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THE VARIATION OF ORGANS OF INDIVIDUAL PLANTS

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INTRODUCTION

Recent biometrical work has been largely concerned with characters of individual plants and animals. One or more characters of each individual have been counted or measured and the means and variances of different populations have been compared. The main stress has been on the comparison of means, and in many cases the variances were only estimated in order that the significance of differences between means might be determined. Where the samples were large enough to allow of a comparison of variances, high variance was often ascribed to genetical diversity in the population sampled, but sometimes to the lesser canalization of development of some genotypes compared with others.

However some data are available about the variation of homologous organs in the same individual. They are seldom adequate. Pearson, Lee, Warren, Fry, Fawcett and others (1901) published extensive data on homotyposis in twenty plant species, and showed that measurements or counts of organs on the same plant were correlated, that is to say, that a population of leaves (for example) from one tree was less variable than a population of leaves from many trees. But they did not examine many organs per plant. For example they counted the numbers of veins, pinnae, or prickles on samples of 26 leaves from each of 833 trees of 4 species. With such small samples it would seldom be possible to state that the variance of leaves on one tree was greater than that of another of the same species, and their data are never presented so as to make this possible. Harris (1915-1917) later counted seeds in 100 pods from each of 60 plants of *Cercis canadensis*, but again his data do not allow a comparison of variability.

Perhaps the closest analogy to my work is to be found in that of Price-Jones (1929, 1933) and Attfield (1951) who found that the variance of the diameter of red blood corpuscles of men and mice in pernicious anaemia and congenital microcytic anaemias is greatly increased. In this case what is measured is the diameter of a corpuscle in a dried film. The reliability of a measurement can easily be estimated. But each corpuscle can only be dried once, and this process may contribute errors of unknown magnitude to the observed variances. So while there is no doubt that the variance of corpuscular diameters is increased, the increase may be larger than the authors' estimates.

Professor J. B. S. Haldane suggested that I might study the variation in petal number of flowers of *Nyctanthes arbor-tristis*. I found (1958a, 1958b, 1959) that the variances as well as the means of different trees differed significantly, and that the variance increased greatly during a season, while the mean changed much less. I obtained similar results with two Oleaceous plants of a winter-flowering variety of *Jasminum* *multiflorum*. and two of a summer-flowering variety of the same species. I noticed (1958b) that the leaves of *Nyctanthes arbor-tristis* had completely different patterns of variation on different trees, and as this is perhaps the simplest phenomenon observed, I shall describe it first.

Variation in the Leaves of the same Plant

Nyctanthes arbor-tristis Linn. (Bengali *Sephalika*, Hindi *Harshingar*, *Parijat*) is a member of the Verbenaceae (formerly of the Oleaceae), and grows as bushes seldom exceeding 8 metres in height. The leaves are heterophyllous (see Fig. 1) and are usually opposite decussate but sometimes superposed. Some leaves are entire and others dentate, the number of teeth varying from 0 to 20. The tooth number varied on leaves of the same tree, or even of the same pair. Eight trees in the compound of the Indian Statistical Institute were studied in 1956. On the first seven trees three or four branches were selected at random, and the tooth number of every leaf on these branches was counted. On the eighth tree all the nine branches were studied separately.

The numbers of teeth on the samples from the eight trees are given in Table 1, and analysed in Table 2. In each case there is a modal number of zero (the apex not being counted as a tooth). It is clear that the distributions from trees 5, 3, and 7 are strongly bimodal. The value of the non-zero modes is not however certain. Thus on tree 3, 38 is not significantly greater than the neighbouring values of 30 and 29 at the 5% level of significance. There are a number of other modal values, but they are not significant. For example on tree 7 there is a mode at 6. But it is only significant if 11 is significantly greater than the number of leaves with 7 teeth, which is 4. The probability that if 15 leaves are taken at random from a large mixture of equal numbers of leaves A and B, the number of B should be 4 or less is $\frac{1941}{32768}$ or 0·059. It would be surprising if no such "false modes" were found. The mode at 2 in tree 8 is quite significant ($\chi_1^2 = 8{\cdot}15$). But it is probably due to symmetry. As will be shown elsewhere, these leaves are highly symmetrical, the correlation between numbers of teeth on the two sides being 0·9368. If there is only one tooth on the right side there is usually only one on the left.

In Table 2, all the statistics calculated give some information. The trees are arranged in order of observed means, but the first three do not differ significantly. It is clear that the trees fall sharply into two classes. In the first class most leaves are entire, and except for a mode at 2 teeth, which was present, but not statistically significant in trees 1 and 6 as well as 8, the distributions were J-shaped. In the second class less than a quarter of the leaves are entire, and the tooth number shows a second mode.

In order to get more information as to the variation I counted all the leaves on nine branches of tree 8. The results are given in Table 3 and analysed in Table 4. It is seen that all branches had the same kind of distribution of tooth numbers though in some the mode at 2 teeth is not apparent. As a test of homogeneity I calculated χ^2 for the frequencies of dentate leaves on the nine branches. This is 37·04 for 8 degrees of freedom. P=0·00002, so there is no doubt of the heterogeneity. But more

Table 1. *The numbers of teeth on leaf samples from eight trees of* Nyctanthes arbor-tristis

Number of teeth	Frequencies of leaves in tree															
	4 Partly shaded		2 Exposed		1 Exposed		8 Partly shaded		6 Shaded		5 Partly shaded		3 Shaded		7 Exposed	
	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)
0	250	80·65	253	71·67	250	81·19	1083	71·72	159	66·51	114	14·59	75	22·00	22	9·36
1	13	4·19	32	9·07	8	2·60	61	4·04	20	8·37	51	6·54	17	5·00	4	1·70
2	12	3·87	25	7·08	17	5·52	98	6·49	21	8·79	61	7·82	12	3·53	8	3·40
3	9	2·90	21	5·95	5	1·62	88	5·83	8	3·35	74	9·49	18	5·29	8	3·40
4	8	2·58	11	3·12	7	2·27	49	3·25	9	3·77	85	10·90	14	4·18	9	3·83
5	11	3·55	7	1·98	6	1·95	48	3·18	10	4·18	75	9·62	26	7·65	7	2·98
6	4	1·29	3	0·85	5	1·62	31	2·05	6	2·51	103	13·21	21	6·18	11	4·68
7	3	0·97	1	0·28	5	1·62	22	1·46	3	1·26	80	10·26	23	6·76	4	1·70
8	—	—	—	—	2	0·65	13	0·86	1	0·42	46	5·90	30	8·82	10	4·26
9	—	—	—	—	1	0·32	3	0·20	2	0·84	41	5·26	38	11·18	22	9·36
10	—	—	—	—	1	0·32	7	0·46	—	—	28	3·59	29	8·53	15	6·38
11	—	—	—	—	—	—	4	0·26	—	—	11	1·41	15	4·41	30	12·77
12	—	—	—	—	—	—	—	—	—	—	6	0·77	13	3·82	23	9·79
13	—	—	—	—	—	—	2	0·13	—	—	3	0·38	4	1·18	20	8·51
14	—	—	—	—	1	0·32	—	—	—	—	1	0·13	4	1·18	9	3·83
15	—	—	—	—	—	—	1	0·07	—	—	1	0·13	—	—	13	5·53
16	—	—	—	—	—	—	—	—	—	—	—	—	1	0·29	10	4·26
17	—	—	—	—	—	—	—	—	—	—	—	—		—	5	2·13
18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0·85
19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0·43
20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0·85
Total	310	100·00	353	100·00	308	100·00	1510	100·00	239	100·00	780	100·00	340	100·00	235	100·00

Table 2. *Analysis of the numbers of teeth on the leaf samples from the eight trees of* Nyctanthes arbor-tristis

Tree	Modes	Median	Mean	S.E. of mean	Variance	% entire	S.E. of %	Insolation
4	0	0	0·632	0·086	2·297	80·65	2·01	Partly shaded
2	0	0	0·705	0·072	1·851	71·67	2·40	Exposed
1	0	0	0·744	0·110	3·709	81·19	2·25	Exposed
8	0,2	0	1·048	0·054	4·362	71·72	1·16	Partly shaded
6	0	0	1·067	0·125	3·711	66·51	3·05	Shaded
5	0,6	5	4·572	0·113	9·881	14·59	1·27	Partly shaded
3	0,9	6	5·544	0·225	17·161	22·00	2·25	Shaded
7	0,11	10	9·209	0·325	24·836	9·36	1·90	Exposed

than half the value of χ^2 is due to branch 8. Even this branch however is not comparable to any of the trees in Table 1. Similarly I have found that dentate leaves are not much more or less frequent in the distal part of a branch than in its proximal part, and one member of a pair may be entire, while the other has many teeth.

Table 3. *Numbers of teeth on the leaves of the nine branches of tree 8 of* Nyctanthes arbor-tristis

Number of teeth	Number of leaves on branch									Total
	1	2	3	4	5	6	7	8	9	
0	166	76	123	167	168	158	93	61	71	1083
1	12	4	4	6	17	3	—	8	7	61
2	18	5	5	13	18	11	1	14	13	98
3	18	6	6	9	19	7	5	10	8	88
4	7	4	7	3	11	6	5	3	3	49
5	5	6	5	7	5	4	7	5	4	48
6	3	1	3	1	3	9	3	5	3	31
7	2	1	2	2	5	4	1	3	2	22
8	—	—	5	2	1	2	—	2	1	13
9	—	—	—	1	—	—	—	2	—	3
10	—	1	2	1	—	1	—	2	—	7
11	—	—	3	1	—	—	—	—	—	4
12	—	—	—	—	—	—	—	—	—	—
13	—	—	—	1	—	1	—	—	—	2
14	—	—	—	—	—	—	—	—	—	—
15	—	—	—	1	—	—	—	—	—	1
Total	231	104	165	215	247	206	115	115	112	1510

Table 4. *Results of total branch-wise enumeration of leaves for teeth number from tree 8 of* Nyctanthes arbor-tristis

Branch	1	2	3	4	5	6	7	8	9	Total
Entire leaves	166	76	123	167	168	158	93	61	71	1083
Dentate leaves	65	28	42	48	79	48	22	54	41	427
%dentate	28·1	26·9	25·5	22·4	32·0	23·3	19·1	46·9	36·6	28·3
χ^2	0·002	0·09	0·65	3·76	1·67	2·52	4·74	19·78	3·83	37·04

Discussion

Bimodal variation in leaf shape is not rare in plants, but this is usually because the shapes of young and old leaves are very different, as in *Leonurus sibiricus*. Bimodal variation in flower, fruit and seed structure and size is not at all rare, but it almost always seems to be determined by position on the plant. Salisbury (1942, pp. 30-32) describes a number of cases, mostly in the Compositae and Cruciferae. What is certainly unique in the case described is the fact that some trees show bimodal distributions while others do not. The difference is certainly independent of insolation, and cannot depend on differences of soil or water, since trees growing close together differed. It seems highly probable that it is genetically determined, and it may well be due to a single gene substitution.

Variation in Petal Number on the same Plant

Method

The gamopetalous flowers of *Nyctanthes arbor-tristis* (Fig. 2) open about evening and are shed during the following night. The number from a single tree has a mean value of about 250, though it may be as high as 1492, and falls off at the end of the season. The flowers from each tree were collected in the morning, and sorted into groups with the same number of petals. These groups were then counted. About one flower in 500, or more probably a smaller fraction, had an incompletely divided pair of petals. Such a pair was counted as one petal. Had it been counted as two, means would have been increased by 0·002 or less, and standard deviations, if at all, by a smaller amount. This would have affected none of my conclusions. Each flower was observed twice, when assigned to its heap, and less carefully, when the heap was counted. The flowers with 4, 8, 9 and 15 petals were very infrequent, and I am sure that none were incorrectly assigned to these groups. It is possible that a flower with 8 petals was assigned to the pile with 7 petals and more likely that misclassification occurred between the groups with 5, 6, and 7 petals, though it is most improbable that any with 4 petals was assigned to the group with 5. If one or more such errors occurred they are perhaps more likely to have lowered variances than raised them.

Between 26.9.55 and 11.1.56 I examined daily all flowers from three plants, and the total number of flowers examined was 76,753. On five days out of these 108 the flowers had been collected by others before sunrise for religious purposes. I also examined 82,173 flowers from 17 plants, including the three examined in the previous year from 24.9.57 to 21.10.57 and 30.10.57 to 13.11.57. Due to circumstances beyond my control, I could not examine flowers during the rest of that season. Because of the large number of trees under investigation only a very small sample of flowers could be examined from each of the 17 trees during 1957. To establish differences in the variation in petal number during different parts of the season a much larger sample size is necessary, so this was not considered for the 17 plants examined during 1957. But the total number of flowers examined for each of the 11 trees was large enough to establish differences in the variation in them and hence analysis on this was made, and is included in this paper. The plants of this species in the compound of the Institute were numbered 1 to 23, but six of these did not flower in 1957. The seven trees numbered 1 to 7 in the study of leaves were so numbered.

Between 18.12.1957 and 13.2.1958 I examined 7,310 flowers from two plants of *Jasminum multiflorum* var. *alba* (formerly known as *J. pubescens*), Bengali *Kund*, an ornamental jasmin, which forms bushes up to 1 metre in height. The gamopetalous flowers (Fig. 4) which open about evening were plucked daily.

Between 10.2.1958 and 16.6.1958, 15,809 flowers (including 7 double flowers) of two plants of *Jasminum multiflorum* var. *rubescens* (Fig. 3) were examined by myself, and by Prof. J. B. S. Haldane during my absence for four weeks. All four *Jasminum* plants were examined during their entire flowering periods. In view of the wide range of petal numbers and the small number, usually less than 100, of flowers per day, the flowers were not arranged in heaps of the same petal numbers, but each was recorded separately.

Variation in Flowers of *Nyctanthes arbor-tristis*

The grand total for 17 trees in two seasons is given in Table 5.

Its most surprising feature is the single flower with 15 petals. Unlike the many petalled *Jasminum* flowers described later, this showed no sign of duplicity. It is perhaps of interest as showing the unsatisfactory character of the range as a measure of variation. A sample of 50 flowers would probably have a range of only 2 (5-7). A sample of 1000 would probably have a range of 4 (4-8), but even a sample of 10,000 would be unlikely to attain a range of 5 (4-9). Finally a single flower, after over 100,000 had been counted, more than doubled the range, raising it from 5 to 11. As it was not observed till over 100,000 flowers had been examined, this is a striking example of the danger of using the range to describe a biological population, whatever may be its justification in industrial statistics.

Table 5. *Overall frequency distribution of petal numbers in flowers on three trees of* Nyctanthes arbor-tristis *in 1955-'56 and seventeen in 1957*

Number of petals	4	5	6	7	8	9	15	Total
Number of flowers	451	29147	109345	18956	1012	14	1	158926
% of total	0·284	18·340	68·801	11·928	0·637	0·009	0·0006	100·000

There is clearly a strong but not overwhelming tendency to produce the normal number of six petals. It will be seen that 68·80±0·12% of all the flowers had the modal number of six petals. In most earlier work on variation of petal number only a minority of flowers had the modal number. Here we clearly have a condition intermediate between the variable sepal number found by Yule (1901-1902) in *Anemone nemorosa* for example, and the situation where thousands of flowers must be examined before a deviation from the standard is found. My data are superficially comparable with those of Browne (1901-1902) who found that 77·1% of a thousand jellyfish *Aurelia aurita* had the modal number of 8 tentaculocysts. However he was studying a population, whilst my results concern individual plants.

Table 6 gives the cumulants k_r and the measures of deviation from normality g_r. In view of the large size of the sample I have calculated the fifth and the sixth cumulants as well as the first four. I also give values k_r', g_r' which would have been obtained had the single flower with 15 petals been absent.

Table 6. *Parameter estimates of the distribution of Table 5;* k_1' *etc. are those found if the fifteen petalled flower is omitted*

k—statistics		g—statistics	
Including the fifteen petalled flower	Excluding the fifteen petalled flower	Including the fifteen petalled flower	Excluding the fifteen petalled flower
$k_1 = +5{\cdot}9432$	$k'_1 = +5{\cdot}9432$		
$k_2 = +0{\cdot}3371$	$k'_2 = +0{\cdot}3371$		
$k_3 = +0{\cdot}0327$	$k'_3 = +0{\cdot}0239$	$g_1 = +\ 0{\cdot}1671 \pm 0{\cdot}0061$	$g'_1 = +0{\cdot}1221 \pm 0{\cdot}0061$
$k_4 = +0{\cdot}1253$	$k'_4 = +0{\cdot}1178$	$g_2 = +\ 1{\cdot}1030 \pm 0{\cdot}0123$	$g'_2 = +1{\cdot}0370 \pm 0{\cdot}0123$
$k_5 = +1{\cdot}3962$	$k'_5 = +0{\cdot}0901$	$g_3 = +21{\cdot}78\ \ \pm 0.027$	$g'_3 = +1{\cdot}405\ \ \pm 0.027$
$k_6 = +1{\cdot}7191$	$k'_6 = +0{\cdot}1011$	$g_4 = +45{\cdot}71\ \ \pm 0.067$	$g'_4 = +2{\cdot}732\ \ \pm 0.067$

The values given above are the estimates of the first six cumulants according to Fisher (1954). The standard error of k_2 is increased by 30% above its value calculated from k_2 alone, because of the high positive value of k_4. A measure of divergence from symmetry is provided by g_1. The distribution is significantly positively skew, but slightly so. A measure of kurtosis is provided by g_2. The distribution is fairly strongly leptokurtic, that is to say, there are more extreme values than would be found in a normal distribution with the same variance. The standard errors of g_1 to g_4 are calculated from a normal distribution, that is to say, they allow an estimate of probability that the sample could have been derived from a normal distribution. This is less than 10^{-80} in each case.

It will be seen that this flower with 15 petals had quite an appreciable influence on k_3 and k_4, and a large one on k_5 and k_6. This demonstrates the fact that even in very large samples it is seldom worth calculating moments beyond the fourth. In calculating the standard error, 0·0014, of the variance estimate k_2, I have allowed for

Table 7. *Frequency distributions of petal numbers in flowers of* Nyctanthes arbor-tristis *from three trees during 1955-'56 and seventeen in 1957*

Number of petals	Number and relative frequencies (% of total) of flowers for tree																			
	10		21		5		9		20		6		18		14		1 (55-56)		1	
	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative
4	75	1·47	49	1·21	40	0·81	29	0·56	32	0·64	19	0·38	13	0·33	5	0·10	87	0·29	13	0·22
5	2524	49·49	1324	32·56	1728	35·06	1779	34·02	1428	28·70	1364	27·56	882	22·60	1169	22·18	4823	16·22	1106	18·29
6	2361	46·29	2605	64·05	2804	56·90	2909	55·63	3154	63·40	3225	65·17	2780	71·23	3604	68·37	22190	74·63	4481	74·12
7	137	2·69	88	2·16	340	6·90	502	9·60	346	6·94	328	6·63	227	5·81	482	9·14	2540	8·54	425	7·03
8	3	0·06	1	0·02	16	0·33	10	0·19	16	0·32	13	0·26	1	0·03	11	0·21	94	0·32	21	0·34
9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	5100	100·00	4067	100·00	4928	100·00	5229	100·00	4975	100·00	4949	100·00	3903	100·00	5271	100·00	29734	100·00	6046	100·00

Table 7—*(contd.)*

Number of petals	Number and relative frequencies (% of total) of flowers for tree																			
	17		3 (55-56)		5		19		7		8		2 (55-56)		2		23		4	
	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative	Absolute	Relative
4	5	0·14	12	0·08	12	0·23	5	0·12	2	0·04	10	0·20	35	0·11	4	0·08	4	0·09	—	—
5	754	20·94	2535	17·82	889	16·74	463	11·28	602	11·66	848	17·10	3619	11·04	387	8·09	578	12·54	345	6·67
6	2447	67·95	9436	66·32	3474	65·42	3119	75·98	3853	74·64	3117	62·86	24106	73·51	3631	75·88	2814	61·07	3235	62·51
7	381	10·58	2160	15·18	897	16·89	494	12·03	666	12·90	920	18·55	4731	14·43	724	15·13	1107	24·02	1462	28·25
8	14	0·39	86	0·60	37	0·70	24	0·59	39	0·76	64	1·29	291	0·89	39	0·82	104	2·26	128	2·47
9	—	—	—	—	1	0·02	—	—	—	—	—	—	8	0·02	—	—	1	0·02	4	0·08
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0·02
Total	3601	100·00	14229	100·00	5310	100·00	4105	100·00	5162	100·00	4959	100·00	32790	100·00	4785	100·00	4608	100·00	5175	100·00

the positive value of g_2 which raises the standard error by 28·8%. On the other hand the standard errors of g_1 to g_4 are those appropriate to a normal distribution only, and merely show the significance of the departure of the sample from normality.

The results for the different trees are set out in Table 7 and analysed in Table 8. The standard errors of the variances are those appropriate to a normal distribution. They should be raised by a factor of $(1+\frac{1}{2}g_2)^{\frac{1}{2}}$, but the sample sizes are not large enough to allow at all precise estimates of g_2. As an alternative measure of spread I calculated for each tree the percentage of flowers which had a number of petals other than 6. For tree 10, I also calculated the percentage deviation from 5. The standard errors of these percentages can be calculated without any doubt. The usual test of significance for the difference of the two variances is only valid when the distributions are

Table 8. *The number of flowers, mean, standard deviation, order of variance and percentage of abnormality of petal number of flowers on 17 trees of* Nyctanthes arbor-tristis *in 1957 and three of them in the season 1955–'56*

Tree number	Number of flowers counted	Mean petal number	Standard error	Standard deviation of petal number	Standard error*	Order of variance in 1957	Percentage of abnormality	Standard error
10	5100	5·5037	0·0081	0·5803	0·0057	10	50·51**	0·70
							53·71	0·70
21	4067	5·6725	0·0084	0·5378	0·0060	6	35·95	0·68
5	4928	5·7086	0·0088	0·6168	0·0062	13	43·10	0·71
9	5229	5·7485	0·0088	0·6347	0·0062	15	44·37	0·69
20	4975	5·7759	0·0083	0·5872	0·0059	11	36·60	0·76
6	4949	5·7882	0·0081	0·5683	0·0057	8	34·83	0·68
18	3903	5·8260	0·0083	0·5180	0·0059	4	28·77	0·72
14	5271	5·8719	0·0077	0·5560	0·0054	7	31·63	0·64
1 (55-56)	29734	5·9237	0·0030	0·5159	0·0021	—	25·37	0·25
1	6046	5·8900	0·0066	0·5135	0·0047	3	25·88	0·56
17	3601	5·9014	0·0095	0·5716	0·0067	9	32·05	0·78
3 (55-56)	14229	5·9840	0·0050	0·5977	0·0035	—	33·69	0·40
3	5310	6·0115	0·0084	0·6122	0·0059	12	34·58	0·65
19	4105	6·0168	0·0080	0·5111	0·0056	2	24·02	0·67
7	5162	6·0267	0·0073	0·5260	0·0052	5	25·36	0·61
8	4959	6·0363	0·0091	0·6441	0·0065	16	37·14	0·69
2 (55-56)	32790	6·0503	0·0030	0·5423	0·0021	—	26·48	0·24
2	4785	6·0851	0·0074	0·5108	0·0052	1	24·12	0·62
23	4608	6·1589	0·0097	0·6605	0·0069	17	38·93	0·72
4	5175	6·2694	0·0088	0·6310	0·0062	14	37·49	0·67

*Neglecting the fourth cumulant.
**Percentage deviation from 5.

normal, and the fourth moments are well determined. The percentage of abnormality is closely related to the standard deviation, but is easier to calculate, and its sampling error does not involve the calculation of the fourth moments. The order of these percentages of abnormal flowers is nearly the same as that of the variances, and they differ very significantly. Thus we may compare the two trees 1 and 14 whose means in 1957 differed slightly, while according to Table 8 the difference of their standard deviations was 5·9 times its standard error. Their percentages of abnormal flowers were $25{\cdot}88 \pm 0{\cdot}56\%$ and $31{\cdot}63 \pm 0{\cdot}64\%$, the difference being 6·8 times its standard error.

We can therefore conclude from Table 8 that each tree had its characteristic mean petal number, and its characteristic variance of petal number, and that these statistics generally differed significantly between different trees. Further it is seen that for trees 1, 2 and 3 the means and variances were very close in the different seasons, though they usually differed significantly. The seventh column shows that the variances of petal number are not correlated positively or negatively with its means. Esscher and Kendall's $\tau = -0{\cdot}029 \pm 0{\cdot}18$. Nor, as might possibly be the case, is the variance least when the mean is nearest to 6. It is possible that the differences between variances as well as means, of different trees, are largely determined genetically. The existence of a group of 4 trees with low standard deviations between 0·5108 and 0·5180, none significantly different, may have a biological meaning.

Variation during the Season

To determine the nature of variation over time the entire flowering season during 1955-1956 was divided into six periods of 15 days each followed by one of 17 days, and the frequency distribution of petal numbers of flowers, mean petal numbers, standard deviations of petal numbers, and the percentages of abnormality for the three trees were computed for each of the seven periods.

The relative frequencies of petal numbers in flowers of trees 1, 2 and 3 for the seven periods of the season were as shown in Table 9.

An examination of Table 9 reveals the facts indicated below.

1. The frequency of the modal class for tree 1 decreased from the first to the fifth period without any appreciable change thereafter; for tree 2, there was a decrease from the first to the seventh period; and for tree 3, the decrease was from first to the fourth period, followed by an increase in the fifth and sixth and a fall again in the seventh period. The standard errors of differences of two percentages were large for the later periods, so that some of the differences described are not significant. The difference between each pair of consecutive periods turns out to be significant for some plants and non-significant for some others, even for the same pair of periods. I should also mention here the surprising behaviour of plant 3 on one day (22.11.55), where the mode shifted from 6 to 5.

2. The relative frequency of the 5 petal class for plants 1 and 2 decreased from the first to the second period, then steadily increased up to the fifth period, and dropped again in the sixth and seventh periods, but that for plant 3 increased slightly in the second period (unlike the other two), then steadily increased up to the fourth period, dropped steadily in the fifth and sixth and increased slightly in the seventh period.

Table 9. *Relative frequencies (% of total) of petal numbers in flowers of* Nyctanthes arbor-tristis *for trees 1, 2 and 3 for seven periods of the season*

	Number of petals	Relative frequencies (%) during						
		26.9.55 to 10.10.55	11.10.55 to 25.10.55	26.10.55 to 9.11.55	10.11.55 to 24.11.55	25.11.55 to 9.12.55	10.12.55 to 24.12.55	26.12.55 to 11.1.56
	4	0·18	0·09	0·12	0·46	0·80	0·89	0·22
	5	13·31	11·73	14·57	21·38	22·23	19·24	15·47
Tree	6	78·95	77·81	75·92	70·94	68·78	68·40	69·06
1	7	7·31	10·04	9·08	6·95	7·84	10·96	14·16
	8	0·25	0·33	0·31	0·27	0·35	0·51	1·09
	9	0·00	0·00	0·00	0·00	0·00	0·00	0·00
Total number of flowers		4485	7770	5880	7452	2884	785	459
	4	0·00	0·00	0·03	0·17	0·32	0·29	0·77
	5	7·99	4·61	10·96	14·56	18·07	13·98	10·46
Tree	6	78·71	76·23	74·65	71·75	68·34	65·13	61·72
2	7	12·70	17·82	13·61	12·83	12·65	17·58	24·49
	8	0·60	1·29	0·75	0·69	0·58	2·88	2·30
	9	0·00	0·05	0·00	0·00	0·04	0·14	0·26
Total number of flowers		3480	7976	7735	7810	4703	694	392
	4	0·03	0·03	0·07	0·15	0·23	0·64	0·44
	5	12·89	14·95	27·87	32·87	22·35	7·68	9·80
Tree	6	72·52	66·92	61·08	60·65	64·29	65·03	62·31
3	7	14·06	17·45	10·64	6·33	12·90	23·45	26·58
	8	0·50	0·65	0·34	0·00	0·23	3·20	0·87
	9	0·00	0·00	0·00	0·00	0·00	0·00	0·00
Total number of flowers		2994	6293	2932	648	434	469	459

3. The relative frequency of the 7 petal class increased in the second period, dropped in the third and fourth, and increased again in the subsequent periods.

4. The trend of change in the relative frequencies of the petal classes 4 and 8 was similar to that of the 5 and 7 respectively.

5. Such changes, as mentioned in paragraphs 2, 3 and 4, can be explained by the drop in mean level in the second of the three main divisions of the periods (see Table 10).

6. The flowers of each tail of the distributions became relatively common late in the season.

The moving means for five days (namely days 1,2,3,4,5 and 2,3,4,5,6 and so on) for the three trees for the season 1955-1956 were computed and the results are represented in Fig. 5.

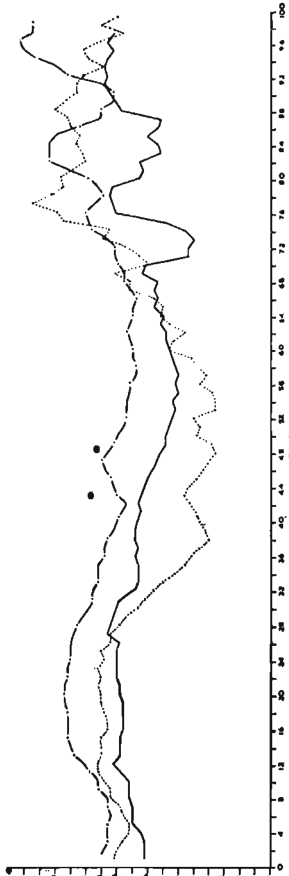

Fig. 5. Moving means of petal numbers of *Nyctanthus arbor-tristis* over five consecutive days for three trees during the season 1955-1956 ———, Tree no. 1; —·—·—, tree no. 2; ·········, tree no. 3.

Table 10. *The number of flowers, mean number of petals, standard deviation and percentage of abnormalities for the three trees of* Nyctanthes arbor-tristis *for the seven periods of the season*

Tree	Statistics \ Period	26.9.55 to 10.10.55	11.10.55 to 25.10.55	26.10.55 to 9.11.55	10.11.55 to 24.11.55	25.11.55 to 9.12.55	10.12.55 to 24.12.55	26.12.55 to 11.1.56
Tree 1	Number of flowers	4485	7770	5880	7452	2884	785	459
	Mean number of petals	5·9414 ±0·0070	5·9880 ±0·0055	5·9488 ±0·0065	5·8520 ±0·0062	5·8471 ±0·0106	5·9096 ±0·0211	6·0044 ±0·0276
	Standard deviation	0·4687 ±0·0049	0·4842 ±0·0039	0·5010 ±0·0046	0·5389 ±0·0044	0·5683 ±0·0075	0·5914 ±0·0149	0·5904 ±0·0195
	Percentage of abnormalities	21·05 ±0·61	22·19 ±0·47	24·08 ±0·56	29·05 ±0·53	31·21 ±0·86	31·59 ±1·66	30·75 ±2·11
Tree 2	Number of flowers	3480	7976	7735	7810	4703	694	392
	Mean number of petals	6·0592 ±0·0081	6·1591 ±0·0056	6·0410 ±0·0060	5·9932 ±0·0063	5·9522 ±0·0086	6·0922 ±0·0254	6·1786 ±0·0344
	Standard deviation	0·4770 ±0·0057	0·5050 ±0·0039	0·5245 ±0·0042	0·5551 ±0·0044	0·5868 ±0·0061	0·6684 ±0·0179	0·6804 ±0·0243
	Percentage of abnormalities	21·29 ±0·69	23·76 ±0·48	25·35 ±0·49	28·25 ±0·51	31·66 ±0·68	34·87 ±1·81	38·27 ±2·46
Tree 3	Number of flowers	2994	6293	2932	648	434	469	459
	Mean number of petals	6·0210 ±0·0099	6·0373 ±0·0075	5·8332 ±0·0113	5·7315 ±0·0224	5·9055 ±0·0289	6·2090 ±0·0300	6·1765 ±0·0290
	Standard deviation	0·5390 ±0·0070	0·5915 ±0·0053	0·6112 ±0·0080	0·5710 ±0·0159	0·6017 ±0·0204	0·6490 ±0·0212	0·6205 ±0·0205
	Percentage of abnormalities	27·49 ±0·82	33·08 ±0·59	38·92 ±0·90	39·35 ±1·92	35·71 ±2·30	34·97 ±2·20	37·69 ±2·26

It will be seen that the mean petal numbers altered in a characteristic way in all the three trees during the season. During the early part of the season the mean was high, being highest during the second week of October, which was followed by a drop, being lowest by the end of November and increasing again late in the season.

The number of flowers, mean number of petals, standard deviations of petal numbers and percentage of abnormalities for the three plants for the seven periods of the season 1955-1956 were as shown in Table 10.

The trend in the mean during the season has already been shown in Fig. 5 and here the same thing has only been repeated for the seven periods. The means for all the plants altered in a similar way with time. Although some of the differences are not significant, the mean increased from first to the second period, then dropped up to the fourth period (and in plant 2 up to the fifth period) and increased again in the subsequent periods. There are, of course, some differences between plants but the trend was more or less the same.

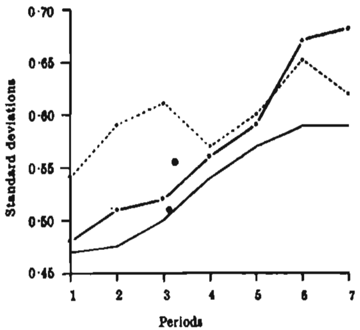

Fig. 6. Standard deviations of petal numbers of *Nyctanthes arbor-tristis* for seven consecutive periods of fifteen days each for three trees during the season 1955-1956.
———— Tree no. 1; ·——·——· tree no. 2; ··········· tree no. 3.

It is seen in Table 10 and in Fig. 6 that the standard deviations increased with time in plants 1 and 2 but that for plant 3 in the fourth and the sixth periods they dropped. Statistical tests were applied to test if the overall differences in the standard deviations for the different periods for each of these plants were significantly different or not. The tests reveal that for plants 1 and 2 the differences were highly significant and that for plant 3 was significant at 5% level.

It is also seen that the percentages of abnormality increased with time and that the increase was highly significant. The percentage of abnormality dropped in the fifth period in plant 3.

Significant increase in the standard deviations of petal numbers as also the percentages of abnormality on the same plant with time clearly indicate that precision in canalization, to follow Waddington's (1942,1957) terminology, falls off with time, and it does so very greatly during the end of the season, the variances sometimes being almost doubled.

Variation in flowers of *Jasminum multiflorum* var. *rubescens*

In 1958, 15,817 flowers were examined and their petal numbers counted. The frequency distributions of petal numbers for the two plants separately and jointly are shown in Table 11.

The number of petals varied from 8 to 17 with a mode at 10. Some flowers showed duplicity and thereby increased the range to 21. It will be seen that 45·19% of all the flowers (including the double flowers) had the modal number of ten petals.

Table 11. *Frequencies of number of petals in flowers of* Jasminum multiflorum *var.* rubescens *for the two plants separately and jointly during 1958*

Number of petals	Frequencies in plant				Total	
	1		2			
	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)
8	167	1·792	119	1·832	286	1·808
9	1919	20·588	1366	21·028	3285	20·769
10	4217	45·242	2931	45·120	7148	45·193
11	2451	26·295	1719	26·463	4170	26·364
12	505	5·418	330	5·080	835	5·279
13	39	0·418	26	0·400	65	0·411
14	12	0·129	4	0·062	16	0·101
15	1	0·011	—	—	1	0·006
16	3	0·032	—	—	3	0·019
17	1	0·011	—	—	1	0·006
18	2(d)*	0·021	1(d)	0·015	3(d)	0·019
19	1(d)	0·011	—	—	1(d)	0·006
20	1(d)	0·011	—	—	1(d)	0·006
21	2(d)	0·021	—	—	2(d)	0·013
Total	9315+ 6(d)	100·000	6495+1(d)	100·000	15810+7(d)	100·000

*d=double flower

Superficially the distributions seem to be asymmetric. To test for normality of the observed frequency distributions, g_1 and g_2 statistics, as suggested by Fisher (1954) and their standard errors if the distributions were normal, were computed and the results are shown in Table 12. In all computations such as g_1, g_2 etc., means and standard deviations the double flowers have been excluded due to the fact that the petal components for such a double flower cannot be determined.

It is seen from Table 12 that except for g_2 for plant 2 (which is just insignificant at 5% level) the other statistics are highly significant. Thus for plant 1, the observed frequency distribution is highly positively skew while for plant 2 the degree of skewness is smaller than plant 1.

Table 12. *k-statistics and g-statistics for the observed frequency distributions of the two plants of* Jasminum multiflorum *var.* rubescens *neglecting the double flowers*

k-statistics		g-statistics	
Plant 1	Plant 2	Plant 1	Plant 2
$k_1 = +10{\cdot}1506$	$k_1 = +10{\cdot}1338$		
$k_2 = +\ 0{\cdot}8125$	$k_2 = +\ 0{\cdot}7794$		
$k_3 = +\ 0{\cdot}2898$	$k_3 = +\ 0{\cdot}1476$	$g_1 = +0{\cdot}3958 \pm 0{\cdot}0254$	$g_1 = +0{\cdot}2145 \pm 0{\cdot}0304$
$k_4 = +\ 0{\cdot}7813$	$k_4 = +\ 0{\cdot}0656$	$g_2 = +1{\cdot}1834 \pm 0{\cdot}0508$	$g_2 = +0{\cdot}1080 \pm 0{\cdot}0608$

The means of petal numbers for plants 1 and 2 were $10{\cdot}1506 \pm 0{\cdot}0093$ and $10{\cdot}1338 \pm 0{\cdot}0110$ respectively. The standard deviations for plants 1 and 2 were $0{\cdot}89796 \pm 0{\cdot}00658$ and $0{\cdot}88555 \pm 0{\cdot}00779$ respectively. Statistical tests were applied to find if the differences in the means and the standard deviations between the two plants were significant. The tests reveal that neither of these differed significantly between the two plants.

VARIATION DURING THE SEASON

The distributions of petal numbers of flowers for eight different periods of the season were as shown in Table 13.

An examination of the table will reveal the facts indicated below.

1. The modal class did not change in either of the plants during the season.
2. The distributions for both the plants remained asymmetric during the season.
3. The range increased in plant 1 in the fifth period from 5 (8-13) to 8 (8-16), in the sixth to 9 (8-17), in the seventh it decreased to 8 (8-16) and then fell to the original range of 5 (8-13) again in the last period; and that for plant 2 rose from 5 (8-13) to 6 (8-14) in the fifth and sixth periods and then dropped to 5 (8-13) again in the seventh and the eighth.
4. Both the plants showed flower teratology, such as production of double flowers, late in the season. In plant 1 double flowers were produced in the sixth period and continued till the last. In plant 2 such a flower was produced in the last (eighth) period. The frequencies of these abnormal flowers were different for the two plants. For plant 1 it was 0·064% while for plant 2 it was 0·015%.

The means and the standard deviations of petal numbers for the two plants for the eight different periods of the season were as shown in Table 14.

An examination of Table 14 will show that the mean decreased from the first up to the fourth period followed by an increase in the fifth and the sixth, and then again declined in the last two periods.

Table 13. *The distribution of petal numbers of flowers for the two plants of* Jasminum multiflorum *var.* rubescens *for different periods of the season*

	Number of petals	Number of flowers for period							
		10.2.58 to 25.2.58	26.2.58 to 13.3.58	14.3.58 to 29.3.58	30.3.58 to 14.4.58	15.4.58 to 30.4.58	1.5.58 to 16.5.58	17.5.58 to 1.6.58	2.6.58 to 17.6.58
Plant 1	8	19	30	53	26	5	7	14	13
	9	269	300	667	303	51	35	204	90
	10	683	613	1482	631	119	94	386	209
	11	437	335	868	353	74	50	218	116
	12	72	75	175	59	22	28	51	23
	13	4	4	9	2	6	5	7	2
	14	—	—	—	—	4	7	1	—
	15	—	—	—	—	1	—	—	—
	16	—	—	—	—	1	1	1	—
	17	—	—	—	—	—	1	—	—
	18	—	—	—	—	—	—	—	2 (d)
	19	—	—	—	—	—	1(d)	—	—
	20	—	—	—	—	—	—	1(d)	—
	21	—	—	—	—	—	2(d)	—	—
	Total number of flowers	1484	1357	3254	1374	283	228+3(d)	882+1(d)	453+2(d)
Plant 2	8	7	21	30	37	9	4	5	6
	9	180	184	403	343	63	100	48	45
	10	511	404	759	774	127	188	93	75
	11	302	295	389	428	86	138	42	39
	12	58	61	58	73	25	38	8	9
	13	3	6	1	8	1	5	1	1
	14	—	—	—	—	2	2	—	—
	15	—	—	—	—	—	—	—	—
	16	—	—	—	—	—	—	—	—
	17	—	—	—	—	—	—	—	—
	18	—	—	—	—	—	—	—	1(d)
	19	—	—	—	—	—	—	—	—
	20	—	—	—	—	—	—	—	—
	21	—	—	—	—	—	—	—	—
	Total number of flowers	1061	971	1640	1663	313	475	197	175+1(d)

On the other hand there is a clear trend of increase in the standard deviation, the maximum being in the sixth period in plant 1 and in the fifth in plant 2, after which there was a decline in the last two periods. But the standard deviations for the last two periods were greater than for the first period.

The data indicate that the mean petal numbers and the standard deviations alter in their characteristic ways during the season, and that there is decrease in canalization of petal number.

Table 14. *The number of flowers, mean number of petals, and the standard deviations of the petal numbers for two plants of* Jasminum multiflorum *var.* rubescens *for the eight periods of the season*

Statistics	Period	10.2.58 to 25.2.58	26.2.58 to 13.3.58	14.3.58 to 29.3.58	30.3.58 to 14.4.58	15.4.58 to 30.4.58	1.5.58 to 16.5.58	17.5.58 to 1.6.58	2.6.58 to 17.6.58
Plant 1	Number of flowers	1484	1357	3254	1374	283	228+3(d)	882+1(d)	453+2(d)
	Mean number of petals	10·1927 ±0·0159	10·1010 ±0·0174	10·1451 ±0·0108	10·0888 ±0·0163	10·3604 ±0·0153	10·4956 ±0·0199	10·1349 ±0·0224	10·1148 ±0·0297
	Standard deviation	0·8638 ±0·0224	0·9072 ±0·0246	0·8689 ±0·0152	0·8544 ±0·0231	1·1515 ±0·0685	1·3430 ±0·0890	0·9413 ±0·0317	0·8939 ±0·0420
Plant 2	Number of flowers	1061	971	1640	1663	313	475	197	175+1(d)
	Mean number of petals	10·2196 ±0·0179	10·2152 ±0·0208	10·0274 ±0·0146	10·1088 ±0·0151	10·2109 ±0·0399	10·2716 ±0·0315	10·0152 ±0·0624	10·0171 ±0·0500
	Standard deviation	0·8228 ±0·0271	0·9176 ±0·0295	0·8385 ±0·0207	0·8718 ±0·0214	0·9985 ±0·0564	0·9706 ±0·0445	0·8781 ±0·0668	0·9354 ±0·0707

Variation in Flowers of *Jasminum multiflorum* var. *alba*

In 1957-1958 I examined 7310 flowers from two plants of *Jasminum multiflorum* var. *alba* and their petal numbers were counted. The frequency distributions of petal numbers for each plant and their grand total are shown in Table 15.

The number of petals varied from 5 to 11 with a mode at 8. Bhatnagar (1957) observed a range of 6-9. 50·3% of the flowers had the modal number of eight petals.

It will be seen that superficially the distributions for both the plants appear to be symmetric. To test for normality of the observed frequency distributions, g_1 and g_2 statistics and their standard errors, suggested by Fisher (1954), if the distributions were normal were computed. The results are shown in Table 16.

It is seen from Table 16 that except for g_1 for plant 1 (which is significant at 5% level but not at 1%) the other statistics are not significantly different from zero. Thus for plant 2, the observed frequency distribution does not deviate significantly from normality while for plant 1 it shows slight skewness.

Table 15. *Frequencies of number of petals in flowers for the two plants of* Jasminum multiflorum *var.* alba *separately and jointly during 1957-1958*

Number of petals	Frequencies in plant				Total	
	1		2			
	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)
5	3	0·08	2	0·05	5	0·068
6	94	2·63	84	2·25	178	2·435
7	1040	29·07	948	25·39	1988	27·196
8	1780	49·76	1897	50·82	3677	50·301
9	608	17·00	730	19·56	1338	18·304
10	51	1·43	71	1·90	122	1·669
11	1	0·03	1	0·03	2	0·027
Total	3577	100·00	3733	100·00	7310	100·000

Table 16. k-*statistics and* g-*statistics for the observed frequency distributions of the two plants of* Jasminum multiflorum *var.* alba *neglecting the double flowers*

k-statistics		g-statistics	
Plant 1	Plant 2	Plant 1	Plant 2
$k_1 = +7·8535$	$k_1 = +7·9338$		
$k_2 = +0·6115$	$k_2 = +0·6185$		
$k_3 = +0·0399$	$k_3 = +0·0295$	$g_1 = +0·0836 \pm 0·0410$	$g_1 = +0·0617 \pm 0·0408$
$k_4 = +0·0209$	$k_4 = +0·0235$	$g_2 = +0·0559 \pm 0·0820$	$g_2 = +0·0614 \pm 0·0816$

The means of petal numbers for plants 1 and 2 were $7·8535 \pm 0·0137$ and $7·9338 \pm 0·0135$ respectively. The means of the two plants were found to be significantly different from one another. The standard deviations of petal numbers for plants 1 and 2 were $0·7820 \pm 0·0092$ and $0·7934 \pm 0·0092$ respectively.

Variation during the Season

The distributions of petal numbers of flowers for four different periods of the season, namely, 18.12.57 to 25.12.57, 3.1.58 to 10.1.58, 20.1.58 to 27.1.58 and 5.2.58 to 13.2.58, are shown in Table 17.

An examination of Table 17 will reveal the facts indicated below.

1. The modal class has changed for plant 1 from 8 to 7 late in the season, but it remains the same for plant 2.

Table 17. *The distributions of petal numbers of flowers for the two plants of* Jasminum multiflorum *var.* alba *for four periods of the season*

	Number of petals	Number of flowers for period			
		18.12.57 to 25.12.57	3.1.58 to 10.1.58	20.1.58 to 27.1.58	5.2.58 to 13.2.58
Plant 1	5	3	—	—	—
	6	45	30	—	—
	7	374	354	59	16
	8	661	641	95	11
	9	185	243	25	4
	10	10	24	3	—
	11	—	—	—	—
Total number of flowers		1278	1292	182	31
Plant 2	5	2	—	—	—
	6	17	17	15	14
	7	219	253	112	110
	8	451	574	201	139
	9	165	266	85	38
	10	14	22	9	1
	11	—	1	—	—
Total number of flowers		868	1133	422	302

2. The distributions for both the plants for the first two periods were nearly symmetric. In the third period, the distributions for both the plants become skew. In the fourth period the distribution for plant 1 was definitely J-shaped, that for plant 2 was significantly positively skew, but not J-shaped. That is to say, on the whole, the distributions tend to be asymmetric late in the season.

The means and the standard deviations of petal numbers for the two plants in the four periods of the season were as shown in Table 18.

An examination of Table 18 will show how for each plant the mean increased significantly from the first period to the second, then returned to the original level in the third and finally went below this level in the fourth. There were some absolute differences, of course, between two sets of plant-wise figures, but the trend in each set was the same. The change in mean petal number, as shown above, was caused by the change in the distributions as shown in Table 17.

On the other hand, the standard deviations altered slightly, being highest in the third period. There was a trend, though not marked, of increase from first to the third period followed by a decline in the fourth for both the plants. Tests both pair-wise and overall, were applied to find out if the standard deviations for the two plants for different periods were significantly different from one another. The tests reveal that the differences were not statistically significant.

Table 18. *The means and the standard deviations of petal numbers for two plants of* Jasminum multiflorum *var.* alba *for four periods of the season*

Statistics \ Period		18.12.57 to 25.12.57	3.1.58 to 10.1.58	20.1.58 to 27.1.58	5.2.58 to 13.2.58
Plant 1	Number of flowers	1278	1292	182	31
	Mean number of petals	7·7903 ±0·0214	7·9048 ±0·0219	7·8462 ±0·0678	7·6129 ±0·1285
	Standard deviation	0·7664 ±0·0152	0·7877 ±0·0155	0·9169 ±0·0479	0·7154 ±0·0909
Plant 2	Number of flowers	868	1133	422	302
	Mean number of petals	7·9240 ±0·0263	8·0229 ±0·0231	7·9076 ±0·0403	7·6755 ±0·0440
	Standard deviation	0·7752 ±0·0186	0·7768 ±0·0163	0·8286 ±0·0285	0·7651 ±0·0311

In view of the fact that when we find so much difference in the variation between plants and also in the same plant with time, perhaps it would not be out of place to comment on Bhatnagar's (1957) observations on the petal number variation in *Jasminum*. According to him the range of petal number in the variety of this species was 6 to 9 which according to my observations was 5 to 11. The smaller range in his case might be, besides other reasons, due to an extremely small sample size. But we have no knowledge of the number of individuals on which his observations were based. Again, it seems that he was satisfied with merely the range of variable floral organs including sepals and petals and went so far as to suggest—"This type of approach can be of great advantage to the systematist who usually has to rely on inconspicuous differences for demarcating varieties and species". I do not share his views and, on the contrary, I believe that the correct approach to determine the exact status of a variety or of a species with regard to variation of such variable structures should be to take into account the distribution, the mode and the variance, with proper consideration of the time factor and not merely the range. The unsatisfactory character of the range as a measure of variation was discussed in detail under "Variation in flowers of *Nyctanthes arbor-tristis*".

Discussion and Conclusion

Organic regulation

Self-regulation, or as Cannon (1932) called it, homeostasis, is one of the most striking charactors of living organisms. While it is most obvious on the morphological level, it has mainly been studied for chemical characters and temperature, because we can see how a change in the environment or in the organism's activity would affect some character of the organism if regulation did not occur. For example, a naked man's internal temperature may not change appreciably (perhaps by 0·1°C) when the temperature around him changes from 15°C to 40°C. The CO_2 content of the arterial blood only rises by about 5% when the CO_2 production per minute is increased fourfold. The temperature of a resting man is very steady, and a failure of temperature regulation is serious. But we can only assess the delicacy of regulation because we can study the effects of changes in external temperature and in heat production.

If we are studying the size of flowers or cells, we do not, in general, know what external or internal changes would make them larger or smaller. Hence experiment is excluded. There are however two more fundamental differences. First of all the parts of organism in question may be formed simultaneously, whereas measurements of temperature etc. are successive.

The second difference is, I think, even more important. If the body temperature rises this is counteracted by sweating, skin vasodilation, and so on, which tend to lower it. In engineering terms there is "negative feed-back". Some substance in the plant must be regulated as, say, glucose, chloride, or thyroxine are in human blood. If there is too much, one process starts up, if too little, another. Near the standard value both are usually in action. We have not even the remotest idea what such a process may be. It might be, for example, that if a tree had produced too many petals on one day, it would tend to produce too few on the next. Again, it may be possible that when a plant has produced 8 petals this is a sign of an excess of some substance, say a hormone, in the branch concerned, and it is rapidly lowered by a self-regulatory process. But this is quite a doubtful hypothesis. It is almost certain that the plant does not react directly to an excess of petals, as an animal can react to a local excess of temperature. Until we know something of the physiology, it is perhaps a little dangerous to use the same word, "regulation", for the processes which keep the temperature and the petal number steady, though I probably shall do so !

It is worth considering if weather effects influence the petal number in different trees. Let us examine the case of *Nyctanthes arbor-tristis*. If an increase in mean petal number from that of the day before had been denoted by a + sign and a decrease by a − sign it might be that on a certain day all seventeen trees gave a + sign. This would only happen by chance once in 2^{17} or 131,072 days, so if it were found it would clearly mean that something had affected all the trees. I think such a situation would occur only if some weather effects influenced the petal numbers in different trees.

To examine this a table has been prepared where an increase in the mean petal number from that of the day before had been denoted by a + sign and a decrease by a − sign. This has been done for all seventeen trees for the season 1957. The samples being too small in November were not considered. Similarly this has been done for three trees in 1955-1956. The results are shown in Tables 19 and 20 respectively.

It will be seen that there was not a single day when all were + or − We may summarise Table 19 as Table 21 where the numbers of + trees in a day are shown.

The mean is 8·238, the variance 3·59, whereas that expected on the basis of pure chance is $\frac{17}{4}$ or 4·25. If there were a tendency for increases to occur on some

Table 19. *Turning points of means of petal numbers for seventeen trees of* Nyctanthes arbor-tristis *for the season 1957*

Date	Turning points of means of petal numbers in tree																	Total	
	1	2	3	4	5	6	7	8	9	10	14	17	18	19	20	21	23	+	−
Sept. 25	−	+	−	−	−	+	+	−	+	+	+	−	−	−	−	+	+	8	9
26	−	+	+	+	+	−	−	+	−	−	−	−	+	−	+	−	−	7	10
27	+	−	−	−	+	−	+	−	−	−	−	+	−	+	+	−	−	6	11
28	+	−	−	+	−	+	−	+	+	+	+	+	−	−	−	−	+	9	8
29	+	+	+	−	+	+	+	−	−	−	−	−	−	+	+	+	−	9	8
30	−	−	+	+	−	−	+	+	−	+	−	+	+	+	+	+	+	11	6
Oct. 5	−	+	+	−	−	+	+	+	+	−	+	−	+	−	+	−	−	9	8
6	+	−	−	−	+	+	+	−	−	−	+	+	+	−	+	+	−	9	8
7	−	+	−	−	+	+	+	−	−	−	−	+	+	+	+	−	+	9	8
8	−	−	+	−	−	+	−	−	+	+	−	−	−	+	−	+	−	6	11
9	−	+	+	+	−	−	+	−	−	+	+	−	−	+	+	+	+	10	7
10	+	−	+	+	+	−	−	+	−	+	−	+	+	−	−	−	−	8	9
11	−	−	−	−	−	+	+	−	−	+	−	+	+	+	+	−	−	7	10
12	−	+	+	+	−	+	−	+	−	−	+	−	−	−	+	+	+	9	8
15	−	−	−	+	−	−	+	+	+	−	−	+	−	−	−	+	+	7	10
16	+	+	+	−	−	−	−	+	−	−	−	+	−	−	+	−	+	7	10
17	−	−	−	+	+	+	−	+	+	+	−	+	+	+	−	+	−	10	7
18	+	−	−	−	−	−	+	−	−	+	+	−	−	−	+	−	+	6	11
19	−	+	+	+	+	−	+	−	+	−	+	+	+	+	−	−	+	11	6
20	+	−	−	−	−	−	−	−	−	−	−	−	+	−	+	+	−	4	13
21	−	+	+	−	+	+	+	−	−	+	+	+	−	−	+	+	+	11	6

day, it would exceed 4·25. Similarly the 3-tree table (Table 20) may be summarised as follows (Table 22).

$\chi^2_3 = 1\cdot93$ which is very low. There are 26 complete agreements where $22\cdot25 \pm 4\cdot085$ is the expectation. So there is no evidence for synchronization. Hence it is clear from the above analysis that weather effects had no appreciably sensitive influence in regulating petal number.

Again, it might be, for example, that if a tree had produced too many petals on one day it would tend to produce too few on the next. This does not imply that the tree had "feed-back" as to the number of petals. If so, successive pairs + +

Table 20. *Turning points of means of petal numbers of* Nyctanthes arbor-tristis *for three trees for season 1955-'56*

Date	Turning points in tree 1	2	3	Date	Turning points in tree 1	2	3	Date	Turning points in tree 1	2	3
Sept. 26				Oct. 29	+	–	–	Dec. 1			
27	–	–	–	30				2	+	+	–
28	–	–	+	31				3	–	–	+
29	+	+	–	Nov. 1	+	–	–	4	+	–	–
30	+	–	+	2	–	+	+	5	–	+	–
Oct. 1	–	–	–	3	+	–	–	6	+	+	+
2	+	–	–	4	+	+	–	7	–	+	–
3	+	–	+	5	–	–	+	8	+	+	–
4	+	+	–	6	–	+	–	9	–	–	+
5	–	–	+	7	+	–	+	10	+	–	+
6	+	+	–	8	–	–	+	11	–	+	–
7	+	–	+	9	–	+	–	12	+	–	+
8	–	+	–	10	+	+	+	13	–	+	–
9	+	–	+	11	+	–	–	14	–	+	+
10	+	+	+	12	–	+	+	15	+	–	–
11	+	+	–	13	–	–	–	16	+	+	–
12	–	–	–	14	+	+	–	17	–	–	+
13	+	+	+	15	–	+	+	18	–	–	+
14	–	–	+	16	+	–	–	19	–	+	–
15	–	–	–	17	–	–	+	20	–	+	+
16	+	+	+	18	–	+	–	21	–	+	+
17	–	–	–	19	+	+	+	22	+	+	–
18	+	+	+	20	–	–	–	23	+	–	+
19	–	–	–	21	+	+	+	24	–	–	–
20	+	–	+	22	–	–	–	25			
21	–	–	–	23	–	+	+	26			
22	–	+	+	24	+	–	+	27	+	+	–
23	+	+	–	25	+	–	+	28	–	–	+
24	+	+	+	26	–	–	–	29	+	–	+
25	–	–	–	27	–	+	+	30	+	+	+
26	+	–	–	28	+	+	+	31	–	–	–
27	–	+	+	29							
28	–	–	–	30							

or – – on the same tree should be rarer than the expected frequency of 1/3 and *changes in signs* should be more than the expected frequency of 2/3.

The results show that in fact the number of successive pairs + + and − − for the three trees were 28, 32 and 20 where the expectation was 28·3. The differences between the observed and the expected numbers are not at all significant. Again, the number of turning points for the three trees were 57, 53 and 65 where the expectation was 56·7. The differences between the observed and the expected numbers are not at all significant.

Table 21. *Numbers of + trees of* Nyctanthes arbor-tristis *in a day*

Number of + trees	4	5	6	7	8	9	10	11	Total
Number of days	1	0	3	4	2	6	2	3	21

Table 22. *Numbers of + trees of* Nyctanthes arbor-tristis *in a day*

Number of + trees	0	1	2	3	Total
Number of days: observed	15	29	34	11	89
expected	11·125	33·375	33·375	11·125	

If a craftsman produced articles with much the same mean dimensions in the course of a day's work, but the variance around this mean increased progressively, we should say that he was getting fatigued. It might be possible to trace this fatigue to a decline in the efficiency of 'negative feed-back'. It is not so easy to apply this notion to a plant even when the variance increased progressively during the season. Heslop-Harrison (1959) observed that for plants of *Cannabis sativa* (hemp) grown in day and night temperatures of 22°C, mean tepal number is 4·98 and within-plant variance 0·0185; with a day temperature of 22°C and night temperature of 10°C., the mean is slightly shifted to 4·79, but the variance shoots up to 0·3289. He observed similar results with stamen number in plants of the same species. The weather became progressively cooler during the flowering season of *Nyctanthes arbor-tristis*, and the increased variance might be ascribed to this. However, the temperature was rising during the flowering season of the *Jasminum* described in this paper.

There are a number of more or less superficially comparable results on the variation between individual members of different clones of protozoa and pure lines of plants, inbred lines of mice and the like. For example, Pearl (1906-1907) observed significant differences in the variation between members of different clones of the protozoon *Chilomonas*. Went (1957) published results on the members of a clone. He observed that the variance was least when the mean height was greatest. Perhaps the most comparable character studied so far in animals is by Price-Jones (1929, 1933) on the diameters of human red blood corpuscles. Here the coefficients of variation differed between normal individuals and were greatly increased in pernicious anaemia. Attfield (1951) subsequently extended this work to inbred lines of mice and confirmed the previous observations.

However, perhaps none of the previous observations are quite parallel to the present one as they were studying populations (plants or animals) whereas I was studying individual plants and over time. Dronamraju (1961) published some data on *Bauhinia acuminata* L. after my preliminary reports (1958a, 1958b, 1959) on *Nyctanthes*. He found bimodality in style length which is comparable, but not identical, with my results on leaves of *Nyctanthes*. The differences in the means of style length both between bushes and during the season are somewhat comparable with my results on the means of petal numbers. But he did not give the variance figures. For a character as well regulated as the petal number very large samples are needed. Samples of 500 flowers or less would not reveal differences of the order found. Since most work of this kind has been done on herbs no comparable observations are on record. These data are likely to open up a nearly new field of research since previous workers have seldom counted enough organs on the same plant to establish differences in the variation between different plants, still less with time.

Whatever may be the nature of the regulatory process, its efficiency can be measured. I suggest that the variance of a metrical character may be as important a property of an organism as its mean, and should be measured on a number of species.

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Summary

The distribution of tooth numbers on leaves of *Nyctanthes arbor-tristis* Linn. was approximately unimodal on five trees, The modal number being zero, and bimodal on three, the modes being zero and six to ten. The modal number of petals of flowers on 17 trees of this species was six in 16 trees and five in one. The variances as well as the means of the trees differed significantly. During a flowering season of four months the mean petal number on three trees fell by 2% to 5% and then rose again. The variances rose steadily and were from 20% to 40% greater at the end of the season than the beginning. Similar increases in variance of petal number were observed in two plants of a winter-flowering variety of *Jasminum multiflorum* over two months, and two plants of a summer-flowering variety of the same species over four months. It may be said that canalization broke down during the season in each case.

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PLATE 7

Fig. 1. Heterophyllous leaves of *Nyctanthes arbor-tristis* showing variation in numbers of teeth.

PLATE 8

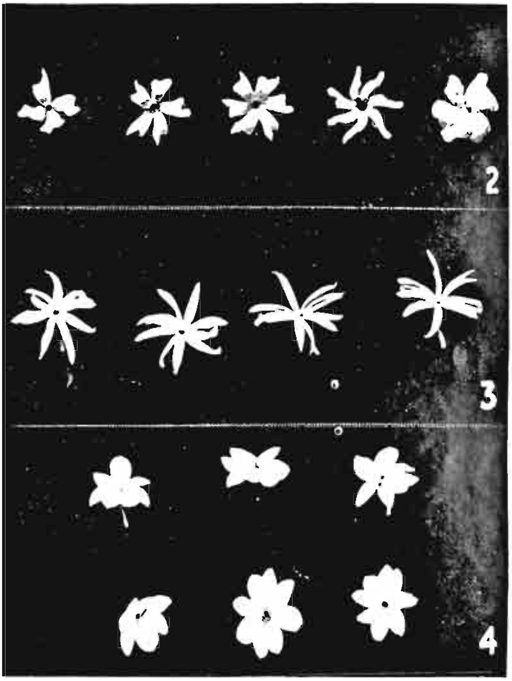

Fig. 2. Flowers of *Nyctanthes arbor-tristis* showing petal number variation.
Fig. 3. Flowers of *Jasminum multiflorum* var. *rubescens* showing petal number variation.
Fig. 4. Flowers of *Jasminum multiflorum* var. *alba* showing petal number variation.