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Yield Stability and Population Diversity in Oats (*Avena* sp.)

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Summary. The relationship between yield stability and populations containing various numbers and combinations of diverse homozygous and homogeneous lines was examined in an environment in which considerable variability occurs among and within growing seasons. Two groups (1,2), each containing 15 populations (4 pure lines grown singly and 11 multilines consisting of mechanical mixtures of all possible 2,3 and 4 way combinations of these 4 pure lines) were tested in each of 5 consecutive years. The pure lines in group 1 and 2 were selected on the basis of previous yield and yield variability respectively. In group 1, no significant differences were found among the 5 year means or the deviation mean squares of the 15 populations but highly significant differences among regression coefficients were present. The regression coefficients of the 4 pure lines differed considerably, indicating that this stability parameter was genetically influenced. The regression coefficients of the multilines tended towards unity regardless of the regression coefficients of the pure lines involved. In group 2, highly significant differences were found among the 5 year means, regression coefficients and deviation mean squares of the 15 populations. No consistent, predictable pattern was apparent between the mean and stability values of the pure lines and the multilines in which they were included. Differences between the 2 groups suggest that higher yield and greater stability result in the multilines if relatively high yielding pure lines are selected for inclusion. In general, the results indicated that multilines containing a number of diverse homozygous and homogeneous pure lines have satisfactory yields and enhanced yield stability. However, adequate testing of the pure lines and potential multilines over a broad range of environments is essential to determine desirable combinations.

Key words: Homeostasis – Composite Population – Stability Indexes – Genotype x Environment Interactions – Stability Parameters

Introduction

Genotype x environment interactions involving such complex quantitative characters as grain yield represent a major problem in plant improvement programs. The most promising method to reduce this factor to a minimum is to use multiline rather than genetically uniform populations (Allard and Bradshaw 1964). Technically, the degree of genetic diversity possible in multiline populations is extremely broad, ranging from restricted mixtures of isolines differing only at a single locus controlling disease resistance (Browning and Frey 1969) to diverse mixtures of pure lines widely different in many genetic traits (Jensen 1952). In most commercial species, the acceptance of multilines require that they be relatively uniform for certain characters such as height, maturity and seed factors. This problem would be of minor significance with restricted multilines but would become increasingly important as genetic diversity was widened. However, multilines containing the greatest amount of genetic diversity possible would probably be more effective in reducing the genotype x environment interaction unless the genotype x environment interaction is closely associated with disease incidence. Thus, the major difficulty in developing acceptable diverse multiline populations is the selection of pure lines which, in competition, complement each other in their response to various environments and still, in combination, satisfy the uniformity requirements.

In self-pollinated crops such as oats, the use of diverse multilines could be advantageous especially in geographical areas where extreme environmental fluctuations occur. This study was designed to evaluate grain yield stability of multiline populations containing various numbers of pure lines over a 5-year period in an area where considerable variability occurs among and within growing seasons. Substantial genetic variability among the pure lines was present but all multilines tested met necessary uniformity standards.

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Materials and Methods

For this study, 8 lines were selected from 89 lines which had been tested in this area for 6 years (1964-1969) in replicated trials. The description and derivation of this lines were reported previously (Pfahler 1971; Pfahler 1972). Since all 89 lines resulted from an increase of single plants in at least the F_6 generation of a very wide cross, each line was considered highly homozygous and homogeneous. Although much diversity existed among the 8 lines selected, all were adapted to the southeastern United States and had approximately the same maturity. No marked differences in disease resistance were apparent.

Two groups (1, 2), each containing 4 of these pure lines were developed. The lines (A, B, C, D) in group 1 were selected on the basis of producing the highest yield among the 89 lines in at least 1 out of the 6 years (1964-1969) tested: A had the highest yield in 1968 and 1969; B in 1966 and 1967; C in 1964; and D in 1965. The lines (W, X, Y, Z) in group 2 were selected on the basis of environmental variability over the 6 years (1964-1969) tested and included the complete range found among the 89 lines. The environmental variability values ($\sigma^2_{\log\ 10}$) of W, X, Y and Z were 0.0227, 0.2815, 0.4360 and 0.5391 respectively. For 5 years (1973-1977) the 4 pure lines in each group were tested singly along with the multilines which contained all possible 2, 3 and 4 way combinations of the 4 pure lines in the group. The multilines in both groups were identified by combining the letters of the pure lines included. As an example, multiline ABCD contained the 4 pure lines A, B, C and D while XYZ was a multiline containing 3 pure lines X, Y and Z. Each group was tested as a separate experiment in the same area each year.

Each year before planting, each of the 11 multiline combinations in each group was made up by mechanically mixing appropriate proportions of the pure lines involved. The proportions were determined using germination and seed weight data so that each multiline contained equal numbers of viable seeds from each pure line included.

A randomized complete block with 5 replications was used each year for each group. Each plot consisted of 3 rows, 305 cm in length with 46 cm between rows. Grain yield in g/plot was taken on the center row. The planting rate was 1 viable seed/cm of row which is aproximately equal to the recommended rate.

Within each group, the response of the 15 populations to the years tested was expressed using the procedure suggested by Eberhart and Russell (1966). With this method, the response of a population to a series of environments is expressed using 3 values; mean yield over all environments and 2 stability parameters, regression coefficient (b value) and deviation mean square. In general, a desirable population is one with the highest mean yield, a regression coefficient of unity and a deviation mean square of zero. To minimize variance heterogeneity and maximize regression linearity, a log 10 transformation of the data was made before analysis. For yield and regression coefficient, expected values for the multilines were calculated. These expected values of each multiline were the arithmetic mean of the yields or the regression coefficients of the component pure lines grown singly and were based on the assumption that the effects of the pure lines within the multiline were additive. Minimum differences for significance in the tables were obtained by means of the revised Duncan's ranges using for p only the maximum number of values to be compared (Harter 1960).

Table 1. Analyses of variance of the transformed (log 10) yield results from each group

Source of variation	d.f.	M.S. Group 1	M.S. Group 2
Population (P)	14	0.03163	0.19316[a]
Year (Y) + (PxY)	60	0.41184	1.13734
Y(linear)	1	23.15057	63.15830
PxY (linear)	14	0.05681[a]	0.25238[a]
Pooled deviations	45	0.01699	0.03442[a]
Error	300	0.01514	0.01077

[a] Significant at the 1% level

Table 2. Yield and stability values of the populations in group 1. The expected values are the arithmetic mean of the pure lines present in each multiline

Population		Mean yield		Regression coefficient		Deviation mean
Type	Composition	Actual[a]	Transformed	Observed[b]	Expected	square
Pure line	A	223.1	2.20897	1.53093		0.00379
	B	206.5	2.35705	0.87755		0.00000[c]
	C	223.2	2.29746	0.71968		0.00168
	D	216.1	2.27730	0.80325		0.00456
Multiline	AB	233.5	2.26164	1.19600	1.20424	0.00000[c]
	AC	242.9	2.30364	1.00405	1.12531	0.00121
	AD	228.9	2.27625	1.09261	1.16709	0.00000[c]
	BC	214.2	2.26014	0.09453	0.78962	0.00279
	BD	246.1	2.31857	0.97878	0.84040	0.00000[c]
	CD	220.4	2.28483	0.89005	0.76147	0.00036
	ABC	210.0	2.24257	0.97392	1.04272	0.00000[c]
	ABD	245.4	2.31081	1.08841	1.07058	0.00000[c]
	ACD	224.4	2.25416	1.09188	1.01795	0.00311
	BCD	233.0	2.29443	0.96540	0.80016	0.00000[c]
	ABCD	232.5	2.30414	0.88087	0.98285	0.00000[c]

[a] g/plot: 100g/plot = 861 kg/ha or 20 bushels/acre
[b] Minimum differences for significance are 0.19924 and 0.26248 at the 5 and 1% level respectively
[c] Calculated value less than zero but assumed zero

Results

Group 1

Statistically significant F values were found only for the P × Y (linear) interaction indicating that differences among the regression coefficients of the 15 populations were present (Table 1). According to the model, a b value of 1.0 indicates a stable population over the environments tested. However, the variability of the environments in an important factor and in large part determines the usefulness of this stability parameter. For group 1, the environmental indexes for each year were as follows, with the actual mean (g/plot) in parentheses: 1973 = 2.32277 (221.3); 1974 = 1.87515 (82.1); 1975 = 2.17342 (153.5); 1976 = 2.60576 (411.2); and 1977 = 2.44003 (283.3). The variability among years was extremely large with the mean actual yield in 1976 being almost 5 times that in 1974.

Substantial differences among the regression coefficient of the 4 pure lines grown singly were obtained (Table 2). A had a b value (1.53093) significantly higher than both the other 3 pure lines and 1.0 indicating that A had a lower than average yield in the years with generally low yields and a higher than average yield in the years with generally high yield. B, C and D with b values considerably less than 1.0 responded in an opposite manner with higher yields in low yielding years and lower yields in high yielding years. Apparently, genetic differences among the pure lines for this stability parameter are present. The observed regression coefficients of the multilines differed considerably from the arithmetic mean of the pure lines grown singly. In most multilines, the observed regression coefficients more closely approached unity rather than the arithmetic mean indicating not only that the multilines had greater stability but that the effects of the pure lines in the multiline were not additive for this parameter. However, the direction and magnitude of this effect was modified by the number and the pure lines involved.

Group 2

Highly significant F values were found for population, the P × Y (Linear) interaction and the pooled deviations (Table 1). According to the model, the most desirable population would have a high mean yield over the environments tested, a b value of 1.0 and a deviation mean square of 0. In group 2, differences among the populations were present for all these parameters.

As in group 1, the environmental indexes used to determine these parameters are vitally important. For group 2, the environmental indexes for each year were as follows, with the actual mean (g/plot) in parentheses: 1973 = 2.31598 (214.6); 1974 = 1.43065 (35.4); 1975 = 1.92413 (86.6); 1976 = 2.56572 (402.9); and 1977 = 2.37318 (240.3). The variability among years was extremely large with the mean actual yield in 1976 more than 11 times as large as that in 1974.

Significant differences were present among the mean yields of the pure lines grown singly with W having the highest yield, Y intermediate and X and Z the lowest (Table 3). The yield of most multilines was intermediate in relation to the pure lines grown singly. However, the yield of some multilines differed substantially from the intermediate value indicating that the effect of certain pure lines was not additive when included in a multiline. As an example, WY yielded about the same as Y which had an intermediate yield when grown singly but was the lower yielding pure line in this multiline. No multiline containing W which was the highest yielding pure line equalled the yield of W grown singly. However, X and Z which had approximately equal yields but were the lowest yielding among the pure lines produced a multiline XZ whose yield considerably exceeded both pure lines grown singly.

Substantial differences among the regression coefficients of the 4 pure lines grown singly were found indicating that genetic diversity for this stability parameter was present (Table 3). In relation to the multilines, differences between the observed and expected regression coefficients were quite pronounced in some cases. However, unlike group 1, the regression coefficients of the multilines did not approach unity more closely than the arithmetic mean of the pure lines grown singly. The same unpredictability was evident in the deviation mean squares (Table 3). Thus, it appears as if the mean and stability parameters of the multilines cannot be accurately predicted from those of the pure lines grown singly.

Discussion

In the model proposed by Eberhart and Russell (1966), an ideal population is one which has the highest yield over a broad range of environments, a regression coefficient or b value of unity and a deviation mean square of zero. The results of this study indicated that some multilines containing a mixture of diverse pure lines approached this ideal more closely than their component pure lines in the environments tested. Although the yield and stability parameters of the multilines were associated with those of their component pure lines grown singly, substantial differences among the pure lines when mixed in various multiline combinations were found. Apparently, an intergenotypic interaction occurs in the multilines so that the yield of each component pure line or genotype depends on the other component pure lines or genotypes in the

Table 3. Yield and stability values of the populations in group 2. The expected values are the arithmetic mean of the pure lines present in each multiline

Population		Mean yield			Regression coefficient		Deviation mean
Type	Composition	Actual[a]	Transformed		Observed[c]	Expected	square
			Observed[b]	Expected			
Pure line	W	243.0	2.32115		0.51452		0.00450[e]
	X	168.5	2.02788		1.14207		0.00000[d]
	Y	201.3	2.13472		1.06260		0.00000
	Z	161.9	1.95465		1.43749		0.03253[f]
Multiline	WX	195.6	2.17862	2.17452	0.76826	0.82830	0.00623[e]
	WY	204.9	2.19786	2.22794	0.78423	0.78856	0.00628[e]
	WZ	204.6	2.20740	2.13790	0.72288	0.97601	0.00492[e]
	XY	204.2	2.13154	2.08130	1.06544	1.10234	0.00000[a]
	XZ	188.3	2.05430	1.99127	1.21523	1.28978	0.00414[e]
	YZ	194.5	2.08579	2.04469	1.24728	1.25005	0.00292
	WXY	199.1	2.17266	2.16125	0.82346	0.90640	0.00809[f]
	WXZ	193.6	2.13796	2.10123	0.91466	1.03136	0.00068
	WYZ	198.0	2.12993	2.13684	1.03496	1.00487	0.00000[d]
	XYZ	180.1	2.04168	2.03908	1.24278	1.21405	0.00326
	WXYZ	201.7	2.14288	2.10960	1.02452	1.03917	0.00049

[a] g/plot: 100 g/plot = 861 kg/ha or 20 bushels/acre
[b] Minimum differences for significance are 0.12684 and 0.16711 at the 5 and 1% level respectively
[c] Minimum differences for significance are 0.28359 and 0.37361 at the 5 and 1% level respectively
[d] Calculated value less than zero but assumed zero
[e,f] Significantly different from zero at the 5 and 1% level respectively

multiline. This interaction among pure lines for yield have been reported in other self-pollinated cereal crops (Jensen 1952; Simonds 1962).

Many factors varying in their effect and intensity can contribute to this intergenotypic interaction in multilines (Allard and Bradshaw 1964; Allard and Jones 1969). Yield represents a final character resulting after many developmental and biochemical pathways from germination to maturity have been involved. Thus, yield can be influenced by genotypic differences in growth rate and development, plant type, disease resistance and efficiency in the uptake and utilization of water, nutrients and light. The effects of some, if not all of these factors in a multiline situation, would be amplified in a crop species such as oats in which plants are grown in close proximity to each other and as a result, interplant competition is relatively intense. Another important contributing factor, if multilines containing a mixture of diverse pure lines are involved, is that the diversity among pure lines for certain morphological and/or physiological characters would probably intensify this intergenotypic interaction. The impact of this intergenotypic interaction is further complicated if production is in a geographical area where considerable variability within and among years is present and where substantial genotype × year interactions would be expected. In this experiment, the extremely large year differences in yield were probably the result of temperature and moisture conditions during the growing season. Little or no soil type or fertility differences were expected since all experiments were conducted in the same area under similar fertility practices. Also, possible differences in disease resistance among the pure lines did not appear to be a major contributing factor since in all years, the disease spectra and their severity were very limited. At the present time, little information is available to interpret the effect of these numerous factors and their interactions on a dynamic living system in which change occurs from germination to maturity (Allard and Bradshaw 1964).

In plant improvement programs with self-pollinated, closely-spaced crop species, the reduction of the genotype × environment interaction is of prime concern. Until recently, the commercial use of homogeneous and homozygous lines which display differing degrees of individual buffering (Allard and Bradshaw 1964) to various environments has been practiced. Although individual buffering capacity has been recognized as a genetic trait (Bhullar et al. 1977; Johnson et al. 1968; Frey 1972), the development of pure lines using individual buffering as a selection criterion is an involved and complex procedure. The difficulty of selecting buffered pure lines is emphasized by the fact that isolines derived by 6 backcrosses and presumably differing in only one disease resistant locus differed significantly in yield and stability parameters although they were quite homogeneous for plant height, general

appearance, heading date and seed traits (Frey 1972). The results of the study reported here indicated that multilines containing a mixture of diverse pure lines have reduced genotype x environment interaction and thus, represent a more desirable alternative to pure lines especially in an area with considerable environmental variability. However, differences in intergenotypic interaction among the pure lines complicate the development process since testing of the pure lines and potential multilines over a broad range of environments is essential to determine the most desirable buffered multilines. This development process can be somewhat simplified by selecting only high yielding pure lines for consideration since the yield of pure lines was found to be positively correlated with yield stability (Pfahler 1972) and this study showed that the most desirable multilines resulted when relatively high yielding pure lines were included in the multiline.

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