DEVELOPMENTAL INSTABILITY IN LEAVES AND FLOWERS OF *NICOTIANA TABACUM*

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ORGANS which are periodically repeated in plants show a more or less quantitative variation in spite of being governed by the same genotype. This variation is considered to be due, in addition to local fluctuation in environmental conditions outside and/or inside the plant body, to mistakes in the developmental course of organs resulting probably from the intrinsic nature of the organisms.

That the magnitude of such quantitative variability of a given organ is genotype-dependent and susceptible to selection pressure has been demonstrated experimentally for the lateral asymmetry of sternopleural chaeta number in Drosophila (MATHER 1953; REEVE 1960, and other publications). In plants, *Nicotiana rustica* was used for the study of within-line variability in plant height, flowering time, leaf length and number of capsules per plant (JINKS and MATHER 1955) or the study of intra-individual variability of stamen and pistil length and leaf shape (PAXMAN 1956). It was concluded from those investigations that the within-genotype variability in those characters was again genotype-dependent.

The intragenotypic variability of quantitative characters which is considered to result from errors in developmental processes, though it might involve effects of undiscernible environmental influences, is called developmental instability, a phenomenon interesting from the viewpoint of genetics and evolution. For example, developmental instability in some traits of a panicle of rice induced SAKAI and SHIMAMOTO (1965) to investigate developmental relationships among them. It is also of great interest to inquire into what role developmental instability might play in adaptation, survival or fitness as well as production of higher organisms.

For the last few years, the writers have conducted a few experimental studies on developmental instability in foliar and floral organs of *Nicotiana tabacum* L. This paper deals with the results of those studies which were carried out under the financial support of Japan Monopoly Bureau, to which our thanks are due.

MATERIALS AND METHODS

Eleven varieties of *Nicotiana tabacum* were used. Among them are two varieties which are adapted to cigar production, i.e. Sumatra and Connecticut Broad Leaf, four varieties for cigarette production, i.e. Virginia Gold, Bright Yellow, Hicks and Moore Field Franagan, two local varieties of Japan, Daruma and Ibusuki, and three not released varieties, i.e. Nicotine-free tobacco, T.I. 448 A and Ambalema. The last three are those which are in possession of specific characters such as low nicotine content or disease resistance.

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Fifteen plants of each variety were planted in rows. From these, three plants of each variety were selected at random for the investigation.

As illustrated in Figure 1, all leaves at maturity were measured for their width (W), width of left (L) and right (R) halves of the blade, intervein distance on the mid-rib (D), and difference between the largest and the smallest distance between two adjoining veins (d_{i_1} and d_{i_2}) together with the average length of the two veins concerned (m_i). Attention was paid to exclude from the measurements veins developing near either end of a leaf. On the basis of those measurements, developmental instability of leaves was measured in three ways: (1) by the amount of asymmetry (A), or absolute difference between the sides of a leaf divided by the maximal width of the leaf; (2) by the vein-distance variability (D), i.e. intraleaf variation expressed in terms of standard deviation of intervein distance on the mid-rib divided by the average intervein distance; (3) by the vein-deviation index (I), i.e. absolute difference between largest and smallest distance between two adjoining veins divided by the average length of two veins concerned. They are:

$$A = \frac{|L - R|}{W}$$

$$D = \frac{\sigma D}{\bar{D}}$$

$$I = \frac{|d_{i_1} - d_{i_2}|}{m_i}$$

For investigation of developmental instability of flower characters, nine of the 11 varieties were used. About 20 flowers per plant were investigated for length of stamens and pistils on the same three plants which were used for the leaf measurements. As a rule, a flower has five stamens, four of which are of about the same length while the remaining one is much shorter. Developmental instability in male organs was measured by variation among the four long stamens within each flower, on the one hand, and variation among flowers within plants in average length of the four stamens, on the other. Developmental instability in female organs was investigated by within-plant between-flower variation in pistil length. Variation in stamen and pistil length was expressed in terms of within-flower or within-plant standard deviation.

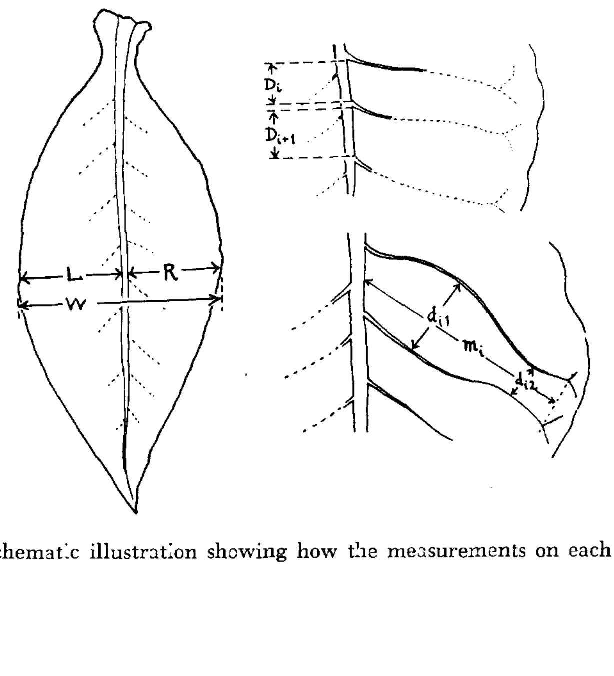

FIGURE 1.—Schematic illustration showing how the measurements on each leaf were taken.

EXPERIMENTAL RESULTS

Results will be described first for the varietal comparison of foliar and floral instabilities, followed by interrelations between those instabilities and lastly for a few properties of developmental instability, especially of leaves.

(1) *Varietal difference in developmental instability of leaves:* Figure 2 shows two leaves of tobacco plants, one from the Ambalema variety and the other from Coker 139. It may be noticed in these photographs that the two varieties differ from each other with respect to their leaf structures. Coker 139, (Figure 2A) has a leaf in which the sides are approximately symmetrical and the distribution of veins is very regular, while the leaf of Ambalema of Figure 2B is highly asymmetrical and the veins are irregularly distributed.

The degree of irregularity in the construction of a leaf was measured in three ways as explained in the preceding section. The analysis of variance of three indices of foliar instability is presented in Table 1, and their mean values for the 11 varieties are shown in Table 2. From Table 1 we find that asymmetry, vein-distance variability and vein-deviation index are statistically highly significant between varieties. Vein-deviation index was statistically significant between plants even within the same variety. From Table 2, we find that the two varieties, Ambalema and T.I. 448 A, are in possession of very high instability for the three indices, while Connecticut Broad Leaf and Sumatra are lowest. It is of interest that the latter two are varieties which are grown for cigar production. It was our initial assumption that highly productive commercial varieties would be low in developmental instability at least for foliar characters. To our surprise, however, they were found to be moderately unstable: Hicks, Bright Yellow and Virginia Gold are those which are highly productive with moderate instability in leaf organs.

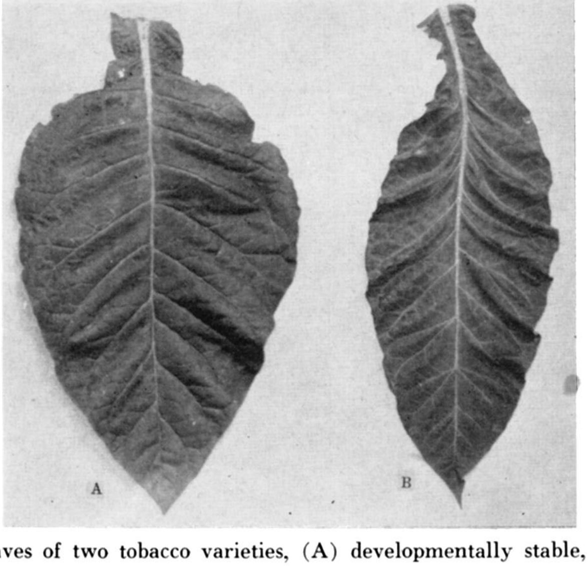

FIGURE 2.—Leaves of two tobacco varieties, (A) developmentally stable, (B) unstable. A: Coker 139, B: Ambalema.

TABLE 1

Analysis of variance for three indices of instability in tobacco leaves.

Source of variation	Degrees of freedom	Mean squares		
		Vein-distance variability	Vein-deviation index	Asymmetry
Between varieties	10	41.0783**	610.64**	0.2378**
Between plants within varieties	22	0.4926	22.19**	0.0443
Between leaves within plants within varieties	579	0.6019	10.75	0.0530

** Exceeds the 1% level of significance.

TABLE 2

Instability values of foliar characters in 11 varieties of tobacco

Variety	Vein-distance variability (×10)	Vein-deviation index (×100)	Asymmetry (×100)
Ambalema	4.36	19.39	4.19
T.I. 448 A	4.54	18.77	3.02
Daruma	3.28	16.27	3.29
Ibusuki	3.22	15.45	2.97
Moore Field Franagan	2.91	15.05	2.67
Hicks	3.11	14.11	3.47
Bright Yellow	2.76	13.81	2.57
Nicotine-free Tobacco	2.53	13.95	2.48
Virginia Gold	2.58	11.31	3.07
Sumatra	2.46	11.71	2.40
Connecticut Broad Leaf	2.25	8.62	2.15

TABLE 3

Analysis of variance of three indices of instability in tobacco flowers

Source of variation	Degrees of freedom	Mean squares		
		Interflower variability of pistil length	Variability in stamen length	
			Intraflower	Interflower
Between varieties	8	2.0573**	0.1264*	0.3101
Within varieties	18	0.3657	0.0456	0.4572

*, ** Exceed the 5% and 1% significance levels, respectively.

(2) *Developmental instability in flowers:* Irregularity in flower organs, or developmental instability in flowers was measured: (1) by variation in length among four long stamens in a flower; (2) by variation in average stamen length among flowers within the same plant, or (3) by intraplant interflower variation in pistil length. We have investigated about 20 flowers from each of three plants of each of nine varieties. The three indices of floral instability were expressed by standard deviations as stated before. Table 3 presents the analysis of variance of the data obtained.

TABLE 4

Instability values in floral characters in nine tobacco varieties

Variety	Interflower variability in pistil length	Variability in stamen length	
		Intraflower	Interflower
Ambalema	2.08	1.19	1.97
T.I. 448 A	1.31	1.07	1.47
Daruma	1.62	0.86	1.44
Ibusuki	1.35	0.73	1.35
Moore Field Franagan	2.24	1.01	1.76
Bright Yellow	3.88	1.32	1.89
Nicotine-free Tobacco	1.80	0.90	1.83
Sumatra	2.98	1.44	1.88
Connecticut Broad Leaf	2.44	0.93	1.97

Table 3 shows that intraflower variability of stamen length and intraplant variability of pistil length are statistically significant between varieties. Developmental instability measured by variation in pistil and stamen length of nine varieties is presented in Table 4.

It is found from Table 4 that Bright Yellow and Sumatra are developmentally highly unstable while Ibusuki is very stable so far as flower characters are concerned.

(3) *Interrelationship between developmental instability of leaf and that of flower organs:* Table 5 presents correlation coefficients among different instability indices of floral as well as foliar characters. From Table 5, we find that three instability indices of foliar characters are mutually positive and highly correlated, and the same also holds among the three floral instabilities, but correlations between foliar and floral instabilities are low and more or less negative rather than positive. This may mean that the same factors are responsible for developmental instability in veins and blades, and factors for developmental instability for flowers are the same for pistils and stamens, but both groups of factors are

TABLE 5

Intervarietal correlations among instabilities in foliar and floral organs of tobacco

	Vein-deviation index	Asymmetry	Interflower variability in pistil length	Intraflower variability in stamen length	Interflower variability in stamen length
Vein-distance variability	.9170**	.8102**	—.4961	—.0132	—.3139
Vein-deviation index	....	.8517**	—.5018	—.0747	—.3832
Asymmetry	....	....	—.3533	—.0219	—.1666
Interflower variability in pistil length	....	....	....	.7474*	.6466
Intraflower variability in stamen length	....	....	....	....	.6103

*, ** Exceed the 5% and 1% significance levels, respectively.

different from each other. In order to examine this situation more precisely, a discriminant function for the foliar instability, on the one hand, and that for the floral instability, on the other, were worked out. The discriminant function, L, for leaves of each variety was constructed by

$$L = 2\,Y_1 + 6\,Y_2 + 3\,Y_3,$$

where Y_1 stands for vein-distance variability, Y_2 for vein-deviation index, and Y_3 for asymmetry. The discriminant function, F, for the flowers was

$$F = 3X_1 + 10\,X_2 + 9\,X_3,$$

where X_1 stands for intraflower variability in stamen length, X_2 the intraplant variability in stamen length, and X_3 the intraplant variability in pistil length. Table 6 presents those discriminant functions for the nine varieties investigated. Table 6 again confirms the view that both developmental instabilities detected in leaves and flowers are not correlated, being probably controlled by separate genetic factors.

(4) *Is the bilateral asymmetry in a leaf of tobacco directional or fluctuating?* In the descriptions given so far, the asymmetry of the leaf sides has been measured by the absolute difference between them. It needs to be definitely known, however, if the asymmetry in a tobacco leaf is directional or fluctuating. This enquiry requires finding out: (1) if there is a species-specific or genotype-specific directional asymmetry, that is, for example, if the left side is always larger than the right for the whole species or whole genotype; (2) should the asymmetry not be directional, being fixed in a species or genotype, if there might occur a directionality fixed per plant, one plant being left-sided while another was right-sided; (3) should the directionality not be individually fixed, if there might still be a localized directionality in a plant, such that, for instance, when a group of nearby leaves in a plant is all left-sided, another group in the same plant might form a cluster of right-sided ones.

If the asymmetry is directional and species- or genotype-fixed, the value of left-side minus right-side of every leaf will be invariably plus or minus within a

TABLE 6

Comparison between foliar (L) *and floral* (F) *instabilities collectively expressed by discriminant functions of tobacco varieties*

Variety	Foliar instability L	Floral instability F
Ambalema	2.161	4.199
T.I. 448 A	2.129	2.960
Daruma	1.732	3.156
Ibusuki	1.658	2.464
Moore Field Franagan	1.567	4.079
Bright Yellow	1.444	5.778
Nicotine-free Tobacco	1.417	3.720
Sumatra	1.265	4.994
Connecticut Broad Leaf	1.030	4.485

r between L and $F = -0.3145$ for 7 degrees of freedom.

given species or genotype. If the asymmetry is directional and individually fixed, then the values of asymmetry obtained from leaves of a single plant would be either definitely plus or definitely minus. As a result, sums of individual leaf values of asymmetry per plant would show a bimodal frequency of distribution with a depression around the zero point. The following studies have been conducted in order to answer these questions.

Sixteen lines, separated at random from the Hicks variety, were used in the study. Eight leaves from each of five plants selected at random from each line were investigated for the degree of bilateral asymmetry of leaves. As a matter of fact, no leaf was found to be completely symmetrical so far as the Hicks variety was concerned.

Now, let the probability of a leaf having a plus value, that is, having the left side larger than the right, be p, then the probability of the value being minus will be $(1-p)$. Eight leaves per plant may take combination of left- and right-sidedness according to the expansion of $[p+(1-p)]^8$. If there is any species-specific, genotype-specific or individually fixed tendency toward directional asymmetry, then $p \gg 0.5 \gg (1-p)$ or $(1-p) \gg 0.5 \gg p$ on the species, genotype or individual level, which results in a Poisson or a skewed distribution of individual plants on each level. On the other hand, if the asymmetry is not at all directional, or fluctuating by chance in every leaf, then it is expected that $p=(1-p)=0.5$ which brings about a bell-shaped distribution of individual plants. Table 7 and Figure 3 present the theoretical and observed frequency distributions. The observed distribution is found to be not significantly different from the binomial distribution with $p=1-p=0.5$. The distribution is fairly strongly leptokurtic, that is to say that there are more intermediate plants than would be found in a binomial distribution. Whatever else it might mean, it may here be right to merely conclude that the asymmetry is not at all directional, neither species- or genotype-specific nor individually fixed.

The third question—if there might be a localized directionality within a single plant—still remains to be settled. We may inquire if there might be a tendency for two successive leaves to show the same sidedness more frequently than would be expected on the assumption of randomness. To settle this question, two successive leaves were compared in respect of asymmetry. If a given leaf is left-sided a +1 value is assigned to it, while a −1 value is assigned for a right-sided leaf.

TABLE 7

Theoretical and observed frequencies of plants having left-sided and right-sided leaves in given numbers among eight

	Number of leaves left-sided (above) and right-sided (below)									
Left-sided: Right-sided:	0 8	1 7	2 6	3 5	4 4	5 3	6 2	7 1	8 0	Total
Number of plants observed	0	3	6	13	30	13	9	4	1	79
Number of plants expected*	0.31	2.47	8.64	17.28	21.60	17.28	8.64	2.47	0.31	79

$0.50 > P > 0.25$ for agreement between observed and expected distributions.
* Expected number of plants for $p=1-p=0.5$.

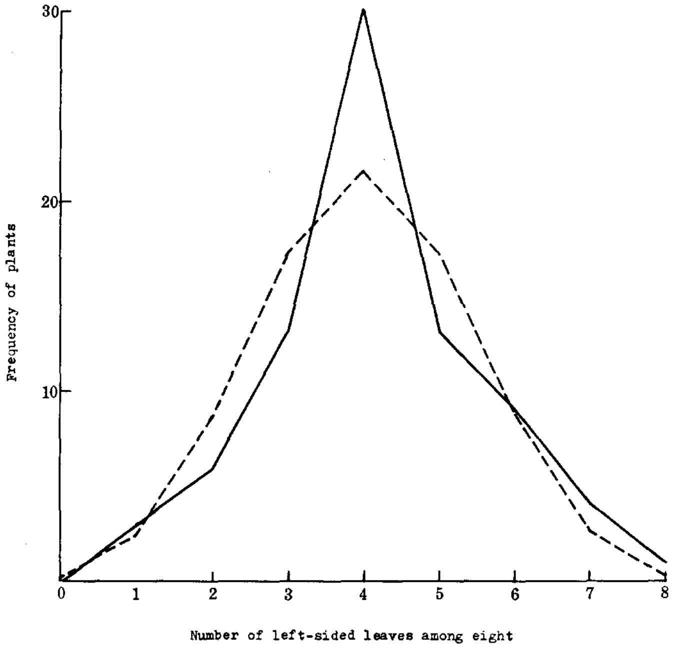

FIGURE 3.—Theoretical and observed frequency distribution of plants having 0 to 8 left-sided leaves. Solid line: Observed. Broken line: Theoretical, computed on the assumption that $p = 1 - p = 0.5$.

Correlation was computed for every two successive leaves to find out whether they tend to have a localized directional asymmetry.

The 79 plants described in Table 7 were examined for the correlation of asymmetry between ith and $(i + 1)$th leaves, $(i + 1)$th and $(i + 2)$th, and so on. The number of leaf pairs examined was 559 and the correlation coefficient obtained was $r = 0.0266 \pm 0.0424$. The approximately zero value of the correlation tells that there is no influence of the older leaf on the younger one in respect of direction of asymmetry.

Thus, the following conclusion has been drawn from this study: The bilateral asymmetry in tobacco leaves is not at all directional, but fluctuating, one side being larger than the other at random per leaf.

(5) *Developmental order of leaves and instability:* The next subject of study was to examine if the degree of developmental instability of leaves varied according to stages of plant growth. Eight varieties were used in this study. Two of them, i.e. T.I. 448 A and Ambalema, had a very high instability for the three leaf characters as shown in Table 2, and were designated as H. Two other varieties, Sumatra and Connecticut Broad Leaf, were designated as L owing to their very low instability. Four intermediate varieties in respect of instability were also included; they were Daruma, Ibusuki, Hicks and Bright Yellow, which were designated as M. Leaves from the top to the base of a plant were divided into seven height-groups, and asymmetry, vein-distance variability and vein-deviation

TABLE 8

Analysis of variance of three indices of foliar instability at seven height-levels in eight varieties of tobacco

Source of variation	Degrees of freedom	Mean squares		
		Asymmetry	Vein-distance variability	Vein-deviation index
Variety	7	8.8271**	13.5624**	107.8821**
Height	6	1.1173	.2772	6.5863
Variety × height	42	2.5493*	.3695**	5.5284**
Error	112	1.5364	.1608	2.9025

*, ** Exceed the 5% and 1% levels of significance, respectively.

index were compared among those groups. Analysis of variance of the data is presented in Table 8.

It is seen from Table 8 that the height effect is nonsignificant, but the interaction between variety and height is significant. It means that positions on the stem may influence developmental instability of a leaf in a genotype-specific way. Figure 4 shows, as an example, the relation between height and vein-

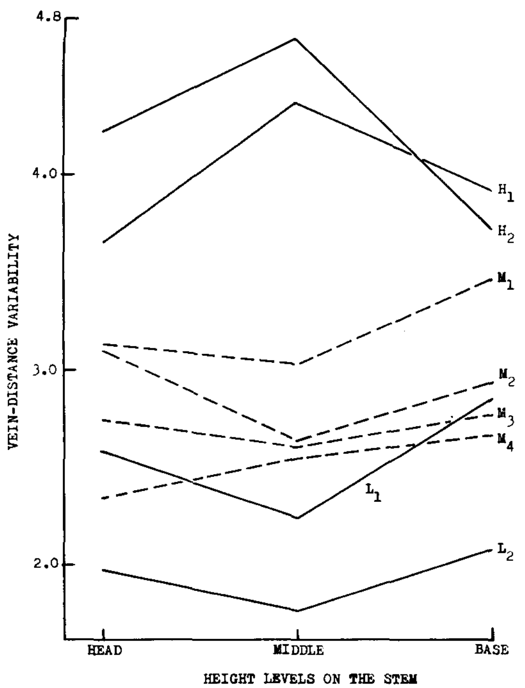

FIGURE 4.—Relation between vein-distance variability and height-level of the leaf on the stem in eight varieties of tobacco. H, M and L are varieties whose foliar instability is high, intermediate and low, respectively. H_1: T.I. 448 A, H_2: Ambalema. M_1: Daruma, M_2: Hicks, M_3: Ibusuki, M_4: Bright Yellow. L_1: Sumatra, L_2: Connecticut Broad Leaf.

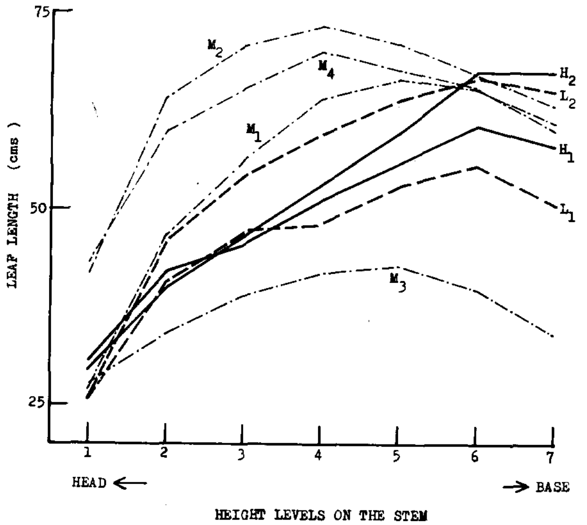

FIGURE 5.—Leaf size (length in cm) on seven height-levels on the stem. H_1: T.I. 448 A, H_2: Ambalema. M_1: Daruma, M_2: Hicks, M_3: Ibusuki, M_4: Bright Yellow. L_1: Sumatra. L_2: Connecticut Broad Leaf.

distance variability in eight varieties, seven height-groups in the original data being regrouped into three for the convenience of comparison.

We find from Figure 4 that developmental instability was highest at the intermediate height in H varieties, but was intermediate or low in others. It is then of interest to know whether or not the instability is related to leaf size. Figure 5 shows leaf size in relation to position on the stem in different varieties. It is found from Figure 5 that some varieties show the maximum leaf growth at the intermediate position, but varieties of interest for the present discussion, i.e. H as well as L varieties, show the maximum leaf growth at the position near the base. It is thus concluded that the developmental instability is not related to leaf size.

DISCUSSION

As described in the introduction, a number of investigations have been conducted on the bilateral asymmetry of sternopleural chaeta number in Drosophila, providing evidences that the asymmetry is a genetically determined trait. In plants, there are also several investigations on developmental instability, but genetic studies are rather few. In *Nicotiana rustica*, JINKS and MATHER (1955) and PAXMAN (1956) have found that developmental instabilities of various characters were genetic. The present paper describes intraplant or even intraorgan variability of such components as leaf blades or veins, on the one hand, and stamen length or pistil length, on the other.

The findings that varieties of tobacco differ with regard to developmental instability in leaves and reproductive organs suggest that the instability here should also be genetic. This is consistent with conclusions drawn from the experiments given above.

Another conclusion drawn from the present study and confirming PAXMAN's work is that developmental instabilities in reproductive organs are correlated, and the same also holds for leaf characters, but floral instability and foliar instability appear to be independent of each other. SAKAI and SHIMAMOTO (1965) have presented a hypothetical scheme to show that correlation between developmental instability in different parts of organs which are found to be controlled pleiotropically by the same genes may reveal their developmental relationships. We are not aware to what extent the same genes are pleiotropically governing the formation of flower and leaf organs in tobacco, but we may consider BERG's opinion (1960) that reproductive parts and vegetative parts in *Nicotiana alata* are not correlated phenotypically with each other, showing the presence of "correlation pleiades". It may thus be possible to assume for the present, that genes responsible either for organ formation or developmental instability or stability might be different between leaf and flower organs in tobacco. It is an interesting subject of study to investigate to what extent vegetative characters are independent genetically, as well as developmentally, from flower characters in this species.

With regard to varietal difference in developmental instability in leaves, it is important to point out that Connecticut Broad Leaf and Sumatra are cigar-tobaccos and must have been particularly selected for structural uniformity or for some intensive buffer against the occurrence of errors in leaf development. Higher instability in leaves of commercial varieties for cigarette production than in cigar-varieties might hint that developmental instability could play a role either in productivity or adaptability. Future studies are desired to answer this question.

It is known that there is a phenomenon of "right-handedness" and "left-handedness" in plants. This developmental character was found to be species-specific or genotype-dependent in some cases, for example, right- and left-handedness of spikelets in wheat and Aegilops species (KOJIMA, MUKAI, SUEOKA and ONO 1955; SUEOKA and MUKAI 1956). In other cases, however, it was found to be nonheritable (DAVIS 1962 and 1963 in coconut palm). This right- or left-handedness, however, appears to be different from the present asymmetry and cannot be compared with it.

VAN VALEN (1962) has divided asymmetrical development in organisms into three categories: (1) directional asymmetry; (2) antisymmetry; and (3) fluctuating asymmetry. It has been demonstrated in the present study that in *Nicotiana tabacum*, bilateral asymmetry of leaves is not at all directional, but it is a fluctuating asymmetry or antisymmetry. In other words, either side, left or right, of a blade is growing better than the other only by chance. It is important to recognize that the asymmetry of each leaf in tobacco is determined individually, being not at all influenced by its preceding or successive leaf. It suggests that the development of each leaf could be independent, in one sense or another, from that of the others.

The next problem to be considered is the relation, if any, between developmental instability and stage of plant growth. ROY (1963) investigated intraplant variability of petal number in Nyctanthes and found that the variability tended to increase with time. It was also seen that the percentages of abnormal flowers increased with time, too. The increase in intraplant variability of petal numbers as well as in the percentages of abnormality with time was, according to ROY, due to falling off with time of precision in canalization. It seems to the present writers that this does not always hold because it has been shown in Figure 4 that the occurrence of instability is a result of interaction between growth stage and genotype. In some genotypes, the instability or intraplant variability is highest in a certain growth period while in others it was lowest. Genotypes which increased instability in the middle stage were those less stabilized from the beginning, while genotypes which showed a decrease in instability at the same stage were those rather stabilized. It seems, accordingly, that the activity of a genic system, if any, which does or does not buffer developmental errors, would probably be emphasized at the time when the development of the organ is at its highest, though this need not necessarily be at the stage of the maximum growth of a leaf.

We consider the developmental procedure in organisms to be governed by the law of stochastics rather than by a deterministic process. Should a certain amount of an error in a given character of an organism be at a disadvantage for its survival or fitness, either natural or artificial selection would have resulted in collecting genes which serve as buffer against the occurrence of errors. It might, however, be possible that, under certain circumstances, developmental instability in some characters could be at advantage in natural or artificial selection. It should then be of interest to investigate what relation developmental instability in various characters has had with productivity, adaptability and fitness in higher organisms.

Conclusion: From the descriptions given above, the following conclusions are drawn: (1) Developmental instability measured by bilateral asymmetry or intraleaf variability of vein distribution in tobacco leaves is found to vary among varieties. Cigar varieties are highly stable, while commercially widely grown cigarette varieties are moderately unstable. (2) Developmental instability measured by intraflower or intraplant variability in stamen length and pistil length is also found to vary among varieties. (3) Instability in leaf organs seems to be controlled by different genes from those causing instability of flower organs. (4) Bilateral asymmetry of a leaf is not directional, but definitely fluctuating, that is, left-sidedness or right-sidedness is determined by chance for every leaf, not being influenced by the next older leaf. (5) Extent of developmental instability varies among leaves of a single plant. Leaves developing in the middle of the growth-period show the highest instability in varieties which are intrinsically unstable, while stable varieties show the lowest instability at this stage.

SUMMARY

Tobacco varieties were investigated for developmental instability in leaf and flower organs. Leaf instability was measured by bilateral asymmetry and two kinds of intraleaf variability of vein distribution. Flower instability was measured

by intraflower and intraplant variability of stamen and pistil length. It was found that these instabilities vary among varieties, suggesting that they are governed by genetic factors. Instabilities of leaf parts were found to be positively and highly correlated with each other, and the same also held for floral parts. None of the foliar instabilities investigated, however, proved to be significantly correlated with any of the floral instabilities. Thus, it was concluded that different genes may be responsible for the developmental instability of leaves and flowers. Bilateral asymmetry of tobacco leaves was tested to find out if it was directional or fluctuating. It was found that the asymmetry was wholly fluctuating, that is, left-sidedness or right-sidedness is determined entirely by chance in each leaf. Developmental instability of leaves was found to vary according to their developmental stage. Leaves developing at the middle height of the stem showed an exaggeration of the degree of instability or stability; varieties which were stable showed the maximum stability at the middle stage of growth, while unstable varieties yielded the highest instability at the same stage. This suggests that genes which are in some sense or other responsible for developmental errors might become more active at a certain growth period than at other stages.

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