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Stability Parameters for Comparing Varieties[1]

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ABSTRACT

The model, $Y_{ij} = \mu_i + \beta_i I_j + \delta_{ij}$, defines stability parameters that may be used to describe the performance of a variety over a series of environments. Y_{ij} is the variety mean of the i^{th} variety at the j^{th} environment, μ_i is the i^{th} variety mean over all environments, β_i is the regression coefficient that measures the response of the i^{th} variety to varying environments, δ_{ij} is the deviation from regression of the i^{th} variety at the j^{th} environment, and I_j is the environmental index.

The data from two single-cross diallels and a set of 3-way crosses were examined to see whether genetic differences could be detected. Genetic differences among lines were indicated for the regression of the lines on the environmental index with no evidence of nonadditive gene action. The estimates of the squared deviations from regression for many hybrids were near zero, whereas extremely large estimates were obtained for other hybrids.

GENOTYPE-environment interactions are of major importance to the plant breeder in developing improved varieties. When varieties are compared over a series of environments, the relative rankings usually differ. This causes difficulty in demonstrating the significant superiority of any variety. This interaction is usually present whether the varieties are pure lines, single-cross or double-cross hybrids, top crosses, S_1 lines, or any other material with which the breeder may be working. Comstock and Moll (2) have shown statistically the effect of large genotype-environment interactions in reducing progress from selection.

Stratification of environments has been used effectively to reduce the genotype-environment interaction. The region for which a breeder is developing improved varieties can often be so subdivided that all environments in the subregion are somewhat similar. This stratification usually is based on such macro-environmental differences as temperature gradients, rainfall distribution, and soil types. However, even with this reducing genotype-environment interactions by the stratification of environments, other methods need to be investigated. One such method would be to select stable genotypes that interact less with the environments in which they are to be grown. If stability of performance, or the ability to show a minimum of interaction with the environment, is a genetic characteristic, then preliminary evaluation could be planned to identify the stable genotypes. With only the more stable genotypes remaining for the final stages of testing, the breeder would be greatly aided in his selection of superior genotypes. However, selection for stability is not possible until a model with suitable parameters is available to provide the criteria necessary to rank varieties for stability. The purpose of this paper is to propose such a model and to illustrate its usefulness.

REVIEW OF LITERATURE

The use of genetic mixtures rather than homogeneous, or pure-line, varieties has been suggested as a means to reduce genotype-environment interactions. Jensen (5) suggested that a multiline variety of oats as compared to pure-line varieties would possess greater stability of production, broader adaptation to environment, and greater protection against disease. Allard and Bradshaw (1) suggested that heterozygous and heterogeneous populations offer the best opportunity to produce varieties which show small genotype-environment interactions. They used the term "individual buffering" for individuals where the individual members of a population are well buffered such that each member of the population is well adapted to a range of environments, and "population buffering" if the variety consists of a number of genotypes each adapted to a somewhat different range of environ-

$$T_{12\cdot 3} = \frac{}{2}\,(S_{13} + S_{23}).$$

$$\text{The variance of } \frac{1}{2}\,(S_{13} + S_{23}) = \text{Var}\,\frac{1}{2}\,(S_{13} + S_{23})$$

$$= \frac{1}{4}\,[\text{Var}\ (S_{13}) + \text{Var}\ (S_{23})].$$

When S_{13} and S_{23} are grown in replicated trials at several locations,

$$\text{Var}\ (S_{13}) = \text{Var}\ (S_{23}) = \sigma^2 + r\sigma^2_{ge},$$

where σ^2 is the experimental error, σ^2_{ge} is the genotype-environmental variance of single crosses and r is the number of replications. Then,

$$\text{Var}\ (\hat{T}_{12\cdot 3}) = \frac{1}{2}\,\sigma^2 + \frac{r}{2}\,\sigma^2_{ge}.$$

But if S_{13} and S_{23} are mixed in the same plot and grown as a single entry,

$$\text{Var}\ (\hat{T}_{12\cdot 3}) = \sigma^2 + r(\sigma^2_{ge}/2).$$

Rowe and Andrew (7) found the variance component caused by the variety-environment interactions for yield, ear height, and plant height for five inbred lines of maize and for the 10 possible F_1 entries to be much greater than for the segregating entries derived from these lines. They found no relation between this variance component and the level of heterozygosity of the entries.

Genotype-environment interactions have been of concern to plant breeders for many years. Various procedures have been used to characterize individual varieties for behavior in varying environmental conditions. Performance tests over a series of environments, when analyzed in the conventional manner, give information on genotype-environment interactions, but give no measurement of stability of individual entries. Plaisted and Peterson (6) presented a method to characterize the stability of yield performance when several varieties were tested at a number of locations within 1 year. A combined analysis of variance over all locations was computed for each pair of varieties, n(n-1)/2 pairs for n varieties; and an estimate of σ^2_{VL} was obtained for each pair. Each variety occurred in n-1 analyses, and an arithmetic mean of the σ^2_{VL} estimates was obtained for each variety. The variety with the smallest mean value would be the one that contributed the least to variety × location interactions and, thus, would be considered the most "stable" variety in the tests. If a large number of varieties were tested, this would call for a large number of analyses, n(n-1)/2 for in varieties.

...ironments,

β_i is the regression coefficient that measures the response of the i^{th} variety to varying environments, δ_{ij} is the deviation from regression of the i^{th} variety at the j^{th} environment, and I_j is the environmental index obtained as the mean of all varieties at the j^{th} environment minus the grand mean

$$[I_j = (\sum_i Y_{ij}/v) - (\sum_i \sum_j Y_{ij}/vn)],\ \sum_j I_j = 0.$$

An index independent of the experimental varieties and obtained from environmental factors such as rainfall, temperature, and soil fertility would be desirable. Our present knowledge of the relationship of these factors and yield does not permit the computation of such an index. Until we can measure such factors in order to formulate a mathematical relation with yield, the average yield of the varieties in a particular environment must suffice. However, the varieties must be grown in an adequate number of environments covering the full range of possible environmental conditions if the stability parameters are to provide useful information.

The first stability parameter is a regression coefficient estimated in the usual manner:

$$b_i = \sum_j Y_{ij} I_j / \sum_j I_j^2 .$$

[Finlay and Wilkinson (4) also have used this regression coefficient in studying the adaptation of barley varieties].

The appropriate analysis of variance is given in Table 1. With this model, the sums of squares due to Environments and Variety × Environments are partitioned into Environments (linear), Varieties × Environments (linear) and Deviations from the regression model.

The performance of each variety can be predicted by using the estimates of the parameters where $\hat{Y}_{ij} = \overline{x}_i + b_i I_j$ where $\overline{x}_i$ is an estimate of the μ_i. The deviations $[\hat{\delta}_{ij} = (Y_{ij} - \hat{Y}_{ij})]$ can be squared and summed to provide an estimate of another stability parameter $(\sigma^2_{d_i})$;

$$s^2_{d_i} = [\sum_j \hat{\delta}^2_{ij}/(n-2)] - s^2_e/r,$$

where s^2_e/r is the estimate of the pooled error (or the variance of a variety mean at the j^{th} location) and:

$$\sum_j \hat{\delta}^2_{ij} = [\sum_j Y^2_{ij} - \frac{Y^2_{i.}}{n}] - (\sum_j Y_{ij} I_j)^2 / \sum_j I_j^2 .$$

This model provides a means of partitioning the genotype-environment interaction of each variety into two parts:

(1) the variation due to the response of the variety to

Table 1. Analysis of variance when stability parameters are estimated.

Source	d.f.	S.S.	M.S.
Total	nv-1	$\sum_i \sum_j Y^2_{ij} - C.F.$	
Varieties (V)	v-1	$\frac{1}{n} \sum_i Y^2_{i.} - C.F.$	MS_1
Environments (Env)	n-1 } v(n-1)	$\sum_i \sum_j Y^2_{ij} - (\sum Y^2_{i.}/n)$	
V× Env	(v-1)(n-1) }		
Env (linear)	1	$\frac{1}{v} (\sum_j Y_{.j} I_j)^2 / \sum_j I^2_j$	
V × Env (linear)	v-1	$\sum_i [(\sum_j Y_{ij} I_j)^2 / \sum_j I^2_j]$ - Env(linear)S.S.	MS_2
Pooled deviations	v(n-2)	$\sum_i \sum_j \delta^2_{ij}$	MS_3
Variety 1	n-2	$\left[\sum_j Y^2_{1j} - \frac{(Y_{1.})^2}{n}\right] - (\sum_j Y_{1j} I_j)^2 / \sum_j I^2_j$	
⋮	⋮	⋮	
Variety v	n-2	$\left[\sum_j Y^2_{vj} - \frac{Y^2_{v.}}{n}\right] - (\sum_j Y_{vj} I_j)^2 / \sum_j I^2_j = \sum_j \delta^2_{vj}$	
Pooled error	n(r-1)(v-1)		

Table 2. Analyses of two single cross diallel sets grown in North-Central Iowa.

Source	1945-47		1948-51	
	d.f.	M.S.	d.f.	M.S.
Env (linear)	1	175,331.2	1	114,305.8
Single Crosses (SC)	54	187.2**	27	192.2*
General (G)	10	611.7**	7	296.6**
Specific (S)	44	90.8**	20	155.7*
SC× Env (linear)	54	83.1**	27	84.7
G × Env (linear)	10	191.8**	7	142.0*
S × Env (linear)	44	58.3	20	43.1
Pooled Deviations	330	45.5**	280	60.8**
Average Error		11.2		30.0

* Significant at the 5% level. ** Significant at the 1% level.

varying environmental indexes (sums of squares due to regression); and (2) the unexplainable deviations from the regression on the environmental index.

In the past, the term "stable variety" often has been used to mean a variety that does relatively the same over a wide range of environments. This means that a "stable variety" by this definition performs relatively better under adverse conditions and not so well in favorable environments. Analyses of several sets of data from Iowa State University maize yield trials have indicated that hybrids with a regression coefficient less than 1.0 ($b_i < 1.0$) usually have mean yields ($\overline{x_i}$) below the grand mean. In situations where production does not give a surplus that can be stored, or where long storage is not possible, such a variety may still be the most desirable. However, under conditions such as exist for maize in the United States, the breeder usually wants a variety that does above average in all environments. Hence, he desires a variety with a high mean ($\overline{x}_i$), unit regression coefficient ($b_i = 1.0$) and the deviations from regression as small as possible ($s^2_d = 0$). Hence, the definition of a

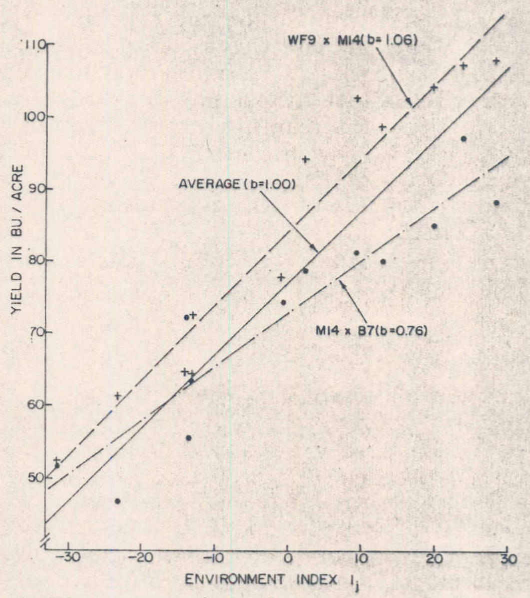

Figure 1. The response of two single crosses to varying environments in North-Central Iowa in 1948-51.

ferences among varieties in their response to a varying environmental index, the F value will be larger. Difficulties arise in obtaining tests of significance when variety deviations are not homogeneous. In these cases, the approximate *t* tests between pairs of effects with different variances [see Steele and Torrie (9)] can be used. However, the F test of differences among varieties (MS_1/MS_3) may be no less valid than the usual F test [MS_1/MS (Variety × Environments)].

The hypothesis that there are no genetic differences among varieties for their regression on the environmental index

$$H_o: \beta_1 = \beta_2 = \ldots = \beta_v$$

can also be tested approximately by the F test,

$$F \approx MS_2/MS_3.$$

The hypothesis that any regression coefficient does not differ from unity can also be tested by the appropriate *t* test. An approximate test of the deviations from regression for each variety can be obtained,

$$F \approx (\sum_j \hat{\delta}^2_{ij}/n\text{-}2)/\text{Pooled error}.$$

The disadvantage of using the average yield of all varieties in a particular environment as the environmental index is evident when the distribution of such tests is considered. If an independent index based on environmental factors could be obtained and de-

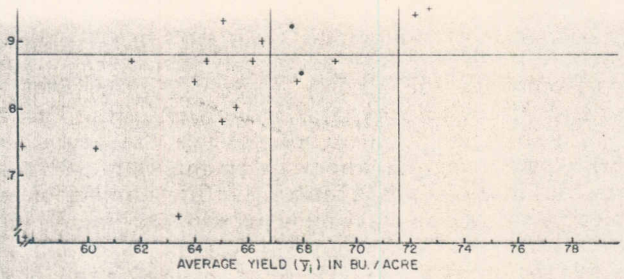

Figure 2. The relation of yield and stability of 55 single crosses grown in North-Central Iowa in 1945-47. Estimates of s^2_d were significant (P = .05) only for those hybrids indicated by +.

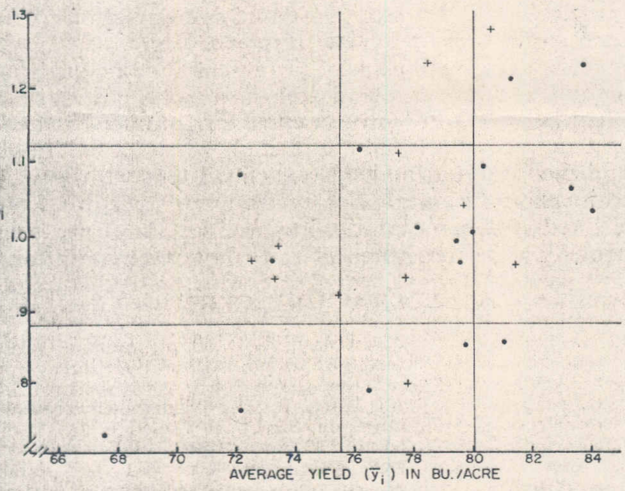

Figure 3. The relation of yield and stability of 28 single crosses grown n North-Central Iowa in 1948-51. Estimates of s^2_d were significant (P = .05) only for those hybrids indicated by +.

squares are not significantly greater than the respective deviation mean squares, there is no evidence that regression coefficients differ because of nonadditive gene action. However, the General × Env (linear) mean squares were significant (P ≈ .05) for both diallels. Figure 1 illustrates the differences in stability of two single crosses and their performance in relation to the average of the test (shown by the solid line). WF9 × M14 is a very desirable hybrid because its performance is uniformly superior ($b = 1.06$, $s^2_d = 0$ and $\bar{x} = 107\%$ of $\bar{\bar{x}}$). In contrast, M14 × B7 is expected to equal or exceed average performance only under very unfavorable conditions ($b = .76$, $s^2_d = 5$ and $\bar{x} = 93\%$ of $\bar{\bar{x}}$).

Figures 2 and 3 give a graphic summary that may be useful in selecting stable hybrids. The vertical

[illegible]					.99	23
[illegible]	67.7	.93	36	--	--	--
R4-66	66.8	.96	45	--	--	--
I205	63.3	.88	53	--	--	--
Average	69.2	1.00	35	77.3	1.00	31
LSD (.05)	2.1	.10	--	2.3	.12	--

Table 4. Analysis of 18 three-way crosses and three single-cross testers grown at 2 locations in North-Central Iowa in 1958-62.

Source	d.f.	M.S.
Total	209	
Env (linear)	1	32,122.7
Entries	20	257.6**
SC vs T-WC	1	142.2
SC	2	52.4
T-WC	17	288.6**
Tester (T)	2	110.7
Lines (L)	5	640.2**
T × L	10	148.4*
Entries × Env (linear)	20	96.6
(SC vs T-WC) × Env (linear)	1	.3
SC × Env (linear)	2	4.2
T-WC × Env (linear	17	113.2*
T × Env (linear)	2	36.7
L × Env (linear)	5	251.6**
T × L X Env (linear)	10	59.3
Deviations	168	64.6**
SC	24	76.4**
T-WC	144	62.6**
Error (Average)		28

* Significant at the 5% level. ** Significant at the 1% level.

Table 5. Average performance of six inbred lines with three testers in North-Central Iowa 1958-62.

Line	$\bar{x}$, bu/A	$\bar{b}$	$\bar{s}^2_d$
B54	118	1.07	57**
N22A	118	.76	29*
B37	117	.78	22
B46	115	.97	61**
B42	113	1.01	28*
W22	106	1.40	10
Average	114	1.00	34
LSD	4	.33	--

* Significant at the 5% level. ** Significant at the 1% level.

lines are one standard deviation above and below the grand mean, whereas the horizontal lines are one standard deviation above and below the average slope ($b = 1.0$). All estimates of s^2_d significantly greater than zero (P ≈ .05) are shown by +. The single cross with above-average performance and satisfactory stability in the 1945-47 diallel is WF9 × Oh28 (indicated by the dot in the center section on the right, Figure 2). WF9 × M14 had above-average performance over environments, but the estimate of s^2_d was 30. In the 1948-51 diallel, two single crosses gave high yields with stability—WF9 × M14 and WF9 × W22 (indicated by the dots in the center section on the right, Figure 3).

The average performances of the lines in crosses are given in Table 3. The line Hy performed consistently better in favorable environments (b=1.15 and 1.15), whereas Os420 performance was relatively better in less favorable environments (b = .95 and .88).

Data for a set of three-way crosses involving three single-cross testers and six inbred lines were available

Table 6. Performance of the testers (single crosses) compared with their average testcross performance (three-way crosses) in North-Central Iowa 1958-62.

Single Cross	Tester			Testcrosses		
	$\bar{x}$, bu/A	b	s^2_d	$\bar{x}$, bu/A	$\bar{b}$	$\bar{s}^2_d$
WF9 × M14	116	1.01	9	115	1.06	41**
WF9 × Oh43	115	.95	56**	113	1.00	36**
WF9 × B14	119	1.06	81**	115	.94	27**
Average	117	1.01	49**	114	1.00	35**
LSD	7	.57	--	3	.23	--

* Significant at the 5% level. ** Significant at the 1% level.

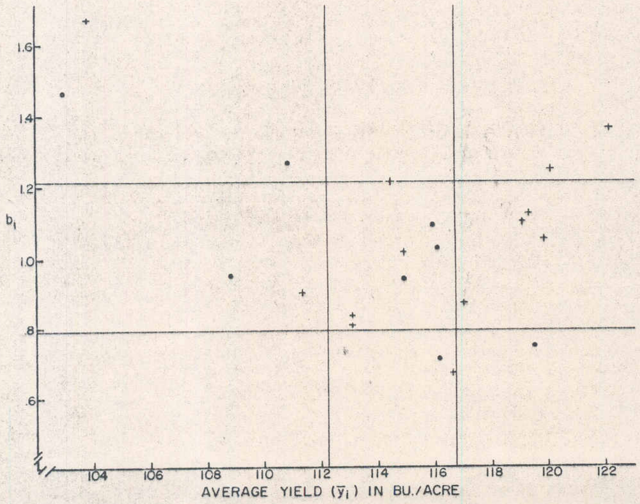

Figure 4. The relation of yield and stability of 18 three-way crosses and three single crosses grown in North-Central Iowa in 1958-62. Estimates of s^2_d were significant (P = .05) only for those hybrids indicated by +.

for two locations in North-Central Iowa for 1958-62. The analysis of variance is presented in Table 4. The difference in the response of three-way crosses to varying environments was due to the different responses of the lines as indicated by the large Lines × Env (linear) mean square. As with the single-cross data, there was no indication that regression coefficients (b_i) differed because of nonadditive gene action, since the Tester × Line × Env (linear) mean square was similar to the three-way cross pooled deviation. As shown in Table 5, three-way crosses involving W22 performed much below average in unfavorable environments, whereas N22A and B37 did extremely well under less favorable conditions. The performance of B37 in three-way crosses was much more predictable than hybrids involving B54 or B46, as indi- presented in Figure 4. None of the three-way crosses falling in the center section to the right had a nonsignificant deviation mean square. However, the hybrid (WF9 × M14) N22A ($\bar{x}$ = 119.8, b = 1.05, s^2_d = 41) is the most nearly acceptable even though s^2_d is larger than desirable. (WF9 × B14) B37 ($\bar{x}$ = 119.5, b = .74, s^2_d = 0) would be especially good under less favorable environments but not as good under favorable conditions. The hybrid with the highest mean yield (WF9 × M14) B37 is unacceptable for both stability parameters ($\bar{x}$ = 122.2, b = 1.37, s^2_d = 103).

Although the inbred lines of maize in this experiment differed in their average responses to varying environments, the Variety × Env (linear) sum of squares was not a very large proportion of the Variety × Environmental interaction. Hence, the second stability parameter (s^2_d) appears very important. Because the variance of s^2_d is a function of the number of environments, several environments with minimum replication per environment are necessary to obtain reliable estimates of s^2_d. However, a good estimate of the regression coefficients can be obtained from a few environments if they cover the range of expected responses. Because large deviations were obtained for some lines and crosses, the data were fit to a quadratic model. The reduction in the deviation mean square was negligible, however, so that large deviations were not caused by a quadratic response.

Since the distribution of rainfall is a major environmental factor, early and late dates of planting can often be used to obtain an extra environment at each location. Similarly, low and high plant populations, and medium and high rates of fertilizers, can be used to increase the number of environments possible from a fixed number of locations, and at the same time provide a greater range of environmental conditions.

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