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GENETIC BASIS OF PLANT STABILITY IN *ARABIDOPSIS THALIANA*[1]

I. Fluctuation of heritability and correlation

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Abstract

Nine genetical lines of *Arabidopsis thaliana* and their F_1 hybrids were used to study the fluctuation of heritability and the correlations of fresh weight between two of the several developmental stages (including flowering time). Heritabilities were significant only at the flowering time, and the fresh weight of the first developmental stage. It decreased rapidly after the first stage but increased again at the later stages. Phenotypic correlations of fresh weights were inversely related to the distance between developmental stages, i. e., approached maxima between two consecutive stages. Correlations between flowering time and fresh weight of the first stage and the last were positive, but negative with the third and the fourth. Genotypic correlations showed slightly positive or negative value bewteen early and middle stages but were highly positive at later stages. Canonical analysis was made for the phenotypic correlation. Second canonical correlation was found related to the growth curve form using fresh weights. The causes of fluctuations of heritability and correlation are interpretated and discussed.

Introduction

Arabidopsis thaliana has no commerical value. However, it is a widely distributed and well adapted species in various geographical locations. In addition, it is homozygous with short life cycle, and provides adequate sources of genetic diversity. Culturing of the plant as experimental materials requires small space, thus, environmental conditions can be easily controlled. It is therefore a convenient material to study basic problems in biology.

Finlay (1963) and Griffing *et al.* (1963) stated that much of the phenotypic stability of the $\bar{F}_2$ can be attributed to the accentuated heterotic effect in the unfavorable environment. However genetical basis of the plant stability have never been reported.

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Wu (1970) reported that the fresh weight stability of *Arabidopsis thaliana* fluctuated with developmental stages. The fluctuations differed significantly among genetical lines, and each line seemed to have a constant tendency. Thus, the fluctuation of stability was considered a genetic character.

This paper reports the fluctuations of heritability, phenotypic and genotypic correlations, of fresh weights at various developmental stages as well as flowering time.

Material and Methods

Nine genetical lines of *Arabidopsis thaliana* were used in this study, i.e., Estland, En, EG-5, Co-1, Po-1, LM-4, C, A 136, and GR 1,4, Diallel crosses, including reciprocals and selfings were made between lines. Tne Plants were grown with five replicates in 12 different environments.

The treatments consisted of six different artificial conditions as shown in the Table 1. Each condition has two levels of fertilization. Thus, the experiment involved a total of 12 different environments. The plants were cultured in sand, and added with either tap-water only (one level of the fertilizer), or nutritional solutions (another level of the fertilizer). The chemicals of the nutritional solution are as follows:

A:
- NH_4NO_3 363 g
- KCl 273 g
- KH_2PO_4 242 g
- $MgSO_4 \cdot 7H_2O$ 1,544 g

B:
- $Ca(NO_3)_2$ 739 g
- HCl (12%) 700 ml
- $FeCl_3$ (6%) 1,685 ml

Chemicals of A or B were solved in the distilled water with a volum of 14 liters, then 20 ml of A and B solutions repectively, were mixed and diluted

Table 1. *Artificial weather conditions*

	Light		Temperature (°C)	
	Intensity (lux)	Time (hrs)	Day	Night
1	10,000	14	25	20
2	24,000	14	27	22
3	5,500	14	30	25
4	natural light and natural day-length		25	20
5			20	20
6			30	25

with tap-water to 9 liters for application, and pH of the solution was adjusted to 6.5 with 10% HCl. Renewal of cultural solution was made at every four days.

The characters for measuring were fresh weight and flowering time. The fresh weights of five plants from each line or F_1 hybrids were measured weekly at random from the first week (abbreviated as FW-1) to the seventh week (FW-7), i.e., from germination to maturity of early lines, and also measured at harvesting time (Wm.) The flowering time (FL-T) was recorded as number of days from the germinating date to the date when the first flower appears. All plants were recorded on a single plant basis, and the mean value of five plants was used for statistical analysis.

Statistical Analysis

The analyses of variance and covariance were used to study the components of variance. Those components were also used to estimate the phenotypic and genotypic correlations and the heritability in broad sense of each developmental stage. The analysis of variance and covariance is shown in Table 2, and the estimating formulae are shown in equations (1) to (5).

Table 2. *Analysis of variance and covariance*

Sources of variation	*df*	Variance/ covariance	Expectation
Genotypes	$n-1$	$V_{ii'}$	$\sigma^2_{e_{ii'}}+r\sigma^2_{g_{ii'}}$
Error	$n(r-1)$	$E_{ii'}$	$\sigma^2_{e_{ii'}}$
Total	$nr-1$		

where:

n=number of lines

r=number of environments

if $i=i'$, indicated the same developmental stages, and

V_{ii}=variance of the i th developmental stage

$i\neq i'$, indicated the different developmental stages, and

$V_{ii'}$=covarianc of the i th and i' th developmental stage.

genotypic variance: $$\sigma^2_{g_{ii}}=\frac{V_{ii}-E_{ii}}{r} \quad (1)$$

genotypic covariance: $$Cov_{g_{ii'}}=\frac{V_{ii'}-E_{ii'}}{r} \quad (2)$$

phenotypic correlation: $$r_{p_{ii'}}=\frac{V_{ii'}}{\sqrt{V_{ii}\cdot V_{i'i'}}} \quad (3)$$

genotypic correlation: $$r_{g_{ii'}} = \frac{\mathrm{Cov}_{g_{ii'}}}{\sqrt{\sigma^2_{g_{ii}} \cdot \sigma^2_{g_{i'i'}}}} \quad (4)$$

heritability in broad sense: $$h^2 = \frac{\sigma^2_{g_{ii}}}{\sigma^2_{g_{ii}} + \frac{\sigma^2_{e_{ii}}}{r}} \quad (5)$$

The significant test of phenotypic correlation had been made according to the general method of that test. The significant test of heritability was made by the F′-test. The canonical analysis was used to estimate the relationship between the different developmental stages of two groups.

Results

The results of the statistical analysis are shown in Table 3.

Table 3. *Heritability, phenotypic and genotypic correlations among the fresn weight of seven growth periods, max. fresh weight and flowering time*

	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	Wm	FL-T
FW-1	0.48**	0.92	-0.25	-0.29	-0.14	0.36	0.68	0.94	0.70
FW-2	0.59**	0.11	0.17	0.10	0.24	0.75	0.98	1.00	0.73
FW-3	0.30*	0.73**	0.02	1.00	1.00	0.98	0.79	0.65	-0.04
FW-4	0.23*	0.57**	0.85**	0.04	1.00	0.70	0.44	0.24	-0.23
FW-5	0.25*	0.45**	0.69**	0.87**	0.02	0.92	0.79	0.70	-0.02
FW-6	0.26*	0.38**	0.56**	0.74**	0.90**	0.04	0.97	0.95	0 38
FW-7	0.27*	0.29**	0.38**	0.53**	0.71**	0.89**	0.07	1.00	0.59
Wm	0.14	0.10	0.00	0.07	0.13	0.31**	0.51**	0.15	0.95
FL-T	0.23*	-0.03	-0.23*	-0.23*	-0.19	-0.09	0.03	0.44**	0.60**

Genotypic and phenotypic correlations are shown on the right and left sides of the diagonal, respectively, and the heritabilities are shown on a diagonal line.
** and *: Significance at 1% and 5% level, respectively.

1. *The fluctuation of heritability*

As shown on a diagonal line of Table 3, the heritabilities of FW-1 and FL-T were significant at 1% level, but the heritability of FW-2 to FW-7 as well as Wm are non-significant. The high heritability of fresh weight in the first week indicated that the seeds nutrition were highly different among various genotypes. On the other hand, the growth of fresh weight in the first week was rarely effected by the environment. The heritability of fresh weight significantly decreased from the second week. The decrease become drastic from the third week to the sixth. This decreasing tendency expressed that the effect of environment to fresh weight during these periods. The

heritability of Wm was insignificantly large than FW-7. The h^2 of FL-T was 0.60. It was statistically significant, so this character was found to be difficultly affected by environment.

2. *The fluctuation of phenotypic correlation*

The phenotypic correlation of fresh weight in seven developmental stages, Wm and FL-T are also shown in the Table 3 on the left side of diagonal. These results indicated significant correlations among all possible combinations of seven developmental stages. The correlations between Wm and FW-6 or FW-7 were also significant at 1% level. Larger correlation coefficient was obtained between any two consecutive developmental stages.

The positive correlations were significant between FL-T and FW-1 or Wm. The negative correlations were significant between FL-T and FW-3 or FW-4. The correlations between FL-T and others were insignificant.

3. *The fluctuation of genotypic correlation*

The genotypic correlations of fresh weight in different developmental stages and FL-T are shown on the right side of the diagonal of Table 3. The estimated value and the tendency of fluctuation of the correlation differed significantly from those of the phenotype. That all phenotypic correlation of the fresh weight between two developmental stages are positive, but the genotypic correlation, between FW-1 with FW-3 FW-4 and FW-5 are negative.

Low genotypic correlations were obtained between the early and middle developmental stages. The correlation coefficients were increased between the Wm and the fresh weight of late developmental stages. The genotypic correlation between FL-T and the fresh weight of each developmental stage has the same tendency as described in the phenotypic correlation. All estimated genotypic correlations are larger than the corresponding phenotypic correlations. The correlations between FL-T with FW-2 and FW-6 were positive.

4. *Canonical analysis*

Phenotypic correlations were used for canonical analysis. The developmental stages were divided into two parts between the fourth and the fifth weeks. Stages FW-1 to FW-4 were considered as X-group, and those of FW-5, -6, -7, Wm and FL-T as Y-group. The first canonical correlation between variates of X and Y groups showed 0.8872, with the following canonical vectors:

$$\begin{cases} \alpha^{(1)\prime} = (-0.0793 \quad 0.0919 \quad 0.1257 \quad -1.1344) \\ \beta^{(1)\prime} = (-1.0954 \quad -0.0627 \quad 0.2570 \quad -0.0845 \quad 0.0536) \end{cases}$$

If the greater vector in each variate is scaled to unity, the canonical responses are:

$$\begin{cases} u_1 = 0.0641(\text{FW-1}) - 0.0852(\text{FW-2}) - 0.1523(\text{FW-3}) + (\text{FW-4}) \\ v_1 = (\text{FW-5}) + 0.0572(\text{FW-6}) - 0.2346(\text{FW-7}) + 0.0772(\text{Wm}) - 0.0489(\text{FL-T}) \end{cases}$$

The weight of FW-4 was approximatly 15.6, 11.7 and 6.6 times of FW-1, FW-2 and FW-3, respectively in the canonical variate for the subtest set of the X-group. Similarly, its correlative in the concomitant vatiates weight FW-5 17.5, 4.3, 13.0 and 20.4 times to that of FW-6, FW-7, Wm and FL-T, respectively. The major link between the sets appears to be (FW-4~FW-5) one.

If the first characteristic root 0.7871 is replaced by the smaller root 0.1478 in the preceding methods, following second canonical responses can be obtained:

$$\begin{cases} u_2 = (\text{FW-1}) - 0.1316(\text{FW-2}) - 0.7249(\text{FW-3}) + 0.3979(\text{FW-4}) \\ v_2 = -0.0445(\text{FW-5}) - 0.3530(\text{FW-6}) + 0.9989(\text{FW-7}) - 0.3831(\text{Wm}) + (\text{FL-T}) \end{cases}$$

The major link between the sets was different with the first canonical responses and appears to be (FW-1~FL-T).

Two additional canonical analyses for phenotypic correlations were conducted by dividing the developmental stages at FW-3 and FW-4, and at FW-2 and FW-3 respectively. The major links between the two sets appears to be (FW-3~FW-4) and (FW-2~FW-3) at the first canonical responses, and (FW-1~FW-7) and (FW-1~FL-T) at the second canonical responses, respectively.

Canonical analysis failed to obtain in genotypic correlations, because the solution of the sample-correlation matrix did not exist.

Discussion

The results indicated that the heritability, phenotypic and genotypic correlations of fresh weight fluctuated with developmental stages.

The heritability was largest at the FW-1 stage, decreased with the subsequent developmental stages, but increased again as the plant reached maturity. The fresh weight was severely affected by environment at the intermediary developmental stages. Thus, selection based on the fresh weight of these stages is not effective.

The phenotypic correlation between Wm and FW-1 is 0.14. It is insignificant. However, their genotypic correlation is 0.94. So the selection based on fresh weight at the early stages of development may be effective. The phenotypic correlations of fresh weight approached maximum at the nearest developmental stages. This is considered a natural phenomenon of plant growth. No such tendency was found for genotypic correlation, however.

The genotypic correlations of Wm and the fresh weight of each developmental stage are higher in the early and the late stages than those in the middle stages. Based on the difference in flowering time among the lines investigated, following interpretations are made with regard to the genotypic correlation of Wm and fresh weight of various developmental stages. Firstly, four lines of different flowering time (the flowering time and maturity date

have a positive correlation, so we only considered of flowering time) and different growth habit (the Wm are also different each other) are shown Fig. 1. Wm_1 is an early line with large Wm, Wm_1', also an early line but with small Wm. Wm_2 is a late maturity line with large Wm, and Wm_2', a late maturity line with small Wm. In the fourth week of development, for example, the fresh weight of the Wm_1' should be larger than the Wm_2, though the maximum fresh weigh, Wm, of Wm_2, is larger than Wm_1'. Because the growth rate of the Wm_1' is larger than the Wm_2 at this developmental stage due to the natural of growth habit, the genotypic correlations of Wm and the fresh weight of this stage, therefore, are small.

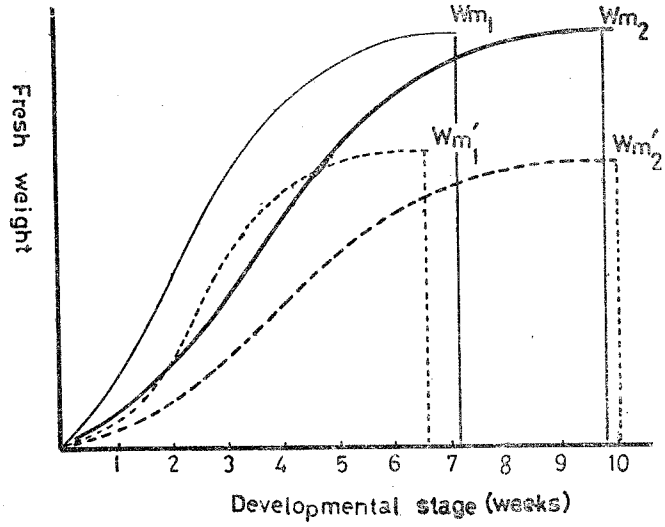

Fig. 1. Growth habit

The phenotypic and genotypic correlations of FL–T and fresh weights of various stage are also fluctuated with developmental stages. This phenomenon is also interpretated as the genotypic correlations of Wm and the fresh weight of each developmental stage as described in the preceding paragraph. On the other hand, the early lines flowered in three to four weeks after sowing. The fresh weights of these lines in the fourth week are naturally heavier than those of the late maturity lines at the same period. Hence the correlations are negative. In the later developmental stages, the fresh weight of the lines increased. The correlation of FL–T and fresh weight therefore is positive.

According to the three first canonical correlations obtained, the major link between the sets appears at the three dividing stages artificially chosen. For example, if the developmental stages were divided between the fourth and the fitfh week, the major link between these two sets would appear at the same stages. The results of the second canonical analysis that the major

link between the sets mostly appears at the first week (FW-1) and either at the seventh week (FW-7) or at the flowering time (FL-T). So the second canonical correlation was weighted at the early and the last stages. The form of a growth curve is pretty well controlled by the fresh weights of the first and the last stages of development. Second canonical correlation therefore will indicate the form of growth curve.

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植物安定性之遺傳學研究

I. 遺傳力及相關之變動

鄔 宏 潘

利用 *Arabidopsis thaliana* 之九系統及其全互交之 F_1 爲材料，研究各生育期之生體重及開花期之遺傳力，表現型相關以及遺傳相關，並比較在發育過程中之變動情形。由結果知：遺傳力在發芽後第一星期時之生體重及開花期較顯著並較大，其他生育期之生體重則不顯著且隨着發芽之促進而遂漸減小。但到生育後期又變大，有一定的變化趨勢。表現型相關在生育期愈接近時愈大。開花期與生育初期及後期之生體重間之表現型相關爲正值，但與中期生體重間則呈負值。此現象如從生長曲線之型態探討，則可給予適當之解釋。遺傳相關在生育初期及中期較小而在後期則較大，由此可知環境因素之影響在初期及中期時較大，而後期較小。利用表現型相關進行正準相關分析結果知，第二正準相關係數似與生長曲線之型態有關，而第一正準相關係數之結果，則難加以解釋。

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