Theor Appl Genet (1991) 81:79–82

THEORETICAL AND APPLIED GENETICS

Prediction of F_3 row performance from F_2 individual plant data in oats[*]

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Received May 4, 1990; Accepted July 13, 1990
Communicated by A.R. Hallauer

Summary. Parameters estimated from a Gardner-Eberhart analysis of the F_2 generation of a six-parent diallel in oats (*Avena sativa* L.) were used to compare methods for predicting the performance of F_3 row plots. The prediction methods were: (1) individual F_2 plant performance (F2I), (2) parent average plus F_2 plot deviations (PF2), (3) parent average plus weighted F_2 plot deviations (PF2P), (4) best linear unbiased prediction (BLUP) of parent average plus F_2 plot deviations (BPF2), and (5) BLUP plus weighted F_2 deviations (BF2). The F_2 single-plant traits used for prediction were biological yield to predict F_3 biological yield, whole plant and primary tiller grain yield for prediction of F_3 grain yield, and whole plant and primary tiller harvest index (HI) to predict F_3 HI. Prediction methods were evaluated by correlations between predicted and observed F_3 performance. Prediction methods and traits for which correlations were greater than for F2I included: BF2 for biological yield, PF2, PF2P and BF2 for whole plant grain yield, PF2, BPF2, and BF2 for primary tiller grain yield. None had a correlation significantly greater than F2I for either measure of HI, where heritability was large. PF2 is the recommended method for traits with low heritability because of its simplicity and because it had the largest or nearly the largest correlation for each of the yield traits. F2I is the recommended method for traits with larger heritability.

Key words: *Avena sativa* L. – Grain yield – Biological yield – Harvest index – Early generation selection

Introduction

Breeders of oats (*Avena sativa* L.) and other self-pollinated cereal crops must advance large numbers of genotypes through segregating generations before a superior cultivar is identified. An effective method of eliminating a portion of the material early in the evaluation process could result in significant reductions in evaluation costs. Studies on the effectiveness of selection in early generations have been conducted, and the general conclusion is that response to selection in early generations is poor (Wricke and Weber 1986). Reasons offered by Wricke and Weber (1986) for the poor response to selection in early generations include: (a) seed quantities available in early generations are not adequate for evaluation in replicated experiments over several environments; (b) plant spacing used in early generations does not provide for competition that exists in dense stands used in culture and, hence, does not permit accurate assessment of genetic potential under commercial culture conditions; and (c) genetic effects associated with heterozygosity in early generations hampers accurate identification of additive effects of genes that will function in later generations. Indeed, methods like bulk or single-seed descent are used in many breeding programs with self-pollinated crops, and any attempt at selection is delayed until homozygosity is essentially reached.

Frequently, inheritance studies are conducted in small grains where detailed data are collected on individual plants in early generations. It would be desirable, in many instances, to enter genetic material from such studies into the cultivar development phase of the breeding program. Procedures that utilize information collected on individual plants in such studies to more accurately select elite genotypes for further evaluation would be helpful. The results of a comparison of five different meth-

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Table 1. Mean-square expectations for analysis of oat F_2 diallel

Source	*df*	Expected mean squares
Parent lines	5	$(\sigma_w^2/18.896)+\sigma_e^2+6.456\sigma_s^2+24.266\sigma_{h_i}^2+0.018\sigma_{\bar{h}}^2+14.244\sigma_p^2$
Average heterosis	1	$(\sigma_w^2/18.896)+\sigma_e^2+1.779\sigma_s^2+16.442\sigma_{h_i}^2+24.668\sigma_{\bar{h}}^2$
Parent heterosis	5	$(\sigma_w^2/18.896)+\sigma_e^2+3.542\sigma_s^2+12.917\sigma_{h_i}^2$
Specific heterosis	8	$(\sigma_w^2/18.896)+\sigma_e^2+10.00\sigma_s^2$
Residual[a]	146	$(\sigma_w^2/18.896)+\sigma_e^2$
Plants in plots	3,058	$(\sigma_w^2/18.896)$

[a] Residual includes maternal, reciprocal, and error effects in the original model

ods of prediction of F_3 row-plot performance based on performance of individual F_2 plants from a diallel cross in oats are reported in this paper.

Materials and methods

A diallel cross, including reciprocals, was constructed from six oat cultivars and experimental lines – 'Ogle', 'Orbit', 'Hazel', 'Dal', PA-2250, and PA-12422 – by hand-crossing during the winter of 1983–84. Eight F_1 plants of each of the 30 possible combinations and the parents were grown in the greenhouse during the winter of 1984–85. Two of the crosses, Hazel/PA-12422 and its reciprocal, were sterile and produced no F_2 seed, resulting in a total of 34 entries (28 crosses and 6 parents) in the experiment. Resulting seeds were used to plant an experiment in the field on April 16, 1985. A randomized, complete block design with five replications of 25 plants per plot was used. Plants were spaced 7.6 cm apart in rows that were 1.8 m long, with 17.8 cm between rows. Data were collected on all but the end plants in each plot. Data collected on F_2 plants and parents included biological yield (grain plus straw yield), whole plant grain yield, primary tiller grain yield, whole plant harvest index (HI = grain yield/biological yield), and primary tiller HI.

Seed from 20, randomly selected F_2 plants were used to establish the F_3 experiment. In some cases, one of 20 random selections did not have enough seed for the F_3, and seed from an end plant from the same F_2 family was used for the F_3. The F_3 experiment was established in two replications of a randomized, complete block design on March 31, 1986. Each replication contained 10 of the 20 families from the F_2 generation seeded at the rate of 50 seeds in a 1.2-m long row. Assignment of families to replications in the F_3 was at random, and replication effects in the F_3 were not significant and were thus ignored in the prediction procedure. Data collected in the F_3 experiment included biological yield, grain yield, and HI for each row. Because we were interested in predicting performance of segregating progeny, no attempt was made to predict performance of the parents that were included in the F_3 experiment. The elimination of the parents plus those F_3 rows that came from seed on the end plants in the F_2 experiment resulted in a total of 467 F_3 rows for which F_2 plants with data were available.

Both experiments were conducted at the Rock Springs Research Center near University Park/PA. Additional details on field procedures for the F_2 and F_3 experiments were given by Kolb et al. (1990).

Data from the F_2 experiment were analyzed according to the linear model:

$$y=u+\mathbf{X}r+\mathbf{Z}_1 p+\mathbf{Z}_2 \bar{h}+\mathbf{Z}_3 h+\mathbf{Z}_4 s+e+w \quad (1)$$

where:

y = the vector of observed values in the F_2 experiment,
u = a constant
$\mathbf{X}$ = a matrix of 0's and 1's expressing the occurrence of replication effects, r,
$\mathbf{Z}_i$ = coefficients of 0's and 1's for parent, p, average heterosis, $\bar{h}$, line heterosis, h, and specific combining ability effects, s, respectively,
e = an error term for plots, and
w = a vector of within-plot effects of individual plants.

The above model is the same as that of Gardner and Eberhart (1966), expressed in matrix terms. Although reciprocal crosses were included in the diallel, maternal and reciprocal effects were not included in the model used in our analysis here. Data collected in the F_3 experiment were used only for comparison of the effectiveness of the prediction methods, and were not subjected to a statistical analysis. Results of an analysis of the F_3 data were given by Kolb et al. (1990).

The analysis of the F_2 generation was conducted in two steps: calculation of plot means and variation within plots, followed by the method of unweighted means analysis. The missing cross and its reciprocal required statistical methods for unbalanced data. Methods presented by Searle (1971) were followed in the analysis and in the derivation of mean-square expectations, following Henderson's Method III as described by Searle (1971). Coefficients of the variance components are shown in Table 1.

Five methods of predicting F_3 performance from F_2 data and parameters estimated from F_2 data were compared:

1. F2I, or individual F_2 plant performance, where

$$\hat{y}_{F_3}=y_{F_2}, \quad (2)$$

where y_{F_2} = the observed value of the individual F_2 parent of the F_3 row. This method is equivalent to selection of individual F_2 plants on the basis of observed performance with no adjustment.

2. PF2, or parental means plus unweighted F_2 plot deviations, where

$$\hat{y}_{F_3}=(1/2)\,(\bar{y}_{P_g}+\bar{y}_{P_h})+(1/2)\,(y_{ghij_{F_2}}-y_{ghi\,.\,F_2}), \quad (3)$$

where $\bar{y}_{P_g}$ = the mean of parent g and $\bar{y}_{P_h}$ = the mean of parent h from the analysis of the F_2 experiment, $y_{ghij_{F_2}}$ = the observed value of plant j from the cross between parents g and h in replication i of the F_2 experiment, and $y_{ghij_{F_2}}$ = the mean of the plot in which the plant appeared. The adjustment of individual plant values to deviations from the plot mean was done to remove replication effects in the F_2 experiment. This prediction formula was derived from simple calculations, based on expected values for parents and the F_2 in a two-allele population.

3. PF2P, or a weighted average of the parental mean and individual F_2 plot deviations, where

$$\hat{y}_{F_3}=(v_1/2)\,(y_{P_g}+y_{P_h})+(v_2/2)\,(y_{ghij_{F_2}}-y_{ghi.{F_2}}), \tag{4}$$

where y's with similar subscripts are as defined for PF2, and

$$v_1=(s_p^2/s_{Ph}^2),$$

with s_p^2 = the estimate of the parent variance component (Table 1), and

$$s_{Ph}^2=(s_w^2/18.896)+(s_e^2/20)+(s_s^2/40)+(s_{h_i}^2/100)+(s_{\bar{h}}^2/460)+(s_p^2/100),$$

where s_i^2 indicates the estimate of variances shown in Table 1; and

$$v_2=(s_p^2/s_{PI}^2),$$

with s_p^2 as defined above and $s_{PI}^2=s_w^2+s_e^2+s_s^2+s_{h_i}^2+s_{\bar{h}}^2+s_p^2$.

4. BPF2, or best linear unbiased prediction of parental means plus unweighted F_2 plot deviations, where

$$\hat{y}_{F_3}=(1/2)\,(\hat{y}_{P_g}+\hat{y}_{P_h})+(1/2)\,(y_{ghij_{F_2}}-y_{ghi.{F_2}}), \tag{5}$$

where $\hat{y}_{P_g}$ and $\hat{y}_{P_h}$ are the estimated means for parents g and h from the equation

$$\hat{y}_{F_2}=\mathbf{V}_G\,\mathbf{V}_P^{-1}(y_{F_2}-\mathbf{y}.),$$

with y_{F_2} = the vector of F_2 entry means, and

$$\mathbf{V}_G=(s_p^2/2)\,\mathbf{Z}_1\mathbf{Z}_1'+(s_{\bar{h}}^2/2)\,\mathbf{Z}_2\mathbf{Z}_2'+(s_{h_i}^2/2)\,\mathbf{Z}_3\mathbf{Z}_3'+(s_s^2/2)\,\mathbf{Z}_4\mathbf{Z}_4' \tag{6}$$

with $\mathbf{Z}_i$ as defined in Eq. 1, and

$$\mathbf{V}_P=\mathbf{V}_G+[s_e^2+(s_w^2/18.896)]\,\mathbf{I}.$$

BPF2 was based on a modification of results presented by Henderson (1975, 1977).

5. BF2, or best linear unbiased prediction of parent means plus a weighted average of individual F_2 plot deviations, where

$$\hat{y}_{F_3}=(1/2)\,(\hat{y}_{P_g}+\hat{y}_{P_h})+(v_2/2)\,(y_{ghij_{F_2}}-y_{ghi.{F_2}}), \tag{7}$$

where $\hat{y}_{P_g}$ and $y_{ghij_{F_2}}$ are as defined for BPF2 and v_2 is as defined for PF2P.

Several other methods, including best linear unbiased prediction of the entire vector of entry means from the F_2 experiment, were attempted. Each of these methods was found to be inferior to those mentioned above and the results are not presented.

Correlations between observed and predicted F_3 means were computed in the evaluation of the methods. Predictions were made only for the 467 F_3 rows for which F_2 plants with data were available. Fisher's z-statistic as described by Snedecor (1957) was used in a one-tailed test ($P=0.10$) to identify those correlations that exceeded the correlation for F2I.

Results

The estimate of the within-plot variance was much larger than estimates of the other variance components for biological yield, whole plant grain yield, and primary tiller grain yield (Table 2). The within-plot variance was approximately the same magnitude as the variance for parents for both measures of HI. The variance component attributed to parents was significant and was the largest of the genetic variance components for each of the traits included in the study. Variances associated with average heterosis and line heterosis were significant for biological yield and both measures of grain yield, but estimates of these components were negative and were assumed to be zero for HI. No estimate of variation associated with specific combining ability was significant, and the estimate of this component was negative and assumed to be zero for biological yield.

Table 2. Estimates of variance components for indicated traits

Component[a]	Biological yield	Grain yield		Harvest index	
		Whole plant	Primary tiller	Whole plant	Primary tiller
s_p	0.9748*	0.2418*	0.0496*	11.4164*	10.4470*
$s_{\bar{h}}$	0.6021*	0.1402*	0.0350*	0[b]	0
s_{h_i}	0.5537*	0.1390*	0.0046*	0	0
s_s	0	0.0018	0.0011	0.1326	0.1140
s_e	3.4875	0.6647	0.0210	1.0844	1.3738
s_w	42.2097	11.2528	0.3770	12.9210	11.9851

[a] Estimates of components as defined in Table 1

[b] Zero was inserted for negative estimates

* Indicates variance components associated with mean squares that were significant in a $P=0.05$ F-test

Table 3. Correlations between predicted and observed F_3 values for different methods

Prediction method	Biological yield	Grain yield		Harvest index	
		Whole plant	Primary tiller	Whole plant	Primary tiller
F2I	0.133	0.104	0.236	0.554	0.476
PF2	0.202	0.190*	0.327*	0.356	0.334
PF2P	0.160	0.189*	0.278	0.454	0.436
BPF2	0.193	0.182	0.320*	0.463	0.452
BF2	0.221*	0.198*	0.316*	0.479	0.480

* Indicates correlations significantly greater than that for F2I in a one-tailed t-test at $P=0.10$

$n=467$ for all correlations

The largest correlation between predicted and observed F_3 biological yield was observed with BF2, and this was the only correlation for biological yield that was significantly greater than that for F2I (Table 3). Correlations for PF2 and BPF2 were similar to that for BF2, and the correlation for PF2P was intermediate in magnitude. Based on the magnitudes of the estimated correlations, predictions of F_3 biological yield on the basis of F_2 individual plant data with BF2, BPF2, and PF2 should be similar and should be superior to F2I.

Correlations between observed and predicted F_3 grain yield were greater for the prediction based on primary tiller than for that based on whole plant F_2 grain yield, but relative rankings of the methods were similar (Table 3). Kolb et al. (1990) also reported that primary tiller grain yield in the F_2 was a better predictor of F_3 grain yield than was whole plant F_2 grain yield. The smallest correlation with both measures of F_2 grain yield was observed with F2I. Correlations with PF2 and BF2 for both measures F_2 grain yield, with PF2P for F_2 whole plant grain yield and with BPF2 for primary tiller grain yield, were significantly greater than corresponding correlations with F2I. The difference between the correlation with F2I and the other methods was larger for the estimate based on F_2 whole plant than for that based on primary tiller grain yield.

The relative ranking of the correlations with the different methods of prediction for HI was very different from that for the other traits in the study, and no method had a correlation significantly greater than that for F2I (Table 3). In fact, some of the correlations would have been significantly less than that for F2I in a two-tailed test. The correlations between observed and predicted F_3 HI were larger than those for the other traits. Heritability for HI has been reported to be high (Rosielle and Frey 1977; Kolb et al. 1990), and larger correlations would be expected for traits with higher heritability. The results with HI indicate that adjustments made in the prediction methods can be detrimental for traits with higher heritability.

Discussion

The results of our analysis confirmed the results of others (Hanson et al. 1979; Knott 1972; McGinnis and Shebeski 1968), who indicated that early generation selection for traits with low heritability in small grains would not be very effective. We found methods, however, that would significantly improve predictions of F_3 row-plot performance on the basis of data collected on individual F_2 plants for traits with low heritability. Our correlations between predicted and observed F_3 grain yield were similar to those reported by Robertson and Frey (1987), who evaluated the honeycomb design of Fasoulas (1973) for prediction of hill plot performance, based on individual plant data with F_{10}-derived lines. Our largest correlations based on F_2 whole plant yield were slightly smaller and those based on F_2 primary tiller yield were slightly larger than those reported by Robertson and Frey (1987). An important difference between our experiment and that of Robertson and Frey (1987) is that our experiment included segregating generations instead of F_{10}-derived lines. The genetic variation within segregating lines is one of the sources of variation that would reduce effectiveness of prediction (Wricke and Weber 1986), and the reduction should be greater for traits of low heritability. A comparison of our results with those of Robertson and Frey (1987) suggests that adjustments can be found that reduce the effect of this variation.

When we started this analysis, we expected that a prediction based on best linear unbiased prediction (Henderson 1975) of the vector of F_2 entry means, BPF2 and BF2, would be among the better methods. Although this expectation was confirmed, these methods were never significantly superior to the methods based on averages of the parents, PF2, and PF2P. The diallel from which parameters were estimated was small and contained parents selected for differences in traits related to yield. Thus, most of the requirements for estimation of variance components (Baker 1978) were not satisfied. The failure to meet assumptions required for estimation of the genetic variances may have contributed to the poorer prediction of the best linear unbiased prediction methods.

We concluded that PF2 probably is the best method for prediction of F_3 grain or biological yield from F_2 individual plant data in experiments that contain the parents and the segregating generations. This conclusion was based on the fact that the method is simple and accuracy was not significantly different from the method with the largest correlation. Prediction based on F_2 primary tiller yield would be recommended over that based on F_2 whole plant yield. PF2 was inferior to F2I for HI, a trait with higher heritability. The results indicate that although PF2 is effective for traits with lower heritabilities, it should not be used for traits with higher heritabilities. At this point, we do not know the heritability level beyond which the method should not be used.

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