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STUDIES ON THE METHODS OF ESTIMATING PLANT STABILITY[1][2]

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Abstract

Various methods are available to estimate the interactions between genotype and environmental effects. However, the parameters of stability estimated from these methods frequently fail to evaluate the quadratic responses between genotypes and environments adequately. In the present study, two estimation methods were developed for the stability of quantitative characters of a population when the response presented in quadratic form under different environments; (1) mean value of curvature of the curve and (2) Hamiltonian of the quadratic equation. To demonstrate these two estimated methods, two lines of ***Arabidopsis thaliana*** and their hybrids F_1 and F_2 were used for analysis.

Introduction

Various methods are available to estimate the interaction between genotypic and environmental effects. Finlay and Wilkinson (1963) using barley varietal traits and measuring the yields on a logarithmic scale, computed a linear regression coefficient of mean individual yield on the mean yield for each site and each season. The regression coefficient was then used as a measurement of the phenotypic stability of a variety. Eberhart and Russell (1966) developed another method for measuring the stability of populations growing from single and three-way crosses in maize, also based on the regression technique. The method was calculated on environmental index for each environmental factor used for a series of trials as the mean of all varieties at one environment minus the grand mean of all environments of the trials. Eberhart and Russell (1966) have pointed out that both regression coefficient and deviation from regression of a variety on the environmental indices should be considered as parameters for measuring the stability of a variety. The regression method of stability analysis was then applied for plant variety testings (Baker, 1969;

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Breese, 1969; Johnson *et al.*, 1968; Walton, 1968; and others), and for material sciences (Mandel *et al.*, 1969; 1971) elsewhere.

Several modified joint regression analyses were also developed by Perkins and Jinks (1968), Tai (1971), Hardwick (1972) and Hardwick *et al.* (1972). Those methods were successfully applied to assess the stability of a variety to the environment, as well as that of variety trials to genetical background for many organisms. But Fripp (1972) has pointed out that any bias introduced by the use of environmental indices (non-independent environmental measure) makes differences either to the ranking of the genotypes according to the magnitude of their linear regression coefficients or to the proportion of the genotype-environmental variation accounted for by the heterogeneity of these regressions when compared with the results of analyses of regression against various independent but biological measures. Bucio Alains *et al.* (1969) have been used an independent assessment of the environment and linear regressions account for all the significant genotype-environmental interactions. The regression functions provide reliable predictions over both environments and generations. Okuño *et al.*, (1971) and Perkins (1972) has applied principle components analysis to study the genotype-environmental interaction components of variations and explained their relationship to the analyses of linear regression, against a non-independent environmental measure, and the deviation from linear regression.

However, the parameters of stability of a variety estimated from these methods frequently fail to evaluate the non-linear responses between genotypes and environments adequately. In the present study, two methods were therefore, developed to measure the stability parameter of quantitative character of a population when the response presented in quadratic form under different environments.

Statistical Method

Two methods were used to estimate the parameter of stability of a population, when the response of the population represented in quadratic form to an independent environmental measurement.

Assume that the response of a population performance to various environments presented in quadratic form;

$$W_i = aT_i^2 + bT_i + c \quad \cdots\cdots (1)$$

where W_i is an observed value of a population grown at the ith environment ($i=1, 2, \ldots, n$), T_i is an independent ith environmental measure, a, b and c are the coefficients of the equation which can be estimated from the experimental data.

Method I The curvature of the equation (1) will be represented as a measure of the parameter of stability. Because, if the curvature approaches to 0, it is shown that the curve line is nearly presented to linear, and the response of a population to the various environments is becoming stable. If the curvature approaches to ∞, the response is becoming unstable. The curvature is the reciprocal of the curvatural radius of a curve function, and the curvatural radius is;

$$\rho=\left|\frac{(1+W'^2)^{3/2}}{W''}\right|=\left|\frac{\left[1+\left(\frac{dW}{dT}\right)^2\right]^{3/2}}{\frac{d^2W}{dT^2}}\right| \qquad (2)$$

where;

$$\left.\begin{aligned}\frac{dW}{dT}&=2aT+b=p\\ \frac{d^2W}{dT^2}&=2a\end{aligned}\right\} \qquad (3)$$

so the curvatural radius becomes;

$$\rho=\left|\frac{[1+(2aT+b)^2]^{3/2}}{2a}\right| \qquad (4)$$

hence, the curvature is;

$$\rho^{-1}=\left|\frac{[1+(2aT+b)^2]^{3/2}}{2a}\right|^{-1} \qquad (5)$$

therefore, the stability parameter will be estimated from this equation. But the value of ρ^{-1} is changeable according to the value of the environmental measure T, therefore, the simple mean value of ρ^{-1} is used for measuring the parameter of stability of a curve function, i.e., ρ_m^{-1}.

Method II Assume equations (3) represented the dynamic system of the equation (1) for a population growth performance, p is the growth rate of this population to the environmental changes, and $H(W, p)$ is the relationship between W and p, then;

$$\frac{\partial H}{\partial T}=\frac{\partial H}{\partial W}\frac{dW}{dT}+\frac{\partial H}{\partial p}\frac{dp}{dT} \qquad (6)$$

if H is constant for different environmental measure T, then;

$$\left.\begin{aligned}\frac{\partial H}{\partial p}&=\frac{dW}{dT}\\ -\frac{\partial H}{\partial W}&=\frac{dp}{dT}\end{aligned}\right\} \qquad (7)$$

in this condition, the value of $H(W, p)$ is a Hamiltonian of equation (1), and can be interpreted as the total energy of this system in the state (W, p), and the constancy of H along trajectories is an expression of the conservation of energy for the system.

Because $\frac{dW}{dT}=p$, and $\frac{dp}{dT}=\frac{d^2W}{dT^2}=2a$, so that;

$$\left.\begin{array}{l} \frac{\partial H}{\partial p}=\frac{dW}{dT}=p \\ -\frac{\partial H}{\partial W}=\frac{dp}{dT}=2a \end{array}\right\} \qquad (8)$$

hence, the solution of equations (8) are;

$$\left.\begin{array}{l} H=\frac{p^2}{2}+\phi(W) \\ H=-2aW+\phi'(p) \end{array}\right\} \qquad (9)$$

then the Hamiltonian function of this system will be expressed as;

$$H(W, p)=\frac{p^2}{2}-2aW \qquad (10)$$

According to this equation, we know that if $|p|\rightarrow 0$, then the H value should be decreased, where p is a change rate of the response to the various environments. When $|p|\rightarrow 0$, the response rate is small and also stable to the environmental measures. So when H value approximate to 0, this population is stable to the environmental change. On the other hand, when $|p|\rightarrow\infty$, the value of H should be increased, and the response of this population will become unstable. Hence, we may calculate the H value of each population to environmental changes, and discover the stability of the population even if the group size of population is variable.

The parameters of H and a of the equation (10) will be estimated by the following two methods.

Method IIa Assume that;

$$\left.\begin{array}{l} Y=\frac{p^2}{2}=\frac{1}{2}\left(\frac{dW}{dT}\right)^2 \\ \eta=2a \end{array}\right\} \qquad (11)$$

than the equation (10) may be transformed to;

$$Y=H+\eta W+e \qquad (12)$$

hence, the value of Y and W may be obtained from the observed values of T and W [see equation (23)], and e is an experimental error, so the equation (12) presents linear regression model, where H and η are the unknown parameters, but can be estimated from the least square method, i.e.;

$$\hat{\eta}=\frac{n\Sigma YW-(\Sigma Y)(\Sigma W)}{n\Sigma W^2-(\Sigma W)^2}$$

$$=\frac{n\Sigma\left(\frac{dW}{dT}\right)^2W-\left[\Sigma\left(\frac{dW}{dT}\right)^2\right][\Sigma W]}{2[n\Sigma W^2-(\Sigma W)^2]} \qquad (13)$$

and

$$\hat{a}=\frac{1}{2}\hat{\eta} \qquad (14)$$

$$\hat{H}=\bar{Y}-\hat{\eta}\bar{W}$$

$$=\frac{1}{n}\left[\frac{1}{2}\Sigma\left(\frac{dW}{dT}\right)^2\right]-\hat{\eta}\frac{1}{n}(\Sigma W)$$

$$=\frac{1}{2}\left\{\frac{\left[\Sigma\left(\frac{dW}{dT}\right)^2\right][\Sigma W^2]-\left[\Sigma\left(\frac{dW}{dT}\right)^2W\right][\Sigma W]}{n\Sigma W^2-(\Sigma W)^2}\right\} \qquad (15)$$

The variance of $\hat{\eta}$ and $\hat{H}$ can be obtained by the method of maximum likelihood, i.e.;

$$V(\hat{H})=\frac{\hat{\sigma}^2\Sigma W^2}{n\Sigma W^2-(\Sigma W)^2}=\left[\frac{1}{n}+\frac{\frac{1}{n}(\Sigma W)^2}{n\Sigma W^2-(\Sigma W)^2}\right]\hat{\sigma}^2 \qquad (16)$$

$$V(\hat{a})=V\left(\frac{1}{2}\hat{\eta}\right)=\frac{1}{4}\left[\frac{n\hat{\sigma}^2}{n\Sigma W^2-(\Sigma W)^2}\right] \qquad (17)$$

where the residual mean square $\hat{\sigma}^2$ is;

$$\hat{\sigma}^2=\frac{1}{n-2}\left\{\left[\Sigma Y^2-\frac{(\Sigma Y)^2}{n}\right]-\left[\frac{(n\Sigma YW-\Sigma Y\Sigma W)^2}{n\Sigma W^2-(\Sigma W)^2}\right]\right\}$$

$$=\frac{1}{4(n-2)}\left\{\Sigma\left(\frac{dW}{dT}\right)^4-\frac{\left[\Sigma\left(\frac{dW}{dT}\right)^2\right]^2}{n}\right.$$

$$\left.-\frac{\left[n\Sigma\left(\frac{dW}{dT}\right)^2W-\Sigma\left(\frac{dW}{dT}\right)^2(\Sigma W)\right]^2}{n\Sigma W^2-(\Sigma W)^2}\right\} \qquad (18)$$

so the significant test of $H=0$ and $a=0$ can be obtained by t-test;

$$t(\hat{H})=\frac{\hat{H}-H}{\sqrt{V(\hat{H})}} \qquad (19)$$

$$t(\hat{a})=\frac{\hat{a}-a}{\sqrt{V(\hat{a})}} \qquad (20)$$

If the calculated t-value is larger than that of the theoretical with the degree of freedom, $df=n-2$, at significant level 5% or 1%, it may be concluded that the estimated value of $\hat{H}$ or $\hat{a}$ is significantly different from the value of zero.

Method IIb The another method for estimating the stability parameter of H will simply be obtained after substitute the value of W of equation (1) and the value of p of equation (3) applied to the equation (10), hence;

$$H=\frac{1}{2}p^2-2aW$$
$$=\frac{1}{2}(2aT+b)^2-2a(aT^2+bT+c)$$
$$=\frac{1}{2}b^2-2ac \quad \cdots\cdots (21)$$

So, if the coefficients of the equation (1) were obtained, these coefficients can be used to estimate H value from equation (21). This H value will be estimated constant, because the values a, b, and c are estimated constant. The interpretation of the relationship between H value and response stability is the same as the aforementioned section (Method II).

A Numerical Example

To demonstrate the aforementioned theoretical work, two lines of *Arabidopsis thaliana* (A and B) and their hybrids F_1 and F_2 were planted at six different temperatures; 16°, 19°, 22°, 25°, 28°, 31°C, respectively. The dry weight of the plant was measured on a logarithmic scale, and the data were used to study the stability of the populations. (Griffing *et al.*, 1963)

The quadratic form was used for fitting the relationship between the mean value of a populations' performance in each environment and the independent environmental measurement (temperature). The coefficients of the theoretical quadratic equation, a, b, and c were calculated from the data. The results are shown in the figure 1 and table 1.

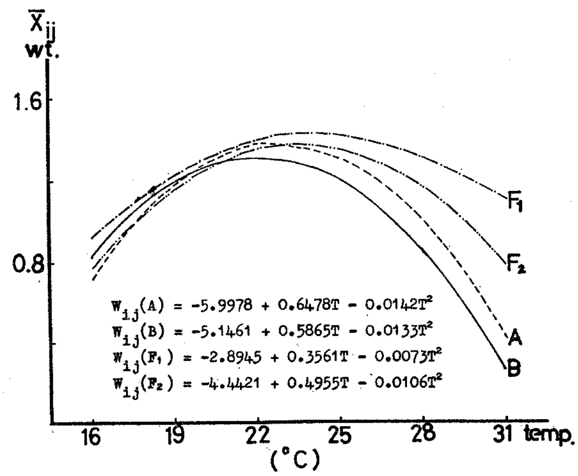

Fig. 1. Temperature response of four populations of *Arabidopsis thaliana*

The linear regression model of Finlay and Wilkinson's method (1963) was also used for studying the stability of these populations. The results are shown in figure 2 and table 1.

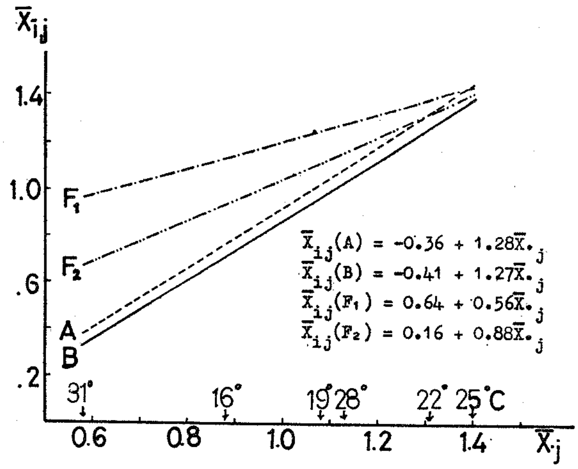

Fig. 2. Linear regression of four populations

The estimated value of curvature (ρ^{-1}) of each population was obtained by equation (5) using the coefficients of quadratic equation, but simple mean value of the curvature (ρ_m^{-1}) over all of independent environmental measure of the population was used for comparing the stabilities.

The $\hat{H}$ value estimation by equation (12) was obtained by the use of simplicity method as described in the follows, disregarding equations (13) and (15). Because;

$$Y_i = H_L + \eta_L W_i + e \quad \text{.......... (22)}$$

where

$$Y_i = \frac{1}{2}p_i^2 = \frac{1}{2}\left(\frac{dW_i}{dT_i}\right)^2 = \frac{1}{2}\left(\frac{W_{i+1}-W_{i-1}}{T_{i+1}-T_{i-1}}\right)^2 \quad \text{.......... (23)}$$

so, if we analyse the linear regression between W_i and $\frac{1}{2}\left(\frac{W_{i+1}-W_{i-1}}{T_{i+1}-T_{i-1}}\right)^2$, then we can simply obtain the estimated value of $\hat{H}_L$ and $\hat{a}_L\left(=\frac{1}{2}\hat{\eta}_L\right)$. Therefore, the value of $V(\hat{H}_L)$ and $V(\hat{a}_L)$ by equations (16) and (17) can be calculated, and the significance test also can be obtained by equations (19) and (20). In this case, the degree of freedom of the error is $n'-2=n-4$.

The another $\hat{H}_Q$ value estimation by equation (21) can be obtained if the coefficients, a, b, and c of quadratic equation have been known. The calculated results of these estimating methods are summarized in the table 1.

From the results of table 1, we find that the performance of a population at each environment against various independent environmental measure (T) is significantly presented in the quadratic form (Method IIb), and it can be fitted by the quadratic regression (Fig. 1). The additional linear regression

Table 1. *Estimated value of the parameter of stability ($\hat{b}$, $\hat{\rho}_m^{-1}$, $\hat{H}_L$ and $\hat{H}_Q$) and the results of its significant test*

Population	A	B	F_1	F_2
Linear regression model				
$\hat{b}$	1.28	1.27	0.56	0.88
$V(\hat{b})$	0.0060	0.0771	0.0400	0.0137
$t(\hat{b})$	4.6096**	16.5523**	2.8005**	7.5161**
Method I				
$\hat{\rho}_m^{-1}$	0.0275	0.0258	0.0144	0.0208
Method IIa				
$\hat{H}_L$	0.0468	0.0408	0.0093	0.0294
$V(\hat{H}_L)$	0.000278	0.000116	0.000002	0.000232
$t(\hat{H}_L)$	2.8077	3.7881*	2.0461	1.9299
$\hat{a}_L$	-0.0175	-0.0160	-0.0029	-0.0107
$V(\hat{a}_L)$	0.000057	0.000026	0.000003	0.000042
$t(\hat{a}_L)$	-2.3221	-3.1325*	-1.6295	-1.6481
Method IIb				
$\hat{a}$	-0.0142	-0.0133	-0.0073	-0.0106
$\hat{b}$	0.6478	0.5865	0.3561	0.4955
$\hat{c}$	-5.9978	-5.1461	-2.8945	-4.4421
$\hat{H}_Q$	0.0395	0.0351	0.0211	0.0286
F-value (linear)	0.4103^{NS}	1.5751^{NS}	0.4488^{NS}	0.0006^{NS}
F-value (quadratic)	32.7725**	30.9109**	58.6646**	41.8576**

* and **; significant level at 5% and 1%, respectively.

analysis also provided the linear relationship between population and environment, and the regression coefficient can be used for measuring the parameter of stability. But as Hardwick *et al.* (1972) pointed out, that a bias arise because the assumption has to be made in linear regression analysis of which the independent variable is measured without an error. In this example, the independent variable is measured with an error (non-independent environmental index), therefore, the estimated value of the stability parameter accounted by this method, cannot present the unbias estimator for measuring the stability of a population's performance. But we can use this parameter to compare with the other estimating methods described above (Methods I and II).

From the results of table 1, we find that the parameter of stability of each population estimated from these four methods, has an identical tendency among four populations (A, B, F_1 and F_2), and has a good agreement among each other (Table 2). Therefore, the estimator by the two methods; Methods

I and II, can also measure independently the stability of a population's performance. These two methods could have a small error and can be avoided from bias in the linear regression method.

Table 2. *Correlation of the stability parameter for four populations between various estimated methods*

	Method IIa	Method IIb	Linear Reg. Method
Method I	0.9976**	0.9924**	0.9914**
Method IIa		0.9897**	0.9810**
Method IIb			0.9770**

**; significant level at 1%.

From the analytical results of this numerical example, we found that the stability of F_1 and F_2 hybrid populations is more stable than that of their two parental populations, and the F_1 hybrid is most stable than the parents and F_2. (Fig. 1, 2 and Table 1). The cause may be due to the heterosis of hybrids from different genetical backgrounds (Griffing *et al.*, 1963).

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植物適應性的評價方法研究

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適應性之大小爲品種特性之一，對新品種之育成及其推廣甚爲重要。到目前爲止，對其評價的方法很多，而其中以直線廻歸分析法在遺傳學及育種學上應用的較多。但此法係以參試族羣在各環境之平均值作爲該環境之指數而推求者，其估值常受參試族羣的不同而異，缺少客觀標準。本研究提出二種不受參試族羣數之影響，而對環境反應呈二次曲線時的評價方法。