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Studies on the dynamic model of plant adaptation of quantitative characters

III. Diallel analysis

Hsiu-Ying Lu[1] and Hong-Pang Wu[2]

[1] *Department of Agronomy, Taiwan Agricultural Research Institute, Wufeng, Taichung Hsien, Taiwan 41301, Republic of China*

[2] *Institute of Botany, Academia Sinica, Nankang, Taipei, Taiwan 11529, Republic of China*

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Abstract. A full set of diallel cross of nine genetic lines of *Arabidopsis thaliana* was made and used to analyze the mechanism of inheritance of the three types of stability of fresh weight in dynamic model. A dynamic model combining features of Griffing's method with the linear regression was established to assess the combining abilities of combiners and examine the fluctuation of heterosis under different environmental conditions for different growth periods. Analysis of combining ability revealed that inheritance of the three types of stability was controlled predominantly by dominance deviations whereas both additive and dominance effects were equally important. Reciprocal crosses showed lower yield and higher stability than their single crosses. Lack of association between the general combining ability of stability and the phenotypic mean of parents suggested that a desirable parent did not necessarily transmit the high potential yield and low linear response to its progeny. It was also difficult to select a desirable hybrid having above average specific combining effect (SCA) for phenotypic mean and remarkably low SCA for stability. Heterosis with high phenotypic mean and low stability was pronounced under favourable environment at the final stages of growth. Both growth and environment stabilities were heritable and possessed the same genetic constitution by means of Jinks-Hayman's diallel analysis. They were controlled mostly by the dominance effect, but the heritabilities were very samll. Low stability was dominant over high stability and overdominance was obvious. Maternal effects in reciprocal crosses were found. The dominant and recessive alleles in the parents were nearly equal in frequency and number. There seemed to be at least four gene groups affecting stability.

Key words: *Arabidopsis thaliana;* Diallel analysis; Dynamic model; Stability.

Introduction

In the previous study (Wu and Lu, 1988), we obtained that the stabilities of various genetic materials were different, and the stability of F_1 was always less stable than their parents. This phenomenon especially occurred in the F_1 plants with large heterosis and heavy fresh weight, and the stabilities of growth as well as environment were different among reciprocal crosses, therefore, the maternal effect may exist in the inheritance of these stabilities. Wu (1974) had studied on the genetic components of environment stability according to the Jinks-Hayman's method, and found that the gene effects were different among various growth stages. In this study, we proposed a dynamic model combining features of Griffing's method with linear regression to assess the combining abilities and heterosis, and adopted the methods of Jinks (1954) and Hayman (1954a,b) to analyze the genetic components and to study the inheritance of growth and environment stabiliy.

Materials and Methods

Experimental Materials

The experimental materials and cultural methods were described in the previous paper (Wu and Lu, 1988), and the estimated values of growth and environment stability obtained in this study were also used to study the mechanism of inheritance, and combining ability.

Statistical Methods

1. Combining ability

The modified method of Griffing (1956) model of general and specific combining ability was used here. The mean performance of a line, when expressed as a deviation from the mean of all crosses, is called the general combining ability (GCA) of the line. Any particular cross has an "expected" value which is the sum of the GCA of its two parental lines. The cross may, however, deviate from this expected value to a greater or lesser extent, this deviation is called the specific combining ability (SCA) of the two lines. In statistical terms, the GCA is equivalent to the main effect and the SCA is an interaction (Falconer, 1981).

We consider the following mathematical model:

$$\begin{aligned} \mathrm{Y}_{\mathrm{tilj}} = {} & \mu + \mathrm{T}_{\mathrm{t}} + \mathrm{g}_{\mathrm{i}} + \mathrm{g}_{\mathrm{l}} + \mathrm{s}_{\mathrm{il}} + \mathrm{r}_{\mathrm{il}} + \mathrm{E}_{\mathrm{j}} + \alpha_{\mathrm{til}} + \beta_{\mathrm{tj}} \\ & + \mathrm{I}_{\mathrm{ilj}} + \omega_{\mathrm{tilj}} + \frac{1}{\mathrm{q}} \sum_{\mathrm{k}=1}^{\mathrm{q}} \mathrm{e}_{\mathrm{tiljk}} \end{aligned} \tag{1}$$

where $\mathrm{Y}_{\mathrm{tilj}}$ represents the mean value of the i×l th hybrid in the j th environment at the t th growth time ($\mathrm{i}=1,..,\mathrm{a},\ \mathrm{l}=1,..,\mathrm{a},\ \mathrm{j}=1,..,\mathrm{p},\ \mathrm{t}=1,..,\mathrm{m}$). μ is the overall mean. g_{i} and g_{l} is the general combining ability of the i th and l th parent, repectively. s_{il} $(=\mathrm{s}_{\mathrm{li}})$ is the specific combining ability of the i×l th hybrid. $\mathrm{r}_{\mathrm{il}}(=-\mathrm{r}_{\mathrm{li}})$ is the reciprocal effect of the i×l th hybrid. T_{t} is the effect of growth time. E_{j} is the j th environmental effect. α_{til}, β_{tj}, $\mathrm{I}_{\mathrm{ilj}}$ and ω_{tilj} are the effects of interactions between the t th growth time and the i×l th hybrid, the t th growth time and the j th environment, the i×l th hybrid and the j th environment, the i×l th hybrid and the j th environment as well as the t th growth time, respectively. The error term $\mathrm{e}_{\mathrm{tiljk}}$ is independently normally distributed with mean zero and variance σ^2 ($\mathrm{k}=1,..,\mathrm{q}$).

The interaction effects (α_{til}, $\mathrm{I}_{\mathrm{ilj}}$ and ω_{tilj}) are characteristics of the genotypes, thus theorically, they can be partitioned into genetic components of the GCA and SCA as well as reciprocal effect to investigate whether the interaction effects can be attributed to "interactions between growth (environment or growth-environment) and additive or non-additive gene action". That is, the interaction effects may be expressed further as:

$$\begin{aligned} \alpha_{\mathrm{til}} &= \alpha_{(\mathrm{g})\mathrm{ti}} + \alpha_{(\mathrm{g})\mathrm{tl}} + \alpha_{(\mathrm{s})\mathrm{til}} + \alpha_{(\mathrm{r})\mathrm{til}} \\ \mathrm{I}_{\mathrm{ilj}} &= \mathrm{I}_{(\mathrm{g})\mathrm{ij}} + \mathrm{I}_{(\mathrm{g})\mathrm{lj}} + \mathrm{I}_{(\mathrm{s})\mathrm{ilj}} + \mathrm{I}_{(\mathrm{r})\mathrm{ilj}} \\ \omega_{\mathrm{tilj}} &= \omega_{(\mathrm{g})\mathrm{tij}} + \omega_{(\mathrm{g})\mathrm{tlj}} + \omega_{(\mathrm{s})\mathrm{tilj}} + \omega_{(\mathrm{r})\mathrm{tilj}} \end{aligned} \tag{2}$$

where $\alpha_{(\mathrm{g})\mathrm{ti}}$, $\alpha_{(\mathrm{g})\mathrm{tl}}$, $\alpha_{(\mathrm{s})\mathrm{til}}$, $\alpha_{(\mathrm{r})\mathrm{til}}$ and $\mathrm{I}_{(\mathrm{g})\mathrm{ij}}$, $\mathrm{I}_{(\mathrm{g})\mathrm{lj}}$, $\mathrm{I}_{(\mathrm{s})\mathrm{ilj}}$, $\mathrm{I}_{(\mathrm{r})\mathrm{ilj}}$ as well as $\omega_{(\mathrm{g})\mathrm{tij}}$, $\omega_{(\mathrm{g})\mathrm{tlj}}$, $\omega_{(\mathrm{s})\mathrm{tilj}}$ and $\omega_{(\mathrm{r})\mathrm{tilj}}$ represent the GCA and SCA as well as the reciprocal effect of α_{til}, $\mathrm{I}_{\mathrm{ilj}}$ and ω_{tilj}, respectively. If these genetic components of the interactions ($\alpha_{(\mathrm{g})\mathrm{ti}}$,.., $\omega_{(\mathrm{r})\mathrm{tilj}}$) can be accounted for by a linear relationship with T_{t}, E_{j} and β_{tj} respectively, then equation (2) can be written as:

$$\begin{aligned} \alpha_{\mathrm{til}} &= \xi_{\mathrm{il}} \mathrm{T}_{\mathrm{t}} + \eta_{\mathrm{til}} = (\xi_{(\mathrm{g})\mathrm{i}} + \xi_{(\mathrm{g})\mathrm{l}} + \xi_{(\mathrm{s})\mathrm{il}} + \xi_{(\mathrm{r})\mathrm{il}})\ \mathrm{T}_{\mathrm{t}} \\ &\qquad + \eta_{(\mathrm{g})\mathrm{ti}} + \eta_{(\mathrm{g})\mathrm{tl}} + \eta_{(\mathrm{s})\mathrm{til}} + \eta_{(\mathrm{r})\mathrm{til}} \\ \mathrm{I}_{\mathrm{ilj}} &= \mathrm{b}_{\mathrm{il}} \mathrm{E}_{\mathrm{j}} + \delta_{\mathrm{ilj}} = (\mathrm{b}_{(\mathrm{g})\mathrm{i}} + \mathrm{b}_{(\mathrm{g})\mathrm{l}} + \mathrm{b}_{(\mathrm{s})\mathrm{il}} + \mathrm{b}_{(\mathrm{r})\mathrm{il}})\ \mathrm{E}_{\mathrm{j}} \\ &\qquad + \delta_{(\mathrm{g})\mathrm{ij}} + \delta_{(\mathrm{g})\mathrm{lj}} + \delta_{(\mathrm{s})\mathrm{ilj}} + \delta_{(\mathrm{r})\mathrm{ilj}} \\ \omega_{\mathrm{tilj}} &= \phi_{\mathrm{il}} \beta_{\mathrm{tj}} + \theta_{\mathrm{tilj}} = (\phi_{(\mathrm{g})\mathrm{i}} + \phi_{(\mathrm{g})\mathrm{l}} + \phi_{(\mathrm{s})\mathrm{il}} + \phi_{(\mathrm{r})\mathrm{il}})\ \beta_{\mathrm{tj}} \\ &\qquad + \theta_{(\mathrm{g})\mathrm{tij}} + \theta_{(\mathrm{g})\mathrm{tlj}} + \theta_{(\mathrm{s})\mathrm{tilj}} + \theta_{(\mathrm{r})\mathrm{tilj}} \end{aligned} \tag{3}$$

where $\xi_{(\mathrm{g})\mathrm{i}}$, $\xi_{(\mathrm{g})\mathrm{l}}$, $\xi_{(\mathrm{s})\mathrm{il}}$, $\xi_{(\mathrm{r})\mathrm{il}}$ and $\mathrm{b}_{(\mathrm{g})\mathrm{i}}$, $\mathrm{b}_{(\mathrm{g})\mathrm{l}}$, $\mathrm{b}_{(\mathrm{s})\mathrm{il}}$, $\mathrm{b}_{(\mathrm{r})\mathrm{il}}$ as well as $\phi_{(\mathrm{g})\mathrm{i}}$, $\phi_{(\mathrm{g})\mathrm{l}}$, $\phi_{(\mathrm{s})\mathrm{il}}$, and $\phi_{(\mathrm{r})\mathrm{il}}$ are the regression coefficients of the GCA and SCA as well as the reciprocal effect for the interactions α_{til}, $\mathrm{I}_{\mathrm{ilj}}$ and ω_{tilj} on T_{t}, E_{j} and β_{tj}, respectively. The item η_{til} ,..., $\eta_{(\mathrm{r})\mathrm{til}}$, δ_{ilj} ,..., $\delta_{(\mathrm{r})\mathrm{ilj}}$, θ_{tilj} ,..., $\theta_{(\mathrm{r})\mathrm{tilj}}$ are the residuals from regression. Thus the mathematical model of equation (1) will be presented further as:

$$\begin{aligned} \mathrm{Y}_{\mathrm{tilj}} = {} & \mu + \mathrm{g}_{\mathrm{i}} + \mathrm{g}_{\mathrm{l}} + \mathrm{s}_{\mathrm{il}} + \mathrm{r}_{\mathrm{il}} \\ & + (1 + \xi_{(\mathrm{g})\mathrm{i}} + \xi_{(\mathrm{g})\mathrm{l}} + \xi_{(\mathrm{s})\mathrm{il}} + \xi_{(\mathrm{r})\mathrm{il}})\ \mathrm{T}_{\mathrm{t}} \\ & + (1 + \mathrm{b}_{(\mathrm{g})\mathrm{i}} + \mathrm{b}_{(\mathrm{g})\mathrm{l}} + \mathrm{b}_{(\mathrm{s})\mathrm{il}} + \mathrm{b}_{(\mathrm{r})\mathrm{il}})\ \mathrm{E}_{\mathrm{j}} \\ & + (1 + \phi_{(\mathrm{g})\mathrm{i}} + \phi_{(\mathrm{g})\mathrm{l}} + \phi_{(\mathrm{s})\mathrm{il}} + \phi_{(\mathrm{r})\mathrm{il}})\ \beta_{\mathrm{tj}} \\ & + \eta_{(\mathrm{g})\mathrm{ti}} + \eta_{(\mathrm{g})\mathrm{tl}} + \eta_{(\mathrm{s})\mathrm{til}} + \eta_{(\mathrm{r})\mathrm{til}} \\ & + \delta_{(\mathrm{g})\mathrm{ij}} + \delta_{(\mathrm{g})\mathrm{lj}} + \delta_{(\mathrm{s})\mathrm{ilj}} + \delta_{(\mathrm{r})\mathrm{ilj}} \\ & + \theta_{(\mathrm{g})\mathrm{tij}} + \theta_{(\mathrm{g})\mathrm{tlj}} + \theta_{(\mathrm{s})\mathrm{tilj}} + \theta_{(\mathrm{r})\mathrm{tilj}} \\ & + \frac{1}{\mathrm{q}} \sum_{\mathrm{k}=1}^{\mathrm{q}} \mathrm{e}_{\mathrm{tiljk}} \end{aligned} \tag{4}$$

That is, the regression coefficients or stability parameters (ξ_{il}, b_{il} and ϕ_{il}) can be also directly expressed as a linear function of both their GCA and SCA as well as the reciprocal effect, respectively. The estimated values and the sums of squares for GCA, SCA and reciprocal effect of the environment stability ($\mathrm{b}_{(\mathrm{g})\mathrm{i}}$, $\mathrm{b}_{(\mathrm{g})\mathrm{l}}$, $\mathrm{b}_{(\mathrm{s})\mathrm{il}}$ and $\mathrm{b}_{(\mathrm{r})\mathrm{il}}$) can be obtained directly by regressing the GCA, SCA and reciprocal effect of interactions ($\mathrm{I}_{(\mathrm{g})\mathrm{ij}}$, $\mathrm{I}_{(\mathrm{g})\mathrm{lj}}$, $\mathrm{I}_{(\mathrm{s})\mathrm{ilj}}$ and $\mathrm{I}_{(\mathrm{r})\mathrm{ilj}}$) on E_{j} respectively as shown in the left column of Table 1. However, they can also be expressed in terms of b_{il} of Griffing's method as shown in the right column of Table 1. The procedure of estimation of GCA, SCA and reciprocal effect for growth stability (ξ_{il}) and growth × environment stability (ϕ_{il}) and their sums of squares is similar as that of environment stability (b_{il}). The analysis of variance (ANOVA) is summarized in Table 2 with fixed (assuming that the factors T, E, G are fixed) and mixed model (assuming that T, E are fixed and G is random), respectively.

If the linear relationship of (4) exists, we may estimate the heterosis. The heterosis (H_{tilj}) of the i × l hybrid in the j th environment at the t th growth time is defined as the expectation of $[Y_{tilj}-(Y_{tiij}+Y_{tllj})/2]$, under the model (4), H_{tilj} can be estimated as:

$$\begin{aligned}\hat{H}_{tilj}=&\hat{s}_{il}-\frac{1}{2}(\hat{s}_{ii}+\hat{s}_{ll})+\hat{r}_{il}\\&+\ [\hat{\xi}_{(s)il}-\frac{1}{2}(\hat{\xi}_{(s)ii}+\hat{\xi}_{(s)ll})+\hat{\xi}_{(r)il}]\ \hat{T}_t\\&+\ [\hat{b}_{(s)il}-\frac{1}{2}(\hat{b}_{(s)ii}+\hat{b}_{(s)ll})+\hat{b}_{(r)il}]\ \hat{E}_j\\&+\ [\hat{\phi}_{(s)il}-\frac{1}{2}(\hat{\phi}_{(s)ii}+\hat{\phi}_{(s)ll})+\hat{\phi}_{(r)il}]\ \hat{\beta}_{tj}\end{aligned}\tag{5}$$

$$=\bar{H}_{.il.}+\hat{\xi}_{(H)il}\hat{T}_t+\hat{b}_{(H)il}\hat{E}_j+\hat{\phi}_{(H)il}\hat{\beta}_{tj}\tag{6}$$

where $\bar{H}_{.il.}=\hat{s}_{il}-\frac{1}{2}(\hat{s}_{ii}+\hat{s}_{ll})+\hat{r}_{il}$

and $\hat{\xi}_{(H)il}=\hat{\xi}_{(s)il}-\frac{1}{2}(\hat{\xi}_{(s)ii}+\hat{\xi}_{(s)ll})+\hat{\xi}_{(r)il}$

$$\hat{b}_{(H)il}=\hat{b}_{(s)il}-\frac{1}{2}(\hat{b}_{(s)ii}+\hat{b}_{(s)ll})+\hat{b}_{(r)il}$$

$$\hat{\phi}_{(H)il}=\hat{\phi}_{(s)il}-\frac{1}{2}(\hat{\phi}_{(s)ii}+\hat{\phi}_{(s)ll})+\hat{\phi}_{(r)il}$$

These relationships indicate that the heterosis is a multiple regression function of $\hat{T}_t$, $\hat{E}_j$ and $\hat{\beta}_{tj}$. The estimated intercept $\bar{H}_{.il.}$ is the mean heterosis of the i × l hybrid and can be expressed as a linear combination of $\hat{s}_{il}$ and $\hat{r}_{il}$. The estimated slopes $\hat{\xi}_{(H)il}$, $\hat{b}_{(H)il}$ as well as $\hat{\phi}_{(H)il}$ are the partial regression coefficients and can be represented as the linear combinations of $\hat{\xi}_{(s)il}$ and $\hat{\xi}_{(r)il}$, $\hat{b}_{(s)il}$ and $\hat{b}_{(r)il}$ as well as $\hat{\phi}_{(s)il}$ and $\hat{\phi}_{(r)il}$, respectively. That is, the hetreosis may also be directly estimated by using the multiple regression analysis.

2. Genetic analysis of stability

The estimated values of growth stability ($\hat{\xi}_{il}$) and environment stability ($\hat{b}_{il}$) obtained in this study were

Table 1. *Formulae for $b_{(g)i}$, $b_{(s)il}$, $b_{(r)il}$ and their sums of squares*

	In terms of $\hat{I}_{(g)ij}$, $\hat{I}_{(s)ilj}$, $\hat{I}_{(r)ilj}$	In terms of $\hat{b}_{il}$
$\hat{b}_{(g)i}$	$\sum_{j=1}^{p}\hat{I}_{(g)ij}\hat{E}_j/\sum_{j=1}^{p}\hat{E}_j^2$	$\frac{1}{2a}(\bar{b}_{i.}+\bar{b}_{.i})=$ GCA of $\hat{b}_{il}$
$\hat{b}_{(s)il}$	$\sum_{j=1}^{p}\hat{I}_{(s)ilj}\hat{E}_j/\sum_{j=1}^{p}\hat{E}_j^2$	$\frac{1}{2}(\hat{b}_{il}+\hat{b}_{li})-\frac{1}{2a}(\bar{b}_{i.}+\bar{b}_{.i}+\bar{b}_{l.}+\bar{b}_{.l})=$ SCA of $\hat{b}_{il}$
$\hat{b}_{(r)il}$	$\sum_{j=1}^{p}\hat{I}_{(r)ilj}\hat{E}_j/\sum_{j=1}^{p}\hat{E}_j^2$	$\frac{1}{2}(\hat{b}_{il}+\hat{b}_{li})=$ reciprocal of $\hat{b}_{il}$
SS (Het. bet. $b_{(g)i}$)	mq $\{2a\sum_{i=1}^{a}(\sum_{j=1}^{p}\hat{I}_{(g)ij}\hat{E}_j)^2/\sum_{j=1}^{p}\hat{E}_j^2\}$	mq $\{\frac{1}{2a}\sum_{i=1}^{a}(\bar{b}_{i.}+\bar{b}_{.i})^2\}\ \sum_{j=1}^{p}\hat{E}_j^2=$ (SS of GCA of $\hat{b}_{il}$) $\sum_{j=1}^{p}\hat{E}_j^2$
SS (Het. bet. $b_{(s)il}$)	mq $\{\sum_{i=1}^{a}\sum_{l=1}^{a}(\sum_{j=1}^{p}\hat{I}_{(s)ilj}\hat{E}_j)^2/\sum_{j=1}^{p}\hat{E}_j^2\}$	mq $\{\frac{1}{2}\sum_{i=1}^{a}\sum_{l=1}^{a}\hat{b}_{il}(\hat{b}_{il}+\hat{b}_{li})-\frac{1}{2a}\sum_{i=1}^{a}(\bar{b}_{i.}+\bar{b}_{.i})^2\}\ \sum_{j=1}^{p}\hat{E}_j^2=$ (SS of SCA of $\hat{b}_{il}$) $\sum_{j=1}^{p}\hat{E}_j^2$
SS (Het. bet. $b_{(r)il}$)	mq $\{2\sum_{i<l}^{a}\sum^{a}(\sum_{j=1}^{p}\hat{I}_{(r)ilj}\hat{E}_j)^2/\sum_{j=1}^{p}\hat{E}_j^2\}$	2mq $\{\frac{1}{2}\sum_{i<l}^{a}\sum^{a}(\hat{b}_{il}-\hat{b}_{li})^2\}\ \sum_{j=1}^{p}\hat{E}_j^2=$ mq $\sum_{i=1}^{a}\sum_{l=1}^{a}\hat{b}_{il}^2\sum_{j=1}^{p}\hat{E}_j^2-$ (SS of GCA of $\hat{b}_{il}$) $-$ (SS of SCA of $\hat{b}_{il}$) $=$ (SS of reciprocal of $\hat{b}_{il}$) $\sum_{j=1}^{p}\hat{E}_j^2$

where

$\bar{b}_{i.}=\sum_{l=1}^{a}\hat{b}_{il}$, $\bar{b}_{.i}=\sum_{i=1}^{a}\hat{b}_{il}$, $\bar{b}_{..}=\sum_{i=1}^{a}\sum_{l=1}^{a}\hat{b}_{il}=0$

Het. bet. $b_{(g)i}=$ Heterogeneity between $b_{(g)i}$'s

Table 2. *ANOVA of dynamic model of stability with analysis of combining abilities giving expectations of mean square for the assumptions of fixed model and mixed model*

Source	D. F.	Expectation of mean square	
		Fixed model	Mixed model
Time (T)	m-1	$\sigma^2+a^2pq\Psi(T)$	$\sigma^2+a^2pq\Psi(T)+\frac{mpq}{m-1}\sigma^2_\alpha$
Environment (E)	p-1	$\sigma^2+ma^2q\Psi(E)$	$\sigma^2+ma^2q\Psi(E)+\frac{mpq}{m-1}\sigma^2_I$
T×E (β)	(m-1) (p-1)	$\sigma^2+a^2q\Psi(\beta)$	$\sigma^2+a^2q\Psi(\beta)+\frac{mpq}{(m-1)(p-1)}\sigma^2_\omega$
Genotype (G)	a^2-1	$\sigma^2+mpq\Psi(G)$	$\sigma^2+mpq\sigma^2_G$
GCA (g)	a-1	$\sigma^2+2mapq\Psi(g)$	$\sigma^2+2mpq\ \{\frac{a-1}{a}\sigma^2_s+a\sigma^2_g\}$
SCA (s)	a(a-1)/2	$\sigma^2+mpq\Psi(s)$	$\sigma^2+\frac{2mpq(a^2-a+1)}{a^2}\sigma^2_s$
reciprocal (r)	a(a-1)/2	$\sigma^2+2mpq\Psi(r)$	$\sigma^2+2mpq\sigma^2_r$
G×T (α)	(a^2-1) (m-1)	$\sigma^2+pq\Psi(\alpha)$	$\sigma^2+\frac{mpq}{m-1}\sigma^2_\alpha$
g×T ($\alpha_{(g)}$)	(a-1) (m-1)	$\sigma^2+2apq\Psi(\alpha_{(g)})$	$\sigma^2+2pq\ \{\frac{a-1}{a}\sigma^2_{\alpha(s)}+a\sigma^2_{\alpha(g)}\}$
Het. bet. $\xi_{(g)}$	a-1	$\sigma^2+2apq\Psi(\eta_{(g)})+2apq\Psi(\xi_{(g)})\sum_{t=1}^{m}T_t^2$	$\sigma^2+\frac{2pq}{a-1}\sum_{i=1}^{a}\sigma^2_{\eta(g)i}+2apq\Psi(\xi_{(g)})\sum_{t=1}^{m}T_t^2$
residual ($\eta_{(g)}$)	(a-1) (m-2)	$\sigma^2+2apq\Psi(\eta_{(g)})$	$\sigma^2+\frac{2pq}{a-1}\sum_{i=1}^{a}\sigma^2_{\eta(g)i}$
s×T ($\alpha_{(s)}$)	a(a-1) (m-1)/2	$\sigma^2+pq\Psi(\alpha_{(s)})$	$\sigma^2+\frac{2pq(a^2-a+1)}{a^2}\sigma^2_{\alpha(s)}$
Het. bet. $\xi_{(s)}$	a(a-1)/2	$\sigma^2+pq\Psi(\eta_{(s)})+pq\Psi(\xi_{(s)})\sum_{t=1}^{m}T_t^2$	$\sigma^2+\frac{2pq}{a(a-1)}\sum_{i=1}^{a}\sum_{l=1}^{a}\sigma^2_{\eta(s)il}+pq\Psi(\xi_{(s)})\sum_{t=1}^{m}T_t^2$
residual ($\eta_{(s)}$)	a(a-1) (m-2)/2	$\sigma^2+pq\Psi(\eta_{(s)})$	$\sigma^2+\frac{2pq}{a(a-1)}\sum_{i=1}^{a}\sum_{l=1}^{a}\sigma^2_{\eta(s)il}$
r×T ($\alpha_{(r)}$)	a(a-1) (m-1)/2	$\sigma^2+2pq\Psi(\alpha_{(r)})$	$\sigma^2+2\sigma^2_{\alpha(r)}$
Het. bet. $\xi_{(r)}$	a(a-1)/2	$\sigma^2+2pq\Psi(\eta_{(r)})+2pq\Psi(\xi_{(r)})\sum_{t=1}^{m}T_t^2$	$\sigma^2+\frac{4pq}{a(a-1)}\sum_{i<l}^{a}\sum^{a}\sigma^2_{\eta(r)il}+2pq\Psi(\xi_{(r)})\sum_{t=1}^{m}T_t^2$
residual ($\eta_{(r)}$)	a(a-1) (m-2)/2	$\sigma^2+2pq\Psi(\eta_{(r)})$	$\sigma^2+\frac{4pq}{a(a-1)}\sum_{i<l}^{a}\sum^{a}\sigma^2_{\eta(r)il}$
G×E (I)	(a^2-1) (p-1)	$\sigma^2+mq\Psi(I)$	$\sigma^2+\frac{mpq}{p-1}\sigma^2_I$
g×E ($I_{(g)}$)	(a-1) (p-1)	$\sigma^2+2maq\Psi(I_{(g)})$	$\sigma^2+2mq\ \{\frac{a-1}{a}\sigma^2_{I(s)}+a\sigma^2_{I(g)}\}$
Het. bet. $b_{(g)}$	a-1	$\sigma^2+2maq\Psi(\delta_{(g)})+2maq\Psi(b_{(g)})\sum_{j=1}^{p}E_j^2$	$\sigma^2+\frac{2mq}{a-1}\sum_{i=1}^{a}\sigma^2_{\delta(g)i}+2maq\Psi(b_{(g)})\sum_{j=1}^{p}E_j^2$
residual ($\delta_{(g)}$)	(a-1) (p-2)	$\sigma^2+2maq\Psi(\delta_{(g)})$	$\sigma^2+\frac{2mq}{a-1}\sum_{i=1}^{a}\sigma^2_{\delta(g)i}$
s×E ($I_{(s)}$)	a(a-1) (p-1)/2	$\sigma^2+mq\Psi(I_{(s)})$	$\sigma^2+\frac{2mq(a^2-a+1)}{a^2}\sigma^2_{I(s)}$
Het. bet. $b_{(s)}$	a(a-1)/2	$\sigma^2+mq\Psi(\delta_{(s)})+mq\Psi(b_{(s)})\sum_{j=1}^{p}E_j^2$	$\sigma^2+\frac{2mq}{a(a-1)}\sum_{i=1}^{a}\sum_{l=1}^{a}\sigma^2_{\delta(s)il}+2maq\Psi(b_{(s)})\sum_{j=1}^{p}E_j^2$
residual ($\delta_{(s)}$)	a(a-1) (p-2)/2	$\sigma^2+mq\Psi(\delta_{(s)})$	$\sigma^2+\frac{2mq}{a(a-1)}\sum_{i=1}^{a}\sum_{l=1}^{a}\sigma^2_{\delta(s)il}$
r×E ($I_{(r)}$)	a(a-1) (p-1)/2	$\sigma^2+2mq\Psi(I_{(r)})$	$\sigma^2+2mq\sigma^2_{I(r)}$
Het. bet. $b_{(r)}$	a(a-1)/2	$\sigma^2+2mq\Psi(\delta_{(r)})+2mq\Psi(b_{(r)})\sum_{j=1}^{p}E_j^2$	$\sigma^2+\frac{4mq}{a(a-1)}\sum_{i<l}^{a}\sum^{a}\sigma^2_{\delta(r)il}+2mq\Psi(b_{(r)})\sum_{j=1}^{p}E_j^2$
residual ($\delta_{(r)}$)	a(a-1) (p-2)/2	$\sigma^2+2mq\Psi(\delta_{(r)})$	$\sigma^2+\frac{4mq}{a(a-1)}\sum_{i<l}^{a}\sum^{a}\sigma^2_{\delta(r)il}$

Table 2. *Continued*

Source	D. F.	Expectation of mean square	
		Fixed model	Mixed model
$G \times T \times E\ (\omega)$	$(a^2-1)(m-1)(p-1)$	$\sigma^2+q\Psi(\omega)$	$\sigma^2+\frac{mpq}{(m-1)(p-1)}\sigma^2_{\omega}$
$g \times T \times E(\omega_{(g)})$	$(a-1)(m-1)(p-1)$	$\sigma^2+2aq\Psi(\omega_{(g)})$	$\sigma^2+2q\ \{\frac{a-1}{a}\sigma^2_{\omega(s)}+a\sigma^2_{\omega(g)}\}$
Het. bet. $\phi_{(g)}$	$a-1$	$\sigma^2+2aq\Psi(\theta_{(g)})+2aq\Psi(\phi_{(g)})\sum_{t=1}^{m}\sum_{j=1}^{p}\beta^2_{tj}$	$\sigma^2+\frac{2q}{a-1}\sum_{i=1}^{a}\sigma^2_{\theta(g)i}+2aq\Psi(\phi_{(g)})\sum_{t=1}^{m}\sum_{j=1}^{p}\beta^2_{tj}$
residual $(\theta_{(g)})$	$(a-1)(mp-m-p)$	$\sigma^2+2aq\Psi(\theta_{(g)})$	$\sigma^2+\frac{2q}{a-1}\sum_{i=1}^{a}\sigma^2_{\theta(g)i}$
$s \times T \times E\ (\omega_{(s)})$	$a(a-1)(m-1)(p-1)/2$	$\sigma^2+q\Psi(\omega_{(s)})$	$\sigma^2+\frac{2q(a^2-a+1)}{a^2}\sigma^2_{\omega(s)}$
Het. bet. $\phi_{(s)}$	$a(a-1)/2$	$\sigma^2+q\Psi(\theta_{(s)})+q\Psi(\phi_{(s)})\sum_{t=1}^{m}\sum_{j=1}^{p}\beta^2_{tj}$	$\sigma^2+\frac{2q}{a(a-1)}\sum_{i=1}^{a}\sum_{l=1}^{a}\sigma^2_{\theta(s)il}+q\Psi(\phi_{(s)})\sum_{t=1}^{m}\sum_{j=1}^{p}\beta^2_{tj}$
residual $(\theta_{(s)})$	$a(a-1)(mp-m-p)/2$	$\sigma^2+q\Psi(\theta_{(s)})$	$\sigma^2+\frac{2q}{a(a-1)}\sum_{i=1}^{a}\sum_{l=1}^{a}\sigma^2_{\theta(s)il}$
$r \times T \times E\ (\omega_{(r)})$	$a(a-1)(m-1)(p-1)/2$	$\sigma^2+2q\Psi(\omega_{(r)})$	$\sigma^2+2q\sigma^2_{\omega(r)}$
Het. bet. $\phi_{(r)}$	$a(a-1)/2$	$\sigma^2+2q\Psi(\theta_{(r)})+2q\Psi(\phi_{(r)})\sum_{t=1}^{m}\sum_{j=1}^{p}\beta^2_{tj}$	$\sigma^2+\frac{4q}{a(a-1)}\sum_{i<l}^{a}\sum^{a}\sigma^2_{\theta(r)il}+2q\Psi(\phi_{(r)})\sum_{t=1}^{m}\sum_{j=1}^{p}\beta^2_{tj}$
residual $(\theta_{(r)})$	$a(a-1)(mp-m-p)/2$	$\sigma^2+2q\Psi(\theta_{(r)})$	$\sigma^2+\frac{4q}{a(a-1)}\sum_{i<l}^{a}\sum^{a}\sigma^2_{\theta(r)il}$
Error	$ma^2p(q-1)$	σ^2	σ^2

where

$\Psi(X)$ = mean square of X.

eg. $\Psi(T)=\sum_{t=1}^{m}T_t^2/(m-1),\ \Psi(\beta)=\sum_{t=1}^{m}\sum_{j=1}^{p}\beta^2_{tj}/(m-1)(p-1),\ \Psi(\xi_{(g)})=\sum_{i=1}^{a}\xi^2_{(g)i}/(a-1)$ .....etc.

used to study the mechanism of inheritance according to the methods of Jinks (1954) and Hayman (1954a, b).

Analytically, we use the model of Hayman with assumptions: (1) parental homozygosity, (2) normal diploid segregation, (3) no maternal effect, (4) no multiple alleles, (5) no linkage, and (6) no non-allelic genic interaction (epistasis). The first three assumptions are usual ones and, numbers 4 and 5 are made in the interests of simplicity and justified on the basis of probable unimportance. The last assumption is tested by the analysis as a null hypothesis. From the diallel table of reciprocal means, compute the variance of the r th array (Vr) and the covariance between the parents and their F_1 offspring in the r th array (Wr), and test (Wr-Vr) for heterogeneity. The heterogeneity of (Wr-Vr) values indicates the inadequacy of a simple additive-dominance mode of genic interaction. If this is significant, identify the disturbing parents by omitting in turn from the diallel table and the remaining arrays are reanalysed. The limitations and merits of this procedure of determining epistatic members are discussed by Jinks (1954), Hayman (1957, 1963), Johnson (1963) and Jana (1975). When a diallel table with uniform (Wr-Vr) values, analyze its variances to compute the genetic components D, F, H_1, H_2 and h^2 and find their standard errors, then evaluate and interpret the genetic parameters $(H_1/D)^{1/2}$, $H_2/4H_1$, k_d/k_r, h^2/H_2 when the relevant components are significant. The heritability of the character can be estimated by the method of regression of the mean values of F_1 offspring on the value of mid-parent. The order of dominance of the parents, determined by the value of (Wr+Vr). The estimated statistics and their symbols used here are given by Hayman (1954a, b).

Results and Discussion

Analysis of Variance

The ANOVA of dynamic model of stability with analysis of combining abilities for the data of *Arabidopsis thaliana* is shown in Table 3. Each main factor is assumed to be fixed effect. Table 3 shows the

Table 3. *ANOVA of dynamic model of stability with analysis of combining abilities in fresh weight of **Arabidopsis thaliana***

Source	D. F.	M. S.
Time (T)	6	90051.65**
Environment (E)	11	9351.39**
T×E (β)	66	2292.33**
Genotype (G)	80	506.78**
GCA (g)	8	314.53**
SCA (s)	36	775.53**
reciprocal (r)	36	280.75**
G×T (α)	480	154.92**
g×T	48	64.16**
Het. bet. $\xi_{(g)}$	8	352.51**
residual	40	6.49
s×T	216	197.14**
Het. bet. $\xi_{(s)}$	36	1121.99**
residual	180	12.17
r×T	216	132.87**
Het. bet. $\xi_{(r)}$	36	629.49**
residual	180	33.54**
G×E (I)	880	188.44**
g×E	88	204.75**
Het. bet. $b_{(g)}$	8	202.32
residual	80	204.99
s×E	396	161.89**
Het. bet. $b_{(s)}$	36	421.36**
residual	360	135.94
r×E	396	211.36**
Het. bet. $b_{(r)}$	30	290.87*
residual	360	203.41
G×T×E (ω)	5280	60.76**
g×T×E	528	60.48**
Het. bet. $\phi_{(g)}$	8	340.65**
residual	520	56.17**
s×T×E	2376	52.38**
Het. bet. $\phi_{(s)}$	36	670.87**
residual	2340	42.86
r×T×E	2376	69.19**
Het. bet. $\phi_{(r)}$	36	599.57**
residual	2340	61.03**
Error	27216	9.20

**,*: Significant at 1% and 5%, respectively.

high significance in GCA, SCA and reciprocal effect of genotype, indicating that the genetic variation of fresh weight of *Arabidopsis thaliana* was due to both additive and dominance effects. Maternal effect also was a significant source in this trait. The interactions between these genetic components and growth time (T), environment (E), growth x environment (T×E) were highly significant, revealing that the phenotypic plasticity of fresh weigth of *Arabidopsis thaliana* to different developmental stages and environmental variation was genetically controlled by additive and non-additive effects, which included dominance and reciprocal effects. Further, the M.S. due to heterogeneity between regressions for all interactions were highly significant and greater than their respective residuals, except for the GCA x environment (g×E) interaction. The linear proportion for fitting dynamic model with combining abilities were almost greater than 80% (except for the reciprocal effect of G×T interaction) as presented in Table 4. Therefore, a major part of combining abilities of the interactions could be accounted for the difference among regressions of the individual genotypes.

Estimated Values of Combining Abilities

The estimated values of GCA for fresh weight and its three types of stability are shown in Table 5. From the results of correlation analysis of Table 6, simple positive correlations between phenotypic GCA and their linear regression coefficients, respectively, were

Table 4. *The linear proportion for fitting dynamic model with Griffing's method for a 9×9 diallel cross of **Arabidopsis thaliana***

Effect (Line no.)	L0	L	Q	Linear%
G×T int.				
GCA (9)	2	6	1	88.89
SCA (81)	2	69	10	87.65
Reciprocal (36)	1	20	15	58.33
G×E int.				
GCA (9)	9	0	0	100.00
SCA (81)	57	20	4	95.06
Reciprocal (36)	31	0	3	91.67
G×T×E int.				
GCA (9)	1	6	2	77.78
SCA (81)	16	56	9	88.89
Reciprocal (36)	8	21	7	80.56

L0 : model $Y=\bar{Y}.$; L: model $Y=b_0+b_1X.$; Q: model $Y=b_0+b_1X+b_2X^2.$; Linear%: the proportion that interactions can be accounted for by the linear regression coefficient, i.e. (L0+L)/(Line no.)×100.

Table 5. *Estimates of general combining ability (GCA) in dynamic model for stability analysis of* ***Arabidopsis thaliana***

Parent	$\bar{Y}$	ξ	b	ϕ
1 EG-5	-0.0129	-0.0002	0.0573	0.0862
2 Co-1	0.3130	0.0904	0.1914	0.1695
3 En	-0.3215	-0.0873	-0.0489	-0.0133
4 Po-1	-0.0350	0.0026	0.0686	0.1160
5 LM-4	-0.2055	-0.0549	-0.0683	-0.1018
6 C	-0.1043	-0.0243	-0.1017	-0.1061
7 A 136	0.1952	0.0291	-0.0115	-0.0204
8 GR 1,4	-0.0247	-0.0113	0.0058	-0.0453
9 Estland	0.1957	0.0559	-0.0928	-0.0848

$\bar{Y}$: phenotypic mean; ξ: growth stability; b: environment stability; ϕ: growth-environment stability.

Table 6. *Simple and partial (in parenthesis) correlations among general combining ability (GCA) of phenotypic mean, growth stability, environment stability and growth-environment stability indices*

	GCA (ξ)	GCA (b)	GCA (ϕ)
GCA ($\bar{Y}$)	0.9999**	0.8854**	0.8871**
GCA (ξ)		0.8827** (-0.3973)	0.8849** (-0.3234)
GCA (b)			0.9995** (0.9977**)

**,*: Significant at 1% and 5%, respectively.

Table 7. *Correlations between parental performance and its estimates of GCA*

Variables correlated	Correlation coefficient
GCA ($\bar{Y}$) and $\bar{Y}$	0.0989
GCA (ξ) and ξ	0.0494
GCA (b) and b	-0.4857
GCA (ϕ) and ϕ	-0.3943

all significant, indicating that the parents with high GCA of mean performance were sensitive to growth time, environmental stress, or growth-environmental changes. But these associations were not absolute, particularly between g_i and $b_{(g)i}$ (r=0.8854) and between g_i and $\phi_{(g)i}$ (r=0.7607), since there were a few parents with high GCA of mean performance and high stability to environmental or growth-environmental changes. Although there were significantly positive correlation

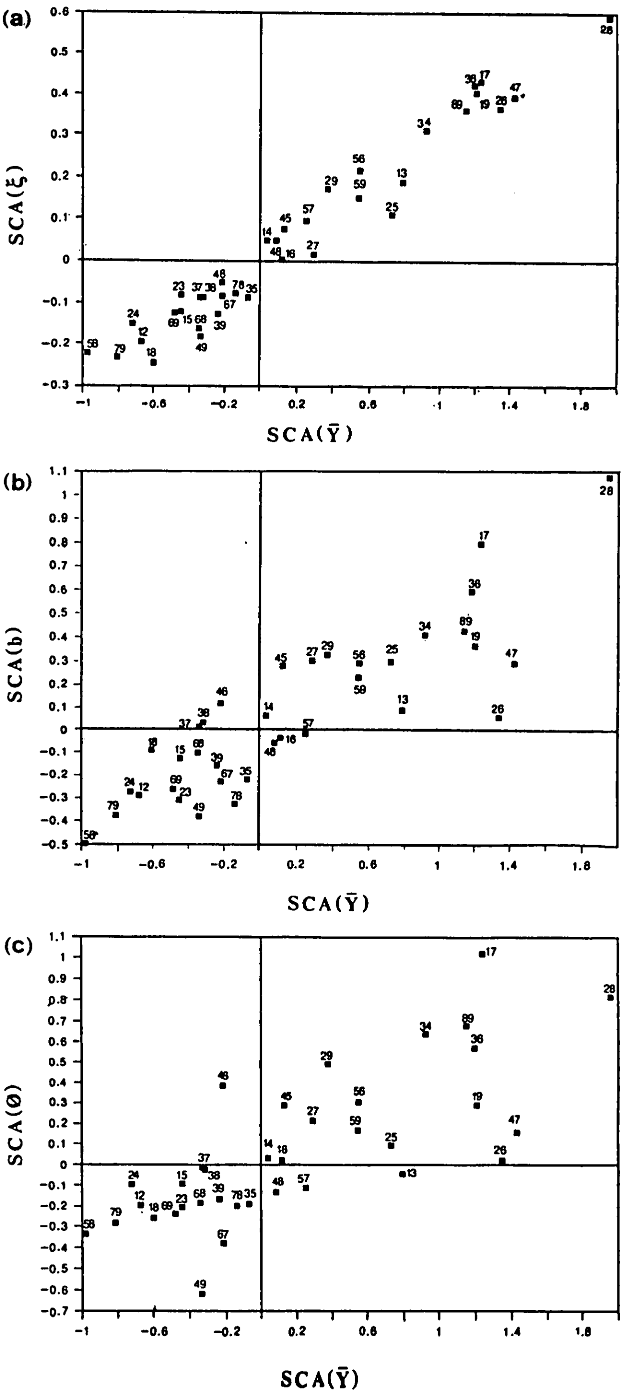

Fig. 1. The relationship between specific combining ability (SCA) for phenotypic mean and (a) growth stability, (b) environment stability, (c) growth-environment stability for F_1 hybrids.

occurred between the linear regressions of GCA from a simple correlation analysis, the high correlation between $\xi_{(g)i}$ and $b_{(g)i}$ as well as between $\xi_{(g)i}$ and $\phi_{(g)i}$ disappeared when the phenotypic GCA was fixed. This suggests that the growth stability is genetically independent of the environment stability and the growth-environment stability, respectively. From Table 5, parental inbreds 7 and 9 with positive GCA estimates for mean performance and regression coefficients ($\xi_{(g)i}$, $b_{(g)i}$) appeared to be the best general combiners, which could transmit average growth and environment stability to their progeny. Lack of association between GCA of stabilities and phenotypic mean of parents by a correlation analysis (Table 7) indicated their independent mode of inheritance. This means that a desirable parent did not necessarily transmit the high yield potential and low linear response (high stability) to its progeny.

The estimated values of specific combining ability (SCA) and reciprocal effect for phenotypic mean and stabilities are shown in Table 8. It was also difficult to select a desirable hybrid having above average SCA for phenotypic mean and remarkably low SCA for linear regressions, because obvious linear relationships between the phentypic SCA and their linear regressions were found in Fig. 1. The estimated values of reciprocal effects of phenotypic mean and linear regressions were almost negative, indicating that reciprocal crosses showed lower yield and lower linear response (higher stability) than their single crosses.

Examination of Fluctuation of Heterosis

Heterosis could be easily assessed by examing the linear combination of growth time, environmental and growth time-environmental indices, respectively. The estimated values of heterosis are shown in Table 9. Almost all F_1 hybrids of *Arabidopsis thaliana* showed positive heterosis, indicating that they have on average a higher yield and lower stability than their parents. Heterosis was pronounced under favourable environments at the final stages of growth.

Estimation of Genetic Components

The results of the heterogeneity test for (Wr-Vr) showed that the corresponding diallel cross did not follow the Hayman's hypothesis (1954a) for both growth stability and environment stability. After excluding the parental inbreds 1, 2, 4, and 8, it permited the remaining entries to adopt Hayman' method to draw the (Vr, Wr) graph (Fig. 2), and to make estimation of the various genetic components, such as D, H_1, H_2, h^2, F and (D-H_1) for each of the two types of stability. The results are given in Table 10.

The high levels of significance of H_1, H_2 and negative values of (D-H_1), indicating that the genetic variances of dominance were greater than the additive genetic variances for both two types of stability. Non-

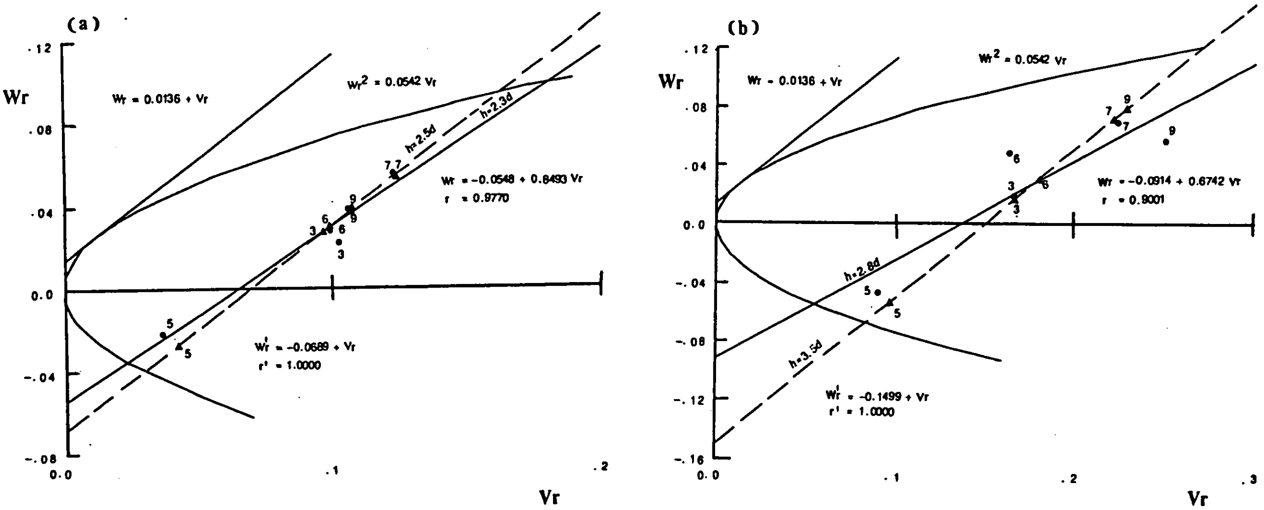

Fig. 2. Wr/Vr graph for (a) growth stability and (b) environment stability of the 5×5 (with array excluded) diallel cross.

Table 8. *Estimates of specific combining ability (SCA) and reciprocal effect in dynamic model for stability analysis of* ***Arabidopsis thaliana***

Genotype		1	2	3	4	5	6	7	8	9
1	$\bar{Y}$	-1.6848	-0.6726	0.7955	0.0374	-0.4420	0.1181	1.2414	-0.6016	1.2085
	ξ	-0.5159	-0.1941	0.1895	0.0499	-0.1206	0.0027	0.4305	-0.2446	0.4027
	b	-0.7808	-0.2861	0.0907	0.0661	-0.1269	-0.0343	0.7953	-0.0907	0.3668
	ϕ	-0.7713	-0.1968	-0.0476	0.0341	-0.0936	0.0219	1.0246	-0.2591	0.2879
2	$\bar{Y}$	0.3696	-2.8750	-0.4450	-0.7203	0.7350	1.3479	0.2957	1.9559	0.3783
	ξ	0.0678	-0.8213	-0.0814	-0.1500	0.1084	0.3643	0.0143	0.5892	0.1706
	b	0.0324	-1.1956	-0.3066	-0.2716	0.2963	0.0576	0.2998	1.0778	0.3284
	ϕ	-0.0320	-1.1450	-0.2061	-0.0953	0.0950	0.0216	0.2154	0.8194	0.4919
3	$\bar{Y}$	-0.2388	-1.4499	-1.5214	0.9243	-0.0699	1.1955	-0.3310	-0.3122	-0.2358
	ξ	-0.1651	-0.4704	-0.4565	0.3127	-0.0868	0.4215	-0.0855	-0.0867	-0.1267
	b	-0.5081	-0.5050	-0.4693	0.4136	-0.2167	0.5967	0.0154	0.0341	-0.1579
	ϕ	-0.7604	-0.6176	-0.5719	0.6398	-0.1899	0.5742	-0.0091	-0.0215	-0.1679
4	$\bar{Y}$	-0.0199	-0.4310	0.0636	-1.3400	0.1345	-0.2130	1.4278	0.0845	-0.3352
	ξ	-0.0081	-0.1385	-0.0085	-0.4925	0.0755	-0.0511	0.3910	0.0462	-0.1816
	b	-0.2433	-0.0350	0.0664	-0.4594	0.2785	0.1189	0.2925	-0.0584	-0.3802
	ϕ	-0.2710	-0.2947	0.0944	-0.6547	0.2877	0.3847	0.1581	-0.1352	-0.6192
5	$\bar{Y}$	0.2418	-0.6190	0.0210	-0.1725	-0.7310	0.5520	0.2547	-0.9817	0.5484
	ξ	0.0131	-0.0766	-0.0852	-0.1518	-0.2164	0.2176	0.0936	-0.2223	0.1511
	b	-0.0419	-0.3087	-0.0507	-0.5023	-0.2441	0.2910	-0.0146	-0.4949	0.2314
	ϕ	-0.0827	-0.1782	-0.1413	-0.5679	-0.1207	0.3038	-0.1149	-0.3345	0.1671
6	$\bar{Y}$	0.0574	-0.2123	-1.2552	0.3672	-0.4817	-1.9688	-0.2129	-0.3406	-0.4783
	ξ	0.0015	0.0107	-0.5453	0.0795	-0.2447	-0.5864	-0.0837	-0.1616	-0.1232
	b	-0.4110	-0.6404	-0.8720	0.2125	0.1259	-0.4361	-0.2292	-0.1022	-0.2624
	ϕ	-0.3286	-0.4155	-0.9204	0.2473	0.0293	-0.5064	-0.3779	-0.1841	-0.2379
7	$\bar{Y}$	-1.0827	-0.2773	-0.0543	0.1949	0.2116	0.2241	-1.7268	-0.1382	-0.8107
	ξ	-0.4271	-0.0696	-0.0731	-0.0020	-0.0927	0.0120	-0.4513	-0.0762	-0.2326
	b	-0.8444	0.0827	-0.2953	-0.0535	-0.0520	0.0861	-0.4594	-0.3254	-0.3743
	ϕ	-1.1267	0.1919	-0.2918	-0.2756	-0.2415	-0.0355	-0.4146	-0.1978	-0.2837
8	$\bar{Y}$	0.1281	-1.3945	-0.3281	-0.4906	-0.6287	-0.3799	-0.2687	-0.8160	1.1500
	ξ	-0.0170	-0.4785	-0.2100	-0.1502	-0.2432	-0.1698	-0.1857	-0.2047	0.3608
	b	0.0941	-0.7438	-0.3177	-0.2210	-0.0677	-0.0506	-0.1172	-0.4721	0.4316
	ϕ	0.0136	-0.7760	-0.4202	-0.1071	-0.1382	-0.1159	-0.2562	-0.3677	0.6805
9	$\bar{Y}$	0.8965	0.0217	-0.2860	0.4479	-0.3893	0.0904	-0.7085	-1.0146	-1.4251
	ξ	0.2307	-0.0527	-0.1671	0.0582	-0.2125	-0.0930	-0.2794	-0.4327	-0.4212
	b	0.0478	0.0928	-0.3807	0.0398	-0.1757	0.1885	-0.0133	-0.1206	-0.1833
	ϕ	0.3262	-0.0699	-0.4151	-0.0350	-0.2244	0.0973	-0.2568	-0.5010	-0.3187

Numerals in the left-hand of diagonal are estimates of reciprocal effects for the phenotypic mean and stability indices; numerals in the diagonal are SCA effects of parents for those; numerals in the right-hand of diagonal are SCA effects of hybrids for those.

Table 9. *Estimates of heterosis in dynamic model for stability analysis of* ***Arabidopsis thaliana***

Genotype		1	2	3	4	5	6	7	8	9
1	(1)		1.9769	2.1598	1.5299	1.0077	2.0023	1.8645	0.7769	3.6600
	(2)		0.5423	0.5106	0.5460	0.2587	0.5554	0.4870	0.0987	1.1020
	(3)		0.7345	0.2077	0.4429	0.3437	0.1632	0.5710	0.6299	0.8967
	(4)		0.7293	-0.1364	0.4761	0.2697	0.3321	0.4909	0.3240	1.1591
2	(1)	1.2377		0.3033	0.9562	1.9190	3.5575	2.3193	2.4069	2.5501
	(2)	0.4067		0.0871	0.3684	0.5507	1.0789	0.5810	0.6237	0.7392
	(3)	0.6697		0.0209	0.5209	0.7075	0.2330	1.2100	1.1679	1.1107
	(4)	0.7934		0.0347	0.5099	0.5497	0.4318	1.1871	0.7998	1.1539
3	(1)	2.6374	3.2031		2.4186	1.0773	1.6854	1.2388	0.5284	0.9515
	(2)	0.8408	1.0279		0.7787	0.1645	0.3977	0.2953	0.0339	0.1451
	(3)	1.2239	1.0309		0.9444	0.0893	0.1774	0.1845	0.1871	-0.2123
	(4)	1.3844	1.2700		1.3475	0.0151	0.1930	0.1923	0.0281	-0.1377
4	(1)	1.5697	1.8182	2.2914		0.9975	1.8086	3.1561	0.6719	1.4953
	(2)	0.5622	0.6454	0.7957		0.2782	0.5679	0.8609	0.2446	0.3335
	(3)	0.9295	0.5909	0.8116		0.1280	0.7792	0.6984	0.1864	-0.0190
	(4)	1.0181	1.0993	1.1587		0.1075	1.2126	0.4171	0.2689	-0.1675
5	(1)	0.5241	3.1570	1.0353	1.3425		1.4202	1.6952	0.0034	0.9977
	(2)	0.2325	0.7039	0.3349	0.5818		0.3743	0.3348	-0.1045	0.2267
	(3)	0.4275	1.3249	0.1907	1.1326		0.7570	0.2852	-0.1888	0.3774
	(4)	0.4351	0.9061	0.2977	1.2433		0.6467	-0.0887	-0.3318	0.2486
6	(1)	1.8875	3.9821	4.1958	1.0742	2.3836		1.8590	0.6719	1.3091
	(2)	0.5524	1.0575	1.4883	0.4089	0.8637		0.4472	0.0642	0.2876
	(3)	0.9852	1.5139	1.9214	0.3542	0.5052		0.3047	0.3013	0.2358
	(4)	0.9894	1.2628	2.0338	0.7180	0.5881		0.0471	0.1371	0.2719
7	(1)	4.0299	2.8739	1.3474	2.7663	1.2720	1.4108		0.8645	0.0567
	(2)	1.3412	0.7202	0.4415	0.8649	0.5202	0.4232		0.0661	-0.0757
	(3)	2.2598	1.0446	0.7751	0.8054	0.3892	0.1325		0.0231	-0.0663
	(4)	2.7443	0.8033	0.7760	0.9684	0.3943	0.1181		-0.0628	-0.1738
8	(1)	0.5207	5.1959	1.1846	1.6531	0.4205	1.4317	1.4019		1.2560
	(2)	0.1327	1.5807	0.4539	0.5450	0.2315	0.4038	0.4375		0.2411
	(3)	0.4417	2.6555	0.8225	0.6284	-0.0691	0.4025	0.2576		0.6387
	(4)	0.2968	2.3518	0.8685	0.4831	0.0479	0.3689	0.4496		0.5227
9	(1)	1.8670	2.5067	1.5235	0.5995	2.0158	1.1283	1.4738	3.2852	
	(2)	0.6406	0.8446	0.4793	0.2171	0.6824	0.4736	0.4831	1.1065	
	(3)	0.8011	0.9250	0.5491	-0.0987	0.6208	-0.1412	-0.0397	0.8799	
	(4)	0.5067	1.2937	0.6925	-0.0975	0.6112	0.0773	0.3398	1.5247	

(1)=$\bar{H}_{.ii}$; (2)=$\xi_{(H)ii}$; (3)=$b_{(H)ii}$; (4)=$\phi_{(H)ii}$.

significant F values were found, suggesting that the positive and negative alleles at these loci are in equal proportions in the parents. The ratios of k_d/k_r, which is close to unity to imply proximity between the numbers of dominant and recessive alleles in the parents (Table 11), generally agreed with the F values.

Ratios computed from the above genetic components provide information on the degree, order, and

Table 10. *Estimates of genetic variance components and their standard errors in the 5×5 diallel cross*

Genetic components	Growth stability	Environment stability
D	0.0542**	0.0542
	±0.0062	±0.0223
H_1	0.3300**	0.6535**
	±0.0166	±0.0602
H_2	0.3197**	0.6378**
	±0.0151	±0.0546
h^2	1.2434**	2.4110**
	±0.0102	±0.0369
F	0.0089	−0.0094
	±0.0154	±0.0557
$(D-H_1)$	−0.2759**	−0.5993**
	±0.0148	±0.0535

**,*: Significant at 1% and 5%, respectively.

Table 11. *Estimates of genetic parameters in the 5×5 diallel cross*

Estimates	Growth stability	Environment stability
$(H_1/D)^{1/2}$		
By graphic	2.25	2.78
By variance	2.47	3.47
$H_2/4H_1$	0.24	0.24
K_d/k_r	1.07	0.95
h^2/H_2	3.89	3.78
Heritability (%)	14.43	7.55
b of Wr/Vr	0.8493	0.6742
	± 0.1069	±0.1884
r of (Wr+Vr)/Yr	− 0.7236	−0.5434
Order of parental dorminance	53697	53679
Order of parental performance	53796	57936

**,*: Significant at 1% and 5%, respectively.

direction of dominance in the inheritance. The mean value of the product of gene frequencies of dominant and recessive alleles at the loci may be presented by $\overline{uv}=H_2/4H_1$ (Table 11). Here, the estimated value of $\overline{uv}$ is 0.24 for both growth stability and environment stability, that is to say, $\bar{u}=\bar{v}=1/2$ for both stabilities, i.e., the positive and negative alleles at these loci are in equal proportions in the parents. This results are consistent with the results obtained from the F values of Table 10. Whether from the graphic result or by using the variance component analysis, the estimated value of $(H_1/D)^{1/2}$ of each stability was greater than one (Table 11), indicating that both growth stability and environment stability showed overdominance. The ratio h^2/H_2 provides an estimate of the number of gene groups which control the character and exhibit dominance to some degree. There are at least four gene groups for these two types of stability (Table 11). Low heritability (14.43% and 7.55%) were obtained in Table 11, since dominance gene action and heterosis played a primary role in these crosses.

The slope of regression line of Wr on Vr is not significantly different from the unit slope for each type of stability (Fig. 1 or Table 11), suggesting that only additive and partial dominance genes existed between the parental gene combinations and that genic interaction did not exist.

In the growth stability, the order of dominance of the parents obtained from (Wr+Vr) is 53697, and the order of performance ($\bar{Y}$) is 53796 (Table 11). This result is in good agreement with the result of Fig. 2. The parent 5 with high sensitivity to growth time carried most of the dominant genes, whereas the parent 6 having higher growth stability contained a less number of dominant alleles than parent 5. The correlation between ($\bar{Y}$) and (Wr+Vr) is not significant (-0.7236), it seems that only weak association between growth stability and the number of dominant genes. In the environment stability, the order of dominance of the parents is 53679, and the order of parental performance is 57936; the correlation between (Wr+Vr) and $\bar{Y}$ is not significant (Table 11). This result is similar as that of growth stability.

From the above results, we may conclude that growth stability and environment stability are heritable and possess the same genetic constitution. They are controlled mostly by the dominance effect, but heritabilities are very small. Low stability is dominant over high stability and overdominance is obvious. Maternal effects in reciprocal crosses were found. These findings agree with those for environment stability obtained by Wu (1974) using linear regression. Westerman (1971) also obtained the same results in the inheritance of environment stability of *Arabidopsis thaliana* by using genotype x location interaction as a stability index. In the present study, it shows that the number or frequencies of dominant and recessive alleles in the parents are nearly equal, and there are at least four gene groups affecting stability. These results are different from those of Wu (1974) who obtained the asymmetry in the distribution of dominant and recessive genes in the parents and one or two gene groups involved. A change in the numerical measure of stability may produce somewhat different information in the number of dominant gene groups when applied Jinks-Hayman's model to study the inheritance of stability.

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植物數量性狀之適應性動態模式之研究
III. 全互交遺傳分析

呂秀英[1] 鄔宏潘[2]

[1]臺灣省農業試驗所
[2]中央研究院植物研究所

利用 *Arabidopsis thaliana* 之 9 個純系及其 F_1 雜交組合鮮重資料，以探討動態模式下三種穩定性的遺傳機制。配合動態模式之組合力分析之結果顯示，三種穩定性之遺傳變異均同時受累加性及顯性作用所控制，累加性遺傳變異甚小於顯性遺傳變異。反交雜種一般較其正交雜種具有較低之表型平均值及高度穩定性。一般組合力效應之大小與平均親本效應之大小沒有明顯的關係，即一個高產且穩定的親種，其雜交組合結果不一定也是高產且穩定。而且很難找到一個表型平均值之特殊組合力(SCA)高而穩定性迴歸估值之 SCA 相當低的雜種組合。高產而低穩定性的雜種優勢，隨著植物之生長發育與所處環境之改善而有增大的趨勢。根據全互交遺傳分析結果，生長穩定性與環境穩定性皆具有相似的遺傳性：其變異主要受顯性作用所支配，故其遺傳率甚小，適應性大者由隱性基因所支配而適應性小者由顯性基因所控制，具有超顯性，且有母質效應存在，正負等位基因平均相對頻度在諸親本間之分布對稱，顯隱性基因則等量存在於兩親，最少顯性基因數爲四對。