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ON THE IDEAL VALUE OF VARYING CHARACTERS II [1])

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CONTENTS

Abstract

In our first paper dealing with this subject we have shown by means of a restricted number of observations made on a comparatively large number (20) of characters found in different plants that there is always a trend towards the development of an "ideal value", i.e. towards the reduction of the degree of variability towards a minimum value.

This time we have made our observations on a much larger scale but on a restricted number of characters, viz. 1) the number of juga in the imparipinnate leaves of *Sorbus aucuparia;* 2) the length of these leaves; and 3) the number of primary rays in the umbels of *Aegopodium podograria.* It appeared that the place where the ideal value is found, is determined by the position which the varying part occupies in the organism. This apparently indicates that the degree of variability is primarily determined by some internal factor.

A similar trend was observed in the degree of variability which is shown by the number of sepals and petals in the flowers of *Ranunculus ficaria* in the course of the flowering period, and in the degree of variability that was found in the shell shape of the Ostracoda *Globorotalites bartensteinii* in the successive layers of the Lower Cretaceous.

1. Introduction

It is not difficult to see that the organisms show in many of their characters a more or less considerable degree of variability. But even a superficial examination suffices to convince us of the fact that every character, no matter how great its variability may be, approaches a definite value. Because of this, even observers who have not been specially trained, can often recognize an organism with a high degree of probability by the aid of the striking, because most common, forms of certain characters.

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This obvious fact has in the past led to the supposition that it ought to be possible to find for every character a fixed value which would be specific, i.e. characteristic for the species. Especially in the beginning of this century there were many biologists who tried to find standard measures for certain characters by way of a painstaking statistical study.

They started from the supposition that it ought to be possible to find a definite average for such a character by measuring its variability in a large number of individuals which had grown up in all realisable circumstances.

We ourselves too accepted in the beginning the view of the old biometricians according to which if one studied a varying character by counting or measuring it in a large number of individuals chosen at random, one would find for this character a regular curve of variation corresponding to the curve of errors based on Newton's binomium or to one of the curves which may be regarded as derived from the latter. Its average value, which in the case of the regular variation curve corresponds to the top, would represent the characteristic or ideal value of that character.

This supposition was founded on the generally accepted opinion that variability was caused by a large number of independent and equivalent factors. In that case the coincidence of all the favourable or of all the unfavourable factors would result in an extreme plus- or in an extreme minus-variant; however it would occur far more often that a number of favourable and a number of unfavourable factors would occur together, and then a value would be obtained which would show a more or less close approximation to the average. What happens in the organism would correspond therefore to what happens in the renowned model constructed by Galton.

It is rather remarkable that, when there was talk of factors, the influence of external factors was as a rule strongly accentuated, while hardly any attention was paid to a possible influence of internal factors; that the latter should not be neglected was shown very convincingly by the results of our own studies.

When we used the methods of the early biometricians we never succeeded in finding such a fixed average value for any character at whatsoever places and times the measurements were made.

Because it was our intention that the choice of the parts we wished to measure, should be completely unbiassed, we originally took no notice of the position which the varying parts occupied on the plants nor of the condition of latter.

Although we were continuously disappointed in our wish to find a fixed average, we were in the course of our measuring and calculating more and more struck by the presence of a regularity which differed from the one we had expected.

This peculiar regularity became obvious when we arranged the variants according to the position which the varying part occupied on the plant. It became more and more evident that the degree of variability is primarily determined by the position which the varying part occupies on the plant and by such factors as the phase of development or growth and the age of the plant. We drew this conclusion from a statistical study of which the results have already been published (Acta Bot. Neerl. **4**: 273, 1955), and which concerned the variability of a fairly large number of characters found in different parts of different plants, e.g.: 1) the ratio between the length of various nerves in palmatifid leaves; 2) the size of the angle between various nerves in palmatifid leaves; 3) the ratio between the length of various nerves as well as the magnitude of the angle between the nerves in a palmatifid leaf; 4) the length of the leaf blade; 5) the ratio between the length of petiole and blade; 6) the relative leaf width in an oval leaf; 7) the number of umbel rays in *Aegopodium podagraria;* 8) the size of the meshes between the reticulated veins in the leaf of *Fagus sylvatica;* 9) the ratio between the number of stomata and the number of epidermis cells in the leaf of *Teucrium chamaedrys.*

Without doubt these characters differ widely. In spite of this, they correspond, as far as their variability is concerned, in the following points; 1) the amount of variability for every character is primarily determined by the position which the varying organ occupies in the organism and by the phase of development of the organism; 2) the degree of variability expressed by the variation-coefficient (V.C.), which always decreases the nearer the part of the plant in which the character occurs, approaches the ideal condition.

The figure for the V.C. that is found in the most perfect form, can therefore be considered to represent the ideal value of the character. In other words we notice in the variability a tendency towards a fixed value; the latter we will call the ideal value.

If the condition mentioned under 1) is fulfilled, this tendency reveals itself in the decrease of the V.C. from a sometimes high value either to zero or at least to a very small one.

In our first publication (l.c.) we gave the results of a more or less general survey of the subject, viz. of a study of the variability of a large number of varying characters in a comparatively small number of specimens. However, in continuing our investigation we limited the number of varying characters and examined a few on a more extensive scale.

In the following study it is our aim to find the ideal value of one particular character, viz. the number of juga in the imparipinnate leaves of the Mountain Ash (*Sorbus aucuparia* L.). We did not try to find a fixed average in randomly chosen leaves, but we determined how the degree of variability varies in the different categories of leaves.

In this study we are not so much interested in the absolute value of the V.C., but rather in its decrease or increase in the various categories that we could distinguish (2.1; 2.2; 2.3).

After having found a certain regularity in the variability of the number of pinnae we tried to ascertain whether the same regularity can be found in another character of the same leaf, viz. in its length (2.4).

When our expectation that we would find here the same regularity, was confirmed, we compared our results with those of our study into the varying number of rays in the umbels of *Aegopodium podagraria* (3.1).

Finally we will give an account of the variability in the number of sepals and petals of *Ranunculus ficaria* (3.2) and in an example taken from the literature on variability, viz. in the fossil *Globorotalites bartensteinii* (Ostracoda) (3.3).

2. Variability in the leaf of the mountain ash

2.1. *The material*

We started our study in 1962 by choosing 5 Mountain Ashes, all 3 years old and approx. 1.50 m high. We chose these trees because, in the midst of many others growing in a large garden, they seemed to have developed fairly regularly.

We studied the variability in the number of juga in the imparipinnate leaves of this tree, because this is an example of discontinuous variability, which has the advantage that the individual values can easily be determined.

After counting the number of juga in all the leaves on that trees we divided the leaves into 3 groups, viz.

a) leaves on long, infertile shoots which we will call dolichoblasts,
b) leaves on the short, infertile shoots, called brachyblasts,
c) leaves on fertile shoots, which we will call anthoblasts.

(To avoid confusion in the terminology we shall use for the older woody products of ramification the term "branch" and for the parts that have developed during the last year, the term "shoot".)

a) Dolichoblasts are hardly ever to be found at the base of the tree; but the top part often consists exclusively of these shoots. The internodes are fairly long, so that it was easy to determine the sequence of the leaves; the latter showed a spiral phyllotaxis. Usually there were about 9 leaves per shoot.

b) The internodes of the brachyblasts are so short that it is practically impossible to determine which is the first leaf (A) and which is the second (B); the position of the higher leaves, C and D, can usually be recognized more easily, because they are implanted closer to the centre and slightly higher; in their case the position they occupy in the spiral phyllotaxis can be recognized more readily than in that of leaves A and B.

These shoots are to be found mainly at the base and in the central part of the tree; they are hardly ever present at the end of the branch, which is the normal place for the anthoblasts.

Because there is a correlation between the number of leaves per shoot and the variability in the number of juga in the individual leaves, we would like to mention here that on the approx. 1350 brachyblasts that we examined in 1962 and 1963, the number of leaves varied from 1–5 per shoot.

In case there were more than 5 leaves the shoot began to resemble a dolichoblast owing to the more pronounced length of the internodes between the higher leaves; for this reason we left those shoots out of consideration as being of uncertain position; anyway there were but very few of them.

c) The internodes of the anthoblasts were always so long that it was easy to determine the sequence of the leaves. Of the approx. 1000 anthoblasts that we examined in the course of 1962, 1963 and 1964, we never found a single one with only 1 leaf (only leaf A), a total of only 19 with 2 leaves (A and B), 26 with 6 leaves (A, B, C. D. E. F) and 6 with 7 leaves (A, B, C, D, E, F, G.)

We therefore confined our study to the leaves on the shoots with 3, 4 and 5 leaves. We also deemed it useful to determine whether there was any difference between the 5 trees in the 3 consecutive years, and, if so, how large this difference was. In 1964 we were forced to limit our attention in the case of the leaves on brachyblasts to the trees I and V, owing to the enormous number of leaves belonging to this category found on each tree.

Furthermore we must mention once again that we did not make a random selection but have counted in the afore-mentioned categories the number of juga in all the leaves (a total of approx. 14 000 leaves). In calculating the S.D. for the following tables we did not use the equation given l.c. 281, but the less accurate one

$$\text{S.D.} = \pm \sqrt{\frac{\sum^{n}(x_i - \bar{x})^2}{n}}$$

Because we are not interested in the absolute value of S.D. and V.C. but only in their decrease or increase, we felt justified in using this simplified equation.

2.2. *Variability in the number of leaves per shoot*

First we determined how many brachyblasts and anthoblasts had 1, 2, 3, 4, 5, 6 or 7 leaves; these countings were made in 1962, 1963 and 1964. (table 1) To facilitate the survey we have given the percentage of shoots belonging to each class as well as the total number of shoots that were examined in the 3 years.

TABLE 1

Number of leaves in the brachyblasts and anthoblasts (Total for all 5 trees).

	Number of leaves per shoot 1	2	3	4	5	6	7	Total number of shoots	Aver.	S.D.	V.C.
Brachybl. 1962	5.3	18.4	41.6	32.2	2.5	—	—	320	3.1	0.90	29
1963	8.0	20.9	51.9	17.2	2.0	—	—	1042	2.8	0.76	27
1964	5.3	27.2	55.2	12.3	—	—	—	1176	2.7	0.73	27
Anthobl. 1962	—	4.8	15.9	44.4	26.9	8.0	—	63	4.2	0.96	23
,, 1963	—	—	7.5	66.5	21.7	3.3	1.0	214	4.2	0.72	17
1964	—	2.7	34.4	48.6	11.7	2.0	0.6	788	3.8	0.84	22

In case of the brachyblasts the variability has hardly changed in the course of the 3 years; with such a high values for the V.C. the difference between 27 and 29 is negligible. Shoots with 3 leaves were by far the most numerous. For the anthoblasts too the variability has hardly changed; here the majority of shoots had 4 leaves.

2.3. *Variability in the number of juga per leaf*

We will now compare the variability in the number of juga per leaf in the 3 afore-mentioned groups of shoots. Because our chief aim was to find the leaf-category with the smallest variability, we will compare the variability in the 3 groups starting with the group with the highest variability, i.c. that with the highest V.C.

a) dolichoblasts

In 1962 we examined approx. 200 and in 1963 approx. 400 dolichoblasts, each with about 9 leaves per shoot. Because in counting the juga of these leaves we discovered that their variability differed according to the position of the leaves at the top, the middle or the bottom of the shoots, we have dealt with these 3 groups separately in table 2; as the total number of leaves per shoot was 9, each of these 3 groups thus consists of 3 leaves.

To reduce as far as possible the enormous amount of figures obtained for the leaves with the different number of juga, we have not given in this table the percentages of leaves with the different numbers of juga; we only give the figures of real importance viz. average, S.D. and V.C. May the statement suffice that the number of juga varied from 4 to 9; however, leaves with 4 juga totalled only 1.5 % of the more than 5000 leaves, and in the same 5000 leaves we only found 1 leaf with 9 juga.

TABLE 2

Variability in the number of juga per leaf in the dolichoblasts.

Position of the leaves on the shoot	1962				1963			
	Number of the leaves	Aver.	S.D.	V.C.	Number of the leaves	Aver.	S.D.	V.C.
Top	643	6.8	0.87	13	1002	6.6	0.88	13
Middle	625	6.1	0.66	11	1190	6.1	0.68	11
Bottom	572	7.0	0.68	9.7	1182	6.8	0.63	9.3

The results obtained in these 2 years differ but slightly. It is remarkable that the average of the 3 lower leaves is the highest one, while their V.C. is at the same time the lowest; this last figure however is never less than 9.

We wondered whether the leaves A (at the bottom of the shoots) might not differ significantly from the leaves B and C. An investigation into this matter gave the following results; table 3.

TABLE 3
Variability in the number of juga of the leaves A and B + C in dolichoblasts.

Position of the leaves	Year	Number of the leaves	Aver.	S.D.	V.C.
A	1962	192	7.1	0.72	10
	1963	314	6.9	0.61	9
B + C	1962	380	6.95	0.66	9.4
	1963	868	6.7	0.58	8.7

Although there is a large difference in the number of leaves in these groups, the values for their average and V.C. do not differ significantly; we conclude that the V.C. of dolichoblasts does not sink below a figure of circ. 9.

b) Brachyblasts
In table 4 we give the results of our countings of the juga in the leaves found on the brachyblasts of the 5 trees in the years 1962 and 1963. As we have already stated, it is extremely difficult to determine on these shoots which is leaf A and which is leaf B; for this reason we have combined the two in this table. We have given the results of A + B on shoots with 1, 2, 3 and 4 leaves per shoot.

TABLE 4
Variability in the number of juga of the leaves A + B on brachyblasts in 1962 and 1963.

Number of leaves per shoot	Position of the leaves	Number of the leaves counted	1962			Number of the leaves counted	1963		
			Aver.	S.D.	V.C.		Aver.	S.D.	V.C.
1	A	16	6.0	0.82	14	82	6.2	0.83	13
2	A + B	115	6.1	0.65	11	416	6.1	0.74	12
3	A + B	220	6.1	0.65	11	1042	6.6	0.54	8.2
4	A + B	252	6.8	0.62	9.1	351	6.7	0.48	7.2

The average shows a definite increase from 6 to nearly 7, while at the same time the V.C. decreases; in shoots with 4 leaves (at least in 1963) the minimum was circa 7.

We also examined all the leaves on the brachyblasts of the trees I and V in 1964. There were so many of them that we did not count them on the 3 other trees; the result of these 2 trees agreed exactly with the results obtained in the 2 previous years, so that we may assume that counting the leaves of the brachyblasts of the trees II, III, IV would not have given any unexpected results.

In table 5 we give a detailed survey of the results of our countings of the juga of the leaves A + B together with the leaves C and D, as this may be regarded as a typical example of the tendency shown by the variability of all leaves on these shoots.

TABLE 5

Variability in the number of juga in leaves on the brachyblasts of trees I and V in 1964

Number of the leaves per shoot	Position of the leaves on the shoot	Tree I				Tree V			
		Total number of leaves	Aver.	S.D.	V.C.	Total number of leaves	Aver.	S.D.	V.C.
1	A	47	5.7	0.86	15	15	5.5	1.1	20
2	A + B	271	6.0	0.82	14	97	5.6	0.73	13
3	A + B	459	6.5	0.82	13	373	6.0	0.44	7.3
	C	209	5.8	0.80	14	180	5.6	0.65	11
4	A + B	77	6.8	0.61	8.9	132	6.2	0.54	8.7
	C	35	6.1	0.63	10	66	6.0	0.68	11
	D	34	5.4	0.83	15	63	5.3	0.89	17

Because these figures demonstrate so typical the tendency which is present in the variability in the number of juga in the leaves of all brachyblasts, we give in table 6 an abstract of table 5, showing the average and V.C. of the various catagories on the brachyblasts of the trees I and V.

TABLE 6

Average and V.C. for the numbers of juga counted in leaves of the brachyblasts of trees I and V in 1964.

Number of leaves per shoot	Value of the average Position of leaves			Value of the V.C. Position of leaves		
	A + B	C	D	A + B	C	D
Tree I						
1	5.7	—	—	15	—	—
2	6.0	—	—	14	—	—
3	6.5	5.8	—	13	14	—
4	6.8	6.1	5.4	8.9	10	15
Tree V						
1	5.5	—	—	20	—	—
2	5.6	—	—	13	—	—
3	6.0	5.6	—	7.3	11	—
4	6.2	6.0	5.3	8.7	11	17

Although there are individual differences between these two trees, a comparison of these figures clearly shows that the average number of juga of the leaves A + B is always higher than the average number of juga found in the leaves C and D; it reaches its highest value in the leaves on the shoots with 4 leaves.

The minimum value of the V.C. on tree V is again to be found on the leaves A + B on the shoots with 3 leaves.

Furthermore we see that the value of the V.C. never sinks below 7 in brachyblasts.

c) Anthoblasts

1) Number of leaves per shoot

The 5 trees flowered for the first time in 1962; but on trees IV and V there were in that year as yet but a very small number of anthoblasts (viz. 1 in IV and 10 in V). In 1963 the total number of anthoblasts counted on the 5 trees was three times as high and in 1964 it was again three times as high as in 1963.

However, even in 1964 we found on some of the trees that some of the groups of leaves which were distinguished by us on account of the number of juga, were represented only by just over 10 examples; in such cases the value found for the V.C. is of little importance and for this reason these small groups have not been included in the following tables.

First we must refer to the figures in table 1 (p. 97) where we gave the variability in the number of leaves per shoot. Here we can see that the number of anthoblasts in the extreme groups with 2, 6 or 7 leaves per shoot was extremely small. Of the total of 1065 shoots observed in the 3 years, only 26 had 2 leaves, 27 had 6, and 8 had 7 leaves. Because of their both relatively and absolutely small number, the figure for their V.C. is not very valuable and for this reason we have omitted them from the tables.

We also see that the majority of shoots have 4 leaves. Of the total of 1065 they account for just under 55 %. We must also mention the fact that the shoots at the end of larger branches usually had 4 or 5 leaves; the shoots with 2 and 3 leaves were usually situated in the middle or lower part of the larger branches. This character in other words showed an anodic development (J.M.; l.c.: 280).

2) Number of juga per leaf in each of the 5 trees

To simplify matters we have given in table 7 the value of the V.C. only for the number of juga in the leaves A and B.

On studying this table it appears that the V.C. is usually less than 7 for leaves A and that it can even reach the value 0.0. The V.C. of the leaves B is usually much higher than that of the leaves A (with the exception of leaf B on the branches with 5 leaves of tree V in 1964).

Trees II and V show the best results. It is noteworthy that tree II showed the best development of all 5 trees, while tree V had developed least in the course of these 3 years.

If we now determine for trees II and V the percentage of leaves with 7 juga in the same categories, we obtain the following result (table 8).

It is worth determining whether there is any difference between the leaves A on anthoblasts at the end of branches and those on anthoblasts which are situated further down the branch. On tree V all 41 leaves A situated on end shoots with 4 leaves had 7 juga and

TABLE 7

V.C. of the number of juga in the leaves A and B on the anthoblasts of the 5 trees.

Position of the leaf	Number of leaves per shoot	Year	Number of tree				
			I	II	III	IV	V
A	3	1962	—	—	—	—	—
		1963	—	—	—	—	—
		1964	7.7	4.6	5.4	5.7	4.5
	4	1962	—	4.1	—	—	—
		1963	6.1	2.1	6.1	9.2	4.5
		1964	7.2	5.9	7.4	6.6	3.4
	5	1962	—	—	—	—	—
		1963	—	1.7	—	—	—
		1964	6.5	6.2	6.0	6.0	0.0
B	3	1962	—	—	—	—	—
		1963	—	—	—	—	—
		1964	6.6	7.2	8.5	5.5	8.9
	4	1962	—	8.0	—	—	—
		1963	11	6.2	8.8	7.8	—
		1964	12	5.4	7.6	4.9	5.9
	5	1962	—	—	—	—	—
		1963	—	3.6	—	—	—
		1964	12	9.6	6.1	8.0	3.6

TABLE 8

Percentage of leaves with 7 juga on anthoblasts with 3, 4 or 5 leaves.

		Number of leaves per shoot		
		3	4	5
Tree II	1962	—	83	—
	1963	—	90	94
	1964	76	80	76
Tree V	1962	—	—	—
	1963	—	85	—
	1964	87	92	100

on the end shoots with 5 leaves all 12 proved to have 7 juga too.

While the numbers of juga in the leaves A on the anthoblasts of the other trees come very close to the ideal value of 7, this tree shows the ideal value for the full 100 %: V.C. = 0.0.

In the variability in the number of juga of its other leaves tree V also presents an ideal picture.

Because the other trees too show the tendency which this tree shows in a most ideal form (i.e. in the decrease of the V.C.) we will gave in table 9 for this tree the V.C. for the number of juga in all categories of leaves on anthoblasts with 3, 4 or 5 leaves. It is noteworthy that on this tree there were no anthoblasts with 2, 6 or 7 leaves; of the exactly 100 anthoblasts 30 had 3, 50 had 4 and 20 had 5 leaves.

One must keep in mind that this table represents an ideal condition to which the other trees tend, but which they do not attain; it is quite possible that somewhere else a tree may be found which would show for the various categories of leaves an even smaller V.C.

TABLE 9

Value of the V.C. for the number of juga in all categories of leaves found on the anthoblasts of tree V (1964).

Number of leaves per shoot*	Position of the leaf on shoot				
	A	B	C	D	E
3	4.5	8.9	28	—	—
4	2.9	5.9	9.0	73	—
5	0.0	3.6	7.7	9.3	69

This table demonstrates very clearly the course of the variability in the number of juga in the different leaves of the anthoblasts. Leaf A always shows the smallest V.C.; for shoots with 5 leaves this even sinks down to 0.0.

If we disregard the uppermost leaf on these shoots, it becomes obvious that for every anthoblast the V.C. for the number of juga increases from its lowest value (0.0) in leaf A to a value of approx. 9 in the uppermost leaf but one. We feel bound to mention here that none of the leaves on the anthoblasts was ever found to have 9 juga, and that only 2 leaves had 8½ juga (this means that one pinna of the ninth jugum was fused with the apical pinna, while the other pinna had remained free).

We can then conclude that the degree of variability in the number of juga in the imparipinnate leaves of the Mountain Ash is determined by 1) the position of the leaf on the shoot; 2) the vegetative or reproductive function of the shoot; 3) the number of leaves per shoot; 4) the position of the shoot on the branch.

These trees showed a tendency towards the production of a 7-jugate leaf. If we take tree V as an ideal example, we may state that the ideal leaf occurs as leaf A on the anthoblasts provided with 5 leaves and situated at the end of the branches.

In some other trees the V.C. reaches for leaf A the value of 0.0 on anthoblasts with 4 leaves; it may even reach that value for leaf B. It is also possible that a tree reaches in a certain category of leaves the ideal value of 0.0 in one year, only to vary more strongly in the following year, with the result that it does not reach the value of 0.0 in any category.

But it is not our intention to define the position of the ideal leaf; in fact, as we have seen that there is no sharply defined position for the ideal leaf; its position is not necessarily the same in all trees of this species.

However, it is obvious that there is a tendency towards an ideal value, and that the nearest approximation to the latter is to be found in leaves which occupy a definite position.

2.4. *Variability in the length of the leaves of the Mountain Ash*

We wondered whether the regularity that we had found in the differences in the degree of variability shown by the number of juga, would also be recognisable in the variability of other characters of these leaves. As the length is easily measurable, we decided to test this possibility by determining the differences in the variability shown by this character. Because we examined this character in the same categories of leaves as were used in our study of the number of juga, it occurred frequently that on some of the trees there were in some of the categories so few examples (less than 10) that it would have served no purpose to determine their V.C.; for this reason they are not included in table 10. The figures of the V.C. in this table are based on a maximum of 46 leaves and on a minimum of 12; normally we examined about 30 leaves in each categorie.

In 1964 we measured the length of leaves of the same 5 trees, and we also measured the same leaf categories for 2 other 5-year-old trees that had developed quite well.

Based on the results of our study of the juga we kept mainly to 7-jugate leaves A; as a random test we also measured leaf B on some of the trees.

As a rule the leaves on the brachyblasts are significantly smaller than the leaves on the anthoblasts (tree VII is an exception).

There are large differences in the length of the leaves on the different trees, but we could not find any connection between their length and the general development of the trees; tree II with its higher average length of 152 mm. is just as well developed as tree VI, where the highest average is 201 mm.

Because of these large differences in the average length of the leaves there is no point in adding up the values found for the same leaf categories in the 7 trees; this has the disadvantage that for several of the trees there are in various categories too few examples to calculate the value of the V.C.

Concerning the V.C. we found here the same trend as in the case of the juga; in most of the trees the lowest value is found in the leaves A on the anthoblasts with 4 leaves.

Sometimes we also found the lowest V.C. value in leaf B on the shoots with 4 leaves (VI) or even in shoots with 5 leaves (VII). We did not determine whether there was any difference in the V.C. in the consecutive years; this would have taken us too far from the main object of this study.

Therefore here too we found a decrease of the V.C., in other words a decrease in the range of the variability which is the larger the more

TABLE 10

Average and V.C. for the length of leaves on the brachyblasts and anthoblasts of trees I–VII.

leaf	Shoot	Number of leaves per shoot	TREE I Aver.	I V.C.	II Aver.	II V.C.	III Aver.	III V.C.	IV Aver.	IV V.C.	V Aver.	V V.C.	VI Aver.	VI V.C.	VII Aver.	VII V.C.
A	Brachyblast	2	—	—	114	6.5	—	—	—	—	—	—	—	—	—	—
		3	131	5.1	122	7.0	136	5.1	132	5.5	136	5.0	155	3.1	135	4.8
		4	—	—	135	4.1	—	—	—	—	153	5.2	152	3.5	—	—
A	Anthoblast	3	154	2.9	149	3.3	164	5.0	—	—	172	3.8	—	—	128	2.8
		4	169	2.4	151	3.1	156	5.0	151	4.8	175	3.9	195	3.8	138	5.4
		5	—	—	152	3.3	—	—	—	—	157	4.2	185	5.7	133	4.4
B	Anthoblast	4	—	—	149	4.0	—	—	—	—	—	—	201	2.8	140	3.0
		5	—	—	—	—	—	—	—	—	—	—	198	6.0	140	2.4

the character (length) develops and this notwithstanding the fact that the amount of increase in the average length is different for every tree.

The variability of both characters, the number of juga and the length of the leaves, show the same trend; *the ideal value, i.c. the value with the smallest V.C., is found in the same categories.*

3. Variability of other characters

3.1. *Variability in the number of umbel rays in Aegopodium podagraria*

In our first publication on the variability of characters we dealt a.o. with the variability in the number of rays in the umbels of *Aegopodium podagraria* (Acta Bot. Neerl. **4**: 306, 1955).

We saw in that time that in the variability of this character too a regularity can be detected, at least if one divides the umbels in groups according to the position they occupy in the plant.

Every umbel is provided with a fairly long stalk springing from the axil of a leaf inserted on the main stem.

At the top of the main stem there is always but one umbel; this umbel we have indicated with the letter "A". There are plants with only this one umbel.

On other plants we find below the umbel A a second group consisting of one or more umbels, each one at the end of a peduncle with a leaf at the base; these plants therefore have the umbels A and B.

There are also plants with 3, 4, 5, 6 or 7 of these groups of umbels, that we have termed resp. C, D, E, F and G umbels. However plants with 7 umbel groups (groups A–G) were found so rarely that we did not study them. Especially on the peduncles of umbels A, B and C we sometimes found a small side shoot that we called a secundary umbel; these were also left out of consideration (Fig. 1).

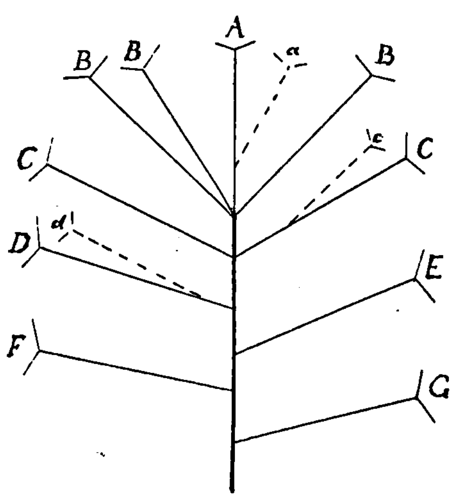

Fig. 1. Position of the umbels in *Aegopodium podagraria*. A–G: primary umbels; a–d: secundary umbels.

In this plant species the umbels are of the compound type.

We only counted the primary rays. The table that we published in 1955 (l.c. p. 306), was the result of a study of 500 plants; we later extended this study to 1065 plants, on which we counted all told approx. 100 000 rays (table 11).

These 1065 plants are divided in 6 groups: group I comprises the plants provided with the umbel groups A–F, group II those with A–E, group III those with A–D, group IV those with A–C, group V those with A and B, and group VI those with A only.

In nearly all cases the umbels were so well developed that it was easy to determine the exact number of rays; this is therefore once again an example of a discontinuously varying character.

We noted that in the groups A, D, E, and F there was usually only one umbel; group B has on the average 2 primary umbels, or even slightly more (II B); in group C there is often also more than one umbel. As to the number of umbel rays we have found that the top umbel (A) has in each of the 6 groups the lowest average; the average number then increases to a maximum which is found in the lowest group but one; (E in I, D in II, C in III, etc.) for the lowest umbel group (F in I, E in II, etc.) the average is always slightly smaller.

In each of the groups I–VI the V.C. is largest for umbel A, decreases progressively for the lower umbel groups and then increases slightly in the lowest umbel. The smallest value is reached for umbel C in group II; here is the average moreover a round figure, viz. 20.0 (accidentally?). In conclusion we can state that the variability of this character is determined by 1) the position the umbel occupies on the main stem; 2) the number of umbels produced per plant.

3.2. *Variability in the number of sepals and petals of Ranunculus ficaria*

Between 15th April and 7th May 1964 we picked every day from about one hectare of deserted wasteland about one hundred flowers of the *Lesser Celandine* and counted the sepals and petals; when we started this study we had no idea of the peculiar variability we were to find.

We looked for as many flowers as possible that had not yet fully opened, so that we might be fairly sure that no petals or sepals had as yet been dropped; the last few days (4th, 5th and 6th May) it became more and more difficult to find intact specimens; when on 7th May the very small number of flowers in the first stages of development showed that the flowering time was over, we stopped our study.

The number of sepals varied from 3 to 6; very rarely did we find a specimen with only 2 sepals. When there were 3, there was an angle of 120° between them. From the fact that, when there were 2, there was also an angle of 120° between them, we concluded that the third sepal had already been dropped; at any rate we did not take these calices into consideration; they were very rare anyway,

TABLE 11

Variability in the number of primary umbel rays on the *Aegopodium podagraria*.

Position of the umbels	Group I: Number of the umbels	I: Aver.	I: V.C.	II: Number of the umbels	II: Aver.	II: V.C.	III: Number of the umbels	III: Aver.	III: V.C.	IV: Number of the umbels	IV: Aver.	IV: V.C.	V: Number of the umbels	V: Aver.	V: V.C.	VI: Number of the umbels	VI: Aver.	VI: V.C.
A	150	13.1	18.3	310	13.6	21	230	14.4	19.3	200	16.3	13.0	120	15.8	12.6	75	15.5	12.4
B	294	18.2	13.4	659	17.9	13.4	418	18.8	13.2	390	19.3	12.3	226	16.7	15.5	—	—	—
C	187	19.9	13.2	366	20.0	11.4	243	19.7	13.0	200	18.9	14.2	—	—	—	—	—	—
D	155	20.8	12.9	310	20.2	12.2	230	19.1	15.0	—	—	—	—	—	—	—	—	—
E	150	21.1	13.4	310	19.2	15.6	—	—	—	—	—	—	—	—	—	—	—	—
F	150	20.9	15.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

certainly in the first weeks of our study. The number of petals varied from 5 to 9. It is possible that in the cases where there were less than 9, a few had already been dropped.

However, we only took flowers into account that had not yet fully opened, so that they were in the first stages of development; furthermore, the regular spacing of the petals in the flowers with a smaller number of them seemed to prove that no petals had as yet been shed; and finally we found these minus variants mainly in the first days of our study when the flowers were still at the beginning of their flowering time so that the petals hardly ever had been shed.

In table 12 we have given the percentages of the various variation classes, as we found them on the various days, as well as their average, S.D. and V.C.

From this table it is clear that on the first day the variation, both among the sepals and among the petals, was quite considerable and that it then became progressively less until on May the 3rd a minimum was reached; on that day of the 163 (!) flowers 98 % had 3 sepals and 95 % had 8 petals (the counting became quite monotonous!).

After May the 3rd the variability, both among the sepals and among the petals, showed a slight increase; we even found for the first time since April the 16th a specimen with 6 sepals.

Although we did not check this, we concluded from this table that each flower did not persist more than a few days. For if each flower had persisted about three weeks, it would have been quite a coincidence if we had, in our random selection over the whole area, always picked just those specimens, that showed the progressive decrease in their number of sepals and petals.

In trying to explain this highly peculiar trend in the variability of the sepals and petals, one is, of course, inclined to look in the first place to the environment.

But we may point out that all conceivable environmental factors varied enormously and quite irregularly in the course of our investigations. Some plants grew in broad sunlight, others in the shade of fairly thick foliage; we found them in ditches as well as on higher parts; sometimes surrounded by grass, sometimes by rotting leaves; sometimes they were on dry ground, sometimes in a fairly damp environment.

The temperature, too, varied unpredictably; sunny days and cloudy or rainy days followed each other without the slightest regularity; strong winds were followed by complete calm, etc.

In any case it is impossible to think of an environmental factor that did not vary considerably and irregularly over the whole stretch and in the course of the weeks in which the flowers were plucked. For this very reason it is remarkable that, in spite of all this, the variability decreased so regularly, the V.C. decreasing almost to 0.0.

It is therefore extremely difficult to regard those highly inconstant external factors as the cause of the perfectly regular decrease in V.C. observed in our study of these 2 characters.

Even more clearly than in the case of the leaves of the Mountain

TABLE 12

Variability in the number of sepals and petals in *Ranunculus ficaria.*

Date	Number of flowers	SEPALS							PETALS							
		3	4	5	6	Aver.	S.D.	V.C.	5	6	7	8	9	Aver.	S.D.	V.C.
April 15	35	43	23	34	—	3.9	0.88	22	3	8	36	53	—	7.1	0.86	12
16	82	32	44	23	1	3.9	0.76	19	—	18	43	39	—	7.2	0.76	15
18	100	57	31	12	—	3.6	0.70	20	1	8	18	72	1	7.6	0.70	9.2
19	100	60	25	15	—	3.6	0.74	21	—	7	29	61	3	7.4	0.69	9.0
20	94	62	26	12	—	3.5	0.69	20	—	6	10	80	4	7.8	0.59	7.6
21	92	66	24	10	—	3.4	0.55	16	—	4	12	76	8	7.9	0.61	7.6
23	77	86	13	1	—	3.1	0.43	14	—	1,5	9	88	1.5	7.9	0.39	4.9
25	100	86	12	2	—	3.1	0.47	15	—	—	5	93	2	8.0	0.26	3.3
27	100	88	9	3	—	3.1	0.46	15	—	2	7	89	2	7.9	0.44	5.5
29	100	90	10	—	—	3.1	0.39	13	—	—	1	98	1	8.0	0.14	1.8
30	100	93	6	1	—	3.1	0.33	11	—	—	5	94	1	8.0	0.24	3.0
May 1	95	92	8	—	—	3.1	0.31	10	—	—	6	93	1	8.0	0.25	3.2
3	163	98	2	—	—	3.0	0.14	5	—	—	4	95	1	8.0	0.22	2.6
4	111	92	6	2	—	3.1	0.37	12	—	2	10	86	2	7.9	0.44	5.6
5	103	93	5	1	1	3.1	0.44	14	—	—	9	90	1	7.8	0.39	4.2
6	126	90	8	2	—	3.1	0.42	14	—	2	5	92	1	7.9	0.33	4.1
7	114	89	10	1	—	3.1	0.36	12	—	—	5	93	2	8.0	0.27	3.4

Ash, we here see 2, probably independent characters, viz. the number of sepals and petals, varying in opposite directions, but otherwise in exactly the same way.

In this species we see again a tendency, both in the case of the sepals, and in that of the petals, toward a definite (ideal) value; in the sepals a low one, viz. 3 and in the petals a high one, viz. 8.

By counting the total number of flowers with a definite number of sepals or of petals, as the early biometricians would have done, we obtain the result depicted in fig. 2.

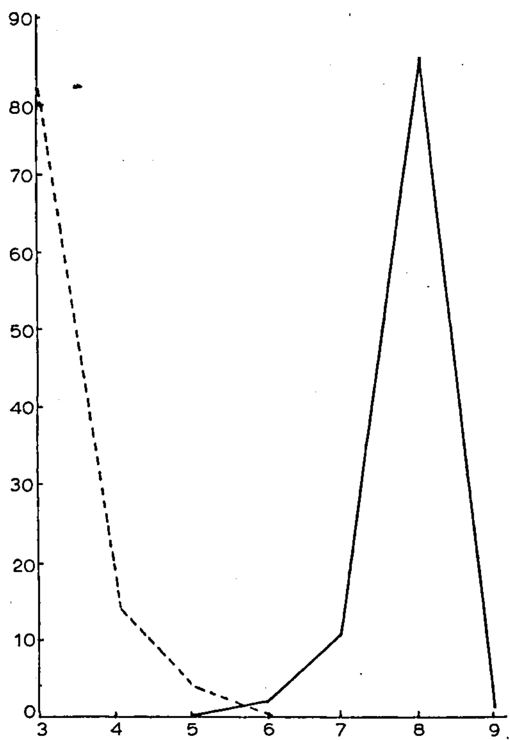

Fig. 2. Frequency of the flowers of *Ranunculus ficaria* differing in the number of sepals and petals. Horizontal: number of sepals and petals. Vertical: percentage of flowers. -------: sepals; ——— petals.

We see two asymmetrical curves, of approximately the same shape as the early biometricians so often had found. The character of these curves is determined by the way in which the flowers were brought together. This way is not sufficiently discriminative to ensure a collection, which, when statistically created, might shed some light on what is going on in the plant.

These curves, therefore, of little or no value to the biologist, because there is no definite connection with processes that are of biological importance; it would therefore be rather pointless to calculate the average, S.D. and V.C. values.

This example demonstrates quite clearly that the haphazard totalling of figures for varying specimens does not lead to useful results.

Biology is here practized as a form of mathematics, instead of by the aid of mathematics.

The mathematical treatment of the figures should be preceeded by their division in groups, which on biological grounds may be regarded as natural ones. Only if this prescription is followed, the differences observed either in the average, the shape of the curve or the V.C. have any meaning.

3.3. *Variability in Globorotalites bartensteinii*

We happened to find in a paleontological journal a study on the variability of a fossil animal. Because we believe that we can draw

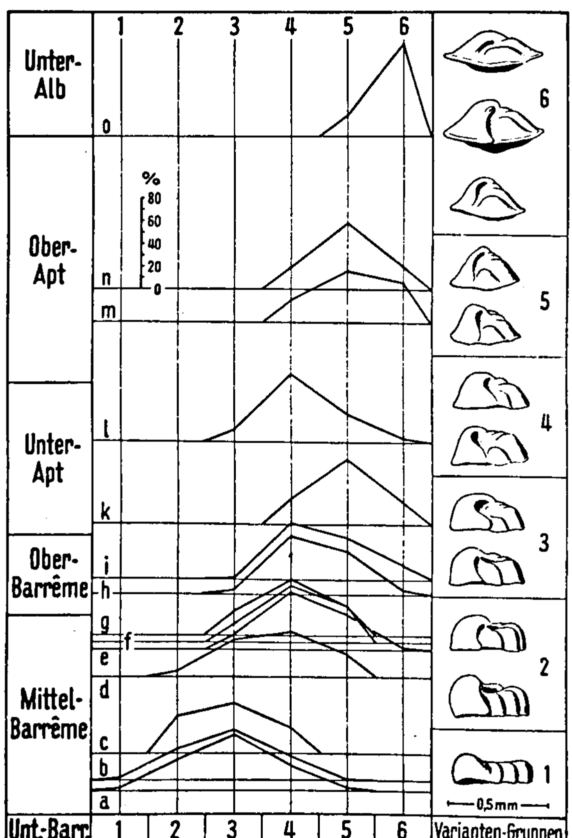

Fig. 3. Frequency of the different shell types of *Globorotalites bartensteinii* found in the consecutive layers of the Lower Cretaceous (after Bettenstaedt). Horizontal: Classes of variants. Vertical: Periods of the Lower Cretaceous. To the right the shell types brought together in the classes 1–6.

TABLE 13

Variability in *Globorotalites bartensteinii.*

Position	Number of specimens	Classes 1	2	3	4	5	6	Aver.	S.D.	V.C.	Period
o	224	—	—	—	—	20	80	5.8	0.43	7.5	Lower-Albian
n	104	—	—	—	19	60	21	5.0	0.63	13	
m	106	—	—	—	20	44	36	5.2	0.75	14	Upper-Aptian
l	64	—	—	10	64	22	4	4.2	0.69	16	
k	54	—	—	—	21	58	21	5.0	0.65	13	Lower-Aptian
i	39	—	—	2	48	36	14	4.6	0.57	12	
h	50	—	—	4	52	40	4	4.4	0.54	12	Upper-Barrian
g	101	—	—	23	50	27	—	4.1	0.71	17	
f	217	—	—	16	50	34	—	4.2	0.79	19	
e	118	—	—	12	50	34	4	4.3	0.73	19	
d	201	—	6	32	40	22	—	3.8	0.82	21	
c	36	—	36	44	20	—	—	2.9	0.73	25	
b	43	4	30	45	21	—	—	2.8	0.82	29	
a	106	4	25	46	21	4	—	3.0	0.89	30	Middle-Barrian
											Lower-Barrian

important conclusions from it, we wish to refer here briefly to this publication.

Bettenstaedt (Paleontologisches Zeitschrift, Bd. 32, 1958) has carried out some statistical investigations with regard to the fossil shells of an Ostracoda (*Globorotalites bartensteinii*); these shells were found in consecutive layers of the Lower Cretaceous; he distinguished 6 classes, which he described as follows; (although the descriptions of these 6 classes are perhaps of little value for the uninitiated, we felt bound to reproduce them for the sake of completeness.) (see fig. 3).

Top view of the shells (approx. 0.5 mm.)	Sum total of the angles (in degrees) between the umbilical and the spiral side.
Class	
1 Rectangular; flat	207–180
2 Rectangular; high	207–180
3 Obtuse-conical; one side oblique	178–155
4 Obtuse-conical; both sides oblique	157–129
5 Pointed-conical; high	130–115
6 Pointed-conical; flat to bell-shaped	115– 85

The specimens were found in layers from the Middle-Barrian to the Lower-Albian, a period covering at least some millions of years. Table 13 gives the percentage with which the classes are represented, as well as their average, S.D. and V.C. Once again we find an increase in the average value in combination with a decrease of the V.C. The small variability in the uppermost series is remarkable; here 80 % of the specimens belong to the ideal class.

Bettenstaedt is of the opinion that this shifting is not due to geological or climatological changes; he ascribes it to an infra-specific ortho-selection.

In this table we again see an obvious trend towards a definite shape. This case is the more peculiar because we see here the same trend in the degree of variability as in the case of the Lesser Celandine; the only directly observable difference is in the length of time; in the Lesser Celandine the whole process takes a few weeks, in this Ostracoda it takes some millions of years.

The decrease in variability can be attributed to an internal force, a trend, as we have said before. In the case of the Lesser Celandine this directed variability has influenced only the phenotype, while in the Globorotalites this trend affects the genotype. This is what Bettenstaedt expresses with the term "infra-specific ortho-selection". However in both cases there is an internal trend which finds its expression in a decrease of the variability.

Finally, from the above it is clear that the varying characters of organisms show a tendency towards an ideal value. What this tendency is, can not be explained. This applies also to the trends observed in the course of the evolution. However, in neither case the fact that we cannot explain it, can warrant a denial of the existence of such a tendency.

ACKNOWLEDGEMENT

At the completion of this study I wish to express my sincere thanks to Prof. C. E. B. Bremekamp (Utrecht), for his valuable advices, his sagacious criticism and his disinterested devotion to my work.