

ON THE IDEAL VALUE OF VARYING CHARACTERS

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I. INTRODUCTION

It is a well-known fact that the leaves of each plant, and also several of its other parts, show such a wide range of diversity, that it is hardly possible to find two corresponding ones that may be regarded as fully identical.

Yet, even a superficial examination of the leaves, to confine ourselves to the latter, leads to the conclusion that, notwithstanding the enormous variability of their characters, they belong in each species to a definite type; this type is, in most cases, characteristic for particular species.

It is but natural that we should try to find a method by the aid of which this type may be recognized in the midst of this, at first sight, rather chaotic diversity. When, by the aid of this method, we have found this type, we will try to express it in a mathematical form. The linnean terminology appears to be insufficient for our purpose. Terms like: "oval, oblong, lobed, split, etc." are not sufficiently precise to deal with the numerous gradations with which we are confronted.

It is a thing of common experience that, how variable a character may be, its average value is met with, as a rule, most frequently, and is therefore its most familiar expression. Even without exact measurements, i.e. simply by direct observation, this average is therefore usually recognizable, though more or less vaguely.

In fact, it is on the ground of this experience that the characters of a species are defined, for this definition rests on the belief, that the

value that is most often met with, is representative for the species.

It is therefore a matter of course that average values are regarded as expressing certain predispositions, which are to be taken as the elements of a specific constitution.

It will be obvious, that in looking for a value that can be accepted as representative of a character in a definite species, which value we will call "the ideal value", we will have to turn our attention to the average values that are found by measuring groups of specimens. However, in order to obtain serviceable averages, it appeared to be necessary to take into account what position the parts of which the characters are studied, occupy in the general plan on which the plant is built.

When we calculated the averages of groups of measurements obtained from leaves occupying corresponding positions on the shoot, we found not only some very satisfactory values but also surprising rules. For this reason we have in the following study always compared leaves which occupy a corresponding position on the shoot. As our investigations went on, we did not confine ourselves to the leaf size, but we studied also other features that are to be observed in the leaf, as the size of the angles between various nerves and the relative length of the petiole and blade: characters of other parts of the plants too were dealt with in the same manner.

It is therefore of primary importance to arrange the parts into natural groups based on the position they occupy in the general plan of the plant: the determination of the average and of the ideal value of a character is then merely a question of measuring and calculating. Only by applying this method it appeared possible to reach our aim, viz. to find for each character the value which we regard as the ideal one.

That often a distinct relation was found between the degree of development of an organ and the position it occupies in the general plan of the organism, is not the only point that deserves our attention. An other point is that the degree of variability too proves to depend upon the position the part occupies in the organism. However, the quantitative and qualitative differences in the variability of these parts has never yet been studied with statistical methods.

This study has taught us, that it is unpractical to calculate averages from quite arbitrarily chosen material, but that the parts that are to be measured should be assembled in groups according to their morphological character, which is determined by the position they occupy in the general plan of the organism: this must be the guiding principle in statistical studies of this kind.

At first view it will perhaps seem strange that this study has not been carried out with clones or pure lines or at least with material of which the genetical constitution is more or less known.

However it should be realized that the most important aim of this study is to obtain some insight into the nature of characters as they appear in species that are met with in nature. We have tried to attain this aim by studying plants of which, on the ground of certain distinctive characters, we were convinced that they belong to a definite species.

The material has therefore, as a rule, been collected from several specifically identical plants; when it has been taken from a single plant this will always be definitely stated.

The choice of the plant species for this study was determined only by the circumstance that these plants were easily at hand: the characters were chosen in such a way that they were as different as possible and that they were easily measurable.

The method described above has not only been applied to the material that we ourselves have collected and measured but also to some series of measurements found in the literature. In this way we wished to test the validity of the rules which had been found in the study of our own material for characters that we ourselves did not investigate. The study was extended to the following characters and species:

Own investigations:

- A. Ratio between the length of various nerves in
 - a. *Acer palmatum* var. *septomlobum*.
 - b. *Acer cappadocicum*.
 - c. *Platanus acerifolia*.
 - d. *Batrachium fluitans*.
- B. Size of the angle between various nerves in
 - a. *Acer cappadocicum*.
 - b. *Platanus acerifolia*.
- C. Ratio between the length of various nerves as well as size of the angle between the nerves in
Tropaeolum lobbianum.
- D. Length of the leaf blade in
 - a. *Acer palmatum* var. *septomlobum*.
 - b. *Acer cappadocicum*.
 - c. *Platanus acerifolia*.
- E. Ratio between the length of petiole and blade in
 - a. *Acer platanoides*.
 - b. *Acer pseudoplatanus*.
 - c. *Batrachium fluitans*.
- F. Relative leaf width in
Ligustrum ovalifolium.
- G. Number of umbel rays in
Aegopodium podagraria.

Testing of the rules found in our own material on data obtained from other investigators: these data regarded:

- A. The size of the meshes between the reticulated veins in the leaf of
Vitis vulpina.

B. The relative length of the internodia in

Fagus sylvatica.

C. The ratio between the number of stomata and the number of epidermis cells in

Teucrium chamaedrys.

ACKNOWLEDGEMENTS

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II. OWN INVESTIGATIONS AND THE RULES DERIVED FROM THEM

A. RATIO BETWEEN THE LENGTH OF DIFFERENT MAIN NERVES IN THE SAME LEAF

In opposition to GOEBEL (1922) UITTEN (1928) was of opinion that the morphological character of a leaf is determined mainly by its venation and not by its outline. He expressed this view in the following way: "It is clear that morphologically it is not the outline but the venation which is of greater importance".

We fully agree with this opinion, for the outline of a leaf is, as this study has shown, primarily determined by the relative length of the nerves and by the size of the angle between them.

Several investigators have tried to detect a regularity in the varying leaf forms. However, by neglecting the structural importance of the nerves and by confining their attention to the outline of the leaf, they remained literally and figuratively on the outline of this problem.

SHULL (1905) arranged the leaf forms of *Sium cicutifolium* according to the sequence in which they appear on the stem, and he came to the conclusion that the most extreme forms are met with in the lower leaves, whereas the variability reaches its lowest value in the upper leaves of the stem. But he only paid attention to the outline of the leaf and he did not at all consider the venation. By this oversight the building plan of the leaf, on which all the varying forms are founded, remained hidden to him.

The same applies to the study which HAMMOND (1941) made of the variability in *Gossypium*.

SMIRNOV and ZHELOCHOVTSSEV (1931) too failed to recognize the structural importance of the venation when they studied the venation of the leaf form in *Tropaeolum majus*. Aside from the fact that they wrongly interpreted the changes in the outline of the growing leaf as conchoidal, they mistakenly regarded the leaf as built up of a number of fields that each are enclosed by two of the main nerves. However it is much more plausible to regard this leaf as composed of fields that are equally developed on both sides of a main nerve; this means that the part enclosed between two main nerves can structurally not be considered as an entity, but forms a combination of two half fields; therefore, as their calculations are based on a view which disregards the real structure of the leaf, their value is to be considered as highly doubtful. AHSBY (1948) ironically remarks: "This is a somewhat Procrustean treatment of the data" (p. 157.), and this seems hit the mark.

A similar objection can be made against THOMPSON (1917) who in discussing the leaf form divides the leaf in sections by arbitrary lines, which intersect the venation. He bases his conclusions regarding the development of the leaf on the changes which these arbitrary sections undergo, disregarding the fact that the leaf form is determined mainly by the venation.

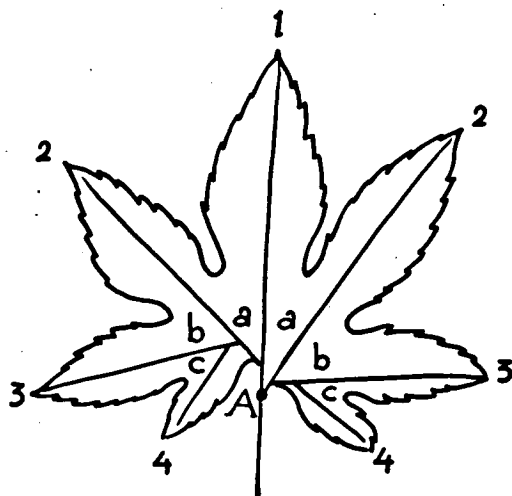


Fig. 1. Indication of the nerves and of the angles between the nerves in a palmatifid leaf. (*Acer palmatum* var. *septemlobum*)

In the conviction that the venation is of primary importance for the form of the leaf, our investigations were in the first place directed to the ratio between the length of the various nerves in several plant species: our principal aim was to find for each plant species a constant value for this ratio.

a. Ratio between the length of the main nerves in the leaf of *Acer palmatum* var. *septemlobum*

The length of the nine main nerves was determined in some hundreds of leaves of this type. The leaves were arranged in groups in according to the position they occupied on the shoot: the nerves were numbered as indicated in Fig. 1.

Further, the length of the nerves 2, 3, and 4 is expressed in percents of that of nerve 1. For this purpose we always took the average length of the two corresponding nerves in the right and in the left half of the leaf.

In this study the sequence in which the leaves are inserted on the shoot is always taken in consideration: the lowest leaf or leaf pair of each shoot is in this study always indicated by the letter "A"; the following one by "B", etc.

When we speak of a higher leaf we always mean a leaf that is inserted higher on the shoot. The word "higher" does not mean that the leaf to which it is applied, is "higher" developed or shows a higher ratio between the length of the lateral main nerves and the central one. As we will see in the course of this study there is in this respect a striking contrast between the leaves of the *Acer* and *Platanus* species.

From leaf class "A" 200 leaves were measured, and these were classified according to their size in 4 groups of 50 leaves: apart from these we measured 50 leaves of each of the leaf classes B, C, E and G, selecting the largest ones, and of the leaf class F 50 leaves of the smallest and 50 leaves of the largest size.

The average length of the nerves 2, 3 and 4 expressed as a percentage of that of nerve 1 was calculated for each group of leaves and these values are given in Table I.

TABLE I
Relative length of the lateral main nerves in the leaves of *Acer palm. sept.*

Position of the leaf	Size group	Number of leaves per group	Aver. length nerve 1 in mm	Aver. length in per cents of nerve 1		
				Nerve 2	Nerve 3	Nerve 4
A	I	50	33	90	65	35
	II	50	42	91	67	38
	III	50	50	91	68	39
	IV	50	56	92	69	40
B		50	48	84	45	19
C		50	52	85	52	19
E		50	45	86	41	19
F	I	50	34	73	38	—
	II	50	49	79	41	—
G		50	39	71	37	—

In considering these results one has to distinguish between ontogenetic development (the growth of a leaf from its first appearance

until it has reached its ultimate size: compare the 4 size groups of leaf class A) and the morphological differentiation. In order to obtain an insight in the latter we should compare the final stage of leaves inserted in different positions on the shoot; viz. the largest leaves of classes A to G. Among the leaves of class A the 50 of size group I remained rather small. We may safely assume that these leaves would have grown no more as they were collected towards the end of the summer, i.e. at a time when all normal leaves are since long full-grown.

The size group II and III form gradual transitions to size group IV: the 50 leaves of these size groups were (nearly) full-grown, not alone ontogenetically but also morphologically: this means that they had attained the highest stage of development that a leaf in the position A can attain.

When we compare the 4 size groups of leaf class A we notice a slight increase for each nerve. The smallest value is found for nerve 2. The maximum is reached in group IV, viz. for nerve 2: 92 %, for nerve 3: 69 %, for nerve 4: 40 %.

This rather striking constancy in the nerve length ratio appears already when the leaves are studied in the bud. To this end the relative nerve lengths of leaves of class A were determined with the aid of a drawing prism: in these leaves the length of nerve 1 proved to vary from 470 μ to 950 μ . The average nerve length ratio was here for nerve 2: 94 %, for nerve 3: 65 % and for nerve 4: 32 % (Table II).

TABLE II

Relative length of the lateral main nerves in leaves of class A in buds of *Acer palm.* var. *sept.*

Number of leaves	Aver. length nerve 1 in μ .	Aver. length in per cents of nerve 1		
		Nerve 2	Nerve 3	Nerve 4
10	474	94	66	31
10	558	96	69	36
10	626	95	67	34
10	744	93	60	27
10	904	90	65	34
Aver. 50	661	93,6	65,4	32,4

Comparison of these figures with those of Table 1 shows that the relative length of the nerves 2 and 3 has already attained its final value when the leaf has reached a length of circ. 0,5 mm, but that the relative length of nerve 4 increases considerably during the growth of the leaf.

It is rather difficult to recognize in these leaf primordia the point where the nerves begin, but in view of the quite satisfactory agreement between the figures, the values given in Table II impress us as trustworthy.

From these data the conclusion may be drawn that the form of the leaf in this *Acer* species undergoes little or no change during its ontogenetic development.

The question whether it is admissible, as we have done here, to conclude from differences in the averages found for small and large leaves to a change in the form of "the" leaf of a species, will be discussed furtheron (p. 296).

When we compare ontogenetically full-grown specimens belonging to the leaf classes A to G it appears that the averages of the nerve length ratio show a considerable decrease; the value for nerve 2 has decreased with $\pm 1/5$; that for nerve 3 with $\pm 1/2$: and nerve 4 becomes so short that it is in the higher leaves no longer accurately measurable.

The average nerve length ratio reaches its highest value in the full-grown leaf of class A. This leaf type shows the highest possible degree of development in the ontogenetic as well as in the morphological sense.

We can recognize a series of morphological stages which have their climax in the leaf class A and show from there to leaf class G a gradual decline; in leaf G appears an anti-climax. This decline from base to top can be called "kathodic".

We will see furtheron that in some other plant species it is on the contrary leaf class A in which the lowest figures are found for the average nerve length ratio, whereas the highest values are reached in the higher leaves; for such an ascending morphological series we will use the term "anodic".¹

Estimation of the measuring errors

Unavoidable errors are made in all our measurements. In the first place in determining the place of origin of the nerves we often make an error of 1 or 2 mm. Moreover the origin of nerve 2 is very often higher at one side of the leaf than at the other. In order to follow everywhere the same line of conduct we have always taken the point where the lower nerve 2 branches off from nerve 1 as the point of origin (point A in Fig. 1).

In addition to this the nerves, especially in full-grown leaves, are very often slightly bent; this always caused a measuring error of some mm. In leaves of 100 mm or more an error of 1 or 2 mm has little importance: however in leaves that are smaller than 20 mm it reaches a value of 5 % or more.

Nevertheless it is not reasonable to suppose that these errors in the hundreds of measurements should all have been made in the same direction. In such large numbers of measurements the positive errors will be compensated by the negative ones. Therefore it seems admissible to assume that the inevitable measuring errors not have had an influence of importance in our calculations of the average.

¹ These terms are taken from a quotation of Heraclitus (fragm. 76. Diels.) „μεταβολὴν ὁρᾷς σωμάτων καὶ γενέσεως ἀλλαγὴν, ὁδὸν ἀνω καὶ κάτω.” “You see changes of bodies and reversal of genesis — a way upwards and downwards”. I owe these terms to H. Höppener, litt. class. dr. (Eindhoven): they express the idea very adequately.

Standard deviation and variation coefficient

All the foregoing conclusions have been based on averages calculated from a number of percentages, i.e. of a number of variates. In order to estimate the magnitude of this variation (the variation width) the standard deviation of these averages was calculated by

means of the usual formula $SD = \pm \sqrt{\frac{\sum^n (x_i - \bar{x})^2}{n(n-1)}}$.

x_i is the value found as average of all the variates and \bar{x} is the value of the individual variate: n is the number of variates. The values found for the SD of the nerve length ratio in the various groups were not directly comparable, for when we find for the SD e.g. a value of 0,5, it makes a great difference whether the relative nerve length is 90 % or whether the latter is 30 %: in the last case the relative importance of the SD is thrice greater than in the first case.

In order to obtain comparable figures we have calculated each time the relative value of the SD, i.e. the value that is known as the variation coefficient (VC) and that is calculated by means of the formula $VC = \frac{100 \times SD}{\text{average}}$.

In the further course of this study we will give the VC for each average as this is a useful measure of the variation width.

However in comparing the values found for the VC it should be born in mind that this should be based on the same number of variates: the value of the SD, and therefore that of the VC too, depends partly on the number of variates. For the magnitude of the numerator in the formula of the SD depends on n and that of the nominator on the square of n , or to be more exact, on $n(n-1)$.

With an increase of n the denominator increases more rapidly than the numerator, with the result that the SD and the VC decrease. In order to obtain comparable values for the VC it is necessary that the groups consist as much as possible of an equal number of leaves. However, when it was impossible to work with groups consisting of an equal number of variates, the following method was applied.

Assuming that the SD of a group of 50 variates was to be compared with that of a group of 100 variates the value obtained in the latter case for the numerator was divided by $\frac{100}{50} = 2$, whereas that of the denominator was divided by $\frac{100 \times 99}{50 \times 49} = 4,041$: from the figure that was obtained in this way the square root would have to be taken. In our example this means that the value calculated for the VC of 100 leaves is to be multiplied by $\sqrt{2,02}$, or roughly by 1,4. In our opinion this is a fully justified procedure when the VC of groups consisting of an unequal number of variates are to be compared.

In Table III the values found in *Acer palmatum* var. *septemlobum* for the SD and the VC of the average nerve length ratio in the leaf classes A and F are given. It appears from this table that the VC decreases when

1) the leaf approaches the end of its ontogenetic development, i.e.

when it reaches its largest size (compare the value found for the nerve length ratio in the different leaf size groups belonging to the two leaf classes)

2) we proceed to the leaf that belongs to the class in which the highest average values are found (compare the leaf classes A and F)

3) when we proceed to the nerve length ratio which shows the highest average value (compare the nerve length ratio for the nerves 2 and 3).

TABLE III

Values found in *Acer palm. sept.* for S D and V C of the average nerve length ratio in leaves belonging to the classes A and F.

Position of the leaf	Number of leaves in size groups	Value of S D				Value of V C		
		Aver. length nerve 1 in mm	Nerve 2 % S D	Nerve 3 % S D	Nerve 4 % S D	Nerve 2	Nerve 3	Nerve 4
A	50	0,66	94 0,81	65 1,23	32 1,10	0,87	1,90	3,40
	50	33	90 0,64	65 0,84	35 0,84	0,71	1,26	2,40
	50	42	91 0,53	67 0,80	38 1,20	0,58	1,22	3,20
	50	50	91 0,55	68 0,53	39 0,73	0,60	0,77	1,90
	50	56	92 0,38	69 0,42	40 0,53	0,41	0,62	1,31
F	50	34	73 1,20	38 0,58		1,60	1,55	
	50	49	79 0,77	41 0,35		0,98	2,08	

Summarizing we may say that the lowest V C of the nerve length ratio was found in the nerve that shows the highest degree of development in an ontogenetic as well as in a morphological sense: in this species it is nerve 2 in full-grown leaves of class A.

The figures given in this table also show that the V C decreases as the average approaches its highest value.

It is of little or no importance that in the regularity with which the series of V C's decreases occasionally a small irregularity occurs (nerves 3 and 4). The absolute figures are not so much of importance as their decrease or increase, and as the place where the lowest value of the V C is found.

The high figure of the V C indicates a high degree of variability in the length of the nerves 3 and 4, but when among such a relatively small number of variates extreme plus- or minus-values occur, the V C will attain even a higher value than one would have expected. However, the general trend of the descending course of the V C parallel to the increase of the average nerve length ratio is not obscured by such occasional irregularities.

The final aim of this study is to determine the optimum degree of development and the value shown by the V C at that stage. It is of little importance to determine the value of the V C's for all those groups of leaves which do not show the optimum degree of development: it will be sufficient to show that they have a higher V C, and

it does not matter how high the latter precisely is. The lowest V C is a diagnostic criterium, and perhaps the most important one, by which the optimal degree of development can be recognized.

A more precise definition of the optimum degree of development

The results of certain studies, which will be communicated further on, raised the question whether the degree of development of the shoot as expressed in the number of leaf pairs, might perhaps have some influence upon the development of the nerves and on their variability, i.e. on the nerve length ratio and its V C.

The leaves of this species grow always in pairs and the number of leaf pairs on each shoot proves to vary considerably. There are shoots with 1, 2, 3, 4 or even more than 6 of leaf pairs. In order to find out whether there is some relation between the nerve length ratio and the number of leaf pairs per shoot, we have calculated the average of nerve length ratio for the nerves 2, 3 and 4 in 6 groups each consisting of 100 leaves belonging to class A as they occur in shoots with respectively 1, 2, 3, 4, and more than 6 leaf pairs (Table IV).

TABLE IV

Average nerve length ratio with its V C in leaves of *Acer palm. var. sept.* belonging to class A and inserted on shoots with 1, 2, 3, 4 and > 6 leaf pairs.

Number of leaf pairs on the shoot	Number of leaf pairs per group	Nerve 1		Nerve 2		Nerve 3		Nerve 4	
		in mm	V C	%	V C	%	V C	%	V C
1	100	45	1,4	89,7	0,32	66,0	0,67	36,6	0,95
2	100	45	0,96	91,4	0,36	70,0	0,73	40,0	1,10
3	100	50	0,68	92,1	0,30	72,4	0,53	40,8	0,90
	100	48	0,71	91,9	0,30	70,6	0,40	39,7	0,88
	200	49	*0,70	92	*0,30	71,5	*0,46	40,2	*0,89
4	100	50	0,74	92,2	0,38	70,7	0,60	38,2	0,97
> 6	100	53	1,13	93,5	0,34	73,7	0,66	41,8	1,50

* V C, if necessary adjusted to a basic number of 100 variates.

It appears from the figures of this Table that the average length of the nerve 1 as well as the average nerve length ratio for the nerves 2, 3, and 4 increase with the number of leaf pairs per shoot.

However, if we look at the figures of the V C than it appears that the leaves of shoots with 3 leaf pairs show the lowest V C : as a control a second group of 100 leaves was studied.

The figures for the average length of nerve 1 as well as those for the nerve length ratio for the nerves 2, 3 and 4 and those for the V C show in these two groups of 100 leaves, especially for nerve 2 and 4, a very good agreement. This strongly corroborates our supposition that these figures may be considered as a trustworthy reflection of a natural relation: that the variation width has reached here its lowest value demonstrates that the leaf shape approaches here its ideal value.

In our first set of investigations we found that the variability of a character decreases as the latter approaches ontogenetically and morphologically its final value. Therefore we concluded that the variation width is a criterium for the rate of development in this sense that a lower degree of variability corresponds to a higher degree of development. The nerve length ratio of the leaves belonging to class A and produced by shoots with more than 6 leaf pairs shows indeed the highest value, but their variability is greater than that found in leaves of shoots with 3 leaf pairs.

However, when we stick to the rule that the ideal value always goes with the lowest width of variation, we come to the conclusion that the nearest approach to the ideal value is found in the leaves produced at the base of shoots with 3 leaf pairs.

We prefer the latter solution and we disengage ourselves therefore from the idea that the highest value of a character is identical with or the nearest approach to the ideal degree of development, i.e. to the degree of development which best expresses the nature of the species.

Although we originally (p. 282) formulated our conclusion in this way that the lowest degree of variability is a criterium, and perhaps the most important one, of the highest average value that a character may reach, it now appears more appropriate to express it in the following way: *the lowest degree of variability (V C) is pre-eminently the criterium of the ideal value of a character.*

Therefore, we come to the conclusion that the ideal value of the nerve length ratio in the leaves of *Acer palmatum* var. *septemlobum* is that which is exhibited by the leaves of class A in shoots with 3 leaf pairs, and that it comes for nerve 2 to 92 %: for nerve 3 to 71,5 %: for nerve 4 to 40,2 %.

The predisposition

From the data of Table I it appears that the leaves that occupy corresponding positions on the shoot form groups in which the nerve length ratio oscillates round a definite average. In each leaf and for each character of the latter a predisposition must be accepted that is determined by the position of the leaf; a local predisposition, therefore, that finds its expression in the figure of the average. In leaf groups that occupy different positions the local predispositions are different; in each of them the characters show their own average.

As the nerve length ratio of individual leaves occupying corresponding positions on the shoot and belonging, therefore, to the same group may deviate rather far from the average, and as the average value found in groups consisting of leaves, that occupy a different position, may sometimes be very close to each other, it is evident that repeatedly leaves will be found with the same nerve length ratio and which nevertheless belong to different groups. These leaves show the same phaenotype but possess a different predisposition.

It is possible to construct a continuous series of values for the nerve length ratio descending from the most extreme plus-variate in a leaf belonging to class A to the most extreme minus-variate in a leaf

belonging to class G (or perhaps to class H or I.)—a complete series of gradual transitions from the highest to the lowest value.

Because of this series of transitions UTTIEN (1939) regards it as impossible to express a specific character in a figure. He says: "It is impossible to express in figures the number of types, for there are complete series of transitions. Reference to a definite type is a question of judgement, that is to say, it is necessarily subjective. This entirely deprives the statistical method of its value." (p. 468).

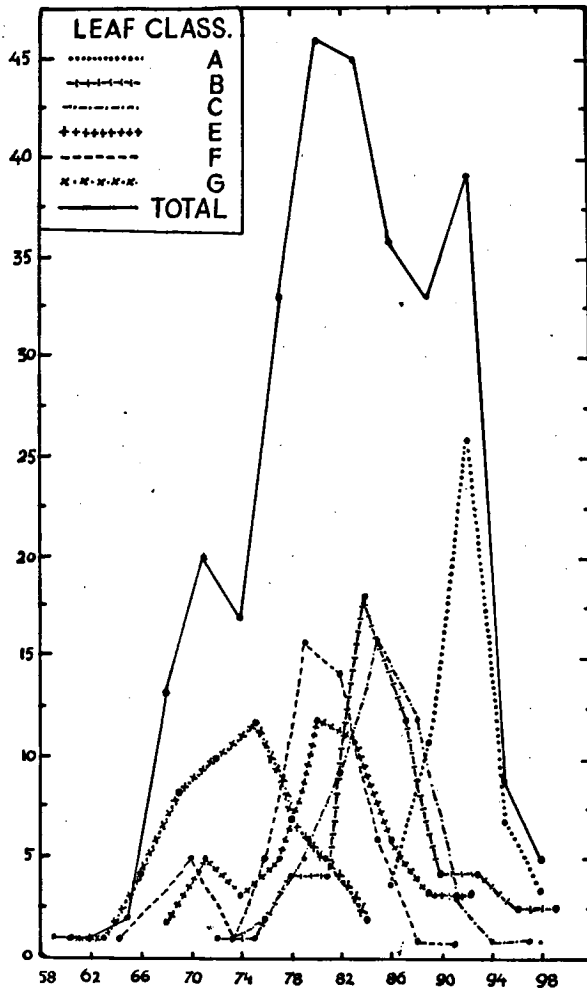


Fig. 2. Nerve length ratio for nerve 2 in per cents measured in groups at 50 leaves belonging to the classes A, B, C, E, F and G and in all these leaves together. Horizontal: Value of the nerve length ratio in per cents.

Vertical : number of leaves in the various classes. (*Acer palmatum* var. *septemlobum*)

The preceding exposition definitely shows that this is an underestimation of the value of the statistical method and, therefore, unacceptable. Indeed, when we collect indiscriminately leaves that occupy different positions on the shoot, than, as we will demonstrate now, it will be impossible to find a significant average.

In order to find out what the result would have been when leaves that occupy different positions on the shoot should have been collected (this is how UITTEN thought that the statistician would obtain his material), we have separately plotted in curves the figures of the nerve length ratio found for nerve 2 in 6 groups each consisting of 50 leaves that respectively belonged to the classes A, B, C, E, F and G (the averages calculated for these groups have been given in Table I), and in addition to these 6 curves we have given a curve comprising all these 300 leaves: in this last-named curve, therefore, the leaves belonging to the classes A, B, C, E, F and G have all been brought together so that the significance of the position they occupy on the shoot has been obliterated (Fig. 2).

We see in this graph that the 6 curves representing leaves belonging to different classes have each but a single top, and that the top of the curve which represent the leaves belonging to class A attains the highest level. The curve that represents the whole lot, on the contrary, shows more tops, and is very irregular. This irregularity is all the more significant as this curve is based on a larger number of leaves, so that we might have expected a greater regularity.

This clearly demonstrates that the curve representing the 300 leaves cannot be regarded as the expression of a homogeneous material, and that its average, therefore, is not to be taken as expressing a definite predisposition: the whole group might be compared to a population, whereas the 6 classes of leaves A to G have the character of pure lines.

The arrangement of the leaves in groups is not arbitrary but was based on our conviction that the leaves possess a certain predisposition that is determined by the position they occupy on the shoot.

It is, of course, impossible to observe this predisposition directly, but this applies to every predisposition. What we observe are differences between the various specimens, in which each time one of the possibilities is realized, but in order to recognize the predisposition it is necessary to apply the described method.

Our final conclusion is that for characters such as the nerve length ratio a definite predisposition is present, which finds its expression in the ideal value and can be expressed in a figure.

b) *The nerve length ratio in leaves of Acer cappadocicum Gled.*

In order to find out whether the rules which were derived from the data given in the foregoing study have a general validity, the nerve length ratio was studied in the same manner in the leaves of another *Acer* species.

The leaves of this species possess, no matter what position they occupy on the shoot, but 5 clearly recognizable main nerves: the

number of the leaf pairs in each shoot is also more limited: leaves of class E are found but seldom.

For a first orientation, i.e. without paying attention to the number of leaf pairs in each shoot, the average nerve length ratio was calculated for two groups of 50 leaves belonging respectively to the classes A and C (Table V).

TABLE V
Nerve length ratio in the leaves of *Acer cappadocicum*.

Position of the leaf	Number of leaves	Aver. length of nerve 1 in mm.	Aver. nerve length ratio in per cents of nerve 1	
			Nerve 2	Nerve 3
A	50	85	92,6	66,8
C	50	65	86,6	55,4

The figures for the average nerve length ratio form just as in the leaves of *Acer palm. sept.* a cathodic series, i.e. the highest average is found in the leaves of class A.

To determine this highest average with greater precision the average nerve length ratio was calculated in 3 groups each of 100 leaves belonging to class A in shoots with resp. 2, 3, and 4 leaf pairs (Table VI).

TABLE VI
Nerve length ratio in leaves belonging to class A in shoots with 2, 3 and 4 leaf pairs of *Acer cappadocicum*

Number of leaf pairs in the shoots	Number of leaves	Average length Nerve 1		Average nerve length ratio			
				Nerve 2		Nerve 3	
		in mm	V C	%	V C	%	V C
2	100	67	2,20	91,3	0,32	69,0	0,88
3	100	80	0,66	92,7	0,27	69,9	0,54
4	100	83	1,07	92,7	0,30	67,7	0,67

The leaves on the shoots with 1 leaf pair are so small that one can say beforehand that the highest value will not be found here, and for this reason they were discarded.

In this species too the leaves of shoots with 3 leaf pairs show not only the highest average nerve length ratio for nerve 2 as well as for nerve 3, but also the lowest V C. Here, therefore, the ideal value of the nerve length ratio is found, and it amounts for this species for nerve 2 to 92,7 % and for nerve 3 to 69,9 %.

Both *Acer* species show, therefore, a striking resemblance in the position of the leaves with the ideal value, as the highest average as

well as the lowest V C are found in the same leaf class. The average nerve length ratio is different for each species, and this value is, therefore, to be taken as characteristic for the species.

c) *Nerve length ratio in the leaves of Platanus acerifolia W.*

At first view it seems that the leaves of this species are very different in form according to the position they occupy at the shoot: most of the leaves belonging to class A are more or less elliptic or ovate, whereas the higher leaves become more and more distinctly palmatifid.

This difference is however more apparent than real, for at a closer examination it appears that in most cases the leaves belonging to class A have a distinctly palmate venation. However, as the nerves are here as yet ill-developed and as the angles between the nerves are small, in most cases the outline of these leaves is unbroken and forms a nearly perfect oval.

Here UTTIEN's idea, that the venation is of primary importance for the leaf form comes to full play; it offers us here a means to reduce all the leaves of this species to the same ground plan, no matter what their outline may be; they are all palmately nerved. In measuring the nerves of this species the same difficulties occur as in the leaves of the *Aceraceae* and they have been solved in the same manner.

The value of the average nerve length ratio and of the latter's V C for leaves occupying successive positions on the shoots are given in Table VII.

TABLE VII
Nerve length ratio and V C in the leaves of *Platanus acerifolia*

Position of the leaf	Number of leaves	Length nerve 1 in mm	Nerve length ratio			
			Nerve 2		Nerve 3	
			%	V C	%	V C
A	100	18-36	75	1,53		
	100	36-46	73	1,18		
	100	70-83	72	1,23	48	3,19
	100	82-125	76	1,05	50	2,35
E	100	18-100	84	0,47		
	100	160-250	82	0,38		
G	100	110-165	85	0,52	65	0,77
	100	165-210	83	0,37	64	0,64
I	100	140-175	85	0,45	65	0,65
	100	175-220	83	0,38	66	0,56

A comparison of these figures shows that the average nerve length ratio for the nerves 2 and 3 as determined for leaves occupying a definite position on the shoot remains practically the same, no matter to which size group the leaves belong; differences of 1 or 2 % are negligible.

The form of the leaves undergoes little or no change during the ontogenetic development.

When we compare the full-grown leaves occupying different positions on the shoot, we notice a clear contrast between this species and the *Aceraceae* studied above: the average nerve length ratio shows here the lowest value in leaf class A, whereas the highest value is attained in leaves that occupy a higher position on the shoot; the successive values for the average show in this species an "anodic" series.

We see in the ontogenetic development of the leaves (compare the smallest and the largest leaves occupying corresponding positions on the shoot) and also as we proceed to higher stages in the morphological series (compare the full-grown leaves occupying successive positions on the shoot, from leaves belonging to the class A to those belonging to the class G (or, eventually, I) a decrease of the V C which reaches its lowest value in leaves belonging to class G.

To determine the highest average value for this species with greater precision the values for the average nerve length ratio and their V C were calculated, first for 100 leaves belonging to class E on shoots with a leaf E as top leaf, and next for 100 leaves belonging to the same class in shoots with leaf G (or a leaf belonging to a higher class) as top leaf.

Furthermore 100 leaves belonging to class G were measured in shoots with a leaf G as top leaf and twice 100 leaves of class G in shoots with a leaf I (or a higher leaf) as top leaf. Finally 100 leaves of class I were measured in shoots with leaf I (or a higher leaf) as top leaf (Table VIII).

TABLE VIII

Nerve length ratio and V C in definite leaves of *Platanus acerifolia* in shoots with a different number of leaves.

Position of the leaves	Class to which the top leaf of the shoot belongs	Number of leaves	Nerve 1		Nerve 2		Nerve 3	
			in mm	V C	%	V C	%	V C
E	E	100	160	0,90	82	0,46	59	1,0
	> G	100	175	0,78	83,5	0,39	62	0,92
G	G	100	160	1,25	83,3	0,40	63	0,75
	> I	100	181	0,80	83,0	0,38	63	0,60
		100	171	0,70	83,6	0,37	63,8	0,56
I	I	100	146	1,45	83,4	0,48	62,7	0,61

From these figures it appears that in the leaves belonging to class E the average nerve length ratio shows a slight increase when the number of leaves on the shoot increases: this increase is accompanied by a diminution of the V C.

The average nerve length ratio in the leaves G show the same value: the V C reaches its lowest value in the shoots with the largest number

of leaves. To check the results we have calculated the average values and their V C for two groups of 100 leaves of this last class. The figures obtained for these two groups show a striking similarity, those for the averages as well as those for the V C. The leaves of class I show nearly the same average values as the leaves of class G, but their V C is higher. This last fact indicates that we cannot regard these leaves as the ideal ones. On the ground of the value of the V C we must accept the value found for the leaves of the class G as the ideal one; it amounts for nerve 2 to 83,3 % and for nerve 3 to 63,4 %.

It is not excluded that the degree of development of the tree has some influence on this ideal value: the V C might be lower in trees which have attained the fullest development. In trees which were in the period of their greatest vigour much more shoots with a larger number of leaves were noted than on trees which already had reached their ultimate height, which were, so to speak, in the autumn of their life.

It is not to be expected that the oldest trees will show the ideal value, no more than that the ideal value of the nerve length ratio is found in the leaves of class I.

However, as no sufficient trees of different age were found in our neighbourhood, we could not study this question.

d) *Nerve length ratio in the leaves of *Batrachium fluitans* Lam.*

This waterplant has stems with a length of 3–4 m and with up to 25 alternate leaves. The submerged leaves consist of the nerves only: there is practically no mesophyll. We never found floating leaves: they are in this species extremely rare.

It is very difficult, and sometimes even impossible, to determine the exact position of the leaves on the shoots, for it is often excluded to determine with some degree of accuracy which leaves belong to "leaf class A".

The stems of these plants are rooting on the lower nodes, and they are in this manner attached to the sandy bottom of the little streams in which they occur. It often happens that leaves are found at the first nodes above the bottom, but sometimes they do not occur below the third node. In such cases it is impossible to decide whether the leaves at the foregoing nodes have already disappeared, as the first leaves die early in the year.

Because of this uncertainty a margin of 2 or 3 leaves should always be allowed in determining the position. For this reason the leaves were arranged in 5 groups: the 100 leaves of each group belong to at least 3 successive classes, viz.

Group I	comprising leaf classes A, B, C.				
" II	"	"	"	"	D, E, F.
" III	"	"	"	"	G, H, I.
" IV	"	"	"	"	J, K, L.
" V	"	"	"	"	M–W.

Each leaf is composed of 3 main nerves: the central one is small and thin (nerve 1); the 2 other ones are longer and thicker (nerve 2) (Fig. 3).

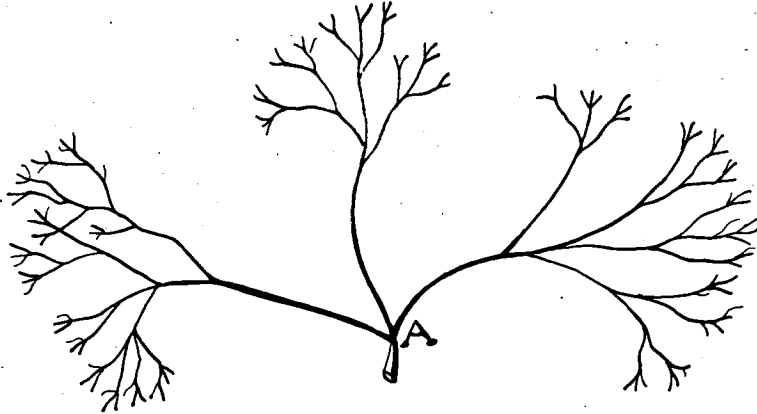


Fig. 3. Leaf of *Batrachium fluitans*. (A: point of origin of the nerves.)

When the leaves are taken from the water for measuring, the ramifications of the 3 main nerves fall together in the form of a brush. In order to measure the length of the nerves the point A, where the 3 main nerves separate, is always taken as the beginning of the nerves and the brush at the top as the end.

The average nerve length ratio for the 50 smallest and for the 50 largest leaves of each group and their V C is given in Table IX. It appears from this table that nerve 1 attains its greatest length in group III, and that there is but little difference between the average nerve length ratio of the 50 smallest and of the 50 largest leaves of each group.

TABLE IX
Nerve length ratio and V C in leaves of *Batrachium fluitans*

Group	Position of the leaves	Number of leaves	Length of nerve 1 in mm	Nerve 2	
				%	V C
I	A.B.C.	50	41-92	123	1,42
		50	130-192	120	1,38
II	D.E.F.	50	41-95	126	1,38
		50	171-216	119	1,08
III	G.H.I.	50	49-142	123	1,69
		50	175-241	120	1,18
IV	J.K.L.	50	44-139	118	1,38
		50	172-233	119	1,02
V	M.-W.	50	20-107	111	1,43
		50	129-216	118	1,02

Comparison of the largest leaves too fails to reveal a marked difference. We can determine therefore the nerve length ratio for all leaves at 119 %.

In each group the average of the 50 largest leaves shows a lower V C and in groups IV and V the V C is the lowest of all. It should be realized that group V comprises the 14-th to the 24-th leaf on the shoot, and this corroborates our opinion that the ideal value of the nerve length ratio is to be found here. We can accept in the leaves of this species on account of the figures for the V C an anodic series.

Sufficient material was collected (it is not of importance for the present to determine the ideal value more precisely) to yield a basis for comparing the variability of the leaf blade with that of the petiole, which will be discussed furtheron.

II. B. THE SIZE OF THE ANGLE BETWEEN THE NERVES

The size of the angle between the nerves of the leaves has also been subjected to a statistical investigation in order to find out whether the rules which pertain to the nerve length ratio are applicable to this character also.

In this study the successive position of the leaves on the shoot has strictly been observed. The angles are called "a, b, c" as is indicated in Fig. 1.

The precise measuring of these angles was often very difficult, especially in full-grown leaves where the nerves are generally rather strongly curved. For this reason the angles have always been measured at the origin of the nerves and not they were derived from the arc at the circumference of the leaf.

Though these angles could rarely be measured with a measuring error of less than 2 or 3 degrees, it is, because of the rather great number of leaves that we have measured, to be expected that the plus and minus deviations will have counterbalanced each other.

TABLE X

Average value of the angle between the nerves in leaves belonging to the classes A and C in *Acer cappadocicum*.

Positions of the leaves	Number of leaves	Nerve 1 in mm.	Angle a		Angle b	
			in degrees	V C	in degrees	V C
A	50	38	45,4	1,4	44,6	2,2
	50	50	43,6		42,6	
	50	65	39,4		39,5	
	50	84	37,0	0,95	36,5	1,6
C	50	32	51,4	1,4	53,6	2,4
	50	46	48,4		49,5	
	50	63	46,2	1,2	45,9	2,1

a) *The size of the angle between the nerves in the leaves of Acer cappadocicum*

As in the leaves of *Acer palmatum* var. *septemlobum* the angles between the nerves are rather small, those of *Acer cappadocicum* with their 2 large angles between the nerves were chosen for this study.

The result of the measurements of groups of 50 leaves belonging to the classes A and C is given in Table X. In the first place it is clear that both these angles in leaf class A as well as in leaf class C decrease as the leaf increases in size and that leaf class C always shows a larger angle than leaf class A. The V C is always lower in the larger leaves than in the smaller ones. The decrease of the V C is here too to be taken as expressing an approach to the ideal value. In order to determine the ideal value of these angles with greater precision, they were studied also in shoots with resp. 2, 3 or 4 leaf pairs (Table XI).

TABLE XI

Average values of the angle between the nerves and their V C in leaf class A on shoots of *Acer cappadocicum* with 2, 3 and 4 leaf pairs.

Number of leaf pairs in the shoots	Number of leaves	Nerve 1 in mm	Angle a		Angle b	
			in degrees	V C	in degrees	V C
2	100	67	39,9	0,88	39,2	0,84
3	100	80	37,7	0,58	34,0	0,65
4	100	83	35,7	0,58	33,4	0,82

From the figures of this table it appears that the angle between the nerves shows the lower V C in leaf class A on shoots with 3 leaf pairs, i.e. at exactly the same place where the lowest V C for the average nerve length ratio was found (Table VI).

For this reason we determine the ideal value of the angles in this species for angle a at 38 degrees and for angle b at 34 degrees.

b) *The size of the angle between the nerves in the leaves of Platanus acerifolia*

In the same manner as in the foregoing species the average value of the angles a and b were measured in this tree (Table XII).

It appears from this table that these angles decrease but little during the ontogenetic development of the leaf, whereas the V C shows a well-marked decrease.

In the same manner as in our study of the nerve length ratio the angles in leaves belonging to the classes E and G were measured in shoots with a different number of leaves in order to determinate the ideal value of these angles with more precision (Table XIII).

Here it appears that with an increase in the number of leaves per shoot also an increase occurs in the average size of the angles between the nerves, whereas the V C at the same time shows a decrease. The values with the lowest V C can be taken as representing the ideal size of the angle in this species. Thus the ideal value for angle a proves to

TABLE XII

Average size of the angle between the nerves and their V C in the leaf classes A, E, and G in *Platanus acerifolia*.

Position of the leaves	Number of leaves	Nerve 1 in mm	Angle a		Angle b	
			in degrees	V C	in degrees	V C
A	100	24	40	1,45		
	100	42	39	1,49		
	100	76	40	1,33	33	2,9
	100	105	39	1,16	35	2,8
E	100	170	45	0,66		
G	100	135	48	0,68	40	0,75
	100	175	47	0,65	39	0,69

TABLE XIII

Average size of the angle between the nerves in leaves of the classes E, G, I in shoots with a different number of leaves in *Platanus acerifolia*.

Position of the leaves	Class to which the top leaf of the shoot belongs	Number of leaves	Nerve in mm	Angle a		Angle b	
				in degrees	V C	in degrees	V C
E	E	100	160	45	0,66	39	0,92
	> G	100	175	46	0,59	40	0,85
G	G	100	160	46,4	0,55	36,0	0,76
	> I	100	181	46,4	0,61	38,6	0,55
		100	171	48,2	0,62	40,2	0,49
I	I	100	146	52,2	0,61	41,9	0,50

be 47,3 degrees and that for angle b 39, 4 degrees, and these values are found in leaves belonging to class G in shoots in which the top leaf belongs to leaf class I (or to a higher class).

Finally it appears that in the leaves of *Acer* the largest angle is accompanied by the highest V C, whereas in the leaves of *Platanus* the largest angle shows the lowest V C. The absolute size of the angle, therefore, can not be taken as indicating the degree of the development. However, when we see that, as a leaf increases in size and thus attains a higher degree of development, the V C of its angle decreases, than the conclusion is admissible that here too the lowest V C is a criterium for the highest degree of development of the character, i.e. for what we have called its ideal value.

It seems justified, therefore, to determine the ideal value of the angle between the nerves in the leaves of *Platanus* as we have done above, i.e. on account of its lowest V C.

II. C THE NERVE LENGTH RATIO AND THE SIZE OF THE ANGLE BETWEEN THE NERVES IN LEAVES OF *Tropaeolum lobbianum* Veitch

In all the preceding investigations we have regarded the equality or inequality of the average nerve length ratio and of the size of the

angle between the nerves in small and large leaves as indicating the absence or presence of changes in these characters during the process of growth.

By comparing average values a conclusion, therefore, was drawn with regard to a change in the form of the leaf, although we did not actually study the latter's ontogenetic development.

It is clearly desirable that leaves should be measured in successive growth stages in order to obtain a direct answer to this question.

This we have done in leaves of *Tropaeolum lobbianum* by means of contact photos, which were taken during the whole course of development. The latter beginning with a just measurable stage and ending with the final stage.

This leaf is very suitable for such a study, because it is from a very young stage totally flat, it is moreover totally glabrous and it has a very smooth outline and easily distinguishable main nerves.

In order to collect material for comparison first the average nerve length ratio and the average size of the angle between the nerves with their V C were calculated in groups of 50 leaves taken from successive position on the shoots: these leaves are indicated from now on as "detached-leaves".

Because in the parallel study the number of leaves was limited necessarily, of these detached-leaves too only groups of 25 were measured: by combining these groups of 25 in pairs, groups of 50 were formed: these groups are indicated as "leaf class BC, DE, FG etc".

The leaf class A is omitted because of its irregular shape and also because its nerves are, in a morphological sense, not yet fully developed.

Since only the nerves 1, 2 and 3 extend unto the margin, the study of the nerves and their angles had been limited to these ones (Table XIV).

TABLE XIV

Nerve length ratio and size of the angle between the nerves in "detached leaves" of *Tropaeolum lobbianum*.

Position of the leaves	Number of leaves	Nerve 1 in mm	nerve length ratio		Angle		Variation coefficient			
			Nerve 2	Nerve 3	a	b	nerve		angle	
							2	3	a	b
BC	50	10	98	72	56	50	1,9	2,9	1,6	1,7
	50	39	101	85	52	47	0,95	1,4	2,1	1,6
DE	50	39	97	87	49	49	0,55	1,1	1,0	1,1
	50	10	94	77	51	49	0,95	1,8	1,3	1,8
FG	50	44	98	88	47	47	0,51	1,4	1,4	1,0
	50	86	98	89	42	44	0,34	0,92	1,1	1,2

On the whole we observed here the same phenomena as in our preceding studies, viz. an increase of the nerve length ratio as the leaves become larger, and also according to the successive position of the leaves on the shoots till the highest value is reached in the

leaf class HI, which also shows the lowest V C: the size of the angles between the nerves too decreases during the growth of the leaf and also from the lower to the higher leaves; the irregularity in the decrease of the V C will be discussed hereafter. We will take the leaf belonging to the class HI as the most ideal one, although a more precise determination of the ideal value has been omitted as it seemed superfluous in this case.

Apart from the study of these "detached-leaves" some other leaves were photographed in their successive stages of development. In this manner 50 series were formed of leaves belonging to class BC and class FG, which furtheron will be called "series-leaves".

In studying the nerve length ratio and the size of the angle between the nerves in each of these series of photos separately, we found that some of them increase, whereas others remain unchanged or show a decrease.

The different nerves and angles of the same leaf show a large degree of independence in their nerve length ratio and in the size of the angle between the nerves.

When we calculate the average values of these "series-leaves" in the same manner as we have done for the "detached-leaves", the same rules emerge (Table XV).

TABLE XV

Nerve length ratio and size of the angle between the nerves and their V C in the "series-leaves" of *Tropaeolum lobbianum*.

Position of the leaves	Number of leaves	Nerve 1 in mm	nerve length ratio		Angles a b		Variation coefficient			
			nerve 2	nerve 3			nerve length ratio		angle a b	
BC	50	11	94	79	54	48	0,88	1,3	1,2	1,6
	50	28	98	86	48	48	0,81	1,1	1,6	1,3
FG	50	11	94	79	51	48	0,54	0,77	0,9	1,0
	50	30	97	85	47	46	0,48	0,71	1,0	1,0

However there is a difference in the absolute values of the nerve length ratio in so far as they are lower in the "series-leaves" than in the "detached-leaves". The difference is too large to be neglected: a plausible explanation can be found, however, in the circumstance that the series-plants developed under unfavourable conditions. They were cultivated in pots, whereas the "detached-leaves" were taken from plants that were growing on a bed in the garden. Moreover the potplants were cultivated in the early summer in a period of abnormally little sunshine and of low temperature (summer 1954).

These plants remained small and the largest leaves occurred in the leaf class EF, whereas but a few leaves were developed afterwards. The plants on the beds in the garden have, on the contrary, reached a

very full growth: their shoots have produced sometimes a great number of leaves (up to leaf M). Meanwhile remembering the word of MENDEL (1865) "No one will seriously maintain that in the open country the development of plants is ruled by other laws than in the garden bed" (otherwise in the pot: J. M.), we will seek the explanation of the difference between the pot- and full-ground-plants in a relation of some other kind.

In our attempts to determine ideal values in the leaves of *Acer* and *Platanus* with greater precision, we noted that the nerve length ratio as well as the size of the angle between the nerves differed considerably in shoots with a different number of leaves: the leaves of shoots with one leaf pair showed a lower average value than those with 2 or 3 leaf pairs. A similar difference will presumably have paid a part in this case.

We should compare the "series-leaves" with the less developed leaves of the shoots with 1 leaf pair, whereas the "detached leaves" would be comparable to those of the better developed shoots, i.e. those with a large number of leaf pairs.

On account of the results to which our studies so far have led, we feel us justified in drawing conclusions from the comparison of average values calculated in groups of corresponding parts with regard to the degree of development of definite specific characters.

TABLE XVI

Number of leaves which show the various differences in nerve length ratio and in the size of the angle between the nerves, observed between the initial and the final stage in the series of photos from the leaves BC and FG in *Tropaeolum lobbianum*.

Difference in per cents between initial and final stage	Nerve 2		Nerve 3	
	Leaf class BC	Leaf class FG	Leaf class BC	Leaf class FG
0	2	5	0	3
	— +	— +	— +	— +
1, 2, 3.	6 13	5 9	2 3	3 12
4, 5, 6.	14	1 23	1 6	7
7, 8, 9.	8	3	15	12
10, 11, 12.	5	2	12	6
13, 14, 15.	2		6	3
16, 17, 18.			3	2
19, 20, 21.			1	—
22, 23, 24.			1	1

Difference in degrees between initial and final stage	Angle a		Angle b	
	Leaf class BC	Leaf class FG	Leaf class BC	Leaf class FG
0	1	1	12	13
	— +	— +	— +	— +
1, 2, 3.	10 1	21 1	16 10	22 5
4, 5, 6.	21	25	6 5	8
7, 8, 9.	13	2	1	1
10	4			1

However, we should never forget that but few specimens conform precisely to the average. We have studied by means of our photos how the nerve length ratio and the size of the angles between the nerves increase or decrease in each of 50 leaves belonging to the classes BC and FG. To this end we calculated the difference in the nerve length ratio and the size of the angle between the nerves that appeared between the first and last stage (Table XVI). This table shows that the nerve length ratio for nerve 2 shows much less extreme differences than that from nerve 3, and that leaves with small differences are more numerous than those with larger ones.

A similar difference is found between the leaves of class FG and those of class BC: this is in good agreement with the fact that the lowest V C is found in the largest leaves of class FG.

The angle a shows only in 2 % of the cases an increase, and the latter, moreover, is very small, whereas the angle b shows in 21 % of the leaves an increase, and this increase is sometimes very large. This explains why for the angle b the difference between the average calculated for the first and last stage is so small: the increase and the decrease of this angle counterbalance each other.

For the angle a, with its stronger decrease in the leaves of class BC as well as in the leaves of class FG, it is much easier to see that it behaves in conformity with the rule that the size of the angle decreases during the growth of the leaf. The large number of leaves that show little or no change in size of the angle b explains perhaps the lack of regularity in the V C that appears in Table XV.

The fact that in the leaf belonging to class FG extreme differences between the first and the last stages are much less numerous and also smaller, demonstrates a decrease in the variability that manifests itself in the value of the V C.

II. D. THE LENGTH OF THE LEAF BLADE

In the course of our study of the nerve length ratio and of the angles between the nerves we could not fail to note that the length of the leaves too varies according to a definite rule.

In order to investigate this rule we have measured during the later part of the summer, i.e. at a time when the growth of the leaves, with few exceptions, is completed, in some plant species the length of the blade in leaves occupying different positions on the shoots. To this end the length of nerve 1 was measured.

a) *Acer palmatum* var. *septemlobum*

In Table I the average length of nerve 1 in leaves occupying successive positions on the shoots has been given; it appears that here too the highest average value is found in leaves of class A, and that the highest leaves show a decrease in the value of the average: the values for the length of the leaves form a similar cathodic series as we found for the nerve length ratio and for the size of the angle between the nerves.

A more precise determination of the ideal length is to be found in Table IV, where the V C's are given. As the lowest value for the latter is to be found at a length of 49 mm, which occurs in leaves of class A on shoots with 3 leaf pairs; it is this value that is to be regarded as the ideal one.

b) *Acer cappadocicum*

From Table V it appears that the leaves of class A show a higher average length than the leaves of class C: this series too is a cathodic one. A more precise determination of the ideal length is to be found in Table VI. Exactly as we found for the nerve length ratio and for the size of the angle between the nerves, the average length of leaves belonging to class A in shoots with 3 leaf pairs shows the smallest V C, so that here the ideal length is to be located.

c) *Platanus acerifolia*

In 4 trees (P, Q, R, S), which were all of about the same height (± 10 m), the average length of the leaves was determined. Moreover in Q the influence of the position the leaves occupy on the tree, was studied. To this end groups of 150 leaves occupying different positions on the shoots and taken partly from the lower branches and partly from branches near the top, i.e. at a height of 8–10 m, were measured (Table XVII).

TABLE XVII
Average length of leaves in different trees of *Platanus acerifolia*.

Tree	Position of the leaves on the shoot	Number of leaves	Position of the shoots on the tree	Aver. length in mm	V C
P	A	150	at the bottom	73	2,3
		150	at the bottom	68	2,3
		150	at the bottom	77	2,1
	D	150	at the bottom	155	0,8
	E	150	at the bottom	168	0,7
	G	150	at the bottom	180	0,6
Q	A	150	at the bottom	63	1,8
		150	at the top	66	2,1
		150	at the top	67	1,8
	D	150	at the top	137	0,7
		150	at the bottom	138	0,6
	F	150	at the bottom	143	0,8
	G	150	at the top	143	0,9
R	G	150	at the bottom	180	0,8
S	A	150	at the bottom	73	2,0

This table shows that:

- 1) the average length shows an increase in the direction of the

higher leaves with the highest value in the leaves of class G; the value found for the length form like those for the nerve length ratio and for the size of the angle between the nerves an anodic series:

2) that the leaves of the lower branches and those from the top region do not show any difference in this respect:

3) that the highest average is accompanied by the lowest V C.

A more precise determination of the ideal value is to be found in Table VIII (and XIII), for which the material was collected from other trees than P, Q, R, S.: this ideal value amounts to 175 (176) mm and is found as well in the leaves of class E as in those of class G, at least in the shoots with the larger number of leaves. It is noteworthy that the V C of the 2 groups of 100 leaves shows hardly any difference, which apparently means that these figures are trustworthy.

It is in the meanwhile very strange that the average values found for all leaf classes in tree "Q" are so much lower than those found in the other trees that the difference can not be neglected as unimportant. This phenomenon is the more remarkable as our study of the nerve length ratio did not reveal such a difference.

We may perhaps find an explanation of this different behaviour in the age of the tree: this one was older than the others- or else in the circumstance that *Platanus acerifolia* is a hybrid.

From the study of these 3 kinds of leaves (*Acer palmatum* var. *septemlobum*, *Acer cappadocicum* and *Platanus acerifolia*) it appears that the variability of the length is determined for the greater part by the position of the leaf on the shoot, and that the greatest length is accompanied by the lowest V C.

II. E. RELATION BETWEEN THE LENGTH OF PETIOLE AND LAMINA

In *Acer platanoides* and *Acer pseudoplatanus* and in *Batrachium fluitans* the average length of the petiole was measured and this value was expressed in per cents of the length of the lamina: its V C was determined too. The leaves were arranged in groups according to the position they occupied on the shoot (Table XVIII). The two species of *Acer* show a rather similar result. In the full-grown leaves of class A the average length of the petiole amounts to 170 mm and they are about $3\frac{1}{2}$ times longer than in the higher leaves belonging to the classes C D. In the lower leaves the petiole is longer than the blade, whereas it attains in the higher leaves hardly 60 % of the blade length.

The values found for the average length of the petiole form, like those found for the blades, a cathodic series with the highest value in the leaves of class A, and here too we find the lowest V C. The greatest length is, therefore, accompanied by the lowest variability.

In *Batrachium fluitans* the leaves were grouped in the same way as in our study of the nerve length ratio (see Table IX). From the data of Table XVIII it appears that the petioles of this species are absolutely (their length in mm) as well as relatively (the length of the petiole expressed in per cents of the length of nerve 1) best developed in group I (leaves ABC), and here too we find once more the lowest V C.

It is very remarkable that the variability of the nerve length ratio reaches its lowest value in the groups IV and V, whereas the petioles show in these groups the highest variability. We observe also in the values found for the average length of the leaf blade in leaves occupying successive positions on the shoot an anodic series, and on the contrary a cathodic series in the values for the length of the petiole.

Finally it appears here again that the highest degree of development of the petiole is accompanied by the lowest degree of variability.

TABLE XVIII

Average length of the petiole expressed in per cents of the length of nerve 1 in *Acer platanoides*, *Acer pseudoplatanus* and *Batrachium fluitans*.

Species	Position of the leaves	Number of leaves	Length nerve 1 in mm	Length of the petiole in mm	Length of the petiole in per cents of the length of nerve 1	V C
a) <i>Acer platanoides</i>	A	40	55	59	108	1,11
		40	125	175	140	0,80
	D	40	85	51	63	3,1
b) <i>Acer pseudoplatanus</i>	A	40	55	47	86	3,6
		40	95	105	111	3,3
		40	140	171	122	2,0
	C	40	45	24	54	4,4
		40	80	47	59	4,1
c) <i>Batrachium fluitans</i>	ABC	50	72	73	102	2,5
		50	154	154	100	
	DEF	50	73	49	68	2,7
		50	183	137	75	
	GHI	50	100	55	55	3,0
		50	202	125	62	
	JKL	50	104	33	32	7,6
		50	198	73	37	
	M/V	50	60	8	13	10,4
		50	174	36	21	

II. F. RELATIVE LEAF WIDTH

HEUSER (1915) has already observed in wheat that there is a correlation between the width of a leaf and its position on the shoot; in this species the leaves increase in width as they approach the top of the shoot.

ABBÉ, RANDOLPH and EINSET (1941) too have observed that the width of the leaf in a variety of corn increases with about 9 % in each successive leaf. In their study they included the leaf primordia and they observed that here too occurs an increase in size that goes parallel with the increase in width in the full-grown leaves.

SNOW and SNOW (1937) have observed that on the surface of the

apex a definite minimum space is required for the development of a new leaf. It is possible (and almost to be expected) that there too a variability is present which determines the rate of growth of the leaves that are formed.

The studies which have been instituted in this direction indicate that, as PEARSELL and HANBY (1926) express it: "It is clear that the main factor determining the shape of the leaf is the rate of growth in the leaf initial" (primordium, J. M.) (p. 120). The question as to the cause of the variability is transferred by these observations from the full-grown leaves to the apical meristem. This does not simplify the solution of this problem, because there is (at least apparently) a striking similarity between the apices in most plant species.

In a great number of leaves collected from different bushes of *Ligustrum ovalifolium* L. and from different successive positions on the shoots of the latter, the length and the width have been measured: then the width was expressed in per cents of length.

In the measurements the following difficulties occurred. The top of the leaves belonging to class A is often found in a withered state; the rounded form of the top of many leaves suggests that here the withered part has already fallen off: such leaves may have a width of 80 % and more.

Moreover, the leaves belonging to the classes A and B, which have a length of a few millimeters only, are very difficult to measure: and it is often impossible to see where the leaf really begins; petiole and blade are often gradually merging one into the other. Notwithstanding these difficulties the values found for the average width in groups of 10 leaves already yield a rather trustworthy result, for they show a handsome similarity; it is not so much the absolute value of the figures but rather the decrease or increase of the successive values for the average which here, as in all similar instances, are of importance.

TABLE XIX
Leaf width in per cents in *Ligustrum ovalifolium*.

Position of the leaves	Number of leaves	Nerve 1 in mm	Leaf width in %	Position of the leaves	Number of leaves	Nerve 1 in mm	Leaf width in %
A	10	2	78	G	10	10	41
	10	4	81		10	15	47
	10	8	75		10	27	49
	10	12	76		10	50	48
	10	16	63		10	65	48
	10	18	69		10	75	48
B	10	7	70		10	78	46
	10	9	73		10	83	48
	10	12	69		10	93	48
	10	13	64	P/Z	10	61	48
	10	18	68		10	69	46
	10	24	66		10	79	47
	10	26	62		10	85	48
	10	29	63				

From Table XIX it appears that the leaves of class A show the greatest relative width, and that the latter decreases from 80 % to 70 % when we proceed from the smallest to the largest leaves. The width of leaves belonging to class B decreases from 70 % to 63 %; those of class G and the higher leaves show for each length an average width of ± 48 %.

This decrease in width can be attributed to a rather strong difference in the rate of growth between the upper and lower half of the leaf. In the leaves of the classes A and B the top half develops at first very strongly so that the top often will already be withered when the basal half is still growing; in this leaf the growth is, according to the terminology of PRANTL (1883), apparently basiplastic. In the leaves that occupy a higher position on the shoot, growth becomes more equally spread over the whole surface, and then the relative width remains unchanged.

In order to diminish the effect of accidentally present extremes on the V C, the groups of 10 leaves have been combined into groups of 20 leaves (Table XX).

TABLE XX
Variation coefficient of the leaf width in *Ligustrum ovalifolium*.

Position of the leaves	Number of leaves	Nerve 1 in mm	Width of the leaves in %	V C
A	20	3	80	4,2
	20	10	76	3,5
	20	17	66	2,8
B	20	8	72	2,2
	20	12	67	3,5
	20	21	67	2,4
	20	27	63	2,6
G	20	13	44	3,0
	20	39	49	2,6
	20	70	48	2,0
	20	88	48	1,7
P/Z	20	65	47	2,0
	20	82	48	1,8

When the small deviations found in the leaves belonging to class B, which can be attributed to the relatively small number of leaves and to measuring difficulties, are left out of consideration, we may conclude from these data that in each leaf class the V C decreases when the size of the leaves increases, and also when we proceed from the lower to higher leaves until the highest value is reached in the leaves belonging to class G.

Here again it appears that the rate of the variability decreases as the character, here the relative width, reaches a higher degree of development.

One might perhaps object against my accepting the relative width of 48 % as the ideal value because the leaves of class A show a relative

width of 80 % and more. However, if we take the absolute width in mm, than the leaves of class G show the highest value. Moreover we may add that in a leaf with a width of 80 % the development was checked by the withering of the top part. For this reason this width is not to be accepted as a normal one, and it can, therefore, not express the ideal form of the character.

II. G. NUMBER OF UMBEL RAYS

In all the foregoing studies there was always a greater or smaller possibility that measuring errors might partly obscure the real situation, although they were never of such importance that the results could have been influenced to a marked degree. Yet it might be useful to supplement these studies into class-variability with one of discrete variability, where measuring errors, if not wholly excluded, are limited to a minimum.

We believe to have found an ideal object for a study of this kind in the umbel rays of *Aegopodium podagraria* L. In the thousands of umbels of which the rays were counted by us, it has happened but seldom that there arose any doubt with regard to the number of these rays.

As the foregoing studies have shown that a definite arrangement of the part according to the position they occupy in the plant is of primary importance in the study of variability, it was our first task to discover in this plant species a suitable arrangement of the umbels of which the rays were to be counted.

In the at first sight rather disorderly arrangement of the umbels of this species a distinct order is to be detected if one pays attention to the manner of branching in this species and to the succession in which the umbels expand.

Thus at the top of the main stem we always find a single umbel, and this proves to be the one that flowers first. It is born by a peduncle at the basis of which we find at least one leaf; this umbel is indicated with the letter "A" (Fig. 4). At the basis of this peduncle arise a number of other peduncles (sometimes 5) which in their turn end in an umbel. These umbels are flowering somewhat later than umbel A, and they are indicated as "B". Lower on the stem there sometimes arise once more one, two or three peduncles ending in umbels that flower after the umbel "B", and that are named "C".

Below these inflorescences some peduncles, each again with an umbel at the top, may arise, but these peduncles always arise single from the main stem: they are called "D, E, F, G"; the umbel G was only found twice among 500 plants.

On the peduncle of umbel A as well as on the other ones occasionally a small branch with a single umbel at the top (secondary umbel) may arise: the rays of these umbels were not counted. The 500 plants were collected from the most different surroundings: in all 49443 umbel rays were counted.

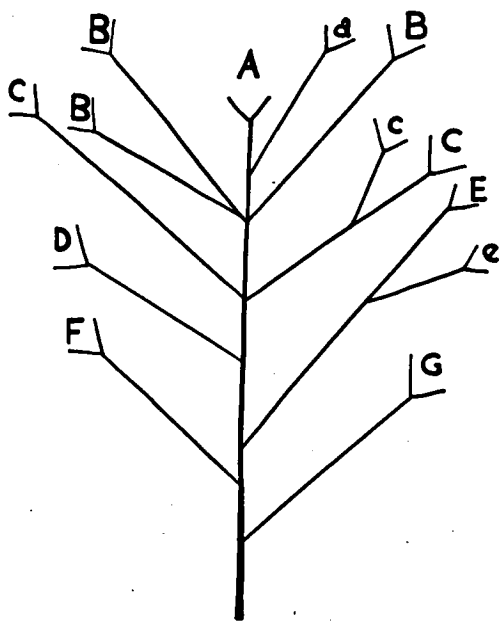


Fig. 4. Sketch of the position of the umbels in *Aegopodium podagraria*.

These 500 plants were divided in 5 groups according to the number of umbels of the classes A, B, C etc. that were present, viz.

Group I	with 6 kinds of umbels belonging to the classes A-F
II	5 " " " " " " A-E
III	4 " " " " " " A-D
IV	3 " " " " " " A-C
V	2 " " " " " " A-B

Since the number of umbels belonging to each of the classes was different (each plant has only 1 umbel of class A but on the average 2 umbels of class B), the V C of the average number of umbel rays was for each class adjusted to a basic number of 100 umbels (Table XXI).

When we look at the average number of rays that are found in the different umbel classes we notice in each group an anodic series, which has nearly always its summit in the umbels belonging to the last but one class.

The increase in the average number is accompanied by a decrease of the V C.

The group of umbels with the highest number of rays (an average of 21,3) is that found in class D of group I with a V C of 1,24 (I D), whereas the group of umbels belonging to class C of group II (II C) shows an average of 20,2 rays with a V C of 1,20.

We are now confronted with the question whether the ideal number of rays is to be seen in class I D or in II C. If we compare the groups I and II, it will be clear that for all corresponding umbel classes the V C is in group II lower than in group I.

We need not attach any value to the exception formed by umbel class A, which shows in group I a lower V C than in group II, as the high value of the V C indicates a high degree of instability, so that occasionally too high or too low value may be expected. Because of

TABLE XXI

Aver. numbers of rays per umbel and its V C in *Aegopodium podagraria*.

Position of the umbels	Group I			Group II			Group III			Group VI			Group V		
	Number of umbels	Aver. number of umbel rays	V C	Number of umbels	Aver. number of umbel rays	V C	Number of umbels	Aver. number of umbel rays	V C	Number of umbels	Aver. number of umbel rays	V C	Number of umbels	Aver. number of umbel rays	V C
A	70	13,4	1,9	180	13,7	2,2	130	14,9	1,9	100	16,2	1,51	20	16,0	0,93
B	120	18,6	1,44	375	18,2	1,4	269	18,4	1,44	205	19,4	1,29	37	17,0	1,4
C	88	20,0	1,35	215	20,2	1,20	135	19,8	1,36	100	19,3	1,50			
D	70	21,3	1,24	180	20,4	1,22	130	18,6	1,6						
E	70	21,2	1,38	180	19,7	1,35									
F	70	20,2	2,7												

the fact that the V C decreases in each group the nearer we come to the umbel class with the highest number of rays and according to the rule that we found repeatedly confirmed in the preceding studies, viz. that the ideal value is recognizable by the lowest V C, the ideal value of the number of rays is for this species represented in the umbel class IIc in plants with 5 umbel classes (A, B, C, D, E): and it amounts to 20,2 umbel rays.

Among the 2263 umbels of which the number of rays was counted, we did not find a single one with 6 or 30 rays, but we found one with 5 and one with 31 rays resp. in class A of group III and B of group IV. These extreme variates were not found in plants with the smallest but with the greatest variability.

Here we notice once again that a high degree of variability does not indicate a high grade of development, but on the contrary, a low one.

Everybody will recognize in an umbel with but 5 rays a kind of "failure". But the umbel with 31 rays is just as well an excess as the other. In this light it is not to be wondered that the ideal value of a character is often not found in parts with the highest value; the lowest V C, however, is always a reliable indication.

III. TESTING OF THE RULES OBSERVED ON DATA DERIVED FROM OTHER INVESTIGATORS

In the literature many studies into the variability of characters are to be found. In some of them the data are given in so much detail that it is possible to apply our own method of investigation to them. In order to extend the scope of the divergent characters our choice has fallen on A) the size of the leaf meshes: B) The relative length of internodia and C) the ratio of the number of stomata and the number of epidermis cells.

A) THE SIZE OF THE LEAF MESHES

BENEDICT (1915) has calculated in *Vitis vulpina* L the size of the meshes between the ultimate ramifications of the nerves in the leaves of young and old plants. He concludes that these meshes are greater in young plants than in older ones. His figures and photos very clearly show a gradual decrease of the size of these meshes with the increase in age of the plants.

He has given a very detailed account not only of the size of these meshes from plant to plant with a record of the age of the latter, but also according to the position the leaves occupy on the shoot. In order to obtain a more easy comparability with our own data we have indicated the successive positions occupied by the leaves on the shoot from the base to the top with the letters A, B, etc. and not with a figure as Benedict has done.

When we calculated from the data given by Benedict the average size of the meshes and its V C for the leaves belonging to the classes A-J in young and old plants we arrived at the results given in Table XXII. From this table it appears that the largest meshes are found in the youngest plants and that the V C likewise is here lower.

TABLE XXII

Aver. size of leaf meshes in respect to the age of the plants in *Vitis vulpina*.

Age of the plants in years	Position of the leaves	Number of leaves	Aver. size of the leaf meshes in square mm	V C
3-5	A-J	42	0,498	0,94
35-70	A-J	45	0,169	2,6

Next to this the average size of the meshes and its V C was determined for leaves of the classes AB and IJ from the 10 youngest and the 10 oldest plants (Table XXIII). It is clear that the meshes are smaller in the higher leaves and the more so as they are taken from older plants. Here too the lowest V C is found in the leaves of the class AB of the youngest plants, i.e. in the leaves which show the largest meshes. Our final conclusion is that the width of variability decreases when the size of the meshes increases or when the leaves reach a higher degree of development.

TABLE XXIII

Aver. surface of leaf meshes in respect to the position of the leaves on the shoots at *Vitis vulpina*.

Age of the plants in years	Position of the leaves	Number of leaves	Aver. surface of the leaf meshes in square mm	V C
3-10	A. B.	20	0,440	3,2
	I. J.	20	0,434	3,7
25-70	A. B.	20	0,205	3,7
	I. J.	20	0,186	4,3

We may regard the decrease in the size of the meshes as the plants grow older as a decline, a sign of senility. In the opinion of *Benedict* photosynthesis and the capacity for water absorption decrease as the plant grows older: at the same time the number of stomata increases but their width decreases: the palissade tissue too is less developed.

It is, therefore, in every respect reasonable to see in the decrease in the size of the meshes a decline.

B) THE RELATIVE LENGTH OF THE INTERNODIA

T. TAMMES (1903) has studied the question whether in shoots of *Fagus sylvatica* the length of the internodia undergoes a change when the leaves are removed. She concluded that the absolute length of the

TABLE XXIV

Length in per cents S D and V C of the internodia in shoots of *Fagus sylvatica* (T. TAMMES. 1903. p. 79)

Position of the internodia on the shoots	B	C	D	E	F	G	H	I	Total length of the shoots in mm
	0,5	2	8	15	18	20	22	14	258
	0,5	4	13	15	17	19	19	12	244
	1,0	6	10	13	17	21	19	11	344
	0,5	2	9	14	18	20	22	14	224
	1,0	5	11	14	18	19	19	14	283
	0,5	3	10	16	18	20	19	13	253
	0,5	3	10	14	16	20	22	14	269
	1,0	5	12	13	17	19	19	14	301
	1,0	1	10	16	18	20	20	12	253
	0,5	0,5	8	16	18	19	21	16	248
	0,5	1	2	13	21	23	23	17	196
	0,5	1	5	17	20	21	21	14	182
	1,0	5	7	13	16	20	23	19	279
	0,5	3	9	11	15	19	22	18	326
	0,5	3	10	13	16	19	20	18	341
Aver. %	0,76	2,96	8,93	14,2	17,8	20,6	21,1	15,0	Aver. length 263
S D			0,72	0,42	0,42	0,29	0,40	0,63	
V C			8	3	2,45	1,45	1,90	4,2	

internodia becomes smaller but that the relative length remains unchanged. She rightly decides that the relative length of these internodia may be regarded as characteristic for this species.

From her data we have chosen one series, and to this series we have applied our method: however, we have first expressed the length of the internodia in per cents of the total length of the shoot (table XXIV).

She has only measured the internodia of 15 shoots of *Fagus sylvatica* but this number will be sufficient to show that the variability in the length of the internodia decreases as the length increases. It is noteworthy that the lowest V C is not found in the longest internodia of class H but in those of class G, and for this reason we recognize these internodia as the ideal ones, but we admit that this idea has here but a dubious value.

The only important fact brought to light by this study is, that the development of this character, the relative length of the internodia, towards its ideal value is on the whole accompanied by a decrease of the variability.

C) THE RATIO BETWEEN THE NUMBER OF STOMATA AND THE NUMBER OF EPIDERMIS CELLS

BEDAUX ¹ (1954) has studied the so-called stomatal index in the leaves of *Teucrium chamaedrys* L.

The stomatal index is the figure that indicates the ratio between the stomata number of and the number of epidermis cells. This relation is expressed in the formula: $I = \frac{100 \times S}{E + S}$; in which S indicates the number of stomata on the lower side of the leaf: (the two guard cells of one stoma are taken as one), and E indicates the number of the epidermis cells on the lower side of the leaf.

In his study BEDAUX always paid attention to the position of the leaves on the stem, because other investigators had found that there was an acropetal increase in the frequency of the stomata. By way of control he has studied the index in 10 successive leaf pairs of one plant.

From his data we have calculated the average value of I, its S D and V C for all leaf pairs as they occur at the plant from the base to the top of the stem: because the number of measurements varied for the groups of leaf pairs from 16 to 24 the V C has been adjusted to a base of 20 for each group of leaf pairs (Table XXV).

Considering that the number of leaves per group was but small, the calculation of the V C yielded quite satisfactory results.

The decrease of the V C is strikingly regular and its V C is the smallest for leaf pair 9: with some reserve, because of the rather low number of measurements, the ideal value of the I is determined at 21,4 (It is remarkable that the value of I of all leaves together is 21,5).

¹ I wish to express my indebtedness to him for his kindness in allowing me the use of his data.

TABLE XXV

Average stomatal index S D and V C in leaves of *Teucrium chamaedrys* (Bedaux)

Position of the leaf pairs	Number of measurements	Aver. Index	S D	V C
1	22	19,5	0,79	4,1
2	24	20,4	0,84	4,1
3	16	22,8	0,87	3,9
5	20	21,1	0,80	3,8
6	20	21,8	0,75	3,4
7	20	22,6	0,69	3,1
8	20	22,7	0,74	3,2
9	20	21,4	0,63	2,9
10	16	21,0	0,63	3,0

On account of the rather small number of measurements it is not to be wondered that a regularity in the increase of the average in the successive leaf pairs is difficult to detect. As the lowest average is found in the leaf pair A the average values probably form here an anodic series. Finally we can see in these data once more a proof that a character varies less as it reaches a higher stage of development.

IV. SPREADING OF THE FREQUENCY OF THE VARIATES

Now that we have attained this point in our investigation, we will turn our attention to the question to what extent the numbers in which the different variates are met with, are identical with or different from those that is to be expected if one assumes that the spreading of the variates should be the same as in the mathematical probability curve or the binomium of Newton.

In order to study this question two divisions were formed from the data of our own studies: division I is made up of groups of data which showed a high V C: division II is made up of groups of data which showed the smallest possible V C.

Of course, the choice of the groups for the first division has been more or less at random: here our only aim was the collecting of groups with a strongly varying character, whereas the second division is made up of groups exhibiting characters which approached the ideal value: our final aim was to obtain as great a contrast as was possible.

Here we are only concerned with the number of variates that were found in each variation class, whereas it does not matter in the least that the groups of variates are of a totally different kind (nerve length ratio, size of angles between the nerves in different plant species).

From these different series of measurements we first have put the class with the mean value in one column beneath each other, and we have added up these figures in both divisions I and II.

After this the other classes of plus and minus variates are arranged in columns at equal distances from the mean class and the figures

of each column too are added up (Table XXVI.) This table shows in the first place how many variates are found in each variation class: in this way the spreading of the 500 variates brought together in the divisions I and II over the various classes is obtained, moreover the number of variates in each class is expressed in per cents of the total number. Right at the bottom the percentages are given which were to be expected according to the mathematical probability calculus (the binomial figures). Under the table the nature of the various groups of which the two divisions have been formed, are specified.

From this table it appears that:

1) the frequency curve of division I shows for each group separately a top that is too low; and of course this applies to the curve in which they are all integrated, too.

2) in the groups with the ideal values (division II) the central classes show the nearest approach to the binomial figures: the class with the mean value shows this phenomenon most convincingly.

3) the classes of the most extreme plus and minus variates show relatively the greatest variability and the greatest deviations of the binomial values.

According to the mathematical probability calculus they should have had but a thousandth or a millionth per cent of chance, whereas they are really represented by 1 or 2 % of the total number.

The same method has been applied in *Aegopodium podagraria* to the spreading of the umbel rays over the different classes. Division I of Table XXVII is once more made up of strongly varying groups; division II of groups with low variability; the origin of these groups are indicated too.

We note here too in division II the nearest approach to the binomial values, whereas the mean class contains even a larger number of variates than would have been expected.

It appears, therefore, that the mean class as well as the classes of the extreme minus and plus variates are represented by a larger number of variates than should have been expected on account of the probability calculus. The mean class, therefore, becomes better represented as the ideal value is approached.

V. DISCUSSION AND CONCLUSIONS

Our investigations have led to the conclusion, that one of the various degrees of development that a character shows, should be regarded as the ideal one, and that this ideal development is recognizable by the decrease of the V C to its lowest value. This ideal development, or ideal value of a character, is, as we have seen, not necessary its highest value.

This view is supported by the following facts, all brought to light by our investigations;

1) Each character shows in its ontogenetic development (i.e. from its first appearance until it has reached the end of its development) a diminution in its variability:

TABLE XXVI

Class	—10	—9	—8	—7	—6	—5	—4	—3	—2	—1	Mean
Division I	—	—	2	3	2	3	5	7	7	7	17
	—	2	1	3	3	4	6	5	13	9	14
	—	—	1	2	4	5	7	9	9	18	16
	—	—	—	1	2	3	6	7	7	14	15
	2	6	2	8	6	8	6	8	11	2	8
	2	8	6	17	17	23	31	36	47	50	70
	0,4	1,6	1,2	3,4	3,4	4,6	6,2	7,2	9,4	10,0	14,0
Division II	—	1	—	2	1	4	1	3	17	9	19
	—	—	1	1	—	5	6	9	9	14	12
	—	—	—	3	1	5	4	8	11	12	17
	—	—	—	—	—	—	4	9	11	13	20
	—	—	1	1	—	2	3	5	7	10	16
	—	1	2	7	2	16	18	34	55	58	84
	0	0,2	0,4	1,4	0,2	3,2	3,6	6,8	11,0	11,6	16,8
	0,000001	0,00002	0,0002	0,11	0,46	1,48	3,6	7,4	12,0	16,2	17,6

Division I

- a) = Platanus Leaf I Shoot I nerve -2 (Table VIII)
 b) = Platanus Leaf I Shoot I nerve -3 (Table VIII)
 c) = Acer palm. Leaf A Shoot 4-l.p. nerve -2 (Table IV)
 d) = Acer palm. Leaf A Shoot 2-l.p. nerve -2 (Table IV)
 e) = Acer capp. Leaf A Shoot 2-l.p. nerve -3 (Table VI)

TABLE XXVII

Class	—10	—9	—8	—7	—6	—5	—4	—3	—2	—1	Mean
Division I	—	—	3	3	6	2	5	13	9	25	35
	1	—	—	3	3	5	4	9	10	23	20
	—	1	—	1	—	5	2	3	4	16	14
	—	—	—	—	—	3	5	7	7	9	8
	—	—	—	—	—	2	2	8	5	8	11
	—	1	—	2	3	4	13	16	22	27	23
	1	2	3	9	12	21	31	57	67	108	111
	0,14	0,28	0,41	1,2	1,6	2,9	4,3	7,8	9,3	14,5	15,2
Division II	—	—	—	—	—	—	1	2	8	14	13
	—	—	—	—	—	—	2	6	12	8	11
	—	—	—	—	1	1	5	11	20	44	39
	—	—	—	—	3	—	3	13	16	28	40
	—	—	—	—	1	2	3	6	20	36	41
	0	0	0	0	5	3	14	38	76	130	144
	0	0	0	0	0,6	0,4	1,9	4,8	10,1	17,5	19,2
	0,000001	0,00002	0,0002	0,11	0,46	1,48	3,6	7,4	12,0	16,2	17,6

+1	+2	+3	+4	+5	+6	+7	+8	+9	+10	Nr.	Division I
10	11	7	5	2	7	—	1	2	2	100	a)
7	8	5	6	5	5	2	—	—	1	100	b)
8	11	2	3	—	4	—	—	—	1	100	c)
11	8	6	6	10	—	2	—	2	—	100	d)
6	6	6	1	5	3	2	2	1	1	100	e)
42	44	26	21	22	19	6	3	5	5	500	
8,4	8,8	5,2	4,2	4,4	3,8	1,2	0,6	1,0	1,0	per cents	
14	14	3	10	—	1	—	1	—	—	100	f)
15	12	5	5	2	3	—	1	—	—	100	g)
13	17	6	—	3	—	—	—	—	—	100	h)
19	10	6	6	2	—	—	—	—	—	100	i)
12	13	11	7	6	4	—	1	—	1	100	j)
73	66	31	28	13	8	—	3	—	1	500	
14,6	13,2	6,2	5,6	2,6	1,6	—	0,6	—	0,2	Per cents	
16,2	12,0	7,4	3,6	1,48	0,46	0,11	0,0002	0,00002	0,000001	Binom. relation	

Division II

- f) = Acer palm. Leaf A Shoot 3-l.p. nerve -2 (Table IV)
 g) = Platanus Leaf G Shoot > I nerve -2 (Table VIII)
 h) = Acer capp. Leaf A Shoot 3-j.p. nerve -2 (Table VI)
 i) = Acer capp. Leaf A Shoot 3-j.p. angle a (Table VI)
 j) = Acer palm. Leaf A Shoot 3-j.p. angle a (Table IV)

+1	+2	+3	+4	+5	+6	+7	+8	+9	+10	Nr.	Umbel
20	18	12	8	8	—	2	—	1	—	180	II A
18	17	8	3	3	3	—	—	—	—	130	III A
23	16	7	5	2	1	—	—	—	—	100	IV A
8	6	2	5	2	4	2	2	—	—	70	I F
12	7	9	1	4	1	—	—	—	—	70	I A
24	14	11	6	4	6	2	1	—	—	180	
105	78	49	28	23	15	6	3	1	0	730	
14,4	10,7	6,7	3,9	3,3	2,1	0,8	0,4	0,14	0	Per cents	
13	9	9	8	5	3	2	—	1	—	88	I C
9	6	7	2	6	—	—	1	—	—	70	I D
33	11	18	12	5	1	4	—	—	—	205	II C
26	14	15	10	5	4	1	2	—	—	180	II D
28	27	18	10	8	2	2	—	1	—	205	IV E
109	67	67	42	29	10	9	3	2	0	748	
14,7	9,0	9,0	5,6	3,8	1,3	1,2	0,4	0,26	0	Per cents	
16,2	12,0	7,4	3,6	1,48	0,46	0,11	0,0002	0,00002	0,000001	Binom. relation	

2) In the series of average values obtained in the earlier described manner, i.e. by arranging the material in groups according to the position the parts occupy in the plants, an increase is always to be observed that is accompanied by a decrease of the variability width: it does not matter here, whether this series has its highest value at the base of the shoot (kathodic series) or at the top (anodic series).

The decrease of the variability width always points to a final state of development from which consistently is to be concluded that the lowest variation width is a criterium for the highest degree of development of a character, in the sense of its ideal value. The foregoing studies show that this ideal value is for each character and each species a constant one.

The view, that it is possible to detect for each character a constant value is not shared by all investigators. KLEBS (1906) can be taken as the exponent of the opposite view. He says: "Dieses regelmässige Schwanken um einen Mittelwert ist aber nicht aufzufassen als eine für irgend eine Pflanze notwendige Erscheinung, es ist nicht ein geheimes, inneres Gesetz, das als etwas in der Natur der Pflanze Gegebenes anzunehmen ist Die Wahrscheinlichkeitsrechnung ist eine Methode, die ganz unabhängig von der Natur des Gegenstandes ist und daher über diese Natur nichts auszusagen vermag.

Die Mittelwert eines Markmals, z.B. der Blattgröße, der Internodienlänge, der Zahl der Blütenglieder usw. entspricht der am häufigsten vorkommenden Kombination dieser Faktoren: die selteneren Varianten entsprechen den selteneren Kombinationen.

Aus dem gesagten folgt, dass der Mittelwert keine konstante Grösze sein kann, sondern immer ein Resultat der gerade zufällig vorhandenen Bedingungen ist und sich mit diesen verändern muss. Tatsächlich beobachtet man auch solche Veränderungen des Mittelwertes; wie Weisse, Macleod, de Vries nachgewiesen haben" (S. 304).

KLEBS maintains therefore 1° that constant average values do not exist, and 2° that their non-existence is the necessary consequence of the inconstancy of the external circumstances. Indeed, with regard to statistical investigations carried out "independent of the nature of the object" the critical attitude of KLEBS is justifiable. When we determine average values without paying attention to the predisposition of the parts, which depends upon the position they occupy, than these average values indeed vary according to accidental circumstances (see figure 2 and our exposition on p. 284 seq.).

Some people think that this is caused by the occasional presence of extreme variates. But in this manner the importance of the extreme variates is exaggerated. We should realize that in order to meet extreme variates, which, as everybody will admit, are relatively seldom, a very large number of the variates must be collected. But the larger the number of variates, the smaller is the influence of the extreme ones on the average.

Moreover there is no reasonable ground to assert that the extreme variates will be found in one direction only, either as minus or as plus variates. The chance to find minus variates is always the same as to

find plus variates; as they counterbalance each other they will not, in general, influence the average.

When we collect parts without paying attention to the different positions they occupy, it are the different predispositions, which, as we have seen, are determined by the position of the parts, that influence the value of the average.

Under such circumstances it entirely depends on the position the collected parts accidentally occupied, what the average will be: the chance that in this case the ideal value will appear is practically nil, how great the number of the collected parts may be. However, by applying the above described method, i.e. by restricting the range of positions, from which parts are collected, more and more constant averages will be obtained. This is clearly shown by the outcome of our studies. It appears that the group of variates showing the more precise value of the average exhibits a lower degree of variability. Our investigations show, in direct opposition to the opinion of KLEBS, that it is really possible to find constant averages. The second assertion of KLEBS, which is merely an attempt to declare the first one, need not be considered, as the first is rejected by us.

This opinion with regard to the constancy of the ideal value of a character is not refuted by the fact that by changes of the circumstances the averages too may change. There is no reason to doubt the correctness of the data collected by WEISZE, MACLEOD, DE VRIES, KLEBS and many others, who have demonstrated that it is possible to obtain different averages by changing the environment. The reactions are obviously dependent in a large measure upon external agencies. But we will have to interpret this fact in this way that, when the circumstances are altered in a definite direction, the ideal state will not be attained any more, and the averages that under such circumstances are found, are none of them the ideal one.

We will now turn our attention to the question whether all these natural variations are to be ascribed to internal or to external agencies. Although we have always used the neutral term "variability" is was never our intention to deny the influence of external factors. But on the other side it seems to us that, on account of the data produced by our studies, one has to attribute a greater influence to internal factors than has generally been done.

Very often all variability is identified with modification, which means with changes that are caused by external agencies and that, therefore, are not due to a definite predisposition.

That we should not undervalue the influence of internal agencies on the variability appears from the following observations for which our investigations have furnished the data:

- 1) If the external agencies should influence the variability to any great extent, than one should expect that leaves which during their growth are subjected to a great number of continually changing agencies, should show a greater variability as they approach their full-development: but this is not so. In each of the foregoing studies it

appeared, that the variation decreases as a character reaches a higher degree of development and also therefore as it approaches the end of its development.

2) In leaves in the bud, where the influence of the environmental agencies, if not excluded at all, is certainly limited to a minimum, the greatest variability was observed.

3) In the same parts all characters are varying independently of each other; one shows e.g. an extreme plus value, whereas the other has an extreme minus or a mean value: a striking instance of this mutual independence of the characters is the following:

In *Aegopodium* the umbels with the lowest and the highest number of umbel rays were found in plants where the other umbel classes were represented in this manner:

Umbelclasses		A	B		C	D
plant 1	Number of rays	5	16	17	18	17
plant 2		20	19	31	22	—

How would it ever be possible to ascribe the fact that two umbels that grow together on the same plant and are exposed to the same external agencies should show such a quite different number of rays, to the influence of external agencies?

It is noteworthy too that one umbel may show an extremely low or an extremely high number of rays whereas an other one on the same plant show an average value.

4) In *Batrachium fluitans* the values for the length of the petiole form a cathodic series, whereas the values for the length of the blade form an anodic one. It can hardly be doubted that the petiole and the blade have been exposed to the same external circumstances.

5) In a palmate leaf each nerve varies in its own manner, and the stronger the further it is removed from nerve 1. Here too the environment is the same for the whole leaf:

6) The number of umbel rays in *Aegopodium* does not change during the development of the umbel: it is already fixed in the bud. That external agencies would influence the meristem of these buds to any extent, is hardly to be expected.

The foregoing facts, the number of which could easily be multiplied, demonstrate the great influence of internal agencies on the variability. The fact that we know little or nothing with regard to the character of these internal agencies, may not be a reason to minimize or to neglect their importance.

Because we did not intend to study the different influence of these two kinds of factors, it did not seem necessary to express a view on their mutual relation. But because of the results of our own studies we are inclined to attribute the principal part to the internal agencies, at least in so far as the development of the ideal value of a character is concerned.

GENERAL CONCLUSIONS

The study of a great number of characters in different plant species lead to the following conclusions:

1) for each character the variability is primarily determined by the position the part, by which it is exhibited, occupies in the organism:

2) when the averages calculated for the various groups of parts that occupy corresponding positions in the organism are plotted in the form of a curve, the highest value is found sometimes at the base (kathodic series) and sometimes at the top (anodic series).

3) The width of variability decreases as, for each character

a) the part by which the character is exhibited approaches the end of its development.

b) the group average approaches its optimum value.

The lowest degree of variability is found in characters as they exhibit their ideal development. The latter is a constant value and should be regarded as expressing a specific predisposition.

4) when the ideal value is approached, the number of variates in the central class was sometimes in the material studied by us, found to exceed that which would have been present when the curve had been a binomial one.

VI. SUMMARY

The aim of this study was to find, among groups of parts showing a variable character, one in which the variability is so strongly reduced that the character approaches constancy. This value, which we called the ideal one, is regarded as characteristic for the species.

During this investigation it appeared that this ideal value can only be found, if attention is paid to the position the parts occupy in the plan on which the plant is built (I). First of all we have tried to find in our own material a definite regularity in the variability exhibited by the various characters we studied in different plants (II). After that this regularity was tested on data obtained from other investigators (III).

In a number of leaves of *Acer palmatum* var. *septemlobum* the ratio between the length of the lateral main nerves and that of main nerve I (the longest nerve which at the same time is the middle one) was studied.

By comparing the averages of the varying values found for this ratio in groups of leaves occupying a corresponding position on the shoot but differing in size, we found that these averages show a slight increase when we proceed from the smaller to the larger leaves.

When we compare the averages found in groups consisting exclusively of leaves of the larger size but occupying different positions on the shoot, we saw that the averages show a continuous decrease when we begin with the leaves inserted at the base, and proceed towards those at the top of the shoot.

The averages of the varying values found for the ratio between the length of the lateral main nerves and the central one, proved to reach

their highest value in the leaves at the base of the shoot, no matter which of the lateral nerves was chosen.

Besides one sees that the variation width decreases:

- 1) in leaves which occupy the same position on the shoot, when we proceed from the smaller to the larger ones,
- 2) in the groups of larger leaves when we proceed from the base of the shoot to the top.

As the ratio between the length of the lateral main nerves and that of the central one reaches its highest value in the largest and best developed leaves, we may regard a higher value of this ratio as a criterium for a better development. Whereas an increase in the value of this ratio is always accompanied by a decrease in the variation width, a decrease in the latter too may be interpreted as indicating a higher development; the optimal degree of development, its ideal value, therefore, is recognizable by the decrease of the variation width to its lowest value. When we compare the averages found for the larger leaves inserted at the base of the shoots, which are more or less well-developed (the degree of development is measured by the number of leaf pairs) we see that they are nearly the same; the variation width is in each of these groups smaller than in the shoots with a smaller number of leaf pairs. The smallest value for the variation width was found in shoots with 3 leaf pairs and for this reason we will consider the average calculated for the leaves at the base of these shoots as the ideal value of this character, i.e. the value that is characteristic for this species.

In this way the aim of this investigation, the discovery of a constant value that may be regarded as the ideal representation of a varying character, was reached (II A, a).

The same state of things was observed when we studied in the same way the ratio between the length of the lateral main nerves and the central one in *Acer cappadocicum* (II A, b) in *Platanus acerifolia* (II A, c) and in *Batrachium fluitans* (II A, d).

We found but one difference in this material, viz. that in the first named species the ideal value is, just as in *Acer palm. v. sept.*, found in the leaves inserted at the base of the shoot, with a decrease of the average value in the direction of the top (a cathodic series), and that in the two last species the ideal value occurs in the leaves inserted at the top (an anodic series). When for a more accurate determination of the ideal value in each of these species the degree of development of the shoot is taken into account, an almost fully constant value is obtained; in these leaves too the variation width reaches its lowest value. In this way we obtain the ideal value which is to be considered representative for the species.

From the study of the average value of the angle between the various main nerves too it appeared, that the variation width decreases as the angle approaches the ideal value. On account of this decrease in the width of variation the ideal value of this character was determined in *Acer cappadocicum* (II B, a) and in *Platanus acerifolia* (II B, b).

In the foregoing investigations it was assumed that the difference in the relative length of the main nerves or in the size of the angle between the latter, are indicative of the degree of development of the leaf and must, therefore, undergo changes during the growth of the latter.

The first-named assumption was based on the results of a comparison between average determined for groups of smaller and for groups of larger leaves occupying a corresponding position on the shoot.

In order to test the soundness of this assumption we carried out measurements on the leaves of *Tropaeolum lobbianum*. In the first place the average values and the variation width of the proportion between the length of the main nerves and the angles between these nerves were calculated in separately gathered full-grown leaves of different size. After that similar measurements were carried out in the same leaf in successive stages of its development. The necessary material was obtained by means of contact photos. No difference of fundamental importance was found between these two series of measurements (II C).

The study of the average length of leaves of *Acer palmatum* var. *septemlobum* (II D, a) *Acer cappadocicum* (II D, b) and *Platanus acerifolia* (II D, c) has shown that the average length of leaves inserted in successive positions on the shoot show a similar decrease or increase as the average of the proportion between the length of their main nerves.

Besides this it appeared that the greatest average length is accompanied by the lowest variability, and that there is no difference in this respect between leaves at the base and leaves at the top of the tree.

From a study of the averages obtained for the relative length of petiole and blade it appeared that the leaves with the highest average value show the smallest variation width. These measurements were carried out in *Acer Platanoides*, *Acer pseudoplatanus* and *Batrachium fluitans* (II E.)

The relative width of leaves which was studied in *Ligustrum ovalifolium* also shows the same phenomenon, viz. that the greatest width is accompanied by the lowest variability (II F).

The number of rays in the umbels of *Aegopodium podagraria* varies according to the position of the umbels on the stem, or to be more precise, according to the sequence in which they are produced. As an increase in the average number of umbel rays is always accompanied by a decrease in the variation width, the ideal value of this character is assumed to be present in the umbel which shows the lowest variation width (II G).

The method applied in the foregoing studies carried out on material collected by ourselves has also been applied to data which other investigators have found for a number of varying characters.

In the study of the size of the meshes formed by the reticulated veins of *Vitis vulpina* (III A) it appears that the variation width reaches its lowest value in the leaves in which the meshes are largest.

In a study of the internodium length of *Fagus sylvatica* (III B) the variation width proved to be smallest in those shoots in which the internodia were longest.

In *Teucrium chamaedrys* (III C) the variation width in the proportion between the number of stomata and the number of epidermis cells proved to attain its minimum value in the leaves in which this proportion reached its highest average value.

A study of the distribution of the frequency of the variates carried out for those characters of which we have ourselves investigated the variability, showed that the mean class is always best represented, as could be expected.

In the curves representing the varying characters in the groups with the ideal value, the mean class sometimes contains a larger number of variates than there are found in material showing the binomial type of frequency distribution.

The extreme plus and minus variates, which are, of course, present in a small number only, are always more numerous than was to be expected on the assumption that the frequency distribution is of the binomial type (IV).

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