Theor Appl Genet (1993) 87:409–415

THEORETICAL AND APPLIED GENETICS

The area under the function: an index for selecting desirable genotypes

C. M. Hernandez[1,*], J. Crossa[2], A. Castillo[3]

[1] Universidad de Colima, Apdo. Postal 36, Tecomán, Colima, México
[2] International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, México D.F., México
[3] Centro de Estadística y Cálculo, Colegio de Postgraduados 56230, Chapingo, México

Received: 11 July 1992 / Accepted: 20 April 1993

Abstract. The linear regression approach has been widely used for selecting high-yielding and stable genotypes targeted to several environments. The genotype mean yield and the regression coefficient of a genotype's performance on an index of environmental productivity are the two main stability parameters. Using both can often complicate the breeder's decision when comparing high-yielding, less-stable genotypes with low-yielding, stable genotypes. This study proposes to combine the mean yield and regression coefficient into a unified desirability index (D_i). Thus, D_i is defined as the area under the linear regression function divided by the difference between the two extreme environmental indexes. D_i is equal to the mean of the i^{th} genotype across all environments plus its slope multiplied by the mean of the environmental indexes of the two extreme environments (symmetry). Desirable genotypes are those with a large D_i. For symmetric trials the desirability index depends largely on the mean yield of the genotype and for asymmetric trials the slope has an important influence on the desirability index. The use of D_i was illustrated by a 20-environments maize yield trial and a 25-environments wheat yield trial. Three maize genotypes out of nine showed values of D_i's that were significantly larger than a hypothetical, stable genotype. These were considered desirable, even though two of them had slopes significantly greater than 1.0. The results obtained from ranking wheat genotypes on mean yield differ from a ranking based on D_i.

Key words: Genotype × environment interaction – Adaptation – Stability – Desirability index

Introduction

Differential genotypic responses to varied environmental conditions are known, in the classical sense, as genotype – environment interactions (GEI). Their most important effect in plant breeding is to complicate the identification of superior genotypes both for general adaptation and for specific environments.

The most widely used method for selecting high-yielding and stable genotypes is the linear regression approach. It was first proposed by Yates and Cochran (1938) for analyzing a barley yield trial and subsequently used by Finlay and Wilkinson (1963) to examine the adaptation of several hundred barley genotypes. The stability of a genotype is shown by its proportional response to the environmental index (regression coefficient). It is considered to be relatively stable if it has a regression line whose slope is near to 1.0. In general, this is a good criterion for selecting a genotype or a group of genotypes targeted to several environments.

Eberhart and Russell (1966) used the linear regression approach for assessing genotypic yield stability. They proposed pooling the sum of squares for environments and GEI and subdividing it into a linear effect between environments, a linear effect for genotype-environment, and a deviation from regression. The deviation from the regression line of each genotype is considered another stability parameter. A stable genotype has a slope equal to one and a small deviation from regression. However, use of the regression ap-

---

Communicated by A. R. Hallauer

[*] *Present address:* Biometrics Unit, Cornell University, Ithaca, NY 14853, USA
Correspondence to: C. M. Hernandez

proach has been criticized because biological and algebraic interdependencies exist between the slopes and the sum of squares due to deviations from regression (Hardwick and Wood 1972; Westcott 1986).

Several authors have pointed out the statistical and biological limitations of regression analysis (Freeman 1973; Hill 1975; Lin et al. 1986; Westcott 1986; Crossa 1990). Although a genotype slope is the primary stability parameter, not all stable genotypes are desirable, since mean yield is also an important parameter. Often these two parameters complicate a breeder's decision when comparing high-yielding, less-stable genotypes with low-yielding, stable genotypes (Crossa 1988).

In general, the regression model is used to partition the overall response pattern of a genotype into two components: yield performance and stability. However, an analytical method for examining the total behavior of a genotype across the tested environments should consider both of these components simultaneously.

The main objective of this study was to present a simple statistical method for selecting genotypes. The procedure is called the "area under the function" and combines the two principal parameters (regression coefficient and mean yield) which describe genotype performance into a unified desirability index. The method was illustrated with examples from an international maize (*Zea mays* L.) trial and an international wheat (*Triticum aestivum* L. em Thell.) trial distributed by the International Maize and Wheat Improvement Center (CIMMYT).

Methodology for developing a genotypic desirability index

From a breeding perspective, a practical problem of the regression approach is how to reconcile and utilize the two most important parameters, slope and mean yield. Often a high-yielding genotype is not stable (β significantly different from 1.0) or a genotype with $\beta = 1$ may show poor yield response.

Relationship between slope and mean yield production of the i^{th} genotype and a standard genotype

In this section we examine different situations where the response pattern of a specific genotype, given by its slope and mean yield, is compared with the response of a stable genotype.

Consider an experiment where "g" genotypes ($i = 1, 2, \ldots, g$) are evaluated in "e" environments ($j = 1, 2, \ldots, e$). The function that estimates the yield of the i^{th} genotype is

$$Y_i = f_i(I)$$

where $f_i(I) = \mu_i + \beta_i I; \mu_i$ is the mean yield of the i^{th} genotype over all environments and is estimated by $\bar{Y}_{i.}$; β_i is the regression coefficient of the i^{th} genotype on the environmental index (I_j) and is estimated by b_i. The enviromental index is the mean of an environment minus the grand mean ($\bar{Y}_{.j} - \bar{Y}_{..}$).

Let the function that estimates the yield of a standard genotype "s" be defined by

$$Y_s = f_s(I)$$

where $f_s(I) = \mu + I$; μ is the mean of all genotypes in all the environments and is estimated by the overall mean ($\bar{Y}_{..}$). By definition, the standard genotype is stable because $\beta_s = 1$.

The relationships between the two parameters, slope and mean yield production, under the models Y_i and Y_s can be displayed in a diagram where phenotypic values of the i^{th} genotype and the standard genotype are regressed on the environmental indexes (I_a being the lowest-yielding environment and I_b the highest-yielding environment). Figure 1 displays six hypothetical cases. In case 1 the i^{th} genotype is unstable (b_i greater than 1.0); however, it can still be considered a desirable genotype because its yield production is better than that of the standard genotype in all environments (Fig. 1A). In case 2 the i^{th} genotype is unstable (b_i less than 1.0) and its yield is lower than the standard genotype in all environments (Fig. 1B). Note that in both cases GEI exists but without genotypic rank change across environments. In cases 3 and 4 the i^{th} genotype is unstable (b_i is greater than 1.0 in Fig. 1C and less than 1.0 in Fig. 1D) and yield is higher than that of the standard genotype in some high- and low-yielding environments, respectively. Both cases show genotypic rank change across environments. In case 5 the i^{th} genotype is stable ($b_i = 1.0$) and more productive than the standard one (Fig. 1E), whereas in case 6 the i^{th} genotype is stable ($b_i = 1.0$) but the yield is lower than that of the standard genotype (Fig. 1F). When both genotypes are stable ($\beta = 1.0$; case 5 and case 6) it is clear that the i^{th} genotype would be desirable only if it shows a better yield performance than the standard one (case 5). Clearly the response of the i^{th} genotype in Fig. 1A is much more desirable than the response in Fig. 1E. It represents a response to favorable environments and also superiority in stress environments.

For the cases where the i^{th} genotype is unstable but more productive than the standard genotype in all environments (case 1), or unstable and more productive than the standard genotype in only some environments (case 3 and case 4), the decision as to whether or not the i^{th} genotype should be selected is not clear. For these cases it would be useful to obtain an index that includes both stability parameters.

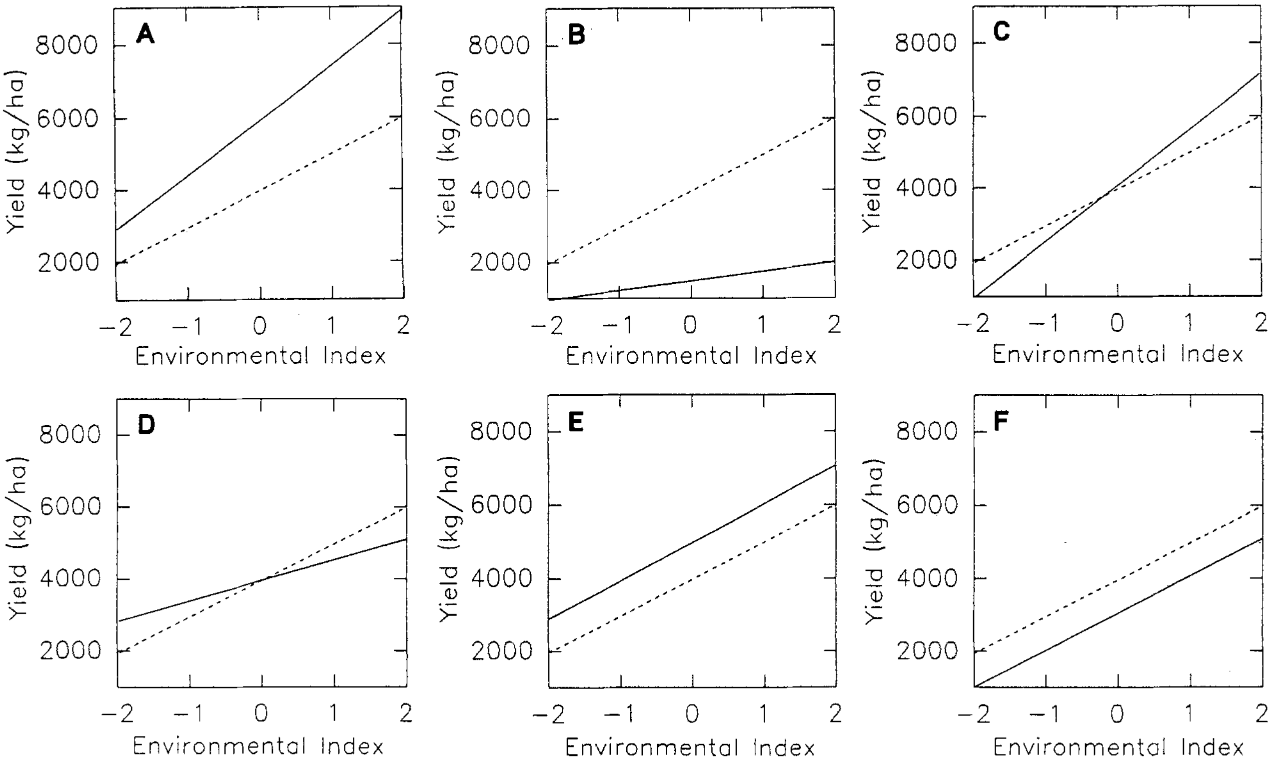


Fig. 1A–F. Six hypothetical linear response patterns of the i^{th} genotype (*solid line*) and the standard genotype (*dashed line*). **A** Case 1. **B** Case 2. **C** Case 3. **D** Case 4. **E** Case 5. **F** Case 6

The desirability index of the i^{th} genotype expressed as the area under the linear function

The area (A_i) under the linear function gives a combined estimate of the influence of both $\bar{Y}_{i.}$ and b_i. Because A_i is an area, it should be converted to a unit of measurement that is easier to interpret. By the fundamental theorem of calculus dividing A_i by the distance between the two extreme environment indexes (I_a and I_b) we obtain the desirability index (D_i): $D_i = A_i/(I_b - I_a)$. This value represents the mean expected yield of the i^{th} genotype expressed in performance units when tested in any of the environments between I_a and I_b.

The area under the linear function (A_i) is the integral of f_i(I) over the range of the tested environments (I_a, I_b) such that

$$D_i = \left[\int_{I_a}^{I_b} f_i(I)d(I)\right] \Big/ (I_b - I_a)$$

$$= \left[\int_{I_a}^{I_b} (\bar{Y}_{i.} + b_i I)d(I)\right] \Big/ (I_b - I_a)$$

$$= \{(\bar{Y}_{i.})(I_b - I_a) + (b_i)[(I_b^2 - I_a^2)/2]\}/(I_b - I_a).$$

Therefore,

$$D_i = \bar{Y}_{i.} + (b_i)C_1$$

where $C_1 = (I_b + I_a)/2$ is the mean of the two extreme environmental indexes and defines the asymmetry of the distribution of environmental indexes around zero ($C_1 = 0$ for complete symmetry). The contribution of the slope to the desirability index increases with asymmetry.

Similarly, the desirability index (D_s) of the standard genotype is defined as the area under its linear function

Table 1. Mean yield (Y_i) (kg ha^{-1}), slope of the regression line (b_i), and desirability index (D_i) in kg ha^{-1}of nine maize genotypes (g_i) at 20 environments (trial 1)

Genotype g_i	Yield Y_i	b_i	D_i
1	4618	0.98	4840
2	4602	0.97	4821^{+}
3	4823	0.95	5038
4	5218	1.31*	5514^{++}
5	5247	1.23*	5525^{++}
6	5330	1.06	5570^{++}
7	4672	0.86	4866
8	4283	0.52**	4401^{++}
9	4930	1.12	5183

*, ** Significant at the 5% and 1% probability level, respectively
$^{+}$, $^{++}$ Significantly different from D_s at the 5% and 1% probability level, respectively

(A_s) divided by the difference between the two extreme environmental indexes ($I_b - I_a$):

$$D_s = A_s/(I_b - I_a)$$

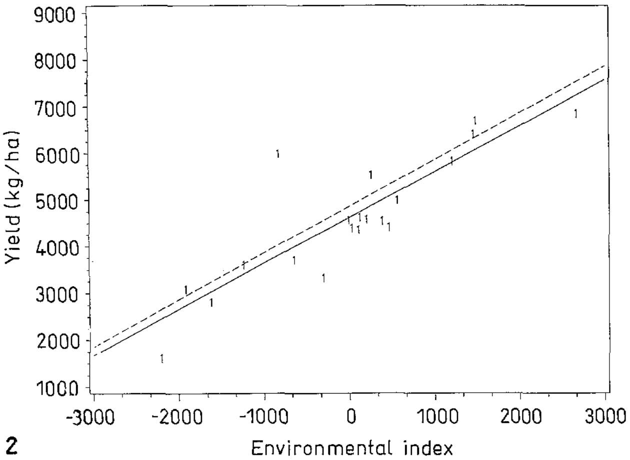
where A_s is the integral of $f_s(I)$ over the range of environments such that

$$D_s = \left[\int_{I_a}^{I_b} f_s(I)d(I)\right] \Big/ (I_b - I_a)$$

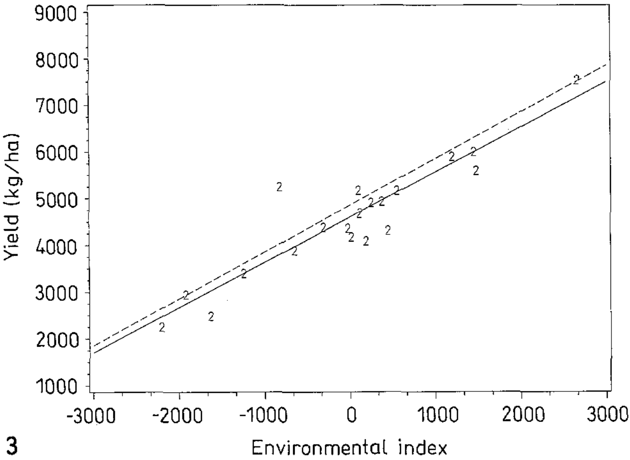
$$= \left[\int_{I_a}^{I_b} (\bar{Y}.. + I)d(I)\right] \Big/ (I_b - I_a)$$

$$= [(\bar{Y}..)(I_b - I_a) + (I_b^2 - I_a^2)/2]/(I_b - I_a) = \bar{Y}.. + C_1$$

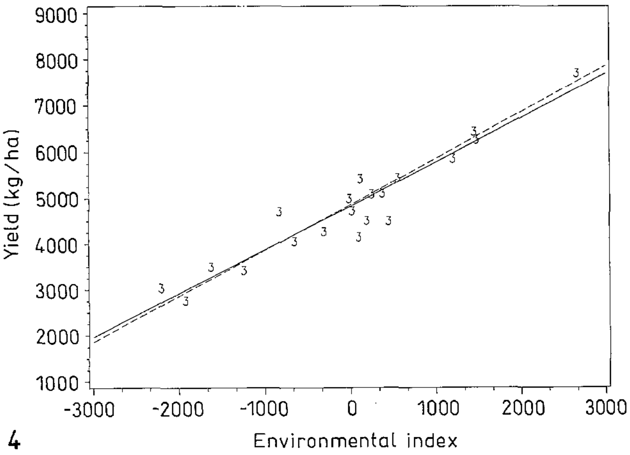
where C_1 is the same as above.



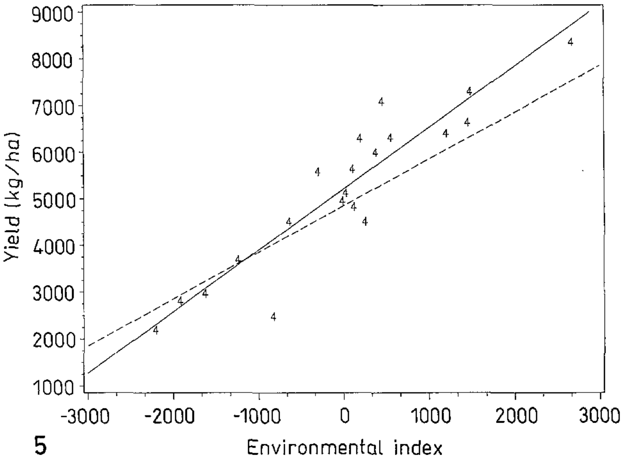
2



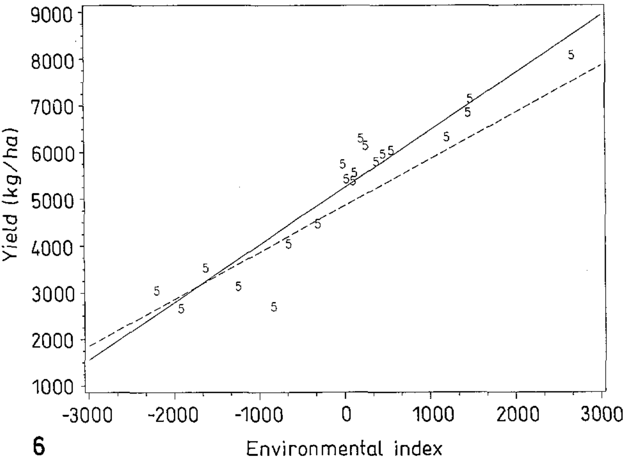
3



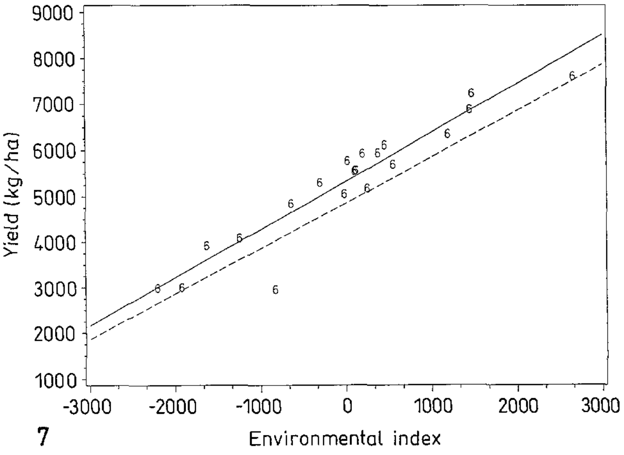
4



5

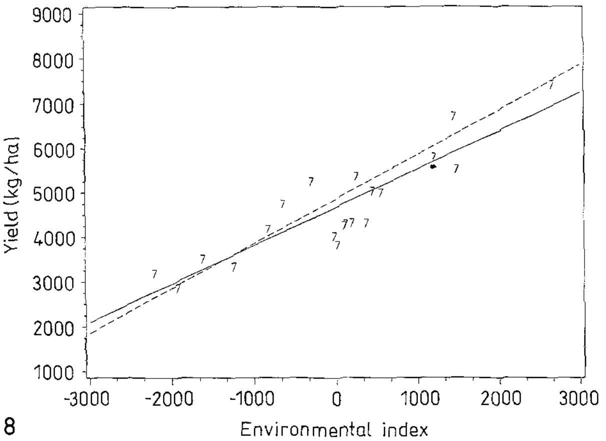


6

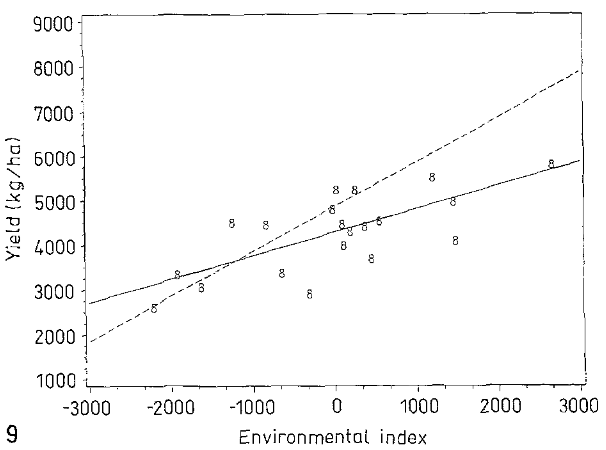


7

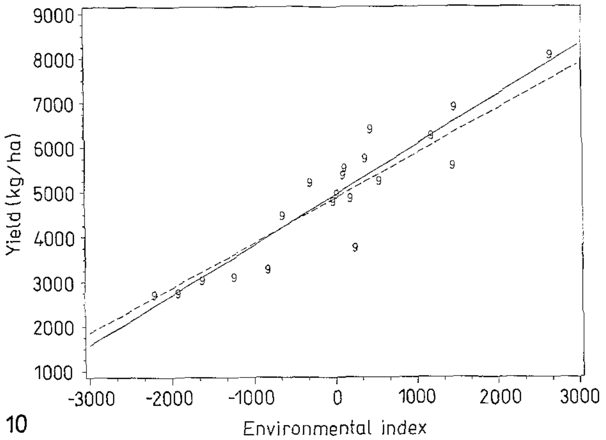
Figs. 2–7



8



9



10

Fig. 2–10. Linear responses of nine genotypes (*solid line*) included in trial 1 and the standard genotype (*dashed line*). *Numbers* identify genotypes

According to these results, the desirability index of a genotype depends on its mean yield, the slope of the regression line, and the asymmetry (C_1) of the experiment. When the two extreme environmental indexes approach complete symmetry – that is $|I_a| = |I_b|$ – then $C_1 = 0$ and D_i and D_s depend on $\bar{Y}_{i.}$ and the overall mean ($\bar{Y}..$), respectively. In this case, the slopes of the genotypes' regression lines do not influence the desirability index, thus the desirable genotypes are those with higher mean yields (higher D_i). However, when the two extreme environmental indexes are asymmetric (C_1 tends to be different than 0), two different cases are possible: (1) when $|I_a| > |I_b|$ and $C_1 < 0$, then D_i and C_1 are inversely related. For two genotypes with the same mean yield the regression line of the desirable one (with higher D_i) will have a smaller slope (b_i); (2) $|I_a| < |I_b|$ and $C_1 > 0$; then D_i and C_1 are directly related. For two genotypes with the same mean yield, the one with greater slope will have a greater D_i.

The desirability index of a genotype with quadratic or cubic responses can also be calculated. For a quadratic response the corresponding coefficient is calculated as $(I_b^3 - I_a^3)/[3(I_b - I_a)]$, whereas for a cubic pattern its coefficient is $(I_b^4 - I_a^4)/[4(I_b - I_a)]$.

Comparing the area under the function of the i^{th} genotype with a constant: hypothesis testing

A linear model-testing methodology (Draper and Smith 1966) is used to test hypotheses about the parameter D_i and its comparison with D_s. Let the vector C' be $(1, C_1)$ and the vector b be $(\bar{Y}_{i.}, b_i)$; then D_i can be written as

$$D_i = C'b$$

and the variance of D_i is estimated by

$$S_{Di}^2 = [C'(I'I)^{-1}C](\text{MSE}/r)$$

where MSE is the pooled error, r is the number of replicates, and I is a matrix containing ones in the first column and the environmental indexes in the second column. To test the null hypothesis Ho: $D_i = D_s$, we use the following F test

$$F_C = \text{MS}_{\text{Ho}}/\text{MSE}$$

where $\text{MS}_{\text{Ho}} = (C'b_i - D_s)^2/S_{Di}^2$. The value F_C is compared with the F value from the table with one degree of freedom (1 df error).

As pointed out in the previous section, those genotypes with values of D_i that are significantly larger than D_s are the most desirable.

Trial 1. A maize experimental variety trial (EVT 16) provides a simple illustration of the use of the area under the model for characterizing desirable genotypes. The trial had nine genotypes tested in 20 international environments in a randomized complete block design with four replicates. The response variable was grain yield (kg ha^{-1}).

The highest yielding genotypes are 4, 5, 6, and 9 (Table 1). Of these, genotypes 6 and 9 are stable (slopes not significantly different from 1.0), whereas genotypes 4 and 5 are unstable (slopes significantly greater than 1.0). The asymmetry of this trial is $C_1 = 226$ ($I_a = -2{,}206$ kg ha^{-1} and $I_b = 2{,}658$ kg ha^{-1}). Therefore, the desirability index for the i^{th} genotype is $D_i = \bar{Y}_{i.} + (b_i)$ (226). The overall mean of the experiment was 4,858 kg ha^{-1}, thus the desirability index for the standard genotype was $D_s = 5084$ kg ha^{-1}. Genotypes 2, 4, 5, 6, and 8 have values of D_i that were significantly different from those of the standard genotype (Table 1). Of these, genotypes 4, 5, and 6 were superior because they had values of D_i that were significantly larger than the standard genotype. In contrast, genotype 8 had the lowest mean yield response and the lowest D_i.

The response pattern of the nine genotypes given by their regression coefficients and mean yields was compared with the response of the hypothetical standard genotype ($b = 1.0$; Figs. 2–10). Deviations from the average response can also be seen from these graphs. Genotypes 1 and 2 represent reference case 6, but only the latter had values of D_i significantly smaller than D_s. Genotype 3 corresponded to case 4, but D_i is not different from D_s (Table 1). Genotypes 4 and 5 belong to case 3; they had slopes greater than one (Table 1) and a D_i that was significantly larger than D_s. Case 5 is typified by genotype 6, which showed the highest mean yield and therefore the largest desirability index. Genotypes 7 and 8 fall into case 4; however, the latter had a slope that was less than 1.0 and a D_i significantly smaller than D_s (Table 1). Genotype 8 not only had a low D_i but has large deviations from regression (Fig. 9). Although genotype 9 belongs to case 3, its D_i does not differ significantly from D_s.

For this trial, mean yields were the predominant factor contributing to D_i and were highly correlated with the desirability index. However, for trials with a higher asymmetry than that of EVT 16, the slope of the regression line will have a greater influence on D_i and thus the results of ranking genotypes on mean yield should differ from a ranking based on D_i.

Table 2. Mean yield (Y_i) (kg ha^{-1}), slope of the regression line (b_i), and desirability index (D_i) in kg ha^{-1} of 18 wheat genotypes (g_i) at 25 environments (trial 2)

Genotype g_i	Yield Y_i	b_i	D_i
1	4671	0.96	5840
2	4694	0.97	5875
3	4289	0.95	5446^{++}
4	4913	1.04	6180^{++}
5	5003	1.10*	6343^{++}
6	4794	0.98	5988
7	4841	1.01	6071
8	4337	1.05	5616
9	4920	0.98	6114^{++}
10	4544	0.83*	5555^{++}
11	4487	0.89	5571^{++}
12	4716	1.04	5983
13	4320	1.04	5587
14	4715	1.00	5933
15	4661	1.16*	6074
16	4587	0.91	5695
17	4607	1.02	5846
18	4654	1.02	5896

*,** Significant at the 5% and 1% probability level, respectively

$^{+}$,$^{++}$ Significantly different from D_s at the 5% and 1% probability level, respectively

Trial 2. These data come from an elite spring wheat trial (ESWYT 8) that included 18 genotypes planted in 25 international environments in a randomized complete block design with three replicates. Grain yield is the response variable (kg ha^{-1}).

Genotype 5 has the highest mean yield but it is unstable because has a slope significantly different from one ($b_i = 1.10$) (Table 2). Genotype 5 has the highest D_i (6343 kg ha^{-1}) followed by genotypes 9 and 4 with D_is of 6114 and 6180 kg ha^{-1}, respectively. Genotype 15 has a relatively high mean yield (4660 kg ha^{-1}) but according to its slope ($b_i = 1.16$) it is unstable (Table 2). The asymmetry of this trial is $C_1 = 1218$ ($I_a = -3546$ kg ha^{-1} and $I_b = 5982$ kg ha^{-1}), that is, trial 2 is about five times more asymmetric than trial 1. The desirability index for the i^{th} genotype is $D_i = \bar{Y}_{i.} + (b_i)(1218)$, whereas $D_s = 5870$ kg ha^{-1}.

For this trial, both mean yield and slope were important factors contributing to D_i. The results of ranking genotypes on mean yield differ from a ranking based on D_i. For example genotype 9 was ranked second based on mean yield and third based on D_i; genotype 4 ranked third based on mean yield and second based on D_i; genotype 15 ranked tenth based on mean yield and fifth based on D_i.

Conclusions

The desirability index, expressed as the area under the regression function, attempts to quantify what most plant breeders actually do; that is, to use both the mean yield and the regression coefficient for determining the desirability of a genotype. This index can facilitate the breeder's decision when selecting superior genotypes especially when high yeilding genotypes have slope greater than one (i.e., genotypes 4 and 5 on the maize trial). For trials where the environmental indexes are fairly symmetric (trial 1), the genotypic desirability index is highly dependent on the mean yield. In this case, superior genotypes whether selected by their mean yield or by their desirability indexes are the same. However, for trials with a more asymmetric distribution of environmental indexes, such as trial 2, the slope of the regression line is an important factor, and therefore selecting on the basis of mean yield will indentify different genotypes from those selected using the desirability index.

Acknowledgements. The authors thank Drs. F. Marquez, C. O. Gardner and C. Qualset for their helpful comments on the manuscript. We also gratefully acknowledge the contribution of those involved in the national research programmes who carried out the numerous experimental variety trials.

References

Crossa J (1988) A comparison of results obtained with two methods for assessing yield stability. Theor Appl Genet 75:460–467

Crossa J (1990) Statistical analyses of multilocation trials. Adv Agron 44:55–85

Draper NR, Smith H (1966) Applied regression analysis. John Wiley and Sons, New York

Eberhart SA, Russell WA (1966) Stability parameters for comparing varieties. Crop Sci 6:36–40

Finlay KW, Wilkinson GH (1963) The analysis of adaptation in a plant breeding program. Aust J Agric Res 14:742–754

Freeman GH (1973) Statistical methods for the analysis of genotype-environment interaction. Heredity 31:339–354

Hardwick RC, Wood JT (1972) Regression methods for studying genotype-environment interactions. Heredity 28:209–222

Hill J (1975) Genotype-environment interactions – a challenge for plant breeding. J Agric Sci 85:477–493

Lin CS, Binns MR, Lefkovitch LP (1986) Stability analysis: where do we stand? Crop Sci 26:894–900

Westcott B (1986) Some methods of analyzing genotype-environment interaction. Heredity 56:243–253

Yates F, Cochran WG (1938) The analysis of a group of experiments. J Agric Sci 28:556–580