DIALLEL ANALYSIS OF STYLE AND FILAMENT LENGTH AND THEIR DEVELOPMENTAL INSTABILITIES AND QUANTITATIVE DIFFERENTIATIONS IN TOBACCO PLANTS, *NICOTIANA TABACUM*

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Organs which are repeatedly formed to play the same role in a single plant are likely to show more or less quantitative variation in spite of being governed by the same genotype. Such an intra-genotypic variability of quantitative characters may comprise the following attributes: The first one is the so-called developmental instability (SAKAI and SHIMAMOTO, 1965 a) or stability (PAXMAN, 1956), which is considered to result from stochastic errors occuring during the developmental process of organs. The second is the quantitative differentiation observed among homologous organs not due to developmental errors, but to a genotype-determined strategy of the plant. It may well be that these two attributes, developmental instability and quantitative differentiation, are characters comparable to other metric characters such as weight, length, and so on in plants.

The present paper describes the result of an investigation into the genetic basis for the size of floral organs and also for developmental instability and quantitative differentiation of those organs by means of diallel crossing in *N. tabacum*, and the discussion of the relationships and differences between them from the viewpoint of development of floral organs.

Materials and methods

Crosses among six varieties (see Table 1) of *N. tabacum* in all possible combinations were made including reciprocal crosses. The parental and F_1 plants were grown in the field. The experiment had two blocks, each consisting of 36 plots of 30 F_1 and 6 parental varieties. Each plot included eight plants.

The style length excluding the stigma and the five filament lengths

excluding the anther were measured in twenty flowers from each plant. The pistils and stamens for investigation were collected in one lot from the terminal inflorescence after anthesis. This data provides the following measurements of size, developmental instability and quantitative differentiation of floral organs.

Size characteristics:

(a) Style length (*SL*)

(b) Length of the shortest filament from each flower (*FS*)

(c) Mean length of the four longer filaments from each flower (*FL*)

Developmental instabilities (expressed as the standard deviation among the twenty flowers for each plant):

(a) Variation of style length among flowers within plants (*VSL*)

(b) Variation of the shortest filament length among flowers within plants (*VFS*)

(c) Variation of mean length of the four longer filaments among flowers within plants (*VFL*)

Quantitative differentiation:

(a) Variation among the four long filaments within a flower (*VW*), which was expressed as the standard deviation among the four longer filaments for each flower. As the next filaments to the shortest one are usually longer than other two longer filaments (SHIMAMOTO, 1967), this variation may be used as a determination of quantitative differentiation.

(b) Difference between *FL* and *FS*(*D*)

The model presented by HAYMAN (1954) was employed for the diallel analysis.

Results

a) Size characters.

The lengths of style and filament recorded in the diallel crosses of the six parents are presented in Table 1, whilst analyses of variances of the full results given in Table 2, indicating that significance exists for a, b_3, and d items in all of the characters in question, and for the c, b_1, and b_2 items in *SL* and at b_1 in *FL*, respectively.

The degree of directional dominance $(F_1-(P_1+P_2)/2)$ were positive in all combinations of all size characters and in average, +1.73, +0.86 and +1.17 (mm.) in *SL*, *FS* and *FL*, respectively and were singificant at the first and third ones, indicating that the size characters in floral organ showed the positive dominances generally.

TABLE 1. Family means of the three measurements of the lengths of style and filament.

♂ / ♀		A	B	C	D	S	T
	SL	35.5	39.0	36.5	36.8	36.8	34.2
A	*FS*	27.1	26.9	26.5	29.3	26.9	25.4
	FL	31.5	33.3	33.0	34.1	32.6	29.9
	SL	38.7	38.7	34.9	33.7	37.5	37.3
B	*FS*	27.8	25.4	24.2	25.6	25.1	24.7
	FL	34.0	31.3	30.5	31.3	31.2	31.1
	SL	35.7	35.0	29.7	33.9	35.3	34.5
C	*FS*	25.8	23.7	21.4	25.8	24.8	24.4
	FL	32.2	30.0	26.2	31.7	30.6	30.3
	SL	34.5	38.0	33.8	32.0	35.3	35.6
D	*FS*	26.5	26.6	25.4	26.4	26.6	26.5
	FL	31.3	32.4	31.3	30.4	31.9	31.5
	SL	37.5	36.8	34.4	35.1	34.3	35.2
S	*FS*	27.0	25.5	23.6	26.2	24.5	24.8
	FL	32.7	31.1	39.2	31.8	29.2	30.2
	SL	33.8	37.5	34.5	35.4	36.0	32.1
T	*FS*	25.4	25.4	24.3	26.5	25.3	23.6
	FL	30.2	31.1	30.4	31.4	30.6	27.4

Note: Upper: Style length (*SL*) in mm.
Middle: Short-filament length (*FS*) in mm.
Bottom: Long-filament length (*FL*) in mm.
Each parent name
A: Ambalema B: Bright Yellow C: Connecticut Broad Leaf
D: Daruma S: Sumatra T: T.I. 448 A

b) Developmental instabilities.

Mean values of developmental instabilities are presented in Table 3 and analyses of variances are shown in part of Table 2. The three measurements of developmental instability were significant for both the additive and dominance items.

Directional dominances of developmental instability were -0.40, -1.47 and -1.35 in *VSL*, *VFS* and *VFL*, respectively and the latter two measurements were significant at the 5% level. Thus F_1's were less variable than their parents on average, contrasting larger F_1 in size characters. But some F_1's were positive.

The manner of the inheritance of developmental instability was not differ-

TABLE 2. Analysis of variances for each character.

Items	d.f.	*SL*	*FS*	*FL*	*VSL*	*VFS*	*VFL*	*VW*	*D*
		mean squares							
$a^{\#}$	5	31.648***	21.024***	17.097***	10.360***	8.575***	5.229**	21.767***	3.210**
b	15	9.937***	1.499***	4.914***	3.345***	4.359***	3.788***	3.647***	1.141***
b_1	1	42.849**	10.643	43.542*	2.288	31.152*	26.352*	2.070	11.130
b_2	5	2.362*	0.733	1.640	2.452*	2.622	4.725***	2.093*	0.255
b_3	9	3.822***	0.908***	2.440***	3.959**	2.347**	0.760	4.686***	0.523**
c	5	1.229*	0.456	0.338	1.224	1.253	1.747**	0.918	0.036
d	10	2.115***	1.080***	1.160***	2.139*	1.423	1.078	2.415***	0.102
Blocks (B)	1	0.125	0.307	0.376	0.700	0.040	0.009	1.307	0.004
$B\times a$	5	0.564	0.044	0.316	0.304	0.150	0.334	0.088	0.205
$B\times b$	15	0.293	0.147	0.197	0.446	0.375	0.271	0.578	0.151
$B\times b_1$	1	0.049	0.584	0.107	0.251	0.125	0.128	1.863	0.191
$B\times b_2$	5	0.261	0.168	0.343	0.335	0.638	0.107	0.288	0.315
$B\times b_3$	9	0.338	0.086	0.125	0.529	0.257	0.377	0.596	0.056
$B\times c$	5	0.207	0.164	0.125	0.281	0.376	0.109	0.256	0.031
$B\times d$	10	0.118	0.121	0.119	0.566	0.925	0.605	0.257	0.063
Block interactions	35	0.269	0.127	0.181	0.436	0.500	0.352	0.370	0.117

***, **, *: Significant at the 0.1%, 1%, and 5% levels, respectively.
#: The same as HAYMAN (1954)'s notation. Each item tested against its own interaction.

TABLE 3. Family means of the three measurements of the developmental instability of flower organ.

♂ / ♀		A	B	C	D	S	T
	VSL	10.6	11.4	10.7	9.9	10.0	11.4
A	*VFS*	11.7	10.2	9.5	8.4	9.8	12.7
	VFL	10.7	9.2	7.5	9.1	8.3	8.8
	VSL	11.2	9.6	10.5	8.4	8.8	10.1
B	*VFS*	9.6	10.6	10.6	9.1	8.5	9.0
	VFL	9.5	8.3	8.2	7.3	8.6	8.5
	NSL	11.7	8.5	13.8	10.1	10.8	10.6
C	*VFS*	10.5	9.1	13.3	9.2	9.7	9.9
	VFL	9.4	8.1	13.4	8.3	8.9	10.1
	VSL	13.1	10.2	8.5	9.4	9.8	7.9
D	*NFS*	10.0	11.0	9.0	9.6	9.7	8.8
	VFL	8.4	8.7	7.8	9.2	7.5	8.3
	VSL	9.7	9.0	12.4	9.5	9.8	9.7
S	*VFS*	10.6	9.2	8.3	9.1	10.0	9.7
	VFL	8.4	9.0	8.2	7.5	8.8	7.9
	VSL	10.8	10.7	11.7	8.0	8.4	10.2
T	*VFS*	12.3	11.3	10.5	9.5	8.9	14.1
	VFL	11.3	9.5	7.9	8.4	8.4	10.8

Note: Upper: Variation of style length within plant (*VSL*)
Middle: Variation of short filament length within plant (*VFS*) } in σ
Botton: Variation of long filament length within plant (*VFL*)
Parent names are shown in Table 1.

ent from that of the size character from the viewpoint of quantitative inheritance which was controlled by both nuclear genes and cytoplasmic effects.

c) Quantitative differentiations.

The family means of two measures of quantitative differentiation are presented in Table 4 and analyses of variances are given in last two columns of Table 2. It was found that a and b_3 items were significant. This confirmed that quantitative differentiations were also under genetic control. In addition the significance of the d item in *VW* implied the existence of the specific reciprocal difference. Two crosses, between B and D and between C and T, exhibited the greatest diversity between reciprocal F_1's, as can be seen in Table 4. In crosses between B and D, F_1 plants took clearly after the female parent, but in cross between C and T, no directional effect could be detected.

TABLE 4. Family means of the two measurements of the quantitative differentiation of filament length.

♂ / ♀		A	B	C	D	S	T
A	*VW*	13.3	15.1	12.7	12.8	14.3	12.3
	D	4.5	6.5	6.5	4.8	5.2	4.5
B	*VW*	16.1	14.4	10.7	9.6	12.3	12.9
	D	6.2	5.9	6.4	5.7	6.1	6.4
C	*VW*	13.0	11.4	10.1	11.2	11.2	16.0
	D	6.4	6.3	4.8	6.0	5.8	5.9
D	*VW*	11.4	13.6	11.7	8.7	11.9	10.9
	D	4.8	5.9	6.0	4.1	5.3	5.0
S	*VW*	15.3	11.7	9.9	12.5	12.9	12.2
	D	5.7	5.6	5.6	5.6	4.7	5.4
T	*VW*	11.1	14.3	11.1	11.2	11.3	11.1
	D	4.8	5.8	6.1	5.0	5.3	3.8

Note: *VW*: Variation within four long filaments in σ. *D*: Difference between short-filament length (*FS*) and long-filament length (*FL*) in mm. Parent names are shown in Table 1.

TABLE 5. Relationships between lengths and their developmental instabilities.

		SL	*FS*	*FL*	
VSL	a	−0.201	0.438	0.631	*SL*
	b	−0.272	0.970***	0.959***	
	b_2	−0.586	—	—	
	b_3	−0.036	0.949***	0.928***	
	c	—	—	—	
	d	−0.100	0.712*	0.827**	
VFS	a	0.552	−0.196	0.921**	*FS*
	b	0.363	−0.848***	0.971***	
	b_2	—	—	—	
	b_3	0.091	−0.781**	0.949***	
	c	—	—	—	
	d	—	—	0.955***	
VFL	a	0.811*	0.928**	−0.296	*FL*
	b	0.519*	0.711**	−0.812***	
	b_2	0.234	—	—	
	b_3	—	—	—	
	c	—	—	—	
	d	—	—	—	
		VSL	*VFS*	*VFL*	

Note: Each hyphen means that its corresponding variance is not significant. (see Table 2)

***, **, *: Significant at the 0.1%, 1% and 5% levels, respectively.

d) Relationships among three kinds of the characteristics.

As shown in the upper-right of Table 5, there was a strong correlation between *FS* and *FL* in all the items in which the significant differences were recognized in Table 2, and the correlations between style length (*SL*) and filament lengths (*FS* and *FL*) were discernible in *b* and *d* items, but not in the *a* item. Therefore, there are independent additive genes controlling the style from the filament lengths. In the relations among the developmental instabilities given in the bottom-left of Table 5, the significant coefficient of correlation in *a* and *b* items between *VFL* and *VFS* was observed. No *VSL* correlated with *VFS*, but did slightly with *VFL* in *a* and *b* items. If the working hypothesis presented by SAKAI and SHIMAMOTO (1965 a) was applied to the system of developmental relationship among style and filament, short filament (*FS*) and long filament (*FL*) would be developmentally closely related to each other and style would developmentally more related to the long filament than the short filament.

Diagonal terms in Table 5 showed the relationships of the size characteristics with their developmental instabilities, respectively. All of correlation coefficient were negative, and the filament lengths correlated strongly with their developmental instabilities at *b* item, indicating that the shorter the lengths of filament were, the higher the developmental instabilities were and

TABLE 6. Relationships between quantitative differentiation and other characters in question.

		SL	*FS*	*FL*	*VSL*	*VFS*	*VFL*	*D*
VW	*a*	0.911*	0.469	0.622	0.143	0.161	0.076	0.237
	b	0.586*	0.581*	0.585*	−0.018	−0.209	−0.278	0.547*
	b_2	0.232	—	—	−0.076	—	−0.125	—
	b_3	0.753*	0.714*	0.828**	0.370	−0.280	—	0.844**
	c	—	—	—	—	—	—	—
	d	0.826**	0.605*	0.649*	0.044	—	—	—
D	*a*	0.336	−0.434	−0.049	0.314	−0.117	0.045	
	b	0.878***	0.870***	0.962***	−0.320	−0.749**	−0.802**	
	b_2	—	—	—	—	—	—	
	b_3	0.756*	0.798**	0.908***	−0.109	−0.383	—	
	c	—	—	—	—	—	—	
	d	—	—	—	—	—	—	

***, **, *: Significant at the 0.1%, 1% and 5% levels, respectively. Each hyphen is the same mean as Table 5.

vice versa.

The two measures of quantitative differentiation in filament length were correlated positively and significantly at *b* item, especially for b_3, with each other (Table 6) and with the lengths of style and filament. Furthermore, *VW* was correlated also at *d* item with the size characters. Of the relationships between quantitative differentiations and developmental instabilities, only *D* was correlated negatively and significantly with *VFS* and *VFL* for the *b* item.

Discussions

After a plant organ has differentiated, its normal metric characters might be determined quantitatively by the three kinds of genetic factors. First there are the genetic factors controlling size of the quantitative character, second the genetic factors controlling the canalization of organ developing or variability within the same genotype, which is characterized by developmental instability, and third the genetic factors controlling quantitative differentiation which make homologus organs differentiate larger or smaller organs determinately and quantitatively. It was shown in Table 2 that these three characteristics were governed by the genetic factors. Furthermore, the developmental instabilities and the quantitative differentiations were largely manipulated by the additive and dominance factors as well as the size characters. The apparent difference in F_1 progenies between the size characters and the developmental instabilities was that the former was positive and the latter was negative, in directional dominance. Such a phenomenon has been observed generally in cross-pollinated plants, and on this interpretation, heterozygosity contributed to the stability in development of organ of F_1 plants. But in the present results for tobaccoplants, which is self-pollinated, the stability of the F_1 could depend on the effects of genic control, not heterozygosity, on the developmental instability, because developmental instabilities of F_1 were not always lower than that of their parents.

The close relationships among the size characters of floral organ of *Nicotiana tabacum* (see Table 5) confirmed partially the correlation pleiades, which BERG (1960) observed in *Nicotiana alata*, for dominance, but not for additive effects. Correlation pleiades should be reduced in self-pollinated plants such as *N. tabacum* which might not require the complete balance of style length with filament length as observed on an entomophilous flower plant.

Based on the correlations among the size characters and among the developmental instabilities, the developmental relationships among style and filaments are estimated by the hypothetical scheme defined by SAKAI and

SHIMAMOTO (1965 a). The relationships in additive item between style and long filament were non-significant at the size and significant at the developmental instability. Thus, though the additive genes controlling the style length were different from those controlling the long filament, they would appear to pursue a common pathway in the process of their development. Furthermore, the style correlated significantly in developmental instability with the long filament and not with short filament, suggesting that since style may carry more similar developmental errors to long filament than to short filament, a role of pollen donor could be greater at long filaments than short filament.

The present data (Table 6) showed that quantitative differentiations correlated positively with size characters and negatively or not at all with developmental instabilities. Though both the quantitative differentiation and developmental instability express the characteristics of intra-plant variability of quantitative characters, they were possibly conditioned under the control of the different genetic factors.

In plant breeding, for example in cereals, intra-variance or inter-tiller variance of characters controlling ear conformation might be of importance (PARODA, 1971), from the viewpoint of synchrony of character. Such a characteristic may be partitioned into the developmental instability and quantitative differentitation as the present paper has considered. If we can ascertain which metrics contribute to asynchrony of a character and both developmental instability and quantitative differentiation are under genetic control as in the present material of *N. tabacum*, we can reduce the degree of the asynchrony of its character by means of the appropriate breeding method.

We have observed genetic variation in developmental instability and quantitative differentiation and generally we can also determine genetic variation in phenotypic plasiticity (see BRADSHAW, 1965). These three characteristics may also be associated with and interact with non-genetic variability within the genotype. It should thus be of interest to investigate what relationships exist between these various characters.

Summary

The objective was to determine the genetic control of variations of size, its developmental instability and quantitative differentiation of floral organs from a set of diallel crosses between six varieties of *Nicotiana tabacum* and to discuss the significances of intra-genotype variability.

The three kinds of measurements of quantitative characters each show

the characteristics of quantitative inheritance. Style and filament lengths are under common genetic control but with specific factors operative. Similar results apply to their developmental instabilities. Since developmental instability and quantitative differentiation are found to be negatively correlated or independent, there is evidence to suggest that they are not always under common genetic control.

Developmental instability and quantitative differentiation are discussed from their implications to plant breeding.

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