Studies on the dynamic model of plant adaptation of quantitative characters

II. Estimation of genetic parameters[1,2]

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Abstract. Nine genetical lines of *Arabidopsis thaliana* and their F_1 hybrids for all cross combinations were used to demonstrate the dynamic model with genetical parameters. In this study the genetic parameters of growth, environment and growth × environment stability of quantitative character were estimated by the linear model from genotype × growth, genotype × environment and genotype × growth × environment interactions, respectively. The cluster analysis was used for grouping genotypes according to the three types of stability for each genotype and classified genotypes into eight categories. The results showed that all parental lines were more stable, and 93.8% of genotypes possessed more stable or stable in these three types of stability. Almost all of the F_1 hybrids showed more unstable than their parents. Significant positive correlations among the three stability indices were obtained.

Key words: Adapation; *Arabidopsis thaliana*; Cluster analysis; Dynamic model; Genetical parameter; Stability.

Introduction

The adaptability of plants to the environment is heritable. The inheritance of adaptation to the environment can be estimated by various methods, but the linear regression method is useful to evalute the adaptation of a quantitative character to the change of environments and can be applied in many cases (Bucio Alanis, 1966; Bucio Alanis and Hill, 1966; Finlay and Wilkinson, 1963; Lu and Wu, 1986; Perkins and Jinks, 1968; Westerman,

1971; Wu, 1972). However, the parameter of the linear model differes as experimental materials and environmental conditions changes. Thus, a estimater obtained may only be a relative value. Furthermore, a quantitative character of a plant often varies with time when it is at different stages of growth and development. In the previous research, a dynamic model was established to integrate the time factor into the linear model to elucidate the three types of stability of genotypes, i.e., growth stability, environment stability and growth × environment stability (Lu and Wu, 1987). The purpose of present study is to continue to develop the simple genetic model for the estimation of the stability of parameters of both parents and

F_1 hybrid for the three types of stability described above. That is, the aim is to extend the applicability of dynamic model to cover many inbred lines and the crosses between them by inducing genetical components into the model. The fresh weight of *Arabidopsis thaliana* was used as a material to test the reliability and applicability of this empirical model.

Statistical Models

Based on the mathematical model of Mather and Jones (1958), Bucio Alanis (1966) and Perkins and Jinks (1968), the mean phenotypic values of the parents (P_1 and P_2) and their F_1 hybrid can be shown as:

$$\left. \begin{array}{l} P_1 = \mu - d + E - g_d \\ P_2 = \mu + d + E + g_d \\ F_1 = \mu + h + E + g_h \end{array} \right\} \quad (1)$$

where μ = population mean, d = additive effect, h = dominance effect, E = environmental effect, g_d and g_h is the interaction effect between environment and additive as well as environment and dominance gene, respectively.

If y_{tijk} represents the observed value of the ith genotype in the jth environment for the kth plant at the tth growth time, then

$$y_{tijk} = \mu + T_t + G_i + E_j \\ + \alpha_{ti} + \beta_{ij} + g_{ij} + r_{tij} + e_{tijk} \quad (2)$$

where α_{ti}, g_{ij} and r_{tij} are the interaction effect between genotype × growth time, genotype × environment, and genotype × growth time × environment, respectively. In the previous study (Lu and Wu, 1987), we obtained the following relationships:

$$\left. \begin{array}{l} \alpha_{ti} = \xi_i T_t + \eta_{ti} \\ g_{ij} = b_i E_j + \delta_{ij} \\ r_{tij} = \phi_i \beta_{tj} + \theta_{tij} \end{array} \right\} \quad (3)$$

Hence, equation (2) may be written as:

$$y_{tijk} = \mu + (1 + \xi_i) T_t + G_i \\ + (1 + b_i) E_j + (1 + \phi_i) \beta_{tj} \\ + \eta_{ti} + \delta_{ij} + \theta_{tij} + e_{tijk} \quad (4)$$

where ξ_i, b_i and ϕ_i are the regression coefficents, and respectively represents the growth, environment and growth × environment stability of the ith genotype. Therefore, the genetical models of equation (4) may be expressed as:

$$\left. \begin{array}{l} P_{tijk} = \mu + (1 + \xi_i) T_t + d_i \\ \quad + (1 + b_i) E_j + (1 + \phi_i) \beta_{tj} \\ \quad + \eta_{ti} + \delta_{ij} + \theta_{tij} + e_{tijk} \\ P_{tijk} = \mu + (1 + \xi_i) T_t + d_i \\ \quad + (1 + b_i) E_j + (1 + \phi_i) \beta_{tj} \\ \quad + \eta_{ti} + \delta_{ij} + \theta_{tij} + e_{tijk} \\ F_{t(ii)jk} = \mu + (1 + \xi_{(ii)}) T_t \\ \quad + h_{(ii)} + (1 + b_{(ii)}) E_j \\ \quad + (1 + \phi_{(ii)}) \beta_{tj} + \eta_{t(ii)} + \delta_{(ii)j} \\ \quad + \theta_{t(ii)j} + e_{t(ii)jk} \end{array} \right\} \quad (5)$$

The ANOVA and the estimated method of ξ, b and ϕ are the same as described previously (Lu and Wu, 1987). Equation (5) are expressed in a way analogous to Finlay-Wilkinson type of analysis, and the $(1 + \xi_i)$, $(1 + b_i)$ and $(1 + \phi_i)$ can be also written as ξ_i', b_i' and ϕ_i', respectively. Throughout this article the latter notations are used to denote the three types of "stability index".

Materials and Methods

Nine genetical lines of *Arabidopsis thaliana* were selected from the previous research (Lu and Wu, 1987) according to their characteristic of various stabilities (Table 1), and single cross and reciprocal crosses between those lines were made. Parents and their F_1 hybrids for all cross combinations were used in this study. The experimental methods were the same as described in the previous paper (Wu, 1972). They were reared with five replicates (plants) under twelve different environments consisting of combinations of six

different artificial weather conditions and two levels of fertilization: cultured in sand and added

Table 1. *Simple classification of various stability for 24 genotypes of Arabidopsis thaliana*

Growth stability	Environment stability	Growth-environment stability		
		More stable	Stable	Unstable
More stable	more stable	F 21 Co-1* (2) 51 D	—	—
	stable	—	—	—
	unstable	—	—	—
Stable	more stable	GR 1, 4* (8) SI-2 JA-2	—	—
	stable	—	AU GR 2, 3 Estland*(9) En*(3) Wil-2 F 140 Hm LM-4*(5) 51 Ch-1 F 26 LM-1 51 A	C* (6)
	unstable	—	—	—
Unstable	more stable	—	—	—
	stable	—	A 136* (7)	—
	unstable	—	—	Po-1*(4) EG-5*(1) φy-0

* Selected for genetical study in this research. The number in parentheses is the code number of the parent used in Table 4.

with water, with or without nutritions. The mean fresh weight of five plants from each line or hybrid was recorded weekly at random from the first week to the seventh week.

Results and Discussion

Analysis of Variance

The ANOVA for the data of each week is shown in Table 2, and the ANOVA of combined data for seven weeks is shown in Table 3. Both of ANOVA are assumed to be fixed effect for each main factor. Table 2 shows the high significance in genotype × environment interaction. Both the heterogeneity between regressions mean square (M.S.) and corresponding residual M.S. were highly significant, indicating the presence of both linear and non-linear components of interaction variation in these data. But the heterogeneity between regressions M.S. were greater than its residuals, indicating that a major part of interaction variation is accounted for by differences in these linear regressions. The linear proportion (following Fripp and Caten's 1971 definition) of genotype × environment interaction approximated to 60% for each week.

Table 3 shows the results of combined analysis. Similar results of the interaction effect were obtained as given in Table 2. The linear propor-

Table 2. *ANOVA for seven periods of 9×9 diallel cross (G, E are fixed models)*

Source	D.F.	M.S.						
		1	2	3	4	5	6	7 (week)
Environment (E)	11	.362**	10.623**	114.163**	409.99**	1,559.88**	5,003.86**	16,006.18**
Genotype (G)	80	.142**	.988**	4.193**	20.61**	72.85**	286.29**	1,051.20**
G×E	880	.007**	.215**	1.752**	7.83**	33.05**	130.55**	379.59**
Het. bet. reg.'s	80	.017**	.411**	4.431**	15.43**	54.17**	180.37**	587.49**
Residual	800	.006**	.196**	1.484**	7.07**	30.93**	125.57**	358.80**
Error	3,888	.001	.022	.317	1.74	6.81	14.61	40.97
Total	4,859							
Linear proportion (%)		75.35	69.16	77.90	72.00	66.25	59.90	63.23

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

Table 3. *ANOVA for dynamic model in the fresh weight of 9×9 diallel cross of* **Arabidopsis thaliana**

Source	D. F.	M. S.	Linear proportion
Time (T)	6	90,051.65**	
Environment (E)	11	9,351.39**	
Genotype (G)	80	506.78**	
T × E	66	2,292.33**	
G × T	480	154.92**	
Het. bet. reg.'s	80	823.46**	98.55%
Residual	400	21.21**	
G × E	880	188.44**	
Het. bet. reg.'s	80	340.73**	66.90%
Residual	800	173.21**	
G × T × E	5,280	60.76**	
Het. bet. reg.'s	80	605.75**	93.25%
Residual	5,200	52.37**	
Error	27,216	9.20	
Total	34,019		

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

tions were 98.55%, 66.90% and 93.25% for genotype × growth time, genotype × environment and genotype × growth time × environment interaction, respectively.

Estimated Value of the Parameter of Stability

The estimated values of the phenotypic mean and three types of regression coefficient (stability index), for parents and F_1 hybrids are illustrated in Table 4. All the growth stability indices (ξ_i') of genotypes were significantly different from zero, indicating the presence of linear function of interaction variation for each parent or hybrid. Environment stability indices (b_i') were also significantly differed from zero except for the F_1 hybrids of the cross-combinations of C×EG-5 (61), C×Co-1 (62) and C×Estland (69). Similar results were found in the growth × environment stability indices (ϕ_i'), except the F_1 hybrid of En × EG-5 (31). Therefore, a major part of the interaction variation could be accounted for by the difference among regressions of the individual genotypes,

and genetic parameter for the different genetical materials were then obtained. The mechanism of inheritance for each type of stability will be the object for future study.

Grouping of Genotypes Based on the Estimated Value of Stability

The method of cluster analysis (Lin and Thompson, 1975) was used for grouping of genotypes according to the stability of each genotype. For the growth stability (genotype × growth time interaction), eight groups were obtained when the clustering was stopping after the samllest dissimilarity index exceeded the critical F-value (5%). These groups and their corresponding genotypes are illustrated in Table 5-(a). This result would be helpful in selection for genotypes with widely adaptation. In the group I of growth stability, parental lines of EG-5 (11), Co-1 (22), En (33) and C (66) showed more stable in growth, the estimated value of growth stability index was less than 0.5. In the groups II and III, parental lines of Po-1 (44), LM-4 (55), A136 (77), GR 1, 4 (88) and Estland (99) showed stable, the estimated value was less than 1.0 but larger than 0.5. All parental lines were more stable or stable in growth, and most of the F_1 hybrids showed less stable than their parents. For the environment stability (genotype × environment interaction), the estimated values of b_i' were clustered into three groups (Table 5-(b)). Group I showed more stable in environmental changes, including nine parental lines and 41 cross-combinations. Group II with 30 cross-combinations possessed the environmental stability. Only one cross-combination (28) was unstable in group III, and had the largest performance in fresh weight. In the growth-environment stability (genotype × growth time × environment interaction), the estimated values of ϕ_i' were divided into three groups (Table 5-(c)), and the results were consistent with the above grouping of environment stability.

Furthermore, based on the three types of

Table 4. *The estimates of phenotypic mean and three stability indices for the parents (diagonal) and* F_1 *hybrids of 9×9 diallel cross*

Parent		1	2	3	4	5	6	7	8	9
1	Ȳ	2.12**	3.09	4.53	3.84	2.93	3.78	6.34**	3.07	4.33
	ξ'	.48**	.83**	1.27**	1.06**	.81*	.98**	1.89**	.76**	1.23**
	b'	.33**	.93**	1.61**	1.44**	.90**	1.33**	2.69**	.88**	1.28**
	φ'	.40**	1.09**	1.79**	1.51**	.97**	1.33**	3.22**	.77**	.96**
2	Ȳ	3.83	1.59**	4.83*	3.82	5.30**	5.60**	4.92*	7.47**	4.70
	ξ'	.96**	.36**	1.39**	1.08**	1.22**	1.42**	1.20**	2.15**	1.37**
	b'	1.00**	.19*	1.34**	1.02**	1.73**	1.79**	1.40**	3.02**	1.33**
	φ'	1.03**	.19**	1.57**	1.48**	1.34**	1.50**	1.17**	2.72**	1.65**
3	Ȳ	4.06	1.93**	1.67**	4.34	3.22	5.86**	3.43	3.50	3.76
	ξ'	.94**	.45**	.37**	1.24**	.86**	1.86**	.93**	1.02**	1.01**
	b'	.59**	.33**	.43**	1.37**	.72**	2.32**	1.25**	1.31**	1.08**
	φ'	.26	.33**	.40**	1.65**	.84**	2.38**	1.25**	1.34**	1.15**
4	Ȳ	3.80	2.96	4.47	2.42**	3.90	3.12	5.23**	4.35	3.21
	ξ'	1.04**	.80**	1.22**	.51**	1.18**	.85**	1.42**	1.19**	.82**
	b'	.95**	.95**	1.50**	.68**	1.78**	.87**	1.40**	1.24**	.56**
	φ'	.97**	.90**	1.84**	.58**	1.87**	1.15**	1.53**	1.04**	.45**
5	Ȳ	3.42	4.06	3.26	3.56	2.69*	4.56	3.87	3.25	4.76
	ξ'	.84**	1.07**	.69**	.87**	.67**	1.38**	1.16**	.95**	1.36**
	b'	.82**	1.11**	.62**	.78**	.62**	1.00*	.90**	.51*	1.25**
	φ'	.81**	.98**	.55**	.73**	.68**	1.07**	1.00**	.66**	1.20**
6	Ȳ	3.89	5.18**	3.35	3.85	3.60	1.66**	3.49	3.75	3.36
	ξ'	.98**	1.44**	.76**	1.01**	.89**	.37**	.91**	.97**	1.00**
	b'	.51	.51	.57**	1.30**	1.25**	.36**	.57**	.85**	.35
	φ'	.67*	.67*	.53**	1.64**	1.13**	.28**	.53**	.78**	.47*
7	Ȳ	4.18	4.36	3.32	5.62**	4.29	3.94	2.50**	4.14	4.12
	ξ'	1.03**	1.06**	.78**	1.42**	.98**	.93**	.61**	1.13**	1.13**
	b'	1.00**	1.56**	.66**	1.30**	.85**	.74**	.52**	.79**	.53**
	φ'	.96**	1.56**	.67**	.98**	.52**	.46**	.54**	.99**	.87**
8	Ȳ	3.32	4.68	2.85*	3.37	1.99**	2.99	3.60	2.97	6.17**
	ξ'	.73**	1.19**	.60**	.89**	.47**	.63**	.76**	.77**	1.84**
	b'	1.07**	1.53**	.67**	.79**	.37**	.75**	.55**	.54**	1.47**
	φ'	.80**	1.17**	.50**	.83**	.38**	.55**	.48**	.54**	2.05**
9	Ȳ	6.12**	4.74	3.19	4.11	3.98	3.54	2.71*	4.14	2.80*
	ξ'	1.69**	1.26**	.67**	.94**	.94**	.82**	.57**	.97**	.69**
	b'	1.38**	1.52**	.32**	.64**	.89**	.73**	.51**	1.22**	.63**
	φ'	1.62**	1.51*	.32**	.38**	.76**	.67**	.35**	1.05**	.51**

**, * Phenotypic means (Ȳ) significantly differ from grand mean (3.83±1.09 g) or stability indices significantly differ from zero at 1% and 5% level, respectively.

stability for each genotype simultaneously, the experimental materials comprised eight categories as shown in Table 6. From these results, it reveals that: (1) all parental lines showed more stable in three types of stability, (2) almost all of the genotypes (93.8%) presented more stable or stable in these three stabilities, and (3) almost all of the F_1 hybrids showed more unstable than their parents.

Correlation Analysis

Table 5 illustrates that the phenotypic performance (y_i) was positively associated with the regression coefficients of ξ_i', b_i' and ϕ_i', respectively. Therefore, the analyses of simple and partial correlation were made (Table 7). From the results of Table 7, simple positive correlations between $\bar{y}_i$ and linear regression coefficient of ξ_i', b_i' and ϕ_i', respectively, were all significant, indicating that the genotypes with high mean performance were sensitive to growth time, environmental stress, or growth-environmental changes. But these associations were not absolute, particularly between $\bar{y}_i$ and b_i' $(r = 0.8019)$ and between $\bar{y}_i$ and ϕ_i' $(r = 0.7607)$, since there were a few genotypes with high mean performance and

Table 5. *Grouping of genotypes in a 9×9 diallel cross*

Group	Genotypes[a]	Line no.	Fresh weight	Stab. index[b]
(a) For G×T interaction				
I	11 22 32 33 66 85	6	1.83±0.22	0.42±0.06
II	44 53 55 77 83 86 93 97 99	9	2.82±0.29	0.63±0.06
III	12 15 18 35 37 42 46 49 51 54 58 63 65 67 73 81 84 87 88 96	20	3.29±0.22	0.83±0.06
IV	14 16 21 24 31 38 39 41 45 52 57 61 64 68 69 71 72 75 76 78 79 94 95 98	24	3.93±0.23	1.02±0.07
V	13 19 23 25 27 29 34 43 48 56 59 82 92	13	4.65±0.27	1.27±0.08
VI	26 47 62 74	4	5.41±0.23	1.43±0.01
VII	17 36 89 91	4	6.12±0.20	1.82±0.09
VIII	28	1	7.47	2.15
(b) For G×E interaction				
I	11 12 15 18 21 22 24 31 32 33 35 39 41 42 44 46 49 51 53 54 55 57 58 61 62 63 66 67 68 69 71 73 75 76 77 78 79 81 83 84 85 86 87 88 93 94 95 96 97 99	50	3.26±0.75	0.68±0.22
II	13 14 16 17 19 23 25 26 27 29 34 36 37 38 43 45 47 48 52 56 59 64 65 72 74 82 89 91 92 98	30	4.66±0.81	1.47±0.34
III	28	1	7.47	3.02
(c) For G×T×E interaction				
I	11 12 15 18 22 31 32 33 35 42 44 46 49 51 53 54 55 58 61 63 66 67 68 69 73 75 76 77 81 83 84 85 86 87 88 93 94 95 96 97 99	41	3.09±0.68	0.59±0.21
II	13 14 16 19 21 23 24 25 26 27 29 34 36 37 38 39 41 43 45 47 48 52 56 57 59 62 64 65 71 72 74 78 79 82 89 91 92 98	38	4.48±0.73	1.34±0.37
III	17 28	2	6.91±0.80	2.97±0.35

[a] Genotype kk' is the line $k \times k'$ in a diallel cross, e.g. $11 = 1 \times 1$, etc.
[b] Stab. index: ξ_i', b_i' or ϕ_i'.

low linear sensitivity, i.e., more stable to environmental changes, and *vice versa*. This suggested that the phenotypic performance and linear response could be combined according to the dictates of the situation. Therefore, one may select for genotypes with above-mean performance and general adaptation. There were significantly positive simple and partial correlations occurred between the three stability indices (Table 7). The presence of positive correlation (significantly differed from zero in 5% level) between growth stability (ξ_i') and environment stability (b_i') implied that a genotype which is stable in growth may be also stable in environmental changes. It is different from the results shown in the previous report (Lu and Wu, 1987). However, the same conclusions were obtained in the significant test of partial correlation between ξ_i' and ϕ_i' as well as b_i' and ϕ_i'.

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Table 6. *Simple classification of various stability for 9×9 diallel cross*

Growth stability	Environment stability	Growth-environment stability		
		More stable	Stable	Unsatble
More stable	more stable	11 12 15 18 22 32 33 35 42 44 46 49 51 53 54 55 58 63 66 67 73 77 81 83 84 85 86 87 88 93 96 97 99	—	—
	stable	31 61 68 69 75 76 94 95	37 65	—
	unstable	—	—	—
Stable	more stable	—	21 24 39 41 57 62 71 78 79	—
	stable	—	13 14 16 19 23 25 26 27 29 34 38 43 45 47 48 52 56 59 64 72 74 82 92 98	—
	unstable	—	—	—
Unstable	more stable	—	—	—
	stable	—	36 89 91	17
	unstable	—	—	28

Table 7. *The simple correlations between phenotypic mean ($\bar{Y}_{.i.}$) and three stability indices (ξ_i', b_i' and ϕ_i') as well as the partial correlations (in parenthese) between three stability indices for a 9×9 cross*

	ξ_i'	b_i'	ϕ_i'
$\bar{Y}_{.i.}$	0.9657**	0.8019**	0.7607**
ξ_i'		0.8172** (0.2759*)	0.8304** (0.5683**)
b_i'			0.9357** (0.8398**)

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

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植物數量性狀之適應性動態模式之研究

II. 遺傳介量之估計

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利用 *Arabidopsis thaliana* 之9個純系及其 F_1 雜交組合資料，配合所建立的含有遺傳介量之動態模式，以估算這些遺傳背景相異之實驗材料的三種穩定性，且依動態模式下之分羣方法進行單一穩定性之分類，並進而將各基因型的三種穩定值做綜合分類，獲知9種親本在生長時間、環境或時間環境作用下均表現極爲穩定，而 93.8% 的基因型顯示三種穩定性爲穩定或極穩定，但絕大多數 F_1 雜交種之穩定性不如其雙親。三種穩定性的相關分析結果，也顯示三種穩定性與表型平均值間均存在有正相關關係。