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STUDIES ON THE GENOTYPE—ENVIRONMENT INTERACTION OF *ARABIDOPSIS THALIANA*[1,2]

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Abstract

Fourteen inbred lines of *Arabidopsis thaliana* and four of their F_1 hybrids were used to study the genotype × environment interaction at three temperature regimes under artificial or natural light conditions. Four quantitative characters were studied: flowering days, leaf/petiole ratio, plant height and rosette size. The plant height and rosette size were expressed on an exponential and reciprocal scale, respectively. By using linear regression and multiple regression analysis for G×E interactions, the results were summarized as follows:

1. The multiple regression analysis could elucidate the linear relationship between the interaction of genotype and two environmental factors. In three quantitative characters, flowering days, leaf/petiole ratio and plant height studied, the interactions of genotype with environments (G×T, G×L) could be expressed as a linear function of the environmental effects respectively. But the genotype × temperature × light interaction could not be represented by linear response in all plant characters.

2. The genotype × environment interaction could be analyzed with linear regression on the given temperatures under artificial light for all plant characters and under natural light for plant height.

3. Extending the regression analysis for inbred lines to the F_1 generation, the genotype × environment interactions of certain F_1 hybrids showed linear in relation to the temperature effect. Cross F10×F57 and F10×Wil-2 showed greater heterosis in rosette size at a higher temperature, whereas cross F10×Est-0 showed greater heterosis in plant height at a lower temperature. The expression of heterosis varied with environmental conditions.

4. Based on the relationship between linear regression coefficient and phenotypic mean, adaptation and performance of genotypes were compared.

Key words: *Arabidopsis thaliana*; genotype × environment interaction; linear regression; multiple regression; stability; plasticity; genetic parameter method; heterosis.

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Introduction

In quantitative characters, the relative performance of different genotypes often varies from one environment to another. This phenomenon is known as genotype × environment (G × E) interaction, and various methods have been proposed for its statistical analysis. Many authors have shown that the performance of an individual genotype can be expressed as a linear function of an environment variable (Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Perkins and Jinks, 1968a, b; Hardwick and Wood, 1972; Tan *et al.*, 1979; Barker *et al.*, 1981). In Eberhart-Russell's model, an environmental index was measured by mean performance of all genotypes grown in an environment, and the performance of individual genotype was regressed on the environmental index. Both the regression coefficient and residual mean square from regression should be considered as parameters for measuring the phenotypic stability of individual genotypes under test. Although there are other useful measures of stability, like the ecovalence (Wricke, 1962) and the coefficient of determination (Pinthus, 1973), they are highly correlated with the stability parameters from regression analysis. Hence, the regression coefficient is a useful statistic for measuring the stability of crop species except for perennial forage species (Langer *et al.*, 1979; Nguyen *et al.*, 1980; Becker, 1981; Gray, 1982; Hill and Baylor, 1983).

Regression analysis reveals that the response of genotypes to environmental conditions is essentially linear, even though the environmental index embodies diverse physical factors such as temperature, light, nutrient, soil type, etc., each of them can vary continously and independently of one another. It is customary in variety trials to assume that the environmental variable is just an amalgam of several factors. In many instances, however, this assumption is not justified. Particular attention may be paid to those environmental factors and to determine how much of the observed variation is due to each individual factor, or composite factor derived from them. Freeman and Dower (1973) and Freeman and Crisp (1979) argued that the use of several multivariate techniques (principal component analysis, canonical analysis, and factor analysis) to partition treatment effects gives no additional information than the analysis of variance. Therefore, they are not been widely used in the analysis of G × E interactions. In fact, the linear regression technique will continue to play an important part in furthering our understanding of G × E interactions because it does have the twin merits of simplicity and biological relevance. In the present study, a multiple regression method is developed for fitting model, and for suggesting criteria with which decisions can be made in terms of the parameters defined by such a new regression model.

Another point reported in this paper is to extend the linear regression technique for inbred lines to the F_1 generation. "Genetic parameter method" developed by

Bucio Alanis and Hill (1966) is adopted, because an environmental index based on the inbred parents will also supply an independent measure for the F_1 generation. This approach may lead to identifing the practical application of a procedure by which G × E interactions can be examined in greater details with an increased accuracy in estimates of genetic components and heterosis over environments.

Materials and Methods

Arabidopsis thaliana (L.) Heynh. is an annual species of the family Cruciferae. It is self-pollinated, has a short life cycle, and is wildly distributed geographically. Its most conspicuous variation is in the response of flowering to natural day-length and temperature regimes (Barthelmess, 1967; Westerman, 1970, 1971; Rédei, 1975). It is a suitable material for the study of G × E interactions.

Fourteen inbred lines and four F_1 hybrids of *Arabidopsis thaliana* were used in this study. They were: F4, F10, F26, F57, F104, V46/6, V50, V198, Wil-2, Est-0, Oy-0, En-2, GR 1.4, Hm, F10 × F57, F10 × Est-0, F10 × Wil-2 and Wil-2 × V46/6. The plants of each line and hybrid were sand-cultured in pots (18 cm in diameter) watered with nutritional solution described by Wu (1972). They were grown under six environmental conditions consisting combinations of three different day/night temperature regimes, (20-22)/(15-17)°C, (25-27)/(20-22)°C and (30-32)/(25-27)°C, and two light conditions (artificial illumination of 20,000 lux with a 15-h daylength, and natural light) during the experiment period from April 1983 to December 1984 in Taipei.

The characters studied were flowering days, leaf/petiole ratio (L/P), plant height and rosette size at flowering. The flowering days was recorded as number of days from seed germination to the first flowering. The plant height and rosette size were expressed on a exponential and reciprocal scale, respectively. There were three replicates per treatment.

Statistical Models

Linear Regression and Multiple Regression

The performance y_{ijk} of the k^{th} ($k = 1, \ldots, r$) replicate of the i^{th} ($i = 1, \ldots, s$) genotype in the j^{th} ($j = 1, \ldots, t$) environment can be written as

$$y_{ijk} = m + V_i + E_j + g_{ij} + e_{ijk} \qquad (1)$$

where,

m = the grand mean;
V_i = the effect of the i^{th} genotype subject to $\Sigma_{i=1}^{s} V_i = 0$;
E_j = the effect of the j^{th} environment subject to $\Sigma_{j=1}^{t} E_j = 0$;

g_{ij} = the G × E interaction of the i^{th} genotype in the j^{th} environment subject to $\sum_{i=1}^{s} g_i = \sum_{j=1}^{t} g_j = 0$;

e_{ijk} = the experimental error contributed by the k^{th} replicate of the i^{th} genotype in the j^{th} environment assuming to follow NID $(0, \sigma^2)$.

The model used by Finlay and Wilkinson (1963) and by Perkins and Jinks (1968a) involves the regression of g_{ij} on E_j effects ($g_{ij} = \beta_i E_j + \delta_{ij}$), i.e.,

$$y_{ijk} = m + V_i + (1 + \beta_i) E_j + \delta_{ij} + e_{ijk} \qquad (2)$$

where β_i is a linear regression coefficient for the i^{th} genotype with a contraint $\sum_{i=1}^{s} \beta_i = 0$, and δ_{ij} is the residual from the regression line for the i^{th} genotype in the j^{th} environment where $\sum_{i=1}^{s} \delta_{ij} = \sum_{j=1}^{t} \delta_{ij} = 0$. The estimator of β_i can be obtained by the least squares method. The result of ANOVA is shown in Table 1.

The model is therefore concerned with the characterisation of each genotype in terms of a phenotypic mean $\bar{y}_{i..}$, and a regression coefficient b_i (estimator of β_i) describing its sensitivity to a specific environmental fluctuation, in which the environmental factors involved are complicated and unmeasurable.

To present the magnitude of G×E interactions, a linear function of a number of environmental factors and the multiple regression method were proposed. In the present study two environmental factors were considered, namely, temperature (T) and light (L). Consequently, the basic model for the analysis of data from a genotype V_i grown in temperature T_j and light L_k for h replicate is:

$$y_{hijk} = m + V_i + T_j + L_k + (VT)_{ij} + (VL)_{ik} + (TL)_{jk} + (VTL)_{ijk} + e_{hijk} \qquad (3)$$

where

y_{hijk} = the observed performance of i^{th} $(i = 1, \ldots, v)$ genotype in the j^{th} $(j = 1, \ldots, t)$ temperature and the k^{th} $(k = 1, \ldots, l)$ light for h^{th} $(h = 1, \ldots, r)$ replicate ;

m = the grand mean ;

V_i = the i^{th} genotypic effect subject to $\sum_{i=1}^{v} V_i = 0$;

T_j = the j^{th} temperature effect subject to $\sum_{j=1}^{t} T_j = 0$;

L_k = the k^{th} light effect subject to $\sum_{k=1}^{l} L_k = 0$;

VT ($\sum_{i=1}^{v} VT_{ij} = \sum_{j=1}^{t} VT_{ij} = 0$) and VL ($\sum_{i=1}^{v} VL_{ik} = \sum_{k=1}^{l} VL_{ik} = 0$) are the first order interactions; VTL ($\sum_{i=1}^{v} VTL_{ijk} = \sum_{j=1}^{t} VTL_{ijk} = \sum_{k=1}^{l} VTL_{ijk} = 0$) is the second order interaction; e_{hijk} = the experimental error contributed by the h^{th} replicate of the i^{th} genotype in the j^{th} temperature and the k^{th} light and is assuming to follow NID $(0, \sigma^2)$.

The three G × E interactions (VT, VL and VTL) can be expressed as linear functions of the environmental indices T, L and TL, respectively, and hence,

Table 1. *ANOVA*

Source	D. F.	S. S.	M. S.	$\mathcal{E}$(MS)
Environment (E)	$t-1$	$SS_E=vr\sum_{j=1}^{t}(\bar{y}_{.j.}-\bar{y}_{...})^2$	MS_E	$\sigma_e^2+\frac{vr}{t-1}\sum_{j=1}^{t}E_j^2$
Genotype (V)	$v-1$	$SS_V=tr\sum_{i=1}^{v}(\bar{y}_{i..}-\bar{y}_{...})^2$	MS_V	$\sigma_e^2+\frac{tr}{v-1}\sum_{i=1}^{v}V_i^2$
G×E (g)	$(v-1)(t-1)$	$SS_g=r\sum_{i=1}^{v}\sum_{j=1}^{t}(\bar{y}_{ij.}-\bar{y}_{i..}-\bar{y}_{.j.}+\bar{y}_{...})^2$	MS_g	$\sigma_e^2+\frac{r}{(v-1)(t-1)}\sum_{i=1}^{v}\sum_{j=1}^{t}g_{ij}^2$
Het. bet. reg.'s (b)	$v-1$	$SS_b=r\sum_{i=1}^{v}[\sum_{j=1}^{t}(\bar{y}_{.j.}-\bar{y}_{...})(\bar{y}_{ij.}-\bar{y}_{i..}-\bar{y}_{.j.}+\bar{y}_{...})]^2/\sum_{j=1}^{t}(\bar{y}_{.j.}-\bar{y}_{...})^2$ $=r\sum_{i=1}^{v}b_i^2\sum_{j=1}^{t}E_j^2$	MS_b	$\sigma_e^2+\frac{r}{v-1}\sum_{i=1}^{v}\sigma_{\delta i}^2+\frac{r}{v-1}\sum_{i=1}^{v}b_i^2\sum_{j=1}^{t}E_j^2$
Residual (δ)	$(v-1)(t-2)$	$SS_\delta=r\sum_{i=1}^{v}[\bar{y}_{ij.}-\bar{y}_{i..}-\bar{y}_{.j.}+\bar{y}_{...}-b_i(\bar{y}_{.j.}-\bar{y}_{...})]^2=SS_g-SS_b$	MS_δ	$\sigma_e^2+\frac{r}{v-1}\sum_{i=1}^{v}\sigma_{\delta i}^2$
Error (e)	$vt(r-1)$	$SS_e=\sum_{i=1}^{v}\sum_{j=1}^{t}\sum_{k=1}^{r}(y_{ijk}-\bar{y}_{ij.})^2$ $=SS_T-SS_E-SS_V-SS_g$	MS_e	σ_e^2
Total (T)	$vtr-1$	$SS_T=\sum_{i=1}^{v}\sum_{j=1}^{t}\sum_{k=1}^{r}(y_{ijk}-\bar{y}_{...})^2$		

Het. bet. reg.'s=Heterogeneity between regressions.

$$\left.\begin{aligned}(VT)_{ij} &= \beta_{Ti}\,T_j + \delta_{ij}\\ (VL)_{ik} &= \beta_{Li}\,L_k + \delta_{ik}\\ (VTL)_{ijk} &= \beta_{TLi}(TL)_{jk} + \delta_{ijk}\end{aligned}\right\} \qquad (4)$$

where regression coefficients β_{Ti}, β_{Li} and β_{TLi} may be estimated from the least squares solutions, i.e.,

$$b_{Ti} = \sum_{j=1}^{t} \widehat{VT}_{ij}\,\widehat{T}_j \Big/ \sum_{j=1}^{t} \widehat{T}_j^2$$

$$b_{Li} = \sum_{k=1}^{l} \widehat{VL}_{ik}\,\widehat{L}_k \Big/ \sum_{k=1}^{l} \widehat{L}_k^2$$

$$b_{TLi} = \sum_{j=1}^{t}\sum_{k=1}^{l} \widehat{VTL}_{ijk}\,\widehat{TL}_{jk} \Big/ \sum_{j=1}^{t}\sum_{k=1}^{l} \widehat{TL}_{jk}^2$$

where, $\widehat{VT}_{ij} = \bar{y}_{.ij.} - \bar{y}_{.i..} - \bar{y}_{..j.} + \bar{y}_{....}$, $\widehat{VL}_{ik} = \bar{y}_{.i.k} - \bar{y}_{.i..} - \bar{y}_{...k} + \bar{y}_{....}$, $\widehat{VTL}_{ijk} = \bar{y}_{.ijk} - \bar{y}_{.ij.} - \bar{y}_{.i.k} - \bar{y}_{..jk} + \bar{y}_{.i..} + \bar{y}_{..j.} + \bar{y}_{...k} - \bar{y}_{....}$; and δ_{ij}, δ_{ik}, δ_{ijk} are the residuals from the fitted regression line, respectively. Thus the model can be written as equation 5, and the result of the analysis of variance is shown in Table 2.

$$y_{hijk} = m + V_i + (1+\beta_{Ti})\,T_j + (1+\beta_{Li})\,L_k + (1+\beta_{TLi})\,(TL)_{jk} + \delta_{ij} + \delta_{ik} + \delta_{ijk} + e_{hijk} \qquad (5)$$

From the ensuing joint regression analysis, the sum of squares of G×E interaction may be partitioned into two orthogonal items, i.e., one measuring the portion of the G×E interactions which is due to differences between the regression lines (linear component), and the other measuring the residuals of the observed values (non-linear component). If the heterogeneity between regressions M.S., or the residual M.S. or both are significant, G×E interactions are present. Therefore: (A) if only the heterogeneity M.S. is significant, within the limits of sampling error, we can predict all the G×E interactions for each genotype from the linear regressions on the environmental values; (B) if only the residual M.S. is significant, there is either no linear relationship, or no simple relationship exists between the G×E interactions and the environmental values, and hence no predictions can be made by the present approach; (C) if both items are significant, not all the interactions of genotypes can be accounted for by the linear component, the practical usefulness of predictions will depend on the relative magnitudes of the two M.S.'s. In the latest case, Perkins and Jinks' (1968b) method can be used to examine the non-linear component of G×E interaction. Correlations can be obtained from the residuals from the linear regressions over environments for each pair of genotypes to assess the relative similarities in their interactions, which are not accounted for by the linear component. There will be no correlation if the direction and magnitude of the residual in each environment is independent for each of

Table 2. *ANOVA*

Source	D. F.	S. S.
Environment	$tl-1$	$SS_{Env.}=vr\sum_{j=1}^{t}\sum_{k=1}^{l}(\bar{y}_{..jk}-\bar{y}_{....})^2$
Temperature	$t-1$	$SS_T=vlr\sum_{j=1}^{t}(\bar{y}_{..j.}-\bar{y}_{....})^2$
Light	$l-1$	$SS_L=vtr\sum_{k=1}^{l}(\bar{y}_{...k}-\bar{y}_{....})^2$
Temp. × Light	$(t-1)(l-1)$	$SS_{TL}=vr\sum_{j=1}^{t}\sum_{k=1}^{l}(\bar{y}_{..jk}-\bar{y}_{..j.}-\bar{y}_{...k}+\bar{y}_{....})^2$
Genotype	$v-1$	$SS_V=tlr\sum_{i=1}^{v}(\bar{y}_{.i..}-\bar{y}_{....})^2$
G × Env.	$(v-1)(tl-1)$	$SS_{V\times Env.}=r\sum_{i=1}^{v}\sum_{j=1}^{t}\sum_{k=1}^{l}(\bar{y}_{.ijk}-\bar{y}_{.i..}-\bar{y}_{..jk}+\bar{y}_{....})^2$
G × Temp.	$(v-1)(t-1)$	$SS_{VT}=lr\sum_{i=1}^{v}\sum_{j=1}^{t}(\bar{y}_{.ij.}-\bar{y}_{.i..}-\bar{y}_{..j.}+\bar{y}_{....})^2$
Het. bet. reg.'s	$v-1$	$SS_{b_T}=lr\sum_{i=1}^{v}b_{Ti}^2\sum_{j=1}^{t}T_j^2$
Residual	$(v-1)(t-2)$	$SS_{\delta_T}=lr\sum_{i=1}^{v}[\bar{y}_{.ij.}-\bar{y}_{.i..}-\bar{y}_{..j.}+\bar{y}_{....}-b_{Ti}(\bar{y}_{..j.}-\bar{y}_{....})]^2$ $=SS_{VT}-SS_{b_T}$
G × Light	$(v-1)(l-1)$	$SS_{VL}=tr\sum_{i=1}^{v}\sum_{k=1}^{l}(\bar{y}_{.i.k}-\bar{y}_{.i..}-\bar{y}_{...k}+\bar{y}_{....})^2$
Het. bet. reg.'s	$v-1$	$SS_{b_L}=tr\sum_{i=1}^{v}b_{Li}^2\sum_{k=1}^{l}L_k^2$
Residual	$(v-1)(l-2)$	$SS_{\delta_L}=tr\sum_{i=1}^{v}[\bar{y}_{.i.k}-\bar{y}_{.i..}-\bar{y}_{...k}+\bar{y}_{....}-b_{Li}(\bar{y}_{...k}-\bar{y}_{....})]^2$ $=SS_{VL}-SS_{b_L}$
G × Temp. × Light	$(v-1)(t-1)(l-1)$	$SS_{VTL}=r\sum_{i=1}^{v}\sum_{j=1}^{t}\sum_{k=1}^{l}(\bar{y}_{.ijk}-\bar{y}_{.ij.}-\bar{y}_{.i.k}-\bar{y}_{..jk}+\bar{y}_{.i..}+\bar{y}_{..j.}+\bar{y}_{...k}-\bar{y}_{....})^2$
Het. bet. reg.'s	$v-1$	$SS_{b_{TL}}=r\sum_{i=1}^{v}b_{TLi}^2\sum_{j=1}^{t}\sum_{k=1}^{l}(TL)_{jk}^2$
Residual	$(v-1)(tl-t-l)$	$SS_{\delta_{TL}}=r\sum_{i=1}^{v}[\bar{y}_{.ijk}-\bar{y}_{.ij.}-\bar{y}_{.i.k}-\bar{y}_{..jk}+\bar{y}_{.i..}+\bar{y}_{..j.}+\bar{y}_{...k}-\bar{y}_{....}-b_{TLi}(\bar{y}_{..jk}-\bar{y}_{..j.}-\bar{y}_{...k}+\bar{y}_{....})]^2$ $=SS_{VTL}-SS_{b_{TL}}$
Error	$vtl(r-1)$	$SS_e=\sum_{h=1}^{r}\sum_{i=1}^{v}\sum_{j=1}^{t}\sum_{k=1}^{l}(y_{hijk}-\bar{y}_{.ijk})^2$ $=SS_{Total}-SS_{Env.}-SS_V-SS_{V\times Env.}$
Total	$vtlr-1$	$SS_{Total}=\sum_{h=1}^{r}\sum_{i=1}^{v}\sum_{j=1}^{t}\sum_{k=1}^{l}(y_{hijk}-\bar{y}_{....})^2$

Het. bet. reg.'s=Heterogeneity between regressions.

two genotypes. The correlation will be significantly positive if the residuals in each environment are in the same direction and have the same relative magnitudes for the two genotypes, or significantly negative if the residuals are in opposite directions to the same relative degree. Genotypes are divided into groups consisting of genotypes which are relatively homogeneous in their interactions with environmental differences, and to see whether or not this can lead to a reduction in the non-linear component of G×E interaction.

Genetic Parameter Method

In the above-mentioned models, we have confined our attention to the case of inbred lines. The methods developed by Bucio Alanis and Hill (1966) and Perkins and Jinks (1968a) are used to develop the genetic model of stability.

The observed performance of F_1 hybrid ($F_{(il)jk}$) and it's parents (P_{ijk} and P_{ljk}) of the k^{th} replicate in the j^{th} environment are expressed as:

$$\left.\begin{aligned} P_{ijk} &= m + d_i + (1+\beta_{di})E_j + \delta_{ij} + e_{ijk} \\ P_{ljk} &= m + d_l + (1+\beta_{dl})E_j + \delta_{lj} + e_{ljk} \\ F_{(il)jk} &= m + h_{(il)} + (1+\beta_{h(il)})E_j + \delta_{(il)j} + e_{(il)jk} \end{aligned}\right\} \quad (6)$$

where m, β_h, β_d, δ and e are the same as those above-mentioned. But, we consider the effect of genotype, as either the additive effect for the parents [d] or the dominance effect for the F_1 [h], the parameter are written with the subscript "h" or "d" to indicate that it is related to the G×E interaction of heterozygous or the homozygous genotype. The environmental values E_j for $F_{(il)jk}$ are now calculated as:

$$\hat{E}_j = \sum_{k=1}^{r} (P_{ijk} + P_{ljk})/2r - \hat{m} \quad (7)$$

and are not the same as defined in Eberhart and Russell's model. The E_j value based on the inbred parents may differ from one F_1 to another, and hence provides an independent assessment of the environment. With constraints $\sum_{i=1}^{s} d_i = 0$, $\sum_{j=1}^{t} E_j = 0$, and $\sum_{i=1}^{s} g_{ij} = \sum_{j=1}^{t} g_{ij} = 0$, and by using least squares method, the estimators can be obtained as follows:

$$\left.\begin{aligned} \hat{m} &= \sum_{j=1}^{t}\sum_{k=1}^{r} (P_{ijk} + P_{ljk})/2tr \\ \hat{d}_i &= \sum_{j=1}^{t}\sum_{k=1}^{r} (P_{ijk} - P_{ljk})/2tr = -\hat{d}_l \\ \hat{d}_i + \hat{g}_{ij} &= \sum_{k=1}^{r} [P_{ijk} - (1/2)(P_{ijk} + P_{ljk})]/r = -\hat{d}_l - \hat{g}_{lj} \\ \hat{h}_{(il)} &= \sum_{j=1}^{t}\sum_{k=1}^{r} F_{(il)jk}/tr - \hat{m} \\ \hat{h}_{(il)} + \hat{g}_{(il)j} &= \sum_{k=1}^{r} [F_{(il)jk} - (1/2)(P_{ijk} + P_{ljk})]/r \\ \hat{g}_{ij} &= b_{di}\hat{E}_j + \hat{\delta}_{ij} = -\hat{g}_{lj} \\ \hat{g}_{(il)j} &= b_{h(il)}\hat{E}_j + \hat{\delta}_{(il)j} \end{aligned}\right\} \quad (8)$$

This method will be illustrated with reference to the quantitative characters of the four F_1 hybrids and their parents grown under different temperature conditions.

Results

1. *Simple Regression Analysis for Inbred Lines Grown in Different Temperature Regimes*

(1) Under artificial light

The result of ANOVA of the data for inbred lines under artificial light is shown in Table 3. The G×E interaction was classified into the portion due to heterogeneity of regression of respective genotypes on temperature means, and the residual portion due to deviation from regressions (cf. equation 2). The heterogeneity of regression among genotypes was significant in all traits (A, B, C and D in Table 3), except those of plant height and rosette size with non-transformed data (C′ and D′ in Table 3). The residual M.S. was also significant only in plant height (exponential transformed data). With the plant height data, the fourteen inbred lines could be divided into two groups differing in regression by using Perkins and Jinks' method, as shown in Table 4.

Accordingly, the additive genetic (genotypic effect), and linear (heterogeneity between regressions) and non-linear (residual) portions of G×E interaction M.S. were each partitioned into those due to "between groups" and "within groups" effects (Table 5). In this analysis, each term was significant when tested against the error M.S., but, the "between groups" difference was highly significant when tested by the "within groups" heterogeneity in both G×E and residual M.S. However, there was no such consistent difference in the additive genotypic effect.

Table 3. *ANOVA for 14 inbred lines under artificial light*

Source	D.F.	A	B	C′	C	D′	D
Environment	2	1344.9285**	5.0888**	4.0613**	107.5795**	47.4499*	0.2147**
Genotype	13	198.8919**	24.6939**	1.0401**	37.5683**	148.8819**	0.2700**
G×E	26	62.4927*	2.5775**	0.3191**	18.9232**	57.3767**	0.1605**
Het. bet. reg.'s	13	91.3037*	4.8091**	0.4242	30.4644**	52.6550	0.3060**
Residual	13	33.6817	0.3458	0.2140**	7.3820*	62.0984**	0.0150
Error	84	33.2223	0.5094	0.0679	3.7291	10.2159	0.0348
Total	125						

A: flowering days, B: L/P, C′: plant height, C: Exp. (plant height),
D′: rosette size, D: 1/(rosette size),
** and *: significant at 1% and 5% level, respectively.

Table 4. *Matrix of significant correlations found between inbred lines under artificial light, for plant height (Exp. transformation)*

		Group													
	Line	1							2						
		1	2	3	4	6	7	10	5	8	9	11	12	13	14
Group 1	1	+	+	+	+	+	+	+	−	−	−	−	−	−	−
	2	+	+	+	+	+	+	+	−	−	−	−	−	−	−
	3	+	+	+	+	+	+	+	−	−	−	−	−	−	−
	4	+	+	+	+	+	+	+	−	−	−	−	−	−	−
	6	+	+	+	+	+	+	+	−	−	−	−	−	−	−
	7	+	+	+	+	+	+	+	−	−	−	−	−	−	−
	10	+	+	+	+	+	+	+	−	−	−	−	−	−	−
Group 2	5	−	−	−	−	−	−	−	+	+	+	+	+	+	+
	8	−	−	−	−	−	−	−	+	+	+	+	+	+	+
	9	−	−	−	−	−	−	−	+	+	+	+	+	+	+
	11	−	−	−	−	−	−	−	+	+	+	+	+	+	+
	12	−	−	−	−	−	−	−	+	+	+	+	+	+	+
	13	−	−	−	−	−	−	−	+	+	+	+	+	+	+
	14	−	−	−	−	−	−	−	+	+	+	+	+	+	+

Significant correlations + or −, P<5%.

Table 5. *The genotype, G×E and residual mean squares each classified into "between groups" and "within groups" portions by dividing the 14 inbred lines into two groups, for plant height under artificial light (Exp. transformation)*

Source	D. F.	S. S.	M. S.	V. R. [(i)/(ii)]
Genotype	13	488.3878	37.5683	
(i) Bet. groups	1	11.3650	11.3650	0.2859
(ii) Within groups	12	477.0228	39.7519	
G×E				
Het. bet. reg.'s	13	396.0374	30.4644	
(i) Bet. groups	1	264.0283	264.0283	24.0009**
(ii) Within groups	12	132.0091	11.0008	
Residual	13	95.9658	7.3820	
(i) Bet. groups	1	63.9782	63.9782	24.0011**
(ii) Within groups	12	31.9877	2.6656	

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

(2) Under natural light

With the data from plants grown under natural light, the G×E interaction was significant only in plant height (Table 6).

Table 6. *ANOVA for plant height of 14 inbred lines under natural light*

Source	D. F.	A	B	C	D
Environment	2	445.1677**	0.1686	86.9780**	0.1682**
Genotype	13	125.2753**	1.2840**	2.1465**	0.0288**
G×E	26	33.1838	0.0826	2.3612**	0.0053
Het. bet. reg.'s	13	28.7145	0.0824	4.2755**	0.0068
Residual	13	37.6530	0.0828	0.4469	0.0039
Error	84	29.5318	0.1093	0.8687	0.0042
Total	125				

A: flowering days, B: L/P, C: Exp. (plant height), D: 1/(rosette size),
** and *: significant at 1% and 5% level, respectively.
Het. bet. reg.'s=Heterogeneity between regressions.

Table 7. *ANOVA for 14 inbred lines*

Source	D. F.	A	B	C	D
Environment	5	1268.0635**	4.3901**	94.8823**	0.1682**
Temperature	2	346.3328**	3.0105**	191.1124**	0.0271
Light	1	2760.1416**	11.4360**	85.2965**	0.0758
Temp.×Light	2	1443.7604**	2.2468**	3.4450	0.3555**
Genotype	13	234.6313**	18.0965**	27.0762**	0.1641**
G×E	65	56.1778**	2.6403**	11.0415**	0.0933**
G×Temp.	26	33.3419	1.1958**	15.8014**	0.0871**
Het. bet. reg.'s	13	49.5344*	2.1418**	27.3190**	0.0250
Residual	13	17.1493	0.2498	4.2839*	0.1491**
G×Light	13	89.5360**	7.8814**	12.6386**	0.1347**
Het. bet. reg.'s	13	89.5360	7.8814	12.6386	0.1347
Residual	0	—	—	—	—
G×Temp.×Light	26	62.3346**	1.4643**	5.4830**	0.0788**
Het. bet. reg.'s	13	6.5965	0.0006	0.4707	0.0678
Residual	13	118.0726**	2.9280**	10.4952**	0.0898**
Error	168	31.3771	0.3093	2.2989	0.0195
Total	251				

A: flowering days, B: L/P, C: Exp. (plant height), D: 1/(rosette size) size,
** and *: significant at 1% and 5% level, respectively.
Het. bet. reg.'s=Heterogeneity between regressions.

2. *Multiple Regression Analysis for Inbred Lines at Different Temperature Regimes under Different Light Conditions*

The results of ANOVA involving multiple regression analysis is given in Table 7. Most of the items were highly significant when tested against the error, but, comparisons of the heterogeneity between regressions and the residual of three compoents of G×E were of primary interest in this study. On flowering days, two interaction (G×T and G×L) were significant, while the residuals were non-significant when tested against the error. This means that the two interactions can be expressed by a linear function of two environmental indices (temperature and light), respectively. In other words, the value of flowering days of each genotype can be predicted by equation 5.

Two other traits, L/P and plant height, showed a similar trend as of flowering days, namely, the interactions of G×T and G×L could be expressed by a linear function of the environmental indices. However, in the G×T×L interaction, residual M. S. was significant but the heterogeneity between regressions was not significant when tested against the corresponding residual M. S. Hence, the three-way interactions could not be represented by linear responses.

In addition, similarly as found in the regression analysis of plant height under artificial light, the M. S. for plant height due to heterogeneity between regressions and the corresponding residual M. S. for G×T interaction were both significant. Therefore, the inbred lines were devided into two groups on the basis of their correlation matrix (Table 8). In this case, line F10 (line no. 2) which was in group 1 previously was moved to group 2. Possibly, the plant height of line F10 would be sensitive to light conditions.

3. *Measurement of Phenotypic Stability*

The estimated values of $\bar{y}_{i..}$ and b_i for flowering days of each line under artificial light are given in Table 9, and the graphic relationship of b_i and $\bar{y}_{i..}$ are presented in Fig. 1. Lines F10, V50, V198, Wil-2, Est-0 and Oy-0 were early-flowering and showed a high stability of flowering days. Line F4 was late-flowering ($\bar{y}_{i..}=42.7$ days) and was relatively stable, whereas Hm was a early-flowering and its flowering days was unstable or plastic. The regression coefficient of line F26 significantly differed from zero. This would be resulted from an unusually plastic response.

As mentioned above, the response of plant height to temperature could be expressed by a linear regression (Table 6). The relationship between performance ($\bar{y}_{i..}$) and regression coefficient (b_i) is shown in Fig. 2 for plants grown under natural and artificial light conditions. The regression analysis of the data showed that certain inbred lines were stable while others were more plastic in the response of plant height to temperatures.

Table 8. *Matrix of significant correlations found between inbred lines, for plant height (Exp. transformation)*

Group	Line	Group 1						Group 2							
		1	3	4	6	7	10	2	5	8	9	11	12	13	14
1	1	+	+	+	+	+	+	−	−	−	−	−	−	−	−
	3	+	+	+	+	+	+	−	−	−	−	−	−	−	−
	4	+	+	+	+	+	+	−	−	−	−	−	−	−	−
	6	+	+	+	+	+	+	−	−	−	−	−	−	−	−
	7	+	+	+	+	+	+	−	−	−	−	−	−	−	−
	10	+	+	+	+	+	+	−	−	−	−	−	−	−	−
2	2	−	−	−	−	−	−	+	+	+	+	+	+	+	+
	5	−	−	−	−	−	−	+	+	+	+	+	+	+	+
	8	−	−	−	−	−	−	+	+	+	+	+	+	+	+
	9	−	−	−	−	−	−	+	+	+	+	+	+	+	+
	11	−	−	−	−	−	−	+	+	+	+	+	+	+	+
	12	−	−	−	−	−	−	+	+	+	+	+	+	+	+
	13	−	−	−	−	−	−	+	+	+	+	+	+	+	+
	14	−	−	−	−	−	−	+	+	+	+	+	+	+	+

Significant correlations + or −, P<5%.

Table 9. *The $\bar{y}_{i..}$ and b_i values of inbred lines under artificial light for flowering days*

Line		$\bar{y}_{i..}$	b_i
1	F4	42.7	0.04
2	F10	27.6	−0.16
3	F26	32.9	1.62*
4	F57	31.2	0.73
5	F104	36.4	−0.63
6	V46/6	35.6	0.72
7	V50	30.0	−0.08
8	V198	29.7	−0.07
9	Wli-2	30.4	−0.21
10	Est-0	29.3	0.06
11	Oy-0	28.6	−0.43
12	En-2	28.0	−0.87
13	GR1.4	36.2	0.29
14	Hm	24.4	−0.99
Total mean		31.6	

L. S. D.=9.36 (P<5%), 12.40 (P<1%),
Environmental index=−4.12, −2.33, 6.45,
** or * reject H_0: $\beta=0$, ($\alpha=1\%$, $\alpha=5\%$),
$\bar{y}_{i..}$: phenotypic mean,
b_i: regression coefficient.

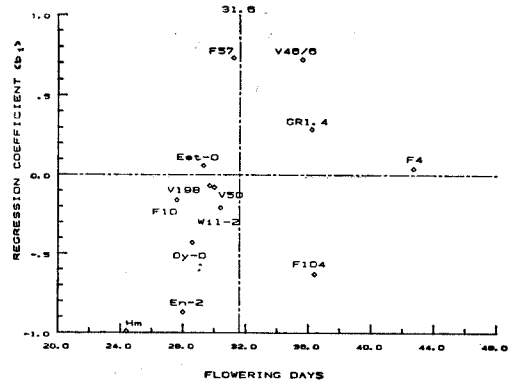
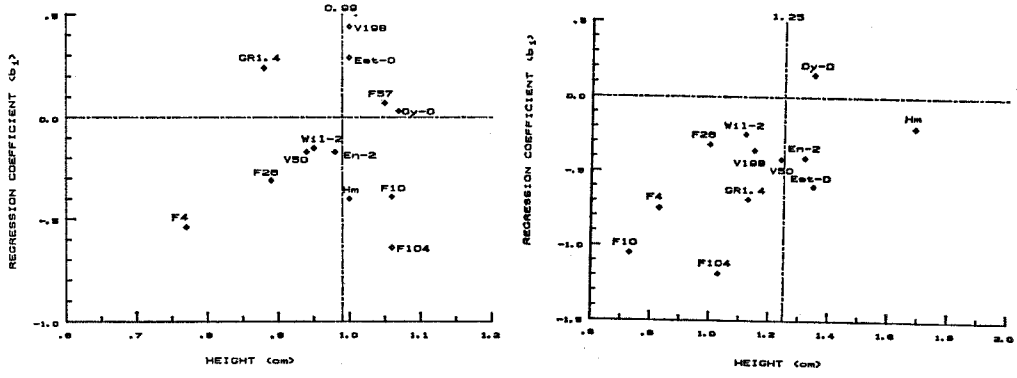


Fig. 1. The relation of phenotypic mean and regression coefficient for flowering days of inbred lines under artificial light.



(A) (B)

Fig. 2. The relation of phenotypic mean and regression coefficient for plant height of inbred lines under (A) natural, (B) artificial light condition.

The multiple regression analysis (equation 5) yielded several regression coefficients, which could be used for measuring stability or plasticity of a trait in response to temperature, light condition, or their interaction. These are exemplified in Fig. 3.

4. *Regression Analysis of F_1 Hybrid and Its Parents*

Following Bucio Alanis and Hill (1966) and Perkins and Jinks (1968a), the analysis will be illustrated with reference to cross F10×F57.

(1) Rosette size of cross F10×F57

The genetic and interaction components for rosette size (reciprocal transformed data) of parents F10 and F57 and their F_1 hybrid in three different temperatures

are given in Table 10. The linear regression of estimates $(h_{(il)} + g_{(il)j})$ on E_j had a slope $(1 + b_{h(il)})$ of -0.05. The estimates by b_d and b_h can be obtained by subtracting the slopes of the parents and hybrid, respectively, from unity. Thus, b_d was equal to -1.14 and $+1.14$, thereby confirming that the two parents responded differently to changes in temperature. The b_h value of -1.05 differed significantly form zero, indicating that the performance of hybrid changed with temperatures. The regression M.S. was highly significant when tested against the error and residual M.S. The regression equations of the F_1 hybrid and its parents could be written as:

$$(F10)_j = 0.77 - 2.14\ E_j$$
$$(F57)_j = 0.12 - 0.14\ E_j$$
$$(F10 \times F57)_j = 0.12 - 0.05E_j$$

The regression lines are shown in Fig. 4A.

The regression lines for h and d components were plotted together in Fig. 4B.

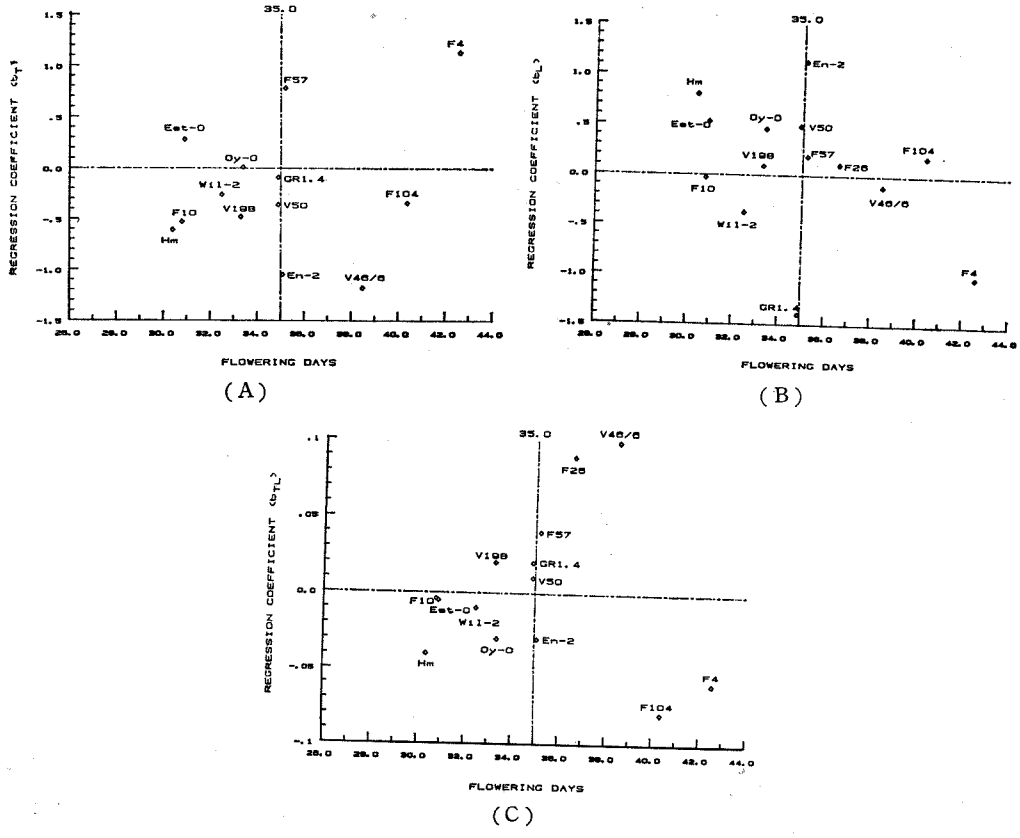


Fig. 3. The relation of phenotypic mean and regression coefficient (A) b_T, (B) b_L, and (C) b_{TL} for flowering days of inbred lines under different environments.

Table 10. *Regression analysis for rosette size of an F_1 hybrid of the cross of F10×F57 grown at three different temperatures*

Item	g			d	b_d
	T_1+	T_2	T_3		
F10 (i)	−0.29	−0.21	0.50	0.32	1.14
F57 (l)	0.29	0.21	−0.50	−0.32	−1.14
F10×F57	0.23	0.23	−0.46	$h_{(il)}$ −0.33	$b_{h(il)}$ −1.05

ANOVA

Source	D. F.	S. S.	M. S.	F([1]/[2])	F([1]/[3])
[1] Regression	1	0.3191	0.3191	25124.8960**	57.7454**
[2] Residual	1	1.3E-5	1.3E-5		
[3] Error	24	0.1326	0.0055		

** and *: significant at 1% and 5% level, respectively.
d: additive effect, h: dominance effect, b_d or b_h: regression coefficient,
g: interaction, $\bar{y}_{i..}$: phenotypic mean, $\bar{y}_{...}=0.44$,
Environmental index: $E_1=-0.22$, $E_2=-0.22$, $E_3=0.44$,
+: day/night temperature: T_1 (20-22)/(15-17)°C,
T_2 (25-27)/(20-22)°C,
T_3 (30-32)/(25-27)°C.

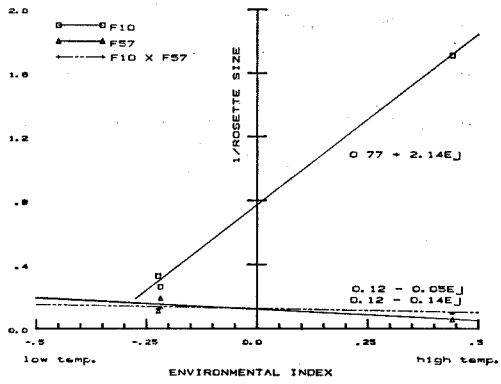


Fig. 4A. Comparison of the phenotypic regressions for cross F10×F57 and its parents in rosette size (reciprocal transformation).

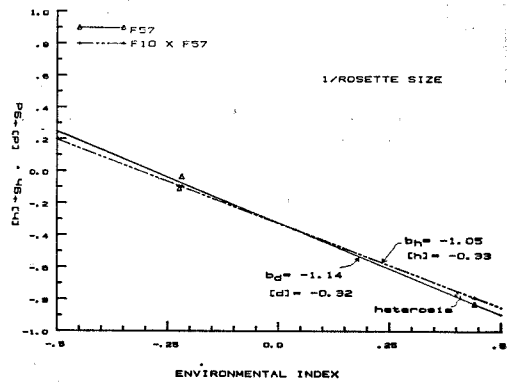


Fig. 4B. The effect of environment on additive [d] and dominance [h] effect of cross F10×F57 in rosette size (reciprocal transformation).

Since b_d and b_h did not differ significantly from each other, the level of dominance would be independent of the environment. However, heterosis was more pronounced under high temperature conditions.

The estimates of b_h and h for various quantitative characters of the four F_1

hybrids are given in Table 11. Three b_h values (marked by +) were significant not only against the error M.S. but also against their own residual M.S., although the latter was itself significant. Because b_h and h values of F10×Wil-2 are similar to those of F10×F57 in rosette size, they have the same results.

(2) Plant height of cross Fi0×Est-0

The regression lines of the parents and their hybrid are shown in Fig. 5A. The estimates of b_d and b_h differed significantly from each other. The genetic implications of this result are interesting, because the expression of dominance for this trait in these populations dependent upon the environment, ranging from apparent overdominance at the lowest temperature through complete dominance to partial dominance at the highest temperature. Heterosis in plant height was more pronounced at low temperature (Fig. 5B).

Table 11. *The $\bar{y}_{i..}$, $h_{(i)}$ and $b_{h(i)}$ fo F_1 hybrids grown at three different temperatures*

F_1	Flowering days			L/P		
	$\bar{y}_{i..}$	$h_{(i)}$	$b_{h(i)}$	$\bar{y}_{i..}$	$h_{(i)}$	$b_{h(i)}$
F10×F57	22.6	−6.75	−0.82	1.40	−0.22	0.87
F10×Est-0	20.7	−6.10	−1.07	1.56	−0.09	0.50
F10×Wil-2	17.2	−11.78	−0.61	1.46	−0.44	−2.01
Wil-2 V46/6	20.5	−12.35	−0.90	1.37	−0.33	−1.79
Total mean	20.3			1.45		
L.S.D.=	11.03 (P<5%), 14.95 (P<1%)			0.55 (P<5%), 0.75 (P<1%)		

F_1	Exp. (height)			1/rosette size		
	$\bar{y}_{i..}$	$h_{(i)}$	$b_{h(i)}$	$\bar{y}_{i..}$	$h_{(i)}$	$b_{h(i)}$
F10×F57	5.57	1.38	−0.57	0.12	−0.33	−1.05†
F10×Est-0	4.13	0.99	−1.20†	0.16	−0.31	−0.87
F10×Wil-2	3.64	0.95	−0.37	0.16	−0.30	−0.98†
Wil-2×V46/6	6.17	−0.43	−0.18	0.12	0.01	−0.48
Total mean	4.88			0.14		
L.S.D.=	2.28 (P<5%), 3.09 (P<1%)			0.13 (P<5%), 0.07 (P<1%)		

† sig. when tested against the MS (Res.) and MS (Error),
h: dominance effect, b_h: regression coefficent, $\bar{y}_{i..}$: phenotypic mean.

Discussion

The experimental results presented have illustrated that the regression anal ysis proposed by Perkins and Jinks (1968a,b) is a powerful tool in the analysis of

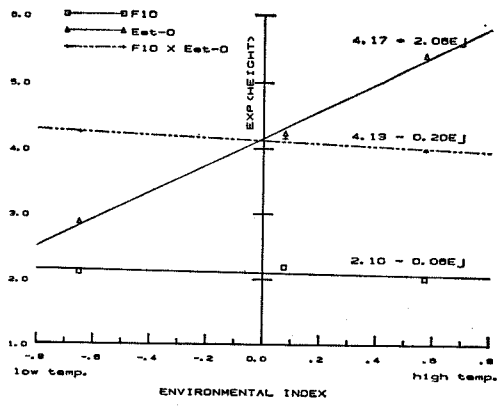


Fig. 5A. Comparison of the phenotypic regressions for cross F10×Est-0 and its parents in plant height (exponential transformation).

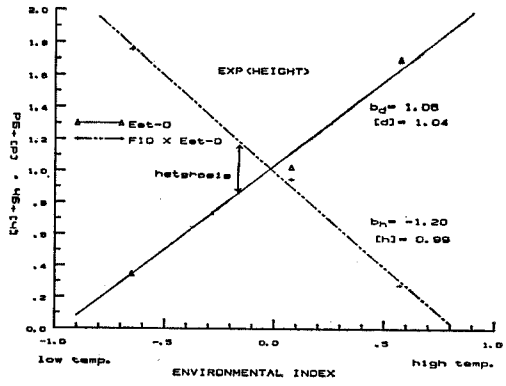


Fig. 5B. The effect of environment on additive [*d*] and dominance [*h*] effect of cross F10×Est-0 in plant height (exponential transformation).

G×E interactions. We have examined additive genetical component, V(d_i), linear regression coefficient, b_i, and non-linear residual, δ_{ij}. In some traits, the linear portion could account for a greater part of the G×E interaction. On the other hand, in plant height, the interaction was accounted for mainly by the non-linear component. After grouping of inbred lines according to their response to environment, linear (heterogeneity between regressions) and non-linear (residual) components of the G×E interaction showed significance. This implies that dividing the lines into groups which are internally homogeneous has achieved a reduction in the residual M. S.

The linear regression coefficient accounted for a greater part of G×E interactions. It is a useful measure of the response of a genotype to the given environments. A genotype with an average sensitivity will have a *b* value of zero (Bucio Alanis *et al.*, 1966) or a (1+*b*) value of 1.00 (Yates and Cochran, 1938). Such a genotype shows no particular G×E interaction, and is stable. On the other hand, a genotype which is unstable or plastic will have a *b* value different from zero. Phenotypic stability and plasticity are of primary importance in plant breeding. Yield stability is an important requirement in crops, but does not make sense in wild plants. *Arabidopsis thaliana* is a wild plant, in which phenotypic plasticity plays a role in adaptation. Even so, both two points have been considered in this paper. We have concentrated on statistical rather than biological aspects.

There are two possible source of bias in the estimation of regression coefficients according to the method of Perkins and Jinks (1968a), and some modified methods are suggested which removes such biases. The first bias is arised from the use of environmental index represented by the mean value for all genotypes as an inde-

pendent variable. Its variance contains an error component presumed to be uncorrelated with the dependent variable (Sprent, 1969; Wright, 1976). Provided that a large number of genotypes are included in the experiment (Hardwick and Wood, 1972), or an independent assessment of the environment can be obtained by using control genotypes (Freeman, 1973), the bias which results should not prove serious in practice. The second bias is resulted from the genotypic values regarded as random (Freeman and Perkins, 1971), presumably giving rise to a spurious element of correlation which may differ from genotype to genotype. In the majority of cases, the genotypic values can be properly regarded as fixed (Wright, 1976), and, provided that the error variance is homogeneous by grouping method (Perkins and Jinks, 1968b), or under the usual assumptions in analysis of variance (Tai, 1971), there will be no second bias in the normal estimate of regression coefficients. Hence, the use of present data from fourteen inbred lines for statistical analysis, may reduce the first bias to some extent. In addition, the second bias can be removed by using Perkins and Jinks' grouping method.

Mutiple regession analysis is essentially an extensiion of the simple regression analysis. Multiple regression can assess the simultaneous effects of a number of well-controlled environmental factors. Nevertheless, in a field trial, data should be first examined by principal component analysis, or equivalent techniques to show which particular environments contribute to the interaction. Then, multiple regression analysis can be used to interpret the linear relationship between the interactions and the environments.

Finally, from a biometrical standpoint, we extended the analysis already described for inbred lines to the F_1 generation. From the results presented, the effect of G×E interaction shows to be linearly related to the envirnmental effect. Such a relationship has important practical applications from a breeder's point of view. This enables a breeder to obtain more reliable estimates of additivity, dominance and heterosis, and hence to predict with greater accuracy the rate of genetic progress under selection for any given trait. Bucio Alanis *et al.* (1969) pointed out, in the absence of non-allelic interactions, this approach may be equally useful in predicting performance over generations. An environmental index, based on the inbred parents, will also supply an independent measure for the segregating generations.

Acknowledgements

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Arabidopsis thaliana 之遺傳與環境交感效應之研究

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本研究係利用 *Arabidopsis thaliana* (L.) Heynh. 之14個自交系及4種 F_1 雜交組合，於人工照明與自然日照等兩種條件下，配合三種不同的溫度處理，探討始花日數、葉長與柄長之比、株高及株叢面積等四種性狀之基因型與環境間的交感效應。

依直線廻歸分析法及複廻歸多環境指標法探討基因型與環境之交感效應，獲得下列結論：

1. 建立複廻歸多環境指標之模式以探討基因型與環境間之交感效應結果，始花日數，葉長與柄長之比及株高之基因型與溫度、光照間的二次交感效應與其環境指標間都呈直線關係，而所有自交系的四種性狀在綜合溫度及光照因子之環境下，其交感效應均不能以直線關係表示之。

2. 人工照明下，所有自交系之始花日數及葉長與柄長之比兩性狀的基因型與溫度間之交感效應都可用直線廻歸模式分析，而且株高經指數轉換，株叢面積經倒數轉換後，也能獲致良好的結果，其交感效應與溫度之間亦具有直線關係。然而在自然日照下，則除經轉換後的株高外，交感效應並不存在。

3. 一部份雜交組合及其親本對溫度之反應，呈直線廻歸模式。F10×F57 與 F10×Wil-2 兩雜交組合之株叢面積，在高溫時雜種優勢較易表現；而 F10×Est-0 之雜交組合的株高，則在溫度愈低下，雜種優勢之表現愈明顯，此暗示雜種優勢之表現因性狀及環境之不同而異。

4. 利用廻歸係數估值與性狀平均值間之關係，可以比較基因型在不同環境下的適應性及性狀之表現。