

ENVIRONMENTAL INDICES FOR THE ANALYSIS OF GENOTYPE X ENVIRONMENT INTERACTION IN MAIZE

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ABSTRACT - One independent (physical) and two partially independent (biophysical) indices were compared with a dependent (biological) index for two sets of yield trials in maize (Zea Mays L.). The object was to investigate whether the environmental response of maize genotypes would be affected by different measures of the environment. The four types of indices gave remarkably similar partitioning of the G X E interaction. Although magnitude of the regression coefficients (b-values) changed markedly with change in type of environmetal index, ranking of the genotypes was little affected. Therefore, interpretation of the data was not affected by the type of environmental index used to assess the environment. KEY WORDS: Zea mays L.; Environmental response; Phenotype stability; Joint regression analyis.

INTRODUCTION

Failure of genotypes to respond consistently to variable environmental conditions is termed genotype x environment (G X E) interaction. Because G X E interaction reduces the predictability of genotypic performance from phenotypic measurement, it is a common practice of plant breeders to grow a set of genotypes in different environments. Data collected from such trials are subjected to one or more statistical analyses. In the last two or three decades, analysis of variance followed by joint regression analysis is the most common approach to the problem. In joint regression analysis, genotypic means in each environmental are regressed on environmental indices, which are obtained as the environmental means per se, or as environment means minus the grand mean. The linear regression coefficient (b₁) and the deviation from linearity (s2,) for each genotype are then compared with theoretical values to determine significant deviations (YATES and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Perkins and Jinks, 1968). This technique has been used to partition G X E interaction in many crop species and a lot of information has accumulated in the literature in the last two or three decades (see for example Freeman, 1973).

This technique, however, has the serious statistical flaw that the «independent» variables in the regression analyses are not truly independent of the phenotypic variables regressed on them. Some ways in which independent environmental variables might be obtained were proposed by Freeman and Perkins (1971) and these were grouped into four major categories by Fripp (1972); that is: - 1) trial genotypes and those for the development of environmental indices as different replicates of the same material; - 2) inclusion of an assessment set of genotypes which are closely related to trial genotypes; - 3) inclusion of a single, or a limited number of assessment genotypes; and 4) use of independent, physical measures.

Several studies have been conducted in which the different independent biological measures of the environment (i.e., 1-3 above) were compared with the standard practice; i.e., use of trial genotypes as measures of the environment (Freeman and Perkins, 1971; Fripp and Caten, 1971; Fripp, 1972; Perkins and Jinks, 1973; Fatunla and Frey, 1976). Most of these studies led to the conclusion that the analyses differed little in ranking genotypes for environmental response. There are, however, only a few studies in which independent physical environmental indices have been compared with the standard practice. FRIPP (1972) compared both biological and physical measures of the environment in the study of environmental response of growth rate in a fungus, Schizophyllum commune. He concluded that «the partitioning of the between environments and genotype X environment sums of squares, the ranking of the b, values, and the amount of variation accounted for by the reegressions are very similar» for all methods studied. However, there was a tendency for linearity of the regression to decrease as the measures of the environment became more distantly related to the trial genotypes.

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In our study, an independent physical index and two partially independent (biophysical) measures of the environment were compared with the standard index for two sets of yield trials in maize (Zea mays L.).

MATERIALS AND METHODS

Grain-yield data used in this study were obtained from two sets of experiments conducted at the Teaching & Research Farm of the University of Ife, Ile-Ife, Nigeria; a tropical rainforest location (7° 28'N, 4° 33'E, approx. 244 m altitude). In expt. I, 10 cultivars of maize were

planted at bi-weekly intervals from 2 March to 25 May, 1978 in a split-pot design with plant densities (18,235; 26,667 and 44,444 plants/ha) as main plots and cultivars as subplots. Each planting was replicated twice. In expt. II, 16 genotypes, consisting 5 open-pollinated cultivars and 11 varietal hybrids, were grown in randomized complete-block designs on seven irregularly spaced planting dates form 31 March to 8 September, 1981. Each planting had 4 replicates. Details of cultural practices were reported previously (FAKOREDE, 1985). Harvesting was done by hand, ears shelled mechanically and grain yield was converted to t/ha at 15% moisture content.

Conventional analysis of variance (AOV) was done each year. Because density effect was not significant in 1978, a second ACV was performed in which the 3 densities were treated as additional replicates (i.e., the second AOV had 6 reps.) and this was used in the GXE analyses for that year.

The four types of environmental indices considered were (i) biological or standard index, (ii) biophysical I, (iii) biophysical II, and (iv) physical. Both biophysical index I and II were obtained each year by regressing environmental mean yield on several climatic variables in a stepwise multiple regression model (for details, see FAKOREDE and OPEKE, 1985). Observed values for the first climatic variables (X₁) identified in the model were substituted into the prediction equation to obtain the predicted yield for each environment and this was used as biophysical index I; i.e.;

$$\hat{Y} = m + b_1 x_1 \dots (1).$$

Predicted yield from the first two variables $(x_1 \text{ and } x_2)$ identified in the regression model were used as biophysical index II; i.e. $Y = m + b_1x_1 + b_2x_2$(2).

For the physical index, value of x_1 for each environment was used *per se*. In all cases, environmental indices (I_j) were computed as the deviation from the grand mean for all values in each types of environmental assessment.

The $G \times E$ analysis of EBERHART and RUSSELL (1966) was used. This model can be represented as:

$$Y_{ij} = \bar{x} + b_i I_j + d_{ij}$$
(3)

were Y_{ij} is mean yield of the ith genotype at the jth environment; b_i is the regression of Y_{ij} on I_j ; d_{ij} is the deviation from regression of the ith genotype at the jth environment. In this model,

$$b_i = \xi_i \, \gamma_{ij} \, I_j / \xi_j \, I_j^2$$

and

$$s_{d_i}^2 = \xi_i d_{ij}^2 / E-2 = \xi_j (Y_{ij} - y_i - b_i I_j)^2/E-2....(5)$$

where y_i is the mean yield of the ith genotype over all environments and E is number of environments.

In addition to b_i and $s_{d_i}^2$ values, following statistics were used to compare the different types of environmental indices.

- (i) $r_E = \text{correlation values between two indices.}$ Fripp (1972) used ϵ_j and Z_j to represent dependent and independent indices, respectively.
- (ii) $b_A = average regression coefficient, which was obtained by regressing average yield in each environment on environmental indices.$
- (iii) $t_i = \text{approximate t-value for testing whether } b_i \text{ differs from } b_A; \text{ each t value was calculated as } t_i = \frac{b_j b_A}{\sqrt{s_{dj}^2/\xi I_j^2}} \text{ and was compared with table t at 0.05 level of probability and } s_{di}^2 \text{ degrees of freedom.}$
- (iv) $r_A{}^2 = coefficient$ of determination for the average regression coefficient, a convenient mean of assessing the degree of linearity obtained.
- (v) $r_s = \text{Spearman's rank correlation coefficient between the corresponding } s_{d_i}^2$ values from two analyses.

RESULTS 💆

Regression of environmental mean yield on several weather factors in a stepwise fashion produced the results summarized in Table 1. Each year a single variable explained over 80% of the yield variation, and addition of a second variable improved the fit but little; only increases of 6 and 3% for the two years.

TABLE 1 - Prediction equations for the regression of grain yield on weather variables in 1978 and 1981

Year	Prediction equation	R ²
1978	$\hat{Y} = 50.92 - 0.58X_1$	0.84
	$\hat{Y} = 92.92 - 1.02X_1 - 0.17X_2$	0.90
1981	$\hat{Y} = 14.00 - 0.008X_3$	0.89
	$\hat{Y} = 19.67 - 0.007X_3 - 0.38X_4$	0.92

X₁ = maximum relative humidity, X₂ = potential evaporation

 X_3 = accumulated heat units and X_4 = minimum temperature.

The joint regression analyses for the yield data are presented in Table 2. As expected, highly significant genotypic differences occured each year. Both years, the E linear (equivalent to the "combined regression" source of variation of Freeman and Perkins, 1971) was highly significant for all types of environmental indices and accounted fot the largest proportion of environment + (G x E). In 1978, the G x E linear (equivalent to "heterogeneity

TABLE 2 - Mean squares from four methods of stability analysis of variance for grain yield of maize in two years

			Mean squares					
Source	df	Biolo- gical	Biophy- sical I	Biophy- sical II	Physical			
			1978					
Genotype (G)	9	135.01**	135.01**	1 35.01**	135.01**			
Environ. + (GxE)	60	1.12						
Elinear	1	58.08**	50.34**	54.05**	50.34**			
GxElinear	9	0.42**	0.41	39	0.41			
Pooled dev.	50	0.11	0.27	0.20	0.27			
Pooled error	315	0.11	6.20	6.20	6.20			
			1981	· -				
Genotypes (G)	15	1.52**	1.52**	1.52**	1.51**			
Environ. + (GxE)	96	1.14**	= = :		_			
E. linear	1	86.38**	76.38**	74.51**	76.69**			
GxE _{linear}	15	0.30	0.25	0.26	0.25			
Pooled dev.	80	0.23**	0.36**	0.39**	0.36**			
Pooled error	315	0.172	0.172	0.172	0.172			

^{*, **} Significant at 0.05 and 0.01 levels of probability, respectively.

of regression" of Freeman and Perkins) for the biological index and the pooled deviations for all indices in 1981 were highly significant. These two items plus the E linear showed that both years, the four types of indices gave remarkably similar partitioning of the G x E interaction. Relative to the biological index, however, mean squares associated with E linear and G x E linear tended to decrease, whereas those associated with pooled deviations increased for the other indices. Our data corroborate those of Fripp (1972) who found a tendency for the heterogeneity of regression to decrease as the environmental indices became less directly related to the trial data.

Except for the biological index in 1978, the G x E linear source of variation was not significant (Table 2). Generally, the E linear accounted for the largest proportion of environment + (G x E) source of variation regardless of type of index used (75 to 86% in 1978 and 68 to 79% in 1981). Usually, the G x E linear explained only 3-6% of the environ. + (G x E) sum of squares even for the biological index that was significant in 1978 (Table 3). Therefore, within the limits imposed by sampling error, most of

TABLE 3 - Average linear regression coefficients (b_A) and the proportions of environment + (GxE) sum of squares associated with the regression parameters for four environmental indices of maize in two years

	Biological index		Biophysical index I		Biophysical index II		Physical index	
				S		Q ²	-	
Parameter	1978	1981	1978	1981	1978	1981	1978	1981
b _A	1.00	1.00	0.984	1.572	1.007	1.112	0.575	0.013
Proportion of SS due	to							
Elinear (i.e. r _A)	0.86	0.79	0.75	0.70	0.80	0.68	0.75	0.70
G x E _{linear}	0.06	0.04	0.05	0.03	0.05	0.04	0.05	0.03
Pooled deviations	0.08	0.17	0.20	0.26	0.15	0.29	0.20	0.26

the G x E interaction for the genotypes under study was explained by the E linear item and the linear response to environment was generally homogeneous among genotypes for each of the different indices investigated. Whereas absolute magnitude of the b_A values changed markedly with change in type of environmental index (Table 3), ranking of the genotypes for s²_{di} was little affected (Table 4) and rank correlation coefficients of s²_{di} values among the indices were high (Table 5). Similarly to Fripp's data, the physical index gave unusual b_A values (Table 3), particularly in 1981 when accumulated heat units was the physical index. For our data, therefore, a unit change in the physical index would be expected to produce less than a unit change in grain yield.

The $r_A{}^2$ values were generally larger for the biological index than the others (Table 3). As would be expected, $s_{\rm d}{}^2$ values were generally smallest for the biological index and were about equal for biophysical I and physical indices (Table 4). Infact, for all parameters considered here except b_A (i.e., mean square, rank values, $s_{\rm d}{}^2$ and r_A) biophysical I and physical indices had nearly the same values. Rank correlations for the $s_{\rm d}{}^2$ (Table 5) also indicated a near-perfect-to-perfect relationship between the two indices.

The similarity between the biophysical I and physical indices was not surprising. Biophysical index I was derived from the same physical factor (x) used as the physical index by the linear equation Y = a + bx where a and b are fixed quantities. Therefore the ranking of environments would not be excepted to change whether they were identified by x (physical index) or Y (biophysical index I).

To test the adequacy of the physical variables in our study, we carried out possible regressions of the environmental indices, and the results are presented in Table 5. In 5 of 6 cases, the biophysical and physical indices $(Z_i$'s) accounted for only 55-72% of the variation in the biological index $(\in_i$'s) whereas the Z_i 's explained 77-100% of the variation inter se.

DISCUSSION

The primary objective of this study was to compare two partially dependent (biophysical) and one independent (physical) measures of the environment with a dependent (biological) index. Results of the analyses clearly showed that the four indices led to the same interpretation. In other words, partitioning of the $G \times E$ sum of squares, the r_A^2 values, and ranking

	Mean Yield	Biological	index	Biophysical	index	I Biophysical	index II	Physical	index
GENOTYPE	(t/ha)	$s_{\mathrm{d_i}}^2$	rank	$s_{\rm d_{\it i}}^2$	rank	$s_{\mathrm{d_i}}^2$	rank	$s_{\mathrm{d_i}}^2$	rank
FARZ 27 x FARZ 26	3.34	1464	12	3499	8	4032*	6	3440	9
FARZ 34 x FARZ 26	2.56	4367*	2	6417**	2	8059**	1	6383**	2
FARZ 34 x TZSR-W	3.12	2171	8	4200*	5	3809*	7	4152*	5
FARZ 34 x FARZ 27	3.12	1635	10	1475	16	2054	16	1442	16
TZSR-W x TZSR-W-1	2.63	2306	7	2806	11	2824	13	2929	10
FARZ 27 x TZSR-W	3.11	808	15	2875	10	4208*	5	2858	11
FARZ 26 x TZSR-W	2.67	836	14	3430	9	3035	11	3393	8
FARZ 26 x TZSR-W-1	2.65	1953	13	3688	6	3358	9	3645	6
FARZ $7 \times TZE_4$	2.47	3044	4	5355**	4	5009*	3	5194**	4
FARZ 23 x TZE ₄	2.74	1521	11	1791	15	2887	12	1746	15
TZSR-Y-1 x TZE ₄	2.34	2893	6	2536	12	3318	10	2522	12
FARZ 27	2.55	683	16	2179	13	2360	14	2137	13
FARZ 34	2.57	4321*	3	6054**	3	4965*	4	6020**	3
FARZ 7	2.12	2141	9	1936	14	2093	15	1925	14
FARZ 23	1.93	2991	5	1936	7	3702	8	3510	7
ΓZE_4	1.55	5339**	1	6554**	1	6052**	2	6555**	. 1

¹ Actual values were multiplied by 10000 to eliminate decimal points.

^{*, **} Significant at 0.05 and 0.01 levels of probability, respectively

TABLE 5 - Spearman's rank correlation coefficients of s_{3i}^2 values (upper diagonal) and coefficients of determination from all possible regressions among \in i and Z_i values (lower diagonal) for grain yield of maize in two years

	р и			**************************************		
		Biological	Biophy- sical I	Biophy- sical II	Physical	
Biological					A	
	1981		0.609*	0.553*	0.622*	
Biophysical						
I	1978	0.554*				
	1981	0.666*		0.897**	0.994*	
Biophysical						
II	1978	0.721**	0.801**			
	1981	0.904**	0.767**		0.859**	
Physical						
	1978	0.555*	0.998**	0.799**		
	1981	0.666**	1.000**	0.769**		

^{*, **} significant at 0.05 and 0.01 levels of probability, respectively.

of genotypes for s_d² values were identical for the four indices. Similarly to conclusions reached by Fripp (1972), none of the methods used in assessing the environment in these yield trials can unconditionally be said to be the best. Therefore, our data showed that use of the dependent biological index in analysis of G x E interaction provides satisfactory, agronomically acceptable results. Actually, there was a tendency for less of the G x E

component to be explained by the linear regressions of non-dependent relative to dependent indices: that is, the r_A^2 values were lower, pooled deviation mean squares and $s_{d_i}^2$ were larger, and in 1981 more of the $s_{d_i}^2$ were significant for biophysical and physical indices than the biological index. As noted by F_{RIPP} (1972), this trend suggests that the environmental indices should be as closely related to the trial genotypes as possible. However, there could be an advantage in using indices that detect more significant $s_{d_i}^2$ than others. Significant $s_{d_i}^2$ indicates a non-linear response to the environment or interaction with specific environment(s) by a genotype. In the latter case, use of independent physical measures in assessing the production environment might aid the isolation of such specific environmental factors.

The present data are probably not typical of what occurs in many practical situations. First, "environments," used here were planting dates, and response of crops to planting dates are fairly more predictable than to environments involving locations and years. However, use of planting dates in studying effect of weather factors on yield has the advantage of eliminating the confounding effects of other non-quantifiable environmental factors (e.g. soil type) usually associated with different locations. Second, environmental variables considered here are only a few meso-climatic factors (Fakorede and Opeke, 1985), two of which were actually involved in developing the indices. The crop micro-climate should be more directly related to yield than those used here.

Several other environmental factors could be used that would make the Z's and E i's respond to different environments in the same way. Altitude index (Eberhart et al., 1973), moisture-stress index (Corsi and Shaw, 1971) and drought index (Sopher et al., 1973) are some of the environmental factors that could be used in the analysis of G x E interaction in maize. Sprague and Eberhart (1977) stated that when such indices are available, the predicted performance for each genotype in a specific environment is often of greater value than a large series of trials in environments not indexed. However, identification of the specific factor(s) primarly causing G x E interaction is a major limitation to the successful use of physical measures to assess the environment. Hardwick and Wood (1972) suggested the use of multiple regressions to identify such variables. FAKOREDE and OPEKE (1985) used correlations, stepwise multiple regressions and path-coefficent analyses to identify the variables primarily affecting grain yield under the conditions of the present study. Subsequently, one or two most important variables were used to construct one-figure environmental indices evaluated herein.

In conclusion, our data showed that interpretation of the environmental responses of a set of genotypes was little affected by the type of environmental indices used to assess the environment.

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