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GENETIC BASIS OF PLANT STABILITY IN *ARABIDOPSIS THALIANA*

II. Inheritance of stability(1)

HONG-PANG WU

Laboratory of Plant Breeding, University of Tokyo, Tokyo, Japan
and
Institute of Botany, Academia Sinica
Taipei, Taiwan, Republic of China

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Abstract

Nine genetical lines of *Arabidopsis thaliana* and their F_1 hybrids were used to study the genetic basis of fresh weight and flowering time as well as their phenotypic stability (linear sensitivity to the environmental change). The mean expression and linear sensitivity to environments have the same genetic constitution, such as unidirectional gene action, dominant effect and heterosis. All of these increases associated with growth. Dominant effect included the effects of different dominant and recessive gene frequencies. Additive genetic variation was smaller than the non-additive ones. So the selection of these two aspects was limited. The developed and fluctuated genes in growth have identical tendency in mean expression and their linear sensitivity. But the heavy fresh weight and high sensitivity were dominant, and the early flowering time and high sensitivity were recessive. The numbers of dominant gene concerning with phenotypic and linear sensitivity were quite different. The genetic basis of linear sensitivity and mean expression of character were different and dependent upon the environments considered. Each gene system determined the character and its linear sensitivity. The genetical analysis of mean expression in each different environment was also investigated.

Introduction

The phenotypic value of quantitative characters of a plant usually is affected by the interaction of genotype and environment. Therefore, the phenotypic value represented variables among different environments. If the iteraction existed, the character is unstable; otherwise, it is stable. Hence, the variation of this interaction may be used to measure the stability of quantitative characters, when the plants are grown at various environments.

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The smaller the variation is, the more stable the character will be. Thus, the stability becomes a fundamental information for varietal improvement.

Many investigators have studied the measured method of the performance of a set of genotypes, when the genotypes were compared with each other over a number of different environments (Wricke, 1962; Finlay & Wilkinson, 1963; Eberhart & Russell, 1966; Oka, 1967; Perkins & Jinks, 1968a, b; Pederson, 1968, Okuno, 1968, 1971; Knight, 1970; Tai, 1971; Hardwick & Wood, 1972; Perkins, 1972; Wu, 1973; etc.). The performance of an individual genotype can be frequently expressed as a linear function of the environmental variable. The slope of the linear regression is a measure of genotypic stability to the overall of environmental factors. The parameter has been proved to have considerable utility in genetics and plant breeding (Finlay & Wilkinson, 1963; Perkins & Jinks, 1968a, b; Knight, 1970; Westerman, 1970, 1971; Matsuo, 1972; etc.). The parameter was also proved to be fluctuated among developmental stage. (Wu, 1970; Westerman, 1970, 1971). Many breeders have successfully applied this method to their material as an empirical measure of genotypic stability or varietal adaptability, such as Finlay & Wilkinson (1963) and Okabe (1972) in wheat; Okuno *et al.* (1968, 1971) and Matsuo (1972) in rice; Oka (1967) in soybean; Breese (1969) and Suzuki (1972) in grasses; Bucio Alanis (1966a, b) and Perkins (1968a, b) in tabacco, etc.

Barthelmess (1967) indicated that *Arabidopsis thaliana* was a suitable plant to study genotype-environmental interactions. Westerman (1970, 1971) also showed that the response of *Arabidopsis* inbred lines to temperatures varied considerably from one to the others. He obtained two main conclusions: (1) the relationship between the performance of a line and the environmental value was essentially linear with respect to all four characters of flowering time, height, leaf number and siliqua number, and (2) the flowering time appears to be a character whose optimum is brought about by the stabilization of the expression of the genes concerned, with respect to height of most families manifest a variable degree of developmental flexibility. Further studies on the genetical analysis of the developmental phenotype of seven inbred lines with different characters during developemental stages were made and concluded that the inheritance of the average phenotype was predominantly cotrolled by additive variations, though non-additive and reciprocal effects also presented.

In this study, the genetical analysis on the plant fresh weight of *Arabidopsis thaliana* was investigated under different environments and developmental stages. Further studies on the stability of this character were also investigated at different growth stages. The character of flowering time and its stability were also studied here.

Materials and Methods

The experimental materials and methods of this study were the same as described in the previous paper (Wu, 1972).

Statistical Analysis

Analysis of variance (ANOVA) on plant fresh weight and flowering time

Hayman's diallel analysis (1954a) were modified and used to estimate the variances of genetic components and genotype environmental interactions.

Estimating the stability parameter

The Finlay's method (1963) was used to estimate the parameter of stability, i.e., the linear regression coefficient between environmental index (overall mean value of genotypes at each environmental site) and mean phenotypic value of a genotype. The coefficient was taken as a parameter of stability for the genotype at certain developmental stage.

Genetical analysis

The characters of fresh weight of each developmental stage and flowering time, as well as the stability parameter of these two characters were used to study their genetic constitutions according to the modified Hayman's (1954b) diallel analysis.

Results

ANOVA of fresh weight and flowering time

The results of the variance ratios of fresh weight and flowering time are shown in Table 1. From these results, the variations were all significant against experimental error. The variance ratios of each environmental factor were fluctuated among developmental stages. Different tendencies of fluctuation have been obtained from different environmental factors, such as; the light factor (L) which was highly effective to fresh weight in initial and maturity stages, the fertilizer factor (F) affected the late stages, and the temperature factor (T) affected the early stages.

The interactions of light and temperature (LT), fertilizer and temperature (FT), and the interactions among the three (LFT) were mostly occured in the middle stages.

The genotypic variation (G) and the additive genetic variation among parental lines (a) were mostly occurred in the early and late stages, only small amount at the middle stages. The non-additive genetic variation (b), the dominance effect due to the different genetic combinations (b_2) and the

Table 1. *Variance ratio (8 environments)*

Variation	FW-1	FW-2	FW-3]	FW-4	FW-5	FW-6	FW-7	FL-T
Env. (E)	104.94*	308.84*	375.39*	231.74*	225.01*	306.73*	404.98*	6,119.17*
Light (L)	130.41*	787.28*	494.18*	84.64*	2.11	23.03*	175.16*	19,189.18*
Fert. (F)	0.52	52.86*	427.88*	639.67*	938.89*	1,717.19*	2,369.52*	53.40*
Temp. (T)	285.02*	399.19*	321.50*	148.06*	34.39*	2.53	51.58*	1,445.87*
L × F	62.40*	2.19	142.84*	98.52*	36.85*	0.34	35.20*	92.15*
L × T	198.00*	912.05*	1,066.18*	508.63*	408.90*	297.67*	154.75*	11,749.83*
F × T	27.83*	3.18	98.62*	68.60*	80.57*	43.11*	0.04	30.69*
L × F × T	30.42*	5.14*	76.55*	74.03*	73.33*	63.22*	48.62*	173.08*
Lines (G)	114.56*	40.48*	10.02*	9.40*	9.73*	12.82*	16.21*	1,955.59*
a	17.73*	37.39*	8.60*	7.86*	7.04*	12.45*	9.08*	6,236.75*
b	14.42*	21.98*	10.40*	9.83*	11.03*	18.24*	21.50*	750.33*
b_1	63.88*	119.61*	142.84*	117.12*	109.79*	201.84*	269.74*	1,421.53*
b_2	21.50*	18.05*	2.66*	3.29*	3.60*	7.06*	7.43*	1,427.27*
b_3	10.49*	19.53*	7.78*	7.79*	9.57*	14.76*	16.47*	524.91*
c	785.81*	175.68*	31.55*	30.90*	27.82*	10.67*	15.97*	7,228.68*
d	79.18*	26.53*	3.79*	3.15*	3.66*	6.57*	11.52*	775.45*
G × E	5.13*	11.56*	5.36*	3.76*	4.05*	6.12*	8.21*	81.21*
L × G	4.87*	17.87*	9.48*	5.69*	6.79*	10.35*	11.77*	282.86*
F × G	5.16*	9.07*	5.26*	4.56*	4.56*	7.01*	9.80*	37.68*
T × G	4.25*	9.97*	5.36*	3.91*	3.18*	4.60*	7.64*	82.17*
L × F × G	5.64*	9.45*	3.94*	3.11*	3.83*	6.27*	7.36*	34.97*
L × T × G	7.57*	14.26*	5.02*	3.05*	3.73*	4.77*	7.11*	52.24*
F × T × G	4.72*	10.71*	4.26*	3.36*	3.84*	6.05*	8.24*	48.72*
L × F × T × G	3.69*	9.56*	4.18*	2.62*	2.43*	3.81*	5.52*	29.83*

*: Significant at 1% level.

same effect caused by the reciprocal difference (b_3) had a similar tendency as described in the genotypic variation (G). Thus, the genetical difference was caused not only by the additive effect but also by the dominance effect of the genes. The average effect of dominance (b_1) mostly arose in the middle and later stages, i.e., the genes which were concerned in the increase of the fresh weight have an unidirectional gene action. The maternal effect (c) as well as the same effect owing to the reciprocal cross were occurred in the early stages. The maternal effect may decrease during the growth. The interactions between environment and genotype were all significant and fluctuated during the developmental stages. But, the fluctuation has the same tendency as the experimental error during the growth; so, the variance ratio always kept a constant value, hence those interactions may not be concerned with the de-

velopment.

The most important environmental factor to flowering time was the light, the interaction of light and temperature (LT) next, and the fertilizer least. The interaction between genotype and light (LG) was highly significant, and the other interactions were significant at lower levels.

Stability, gene action and growth fluctuating of fresh weight

The Finlay-Wilkinson method was applied to estimate the linear regression coefficient (linear sensitivity), and was taken to measure the parameter of stability genotype. On the other hand, the linear regression may express the relationship between genotypic and environmental means, and the gene action may be expressed by the constant of the linear regression equation (Bucio Alanis 1966b).

Thus, if we have; $Y_{ij}=[d_i]+\beta_i\varepsilon_j$, or $Y_{ij}=[h_i]+\beta_i\varepsilon_j$, where; Y_{ij} shows the phenotypic mean value of the i th genotype (parental or F_1 line) grown in the j th environment, ε_j shows the j th environmental effect, then β_i shows the linear regression coefficient (stability parameter) of the i th genotype, and $[d]$ as well as $[h]$ show the additive and non-additive gene actions in parental and F_1 lines, respectively. The correlation of β_i and d_i (or h_i) among different growth stages are shown in the Table 2.

Table 2. *Simple correlation of stability parameters (right side) and gene effects (left side).*

	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	FL-T
FW-1		0.55*	0.33*	0.24#	0.20	0.32*	0.35*	0.63*
FW-2	0.35*		0.71*	0.54*	0.45*	0.47*	0.41*	0.17
FW-3	0.43*	0.66*		0.76*	0.58*	0.45*	0.24#	−0.09
FW-4	0.28*	0.42*	0.67*		0.79*	0.60*	0.30*	−0.11
FW-5	0.09	0.23#	0.46*	0.76*		0.80*	0.61*	0.02
FW-6	0.06	0.19	0.32*	0.60*	0.77*		0.85*	0.13
FW-7	−0.04	0.11	0.05	0.20	0.49*	0.77*		0.21#
FL-T	0.23#	−0.17	−0.05	−0.01	0.09	−0.02	−0.04	

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

From results of Table 2, we obtained that: (1) The 79.5% and 6.4% of the total lines respectively showed linear and non-linear (curvilinear) relationship between Y_{ij} and ε_j. (2) The response of the genotype to environments almostly showed the same tendency during the growth, i.e., linear or curvilinear responses to growth stages. So, this response may be a characteristic of a genotype. (3) The stability parameter (β_i) of the genotype of growth stages

was fluctuated, and the fluctuated tendency differed among lines, and even in the same recirprocal crosses. (4) The correlations among β_i, d_i or h_i in continuous growth stages of a genotype were significant. This indicated that the stability of a gene slowly changed in the growth.

Genetical analysis on the stability of plant fresh weight

The analyzed genetic results of stability are shown in Table 3. The additive genetical variances (a) of various stages were all significant; therefore, the stability was genetically different among parental lines. The dominances of b, b_1, b_2, and b_3 were significant, and known to be involved in the inheritance of the stability of fresh weight in an unidirectional gene action during the growth. Since the h-value ($h=2(\bar{F}_1-\bar{P})$) was larger than zero, the unstability (large β-value) was dominant over the stability (small β-value) in the character. The genetical variance of each stage was constituted by both additive and dominant genetic variances. The maternal effects (c and d) were also significant, so the different of these effects were also existed among the parental lines. The heritability in broad sense was ranged from 97.36% to 99.72%, but that of narrow sense was from −0.53% to 11.53% only. This difference was caused by the large dominance effect, so the selection for this character was usually uneffective.

Over-dominant was found in each growth stage. The large heterosis was ranged from 21.7% to 135.05%. The ratio of dominant and recessive genes among parental lines was nearly 2.0 for each stage. So, the numbers of dominance genes concerning with the development of the stability for fresh weight in each stage were twice as much as the recessive ones. Owing to $H_1\neq 0$, $H_1-H_2\neq 0$, and $uv\simeq 0.20$ for each stage, the frequencies of dominance and recessive genes were different, and these differences contributed to the portions of dominant variance and effect.

The degree of dominance of each parental lines was obtained after the comparison of variance (V_r) and covariance (W_r). The correlation between (V_r+W_r) value and mean stability of each parental line was also obtained, and the values 0.577, 0.668, 0.762, 0.7753, 0.911, 0.861, and 0.416 were obtained for FW-1, 2, 3, 4, 5, 6, and 7, respectively. From these results, a line which has small β-value (i.e., stable) was recessive, and carried large numbers of positive homogeneous genes which directed the sability to the stable state. On the contrary, a line which has large β-value (i.e., unstable) was dominant. Therefore the stability of fresh weight was conditioned by recessive genes and the unstability by the dominance. This phenomenon is consistent in different growth stages.

Table 3. *Diallel analysis, first and second degree statistic, genetical components and genetic analysis of phenotypic stability parameters.*

ANOVA (MS)	df	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	FL-T
Treatments	80	0.7305*	0.4027*	0.4163*	0.3732*	0.2660*	0.3147*	0.3389*	0.4775*
a	8	0.3172*	0.4914*	0.4453*	0.3965*	0.1529*	0.1758*	0.2042*	0.9228*
b	36	0.2673*	0.3151*	0.4310*	0.3953*	0.3330*	0.4298*	0.3543*	0.0801*
b_1	1	0.2639*	1.2682*	2.1119*	1.8239*	2.4943*	3.0135*	2.9193*	0.1834*
b_2	8	0.1587*	0.2877*	0.1760*	0.2741*	0.1534*	0.1314*	0.1161*	0.0429*
b_3	27	0.2995*	0.2880*	0.4563*	0.3783*	0.3062*	0.4225*	0.3299*	0.0873*
c	8	4.3173*	1.0724*	0.5706*	0.5270*	0.3603*	0.4289*	0.4967*	2.5311*
d	28	0.4193*	0.2985*	0.3375*	0.2943*	0.1853*	0.1737*	0.3142*	0.2745*
Error		0.0184	0.0243	0.0052	0.0232	0.0286	0.0355	0.0312	0.0084
First and second degree statistic									
V_p		0.0386	0.1547	0.0276	0.0748	0.0508	0.0266	0.0245	0.0939
$\bar{V}_r$		0.1513	0.1849	0.2432	0.2197	0.1750	0.2246	0.1885	0.0913
$V_{\bar{r}}$		0.0176	0.0273	0.0247	0.0220	0.0085	0.0098	0.0113	0.0513
$\bar{W}_r$		-0.0036	0.0100	-0.0026	-0.0126	-0.0086	-0.0091	-0.0051	0.0664
t-test		2.9893#	1.7483	6.4351*	3.5586*	2.7089#	3.0393#	1.4728	0.3299
$r(V_r\&W_r)$		0.4340	0.0899	0.3643	0.0279	0.3580	0.0337	0.1357	0.7097#
$\bar{P}$		0.8385	0.6392	0.5433	0.5756	0.5037	0.4544	0.4630	1.1346
$\bar{F}_1$		1.0202	1.0373	1.0571	1.0531	1.0620	1.0682	1.0671	0.9832
Heterosis (%)		21.66	62.29	94.58	82.06	110.86	135.05	130.46	-13.34
Genetical components									
D		0.0203	0.1304	0.0224	0.0516	0.0221	-0.0090	-0.0067	0.0855
F		0.0630	0.2314	0.0574	0.1638	0.0916	0.0345	0.0208	-0.0909
H_1		0.6070	0.7865	0.9964	0.9393	0.7058	0.8630	0.7121	0.1702
H_2		0.4978	0.5817	0.8636	0.7442	0.6087	0.7885	0.6461	0.1434
h^2		0.1247	0.6245	1.0539	0.9028	1.2358	1.4927	1.4473	0.0884
E		0.0184	0.0243	0.0052	0.0232	0.0286	0.0355	0.0312	0.0084
$D-H_1$		-0.5867	-0.6561	-0.9740	-0.8877	-0.6836	-0.8720	-0.7189	-0.0847
Genetic analysis									
$\overline{uv}$		0.2050	0.1849	0.2167	0.1981	0.2156	0.2284	0.2268	0.2106
H_1-H_2		0.1092	0.2048	0.1328	0.1951	0.0971	0.0746	0.0660	0.0268
K_d/K_r		1.7940	2.1315	1.4761	2.1846	2.1559	1.4875	1.3551	0.4529
n		0.2050	1.0736	1.2204	1.2131	2.0302	1.8932	2.2400	0.6161
Heritability (narrow)		1.78	8.56	11.53	5.47	1.62	-0.53	-0.48	20.83
Heritability (broad)		98.39	98.40	99.72	99.30	97.91	97.36	97.75	97.95
Degree of dominance		5.4744 Over-d	2.4560 Over-d	6.6738 Over-d	4.2668 Over-d	5.6453 Over-d	9.8179 Over-d	10.3007 Over-d	1.4110 Over-d

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

The fluctuation of stability and its genetic constitution in different growth stages

From the aforementioned results, the stability of fresh weight was fluctuated in growth stages, and the genetic parameters were also different during the growth. The genetic parameters, except heterosis, maternal effect, and heritability did not change during growth. Those did change during growth were the gene effect, the difference of gene frequencies, the ratio of dominance and recessive genes, and the effective genes of dominance.

But the estimated value of homogeneous recessive genes concerning with fresh weight stability for a parental line was fluctuated with growth. From Fig. 1, line Co–1 has a few homogeneous recessive genes, so, this line was unstable in growth. Lines En, Po–1, C and Estland have a large number of recessive genes, they were stabler than the Co–1. The genes estimated for the stability of line LM–4 were more fluctuated than the others. Therefore the stability parameters was also fluctuated with its gene number during growth. Hence, we concluded that the recessive homogeneous gene controlled the fresh weight to a stable state during growth.

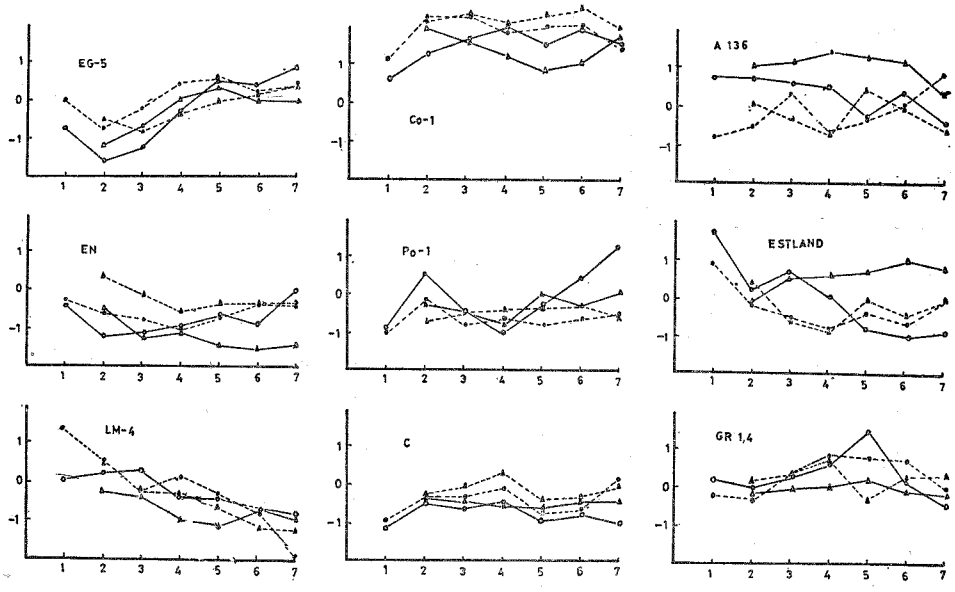

Fig. 1. The change of fresh weight, its stability and (V_r+W_r) value during the growth. ○——○: fresh weight stability; ●——●: (V_r+W_r) value of fresh weight stability; △——△: fresh weight; ▲——▲: (V_r+W_r) value of fresh weight. The horizontal and vertical axes are shown the growth stage in weeks and normally standardized value of mean expression, respectively.

Genetical analysis of fresh weight

The genetical analysis of fresh weight was mentioned in the first section

(Table 1). In this section, we reported the results according to different growth stages, and environments.

1. *Genetical analysis of fresh weight in different growth stages*

The additive genetic effect (D) was less than that of dominant (H_1 and H_2). Heterosis has a tendency to be increased with the growth. Owing to $h>0$, therefore the heavy fresh weight was dominant. For $H_1 \neq H_2$ $\overline{uv} \neq 0.25$, so the dominant effect was partially contributed by the difference of perental gene frequency. The variance of "a" was contributed by additive and dominant gene effects. Ratio of the dominant and recessive genes was 1.5–2.0. The number of dominant genes was more than twice as much as the recessive ones. The number of dominant genes was fluctuated in 6–15, during the growth. The additive gene effect was smaller than the dominant. Therefore, the heavy fresh weight became over-dominance and the hritability in narrow sense was small. Therefore the selections for fresh weight are less efficient in growth stage.

The change of mean fresh weight and (V_r+W_r) value in various growth stages of the ith lines are also shown in Fig. 1. Because of comparing the mean fresh weight and (V_r+W_r) values in different growth stages, these values were normally standardized. From these results, the fluctuating tendency of fresh weight and number of dominant gene agreed with lines, EG–5. Co–1, Po–1, LM–4, C, and GR 1,4. But lines En, A 136, and Estland were also slightly fluctuated. The gene effect of the former line was smaller than the latter two.

2. *Genetical analysis of fresh weight in different environments*

In previous sections, we analyzed the genetic constitution of plant fresh weight in overall environments. The genetic constitutions of fresh weight for several individual environments were analyzed in this section. They were artificial and natural light conditions, with or without fertilizations, and low (25°C in day and 20°C in night) and high (30°C in day and 25°C in night) temperature treatments. The results are summarized as follows.

(1) Of the light conditions, the results are shown in Table 4. The genetical differences were all significant in each stage. The effects of additive genes were smaller than the dominant. The dominant and maternal effects became large, and were associated with growth. The genetical constitutions of these two treatments were the same as described in the previous section. The genetic variation of artificial light treatment was smaller than that of natural light. The gene effect was weaker under artificial than natural lights. The fluctuations of mean weight and (V_r+W_r) values for each line during the

growth are shown in Fig. 2. Lines EG–5, En, and Po–1 have more dominant gene effects under natural light than the artificial, and line Co–1 *vice versa.* In later growth stage, line LM–4 has less numbers of dominant gene under natural light and the fresh weight decreased in the stage, Line C, on the other hand, dominant genes developed under artificial light in later growth stage, and the fresh weight increased. Lines A 136, and Estland developed dominance genes under natural light in later stages, and their fresh weight increased.

Table 4. *Diallel analysis of artificial light*

Variation	df	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	FL-T
Treatments	80	0.1081*	1.18*	6.87*	24.07*	74.42*	299.79*	840.95*	19,389.39*
a	8	0.0129*	1.39*	10.19*	35.36*	68.51*	271.67*	386.81*	101,072.55*
b	36	0.0166*	0.73*	6.98*	28.61*	97.09*	346.37*	855.03*	9,987.30*
b_1	1	0.0725*	4.86*	66.26*	280.87*	1,142.42*	4,009.96*	9,824.49*	26,240.42*
b_2	8	0.0148*	0.71*	2.94*	14.68*	29.21*	89.13*	178.53*	19,901.86*
b_3	27	0.0151*	0.58*	5.99*	23.39*	78.49*	286.90*	723.26*	6,447.88*
c	8	0.7738*	4.38*	14.20*	40.59*	110.78*	608.78*	2,099.62*	29,468.51*
d	28	0.0627*	0.78*	3.69*	10.28*	38.59*	159.66*	592.97*	5,259.90*

Diallel analysis of natural light

Variation	df	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	FL-T
Treatments	80	0.0446*	0.19*	0.74*	8.72*	53.36*	171,14*	629.80*	25,683.90*
a	8	0.0055*	0.05#	0.55	6.83*	45.22*	185.16*	480.73*	33,970.91*
b	36	0.0037*	0.06*	0.66*	6.77*	44.20*	216.63*	823.69*	5,728.71*
b_1	1	0.0223*	0.43*	7.28*	54.66*	247.17*	1,696.24*	8,200.78*	8,647.35*
b_2	8	0.0055*	0.05#	0.35	3.91#	23.04*	84.63*	301.78*	10,103.39*
b_3	27	0.0025*	0.05*	0.51#	5.84*	42.95*	200.93*	705.10*	4,324.10*
c	8	0.3103*	1.06*	1.12*	25.94*	164.85*	215.93*	199.73*	142,551.72*
d	28	0.0325*	0.13*	0.79*	6.86*	35.63*	95.84*	545.98*	15,582.26*

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

(2) Of the fertilizer conditions, the results are shown in Table 5. The genetic variations were all significant except b_2 and additive gene effect at FW–4, 5, 6 and 7 stages. The genetic variation of fertilizer treatment was larger than that of non-fertilizer. This indicated that fertilizer has increased the genetic effect, specially to the mean dominance (*b*) and maternal effects. Fig. 3 shows the fluctuating tendency of dominance genes and the fresh weight in normally standarized value. Lines EG–5, and Co–1 increased in these two characters after fertilizer application except line En. Lines Po–1, LM–4, A 136, and GR 1,4 were uncertain after fertilizer treatments. The

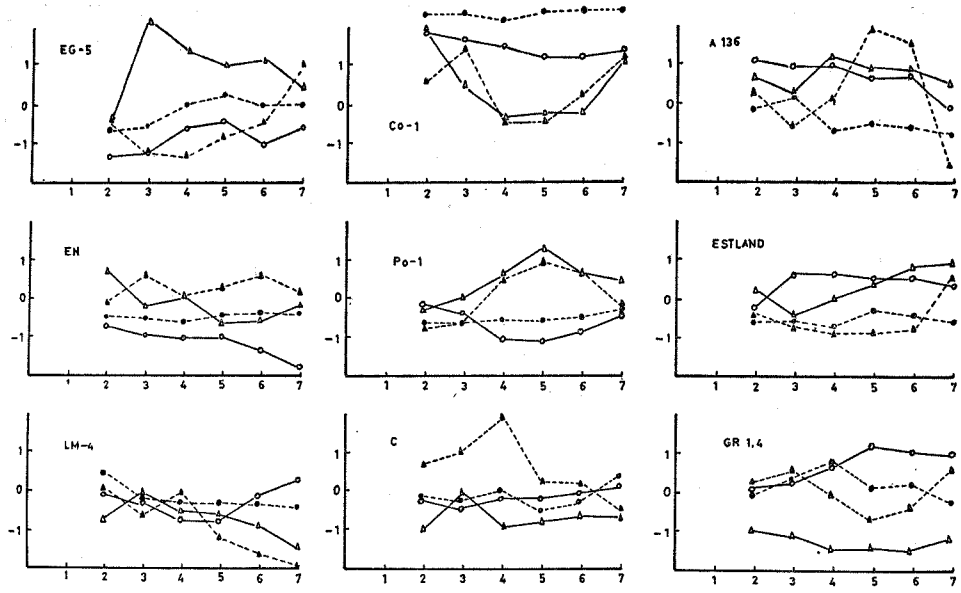

Fig. 2. The change of fresh weight and (V_r+W_r) value under different light conditions. ○——○: fresh weight under artificial light (AL); ●------●: (V_r+W_r) value under AL; △——△: fresh weight under natural light (NL); ▲------▲ (V_r+W_r) value under NL. The horizontal and vertical axes are shown the growth stage in weeks and normally standardized value of mean expression, respectively.

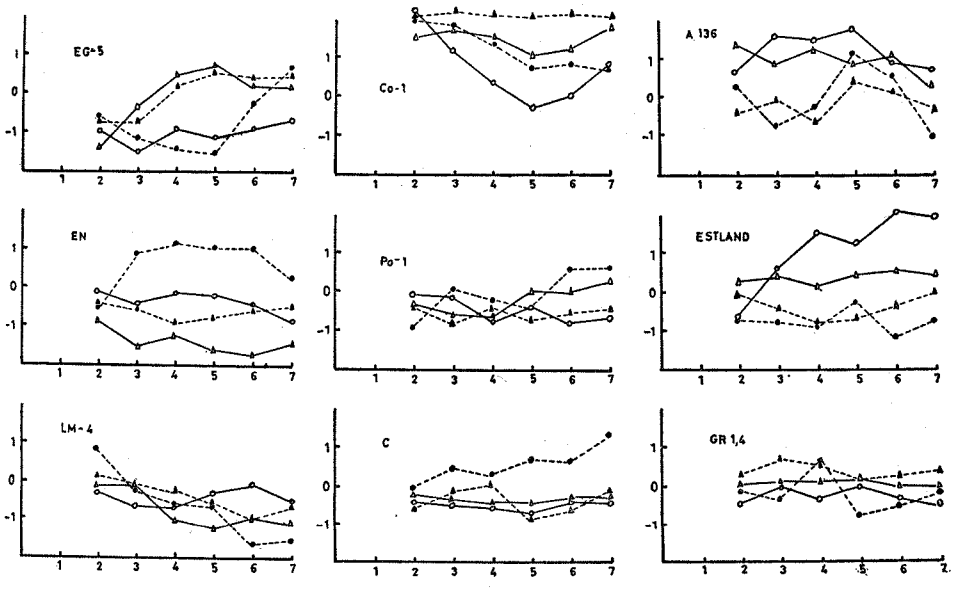

Fig. 3. The change of fresh weight and (V_r+W_r) value under different fertilization conditions. ○——○: fresh weight, without fertilization (NF); ●------●: (V_r+W_r) value under NF; △——△: fresh weight, with fertilization (F); ▲------▲: (V_r+W_r) value under F. The horizontal and vertical axes are shown the growth stage in weeks and normally standardized value of mean expression, respectively.

dominance genes of C line increased in the later stage without fertilization. The fresh weight of Estland increased in the same treatment. Therefore the gene effect of these two lines was different in these two fertilizer treatments.

Table 5. *Diallel analysis of non-fertilizer*

Variation	df	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	FL-T
Treatments	80	0.0746*	0.57*	1.11*	4.47*	14.34*	46.01*	104.58*	21,963.45*
a	8	0.0139*	0.47*	1.11*	4.55*	7.32*	29.40#	65.86	57,091.19*
b	36	0.0080*	0.32*	1.22*	5.60*	16.43*	53.55*	142.41*	8,305.54*
b_1	1	0.0694*	1.69*	15.95*	82.02*	162.09*	585.25*	1,488.30*	22,296.56*
b_2	8	0.0080*	0.30*	0.70#	2.61	10.76	25.24	50.20	15,122.52*
b_3	27	0.0057*	0.27*	0.82*	3.66*	12.72*	42.25*	119.89*	5,767.60*
c	8	0.5083*	2.19*	1.49*	7.49*	31.09*	86.98*	98.63*	86,179.00*
d	28	0.0536*	0.47*	0.86*	2.12*	8.89	29.35*	68.70*	11,139.34*

Diallel analysis of fertilizer

Variation	df	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	FL-T
Treatments	80	0.0724*	0.57*	4.76*	26.15*	93.23*	395.85*	1,589.17*	18,040.20*
a	8	0.0092*	0.52*	4.22*	22.88*	67.15*	297.40*	563.37*	63,660.30*
b	36	0.0102*	0.34*	5.10*	31.67*	135.52*	602.70*	1,862.82*	7,174.73*
b_1	1	0.0241*	2.42*	46.83*	227.89*	1,353.50*	6,450.93*	22,830.64*	11,163.98*
b_2	8	0.0109*	0.31*	1.91*	18.68*	46.41*	163.96*	478 45*	14,539.91*
b_3	27	0.0094*	0.27*	4.50*	28.25*	116.81*	516.10*	1,496.42*	4,844.88*
c	8	0.5243*	2.66*	11.60*	54.79*	97.76*	174.34*	2,223.05*	59,092.52*
d	28	0.0413*	0.29*	2.51*	11.80*	45.06*	221.31*	1,349.31*	7,246.32*

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

(3) Of the temperature conditions, the results of low (25°–20°C) and high (30°–25°C) regions are shown in Table 6. The genetic variations of the two treatments were all significant, except the b_2 of FW-4 in high temperature. But the variation of high temperature was smaller than that of the low. Because plants respire more in the high temperature, anabolism decreased and catabolism increased. Therefore, less amount of fresh weight was obtained in the treatment. The gene effect of fresh weight became small. The genetic constitutions were the same as those from the overall environments.

The fluctuating tendency of dominance genes and fresh weight of each line in temperature are shown in Fig. 4. From these results, lines Co-1, C and A 136 have the same fresh weight in different temperatures, but the numbers of

Table 6. *Diallel analysis of temperature (25°–20°)*

Variation	df	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	FL-T
Treatments	80	0.0426*	0.72*	2.93*	14.19*	46.73*	162.34*	461.30*	10,820.79*
a	8	0.0075*	0.61*	2.16*	8.88*	28.99*	150.12*	463.65*	26,910.64*
b	36	0.0077*	0.42*	2.98*	13.69*	48.89*	188.16*	577.09*	4,194.00*
b_1	1	0.0093*	1.69*	36.35*	142.65*	551.33*	1,970.10*	6,065.64*	4,576.99*
b_2	8	0.0115*	0.26*	0.79*	3.59*	15.48#	54.13*	180.96*	7,238.51*
b_3	27	0.0065*	0.42*	2.40*	11.90*	40.18*	161.88*	491.19*	3,277.58*
c	8	0.2743*	2.70*	8.18*	43.30*	138.77*	235.82*	439.46*	44,515.43*
d	28	0.0313*	0.58*	1.58*	8.04*	22.73*	111.64*	318.00*	5,116.88*

Diallel analysis of temperature (30°–25°)

Variation	df	FW-1	FW-2	FW-3	FW-4	FW-5	FW-6	FW-7	FL-T
Treatments	80	0.0393*	0.17*	0.87*	7.90*	35.80*	110.29*	534.57*	14,665.37*
a	8	0.0124*	0.15*	0.64*	6.32*	18.99*	75.07*	128.00*	56,013.40*
b	36	0.0044*	0.10*	0.72*	5.75*	35.03*	147.54*	585.26*	5,614.98*
b_1	1	0.0401*	0.56*	5.60*	60.39*	195.69*	1,231.14*	5,212.43*	14,620.53*
b_2	8	0.0052*	0.09*	0.36	4.76*	15.83#	76.27*	166.18*	11,336.07*
b_3	27	0.0028*	0.09*	0.64*	6.69*	35.97*	128.53*	538.06*	3,586.26
c	8	0.2710*	0.78*	2.63*	21.02*	87.25*	62.01*	702.10*	46,683.95*
d	28	0.0255*	0.08*	0.63*	4.79*	25.73*	86.26*	537.70*	5,339.24*

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

dominance gene varied in different temperatures. The gene effects of the lines were different. Lines EG–5 and LM–4 have the same fresh weight in early and middle growth stages, but differed with that of later stage, (increasing fresh weight in high temperature). The fluctuating tendency of fresh weight and dominance genes was different in these two lines. Lines GR 1,4 and Estland have heavy fresh weight under low temperature, in middle, and later stage, bue the tendency of dominance genes and fresh weight did not agree with later stage. Po–1 line gained more fresh weight under high temperature in all stages, but in later stage, the numbers of dominance gene was difference in two different treatments.

Genetical analysis of flowering time stability

The data of Table 3 showed that the maternal effect was more efficient than the additive or non-additive genetic effect in flowering time stability. The dominant effect was significant, and the average dominant effect was also large. So the gene action unidirectionally affected the character. The variation of "a" included both additive and dominant effects, and the dominant effect

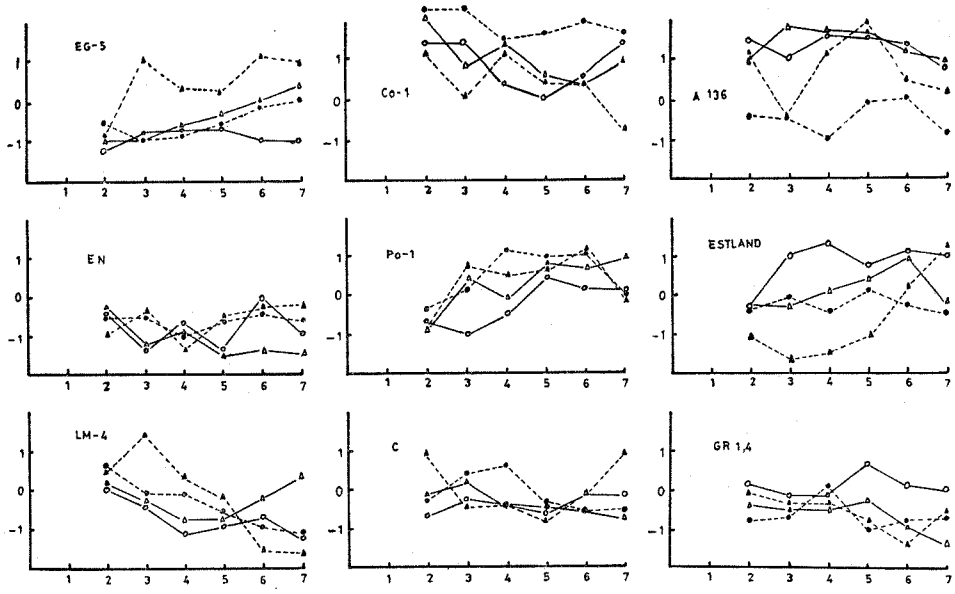

Fig. 4. The change of fresh weight and (V_r+W_r) value under different temperature conditions. ○——○: fresh weight under low temperature (LT); ●------●: (V_r+W_r) value under LT; △——△: fresh weight under high temperature (HT); ▲------▲: (V_r+W_r) value under HT. The horizontal and vertical axes are shown the growth stage in weeks and normally standardized value of mean expression, respectively.

partially involed the different gene frequencies.

Mean stability expressions of the parental lines and F_1 plants were 1.1346 and 0.9832, respectively. Therefore $h<0$, the stability was dominant over the unstability. After comparing the genetic variations, the additive genetic effect (D) was smaller than that of the non-additive ones, H_1 and H_2. So the heritabilities were 20.8% and 98% for narrow and broad senses, respectively. Therefore, selection responsibility of flowering time stability was greater than that of the character of fresh weight stability, but not efficienet. Because $uv\neq0.25$, $H_1\neq H_2$, hence the dominance and recessive gene frequencies of the parental lines were different, so the dominant effect was included in the variation of *"a"* source. The ratio of the dominant and recessive genes was 0.45. Therefore the recessive gene group was greater than the dominant. The correlation between mean stability and (V_r+W_r) value was −0.4036, so the stable lines have dominant homogeneous genes as Co-1, and C. The unstable lines were A 136 and Estland, which have less numbers of dominant gene. (Fig. 5)

Genetical analysis of flowering time

The variation of flowering time among different lines (G) was significant. The maternal (c) and the additive genetic effect (a) were the important factors

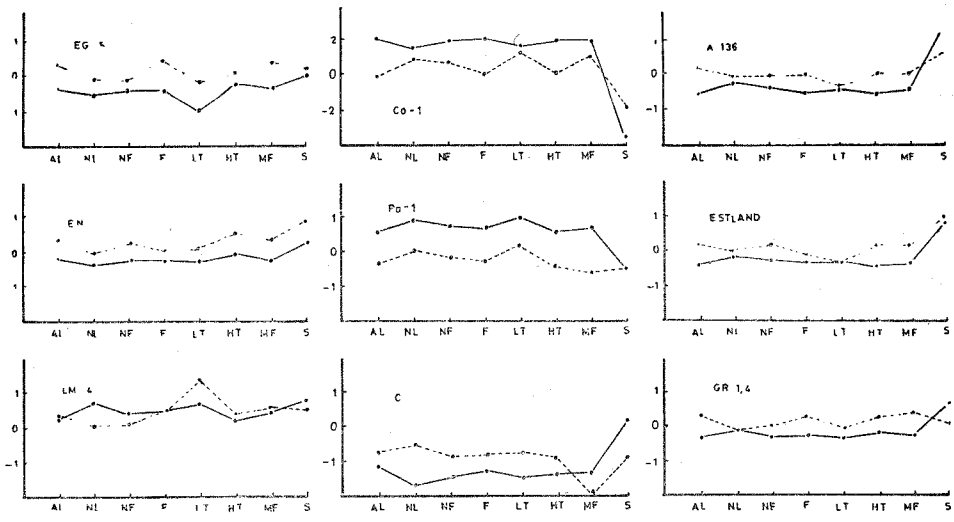

Fig. 5. The change of flowering time, its stability and their (V_r+W_r) value at different environments. AL: artificial light; NL: natural light; NF: without fertilization; F: with fertilization; LT: low temperature; HT: high temperature; MF: mean flowering time; S: stability; •——•: mean expression; ●------●: (V_r+W_r) value. The horizontal and vertical axes are shown the environment and normally standardized value, respectively.

to flowering time. The next important factor was the average dominant effect (b_1), and the dominant gene which unidirectionally controlled and delayed the flowering time. The average flowering times were 53.0 and 58.8 for parental line and F_1 plants, respectively. Hence $h=11.6>0$, so the late flowering was dominant. The differences in dominance among parental lines (b_2) and among different crosses (b_3) were significant, $H_1 \neq H_2$ representing the difference of gene frequencies. So, the additive genetic variance and dominant effect contributed to genetic variation. The maternal effects c and d were significantly existed; so, the cytoplasmic effect partly controlled the inheritance of flowering time.

The estimated values of various genetic variations were 42.26, 431.57, 244.20, 7.36, 134.93 and 1.32 for D, H_1, H_2, F, h^2, and E, respectively. The additive genetic variation was smaller than the non-additive ones. Threfore, the heritabities were 5.88% and 99.82% for the narrow and broad senses, respectively. So the selection was in-efficient. Frequencies of dominant and recessive gene were dffierent, and may cause a dominant effect. The numbers of dominant and recessive genes were the same. Over-dominance existed in this character, and the correlation between flowering time and (V_r+W_r) value of each line was 0.2843. So line Co-1 which has a late flowering time has more dominance genes. Line C flowered early; it has less numbers of dominant gene. (Fig. 5)

The genetical analysis of flowering time in different environments

As described in section 5-2, the genetical analysis of flowering time was made according to different environments. The main results are summarized in follows.

(1) Different light conditions. The genetic variation due to different parental lines and maternal effect under natural light was greater than that of the artificial. On the contrary, the additive genetic variation and dominant effect were rather large in the artificial light condition. The gene action concerning with the flowering time was different under light condition. The array of mean flowering time and dominant gene numbers of each line was not concordant in both conditions (Fig. 5).

(2) Different fertilizer conditions. The genetical difference among parental lines was large, and the average dominant effect as well as the maternal were small under fertilization. The array of mean flowering time and its dominant gene of each line was concordant in no fertilization but it did not agree with those of fertilizer treatment.

(3) Differerent temperature conditions. The variations of genetical difference among parental lines, mean dominant effect, dominant effect owing to the different parental lines as well as unidirectional gene action were large in the high temperature treatment (30°C–25°C), but maternal effect and dominant effect owing to different cross combinations were not affected by the temperature. The array of the mean flowering time and its dominant gene numbers of each line was concordant in the low temperature treatment (25°C–20°C), but not agreed with the high ones.

(4) The genetic constitution of flowering time in each treatment had the same manner as described in section 7.

Discussion

The plant of *Arabidopsis thaliana* can be grown under light of 5,000 lux with daylength of more than 8 hours (Griffing *et al.* 1963; Pederson, 1968) at 10°–30°C (Griffing *et al.*, 1963; Pederson, 1968; Westerman, 1970). In this study, the light intensity was enough to grow the plants. We concluded that the variation caused by light was mainly influenced by the nature of lights, i.e., natural or artificial lights, and daylength. Pederson (1968) has obtained the temperature-dependent stability in his study of *Arabidopsis*. However this stability was not found in this study. This may be due to many environmental factore, snch as temperature, light, and fertilizer involved.

The mean expression (fresh weight or flowering time) and linear sensitivity to environments have the same genetic constitution, such as unidirectionally gene action, dominant effect and heterosis. All of these increases associated

with growth. Dominant effect included the effects of different dominant and recessive gene frequencies. Additive genetic variation was smaller than the non-additive ones. So the selection of these two aspects was limited. The developed and fluctuated genes in growth have identical tendency in mean expression, and linear sensitivity. But heavy fresh weight and high sensitivity were dominant. Early flowering time and high linear sensitivity were recessive. The numbers of dominant gene concerning with phenotypic and linear sensitivity were quite different. The response to the change of environment during growth differed among genotypes. The genetic basis of linear sensitivity and mean expression of characters were different and dependent upon the environments considered. Each gene system determined the quantitative character of fresh weight, flowering time, and its linear sensitivity.

The estimated value of linear sensitivity of genotype will be more accurate when gene (Finlay *et al.*, 1963; Breese, 1969; Okuno, 1971), and environmental number increase. So the parameter which measured the linear sensitivity of a genotype will be considered as a parameter of stability for a quantitative character, and may be taken as a character to analysis the genetic constitution.

The stability of fresh weight, yield of an open-pollinated plant is being concerned with the heterozygosity. The high heterozygosity is always stabler than the homozygosity during environmental change. In self-pollinated plant, the same tendency in yield was found in wheat (Copp *et al.*, 1952), and that of fresh weight in *Arabidopsis* (Griffing *et al.*, 1963). Pederson (1968) has found that the fresh weights of F_1 *Arabidopsis* and F_2 generations were stabler to different environments than those of their parental lines. This is because that the genetic difference of parental lines was greater than their hybrids. In this study, we obtained an inverted results, i.e., the parental lines was stabler to environments than their hybrids.

The relationship between mean expression of flowering time and its linear sensitivity becomes quadratic form. This shows that the early and late flowering times are less sensitive to environments, while the middle stage is high. So the genotype having early or late flowering time may show certain expressions and developped numbers of dominance gene under various environments. And the genotype having middle expression may fluctuate their dominance genes and actions under different environments.

Line A 136 is a early flowering mutant from line Estland. Its mean expression of flowering time remained the same in various environments except in fertilizer treatment. Therefore, the fertilizer factor may give influence to gene actions of early flowering mutant.

Fripp and Caten (1973) has pointed out a positive association between mean expression and linear sensitivity. The correlation was low, however,

approximately 50%. These two aspects was independent upon each other. The association disappears in a set of uniform environments, demonstrating that different genetical systems react in different environments. In certain circumstances, mean expression and linear sensitivity are determined by separate gene systems; this agrees with our results. So the relationship between mean expression and sensitivity is markedly influenced by the environments. Each combination of genotype, environment, and character should be trated as a separate case. Therefore the joint selection for high performance and low sensitivity may be limited by an association between high expression of these two characters. As concluded by Fripp *et al.* (1973), the development of a specially or generally adapted varieties is dependent upon the use of a selected environment.

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植物安定性的遺傳學研究

II. 安定性的遺傳

鄔 宏 潘

日本東京大學植物育種實驗室和中央研究院植物研究所

利用 *Arabidopsis thaliana* 的九系統及其全互交的 F_1 爲材料，探討各生育期的生體重、開花期，以及這些性狀對不同環境的安定性的遺傳。在遺傳結構上，支配這些性狀及其安定性的各別遺傳因子皆具有單向性的因子作用。顯性作用及雜種優勢也存在，而這些作用力皆隨着生長而漸增。顯性作用一部份由顯隱性因子頻度之差異而形成，顯性變異及累加性遺傳變異共同造成遺傳總變異，但顯性變異大於累加性變異，因此性狀本身以及其安定性的選拔效果可能甚低。顯性因子支配着大的生體重，而不同的隱性因子支配着大的安定性。然在開花期方面，則隱性因子支配早期的開花而不同的顯性因子支配其大的安定性。由此可知支配數量性狀及其安定性的遺傳系統不相同，可能分別選得不同的遺傳體系。但在生體重方面外表型平均值及其安定性間呈直線關係，要選得生體重大而又安定的後裔可能性較低，而在開花期方面，則兩者之間呈拋物線關係，開花期早及遲者呈安定狀態而中間者呈不安定，因此各別選得早（或遲）開花而其開花期又安定的後裔的可能性較大。不同環境下的遺傳分析也同時進行之。