Flowering Time Dependent and Independent Components of Interplant Variation of Plant Height in Diallel Cross F_1 of Rustica Tobacco

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The interplant variation of plant height within plot was analyzed in relation to the variation of flowering time using a set of F_1 diallel crosses between six inbred lines of rustica tobacco grown in two environments, the early and late transplantings. The interplant variation of plant height in a genotype was partitioned into two components; the one dependent on flowering time and the residual one independent of flowering time. The former was mainly due to the additive effect of genes and the genetic effects on it were not consistent to the environmental changes. The latter was due to the additive and non-additive effects of genes which were relatively stable against the environmental changes. There was no genetic relationship between the two components in both environments. From these results, it was suggested that the two components of the interplant variation of plant height were controlled by different genetic factors. Neither the dependent nor the residual interplant variation was correlated with the phenotypic plasticity, which was estimated in terms of the ratio of phenotypic difference to the mean value between the environments.

KEY WORDS: *Nicotiana rustica*, interplant variation, intragenotypic variability, developmental instability, diallel analysis.

Introduction

The phenotypic variation among genetically identical plants grown in a certain environment contains variation other than that resulted from environmental causes. Such an intragenotypic variability in a quantitative character is considered to be due to chance fluctuation in developmental process and is known as developmental instability (SAKAI and SHIMAMOTO 1965) or stability (PAXMAN 1956).

PARODA (1971, 1972) demonstrated the importance of uniformity of heading time of the tillers within a genotype in cereals, or synchrony of heading, which influences the subsequent growth of tillers and even the final grain yield. A similar effect must be observed in an interplant variation of a character. For example, it has been pointed out that interplant variations in seedling size and time of its emergence affect the growth (KASPERBAUER and SUTTON 1977, SOETONO and DONALD 1980, KNIGHT 1983). From these reports, the interplant variation in a particular character appears to contain the variations depending on the variations of other characters which have developed in advance, in addition to the independent or residual variations.

But few genetic information on such dependent and residual interplant variations within a genotype has been obtained. Thus, in this paper an attempt was made to partition the interplant variation of a particular character, plant height at flowering time, into the two components, and then their genetic controls and relationships were investigated using F_1 's in a set of diallel crosses between six inbred lines of rustica tobacco (*Nicotiana*

rustica L).

Materials and Methods

The experiment was carried out in 1981 at Experimental Farm of Faculty of Agriculture, Hokkaido University. Six inbred lines listed in Table 2 were crossed in all possible combinations including reciprocal crosses and selfings. After a month of nursing in the greenhouse, plants were transplanted into the field with two replications on May 16 (early) and June 2 (late). Adjacent rows were 75 cm apart and plants were placed 15 cm apart in each row.

Flowering time of the first flower and plant height at flowering time (hereafter called as plant height) were recorded with ten plants which flowered within a week after initial flowering.

The interplant variation of plant height was partitioned into two components according to the following formula,

$$SS_{ph} = r_f^2 SS_{ph} + (1 - r_f^2) SS_{ph},$$

where SS_{ph} is a sum of square of plant height within a plot. r_f is a correlation coefficient between flowering time and plant height over plants within a plot. On account of the normality of distribution, the magnitude of each interplant variation of plant height was estimated in terms of the standard deviation. Namely,

$$\sigma_{ph} = \sqrt{SS_{ph}/(n-1)}, \quad \sigma_d = \sqrt{r_f^2 SS_{ph}}, \quad \sigma_r = \sqrt{(1-r_f^2) SS_{ph}/(n-2)}$$

where $n (=10)$ is the number of plants sampled in a plot.

σ_{ph} is defined as the interplant variation of plant height. σ_d is defined as the interplant variation dependent on the differences in flowering time and σ_r is defined as the residual interplant variation independent of the variation in flowering time. The interplant variation of flowering time itself was also estimated in terms of the standard deviation within a plot, and expressed as σ_{ft} . The diallel analysis was carried out in the way described by HAYMAN (1954).

Results

(i) Variation among F_1 families

Fig.1 shows that variation in σ_{ft} among F_1 families was small and the relationship of σ_{ft} with σ_{ph} was not strong in both environments. Similarly, r_f values varied among families and were not correlated with σ_{ph} in both environments as shown in Fig.2. From these results, it was found that the analysis for the genetic variation in σ_{ph} was possible, being independent of the genetic variations in σ_{ft} and r_f .

The analyses of variance for interplant variation of plant height and its components are presented in Table 1, and the mean values of the F_1 's over two environments in Table 2. It was undoubted that the genetic variations in the interplant variation of plant height and its two components were mostly explained by the additive effect of genes (item *a*). The non-additive effect of genes (item *b*) was observed only in σ_r . A comparison of the mid-parent and F_1 values showed that on an average there was partial dominance towards larger σ_r . Differences between reciprocal crosses (items *c* and *d*) were not obvious for any component of the interplant variation.

Fig. 1. Relationships of the interplant variation of plant height with that of flowering time over diallel F_1 families in the early and late transplantings. Both interplant variations were estimated by the standard deviations within a plot.

Fig. 2. Relationships of the interplant variation of plant height with the correlation coefficient between flowering time and plant height within a plot over diallel F_1 families in the early and late transplantings.

(ii) Environmental and genotype-environment interaction effects

The dependent interplant variation reduced from $\sigma_d=20.2$ in the early transplanting to $\sigma_d=16.0$ in the late one, while the difference was not statistically significant (Table 1). The genotype-environment interaction effect was observed in this component. The interactions of items *a* and *b* with environments exhibited that the both additive and non-additive effects of genes on σ_d were not consistent to the environmental changes. The environmental and genotype-environment interaction effects on the residual interplant variation were rather small.

Table 1. Diallel analyses of variance for the interplant variation of plant height and its two components

Items	d. f.	Mean squares		
		$\sigma_{ph}^{1)}$	σ_d	σ_r
Genotypes, G.	35	3.701**	67.45**	5.731**
$a^{2)}$	5	22.007**	196.92**	26.593**
b	15	3.356	42.82	2.674**
b_1	1	5.746	42.94	4.316*
b_2	5	3.609	12.10	4.116**
b_3	9	2.950*	59.87	1.690
c	5	2.301	47.19	1.441
d	10	1.050	49.78	0.772
Environments, E.	1	12.885	610.79	0.001
Block $\times$ E	2	7.110**	163.40**	0.782
G $\times$ E	35	1.394*	41.65**	0.983*
$a \times E$	5	1.350	95.91**	2.182*
$b \times E$	15	1.408*	26.23*	0.845
$b_1 \times E$	1	3.891*	19.14	1.621
$b_2 \times E$	5	1.917*	37.25*	0.681
$b_3 \times E$	9	0.849	20.89	0.850
$c \times E$	5	1.924*	78.64**	0.385
$d \times E$	10	1.129	19.14	0.890
Pooled error	70	0.813	13.45	0.614

¹⁾ σ_{ph} is the interplant variation of plant height at flowering time. σ_d and σ_r are the dependent and the residual interplant variations, respectively. These three interplant variations of plant height were estimated by the standard deviations within a plot.

²⁾ a ; additive effect of genes. b ; non-additive or dominance effect of genes. b_1 ; mean dominance effect. b_2 ; additional dominance effect of genes. b_3 ; residual dominance effect of genes. c , d ; average and residual reciprocal effects, respectively, cf. HAYMAN (1954).

*, ** Significant at the 5% and 1% levels, respectively. Each mean square of main effect was tested against interaction mean square.

(iii) Relationships among variation components

As shown in Table 3, there was strong positive correlation between σ_{ph} and σ_r in both environments. This correlation was accounted for by the close relationships both in the additive and non-additive effects of genes. σ_{ph} was also positively correlated with σ_d in most items except for item a in the late transplanting. No items in σ_d was correlated with those in σ_r , indicating that the additive and non-additive genes controlling σ_d seemed to be different from those controlling σ_r .

Table 4 shows correlations between two environments in the variation components in question. A positive correlation between the early and late transplantings was recognized in σ_r , where it was ascribable to correlations in both of the additive and non-additive effects of genes. Thus, it was found that the additive and non-additive effects of genes controlling σ_r were relatively stable over two environments. In σ_d , as anticipated from the results of the large genotype-environment interaction shown in Table 1, the correla-

Table 2. Mean values, over two environments, of the interplant variation of plant height and those of the two components in each diallel F_1 family

σ	δ	H ¹⁾	K	M	P	R	T	Mean
H	σ_{ph}	6.20	7.69	5.34	5.76	5.90	8.84	6.62
	σ_d	22.7	22.2	17.0	19.9	14.4	23.2	19.9
	σ_r	3.06	4.93	3.19	3.47	4.96	6.66	4.38
K	σ_{ph}	7.74	7.27	7.43	5.41	6.80	8.44	7.18
	σ_d	22.3	19.8	26.0	15.2	23.7	18.5	20.9
	σ_r	5.71	5.45	4.47	4.10	4.10	7.14	5.16
M	σ_{ph}	5.95	7.22	4.34	5.03	6.16	7.30	6.00
	σ_d	20.8	25.1	14.8	13.5	21.0	14.5	18.3
	σ_r	3.54	4.43	2.72	4.02	3.91	6.53	4.19
P	σ_{ph}	5.60	4.82	5.00	5.28	4.73	6.19	5.27
	σ_d	17.5	13.4	14.4	13.2	10.9	15.3	14.1
	σ_r	3.97	3.75	3.76	4.40	4.02	5.17	4.18
R	σ_{ph}	7.20	5.26	5.78	5.40	5.28	6.60	5.92
	σ_d	26.5	15.1	18.0	19.3	16.8	16.4	18.7
	σ_r	3.86	4.05	4.03	3.09	3.64	5.49	4.03
T	σ_{ph}	8.60	6.13	7.08	6.44	6.71	6.92	6.98
	σ_d	22.8	13.7	18.4	16.6	15.1	14.0	16.8
	σ_r	6.86	5.29	5.73	5.23	5.74	6.18	5.84
Mean	σ_{ph}	6.88	6.40	5.83	5.56	5.93	7.38	6.33
	σ_d	22.1	18.2	18.1	16.3	17.0	17.0	18.1
	σ_r	4.50	4.65	3.98	4.06	4.40	6.20	4.63

¹⁾ Parent names, H : Himlis, K : Korikien, M : Machorka, P ; M. Promoskase 1—4, R : Rustica, T ; Texana.

Table 3. Correlations between the interplant variation of plant height and its two components in the early (above-right) and late transplantings (bottom-left)

	σ_{ph}	σ_d	σ_r
σ_{ph}		G ¹⁾ 0.794**	0.776**
		a ²⁾ 0.787	0.813*
		b ——— ³⁾	0.904**
		b ₂ ———	0.976**
		c 0.948**	0.863*
σ_d	G 0.546**		G 0.272
	a 0.271		a 0.286
	b 0.772**		b ———
	b ₃ 0.840**		b ₂ ———
	d 0.869**		c ———
σ_r	G 0.727**	—0.154	
	a 0.788	—0.376	
	b 0.762**	0.215	
	b ₃ 0.827**	0.410	
	d ———	———	

¹⁾ Genotypic correlation over 36 F_1 families.

²⁾ The same as HAYMAN's (1954) notation, see Table 1.

³⁾ Its corresponding mean square is not significant.

*, ** Significant at the 5% and 1% levels, respectively.

Table 4. Correlations between two environments in the interplant variation of plant height and in its two components

Items	σ_{ph}	σ_d	σ_r
G ¹⁾	0.579**	0.240	0.699**
a ²⁾	0.885*	0.350	0.871*
b	0.411	— ³⁾	0.522*
b ₂	—	—	0.719
b ₃	—	—	—
c	—	—	—
d	—	—	—

1), 2) and 3) The same meanings as in Table 3.

*, ** Significant at the 5% and 1% levels, respectively.

tion between two environments was not detected.

Discussion

Typical two genotypes, as illustrated in Fig. 3, can be imagined with regard to the relationship of plant height with flowering time among plants grown in an environment.

Fig. 3. Schematic diagram of the relationship of plant height with flowering time among plants within a plot. Open circles show a supposed genotype of which interplant variation of plant height depends on the difference in flowering time, and the taller plants are caused by delayed flowering time. Solid circles show another supposed genotype of which plant height has no interrelation with flowering time.

Open circles show plants with a supposed genotype, in which the larger plant heights are caused by the delayed flowering time. Such a genotype has a very high correlation coefficient between the two characters. As a result, it may be expected that the interplant variation of plant height (σ_{ph}) mostly consists of the variation dependent on the differences in flowering time (σ_d). On the other hand, solid circles show plants with another supposed genotype, in which their plant heights vary independently of flowering time, thus the correlation coefficient would be expected to be nearly zero. In such a genotype, the interplant variation may consist of the residual interplant variation (σ_r) in most parts.

In the previous trial using inbred lines, the above two typical genotypes were found but most genotypes contained both σ_d and σ_r with various degree (MIURA *et al.* 1985).

The present experiment using diallel F₁ families indicated that σ_r was due to the additive and non-additive effects of genes, while σ_d was mainly due to the additive effect. The genetic effect on σ_d was strongly interacted with environments as compared with that on σ_r . There was genetical independency of σ_d with σ_r in both environments. Therefore, it was confirmed that

the two components studied were controlled by the different genetic factors.

The intragenotypic variability observed under a certain environment may be ascribable to two genetic factors (SHIMAMOTO 1978). The first is the developmental instability and the second is the quantitative differentiation which makes homologous organs differentiate quantitatively in a certain direction. According to this definition, the dependent inter-plant variation may be concerned with variations responsible for the quantitative differentiation. It is because this component contains the variation due to differences in growth which has linear relationship with differences in flowering time. The residual one may be concerned with the developmental instability because of randomness in the direction of the variation, which corresponds to a low value of r_f in Fig. 2.

Table 5. Correlations between the interplant variations and phenotypic plasticity

	Phenotypic plasticity ¹⁾	
	Plant height	Flowering time
σ_{ph}	-0.072	-0.101
σ_d	-0.061	0.115
σ_r	-0.047	-0.219

¹⁾ Estimated from the ratio of phenotypic difference to the mean value between two environments.

We can also measure the other type of intragenotypic variability by growing genetically identical plants in various environments. The variability expresses the sensitivity to macro-environmental changes and is known as phenotypic plasticity (BRADSHAW 1965). Table 5 shows the relationships between the interplant variations averaged by two environments and the phenotypic plasticity, which was estimated from the ratio of phenotypic difference to the mean value between two environments. It appeared that neither the dependent nor the residual interplant variation resulted from the phenotypic plasticity, since the components were not correlated with the plasticity.

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ルスチカタバコの二面交雑 F_1 における草丈の個体間変異の開花日依存・非依存成分

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遺伝的に均一な個体を同一環境条件下で生育させたとき, ある量的形質で観察される個体間の表現型変異は, 測定誤差や環境条件の微細な変動を除けば, 遺伝子型固有の発育不安定性によっている. このような表現型変異は, 形質間の発育的相互関係を考慮した場合, 他の特定の形質の変異に起因して生じた部分と, それ以外の原因で生じた部分とに分けられる.

本研究では, ルスチカタバコの 6 系統間の正逆交雑による二面交雑 F_1 を供試し, 開花日における草丈の試験区内の個体間変異を, 個体間の開花日と草丈の相互関係をもとに二つの変異成分に分割した. 一方は, 開花日の差異が原因で生じたとみられる依存個体間変異であり, 他方は開花日の差異とは独立な残余の変異である.

依存個体間変異は, 主として遺伝子の相加的效果によっており, 移植日を異にしたとき遺伝子型と環境との相互作用が大きかった (Table 1). 残余の変異は, 遺伝子の相加的效果に加え, 非相加的效果も関与し, 変異の大きい方向に部分優性を示した (Table 2). これら相加的效果および非相加的效果は, とともに環境との相互作用が小さく, 安定的であった (Table 4). 分割されたこれら二つの変異成分は, いずれの環境でも互いに独立した関係にあり (Table 3), 異なった遺伝的支配を受けることが示唆された. さらに, 両変異成分はともに, 形質の環境変化に対する反応能力 (表現型可変性) と相関関係がなかった (Table 5).