, do not achieve complete weed control, and apply little or no inorganic fertilizer to their crops, even after they adopt short,

nitrogen- and density-responsive cultivars that have been selected in HPE (IRRI, 1984). Breeders who select crop cultivars for use in such LPE probably should conduct experiments to determine whether the greatest yield gain in those environments will be obtained by selecting in similar conditions or in HPE. Research aimed at testing the assumed superiority of HPE for selection is needed in developed countries also, because farmers are now seeking to cut production costs by reducing purchased inputs. Our results indicate that greater gains in yield in some low-input, low-productivity cropping systems may result from direct selection than from indirect selection under conditions of extremely high productivity.

SECTION II. SELECTION OF OAT LINES IN LOW-, MEDIUM-, AND HIGH-
PRODUCTIVITY ENVIRONMENTS FOR GRAIN YIELD
UNDER LOW-PRODUCTIVITY CONDITIONS

ABSTRACT

Crop varieties for use in low-productivity environments (LPE) may be selected directly in LPE or indirectly in medium- or high-productivity environments (MPE or HPE, respectively). These contrasting strategies were compared in three selection experiments in which random populations of oat (Avena sativa L.) lines were selected ($i = 10\%$) for grain yield in LPE, MPE, or HPE. Selected lines were then evaluated at each productivity level. The influence of degree of replication of the selection unit on the relative effectiveness of direct and indirect selection for yield in LPE was examined by first selecting on the basis of line means in a total of 4, 3, and 2 replications in experiments 1, 2, and 3, respectively, and then repeating selection based on twice the original number of replications in each experiment. At the lower level of replication, response in LPE to selection in LPE, MPE, and HPE did not differ in experiments 1 and 2, whereas at the higher level of replication, direct selection in LPE gave significantly greater gains than did indirect selection in MPE or HPE. In experiment 3, the largest yield gain resulted from selection in HPE, regardless of the productivity level of the evaluation environment or degree of replication of the selection unit. In all three experiments, the effectiveness of direct relative to indirect selection for yield in LPE increased with increasing replication of the selection unit. Our results show that HPE are not necessarily optimum for selection when the goal is to select genotypes for use in LPE.

Additional index words: Avena sativa L., correlated response, genetic correlation, genotype x environment interaction, replication.

INTRODUCTION

Crop varieties destined for use in stress environments may be selected in either the presence or absence of stress. Few empirical studies have attempted to determine which of these strategies is superior. This is an especially important issue in developing countries where, because of credit constraints, commodity prices, or other reasons, small farmers often apply little or no purchased fertilizer to their crops, use low plant densities, and have incomplete weed control. These production constraints can exist even among farmers who have adopted nitrogen-responsive cultivars selected under high-fertility conditions (IRRI, 1984). It has not been determined whether the greatest yields in such relatively unproductive environments will be obtained from genotypes selected in similar conditions or in high-productivity environments (HPE). This issue is becoming increasingly important in developed countries as well, where farmers are seeking to limit production costs by reducing purchased inputs.

Falconer (1952) suggested that yield in stress, or low-productivity, environments (LPE) and yield in HPE could be considered as separate traits, not necessarily controlled by identical sets of genes. Viewed in this light, the problem of choosing the best productivity level for selecting genotypes for use in LPE is reduced to a comparison of direct and correlated response; should selection be direct, i.e., undertaken in LPE, or should it be indirect, i.e., undertaken in HPE? Authors taking this approach to the problem have shown that the value of a selection

environment is dependent on both heritability of yield in that environment and on the genetic correlation (r_G) of yield in the selection environment with yield in the target environment (Falconer, 1952; Allen et al., 1978; Rosielle and Hamblin, 1981; Atlin and Frey, 1988a). It has also been demonstrated that the relative effectiveness of direct versus indirect selection in LPE is affected by the extent of replication of the selection unit (Atlin and Frey, 1988a).

The best productivity level at which to select cultivars for use in LPE varies among breeding populations, crop species, and target environments. Several studies support the hypothesis that selection for performance in LPE should be conducted indirectly, i.e., in HPE. Pfeiffer (1987) reported that soybean (Glycine max L.) lines selected in early planted environments outyielded those selected in late plantings, regardless of whether they were evaluated in early or late plantings. Similarly, Van Sanford and Matzinger (1983), in a study comparing recurrent selection on low- and high-nutrient media for increased seedling weight in tobacco (Nicotiana tabacum L.), observed that the greatest gains resulted from selection on high-nutrient medium, irrespective of the level at which response was evaluated. An advantage for indirect selection in the absence of stress has also been reported in cotton (Gossypiu hirsutum L.) by Quisenberry et al. (1980), in oats (Avena sativa L.) by Shabana et al. (1980), and in alfalfa (Medicago sativa L.) by Salter et al. (1984). On the other hand, Arboleda-Rivera and Compton (1974) reported that direct selection in drought-stressed environments was superior to indirect selection in the absence of drought for

selecting a drought-hardy maize (Zea mays L.) synthetic, and both Falconer and Latyszewski (1952) and Bateman (1974) observed that direct selection on a poor diet for increased body size in mice was superior to indirect selection conducted at a higher nutritional level.

In light of these conflicting reports, further research on the relative effectiveness of direct and indirect selection in LPE is warranted, to more clearly define situations in which an advantage for direct selection might exist. The specific objectives of our research were (a) to empirically compare direct and indirect selection for grain yield in low-, medium-, and high-productivity environments in populations of previously unselected oat lines, and (b) to determine the effect of increased replication of the selection unit on the relative effectiveness of direct and indirect selection for yield in LPE.

MATERIALS AND METHODS

Selection Protocol

Three experiments were conducted to compare the effectiveness of direct and indirect selection in LPE, medium-productivity environments (MPE), and HPE, using two populations of random oat lines tested in many environments in Iowa. Each experiment was conducted, with minor variations, according to the following general protocol:

1. A series of yield trials, in which a common set of oat lines was tested, was grouped into either two (low and high) or three (low, medium, and high) productivity levels.
2. Within each productivity level, several yield trials were randomly designated selection environments, and remaining trials were designated evaluation environments.
3. Selection for increased grain yield at an intensity of approximately 10% was conducted in the selection environments of each productivity level.
4. Mean yields of lines selected in LPE, MPE, and HPE were measured in evaluation environments of each productivity level to provide estimates of direct and indirect responses.
5. Selection was replicated by randomly redesignating a new set of selection and evaluation environments within each productivity level, and then repeating steps 2 to 4.
6. Estimates of response were analyzed according to the following model:

$$G_{ij} = \mu + l_i + r_j + \epsilon_{ij} \quad (1)$$

where G_{ij} denotes gain under evaluation at a given productivity level that resulted from selection at the i th productivity level in the j th repetition of the selection procedure, μ is the population mean gain, l_i is the effect of the i th productivity level, r_j is the effect of the j th repetition of the selection procedure, and ϵ_{ij} is the residual.

In each of the three experiments, the entire protocol was completed once using a low level of replication of the selection unit, and then was repeated with selection based on twice as many replicates.

Experiment 1

Oat lines for this experiment 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. A random sample of 116 such lines was used in this experiment. The lines were tested in 36 yield trials conducted in Iowa during 1967, 1968, 1972, 1973, and 1986. Yield variation among trials resulted from natural climatic and edaphic factors, and differences among trials in agronomic treatments such as planting date, seeding rate, rotation, and amount of N and P applied (Table 1). Each trial was conducted as a randomized complete-block experiment with two replications. Plots were hills spaced 30 cm apart in perpendicular directions. In all

Table 1. Mean yields, locations, years, and agronomic treatments of oat yield trials used in Experiment 1

| Trial | Mean yield (kg/ha) | Location | Year | Seeds/plot | Rotation ^{a,c} | Fertilizer ^{a,b} (kg/ha) | Planting date |
|-------|--------------------|------------|------|------------|-------------------------|-----------------------------------|---------------|
| 1 | 900 | Castana | 1973 | 30 | CCOM ^d | 0 P | 4/7 |
| | | | | | COMME ^e | 0 P | |
| 2 | 920 | Kanawha | 1972 | 30 | CCCO | 0 N | 4/18 |
| 3 | 980 | Castana | 1972 | 30 | CCOM ^d | 0 P | 4/17 |
| | | | | | COMME ^e | 0 P | |
| 4 | 1200 | Castana | 1986 | 30 | CCOM | 0 P | 4/2 |
| 5 | 1260 | Sutherland | 1986 | 30 | | 17 N, 29 P, 18 K | 5/12 |
| 6 | 1370 | Kanawha | 1973 | 30 | OOOO | 0 N | 4/24 |
| 7 | 1390 | Kanawha | 1986 | 30 | | 52 N, 3 P, 4 K | 5/10 |
| 8 | 1410 | Kanawha | 1986 | 30 | OOOO | 0 N | 4/23 |
| 9 | 1460 | Kanawha | 1972 | 30 | CCCO | 67 N ^f | 4/18 |
| 10 | 1590 | Hinds | 1986 | 30 | | | 5/2 |
| 11 | 1750 | Kanawha | 1986 | 30 | | 52 N, 3 P, 4 K | 4/23 |
| 12 | 1840 | Ames | 1973 | 30 | | 10 N, 40 P, 20 K | 5/16 |
| 13 | 1950 | Sutherland | 1986 | 30 | CCOM ^d | 0 N | 4/22 |
| | | | | | SCOME ^e | 0 N | |
| 14 | 2150 | Kanawha | 1972 | 30 | CCCO | 134 N ^f | 4/18 |
| 15 | 2160 | Kanawha | 1972 | 30 | CCOM | 0 N | 4/18 |
| 16 | 2210 | Sutherland | 1968 | 32 | CBOM | 18 N, 27 P, 20 K | 4/? |
| 17 | 2350 | Castana | 1972 | 30 | CCOM ^d | 59 P | 4/17 |
| | | | | | COMME ^e | 88 P | |
| 18 | 2370 | Ames | 1986 | 30 | | 34 N, 22 P, 28 K | 5/2 |
| 19 | 2430 | Castana | 1973 | 30 | CCOM ^d | 59 P | 4/7 |
| | | | | | COMME ^e | 88 P | |
| 20 | 2510 | Kanawha | 1972 | 30 | OOOO | 0 N | 4/18 |
| 21 | 2610 | Kanawha | 1973 | 30 | | 34 N, 34 P, 34 K | 4/24 |
| 22 | 2790 | Cresco | 1968 | 32 | MMMO | 0 N | 4/? |
| 23 | 3110 | Cresco | 1967 | 32 | MMMO | 0 N | 4/? |

^aBlanks indicate that treatment is unknown.

^bWhen only one element is listed, it is the primary yield-limiting element at the location. Records concerning applications of other elements were unavailable.

^cC represents corn, B soybeans, M meadow, O oats, S sorghum.

^dReplicate 1.

^eReplicate 2.

^fApplied to previous corn crop.

Table 1. (Continued)

| Trial | Mean yield (kg/ha) | Location | Year | Seeds/plot | Rotation | Fertilizer (kg/ha) | Planting date |
|-------|--------------------|------------|------|------------|----------|--------------------|---------------|
| 24 | 3160 | Ames | 1973 | 8 | | 10 N, 40 P, 20 K | 4/22 |
| 25 | 3370 | Ames | 1973 | 30 | | 10 N, 40 P, 20 K | 5/5 |
| 26 | 3470 | Ames | 1986 | 30 | | 34 N, 22 P, 28 K | 3/28 |
| 27 | 3500 | Kanawha | 1972 | 30 | CCOM | 67 N ^f | 4/18 |
| 28 | 3540 | Ames | 1967 | 32 | CBOM | 18 N, 27 P, 27 K | 3/? |
| 29 | 3570 | Sutherland | 1972 | 30 | | | 4/11 |
| 30 | 3590 | Ames | 1973 | 64 | | 10 N, 40 P, 20 K | 4/22 |
| 31 | 3630 | Ames | 1973 | 30 | | 10 N, 40 P, 20 K | 4/21 |
| 32 | 3720 | Ames | 1973 | 32 | | 10 N, 40 P, 20 K | 4/22 |
| 33 | 3750 | Ames | 1972 | 30 | | 10 N, 40 P, 20 K | 4/8 |
| 34 | 3830 | Ames | 1968 | 32 | | 10 N, 40 P, 20 K | 3/? |
| 35 | 3890 | Sutherland | 1973 | 30 | | | 4/5 |
| 36 | 4180 | Kanawha | 1972 | 30 | | 50 N, 50 P, 50 K | 4/19 |

experiments except nos. 24 and 30, the seeding rate was 30 or 32 seeds per plot, which corresponds to approximately 105 kg ha⁻¹. Each trial was bordered on all sides by two rows of hills. Plot areas were hand weeded, and the plants were sprayed with a fungicide (zinc ethylenebisdithiocarbamate until 1973, and the systemic fungicide Bayleton (1-(4-chlorophenoxy)-3,3-dimethyl-1-(1H-1,2,4-triazol-1-yl)-2-butanone) in 1986) as needed to control foliar diseases. Grain yield was the weight of threshed grain from a plot expressed in kg ha⁻¹.

The 36 trials were divided into 3 yield groups (low, medium, and high) of 12. The effects of direct and indirect selection at each yield level, based on line means from either two or four trials, were estimated from 10 repetitions of the general protocol described above.

Experiment 2

The 178 oat lines used in this experiment were extracted by Adegoke (1979) from a bulk population originally derived from a mixture of F_2 seeds from 75 matings. These lines were evaluated in 1983 and 1984 in randomized complete-block trials, each with six replicates, at Castana, Kanawha, and Sutherland, Iowa, which were the low-, medium-, and high-productivity environments, respectively. Mean yields and agronomic treatments for these trials are presented in Table 2. Low yields at Castana were primarily the result of P deficiency. Direct and indirect selection for grain yield were compared at each productivity level and for selection based on line means in 3 or 6 replications at a single location, according to the general protocol outlined above. Repetition of selection was achieved by first designating the 1983 trials as selection environments and the 1984 trials as evaluation environments and then repeating the selection protocol with these designations reversed. Plot type, experimental design, agronomic management, and statistical analysis were as described in Experiment 1.

Experiment 3

In Experiment 3, the 178 lines used in Experiment 2 were tested in a total of 16 unreplicated yield trials in 1978, 1983, and 1984. Locations, mean yields, and agronomic treatments are presented in Table 3. Plot type, experiment layout, agronomic management, and statistical design were as described for Experiment 1. The 16 trials were grouped into two productivity levels, low and high. (Only two productivity levels were

Table 2. Mean yields, locations, years, and agronomic treatments of oat yield trials used in Experiment 2

| Trial | Mean yield (kg/ha) | Location | Year | Rotation ^b | Fertilizer ^a (kg/ha) | Planting date |
|-------|--------------------|------------|------|-----------------------|---------------------------------|---------------|
| 1 | 700 | Castana | 1983 | COMM ^c | 0 N, 0 P, 0 K | 4/26 |
| | | | | CCOM ^d | 0 N, 0 P, 0 K | |
| | | | | COCO ^e | 0 N, 0 P, 0 K | |
| 2 | 700 | Castana | 1984 | COMM ^c | 0 N, 0 P, 0 K | 4/25 |
| | | | | CCOM ^d | 0 N, 0 P, 0 K | |
| | | | | COCO ^e | 0 N, 0 P, 0 K | |
| 3 | 1660 | Kanawha | 1983 | CCOM ^c | 120 N, 30 P, 37 K | 4/27 |
| | | | | CSCO ^d | 120 N, 30 P, 37 K | |
| | | | | CCOM ^e | 60 N, 30 P, 37 K | |
| 4 | 1820 | Kanawha | 1984 | CCOM ^c | 120 N, 30 P, 37 K | |
| | | | | CSCO ^d | 120 N, 30 P, 37 K | |
| | | | | CCOM ^e | 60 N, 30 P, 37 K | |
| 5 | 1910 | Sutherland | 1983 | COMM ^c | 20 N ^c | 5/9 |
| | | | | CCOM ^d | 80 N ^d | |
| | | | | SCOM ^e | 80 N ^e | |
| 6 | 2400 | Sutherland | 1984 | COMM ^c | 20 N ^c | 4/25 |
| | | | | CCOM ^d | 80 N ^d | |
| | | | | SCOM ^e | 80 N ^e | |

^aFor trials 1 and 2, P was the primary yield-limiting element. For trials 3-6, N was limiting. P and K were applied in unknown amounts at Sutherland. In all cases, N was applied to the previous corn crop.

^bC represents corn, M meadow, O oats, S soybean.

^{c,d,e}Replicates 1 and 2, 3 and 4, and 5 and 6, respectively.

constituted in this experiment because, to obtain an unbiased comparison of direct and indirect selection, replication had to be equal at all levels.) Direct and indirect selection for grain yield, based on line means in two or four trials, were compared at each productivity level using ten repetitions of the selection protocol described above.

Table 3. Mean yields, locations, years, and agronomic treatments of oat yield trials used in Experiment 3

| Trial | Mean yield (kg/ha) | Location | Year | Rotation ^{a,b} | Fertilizer (kg/ha) | Planting date |
|-------|--------------------|------------|------|-------------------------|--|---------------|
| 1 | 530 | Castana | 1983 | COMM | 0 N, 0 P, 0 K | 4/26 |
| 2 | 670 | Castana | 1984 | COMM | 0 N, 0 P, 0 K | 4/25 |
| 3 | 1000 | Castana | 1978 | COCO | 29 P ^c , N and K unknown | 4/16 |
| 4 | 1620 | Kanawha | 1983 | CCOM | 120 N ^c , 30 P, 37 K | 4/27 |
| 5 | 1770 | Castana | 1978 | COCO | 29 P + 17,900 manure | 4/16 |
| 6 | 1850 | Sutherland | 1983 | COMM | 20 N ^c , P and K unknown | 5/9 |
| 7 | 1890 | Kanawha | 1984 | CCOM | 120 N ^c , 30 P, 37 K | 4/21 |
| 8 | 1930 | Kanawha | 1978 | CCCO | 0 N, P and K unknown | 4/16 |
| 9 | 2500 | Kanawha | 1978 | CCOM | 67 N ^c , P and K unknown | 4/16 |
| 10 | 2670 | Sutherland | 1978 | COMM | 22 N ^c , P and K unknown | 4/13 |
| 11 | 2670 | Ames | 1983 | | 34 N, 23 P, 43 K | 4/? |
| 12 | 2680 | Ames | 1978 | | 34 N, 20 P, 19 K | 5/11 |
| 13 | 2710 | Castana | 1978 | CCOM | 58 P + 17,900 manure | 4/16 |
| 14 | 2710 | Sutherland | 1978 | CCOM | 90 N ^c , P and K unknown | 4/13 |
| 15 | 2730 | Ames | 1978 | | 34 N, 20 P, 19 K | 4/27 |
| 16 | 3090 | Ames | 1978 | | 34 N, 20 P, 19 K | 4/12 |

^aC represents corn, O oats, M meadow.

^bBlanks indicate that treatment is known.

^cApplied to previous corn crop.

RESULTS AND DISCUSSION

Mean grain yields of the oat lines when tested at each productivity level in Experiments 1, 2, and 3 are presented in Table 4. Mean yields in LPE were only one-third to one-half as great as in HPE, which indicates that LPE imposed severe stress on the oat populations. In Experiment 1, the mean yield in MPE was two-thirds as great as in HPE, but in Experiment 2, there was only a small difference between grain yields in MPE and HPE.

The relative effectiveness of direct and indirect selection for grain yield in LPE varied among experiments and among levels of replication of the selection unit within experiments. In Experiment 1, mean yield gains from selection based upon two trials in LPE, MPE, or HPE did not differ significantly when evaluation was done in LPE (Table 5). When selection was based on four trials at a given productivity level, however, the mean gain from direct selection in LPE was 37% and 77% greater than that obtained from indirect selection in MPE and HPE, respectively. Selection in LPE was significantly inferior to selection in MPE and HPE in producing yield gain under evaluation in HPE. When averaged over all evaluation environments, the gains in mean yield from selection in LPE were only 58% and 71% as great as those resulting from selection in HPE when two and four trials, respectively, were used for selection. These results agree with predictions made by Atlin and Frey (1988a) for the same set of lines and environments. Their predictions, which were based on estimates of heritability within and genetic correlation among productivity levels, indicated that indirect selection in HPE would never be more effective than direct selection in LPE, irrespective of the level

Table 4. Mean grain yields of oat lines tested at two or three productivity levels in Experiments 1, 2, and 3

| Productivity | Mean yield (kg/ha) | | |
|--------------|--------------------|--------------|--------------|
| | Experiment 1 | Experiment 2 | Experiment 3 |
| Low | 1340 | 700 | 1410 |
| Medium | 2480 | 1740 | - |
| High | 3670 | 2160 | 2720 |

of replication. They predicted that selection in MPE would give the greatest yield gain in LPE at low and moderate levels of replication of the selection unit, whereas direct selection in LPE would be most effective when replication was high. The level of replication at which an advantage for direct selection in LPE was predicted to occur, however, was much greater than actually found in this experiment.

In Experiment 2, inadequate repetition of the selection protocol resulted in low precision of the estimates of yield gain from selection. Nonetheless, trends in this experiment were similar to those observed in Experiment 1. When selection was based on line means estimated from only three replications, there was no significant difference between gains resulting from direct selection in LPE and from indirect selection at the other productivity levels (Table 6). However, when line means were estimated from six replications, the yield gain in LPE was significantly greater from direct selection than from indirect selection in either MPE or HPE. Selection environment did not have a significant influence on

Table 5. Gains (% of population mean within productivity levels) from direct and indirect selection for grain yield in low-, medium-medium-, and high-productivity environments: Experiment 1

| Selection environment | | | Evaluation environment | | | |
|-----------------------|----------------------|--------------------|------------------------|--------|------|------|
| No. of trials | Replicates per trial | Productivity level | Low | Medium | High | Mean |
| 2 | 2 | Low | 5.4 | 5.6 | 4.4 | 5.0 |
| | | Medium | 6.1 | 8.0 | 8.1 | 7.7 |
| | | High | 4.1 | 9.6 | 9.7 | 8.8 |
| | | L.S.D. (0.05) | 3.8 | 2.3 | 2.4 | 2.0 |
| 4 | 2 | Low | 10.8 | 9.3 | 4.6 | 7.2 |
| | | Medium | 7.9 | 9.7 | 9.4 | 9.2 |
| | | High | 6.1 | 10.3 | 11.4 | 10.1 |
| | | L.S.D. (0.05) | 3.5 | 2.2 | 1.3 | 1.4 |

Table 6. Gains (% of population mean within productivity levels) from direct and indirect selection for grain yield in low-, medium-, and high-productivity environments: Experiment 2

| Selection environment | | | Evaluation environment | | | |
|-----------------------|----------------------|--------------------|------------------------|--------|------|------|
| No. of trials | Replicates per trial | Productivity level | Low | Medium | High | Mean |
| 1 | 3 | Low | 3.8 | 0.6 | 3.1 | 2.3 |
| | | Medium | 3.6 | 7.2 | 7.1 | 6.5 |
| | | High | -0.3 | 5.2 | 6.4 | 5.0 |
| | | L.S.D. (0.05) | 8.5 | 15.6 | 5.1 | 6.1 |
| 1 | 6 | Low | 11.1 | 4.8 | 5.9 | 6.3 |
| | | Medium | 0.7 | 8.9 | 7.6 | 7.0 |
| | | High | -0.3 | 6.2 | 3.6 | 4.0 |
| | | L.S.D. (0.05) | 6.8 | 8.4 | 3.7 | 4.5 |

gain in grain yield when selected oat lines were evaluated in MPE and HPE, or when gains were averaged over productivity levels.

In Experiment 3, selection in HPE was superior to selection in LPE irrespective of whether evaluation was conducted in high- or low-productivity environments and regardless of whether selection was based on line means from two or four trials (Table 7). However, increasing the number of replications of the selection unit had the same basic effect as in Experiments 1 and 2; it improved the effectiveness of direct relative to indirect selection for yield in LPE. With selection based on line means in two trials, direct selection was only 67% as effective as indirect selection, whereas with four trials, it was 79% as effective. The advantage for selection in HPE observed in this experiment contrasts with the results from Experiments 1 and 2, but agrees with findings reported by Shabana et al. (1980), who tested the same oat lines in a less extensive set of environments.

The discrepancy between the results from Experiments 1 and 2 and those from Experiment 3 and the experiment of Shabana et al. (1980) may be due, in part, to the fact that selection was based on only two to four replications in the latter experiments, whereas four to eight replications of the selection unit were used in Experiments 1 and 2. The effect of increasing replication on gains from direct and indirect selection for yield in LPE can be shown by considering the predicted ratio of correlated to direct response (after Falconer, 1981, p. 291):

$$CR_L/R_L = r_G H_H/H_L \quad (2)$$

where CR_L is the correlated response in LPE to selection in HPE, R_L is

Table 7. Gains (% of population mean within productivity levels) from direct and indirect selection for grain yield in low- and high-productivity environments: Experiment 3

| Selection environment | | | Evaluation environment | | |
|-----------------------|----------------------|--------------------|------------------------|------|------|
| No. of trials | Replicates per trial | Productivity level | Low | High | Mean |
| 2 | 1 | Low | 5.3 | 2.3 | 3.3 |
| | | High | 7.9 | 8.3 | 8.2 |
| | | L.S.D. (0.05) | 1.9 | 2.5 | 2.1 |
| 4 | 1 | Low | 7.1 | 5.7 | 6.2 |
| | | High | 9.0 | 11.6 | 10.7 |
| | | L.S.D. (0.05) | 2.9 | 3.7 | 3.0 |

response to direct selection in LPE, r_G is the genetic correlation between yield in LPE and HPE, and H_H and H_L are the square roots of heritabilities in HPE and LPE, respectively. This relationship shows that correlated response may exceed direct response if heritability is greater in HPE than in LPE and if the value of r_G is moderate to high. When H_H is greater than H_L , as generally is the case for oats evaluated in Iowa (Barrales, 1985; Vega and Frey, 1981; Atlin and Frey, 1988a,b), the ratio H_H/H_L is considerably greater than 1 at low levels of replication, but it approaches unity as replication increases. If r_G is less than 1, a level of replication will exist at which CR_L/R_L also will be less than 1, resulting in an advantage for direct selection in LPE. Estimates of H_H , H_L , and r_G were not presented by Shabana et al. (1980)

and could not be reliably estimated for Experiment 3. However, if these parameters had values similar to those obtained by Atlin and Frey (1988a), direct selection in LPE could not have been advantageous at the low levels of replication of the selection unit used in Experiment 3 and that of Shabana et al. (1980). In general, these results demonstrate that, if H_H is greater than H_L , the effectiveness of direct selection in LPE can increase, relative to selection in HPE, as the number of replications is increased. Because of this relationship, empirical comparisons of the effectiveness of direct and indirect selection for yield in LPE need to be conducted at several levels of replication.

Our results show that one cannot assume that the greatest yield gain in LPE will necessarily result from selection either in HPE or in the environment where H^2 is maximized. Rather, the best productivity level for selection must be identified experimentally, a conclusion previously reached by Allen et al. (1978), Rosielle and Hamblin (1981), and Atlin and Frey (1988a). Equation 2 shows that some portion of gain made in HPE will be expressed in LPE whenever r_G is positive. This, however, does not prove that HPE is the optimum selection environment for yield in LPE because, if r_G is less than 1, some level of replication exists at which direct selection for yield in LPE will be superior to indirect selection in HPE.

These conclusions do not preclude the possibility that a single genotype will be most productive in both LPE and HPE, even when r_G is low. This is because r_G is an average measure of genotype x productivity level interaction for the entire population. Even when r_G for the population

is low, certain exceptional genotypes may interact little with the environment. Likewise, an estimate of r_G that approaches 1.0 does not preclude the possibility that different genotypes may be most productive in LPE and HPE. Our findings are most relevant to preliminary selection in large populations, when the goal is to preserve an elite fraction of the population for recombination or further testing.

Testing the assumption that selection of plant genotypes in high fertility, intensively managed environments will maximize gains in LPE is especially important in breeding programs at international agricultural research centers and in the national breeding programs of developing countries. Developing countries often have a two-tiered agriculture, wherein a small proportion of farmers produces crops commercially, in HPE, and a larger proportion produces, primarily for subsistence, in LPE. In some instances, the differences between these production environments may be so extreme that substantially different gene complements are required to achieve the highest yields in each. To maximize national production when this is the case, breeders will need to select different varieties for LPE and HPE.

SECTION III. PREDICTING THE RELATIVE EFFECTIVENESS OF DIRECT VERSUS
INDIRECT SELECTION FOR OAT YIELD IN THREE TYPES
OF STRESS ENVIRONMENT

ABSTRACT

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 heat-stressed environments. Estimates of r_G between yield in nonstress and yield in P-deficient, N-deficient, and heat-stressed 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 heat-stressed environments, but selection in high-N environments was predicted to result in the greatest yield gain in both low-N and high-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.

Additional index words: Avena sativa L., genotype x environment interaction, genetic correlation, N-deficiency, P-deficiency, heat stress.

INTRODUCTION

When breeding crop varieties for yield in stress environments, it must be 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_s^2 and H_{ns}^2 , respectively), and the genetic correlation between yields in stress and nonstress environments (r_G) (Falconer, 1952; Allen et al., 1978; Rosielle and Hamblin, 1981; Atlin and Frey, 1988a). The relative effectiveness of indirect versus direct selection for a trait such as yield in stress environments can be predicted (after Falconer, 1981, p. 283) as:

$$CR_s/R_s = r_G H_{ns}/H_s \quad (1)$$

where CR_s is correlated response in stress environments to selection in nonstress environments and R_s is response to direct selection in stress environments. Estimates of H_s and H_{ns} have been reported by several authors (e.g., Gotoh and Osanai, 1959; Frey, 1964; Johnson and Frey, 1967; McNeill and 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 x environment interaction (with "environment" meaning "stress level" in this paper) and can, under restricted conditions, be calculated as:

$$r_G = \sigma_G^2 / (\sigma_G^2 + \sigma_{GE}^2) \quad (2)$$

where σ_G^2 and σ_{GE}^2 are genetic and genotype x 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 and Frey, 1988a).

Atlin and Frey (1988a) 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 predicted yield gain was greater for direct selection in LPE than for indirect selection in HPE, even though H^2 was greater in HPE. This prediction was confirmed in an empirical selection experiment (Atlin and Frey, 1988c).

In their selection experiments, Atlin and Frey (1988a,c) grouped low N, low P, and heat-stressed 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 heat-stressed environments in the same population of oat lines used by Atlin and Frey (1988a). 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 obtain data for computing 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 prior to 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 a broadcast application of 59 kg ha^{-1} P prior to planting and the other received 88 kg ha^{-1} , both broadcast preplanting. In 1986, the high-P experiment received a preplant 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 Bayleton (1-(4-chlorophenxy)-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:

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

where Y_{ijk} is the yield of a plot, μ is the experiment mean, $R/E_{k/j}$ is the effect of the kth replicate in the jth year, 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, and ϵ_{ijk} is the residual.

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

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

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 and Bancroft (1952). Heritabilities within P levels, expressed on an entry-mean basis for a reference unit of mean yield from three 2-replicate trials, were computed as:

$$H^2 = \sigma_G^2 / \sigma_P^2 \quad (5)$$

where σ_G^2 and σ_P^2 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 x year covariances. The genetic correlation (r_G) between yield in high-P and low-P environments was calculated as:

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

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 variances 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 prior to 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 non-

Table 1. Analysis of covariance for mean grain yield of 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 x Y | 230 | σ_{GY} |

stressed environments was estimated by pairing, within locations, early and late planted experiments at Ames, Kanawha, and Sutherland. Within a location, early and late planted experiments were conducted in different years. The early trials were sown on 30 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 described for the P and N experiments, except that locations instead of years were considered to be environments in the analyses of variance. It has been shown that under heat stress some oat genotypes produce high yields because they are early maturing and, thus, can avoid the onset of high temperatures, whereas others appear to resist heat stress (Colville Baltenberger and Frey, 1987; Wych et al., 1982). To clarify whether differential maturities were responsible for yield differences among lines tested in heat-stressed environments, r_G was computed between

heading date (number of days from planting until 50% of panicles had emerged from the leaf sheath) measured in early-sown and grain yield in late-sown experiments. Heading dates from Ames in 1967 and 1972, and grain yields from Ames-1973, Kanawha-1986, and Sutherland-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:

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

where $\sigma_{G_{HG}}$ is the covariance of line means for heading date 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 response to selection was computed, after Falconer (1981), p. 291), as:

$$CR_s/R_s = r_G H_{ns}/H_s \quad (8)$$

$$CR_{ns}/R_{ns} = r_G H_s/H_{ns} \quad (9)$$

where CR_s is the correlated response in a stress environment to selection in a nonstress environment, R_s is direct response to selection in a stress environment, CR_{ns} is correlated response in a nonstress environment to selection in a stress environment, R_{ns} is direct response in a nonstress environment, r_G is the genetic correlation between yields in stress and nonstress environments, and H_s and H_{ns} are the square roots of heritabilities in stress and nonstress environments, respectively.

RESULTS AND DISCUSSION

Mean yields, heritabilities, r_G between yields in stress and non-stress environments, and predicted ratios of correlated versus direct response are presented in Tables 2, 3, and 4, for the comparisons 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. Heritability of yield at the low P level was greater than at the high level; thus, if heritability were the only criterion used to decide which environment was best for selection, low-P would be judged superior. 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.

In contrast to the results for the comparison over P levels, r_G between yield in low-N and high-N environments was not significantly different from 1 (Table 3). This suggests that an identical complement of genes 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 maximum response regardless of the N level of the evaluation environment.

Table 2. Heritability^a (H^2) of grain yield in low-P and high-P environments, the genetic correlation (r_G) between yield in low-P and high-P environments, and the predicted ratio of correlated and direct response to selection (CR/R) at each P level

| P level | Mean yield (kg ha ⁻¹) | H^2 | r_G | CR/R |
|---------|-----------------------------------|--------------------|-----------|------|
| Low | 1140 | 0.40 (0.22, 0.54) | 0.52±0.24 | 0.38 |
| High | 2710 | 0.21 (-0.02, 0.40) | | 0.71 |

^aReference unit for H^2 is mean yield in three 2-replicate yield trials. Upper and lower bounds of the 90% confidence interval in brackets.

Table 3. Heritability^a (H^2) of grain yield in low-N and high-N environments, the genetic correlation (r_G) between yield in low-N and high-N environments, and the predicted ratio of correlated and direct response to selection (CR/R) at each N level

| N level | Mean yield (kg ha ⁻¹) | H^2 | r_G | CR/R |
|---------|-----------------------------------|-------------------|-----------|------|
| Low | 1240 | 0.32 (0.12, 0.48) | 1.08±0.16 | 1.09 |
| High | 2850 | 0.38 (0.19, 0.53) | | 0.92 |

^aReference unit for H^2 is mean yield in three 2-replicate yield trials. Upper and lower bounds of the 90% confidence interval in brackets.

Table 4. Heritability^a (H^2) of grain yield in late-planted and early-planted environments, the genetic correlation (r_G) between yield in late- and early-planted environments, and the predicted ratio of correlated and direct response to selection (CR/R) at each planting date

| Planting date | Mean yield (kg ha ⁻¹) | H^2 | r_G | CR/R |
|---------------|-----------------------------------|--------------------|-----------|------|
| Late | 1500 | 0.15 (-0.10, 0.36) | 0.06±0.24 | 0.12 |
| Early | 3970 | 0.63 (0.52, 0.72) | | 0.03 |

^aReference unit for H^2 is mean yield in three 2-replicate yield trials. Upper and lower bounds of the 90% confidence interval in brackets.

The r_G between yield in early- and late-planted environments did not differ significantly from 0 (Table 4), 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 heading date in early-sown 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 was probably 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. Also, they demonstrate that low-P and late-planted environments were responsible for the low r_G

between yield in LPE and HPE reported by Atlin and Frey (1988a). 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 and 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 and Frey, 1987), and instances of specific adaptation of certain genotypes to low-P environments have been observed in a number of species (Gabelman and Gerloff, 1983; Caradus, 1982; Brown et al., 1977). However, little use has been made of such estimates in the development of breeding strategies for stress environments, both because experiments designed to estimate genotype x environment interaction rarely include enough genotypes to obtain reliable estimates of genetic parameters, and because few plant breeders appear to be aware of the nature of the relationship between r_G and σ_{GE}^2 . This relationship is the basis for the quantitative approach described in this paper 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 for developing countries, where a given crop species is often grown in diverse production environments.

GENERAL CONCLUSIONS

In this study, Falconer's (1952) model was used to determine whether oat cultivars destined for use in low-productivity environments (LPE) are best selected directly in LPE or indirectly in high-productivity environments (HPE). The results have important implications for the design of breeding programs. In Section I, it was shown in a population of 116 random oat lines that grain yields in low- and high-productivity environments are traits controlled by a substantially different set of genes ($r_G = 0.59$), and that at high levels of replication of the selection unit, direct selection in LPE is predicted to be more effective than indirect selection in HPE. These results were confirmed in the empirical selection experiments described in Section II. In two of the three experiments, direct selection in LPE was superior to indirect selection in HPE at moderate levels of replication. In Section III, it was predicted that selection for yield in low-P and heat-stressed environments is best conducted directly in the presence of those stresses rather than in nonstress conditions. However, selection for yield under conditions of N deficiency was predicted to be more effective in high-N than in low-N environments.

The most important conclusion arising from this study, and a result previously reached on theoretical grounds by Allen et al. (1978), is that it cannot be assumed a priori that selection is best conducted in highly productive nurseries when the objective of a breeding program is to produce cultivars adapted to LPE. In many cases, it is likely that

selection for yield in LPE should be direct, i.e., in an environment similar to on-farm conditions. This finding is particularly significant for breeding programs in developing countries, where on-farm conditions may differ markedly from the breeder's test environment. Predictions of the relative value of members of a set of candidate selection environments can be accurately obtained via Falconer's method, but there is little evidence to suggest that such predictions have informed the design of breeding programs in international agricultural research centers, where the critical early stages of selection are generally conducted under high-productivity conditions. Such predictions could lead to the design of breeding programs better suited to the needs of the poorest farmers.

It was also demonstrated in Sections I and II that the relationship between direct response to selection in LPE and correlated response in LPE to selection in HPE is not fixed but dependent on the extent of replication of the selection unit. A similar observation has been made by Frey (1965) and Baker and Leisle (1970) in comparisons of response to selection in hill and four-row plots in small grains. In the present study, it was shown that whenever the genetic correlation between yields in LPE and HPE is less than 1.0, direct response to selection in LPE must exceed, at some level of replication, indirect response in LPE to selection in HPE. The choice of whether to select in LPE or in HPE for yield in LPE is thus, in part, a policy decision, dependent on the extent of the resources available to the breeding program as well as on the magnitude of the additional gains in LPE which might be expected

from direct selection.

The prediction methods described in this study are applicable to a large class of plant breeding problems which are, in their essentials, problems of choosing the best selection environment for a given purpose. These methods should be particularly helpful in deciding whether separate breeding programs are required for different cropping systems occurring within the same species and breeding region, but appear to have been previously used in this application only by Pfeiffer (1987) and Weaver and Wilcox (1982). Other authors (i.e., Brakke et al., 1983; Newhouse and Crosbie, 1987) have attempted to make such decisions on the basis of the magnitude of genotype x cropping system interaction mean squares computed from an analysis of variance. The discussion in Section I on the nature of the genetic correlation between expressions of the same trait in different environments (r_G) shows that this is only valid when such interactions are not significant and, consequently, $r_G = 1.0$. Greater familiarity of plant breeders with the methods described herein should lead to more reliable decisions regarding choice of the best selection environment in the presence of genotype x environment interactions.

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APPENDIX

Table A1. Sums of squares from analyses of variance within low-, medium-, and high-productivity environments for grain yield of 116 oat lines

| Source | df | Productivity level | | |
|-----------------|------|--------------------|------------|------------|
| | | Low | Medium | High |
| Environment (E) | 11 | 20454.54 | 31276.20 | 10727.63 |
| Replication/E | 12 | 4588.27 | 11274.44 | 2644.59 |
| Line (L) | 115 | 5746.41** | 16912.05** | 31105.15** |
| L x E | 1265 | 26556.88** | 38108.72** | 48595.03** |
| Error | 1380 | 18550.73 | 30358.56 | 43021.41 |

**Indicates significance at the 1% level of probability. Tests of significance were made only for the effects of lines and lines x environments.

Table A2. Sums of squares, on original, square-root, and standard-unit scales, from analyses of variance combined over low- and medium-productivity levels, for grain yield of 116 oat lines

| Source | df | Scale | | |
|-------------------------|------|----------|-------------|---------------|
| | | Original | Square root | Standard unit |
| Productivity levels (P) | 1 | 256253 | 2350.6 | 0 |
| Environments (E)/P | 22 | 51731 | 749.7 | 0 |
| Replicates (R)/E/P | 24 | 15863 | 234.4 | 495.3 |
| Lines (L) | 115 | 16963** | 234.7** | 652.3** |
| L x P | 115 | 5695** | 64.3** | 153.3** |
| L x E/P | 2540 | 64666** | 981.3** | 2382.7** |
| Error | 2760 | 48909 | 745.8 | 1860.4 |

**Indicates significance at the 1% level of probability. Tests of significance were made only for the effects of lines, lines x productivity levels, and lines x environments within productivity levels.

Table A3. Sums of squares, on original, square-root, and standard-unit scales, from analyses of variance combined over medium- and high-productivity levels for grain yield of 116 oat lines

| Source | df | Scale | | |
|-------------------------|------|----------|-------------|---------------|
| | | Original | Square root | Standard unit |
| Productivity levels (P) | 1 | 169181 | 1564.9 | 0 |
| Environments (E)/P | 22 | 42004 | 422.0 | 0 |
| Replicates (R)/E/P | 24 | 13919 | 152.6 | 306.5 |
| Lines (L) | 115 | 42063** | 371.9** | 1099.8** |
| L x P | 115 | 5954** | 48.8* | 125.4* |
| L x E/P | 2530 | 86704** | 806.7** | 2163.7** |
| Error | 2760 | 73380 | 666.2 | 1848.6 |

*,**Indicate significance at the 5% and 1% levels of probability, respectively. Tests of significance were made only for the effects of lines, lines x productivity levels, and lines x environments within productivity levels.

Table A4. Sums of squares on original, square-root, and standard-unit scales, from analyses of variance combined over low- and high-productivity levels for grain yield of 116 oat lines

| Source | df | Scale | | |
|-------------------------|------|----------|-------------|---------------|
| | | Original | Square root | Standard unit |
| Productivity levels (P) | 1 | 650610 | 7751.4 | 0 |
| Environments (E)/P | 22 | 31182 | 483.5 | 0 |
| Replicates (R)/E/P | 24 | 7233 | 122.3 | 316.9 |
| Lines (L) | 115 | 23977** | 244.3** | 724.2** |
| L x P | 115 | 12874** | 103.1** | 259.6** |
| L x E/P | 2530 | 75152** | 908.5** | 2303.3** |
| Error | 2760 | 61572 | 717.6 | 1940.0 |

**Indicates significance at the 1% level of probability. Tests of significance were made only for the effects of lines, lines x productivity levels, and lines x environments within productivity levels.

Table A5. Sums of squares from analyses of variance (on standard-unit scale) within low- and high-P environments, for grain yield of 116 oat lines

| Source | df | P level | |
|---------------|-----|-----------|-----------|
| | | Low | High |
| Year (Y) | 2 | 0 | 0 |
| Replication/Y | 3 | 38.248 | 242.954 |
| Line (L) | 115 | 155.758** | 103.788 |
| L x Y | 230 | 181.873 | 162.424** |
| Error | 345 | 317.120 | 183.833 |

**Indicates significance at the 1% level of probability. Tests of significance were made only for the effects of lines and lines x years.

Table A6. Sums of squares from analyses of variance (on standard-unit scale) within low- and high-N environments, for grain yield of 116 oat lines

| Source | df | N level | |
|---------------|-----|-----------|-----------|
| | | Low | High |
| Year (Y) | 2 | 0 | 0 |
| Replication/Y | 3 | 179.482 | 16.369 |
| Line (L) | 115 | 145.466** | 214.890** |
| L x Y | 230 | 179.720** | 242.979** |
| Error | 345 | 188.333 | 218.761 |

**Indicates significance at the 1% level of probability. Tests of significance were made only for the effects of lines and lines x years.

Table A7. Sums of squares from analyses of variance (on standard-unit scale) within early- and late-sown environments, for grain yield of 116 oat lines

| Source | df | Sowing date | |
|---------------|-----|-------------|-----------|
| | | Late | Early |
| Location (E) | 2 | 0 | 0 |
| Replication/E | 3 | 13.006 | 1.599 |
| Line (L) | 115 | 168.488 | 245.728** |
| L x E | 230 | 277.664** | 181.018 |
| Error | 345 | 233.842 | 264.655 |

**Indicates significance at the 1% level of probability. Tests of significance were made only for the effects of lines and lines x locations.

Table A8. Sums of cross products from analysis of covariance of line means in low-P and high-P environments, for grain yield of 116 oat lines

| Source | Sums of cross products | |
|-------------|------------------------|-------|
| Year | 2 | |
| Line | 115 | 15.84 |
| Year x line | 230 | 11.74 |

Table A9. Sums of cross products from analysis of covariance of line means in low-N and high-N environments, for grain yield of 116 oat lines

| Year | df | Sums of cross products |
|-------------|-----|------------------------|
| Year | 2 | |
| Line | 115 | 50.43 |
| Year x line | 230 | 23.10 |

Table A10. Sums of cross products from analysis of covariance of line means in early- and late-sown environments, for grain yield of 116 oat lines

| Source | df | Sums of cross products |
|-------------|-----|------------------------|
| Year | 2 | |
| Line | 115 | -0.065 |
| Year x line | 230 | -3.877 |