

## Longitudinal Symmetry in Phanerogamia

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*Phil. Trans. R. Soc. Lond. B* 1909 **200**, 57-115  
doi: 10.1098/rstb.1909.0002

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## II. *Longitudinal Symmetry in Phanerogamia.*

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*Communicated by* Dr. D. H. SCOTT, *F.R.S.*

(Received January 24,—Read February 21,—Received in revised form November 28, 1907.)

### INTRODUCTION.

ALTHOUGH the transverse symmetry of Phanerogamia, as revealed by measurements of the angles of divergence of vegetative and floral leaves, has been very amply investigated, the subject of longitudinal symmetry has scarcely been touched. The reason for this is not far to seek. Early in the history of botany it was discovered that the successive leaves of a flowering plant are separated in a transverse plane by angles that are more or less equal, measurable, and constant under varying conditions; but that the longitudinal distances apart of successive leaves are obviously unequal and affected by external conditions, so that their measurements often seem to form an irregular series.

The first object of this paper is to demonstrate a *graphic method* of recording, in an easily perceptible manner, the quantitative relations existing among the longitudinal distances apart of successive leaves.

Such longitudinal measurements may be of threefold value :—

(i) They are usually capable of more exact estimation than are angles of divergence.  
 (ii) If the longitudinal arrangement of leaves be found to be governed by certain laws of symmetry, and to exhibit inherent features that are certainly independent of mechanical influence, then light will be shed upon the validity of various modern mechanical theories of phyllotaxis, which thrust into the background the consideration of the part played by ancestry and by undetermined physiological characters.

(iii) These measurements may prove to be of value in solving morphological problems, and in providing a statistical basis for the diagnosis of living or fossil species, genera, or families.

The following historical sketch recounts the views held up to the present time in regard to the lengths of internodes.

In 1727 HALES (1) noted that certain stems formed in one season exhibited *an increase and a subsequent decrease in the lengths of their successive internodes.*

In 1842 HARTING (2) again directed attention to this rise and fall in the lengths of the internodes of one axis, but he also proved that the mean lengths of cells taken from the same tissues in the different internodes do not vary proportionately. This

latter fact was confirmed by MOLL (3) in 1876. (And I may here add that my observations on the epidermis of *Lanium album* yield the same result.)

In 1878 ASKENASY (4) added the information that, in some cases, the first internodes of an axis are the longest.

In 1883 MACCHIATI made observations on *Lonicera chinensis*, which WIESNER (5) describes in the following words: "Here a remarkable case occurs, namely, that, independent of external circumstances, the first internodes increase in length, then decrease, and once more increase, until near the end of the shoot is another decrease in the internodes." The probable explanation of this case will be given in the sequel.

Finally, what may be regarded as the view commonly held may be gleaned from a quotation from the new edition of PFEFFER'S 'Physiology of Plants' (6): "The leaves and internodes on every shoot increase in size from below upwards. . . ."

Stress must be laid on the fact that, when the statements given above are true, they concern solely the shoot produced during one vegetative season. On such a shoot it is very common to find that the successive internodes wax and wane in length from below upwards, but, as I shall prove hereafter, this is far from being universal, indeed, many branched herbs provide exceptions.

Only few *explanations* of this increase and decrease of internode-length have so far been put forward. HALES correlated the increase with increased vigour of nutrition, associated with enlarged leaves and rise in temperature, and he attributed the final decrease to rapid hardening of the tissues in the dry, hot summer and to cool autumn nights. Other botanists, too, have ascribed the preliminary increase to rise in temperature in spring, and the final decrease to fall of temperature in autumn, or to deficient supply of water to the growing-points.

These explanations, involving the assumption that external factors are the cause of the phenomenon, are excluded by the following facts :—

(1) In European trees, whose twigs exhibit these internodal features, the internodes have completed their growth in length before the cool autumn days or nights.

(2) In some species of European trees, when two crops of foliage are produced in one normal vegetative season, the internodes produced during that season display a double rise and fall in length (see BÜSGEN, 7).

(3) Trees growing in permanently humid, warm, tropical forest show the rise and fall of internode-length (RACIBORSKI, 8), even though the twigs concerned on one and the same individual tree may have grown out at utterly different times of the year (A. F. W. SCHIMPER, 9).

(4) Some submerged aquatic plants, whose shoots conclude their growth in length before autumn, show the same features in regard to length of internode; this I have proved to be true of *Elodea* and *Myriophyllum*.

(5) Finally, in an interesting paper (10) issued during the somewhat slow progress of my work, TINNÉ TAMMES has proved that the rise and fall in length of the

internode of an axis are independent of the functional activity of the leaves on that axis; this proof she furnished by removing a greater or smaller number of leaves from stems during their growth, and subsequently measuring the mature internodes.

The increase and decrease of internode-length along a shoot produced in one vegetative season are not directly due to variations in temperature, illumination, or water supply; the cause is inherent, as will be proved in detail later in this paper. Such inherent longitudinal symmetry in Phanerogamia has long been recognised, without, however, having been considered. Species, genera, or even families, may be characterised by the possession of radical leaves, or inflorescences of definite form (umbels, capitula, "interrupted spikes," and so forth), in which the successive internodes show inherent correlation as regards length.

So far, I have referred solely to the relative lengths of the internodes along a single axis to which previous observers have confined their attention. In regard to the relative longitudinal symmetry of an axis and its branches, the observations so far published are limited to a few measurements dealing solely with the complete lengths of the stems in question, and to more numerous ones dependent on mere inspection and dealing mainly with inflorescences. Yet definite and remarkable relations subsist between the (relatively) main axis and its (relatively) secondary axes as regards internode-lengths and resultant longitudinal symmetry. The branches provide a most interesting series of deviations from the relatively main axis as regards lengths of their successive internodes; in particular, a branch often shows no increase and decrease in the lengths of its successive internodes. But the relation between axis and its branches as regards internode-lengths can only be clearly appreciated by the employment of some such graphic method as is here introduced.

#### METHOD.

Each measurement was made from the lower face of the base of one leaf at its point of insertion on the stem to the corresponding point in connection with the next higher leaf. Therefore each distance measured was, not an internode, but an internode together with a node. These longitudinal distances in this paper are referred to as *interfoliar spaces or distances*, and the parts of the stem that they represent are termed *segments* (or, sometimes when no inaccuracy of conception is introduced, internodes). For reasons that will become apparent subsequently, when two or more leaves occurred in connection with one node, the longitudinal distances from leaf to leaf at the node were recorded (naturally as zero when the leaves were inserted at exactly the same level). Only exceptionally was any attempt made to measure accurately to less than half a millimetre.

From the measurements of the successive segments, curves were constructed on squared paper (with 10 meshes to the inch) in the following manner. The lengths of

the successive interfoliar spaces were recorded as successive ordinates. Consequently, when two shoots of one species be considered, if the measurements commence at the same point (say at the cotyledonary node, or at the point of insertion of a branch), the two resultant curves are perfectly comparable, that is to say, the ordinates at the same abscissal distances are, in a sense, homologous. The curve thus constructed is termed the *internode-curve*, because it presents a correct picture of the relative lengths of the successive internodes, though the measurements really made were of segments.

The remainder of this paper is divided into two parts :—

- Part I. *Survey of Results*, describing the particular results obtained, though not in minute detail.  
 Part II. *General Considerations and Conclusions*.

#### Part I.—SURVEY OF RESULTS.

##### *Rhinanthus Crista-galli* (LINN.). (Curves 1–4.)\*

A typical *internode-curve* of the main stem of a herb shows an ascent followed by a descent, corresponding to the gradual increase and decrease in length of the successive segments. Two features stand out in reference to the curve: the first is its surprising regularity, and the second is the strong likeness between the curves of all individuals belonging to the same species (under the same environment). This curve is characteristic of the species, though naturally modified by changes in the surroundings. The same characters reappear in the curves of many erect shoots emitted from the subterranean shoots of herbs, also of the year's growth of twigs of trees. This ascending-descending type of curve may, for the sake of brevity, be termed the "normal" curve.

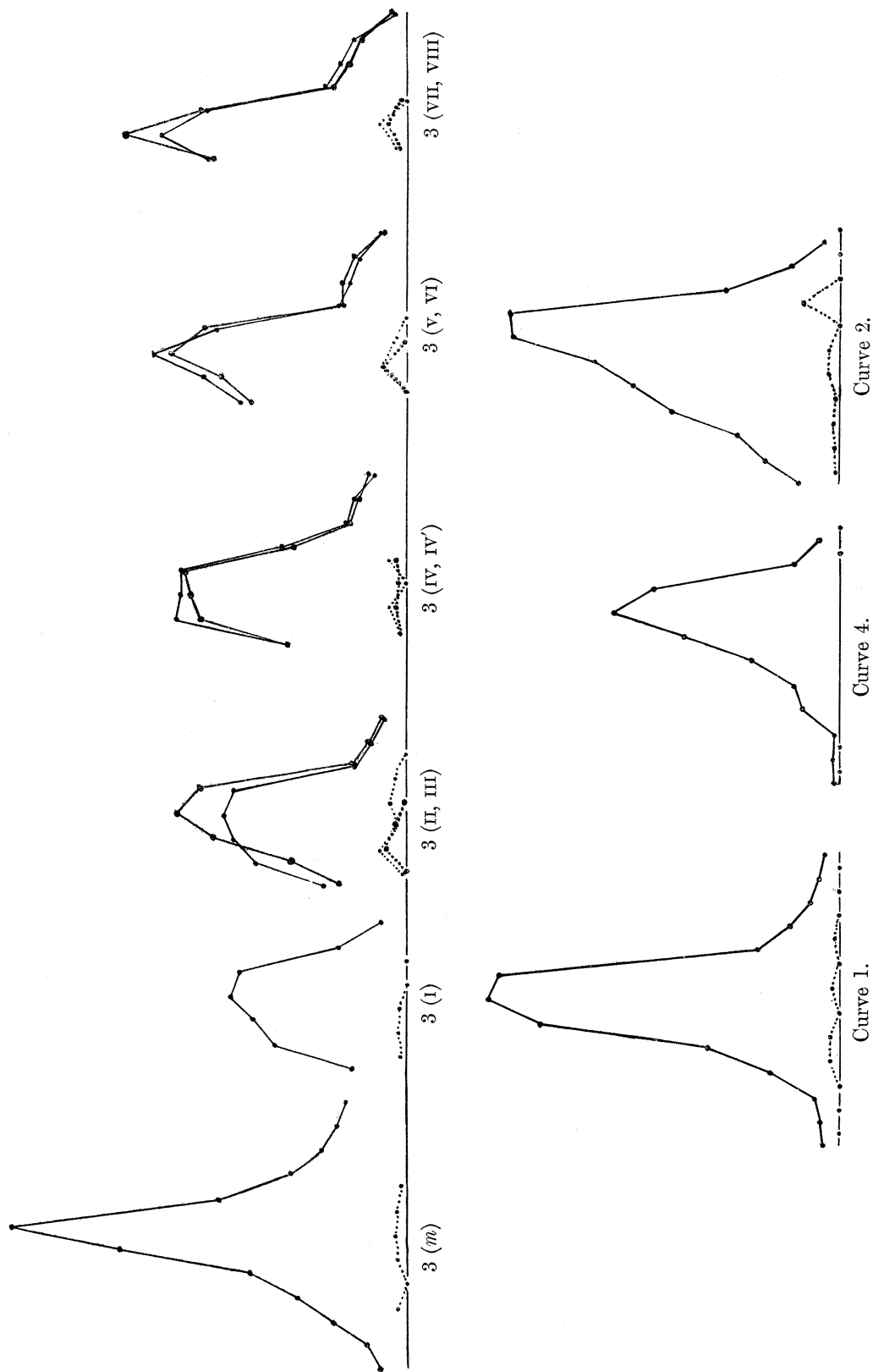
The main stem of *Rhinanthus Crista-galli* (LINN.) excellently illustrates the truth of the preceding remarks. Measurements were commenced at the lowest recognisable node, which may have been in all cases (save a few exceptional ones, hereafter mentioned) the cotyledonary node. In some instances the highest segments measured may not had completed their growth in length.

Twelve specimens of this opposite-leaved species were measured, and in this paper are termed Individuals I–XII. A regular normal *internode-curve* characterises the main stem of Specimens I, II, IV, V, VI, X, and XII, as is rendered clear by an inspection of Curves 1, 2, and 3 (*m*), here printed. The subjoined table gives the statistics. The heading designates the specimen concerned. Each vertical line denotes the lengths of the successive interfoliar distances of one axis in millimetres. The numbers printed in smaller type denote the leaf-displacements at the nodes. After the eleventh segment these were all reduced to zero, that is, the leaves were

\* For general explanation and description of curves, see pp. 112–115.



LONGITUDINAL SYMMETRY IN PHANEROGAMIA.



exactly opposite, so that in the table only the internode-measurements are given after the twelfth horizontal series. The last vertical column gives the sum of the successive horizontal series and thus provides means for constructing the composite or mean internode-curve of these specimens. This composite curve is not printed, but is of remarkable regularity. The maximal measurements are enclosed in square brackets. The letter C in the table denotes the position of the "critical" node, namely, that immediately preceding the acropetal terminal spike. Its varying position shows that the position of the first flowers in the inflorescence does not determine the form of the internode-curve and that the converse is not true.

*Internode Curve of Main Stem of Rhinanthus Crista-galli.*

No. of Internode } }	I.	II.	IV.	V.	VI.	VII.	X.	XII.	Composite curve.
1. . . .	5·5	3	3·5	6	2·5	3	8·5	5·5	37·5
	0	0	0	0	0	0·5	0·5	0	1
2. . . .	7·5	3·5	3·75	10	13·5	5	15·5	8·5	67·25
	0·5	0	0	0	0	0	0·75	0	1·25
3. . . .	10	5	5·5	12	11·5	7	21·5	15	87·5
	1	0	0	0	0·5	0	1	2	4·5
4. . . .	21	11·5	14·5	29	17·5	9·5	35	23	161
	0·75	0	2	1·75	0	0·5	0·5	0	5·5
5. . . .	26	21	28	38	27·5	17	43·5	33·5	234·5
	0	0	2	3·5	1	2	2·5	1·5	12·5
6. . . .	35	27	63	50	42·5	32	51·5	60·5 C(?)	361·5
	0	2	0	1·25	0	0	2·5	2	7·5
7. . . .	44	48·5	[74] C	[63·5]	56	43·5	68·5	84 C(?)	482
	0	2	1·5	1·5	0	1·5	0	2	8·5
8. . . .	[58]	50·5	71·5	61·5 C	55	[45]	[69·5] C	39	450
	0	4	0	0	0	0	7·5	1·5	13
9. . . .	56·5	72·5	17·5	35	[77] C	42·5 C	24	24	349
	1	1·5	1	0	2·25	0	0	0	5·75
10. . . .	36·5	[89] C	10·5	7	34 C	18	10·5	18	223·5
	0	0·5	0	0	0·5	0	0	0	1
11. . . .	14 C	20	6·5	5	13	9	3·5	14	85
	0	0	0	0	0	0	0	0	0
12. . . .	6·5	9·5	4·5	3	6	—	—	12·5	42
13. . . .	—	5	3	—	—	—	—	12	20
14. . . .	—	4·5	—	—	—	—	—	11	15·5
15. . . .	—	—	—	—	—	—	—	5	5

(The internode-curves of Specimens IV, X, and XII are printed respectively as Curves 1, 2, and 3m.)

The secondary (plagiotropous) vegetative axes of herbs display internode-curves different from that of the primary axis (or orthotropous axes). In the herbs that I examined, the following rule prevailed, even when the erect shoots were not true main stems but were relatively main axes springing from underground parts:—*The nearer the insertion of a branch to the base of the main axis, the more closely does its internode-curve conform with that of the latter, and the nearer its insertion to the apex of the main axis, the more does its internode-curve approximate to a purely descending*

curve. Thus the successive branches commencing from below and travelling up the main stem, show in their internode-curves transitions from a normal (ascending-descending) one to a descending one. This is clearly shown in the curves of the branches of Specimen XII of *Rhinanthus Crista-galli* (Curves 3 (I-VIII)).

In *Rhinanthus Crista-galli*, the branches commencing at the "critical" node are basipetal in development. Traced down the main stem, the branches show a relative or even absolute increase of vegetative vigour, as measured by number of foliage leaves, and a decrease of reproduction vigour, as measured by number of flowers. At the critical node the buds may remain dormant, or develop into flowers, or into short branches that soon produce terminal spikes.

The subjoined table giving the statistics is drawn up on the same plan as the preceding one, except that after the first vertical column representing the main stem, the remaining vertical columns refer to the successive branches on it, numbered from below upwards. The pairs of branches in connection with the same node are bracketed. The numbers in the last horizontal line denote the total lengths of the stems (all of which had practically completed their growth in length).

*Main Stem and Branches of Rhinanthus Crista-galli XII.*

	Main stem.	Branch 1.	Branch 2.	Branch 3.	Branch 4.	Branch 4'.	Branch 5.	Branch 6.	Branch 7.	Branch 8.
1	5.5	11.5	17.5	14	25	25	35	32.5	41.5	40.5
	0	1.5	0.5	0	1.5	1.5	0	0	2	1.25
2	8.5	28	32	24	[48]	43	42.5	38.5	[51.5] C	[58.5] C
	0	2	5.5	4	3.5	2	5.25	4.75	5.5	3.5
3	15	32	36.5	40.5	[47.5]	45	[53] C	[49.5] C	42	43
	2	1.75	2	2	0	1.5	2.5	0	0	0.75
4	23	[37]	[38.5] C	[48] C	[47.5] C	[46.5] C	40	42.5	17	15.5
	0	0	3.5	0	3.5	2	0	0	0	0
5	33.5	35 C	36.5	43.5	26	23.5	14.5	13.5	13.5	12
	1.5	0	2.5	0	0	0	0	0	0	0
6	[60.5] C(?)	14.5	11	11.5	12.5	12	12	13.5	11	9.5
	2	0	0	0	0	0	0	0	0	0
7	[84] C(?)	5.5	7.5	8	11	9.5	10	11	2.5	3
	2	—	0	0	0	0	0	0	—	—
8	39	—	4.5	4.5	6.5	7.5	6.5	5	—	—
	1.5	—	—	—	—	—	—	—	—	—
9	24	—	—	—	—	—	—	—	—	—
	0	—	—	—	—	—	—	—	—	—
10	18	—	—	—	—	—	—	—	—	—
	0	—	—	—	—	—	—	—	—	—
11	14	—	—	—	—	—	—	—	—	—
	0	—	—	—	—	—	—	—	—	—
12	12.5	—	—	—	—	—	—	—	—	—
	0	—	—	—	—	—	—	—	—	—
13	12	—	—	—	—	—	—	—	—	—
	0	—	—	—	—	—	—	—	—	—
14	11	—	—	—	—	—	—	—	—	—
	0	—	—	—	—	—	—	—	—	—
15	5	—	—	—	—	—	—	—	—	—
	0	—	—	—	—	—	—	—	—	—
Total	374	168.75	198	200	232.5	219	221.25	210.75	186.5	187.5



These statistics are graphically represented in Curves 3*m* and 3(1)–3(VII, VIII). The internode-curves of the branches inserted successively higher up the main axis show the gradual change from a normal curve towards a purely descending curve, though this is not actually attained. The curves also show the striking resemblances between the internode-curves of the pairs of branches inserted in connection with the same nodes, namely, 2 and 3, 4 and 4', 5 and 5', 7 and 8. In addition, these branches composing the pairs agree tolerably closely in length, as is shown in the table.

The change in the internode-curve of the successive branches is accomplished by a relative (and absolute) lengthening of their basal internodes as the insertion of the branches rises, and, secondly, by a shortening of their more distal internodes. If the lengthening of the basal internodes takes place at a greater rate than the shortening of the distal ones, the internode-curve of the branch concerned will acquire two maxima and show a double ascent and descent. This and the general nature of the changes here discussed are shown in the accompanying illustrations (fig. 1), which

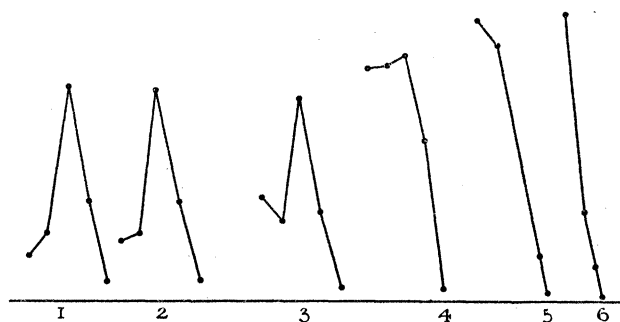


FIG. 1.

show a schematic series of transitions from the internode-curve of the main axis (1) to those of successively higher branches (2–6). This explains the double maximum exhibited by the internode-curves of branches very commonly exhibited at certain heights up a relatively main axis; and probably explains the case already cited of *Lonicera chinensis*, as having been described by MACCHIATI; and above all it throws light on the remarkable nature of the longitudinal symmetry in Chenopodiaceæ about to be discussed. But one important point proved is that there may be introduced into an internode-curve an apparent irregularity—a zigzag—that in reality is evidence of correlated growth and of a transition from one type of longitudinal symmetry to another, but is not due to external influence.

#### *Chenopodiaceæ.*

The internode-curve of a main axis does not always assume the normal form. The main stem of *Atriplex rosea*, for instance, shows “internodes” that are apparently irregular in length, and, at first sight, seem to follow no rule in this respect, except that at the base long and short internodes constantly succeed one another. But the

*internode-curve* at once reveals a hidden type of symmetry, for it assumes a characteristic, but tolerably *regular zigzag form, with a general ascent and descent* (see the plain line in fig. 2). This peculiarity is not confined to single individuals, single

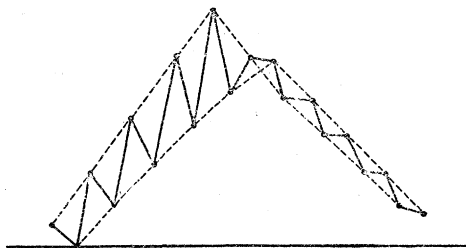


FIG. 2.

species, nor single genera, but it recurs in all the alternate-leaved *Chenopodiaceæ* that I have examined. Moreover, the zigzag reappears in the branches of the same plants. The regular zigzag occurs in the internode-curves of prostrate and erect shoots, of shaded and completely illuminated shoots, in littoral and inland species, in moist and dry soil; moreover, the crests and furrows occur respectively at exactly the same points on corresponding axes. (This statement, of course, does not refer to additional irregularly occurring crests or furrows induced by external change or certain internal changes.) Hence the recurrent zigzag in the internode-curve of alternate-leaved *Chenopodiaceæ* is inherent, and not due to external changes.

Mere inspection makes it evident that this curve can be analysed into two partial curves, or sub-curves, which are normal (ascending-descending) in form, and are made by joining the alternate ordinates in place of the successive ones. (An imaginary case of the kind is shown in fig. 2, in which the two sub-curves are printed in dotted lines.) The upper sub-curve, especially during the ascent of the internode-curve, represents a series of long segments, and the lower sub-curve a series of short segments. Now, if the lower sub-curve be traced to the cotyledonary node, or sometimes to the node above this, it descends to zero, because the leaves become opposite. This suggests that the short segments arise by the separation of two originally opposite leaves at a node, the one leaf being carried relatively upwards; thus the lower sub-curve would denote a series of longitudinal displacements of leaves, changing from an opposite to an alternate arrangement. Hence I term this sub-curve the "*displacement sub-curve,*" or "*displacement curve,*" and the other sub-curve the "*internode sub-curve.*"

Although several explanations of this peculiarity in the *Chenopodiaceæ* present themselves, here evidence is given only in favour of the view which I believe to be correct, namely, that *the alternate-leaved Chenopodiaceæ have a phyllotaxis transitional between alternate and opposite, and that opposite phyllotaxis is primitive in this family.* The evidence is as follows:—

- (i) The zigzag curves are universal in all axes of the various alternate-leaved

Chenopodiaceæ examined, *e.g.*, *Atriplex rosea*, *A. hortensis*, *Salsola Kali*, *Chenopodium Bonus Henricus*.

(ii) Some Chenopodiaceæ are opposite-leaved throughout, and in the sole species (*Salicornia herbacea*) examined the internode-curve of the main axis is a normal one, ascending and descending without the peculiar zigzag. This is shown in Curve 7. The lengths of the successive internodes were in millimetres: 7, 10·5, 10·5, 12, 10, 9, 8, 4·5, 3·25, 2·25, 1·75.

(iii) In various species, transitions from opposite or sub-opposite to alternate phyllotaxis occur, as in *Kirilovia*, *Alexandra*, *Halarchon*, *Halopeplis*, *Rhagodia*, *Petrosimonia*.

(iv) Even in *Atriplex*, whose leaves are mainly alternate, one finds opposite leaves not merely occurring at the base of the main stem, but suddenly reappearing on some branches. This sudden appearance of opposite foliage-leaves high up the plant seems more simply explained as a reversion than as a casual sport.

(v) The angles of divergence of leaves and branches near the base of *Atriplex rosea* approximate to those of decussate phyllotaxis. The first two foliage-leaves being actually or approximately separated by a divergence of 180°, the next pair of leaves are approximately decussate in reference to these, and, in prostrate individuals of *Atriplex rosea*, the decussate arrangement of the first four branches subtended by these leaves is very marked.

(vi) The occurrence of other displacements in the Chenopodiaceæ lends support to the view now put forward: (a) An upward displacement of branches clearly takes place in some axes, so that the branches become supra-axillary. In some instances a distinct ridge of tissue runs from the leaf-axil up the main axis to the point from which the branch appears to emerge, so that the branch clearly looks as if it were "fused" with the main axis; in other instances there is no such ridge. (b) Low down the main axis the subtending leaf of a branch is often carried for some distance up the branch that it should subtend; this appears to be associated with the very early development of these branches.

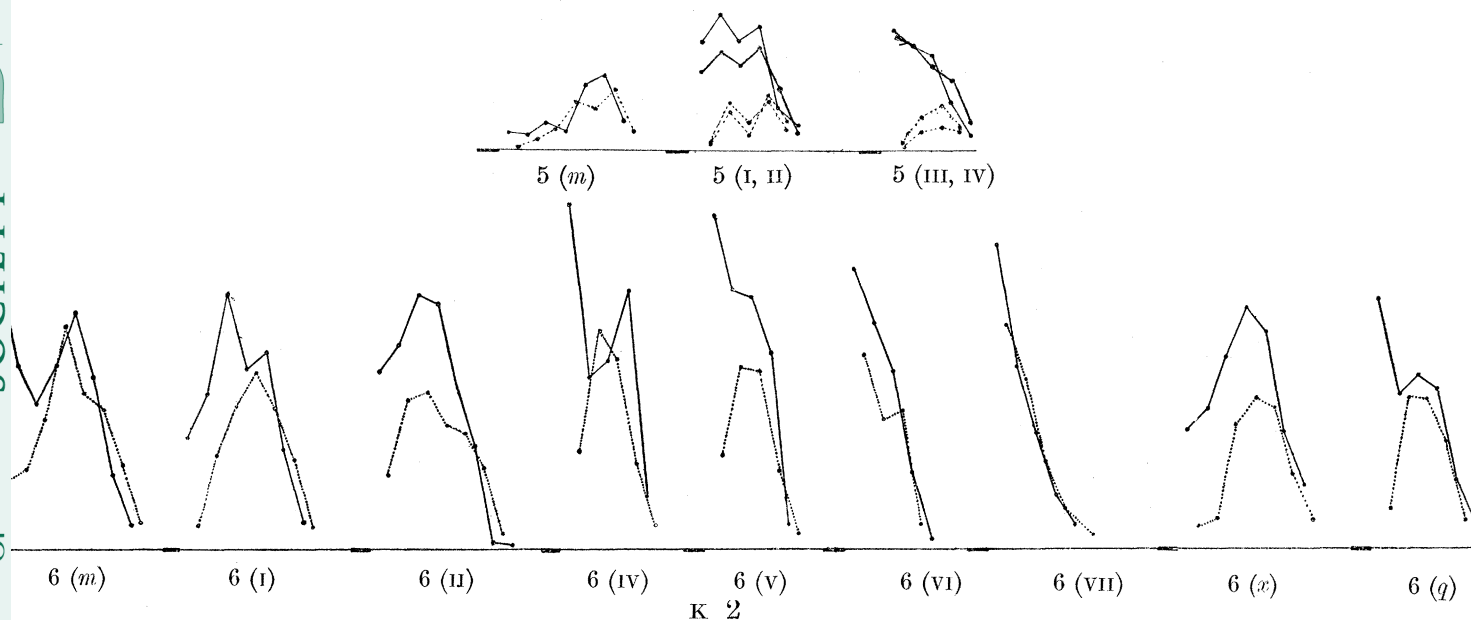
(vii) If the raising of branches and the suggested displacement of the leaves be comparable with an act of "fusion," then evidence in favour of displacement is derived from the prevalence of such fusion in the Chenopodiaceæ. (a) In *Salicornia* it is usually assumed that each pair of leaves is "fused" with the stem for the length of a complete internode. (b) The opposite bracts of *Arthocnemum* and *Pachycornia* are fused, as are the pairs of flowers of *Didymanthus*. (c) Finally, in the inflorescence of *Atriplex rosea* and *Salsola Kali*, branches frequently become supra-axillary by "fusion" with the main axis. As the fused branch does not always cohere straight up the main axis, but is obliquely raised above the leaf-axial, this phenomenon has not been correctly appreciated, and is rendered more puzzling by the simultaneous presence of truly axillary branches, which in reality are accessory branches occurring below the normal (supra-axillary) ones, just as accessory branches occur below normal

axillary ones in the vegetative region of *Atriplex rosea* and others. But the correctness of my interpretation is shown not only by the fused part of the branch sometimes being marked as a ridge on the main axis, but is very clearly confirmed by recording the successive fusion-distances up one main axis in the form of a curve, which assumes a regular form like that of the displacement sub-curve (in connection with the leaves). Hence the production of the so-called *interrupted inflorescence of the Chenopodiaceæ* is, often at least, *due to displacement of leaves and axillary branches*, and is not due, as generally supposed, to atrophy of any leaves.

(viii) The evidence obtained by comparison with other families, especially the Boraginaceæ, will be given later in this paper.

(ix) The theory here propounded is strongly substantiated by the *internode-curves of the branches of alternate-leaved Chenopodiaceæ*. These are *extremely irregular in form*, but, when analysed, produce regular and consistent internode and displacement sub-curves.

The sub-curves of the lower branches on a main stem assume (or tend to assume) the normal form with an ascent succeeded by a descent. But the sub-curves of the successively higher branches gradually change, or tend to change, from the ascending-descending form to the purely descending one, just as do the internode-curves of typical herbs, such as *Rhinanthus*. And, just as in the internode-curve of branches of typical herbs, the change in question sometimes brings with it an additional depression (or a second maximum) in the sub-curves of these *Chenopodiaceæ*; this additional crest and furrow in the sub-curves is obviously quite distinct from those forming the zigzag of the internode-curve. The subjoined tables show the gradual change in longitudinal symmetry of the main axis and branches in three alternate-leaved *Chenopodiaceæ*. The branches are numbered from below upwards, and the tables are constructed on the same plan as those previously given, and the measurements of the displacement-segments are printed in smaller figures. The corresponding internode-curves are Curves 5*m*, 5I-IV, 6*m*, 6I-VII, 6*x*, 6*q*.



*Atriplex rosea*, I 30. [Curves 5m, 5 (I-IV).]

Main stem.	Branch 1.	Branch 2.	Branch 3.	Branch 4.
4·5	28·5	20	31·5	30
0	1·5	1·5	1	1·5
4	35·5	25	27	27
2	10	11·5	5	8·5
7	29	22	25	22
5	4	7	6	11·5
5	32·5	26·5	12·5	18·5
11·5	14·5	12	5	6
16·5	11	15·5	4	7·5
10·5	7·5	5	Bud	Bud
19·5	6·5	4	—	—
15	—	—	—	—
7·5	—	—	—	—
4·5	—	—	—	—
Bud	—	—	—	—
Total length } 110	190	160	125	145

*Atriplex rosea*, 190. [Curves 6m, 6 (I), 6 (II), 6 (IV-VII), 6x, 6q.]

Secondary axis.	Tertiary axes—							Quaternary axis. q.
	1.	2.	4.	5.	6.	7.	x.	
74	29·5	47·5	91·5	88·5	74	80	31·5	66
18	6	19·5	26	25	51·5	59·5	6	10·5
48·5	41	54	46	68·5	60	48	37·5	41
21	25	39·5	58	48·5	34·5	45	8	40·5
38·5	67·5	67·5	50	67	47	30·5	51	45·5
34·5	37·5	41·5	51	47·5	36·5	23	33	40
48·5	48	65	78·5	52	20·5	14	64	42·5
59	47	33	22·5	21	6·5	10·5	40	28
63	52·5	43	14	6·5	2·5	6·5	57·5	18
41·5	37·5	30·5	6·5	4	—	3·5	37·5	7·5
45·5	26·5	27·5	—	—	—	—	31	6·5
37	23·5	21·5	—	—	—	—	19·5	—
20	7·5	2	—	—	—	—	17	—
22·5	6	4	—	—	—	—	7·5	—
6·5	—	1	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—
Total length (approx.) } 585	455	497	444	429	333	320	—	—

Measurements were made along the longest branch (secondary axis) on the main stem, and along the branches (tertiary axes) of that which are numbered successively from below upwards. All these had completed their growth in length. In addition, two shorts still growing were measured: one of these



was a quaternary axis, being the lowest branch of Tertiary axis 1; and the other was a Tertiary axis ( $x$ ) whose position was not recorded. Tertiary axis 2 provided a practical illustration of the value of the graphic method as applied to morphological problems. The measurements were made along it before I had learnt to appreciate the general occurrence of "fusions" between branches and the main axis. After the eleventh measurement, a little branch showed itself on the main axis, and, assuming that the subtending leaf had fallen off, I made the twelfth measurement from the leaf below up to the insertion of this branch. The internode-curve which resulted was found to differ greatly above the eleventh measurement from those of corresponding parts of the other tertiary axes. I therefore re-examined the short in question, and discovered that my twelfth measurement merely recorded the distance above its subtending leaf of a supra-axillary branch. Rectifying my former misinterpretation, the internode-curve became consistent, as is seen in Curve 6 (II).

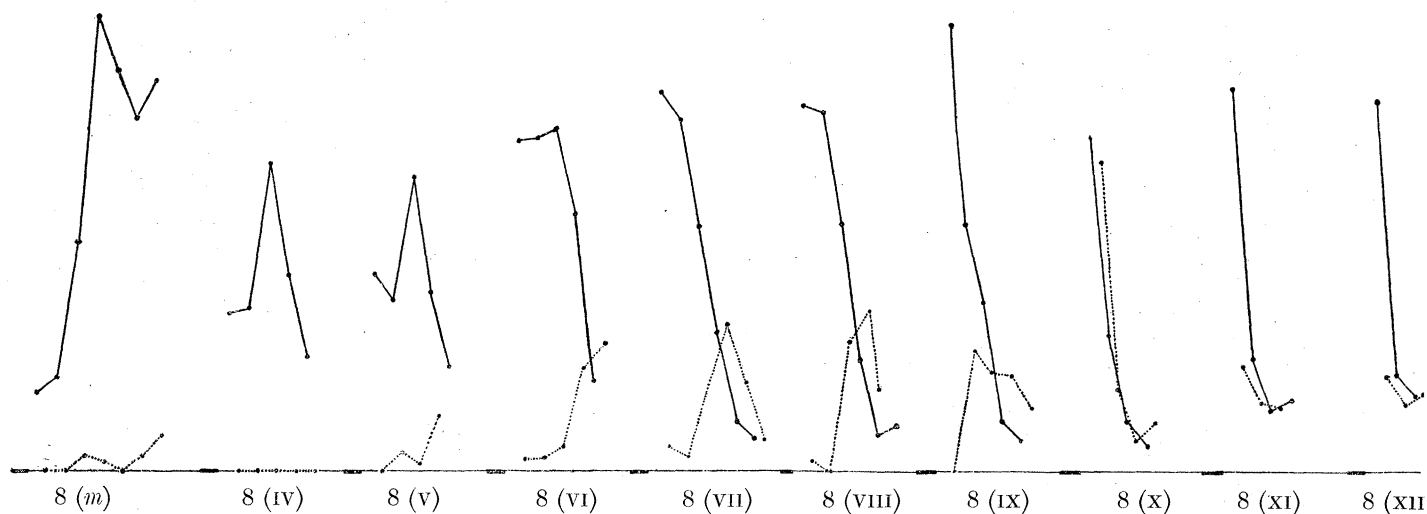
*Atriplex hortensis* (LINN.) 14. [Curves 8m, 8 (I-XII).]

Main stem.	Branch 1.	Branch 2.	Branch 4.	Branch 5.	Branch 6.	Branch 7.	Branch 8.	Branch 9.	Branch 10.	Branch 11.	Branch 12.
20·5	(Dwarf)		41·5	51·5	87	100	96·5	117·5	88	100·5	97·5
0			0	0	3	6·5	2·5	0	81·5	28	25·5
25	—		43	45	88	92·5	94·5	65	35·5	29·5	25·5
0			0	5	3·5	3·5	0	31·5	21·5	18	18
60·5	—		81·5	77	90·5	64·5	65	44·5	13	16	20
4			0	2	6·5	20	34	26	8	17	20·5
119·5	—		52	47	68	36	29·5	13	6·5	19	—
2·5			0	14·5	27·5	38·5	42·5	25·5	12·5	—	—
105·5	—		30	27·5	23·5	13	9·5	8	—	—	—
0			0	—	32·5	23·5	21·5	16·5	—	—	—
93·5	—		—	—	—	8·5	12	—	—	—	—
4			—	—	—	8·25	—	—	—	—	—
103	—		—	—	—	—	—	—	—	—	—
9·5			—	—	—	—	—	—	—	—	—
broken off	—		—	—	—	—	—	—	—	—	—
Length of fruiting terminal part			} ?	98·5	127·5	50·5	67	85	55·5	65·5	50
Approximate total length			—	368	558	465	475	433	322	294	257

The measurements of the first internode-segments of the successive branches form no regular curve such as is generally formed in typical herbs and in *Atriplex rosea*, as the preliminary rise is succeeded by irregularities. The plant was growing close to a wall, and assuming that the irregularities were due to unequal illumination and that the branches approximately preserved this decussate arrangement, Branches 6 and 10, 7 and 11, 8 and 12, would be respectively on the same orthostichies, and there is a remarkable agreement in the lengths of their first internodes, which were respectively 87 and 88, 100 and 100·5, 96·5 and 97·5. On this assumption Branches 7 and 11 would be on the shaded side, 8 and 12 on the lighted side, and therefore 6 and 10 on the shaded: this suggestion is confirmed by the considerable length of Branch 9, which would be opposite to Branch 10.



7.



Similar results were obtained from a number of other Chenopodiaceæ examined (Chenopodium, Salsola, other specimens of *Atriplex rosea* of the prostrate and erect varieties).

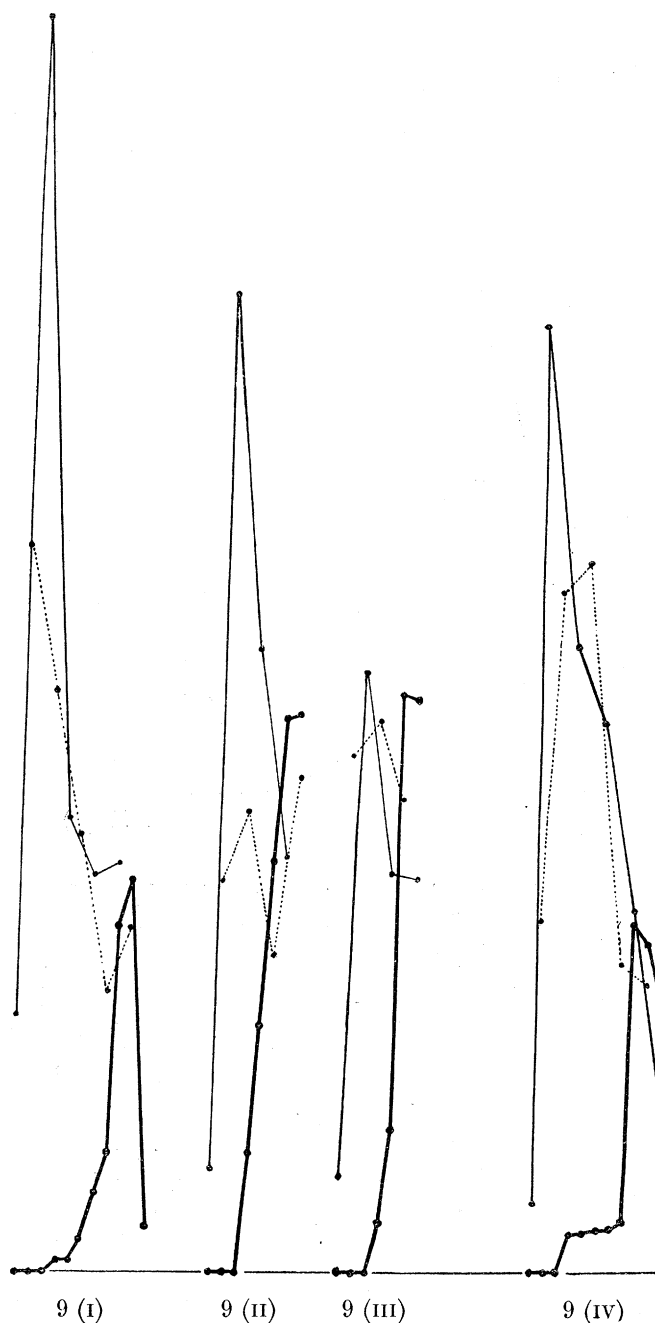
One additional feature stands out in reference to the sub-curves in the successive branches up an axis; the internode sub-curve changes from the normal form to the purely descending form earlier and more completely than does the displacement sub-curve (which, according to my theory, is of more recent phylogenetic origin).

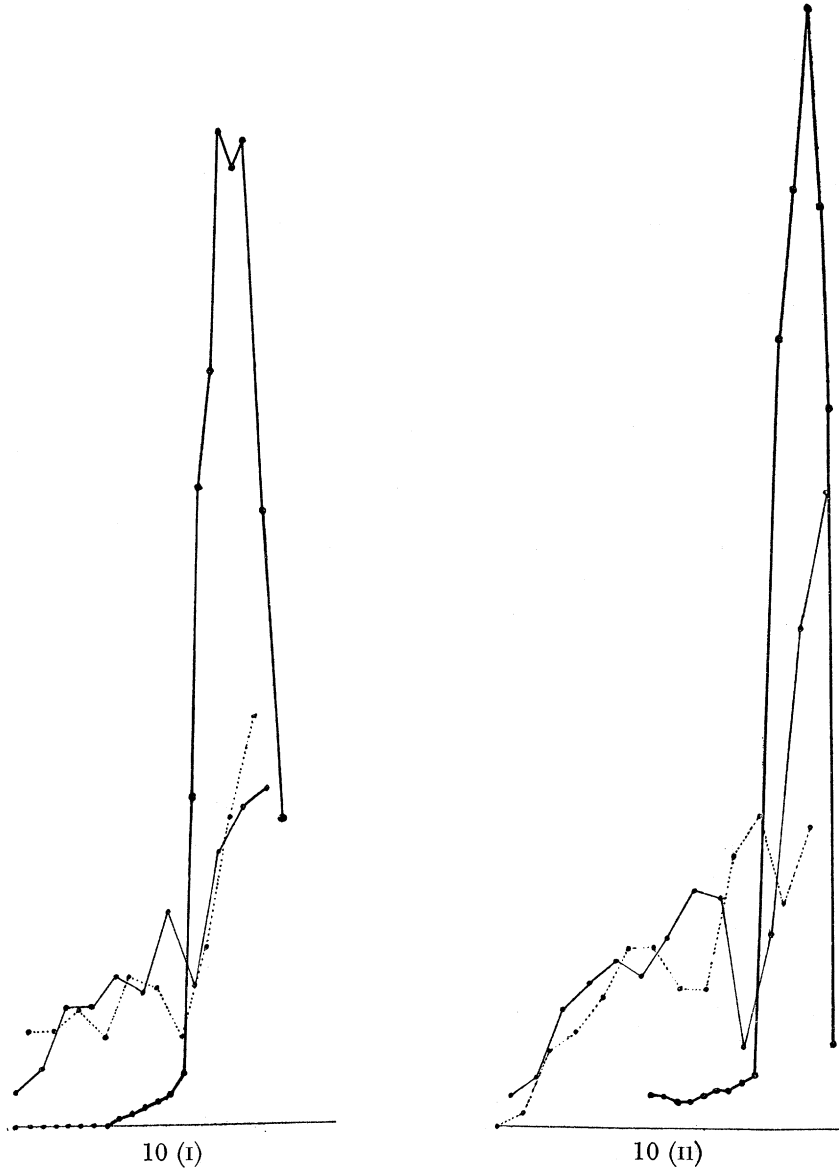
This last feature is a particular illustration of the general truth that, in alternate-leaved Chenopodiaceæ, the *internode sub-curve and displacement sub-curves of the various axes follow two different and by no means synchronous rhythms*—for the two sub-curves of a stem harmonise neither in form nor in period. This alone suffices to prove that the morphological features concerned are not due to external influence. It is also clear, whatever be the explanation, that alternate, not successive, internodes in these Chenopodiaceæ are correlated in growth.

#### *Boraginaceæ.*

The definite form of the displacement-curve of the Chenopodiaceæ suggested a means of testing the truth of the theory here put forward, namely, a reference to plant members, which have admittedly been displaced upwards, as is the case with the extra-axillary branches of *Boraginaceæ*. It is generally conceded that these inflorescences have been moved upwards from the leaf-axils by a process comparable with that which I suggest has rearranged the leaves of Chenopodiaceæ, and which was formerly described as being one of concrescence or fusion. This displacement in the Boraginaceæ is obviously a relatively recent feature, just as is the assumed displacement in the Chenopodiaceæ. Thus the analogy between the two sets of phenomena is complete, though in one case leaves are concerned, and in the other branches.

WYDLER, long ago, noticed that the distances of the successive branches above their subtending leaves increase as the (relatively) main axis is ascended; but, recording these successive measurements in the form of a curve, *the displacement-curve resulting is of startling regularity in the Boraginaceæ* investigated, namely, *Symphytum* and *Anchusa*, as may be seen in the thick plain lines in Curves 9 and 10. In some cases the curve is so regular as to form a straight line (within the limits of possible accuracy of observation) in its ascending portion. In most cases the curve is clearly an ascending-descending one, and in mature condition may, perhaps,





always be so. Furthermore, the *displacement-curve of the branches shows a form characteristic of each species* examined. Hence these observations on the Boraginaceæ not only confirm the view here given in regard to the phyllotaxis of the Chenopodiaceæ, but throw light on laws regulating the longitudinal disposition of members as rearranged by phylogenetically recent changes in the architecture.

In the Chenopodiaceæ, not only are the leaves displaced, but so likewise are often the branches, particularly in the inflorescence region. And in the *Boraginaceæ* there is also evidence of both kinds for displacements, for the *phyllotaxis* seems to be one transitional between opposite and alternate, as is suggested by the following evidence :—

(a) The internode-curves are very irregular, but the sub-curves obtained by

joining the alternate ordinates are more or less regular and consistent, though not to such an extent as in the Chenopodiaceæ. This is shown by the curves of *Symphytum*, *Anchusa*, *Lycopsis*, and *Myosotis*. (Curves 9, 10, 11*m*, 12*m*, 13*m*, 14*m*.)

(*b*) The internode sub-curves of the successive branches up the main stem change in the typical manner from a normal (ascending-descending) form to a purely descending one (Curves 11 (I)–11 (V)), whereas the irregular internode-curves show no such symmetrical change.

(*c*) The angles of divergence of the successive leaves of *Asperugo* and *Lycopsis*, commencing directly above the cotyledons, are 90° and 180°, or approximations to these, and thus indicate a decussate design.

(*d*) Although the majority of *Boraginaceæ* are alternate-leaved, one genus, *Antiphytum*, has opposite leaves; while a number, including *Asperugo*, *Allocarya*, *Eritrichium*, *Harpagonella*, *Pectocarya*, *Suchtelenia*, and *Trichodesma*, have opposite leaves near the base of the main axis, but alternate leaves higher up.

Thus the *Boraginaceæ*, as a whole, like the *Chenopodiaceæ*, may be *opposite-leaved in design*, though alternate-leaved by displacement.

Subjoined are the statistics dealing with the species examined.

*Symphytum officinale* (LINN.). [Curves 9 (I–IV).]

Four shoots, I, II, III, and IV, were cut off close to the ground, and measurements were commenced as near the base as it was possible to measure the internodes. The subjoined table records the results. In this table, corresponding to each shoot, are two horizontal series of figures, the upper of which records the successive interfoliar distances, and the lower series (in brackets) gives the distances above the respective leaves of the branches that should be axillary, that is to say, the lengths of the “fused” portions of the branches.

*Symphytum officinale*.

Shoot I	50·5 (0)	143 (0)	247 (0)	114·5 (2·5)	89·5 (2·5)	86 (6·5)	78 (15·5)	55 (23·5)	80·5 (67·5)	67·5 (77)	(9)
Shoot II	20 (0)	77 (0)	193 (0)	91 (23·5)	122·5 (48·5)	62 (80·5)	82 (109)	97·5 (109)	—	—	—
Shoot III	18·5 (0)	101·5 (0)	118·5 (0)	108·5 (10)	78·5 (28)	93 (113·5)	77·5 (112·5)	—	—	—	—
Shoot IV	14 (0)	69 (0)	186 (0)	133·5 (7·5)	123 (7·75)	140 (8·5)	108 (8·5)	61 (10)	71·5 (69)	56·5 (64·5)	34

The curves (9 (I–IV)) corresponding to these show strong likenesses, particularly between those of Shoots I and IV, and Shoots II and III respectively, and generally



among all four up to the eleventh measurement. The difference between the curve of branch-displacement belonging to Shoot I, and those belonging to Shoots II and III, concerns the final descent shown in the first named. This descent is shown

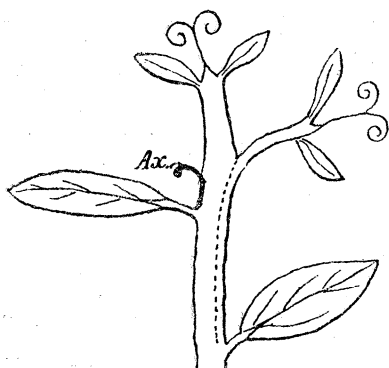


FIG. 3.

because (according to the interpretation here adopted) in Shoot I the end of the relatively main axis was preserved, so that the final measurement was possible, whereas in Shoots II and III the true end of the relatively main axis was obliterated, and no such final measurement was possible. The accompanying diagram (fig. 3) represents the termination of Shoot I (which bore rudimentary flowers), and shows the end of the relatively main axis at *Ax.* The terminal parts of Shoots II-IV were similar, except for the absence of the little stem *Ax.* (and in Shoot III the uppermost terminal branch had only one bract and one scorpioid

cyme in place of two).

The strong resemblance between the internode sub-curves is not accompanied by any close likeness between the leaf-displacement sub-curves. It is worthy of note that the end of each of these sub-curves of Shoot I, and the end of the leaf-displacement sub-curve of Shoot II, is marked by an unusual rise, and that these unusual ascents occur just at the internodes up which the axillary branches are "fused" for the maximal distance. Thus the appearance is given of the "fused" portions of these branches actually stretching the naturally shorter internodes of the relatively main stem to an abnormal length, just as when the displacement-distances of the leaves in other species are naturally shorter than the internodes affected, these seem to be abnormally shortened by the "fusion."

*Anchusa* sp. [Curves 10 (I), 10 (II).]

Two shoots from a garden plant were cut close to the ground. (I, unfortunately, did not record the specific name of the plant, but the results are too interesting to be omitted.) The measurements are recorded in the subjoined tables as in the case of *Symphytum*; the lower horizontal double series in each table is a continuation of the upper series.

The results obtained in general agree with those obtained from *Symphytum*. The absence of any final descent in the internode sub-curves and leaf-displacement sub-curves in like manner may be due to the "fused" portions of the branches imposing their longitudinal symmetry upon the main axis and thus abnormally lengthening the interfoliar spaces of the latter near its end.

It is worthy of note that if we estimate the complete length of a branch as being the sum of the "fused" and the free portions, the curve representing the complete

lengths of branches subtended by leaves 14–22 on Shoot I show a nearly regular ascent and descent (such as is at least often exhibited by the successive secondary branches of a normal herb); whereas the curve of the lengths of the free portions shows a regular descent to zero, followed by a regular ascent.

*Anchusa.*

## Shoot I.

6·5 (0)	18·5 (0)	11·5 (0)	18·5 (0)	23 (0)	23 (0)	23 (0)	17·5 (1·5)	29 (2·5)	29 (3·25)	26 (3·5)	27 (4·5)
42·5 (6)	17·5 (10)	27·5 (64·5)	35 (126)	54 (148·5)	60·5 (196)	62·5 (188·5)	80·5 (194)	66 (120·5)			(60)

## Shoot II.

0	6·5 (0)	3 (0)	10 (0)	15·5 (0)	23·5 (0)	19 (0)	28·5 (0)	26 (0)	33·5 (0)	36 (0)	30·5 (0)	36 (6·5)	37·5 (6·5)	28 (5·75)
47 (5·75)	28 (7)	46 (8)	54·5 (8)	16·5 (9·5)	62 (11)	39 (156·5)	45 (186)	99·5 (222)	60 (183)	126 (143)				(17·5)

*Lycopsis arvensis* (LINN.). [Curves 11*m*, 11 (I–V).]

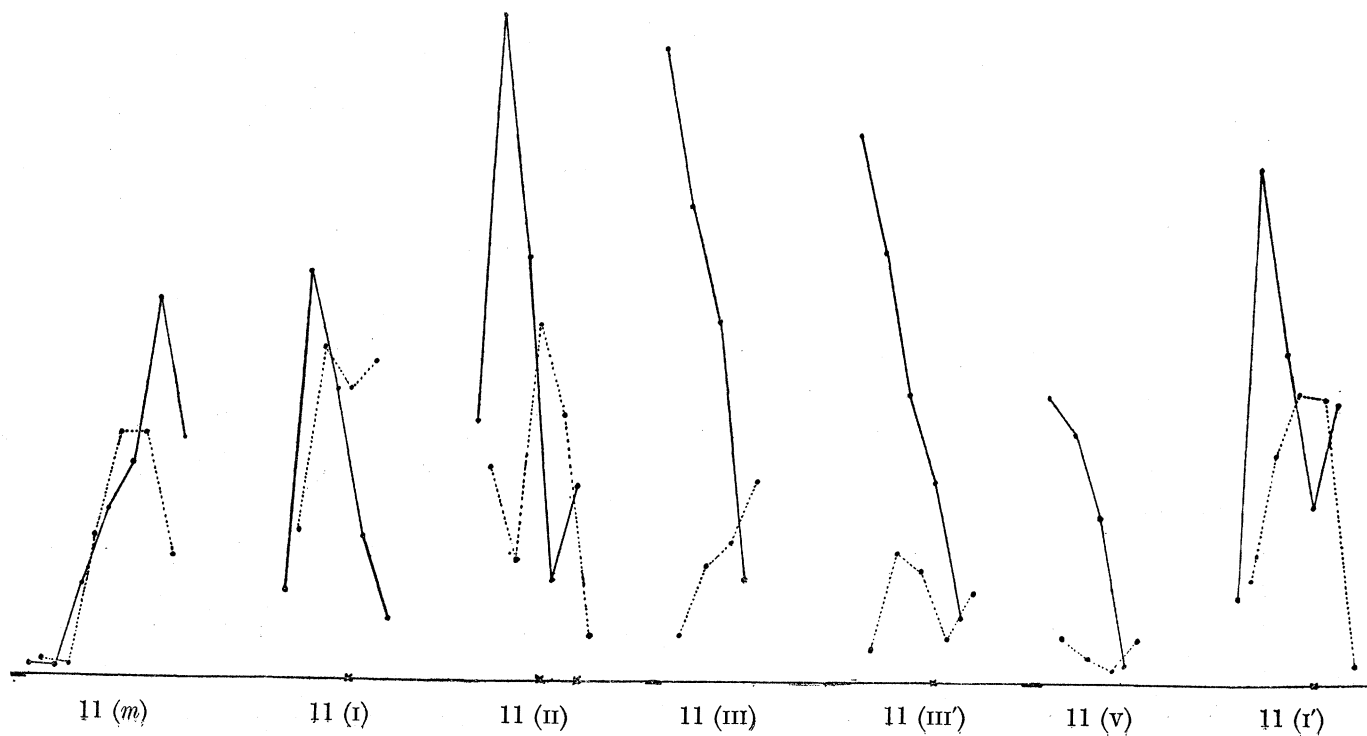
The measurements of this annual species commenced at the cotyledons and solely concerned the distances apart of the successive leaves on the main axis and branches. The subjoined table gives the results obtained. Branches I and I' were subtended by the lowest two foliage-leaves (I and I') which were sub-opposite; Branch II was subtended by the third foliage-leaf; Branches III and III' by the fifth and sixth leaves respectively. Branch V, subtended by the ninth leaf, already showed a terminal forked inflorescence, whereas the seventh and eighth leaves subtended merely short young branches (IV and IV').

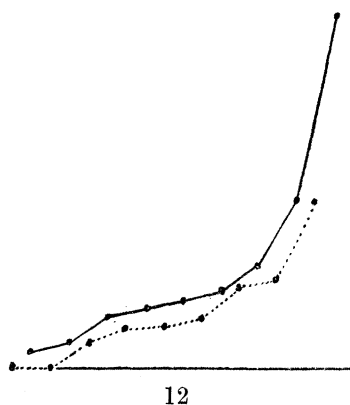
The regularity or consistence of the sub-curves resulting and the irregularity of the internode-curves without analysis is instantly obvious. Moreover, the internode sub-curve of the successive branches changes in the typical manner from the normal to the purely descending form. That the phyllotaxis is thus alternate by displacement is also confirmed by the angular divergence of the lower leaves. The first pair were sub-opposite and decussate in reference to the cotyledons; the sub-opposite second pair of leaves were also almost decussate in reference to the first pair. The right-handed spiral, feebly foreshadowed in the first four leaves, became clear in all the higher ones.

*Lycopsis arvensis.*

Internode lengths (in millimetres).						
Main axis.	Branch I.	Branch I'.	Branch II.	Branch III.	Branch III'.	Branch V.
1·5	17·5	17·5	51·5	125·5	108·5	57
3	29·5	20·5	42	9	6·5	8·5
1·25	80·5	102·5	131	94	85	49·5
2	66	45·5	24	23	25·5	5
18	57·5	65·5	83·5	71	57	33
27·5	58	58	70·5	27·5	22	2·5
33	28	35·5	19·5	20	39·5	3·5
48	63	57	52·5	39·5	8·5	8·5
42	12	55·5	38·5	—	13	—
48	—	3·5	9	—	17·5	—
75	—	—	—	—	—	—
24	—	—	—	—	—	—
47	—	—	—	—	—	—
Total length to terminal fork	412	461	522	409·5	383	167·5

(The ×'s shown on the base-line of the curves denote where axillary inflorescences were "fused" with the relatively main axes.)



*Asperugo procumbens* (LINN.). (Curve 12.)

The measurements of the interfoliar distances along the length of this annual plant were commenced at the cotyledons, and ceased at the termination of the stem. The results and curves confirm the evidence supplied by *Lycopsis*.

In the subjoined table the successive interfoliar distances are recorded in the upper line, and the angular divergences of the two leaves in the lower line (the lower double horizontal series is a continuation of the upper series). The first measurement was from cotyledon to cotyledon, and the second from cotyledon to lowest foliage-leaf.

*Asperugo procumbens* Main Axis.

0 180°	2 90°	0 180°	3·5 90°	3·5 180°	6·5 90°	5·5 180°	8 90°	5·5 ?	9 90° (circa)
6·5 180° (circa)	10·5 90° (circa)	11 ?	14 90° (circa)	12 180°	23 90° (circa)	22·5 180° (circa)	47·5 90° (circa)		

*Myosotis sylvestris* (LINN.). [Curves 13*m*, 13 (IV-X), 14*m*.]

Among a considerable number of stems measured, two belonging to Specimens M16 and M18 were of secondary shoots which were severed from the base of the plant.

The corresponding internode curves are Curves 13 (*m*) and 14 (*m*): the statistics are given below.

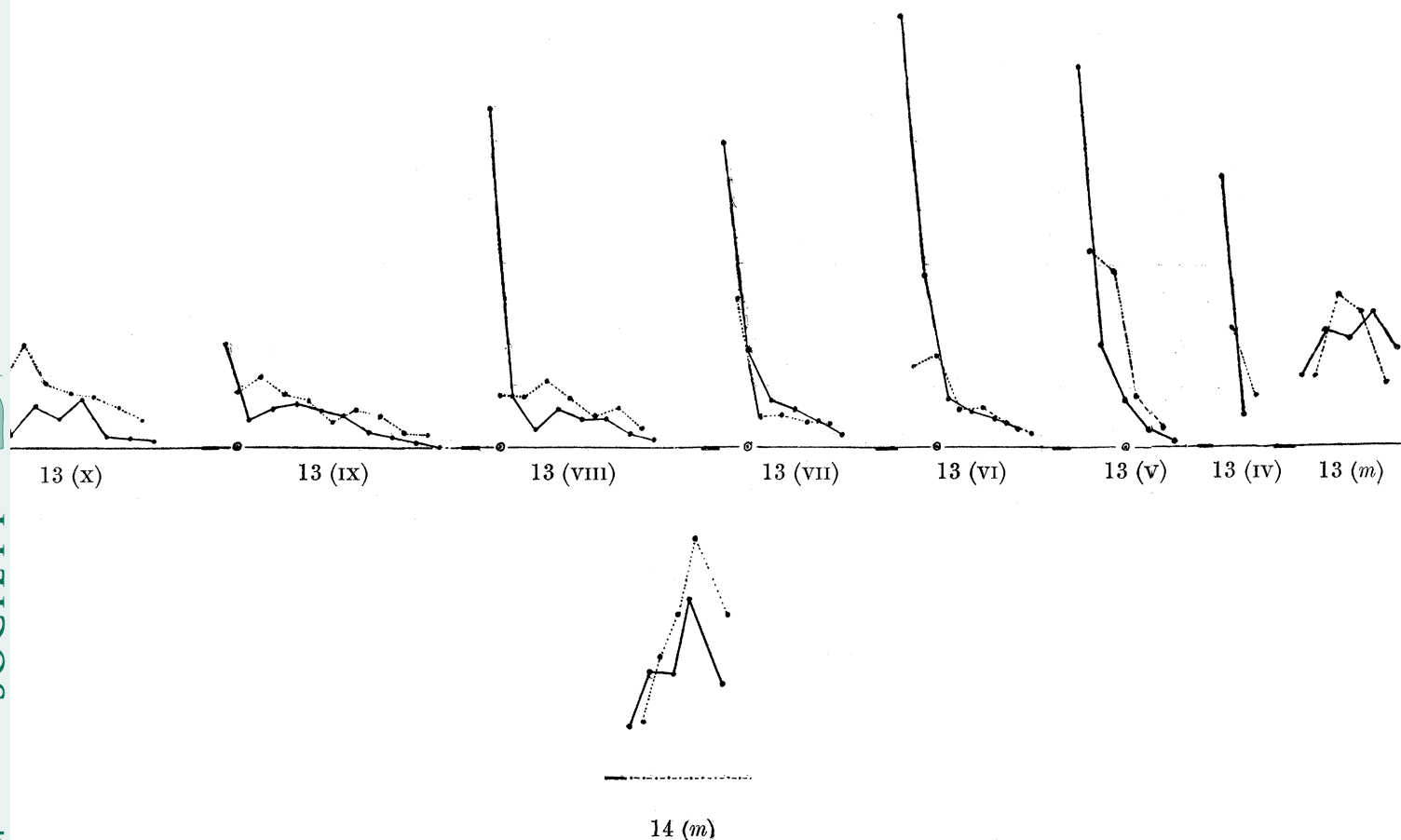
M. 16 . . . .	15	15	24	32·5	23	28	28·5	13	20·5	
M. 18 . . . .	10	10·5	21	24	20	32·5	35·5	48	16	30·5

The resultant curves and sub-curves, as well as the angular divergences observed

in connection with Specimen M18, bear out the view that the phyllotaxis is transitional between opposite and alternate.

In addition, measurements were made along the successive branches of M16. The relatively main axis had at its end a forked dichasium and Branches 10 and 9 were the two arms of the dichasium. The branches are numbered successively from below upwards.

The measurements in the lower portion of the subjoined table all refer to distances from flower to flower, and therefore concern the floriferous (sympodial) part of the axis; thus in each case the fifth horizontal line records the measurements from the lowest flower to the next. The upper portion of the table records all the measurements from the insertion of each branch up to its lowest flower. All the branches were axillary except Branches 9 and 10, which according to current views are the raised axillary branches of the topmost two leaves. The distance of the lowest flower of Branch 10 from the fork was 27 mm., but the distance from the fork to the topmost leaf was 32 mm. Hence the distance of the base of the branch to its first flower must be regarded as  $27 + 32 = 59$  mm. or as 27 mm. Similarly the distance of the base of Branch 9 was  $22 + 52.5 = 74.5$  mm. or 22 mm. The measurements were not continued up beyond the open flowers.



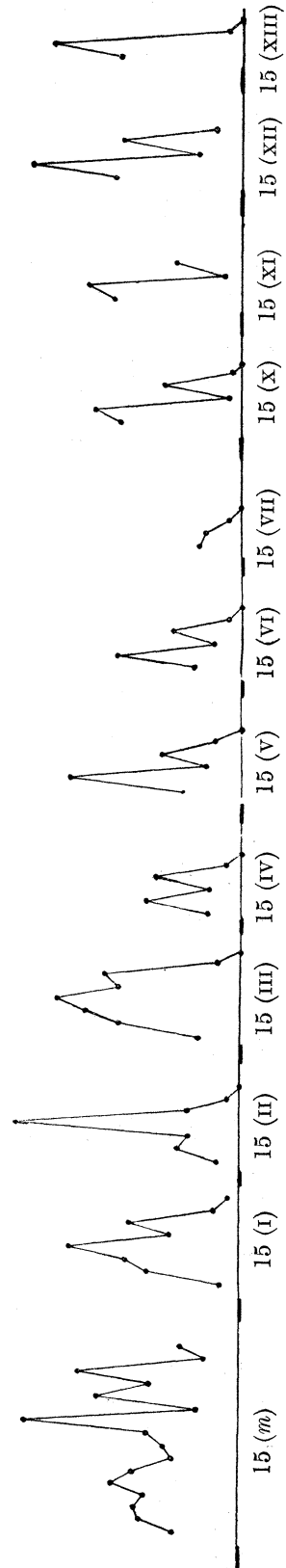




*Solanum Dulcamara*. [Curves 15*m*, 15 (I-XIII).]

Main stem.	Branch I.	Branch II.	Branch III.	Branch IV.	Branch V.	Branch VI.	Branch VII.	Branch X.	Branch XI.	Branch XII.	Branch XIII.
13	4	5	8.5	7	12	9.5	8.5	24.5	26	26	25
20.5	19	13	25	19.5	35.5	25.5	7.5	30	31.5	43	38.5
21.5	23.5	10.75	32	6.5	7.5	6	2.5	2.5	3.5	9	2.75
19.5	35	46.5	38	17.5	16.5	14	0	16	13.5	24.5	0
26.5	14.5	11	25	3.5	5.5	2.5	—	2	—	5.5	—
22	22.5	2.5	28	0	0	0	—	0	—	—	—
14	5.5	0	5	—	—	—	—	—	—	—	—
15.5	2.5	—	0	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—	—
44	—	—	—	—	—	—	—	—	—	—	—
8.5	—	—	—	—	—	—	—	—	—	—	—
29	—	—	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—	—	—
33	—	—	—	—	—	—	—	—	—	—	—
7.5	—	—	—	—	—	—	—	—	—	—	—
12.5	—	—	—	—	—	—	—	—	—	—	—

*Note*.—A number of the shoots terminated in active buds, so that the last measurements in each series do not represent mature segments.



as indicating that the *well-known upward displacements of the leaves in the flowering region of the stem is no sudden phenomenon, but is foreshadowed by leaf-displacements lower down the same stem.* The sub-curves of *Solanum* agree closely with the view that the original phyllotaxis was opposite, and, if so, they seem to denote that the change to the modern alternate arrangement was a more ancient one than in the *Chenopodiaceæ* or *Boraginaceæ*, because *both* the internode and leaf-displacement sub-curves of the successive branches change from the ascending-descending to the purely descending form. *If the original phyllotaxis was opposite in the Solanaceæ, then the familiar phenomenon of the upper displacement of only one leaf of each pair in the inflorescence-region would be merely an obvious illustration of a rule prevailing throughout the whole plant.*

The accompanying tables and that on p. 80 represent the measurements in *Solanum* and *Petunia*.

*Petunia hybrida.* (Curves 16, 17.)

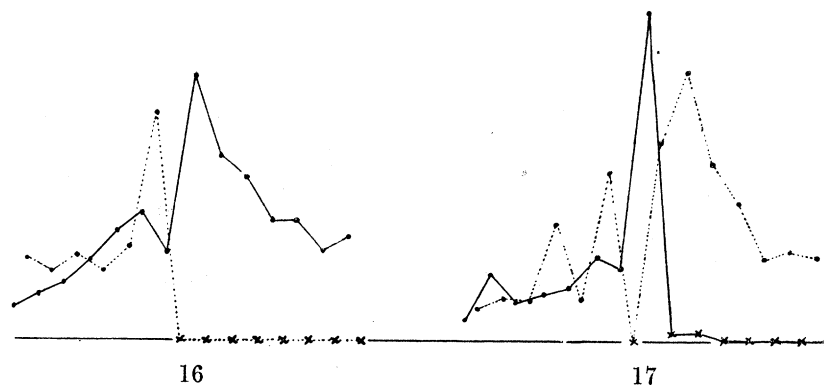
Monopodial Region.

Specimen I .	6	16	9	14	11.5	17	16	14	22	18.5	25.5	45	17.5
Specimen II .	4	6	13	8.5	7.5	8	9	23	10.5	8.5	16.5	33	14

Sympodial Region.

Specimen I .	0	52.5	...	0	36.5	0	32	0	23.5	0	23.5	0	17.5	0	20.5	0
Specimen II .	0	65	39	1.5	53	1.5	35	0	27	0	16	0	17.5	0	16.5	0

The resemblance between the curves of the sympodial portion of the axes is clear if it be remembered that, owing to the introduction of an extra internode and leaf on the sympodial axis of Specimen II, in the sympodial region the dotted sub-curve of Specimen II mainly corresponds with the plain sub-curve of Specimen I, and the likeness between the two is very striking.



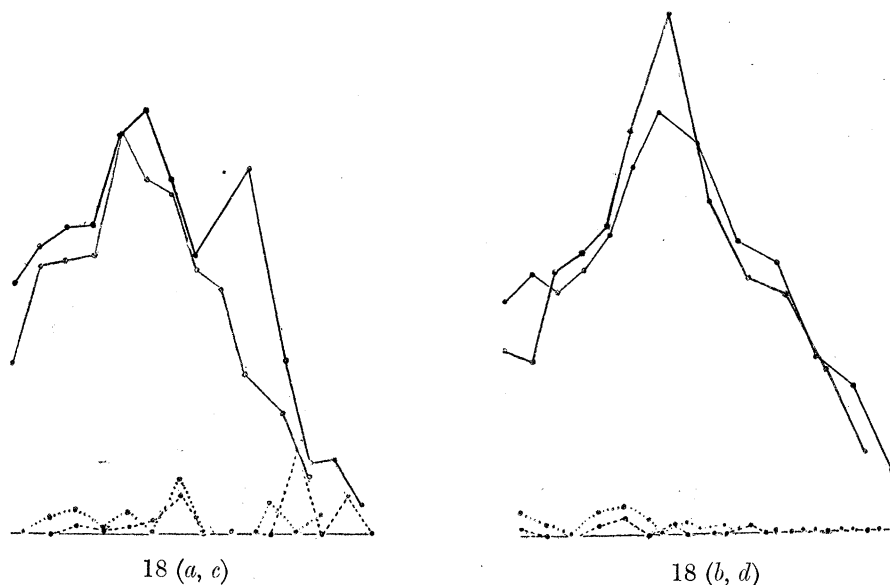
*Fluctuating Displacements.*

So far in dealing with displacements, either assumed or admitted, reference has only been made to advanced and firmly fixed cases as afforded by Chenopodiaceæ, Boraginaceæ, and Solanaceæ, in which the leaf-displacements can be demonstrated or surmised by means of careful measurements of the internode-lengths. It, therefore, seemed advisable to investigate species in which the leaf-displacements do not take place in connection with either all the individuals or all the nodes. Incidentally less advanced displacements serve to demonstrate that even herbs, subject as they are to slight external changes, yet preserve a certain constancy in their longitudinal symmetry and their internode-curves.

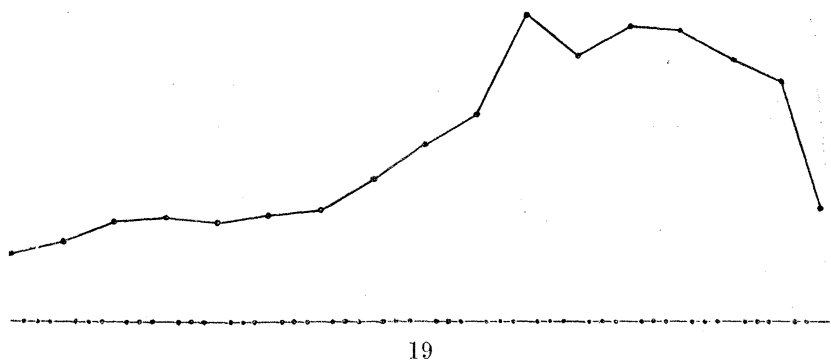
*Lysimachia vulgaris.* (Curves 18–23.)

For this reason *Lysimachia vulgaris* was investigated. The leaves of this species are mostly in whorls (usually dimerous, trimerous, or tetramerous), but on some shoots here and there the leaves become more or less alternate obviously by displacements. The internode sub-curves are more or less regular, but the displacement sub-curves betray no regularity (Curves 18–23); it is particularly worthy of note that when branches of similar position were compared, not only the resultant internode sub-curves, but also the displacement sub-curves showed unmistakable likenesses (Curves 18*bd* and 18*ac*).

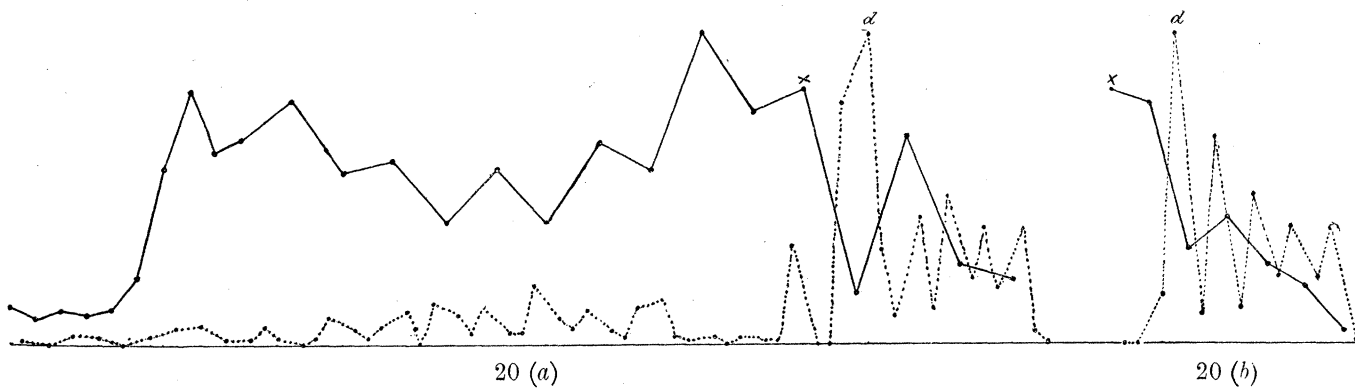
In *Lysimachia* the internode-sub-curve is more irregular the greater the leaf-displacements are, as may be seen by comparing Curve 19 with Curves 20*a* and 22, or by comparing the portions of one curve that are free from displacement with the portions where displacements occur (Curves 23, 20*a*, 20*b*, 22). But in the case of a plant, such as *Lysimachia*, with cyclic leaves, if one leaf be displaced from a node



LONGITUDINAL SYMMETRY IN PHANEROGAMIA.

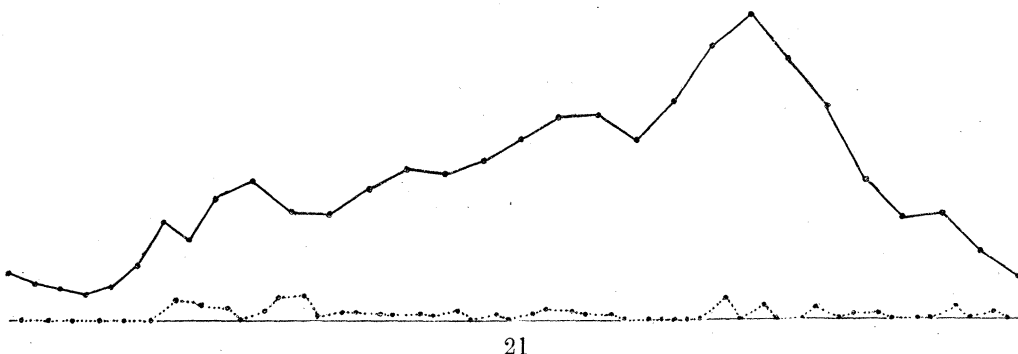


19

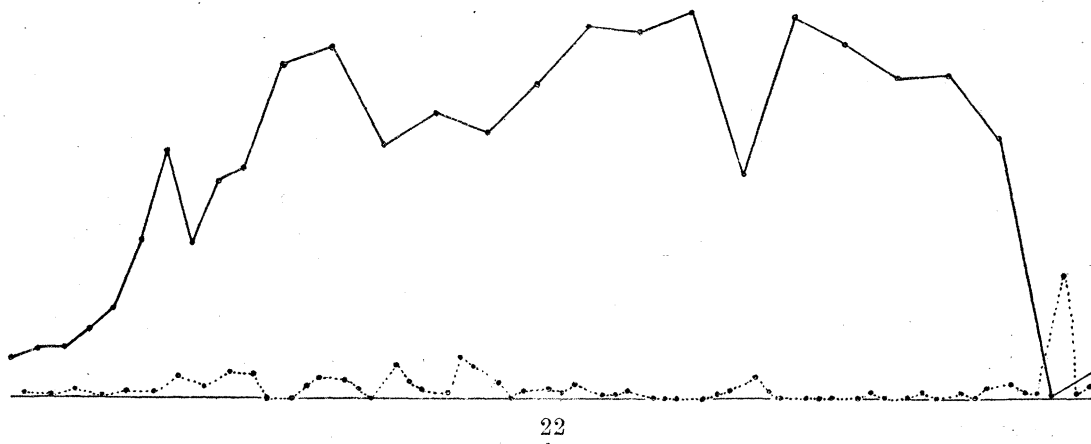


20 (a)

20 (b)

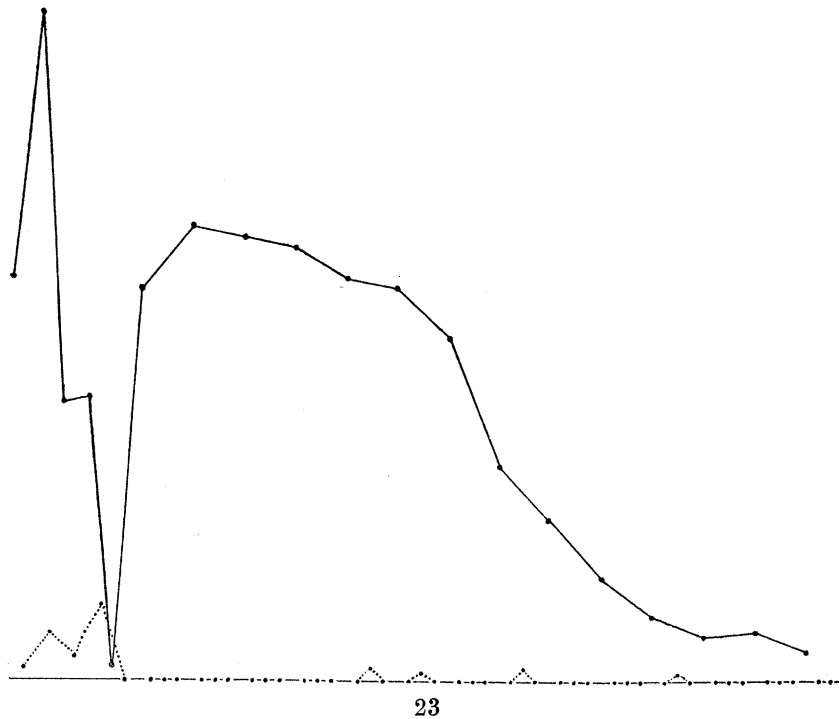


21



22





up along the succeeding internode, it is obvious that the true length of the latter is not registered by the measurement from the raised leaf to the node above. Supposing the other leaves to have remained stationary, the true length of the internode in question would be the sum of the distance of the raised leaf above the lower node, together with the distance from that leaf to the higher node. But even adopting this method of calculation (or similar methods where the whorls have three or more leaves) the internodes associated with displacements are abnormally short in this plant. This suggests that *the act of displacement of a leaf up an internode shortens that internode*, and this shortening is easily comprehensible if we assume that the displacement is due to an actual blending of the leaf-base with the stem. According to the view that the displacement is a case of "fusion," the internode would only be shortened, supposing the length of the fused part of the leaf would naturally have been shorter than the fused part of the internode; but if the fused part of the lateral member were naturally longer than that part of the internode in question, then such concrescence would lead to an abnormal lengthening of the internode, and an abnormal lengthening of this kind probably occurs in the main stem of the Boraginaceæ, as has already been mentioned.

But another very significant point in regard to the leaf-displacements and the internode-lengths of *Lysimachia* can best be realised after a digression in regard to some interesting features concerning the increase and subsequent decrease in the number of leaves at the successive nodes. All the shoots examined had dimerous nodes at the base, but higher up the nodes became trimerous and tetramerous.

Traced upwards, some of the shoots showed all transitions between two and four leaves in a whorl : (i) two simple normal leaves ; (ii) one normal leaf and one leaf with two tips ; (iii) one normal leaf and one bilobed leaf, which subtends either one bud or two ; (iv) one normal leaf and two complete leaves in close lateral juxtaposition ; (v) three equi-distant normal leaves. Similar transitions to a tetramerous condition were seen, in which two bilobed leaves appeared at the lower nodes. These features are illustrated by figs. 4 and 5. Higher up the stems similar transitions in the reverse direction occurred, and culminated in the complete return to the dimerous condition ; these are shown in fig. 6. These changes take place at definite regions of the stem, and sometimes, at least, at sharply determined points, but the remarkable feature upon which stress is laid here is that *alternate, not successive, nodes are closely correlated in their behaviour*. This is made clear by an examination of the table on page 87, which gives the statistics in reference to only one of the plants, Specimen II, examined, and by an inspection of fig. 4, which represents the leaves at the successive nodes of Branch A of Specimen II, commencing at the fifth node.

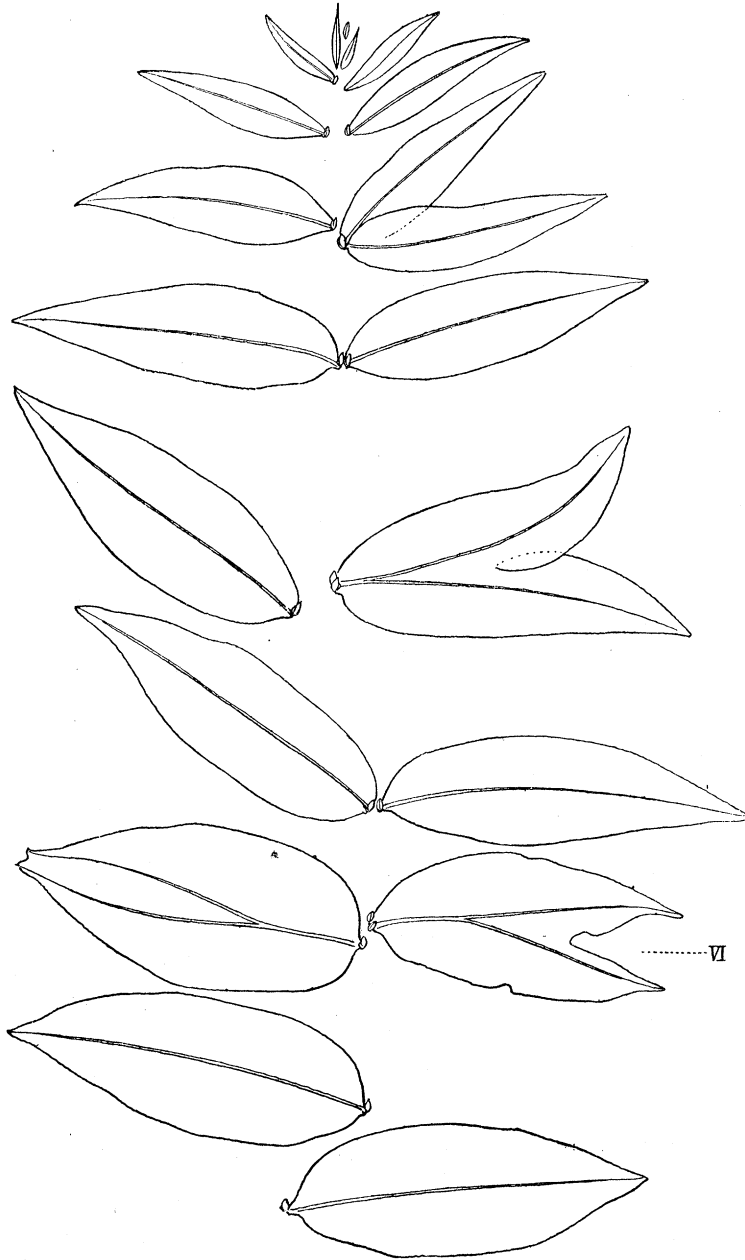


FIG. 4.—Leaves of *Lysimachia* II, Branch A ; VI denotes the sixth node (reduced to  $\frac{1}{2}$ ).

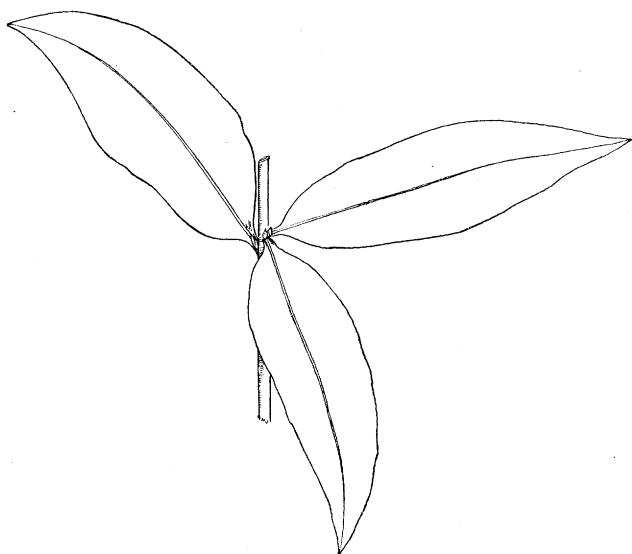


FIG. 5.—Sixth node of *Lysimachia* II, Branch D (reduced to  $\frac{1}{2}$ ).

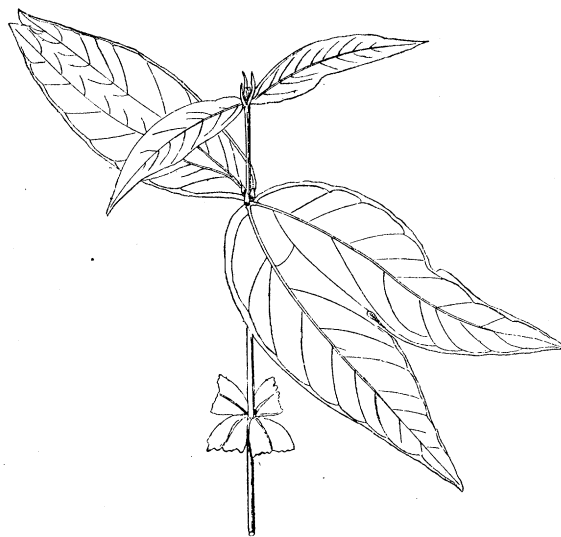


FIG. 6.—*Lysimachia vulgaris*. Tip of shoot, showing tetramery giving way to dimery (reduced to  $\frac{1}{2}$ ).

*Lysimachia vulgaris* II. (Curves 18*a,c* and 18*b,d*.)

An erect shoot severed close to the ground gave off three branches (A, B, and C), arranged in a whorl, and continued above this point for one more internode which was capped by a node. Above this node the shoot had been broken off, and it was functionally replaced by a branch (D) emitted from the topmost node. On all four branches the lower leaves were dimerous, opposite or sub-opposite, and decussate, but exactly at the sixth node a change took place, in the initiation of pleiomorous whorls, without, however, affecting the internode-curve. The nature of the leaves at the successive nodes is indicated in the appended table.

The measurements of the internodes and longitudinal displacements of the leaves show that these seem to conform with the same rule, namely, that *alternate internodes, and associated leaf-displacements, are apparently more closely correlated than successive ones*. As the phyllotaxis of *Lysimachia* is cyclic, this phenomenon may imply that *morphogenous impulses are transmitted along the orthostichies*, and may or may not further imply that stimuli travel along the young or future vascular tissue. A certain amount of confirmation of the rule concerning the close correlation of alternate internodes in plants with phyllotaxis that is cyclic in fact or design is met with in other genera dealt with in this paper; and this rule would serve to explain some of the peculiar but regular zigzags in the internode-curves of those plants.

Subjoined are the statistics dealing with the internodes of the plants observed. In all cases, except Specimen II, the axes measured were erect stems severed close to the ground. The displacements are printed in smaller type.

Lysimachia II.

Node.	Branch A.	Branch C.	Branch B.	Branch D.
VI	1 bilobed leaf subtending 2 buds, 1 double-tipped leaf (fig. 4)	1 bilobed leaf subtending 2 buds, 1 double-tipped leaf	1 deeply bilobed leaf subtending 2 buds, 1 leaf with 2 minute tips	3 simple leaves, of which 2 were inserted in very close lateral juxtaposition at a higher level than the other (fig. 5)
VII	2 normal leaves	2 normal leaves	3 normal leaves, of which 2 were inserted at the same level, but higher up than the other	3 simple leaves, of which 2 were inserted higher up than the other and in close lateral juxtaposition, with their contiguous sides at the same level
VIII	1 deeply bilobed leaf subtending 2 buds; 1 normal leaf	4 simple leaves juxtaposed in pairs, which were superposed upon the leaves at Node VI	3 simple leaves, of which 2 were laterally juxtaposed and approximately on the same orthostichy as the bilobed leaf at Node VI	3 simple leaves, of which 1 was inserted at a lower level than the other 2
IX	2 normal leaves	2 simple leaves subtending 1 small bud each; 1 normal leaf subtending 1 normal-sized bud	3 simple leaves, of which 2 were laterally juxtaposed at a higher level than the other, and superposed on the raised leaves of Node VII	3 simple leaves, of which 1 was inserted at a lower level
X	2 leaves as closely as possible juxtaposed on the orthostichy, on which were the bilobed leaves of Nodes VI and VIII; 1 simple leaf on the opposite orthostichy	1 bilobed leaf approximately superposed on a pair of leaves at Node VIII; 1 simple leaf	3 whorled, simple leaves	3 whorled, simple leaves
XI	2 normal leaves	2 normal leaves	3 whorled, simple leaves	3 whorled, simple leaves

*Lysimachia II.*

Branch A (Curve 18*a,c*): **32·5**, 0—**51·5**, 3—**53**, 4—**54**, 1—**78·5**, 3·5—**69**, 0—**66**, 10·5—**51**, 0—**47·5**, 0—**31**, 0, 5·5—**23·5**, 0—**11**, 3·5.

Branch C (Curve 18*a,c*): **49·5**, 0—**57**, 0—**60**, 1·5—**61**, 0·5—**78·5**, 1—**83·5**, 2·5—**70**, 7·5—**55**, 0, 0, 0—**72**, 0, 0—**34·5**, 16·5—**14·5**, 0—**15**, 7·5—**6**, 0.

Branch B (Curve 18*b,d*): **46·5**, 1·5—**51·5**, 0—**48**, 0—**52**, 2—**59·5**, 3—**72·5**, 0—**83·5**, 2, 0—**77**, 0, 0—**57·5**, 1·5, 0—**53·5**, 0, 0—**35·5**, 0, 0—**28·5**, 0, 0—**11·5**.

Branch D (Curve 18*b,d*): **36**, 4·5—**34**, 2—**51·5**, 0—**55·5**, 4·5—**60**, 5·5—**79**, 2·5, 0—**102·5**, 1·5, 1—**64·5**, 1, 0—**50**, 0, 0—**46·5**, 0, 0—**32·5**, 0, 0—**15**, 0, 0.

*Lysimachia III.* (Curve 19.)

**13—15·5—19—20·5—19—20·5—21·5—28—34·5—40·5—60—52—58—57—51·5—47·5—22.** The displacements were always 0, and have therefore been omitted. Up to the sixteenth node the leaves were tetramerous. At Node XVI there were three leaves—two simple ones, and one bilobed one which subtended two buds. At Node XVII there were two leaves—one simple one, and the other bilobed and subtending two buds.

*Lysimachia VIII.* (Curves 20*a* and 20*b*.)

In this shoot and those subsequently dealt with, the leaves at the base of the stem had fallen off, and were clearly dimerous at the very base, but higher up they gave way to leaves which were laterally juxtaposed in pairs, one pair at each node being either opposite or sub-opposite to the other. Higher up the leaves were tetramerous in the normal way. But in *Lysimachia VIII* the great displacements rendered it impossible to decide whether the phyllotaxis near the top of the stem was tetramerous or trimerous in design. The sub-curves conformed better with the latter assumption, but the sub-curve would be equally consistent if the largest measurements were treated as representing the internodes. So that this plant indicates that where displacements take place in connection with nodes and the number of leaves represented by each (original) node is unknown, there may result an internode-curve which is difficult to analyse. (This is shown in a still more marked degree by *Ænothera*, which will be subsequently described.) From the dubious point of *Lysimachia VIII* onwards the statistics are recorded in duplicate, on the assumption that the leaves are tetramerous and trimerous respectively, and the corresponding curves from that point (×) are given (Curves 20*a*–20*b*): **8**, 0·5—**5**, 0—**6·5**, 1·5—**5·5**, 1·5—**6·5**, 0—**13**, 1·5—**34·5**, 3—**50**, 3·5—**38**, 1—**40·5**, 1, 3·5, 1·5—**47·5**, 0, 1, 5·5—**33·5**, 2·5, 1, 3—**36**, 7, 0, 8—**24**, 5·5, 2, 7·5—**34·5**, 2·5, 2·5, 11·5—**24**, 5, 3·5, 6·5—**39·5**, 2·5, 1, 7·5—**34·5**, 8·5, 1·5, 0·5—**61**, 1, 0, 1—**46**, 0·5, 0·5, 19—×.



*Either*

50, 0, 0, 47·5—10, 61, 18·5, 5·5—40·5, 25, 7, 29—15·5, 13, 22·5, 11—12·5, 22·5, 2·5, 0.

*Or*

50, 0, 0—47·5, 10, 61—18·5, 5·5, 40·5—25, 7, 29—15·5, 13, 22·5—11, 12·5, 22·5—2·5, 0.

The internode sub-curve up to the problematic point × (the 21st measurement) shows two peculiarities: first, a peculiar general descent in the middle of its course; secondly, a regular recurrence of crest and furrow. This general depression between Nodes VIII and XIX coincides with a general rise in the displacement sub-curve. Even by estimating the complete lengths of the internodes as being equal to the distance from the lowest leaf of one node to the lowest of the next, this general depression does not disappear, and as it is not represented in other specimens where displacements are lacking, we assume that it is due to the latter, and shows that the displacement has a shortening effect on the stem. The extent to which displacements and length of internodes vary inversely is shown in the subjoined table. The upper line denotes the length of the successive internodes, the lower line is the sum of the displacements of the three leaves in connection with the nodes.

8 0·5	5 0	6·5 1·5	5·5 1·5	6·5 0	13 1·5	34·5 3	50 3·5	(38) 1	40·5 6	47·5 6·5
33·5 6·5	36 15	(24) 15	34·5 16·5	(24) 15	39·5 11	34·5 10·5	61 (2)	46 20	50	

The minima and maxima of the internodes respectively are associated with maxima and minima of displacements.

The regularly recurrent zigzag of the internode-sub-curve suggests that the alternate internodes are more closely correlated than the successive ones: the maximal displacements at Nodes XIV, XVI, XVIII and XX suggest the same, especially as they all occurred along the same orthostichy.

*Lysimachia IX.* (Curve 21.)

This specimen confirmed the results obtained from the preceding. The following are the measurements obtained: 9·5, 0—7, 0—6·5, 0—5·5, 0—6·5, 0—11, 0—19·5, 4—16, 3—24·5, 2·5, 0—28, 2, 4·5—21·5, 5, 1—21, 1·5, 1·5—26, 1·5, 1—30, 1·5, 0·5—29, 2, 0—31·5, 1, 0—35·5, 1·5, 2·5—40, 2, 1—40·5, 1, 0—35·5, 0, 0—43, 0, 0—54, 4·5, 0—61·5, 3, 0—51·5, 0, 2·5—42, 0, 1—28, 1, 0—20·5, 0, 0—21, 2, 0—13·5, 1, 0—8·5.

*Lysimachia XI.* (Curve 22.)

The curve of *Lysimachia XI* is intermediate in type between those of Specimens VIII and IX. The plant showed, in particular, the raising of adjacent juxtaposed leaves in pairs, which were on the side of the stem opposite to that on which the two lower leaves were inserted. The following are the measurements observed: **8**, 1—**9·5**, 0·5—**10**, 1·5—**14**, 0·5—**18**, 1·5—**31·5**, 1·5—**48·5**, 4·5—**30·5**, 2·5—**42·5**, 5—**45·5**, 5, 0—**66**, 0, 2·5, 4—**69**, 3·5, 2, 0—**49·5**, 7, 3, 1·5—**56·5**, 1, 8, 6·5—**52·5**, 3·5, 0, 1·5—**61·5**, 2, 1, 3—**73·5**, 0·5, 0·5, 2—**72**, 0, 0, 0—**76**, 0, 0·5 1·5—**44**, 4·5, 1·5, 0—**75**, 0, 0, 0—**70**, 0, 1, 0—**63**, 0, 1, 0—**63·5**, 1, 0, 2—**51·5**, 3, 1, 1—**0·5**, 24·5, 0·5, 2·5—**6·5**. The remarkable point is the reduction of the twenty-sixth internode to the length of 0·5 mm. : this interpretation was confirmed by the angular divergence of the leaves at the two nodes concerned, and paralleled by similar reductions in Specimens VIII and I.

*Lysimachia I.* (Curve 23.)

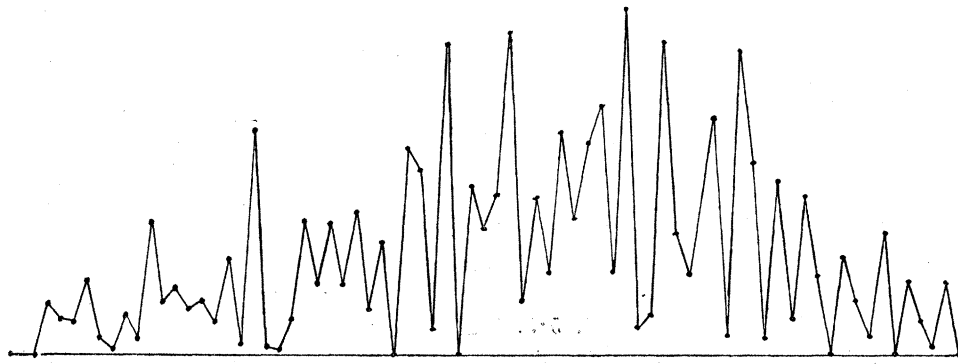
The following are the measurements made: **79·5**, 2·5—**132·5**, 9·5—**55**, 4·5—**56**, 15—**3**, 0—**77·5**, 0, 0, 0—**89·5**, 0, 0, 0—**87·5**, 0, 0, 0—**85·5**, 0, 0, 0—**79**, 0, 2·5, 0—**77·5**, 0, 1·5, 0—**67·5**, 0, 0, 0—**42**, 0, 2, 0—**32**, 0, 0, 0—**21·5**, 0, 0, 0—**12·5**, 0, 1·5, 0—**9**, 0, 0, 0—**9·5**, 0, 0, 0—**6**, 0, 0, 0. The resultant curve contrasts with the others in that the initial numbers are higher, because measurements were commenced higher up the stem. The remarkable early descent of the internode-curve is coincident with the solitary considerable rise in the displacement sub-curve, and is obviously disproportionately greater than the latter.

*Oenothera biennis.* (Curve 24.)

In *Lysimachia vulgaris* it has been shown that when the leaf-displacements occur only on some axes, that their distribution along the axis is irregular; and that when their dimensions are considerable the resultant internode-curve becomes very irregular; and, finally, that when the number of leaves associated with each node is unknown, the analysis of the internode-curve becomes a matter of great difficulty. All these features are repeated in *Oenothera biennis* (Curve 24), whose phyllotaxis is partly cyclic and partly acyclic, and which belongs to the Onagraceæ, whose species may be acyclic or cyclic in phyllotaxis.

Three erect shoots (I, II, and III) from different individuals were cut off close to the ground at points above the densely crowded basal leaves. The measurements did not extend up to the floriferous part of the axis. The curves show a general rise and fall, but such irregularity that I found it impossible to analyse them in such a manner as to indicate the fundamental nature of the phyllotaxis, though I attempted analysis into from two to seven sub-curves. The irregularity of the curves of *Oenothera* seems to indicate that in this fluctuating species the transition from one type of phyllotaxis to the other is now in progress. The following are the measurements made:—

*Cenothera* I.—9·5, 0, 26·5, 0, 21, 25·5, 11, 37·5, 23·5, 22·5, 39·5, 24, 31, 36, 17·5, 36·5, 34, 35, 45, 39·5, 4·5, 70, 4, 41, 45·5, 0, 47, 25·5, 26·5, 63, 9·5, 15, 62·5, 10·5, 42, 0, 23, 38, 19, 35, 18·5, 22, 33·5, 4·5, 29·5, 4, 10, 12, 0, 11·5, 1·5.



24

*Cenothera* II.—5·5, 9, 2·5, 4, 23, 6, 37, 2·5, 6·5, 32, 0, 37·5, 16, 3·5, 25, 63, 23, 1·5, 13, 15·5, 63·5, 54, 0, 31, 34·5, 13, 55·5, 26·5, 36·5, 23·5, 33, 37, 18·5, 4·5, 101·5, 0, 23·5, 33·5, 6, 23·5, 50·5, 18, 21·5, 56, 5·5, 33·5, 4·5, 20, 25, 21, 0, 16, 17·5, 6·5, 10·5, 2·5, 4·5, 3, 19·5, 12, 1, 6·5, 9·5, 1·5, 7, 15.

*Cenothera* III.—0, 0, 0, 10·5, 7, 6·5, 15, 3, 1, 8, 3, 26·5, 10·5, 13, 9, 10·5, 6·5, 19, 2·5, 40, 1·5, 1, 7, 26·5, 14, 26, 13·5, 28·5, 9, 22·5, 0, 41, 37, 5, 62, 0, 33·5, 25, 31·5, 64, 10·5, 31, 16, 44, 27, 42, 49·5, 16·5, 69, 5, 8, 62·5, 24, 16, 47, 4, 60·5, 38·5, 3, 34·5, 7·25, 31·5, 15·5, 0, 19·5, 10·5, 4, 24·5, 0, 14·5, 6·5, 1·5, 14·5, 0.

Only the curve of *Cenothera* III is printed in this paper.

#### *Scrophularia nodosa.*

This plant, on the contrary, shows a transition from opposite to alternate phyllotaxis at a definite region, namely, near the inflorescence. At the transitional region the internode-curve formed resembles that of the *Chenopodiaceæ*, and can be similarly analysed into an internode sub-curve and a displacement sub-curve. The *displacement sub-curve assumes the normal form, showing a rise and fall*, though its regularity is not great. As only the upper part of the stem was measured, the internode sub-curve naturally assumed a descending—though not very regular—form. The sub-curves became more regular on further analysis into two, on the assumption that alternate internodes and displacements are closely correlated.

The two shoots examined gave the following measurements:—

Specimen I.—85, 0, 82, 0, 65, 0, 78, 0, 66, 3, 72, 5, 86, 0, 70, 8, 61·5, 25, 40, 8·5, 46, 24, 24, 17·5, 18, 19, 15·5, 20, 11, 5·5, 11, 9, 7·5, 7, 5, 4·5, 4·5, 3·5.

Specimen II.—4, 77, 0, 71, 5·7, 55, 7, 50, 11, 35·5, 14, 30·5, 18·5, 9, 16, 17, 14·7, 15, 11·5, 15, 19, 15, 8·7, 14, 8, 11·5, 9·5, 6·5, 7·5, 10·5, 7·5, 6, 10, 2·5, 4·5, 4·5, 3·5, 3, 4, 4, 3.

(The curves of these two are not printed in this paper.)

*Other Species examined.*

Measurements were made of three typical opposite-leaved plants belonging to opposite-leaved families: *Lycopus europæus*, *Stellaria media*, and *Lychnis dioica*; and the resultant internode-curves are regular. Less regular are the internode-curves of *Centaurea nigra*, *Senecio Jacobææ*, and *S. vulgaris*, which belong to a family in which the phyllotaxis differs even in the different species of one genus.

In order to demonstrate the final descent of the internode-curve in submerged aquatic plants, measurements were made along the stems of *Elodea canadensis* and *Myriophyllum*. The statistics concerning three axes of the former are subjoined:—

## Elodea XVIII.

Branch 1.—6, 5·5, 4·5, 5·25, 6, 5, 5·25, 5·5, 5·25.

Branch 1a.—3, 3·5, 3·75, 3·75, 3·5, 2·75, 4, 3·5, 3·25, 2.

Branch  $\alpha$ .—9, 10, 9·5, 10·25, 8, 10, 8·75, 8·75, 8·75, 9, 8·5, 9, 7, 6·75, 5·25, 5, 7·75, 6·5, 6, 5·75, 6, 6, 5·75, 6, 6·5, 2·5, 2·5, 2·5.

The shallow internode-curve of *Myriophyllum* showed the final descent, despite of the fact that growth for the season had concluded (in July).

*Sympodial Axes.*

I was desirous of testing the graphic method as a new method of morphological investigation, quite apart from any question of leaf-displacement. I therefore made measurements along reputedly sympodial axes, namely, the floriferous stems of *Myosotis sylvestris* and *Petunia hybrida*, and the tendrilliferous axis of *Ampelopsis hederacea*.

In regard to *Petunia* and *Myosotis*, the results were disappointing, in that the curves showed that the graphic method is not competent to distinguish between a monopodial and a sympodial axis. The statistics dealing with the matter are given on pp. 79 and 81, while Curves 13, 16, and 17 record the results graphically. It may, however, be pointed out that the curves would definitely harmonise with the view that the inflorescence axis in each case represents a cicinnus with the branch on the same side constantly strengthened; and this result is not without interest. But apart from the fact that other interpretations are quite possible (such as leaf-displacements) it is probable that the longitudinal symmetry of inflorescences is, at least, often of a kind different from that of vegetative axes.

*Ampelopsis hederacea.* (Curves 25, 26.)

The construction of internode-curves of this species gave more satisfactory positive results.

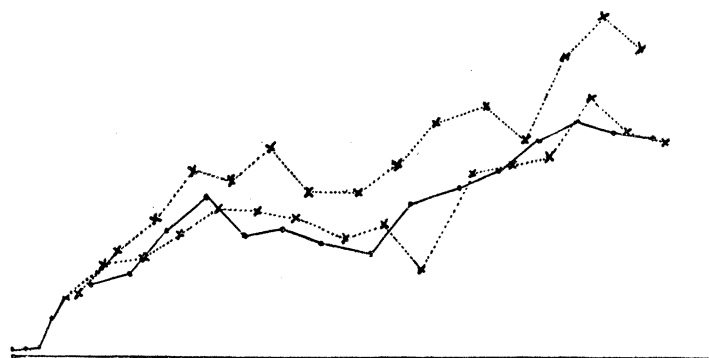
Along the stem the leaves are arranged alternately, and tendrils are inserted opposite to the leaves in such a manner that two tendrilliferous nodes are succeeded by one node without a tendril.



Of the two shoots measured, Ampelopsis I was plucked on November 2, its leaves being red and ready to fall; while the other, Ampelopsis II, was collected later in the year, when the leaves had fallen. Growth in length for the season, had, therefore, concluded in both cases. Ampelopsis II had lost the end of its stem, which was preserved in Ampelopsis I.



25



26

The measurements given below denote the distances apart of the successive leaves. As tendrils are opposite to some of the leaves, a number of the measurements also record the distances of the tendrils from the next lower leaves; these are denoted by a  $\times$  placed after each. In the corresponding curves the  $\times$ 's are placed at the summits of the ordinates that denote the lengths of internodes capped by tendrilliferous nodes, whereas ordinates without the  $\times$ 's denote the other internodes.

The following results were obtained:—

*Ampelopsis I.*—(The measurements did not commence at the base of a branch but at a tendrilliferous node): 30.5  $\times$ , 26, 24  $\times$ , 33.5  $\times$ , 25, 28.5  $\times$ , 36  $\times$ , 25, 22  $\times$ , 27.5  $\times$ , 23, 22  $\times$ , 25  $\times$ , 19, 17  $\times$ , 22  $\times$ , 19, 19.5  $\times$ , 26  $\times$ , 25, 20.5  $\times$ , 31.5  $\times$ , 26, 23  $\times$ , 33  $\times$ , 28, 22.5  $\times$ , 35.5  $\times$ , 27.5, 24.5  $\times$ , 38.5  $\times$ , 26, 27.75  $\times$ , 41.5  $\times$ , 32, 33  $\times$ , 43  $\times$ , 35, 33  $\times$ , 41.75  $\times$ , 31.5, 23  $\times$ , 33.5  $\times$ , 26, 27  $\times$ , 31  $\times$ , 27, 24  $\times$ , 30.5  $\times$ , 19.5, 12  $\times$ , 12.5  $\times$ .

*Ampelopsis II.*—(The measurement commenced at the base of the branch where four scales were visible. The lowest scale was approximately at the insertion of the branch, the second scale was higher up. Thus the first measurement was from the insertion of the branch (or the first scale) to the second scale; the second measurement was from this to the third scale; the third measurement from this to the fourth scale;



and the fourth measurement from this to the first foliage leaf, which had no tendril opposite; the fifth measurement extended to the second foliage leaf and first tendril. Thus, according to generally accepted views, the axis up to this point is a true monopodial one—and above it commences the sympodium): 1, 1.25, 1.75, 7.5, 11.5 ×—12.5 ×, 14.5, 18 ×, 21 ×, 16.5, 20 ×, 27 ×, 25, 24 ×, 36.75 ×, 31.5, 29 ×, 34.5 ×, 24, 29 ×, 41 ×, 25.5, 27.5 ×, 32.25 ×, 22.5, 23.5 ×, 32.5 ×, 20.5, 26.5 ×, 38 ×, 30.25, 17.5 ×, 46.25 ×, 33.5, 36.5 ×, 49.75 ×, 37, 38 ×, 42.75 ×, 43, 40 ×, 59.5 ×, 46.5, 51 ×, 67.5 ×, 44.5, 44.5 ×, 61 ×, 43.5.

The resultant curves are zigzags which show evident periodicity. According to the usually accepted interpretation the axis is a sympodium constructed of the basal portions of successive lateral axes which terminate in tendrils, the branches being alternately stronger and weaker. According to this theory, each strengthened bifoliar branch arises in the axil of the first and only leaf of a weaker branch and bears two leaves, in the axil of the upper of which is a weak unifoliar branch. Accordingly, there should be three kinds of internodes:—

(i) The first internode of the “weaker” branches which is capped by a tendril. This series may be termed “Series A ×.”

(ii) The first (basal) internode of the strengthened branches which is succeeded by a second internode. This series may be termed “Series B.”

(iii) The second internode of the strengthened branches which is capped by a tendril. This series may be termed “Series C ×.”

Accordingly, in the following two tables the recorded measurements are ranged in three horizontal series so that the successive corresponding internodes may be compared. In addition, in the fourth horizontal series the consecutive pairs of measurements of series B and C × are added together so as to show the actual lengths of the strengthened axes from their base to the insertion of the second leaf, that is to the commencement of the tendril apparently opposed to this.

The series of numbers recording the successive internode-lengths and the corresponding curves (see Curve 25) are irregular. But when analysed into three sub-series and three sub-curves in the manner just indicated, *the numbers become ranged into three consistent sub-series, and the irregular zigzag internode-curve becomes analysed into three consistent and tolerably regular sub-curves* (see Curve 26). Now, if the series or internode-curves be analysed into two, four, or five sub-series or sub-curves, no such consistence or regularity results. These facts indicate that, whatever be the interpretation of the *construction of the axis, it is determined by three sets of component units*—morphological or physiological in significance.

This conclusion conforms with the view upheld by ST. HILAIRE, ROEPER, BRAUN, KUETZING, WIGAND, and EICHLER, that the stem of *Ampelopsis* is a concatenation of the basal parts of alternately unifoliar and bifoliar branches, which terminate in tendrils.

## Ampelopsis I. (Curve 25.)

A × . . .	30·5	33·5	36	27·5	25	22	26	31·5	33	35·5	38·5	41·5	43	41·75	33·5	31	30·5	12·5
B . . .	26	25	25	23	19	19	25	26	28	27·5	26	32	35	31·5	26	27	19·5	—
C × . . .	24	28·5	22	22	17	19·5	20·5	23	22·5	24·5	27·75	33	33	23	27	24	12	—
B+C × .	50	53·5	47	45	36	38·5	45·5	49	50·5	52	53·75	65	68	54·5	53	51	31·5	—

## Ampelopsis II. (Curve 26.)

(Monopode : 1, 1·25, 1·75, 7·5, 11·5.)

A × . . .	—	12·5	21	27	36·75	34·5	41	32·25	32·5	38	46·25	49·75	42·75	59·5	67·5	61		
B . . .	7·5	14·5	16·5	25	31·5	24	25·5	22·5	20·5	30·25	33·5	37	43	46·5	44·5	43·5		
C × . . .	11·5	18	20	24	29	29	27·5	23·5	26·5	17·5	36·5	38	40	51	44·5	—		
B+C × .	19	32·5	36·5	49	60·5	53	53	46	47	47·75	70	75	83	97·5	89	—		

*Monopodial* interpretations of the axis are :—

- (i) The tendrils are leaves.
- (ii) The tendrils are emergences.
- (iii) The tendrils are extra-axillary branches (according to NAEGELI and SCHWENDENER, WARMING (partly), PEDERSEN, and VELLEN).

In any of these cases we should expect the internode-measurements to form a regular curve, or one, at most, interrupted at the non-tendrilled nodes.

(iv) The stem is a monopodium with tendrils representing axillary branches that have been upwardly displaced (according to LESTIBOUDOIS and DUTAILLY). Against this view may be cited not only the general nature of the curves, but also the particular absence of any transitional displacement-stages as reflected in the curves.

A regular internode-curve might also be anticipated were the stem a *dichotomous* one with each tendril representing one-half of the dichotomous apex (according to WARMING (in part) and PRILLIEUX).

In short, the curves naturally and readily agree with the sympodial theory, but demand various additional and unfounded assumptions to make them conform with any other theory.

[At the commencement and end the curves of the two shoots measured do not agree, because the base of one and the apex of the other were missing. Both curves show a general fall in the main curve and sub-curves before the final rise and fall, and thus recall the forms of curves of some monopodial branches.]

## Part II.—GENERAL CONSIDERATIONS AND CONCLUSIONS.

Rhythmic change is one of the most marked features in the activity of protoplasm, and the periods of the rhythm vary from exceedingly short ones, as in ciliary movements, to successively longer ones, represented by diurnal variations, the waxing and waning activities of individual cells, up to the period representing the duration of life of the individual plant. Rhythmic physiological activity is often revealed in corresponding structural change, as in the succession of lateral members of different size and shape on an axis, as well as in the succession of internodes of definite but different lengths on the stem of a phanerogam. It has already been shown that this latter feature is inherent, though the precise lengths of the internodes are liable to disturbance by external change. But, in the past, too little attention has been devoted to the inherent nature of this feature, and too much stress laid upon the action of environment. This is particularly shown in the cases where no distinction is made between lengthening (or shortening) of an axis due to increased (or decreased) *length* and increased (or decreased) *number* of internodes, as a result of external change. Compared with woody plants, herbs are more directly and immediately subject to the direct action of changes in the surroundings (except wind); I therefore selected them for investigation, as calculated to give the strongest evidence, and more especially so because the periodicity in the length of internodes in a year's growth of a tree is already well known.

*Normal Internode-curve of a Main Axis.*

It has already been pointed out that the normal curve of a main axis of a herb assumes an ascending-descending form.

The curve at once recalls that representing the grand period of growth of a cell (or of a very short zone), and the question arises as to the connection between the two. What SACHS describes as the "grand period of growth" of a cell involves merely a kinetic conception dealing exclusively with the velocity or rate of growth of a cell. The proposition in question states that a cell grows at first with gradually increasing rapidity, and afterwards with gradually decreasing rapidity, until it entirely ceases to add to its length. It does not define or treat of the duration of growth or the ultimate dimensions attained by the cell. There is a similar "grand period" exhibited in enzyme action, and probably in various physiological activities of cells (assimilation and the like).

The length attained by an internode, on the other hand, depends upon several factors: the original length of the internode, the mean velocity, and duration of its growth. It would seem scarcely necessary to enumerate these three obvious factors, but neglect of the first and third frequently leads botanists into making misleading statements in regard to the effect of external conditions upon plant-form (say in regard to the lengths of axes grown in the shade).

The length attained by an internode depends upon the following sets of factors :—

(A) The number of cells definitely set aside in the growing point to produce internode-tissue (Factor I).

(B) The number of transverse divisions in these initial cells, and this in turn depends upon—

( $\alpha$ ) The rate of cell-division and velocity of correlated cell-growth (Factor II).

( $\beta$ ) Duration of the dividing phase (Factor III).

(C) The amount of growth of each cell after it has ceased to divide ; this in turn depends upon—

( $\alpha$ ) Velocity of cell-growth (Factor IV).

( $\beta$ ) Duration of the growing phase of the cell (Factor V).

The differences in the lengths of the successive internodes of an axis might be due to variations in any of the factors numbered I–V. But comparison with *Nitella* and some other Cryptogamia with single apical cells, as well as estimates obtained by observations on Phanerogamia, entitle us to surmise that Factor I remains constant, and may therefore be eliminated from the question. Furthermore, remembering the constancy of size of the initial cells of an internode, if we assume that rate of cell-division is purely a function of velocity of growth of the cell (in one plant), then only three determinant factors remain in connection with the ultimate length attained by the product of a single cell, namely, the mean velocity of growth of the initial cell originally set apart to produce internode tissue, the duration of the dividing phase, and the duration of the growing phase. MOLL (3) has shown that the number of constituent cells of an internode varies nearly proportionately with the length of the internode, whereas the mean lengths of the individual cells vary in the same sense, but to a disproportionately less extent. This shows that the product of Factors V and VI remains nearly constant, and, therefore, that if the mean velocity of growth of the cell during its ultimate exclusively growing phase be changed in the successive internodes, then the duration of growth must be changed proportionately and in an opposite sense. The internode-curve might thus result from an increase and subsequent decrease in velocity of cell-growth, and duration of the dividing and growing phases, or it might result from a steady increase in one or two of these factors, accompanied by a steady decrease in the other two or one.

But older observations have demonstrated that there is some parallelism between the *amount of growth* in length of an axis at different seasons and the length of the internodes formed at the same times, that is to say, when the stem is growing rapidly, the rapidity is due to the production rather of long internodes than of many internodes. There is therefore a likeness between the curves of the amount of growth of the stem and the lengths of the internodes, and an analogy of these with the curve of the grand period of growth of a cell.



Throughout the preceding discussion it has been assumed that the growth in length of an internode is constant throughout its length, but in reality this is not the case. An internode often grows most vigorously at its middle portion, but sometimes the maximum amount of growth is transferred to the upper or lower end.

The fact that there is no essential connection between the grand period of growth of constituent cells and the internode-curve of a stem is instantly shown by the internode-curves of branches.

*Changes in the Symmetry of Typical Stems.*

Ascending the main stem of a herb, or the year's shoot of a tree, it is not only the internodes that show a successive increase and decrease in dimensions, but so likewise do the leaves. And, in the case of the herb, there is a similar change in the vigour of the successive branches, which, traced from below upwards, often show at first an increase, and afterwards a decrease, in vegetative vigour, as estimated by their total lengths, as well as by the number of leaves and internodes.

The various changes in the dimensions of internodes, leaves, and branches of the (relatively) main stem do not synchronise. This is particularly evident in the case of trees in which the lateral buds destined to grow out most vigorously are inserted near the tip of the year's shoots where the internodes are short, and where the leaves may be of maximum size or small.

The waning activity of the terminal bud is a feature of very general occurrence. Unlimited apical growth in Angiospermæ is rare in temperate plants, and probably so even in tropical ones; the majority of European trees are sympodial in growth. (In the more lowly organised plants, for instance, in coniferous trees, unlimited apical growth seems to be more frequent.) I therefore suggest that the permanent suppression and death of the terminal buds of angiospermous trees at the conclusion of the growing season is not to be regarded as a peculiar phenomenon, but is rather to be viewed as an exaggeration of the weakening of vegetative vigour as expressed in the decreased size of internodes, leaves, and branches (buds often being absent from the axils of the bud-scales). As these changes are not synchronous, and as they affect not only the forms of the leaves but the dimensions of the internodes, it would appear that hypotheses involving the assumed existence of the "flower-building material" or "growth-enzymes" of SACHS and BELJERINCK hardly contribute to the comprehension of these rhythmic processes.

*Longitudinal Displacement of Leaves and Branches.*

The characteristic and regular form of the internode-curves of a typical herb clearly indicates that under a definite set of external conditions the length of an internode is defined by its position. This is demonstrated by an application of the graphic method to herbs with invariably opposite leaves (some Caryophyllaceæ,



Labiatae, and individuals of *Rhinanthus*), and supported similarly by alternate-leaved twigs of trees.

But the typical form of longitudinal symmetry, which has some unknown physiological principle as its cause, is liable to disturbance by changes from one type of phyllotaxis (cyclic or acyclic) to the other, so that the curve representing the successive interfoliar distances is modified; and similarly when branches are raised above the leaf-axils the curve representing the distances apart of the successive branches becomes changed.

Considering first the longitudinal displacement of leaves, when the phyllotaxis is changed from opposite to alternate two results follow:—

- (i) The introduction of new segments, which are *displacement-distances*.
- (ii) A shortening of the original internodes, which become represented by a set of new “internodes.” And it must be noted that the sum of the displacement and the new “internode” is not equal to the estimated length of the original internode.

A distinction must be made between *occasional* longitudinal *displacements* which do not characterise all the individuals of a species, and *invariable displacements* which affect a whole species, genus, or family.

*Occasional* longitudinal *displacements* of leaves are met with in *Rhinanthus Cristagalli*. In this case they are slight, and no definite rule prevailed as to the region of their occurrence, though they often attain a maximum just beneath the terminal inflorescence.

*Lysimachia vulgaris*, like the preceding, may have stems on which the phyllotaxis is approximately or exactly cyclic throughout. Some of its stems, however, show great displacements of the leaves, and these displacements attain a maximum high up the axis. But neither in *Rhinanthus* nor in *Lysimachia* is there a steady rise and fall of the displacement-curve, which, on the contrary, is irregular.

*Invariable* longitudinal *displacements* concern the leaves of all the alternate-leaved Chenopodiaceae investigated, and the branches of a number of Boraginaceae. In these cases the displacement-curve is regular and defined, and on the main axis is of ascending-descending form, while on the successively higher branches of the Chenopodiaceae it, like the internode sub-curve or curve, tends to change to a purely descending form. (In some Boraginaceae the curve of branch-displacement on the relatively main axis may not show the final descent.)

Alternate explanations of the zigzag nature of the chenopodiaceous curve, however, present themselves. It might be suggested that the leaves were originally alternate, but that an additional leaf had been intercalated on each internode. Apart from any lack of evidence in favour of such a view, it may be pointed out that where the phyllotaxis is cyclic and additional leaves are intercalated on the stem (as opposed to being acquired by an increased number of nodes added at the apex), the leaves are added in connection with the nodes, which become pleiomerous,

at least in the cases that I investigated. And when an analogous change takes place by the conversion of an alternate-leaved distichous shoot into a tristichous one, in the hazel for instance, inspection suffices to show that the internode-curve is not converted into a zigzag one like that of the Chenopodiaceæ. Again, it might be suggested that the chenopodiaceous curve is capable of analysis into two sub-curves, not for any morphological reason, nor because of any displacements, but because, for some physiological reason, alternate rather than successive internodes are correlated in growth. Such a correlation is indicated in connection with not only the internodes, but also with the displacements, and the behaviour of the nodes of certain plants already mentioned; but these have one feature in common: their phyllotaxis is cyclic, and, therefore, the leaves at the alternate nodes are on the same orthostichies. Such a common feature would not be shared by the Chenopodiaceæ if their phyllotaxis were originally alternate.

Again, it might be contended that the original phyllotaxis was alternate and that the shortness of the alternate internodes of the main stem of alternate-leaved Chenopodiaceæ is merely a case of correlation, and represents the necessary transitional stages between the opposite insertion of the cotyledons and the alternate insertion of the foliage-leaves. Against such a view may be urged: (i) The various considerations and facts cited in Part I of this paper. (ii) The similar nature of the internode and displacement sub-curves of branches, where no such transition is indicated. (iii) The agreement of the displacement sub-curve with that concerning the displaced branches of the Boraginaceæ or displaced leaves in Scrophularia. (iv) The fact that the displacement sub-curve retains its distinctness high up the main axis, where there is no apparent reason for the occurrence of any correlation dependent upon transition.

I therefore conclude that the zigzag internode-curve of the Chenopodiaceæ is due to displacement, and that the displacement sub-curve in this family and in connection with the Boraginaceæ points to some principle determining the dimensions and distribution on the plant of morphological modifications. In this connection it is worthy of note that in axes with occasional or invariable displacements the maximum displacement by no means coincides in position with maximum length of internodes.

One most interesting result obtained in this work is that the displacements of the leaves and branches along the main stem of Chenopodiaceæ and Boraginaceæ respectively, though they are modifications sufficiently ancient in phylogeny to be hereditary and characteristic of a whole species and probably of many genera, yet conform *with the rule established by DE VRIES in regard to the distribution and dimensions of anomalies on a plant*. Traced up the main axis, DE VRIES found these to increase in number and extent and then decrease. And TINNÉ TAMMES (10) has shown that these changes do not synchronise with those in the internode-length. The rule propounded by DE VRIES does not hold exactly for the occasional leaf-displacements

that I observed, but this may be due in part to the paucity of the specimens of one species that I examined, and in part to the fact that some of the axes I examined were not main ones. Indeed, analogy with the displacement-curve of the chenopodiaceous branches leads me to suggest that DE VRIES' rule will not hold good for the anomalies on branches, but that on some branches inserted high up the plant the anomalies will be found either to be most marked near the base of the branch and decreasingly so towards its tip, or to show two maxima.

Although DE VRIES' rule adds strength to the view here propounded in regard to the significance of the displacement sub-curve in Chenopodiaceæ, its application may not be general. The changes investigated by DE VRIES and TINNÉ TAMMES seem to be in the direction of increasing complexity—the separation of whorled leaves in “contorted” stems, the abnormal multiplication of leaflets of a compound leaf, and the gradual conversion of foliage-leaves into ascidia. But degenerative changes might follow an entirely different rule. Therefore if a plant were changing its phyllotaxis from alternate to opposite by a condensation of the alternate internodes, DE VRIES' rule does not necessarily render it probable that such condensations would be most marked in the same region of the stem as displacements or other changes are. Consequently, until DE VRIES' rule has been shown to apply to simplifying modifications, it will not supply us with even a tentative analogy by which to decide between a change from a primitive acyclic to a cyclic phyllotaxis and the reverse.

Finally arise questions as to the physiological significance of longitudinal displacements and the developmental means by which they are accomplished. In the Boraginaceæ the development of the uplifted branches has been investigated by SCHUMANN (11), KOLKWITZ (12), and ČELAKOVSKY (13). The branch arises at a very early stage in the terminal bud of the main stem, as a lump of tissue separated from the leaf below by a mere line, so that it may be described as axillary. This primordium stretches for some distance up towards the actual apex of the main stem, sometimes beyond the first, second, or even third leaf above. Subsequent elongation of the main stem causes this elevation of tissue to be longitudinally extended and the branch ultimately to be inserted apparently at a considerable distance above the subtending leaf. It is obvious that if the branch arises on a portion of the main stem that has not ceased to elongate, the relatively earlier its time of origin or the higher its position of origin on the main growing point the relatively greater will be its apparent upward displacement, always assuming that the internodes at the point concerned grow with equal vigour. But precocity of origin is also indicated by the fact that the branches are more displaced the relatively or absolutely earlier they sprout. In the cases investigated in this paper, the upper branches are basipetal in order of shooting out, and it is the basal branches on the main stem that shoot out late and are not displaced from the leaf-axil. The gradual creeping of the branch-primordium up the main growing point reaches a climax in the Boraginaceæ when it extends to the actual tip, and a dichotomous dichasium seems to result, or a

dichasium in which the true termination (a flower) seems to be carried up one arm of the dichasium as in *Myosotis*.

It therefore becomes evident that a leaf may be inserted higher up the stem than another leaf, because it arises nearer the actual tip, either before, at same time as, or even subsequent, to the next lower leaf, and the higher up the growing point it arises the more will it be raised. To prove such a type of precocity would be difficult, and the sole observations I have made upon the matter in the *Chenopodiaceæ* is to note that often at least two young leaves which will hereafter be separated by considerable lengths of stem, but which belong to the same node, show distinctions in size. In this connection it is of deep interest to note that in the allied *Caryophyllaceæ* the two leaves at a node, though opposite, are stated to arise at different times. This may be the first step towards the condition in *Chenopodiaceæ*. It is obvious that two leaves inserted at the same level in the bud might become alternate by subsequent differential development on the two sides of the stem, and in this connection the frequent flexuous form of the stem in alternate-leaved *Chenopodiaceæ* is not without interest.

#### *Transverse Displacement of Leaves.*

Individual and phylogenetic leaf-displacements in a longitudinal direction, as statistically demonstrated by the graphic method, may shed light upon the question of transverse displacements of leaves. Their occurrence goes to show that the latter displacements, which are often assumed to have taken place in order to account for change in phyllotaxis, are not to be airily dismissed as unjustifiable assumptions devised to bolster up some untenable hypothesis. On the contrary, analogy with longitudinal displacements would lead us to anticipate the occurrence of transverse ones when the phyllotaxis is changing, and, further, to anticipate that up the stem the angle of displacement would increase and then decrease. So far as I observed, the amount of transverse displacements often varied directly with the longitudinal displacement where the phyllotaxis was changing from cyclic to acyclic, just as it would if either the stem were undergoing constant torsion, or if the displaced leaves were moving along a line directed at a constant angle to the long axis, or, finally, if the angle of displacement increased and decreased as suggested above.

#### *Increase and Decrease in Number of Leaves at a Node.*

In *Lysimachia vulgaris*, as the axis is ascended, there is frequently an increase succeeded by a decrease in the number of leaves at a node, and at transitional regions there are all the stages intermediate between a single leaf, a double-leaf, and two leaves.

Other cases of double-leaves have been observed in *Caprifoliaceæ* (20) where the dimerous nodes are becoming trimerous. Double-cotyledons, together with all the



stages to three or four cotyledons, are very familiar in *Acer Pseudo-platanus* and I have observed double-cotyledons in *Fraxinus excelsior*. PAUL REINSCH (14) has described a seedling of *Fagus sylvatica*, which had one ordinary cotyledon and two small ones; and these were succeeded by two opposite foliage-leaves, one of which was bilobed. In *Acer*, the trimery of the cotyledons is succeeded for some distance up the stem by trimery of the foliage-leaves. Increase in the number of cotyledons without any transitional double-leaves is familiar among Coniferæ and polycotylous Dicotyledones, and similar sudden pleiomery is observable in connection with the foliage and stipule whorls of *Stellata*.

The production of double-leaves where the number of leaves at a whorl is undergoing reduction is less known. In *Bauhinia*, the two distal leaflets of a compound leaf are supposed to have fused to form the single more or less bilobed leaf as it now exists. The needles of *Sciadopitys* are usually regarded as resulting from fused pairs of needles. Finally, continuity of the bases of cotyledous foliage-leaves, stipules, sepals, and petals, which sometimes culminate in the disappearance of the original tips of the connected members are common.

Two views have been promulgated to account for the increased number of leaves at a node. According to what may be termed the *morphological theory*, the increase is due to chorisism of one or more leaves, and the double-leaves represent stages towards this. But according to what may be termed the *physiological theory*, there is no direct genetic type of connection between the more numerous leaves at a node and their predecessors; the growing point of the stem can, it is urged, suddenly produce an increased number of leaves at a node by becoming active at a greater number of points on its periphery.

The *morphological theory* may seem to be the more natural when applied to cyclic leaves, and is favoured by the following considerations:—

(i) Transitional stages between one leaf and two distinct leaves occur on individual plants of *Lysimachia*, *Acer*, and others. While similar stages present themselves in different species of *Sphenophyllum*. Again, certain species of *Alchemilla*, in place of having simple alternate leaves, apparently display whorls of narrow leaves, and, according to GOEBEL (15), each seeming whorl is in reality one divided leaf.

(ii) When the increased number is first attained at a node in *Lysimachia*, two leaves nearly occupy the position of one, and are in close lateral juxtaposition.

(iii) If an additional leaf at a node is to be produced, one of the simplest methods of arranging for its vascular supply is for the leaf to arise in connection with a leaf already established.

(iv) It would appear simple to conceive of a primordium originally destined to produce a leaf arresting its apical development prematurely, and allowing growth to persist on the two sides of the apex. Yet, in reply to this, I would urge that though it seems to be fashionable to explain morphological peculiarities by the assumption that the growing point behaves in a peculiar manner, such an assumption is no



explanation, but is rather a mere ontogenetic description. And in this case such an explanation is doubly incomplete, since it neglects the axillary buds—for in the axil of a bilobed leaf of *Lysimachia* there are often two small collateral buds.

(v) In flowers, members described as “chorised” are known to arise from a common primordium.

According to the *physiological theory*, a node suddenly produces a larger number of leaf primordia and, consequently, of leaves. It is supported by the following considerations :—

(i) GOEBEL (16) has shown that in some cases, at least, the increased number of leaves is associated with reinforced nutrition. Still, it must not be forgotten that the division of a leaf often increases with rise in vigour or additional nutrition.

(ii) A similar phenomenon is witnessed in species of *Pinus* when the dwarf-shoots of vigorous plants produce three in place of two needles, or four or five in place of three ; and the reverse is seen in feebly nourished shoots where a reduction in the number of needles on a spur takes place.

(iii) A possibly analogous case is that of vigorous stool-shoots, with alternate phyllotaxis, in which a distichous arrangement is replaced by a tristichous one. But, even in this case, the assumption that the tristichy is due to a modified process of chorisis is not so strained as might be thought at first, since double-leaves have been observed by DE VRIES in alternate-leaved types (*Castanea*, *Carpinus*, and *Robinia*), as is mentioned in ČELAKOVSKY'S paper (17) ; furthermore, in *Salvinia*, of the three leaves forming an apparent whorl, two (the water-leaf and one subaërial leaf) arise by the division of a single segment of the two-sided apical cell.

(iv) Pleiomery often occurs on vegetative shoots and in flowers without any intermediate stages, such as double-leaves.

According to the physiological view, the double-leaves may be explained as examples of correlation, for instance, in the following manner : If a shoot changes from dimerous to tetramerous whorls, the nodes in the two regions receive, so to speak, different instructions. In the dimerous region the leaves are to be produced at two points separated by angles of  $180^\circ$ , but in the tetramerous region at four points separated by  $90^\circ$ . The change of instruction might take sudden effect, so that tetramerous whorls appeared without any intermediate stages, or the nodes at points between the dimerous and tetramerous regions might receive more evenly balanced, conflicting instructions, and the result would be a compromise. Such a compromise would then be represented by the double-leaves and paired leaves. The nature of the message or instructions seems to be beyond our present powers of apprehension, but it does not seem to me possible to accept the simple explanation that GOEBEL (16) attempts in discussing double-leaves in *Caprifoliaceæ* where the phyllotaxy is changing from dimery to trimery. He writes : “They evidently arise because under the influence of the increased nutrition the shoot forms three instead of two primordia of leaves, and of the three two lie close together ; if the plastic material sufficient for the development

of two leaves flows to these then they remain separate and form two leaves; if this is not the case then one bifid leaf is developed." This does not explain why two leaves should be close together, and it is very doubtful if poverty of nutrition would cause trimery to change back to dimery any more than it can modify the rhythmic succession of nodes of certain relative lengths.

Light is thrown on the matter by the reverse process, that of the reduction in the number of leaves at a node. This may be interpreted either morphologically, as a fusion of one or more pairs of leaves, or physiologically. The morphological view is supported by: (i) the double-leaves in *Lysimachia*; (ii) the very common phenomenon of continuity of the tissue connecting the bases of opposite leaves; (iii) the transitions in the Rubiaceæ between pairs of stipules and interpetiolar stipules; (iv) syncotylous plants; (v) various concrescences in flowers; (vi) concrescences between axis and branch, or leaf and branch; (vii) the double-needles of *Sciadopitys*, and the bilobed leaf of *Bauhinia*. The physiological view is just the converse of that in connection with the increase in the number of leaves, and the double-leaves may represent correlative features or compromises, just as transitions from foliage-leaves to bud-scales, or to coloured floral leaves, represent compromises. But in this case there is no room for the somewhat crude conception of a substance comparable with flower-producing substance, for we cannot conceive of a "one-leaf-producing" or a "two-leaves-producing" substance.

It is clear, however, that in ascending a shoot of *Lysimachia* one can see the gradual replacement of one primordium by two close together, and subsequently by two separated by a normal divergence; and higher up one can observe the gradual creeping together of two leaves until a double primordium eventually gives way to a single one. The most novel and interesting case of this latter process was shown by *Rhinanthus Crista-galli*. Occasionally the main shoot, while giving no sign whatever of any abnormal modification in the internode-curve, changes its phyllotaxy from opposite to alternate. The absence of any zigzag in the internode-curve indicates that the change is not due to displacement. The specimen of *Rhinanthus*, termed *Rhinanthus III*, upon which this statement is based, showed a very peculiar arrangement of its leaves. The two cotyledons were succeeded by two nodes with decussate leaves, and these by six nodes with a solitary foliage-leaf at each; above these was a node with a single bract, and thereafter dimerous nodes with decussate bracts. The following were the measurements of the interfoliar distances, commencing at the two cotyledons:—

0	1·25	0	1·5	0	1	8	9·5	18·5	33	48	39	9·5	0	4·5	0
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The corresponding internode-curve (Curve 4) is very regular, and, in order to show its similarity to the ordinary internode-curve of the main stem of *Rhinanthus*, is constructed in the same manner as if there were two leaves at each node.

In cases such as this botanists would ordinarily conclude that at the nodes affected one leaf had been suppressed in each case, and the other had persisted. But the matter is not so simple. At the transitional region, in one or two specimens there occurred two leaves which were not only laterally approximated towards one side of the stem, but were also asymmetrical with the adjacent halves of the blades somewhat reduced (fig. 7), while in *Rhinanthus* III, at the same point, stood a solitary double-leaf (fig. 8). Thus this reduction from two leaves to one leaf at a node is accomplished

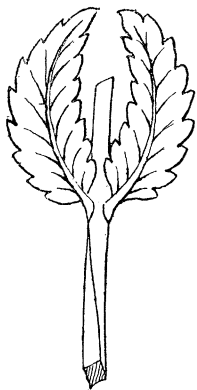


FIG. 7.

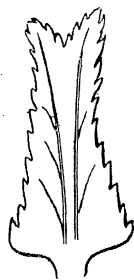


FIG. 8.

by the same means as the reduction of four or three leaves to two in *Lysimachia*; but in this case it causes the phyllotaxis to change from cyclic to acyclic. The process then seems to be one of morphological concrescence or of physiological fusion of impulses.

It is possible that increase and decrease in number of leaves at a node may take place by both kinds of methods. But whichever theory be adopted the facts indicate that a monocotylous embryo may become dicotylous by the process equivalent to chorisis, while a dicotylous one may become monocotylous by the reverse process, without any anatomical evidence persisting in the single cotyledon of any such phylogenetic change (21). The facts also demonstrate that the number of leaves on an axis can decrease or increase on a stem without any corresponding change in the number of original internodes, and that on the one hand opposite phyllotaxis can give way to alternate by the "fusion method" or by displacement, and in the latter case a new set of segments which are intercalary in a phylogenetic sense may arise.

It has already been noted that when the phyllotaxis is cyclic in design the increased (or decreased) number of leaves at the nodes is continued, when once established, for some distance along the stem, but that in this respect alternate and not successive nodes are more closely correlated. This may shed light upon some problems in floral morphology, for instance, upon the nature of the cruciferous flower which might be regarded as showing alternately dimerous and tetramerous whorls. It would also throw a sidelight on the old view that pentamery in a flower may be due to the telescoping together of alternately dimerous and trimerous whorls.

#### *Construction of the Shoot.*

The phanerogamous stem usually, but not universally, shows a clear distinction into nodes and internodes. Apart from anatomical differences between the two, internodes and nodes show a marked physiological distinction, the former being elongating segments and the latter being organ-producing parts.

It will, I think, be admitted that current views regarding the morphological signifi-

cance of internodes are somewhat hazy. In particular, the significance of internodes as segments may be under-estimated because of the failure to distinguish between the ontogenetic addition of internodes at the apex, and the phylogenetic addition by an intercalary method, also because of the now fashionable view that the shoot is the slave of its growing point. In Phanerogamia, however, not only ontogenetically but also phylogenetically the shoot is largely intercalary in origin, in other words, it is easy to conceive of a number of original definite segments which may subsequently undergo modification. The latter conception is favoured by shoots showing ordinary phyllotaxis and a normal internode-curve: in these the relative lengths of the successive internodes are accurately defined, so that the internodes might be compared with the metameres of animals. In families which preserve their acyclic or cyclic phyllotaxis throughout this comparison may be so far justified in that the internodes of allied forms in corresponding positions are in a sense homologous. But it is certainly not always the case that the internodes of an axis are serially homologous; for along one stem the internodes may be of different lineage, as is shown when leaves of a whorl become separated by greater or smaller interfoliar spaces in *Lysimachia vulgaris*, and alternate-leaved Chenopodiaceæ, in the latter of which the alternate internodes are of more recent origin and represent displacements.

The question arises as to the morphological significance of the tissue separating a displaced leaf from its ancestral point of insertion. The question may cease to have any meaning if we assume that the stem is an axis capable, according to circumstances, of emitting leaves wherever these are required or where the growing point and some unknown physiological principle dictate. Although a number of modern botanists seem inferentially to adopt some such view, I shall assume the contrary one, namely, that the segmentation of a stem has a phylogenetic basis, and that the conduct of the growing point is determined in this respect by heredity, as it is, for instance, in the case of the production of leaves characteristic of the species. What, then, is the nature of the tissue *a-b*, separating two leaves A and B which have been relatively displaced from an originally opposite arrangement (see fig. 9). The separation might

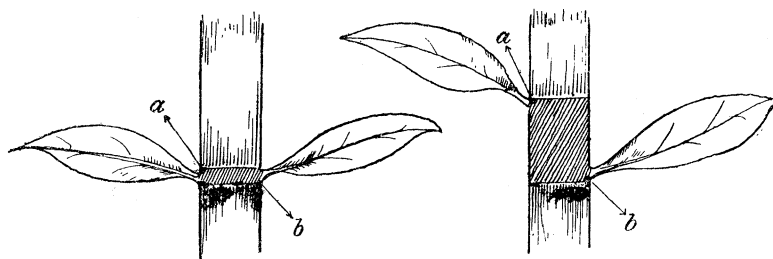


FIG. 9.

be due to a lengthening of the node tissue, but this explanation would not harmonise with the case of the displaced branches of the Boraginaceæ, which may be each raised upward for several internodes.



The simplest explanation would seem to be that derived from an imaginary case of branch-displacement similar to that occurring in Boraginaceæ, but taking place in a stem with a single apical cell. We will further assume that at a certain stage there is set apart a single mother-cell, which will divide anticlinally into an upper daughter-cell destined to produce internode-tissue and a lower daughter-cell destined to give rise to a branch. If there were a tendency for the branch to grow out precociously, and this were revealed by the commencement of its protuberant growth before the mother-cell had divided, then two results follow : (i) The base of the branch might lengthen abnormally in the direction of the axis of the main stem, and seemingly carry the branch upwards, because it is partly constituted of meristem, normally destined to grow in length and add internode-tissue to the main stem. (ii) This elongated base of the branch would represent not branch-tissue alone, but mingled tissue of branch and main axis, because the branch commenced to grow out before the cell-division differentiating between the two took place. Transferring this conception to the Boraginaceæ, a branch is displaced upwards, because its incipient protuberant growth commences before the tissue in that region of the growing point of the main stem has become properly differentiated into meristems destined to produce branch and main stem respectively. This being so, it may be anticipated that the less the upward displacement of a branch the more similar to branch-tissue will be its base, because the relatively later is the inception of the branch and the more completely differentiated are the meristems of branch and main stem. And this anticipation is realised. Low down the stem of Symphytum, where the displacements are at the minimum, the branch is mounted upon a basal cushion of tissue, which extends up the stem for a short distance and has a polished surface contrasting with that of the stem. Higher up the stem, in place of raised cushions, are raised elongated ridges marking the "fused" portions of the branches, but still higher the ridges become more and more indistinct as the displacement increases. Similarly, in the Chenopodiaceæ, the "fused" portions of branches are more clearly marked by ridges the shorter the upward displacement. Thus the tissue connecting the raised branch with a subtending leaf does not exactly represent branch-tissue that has fused with the main stem, but rather represents the result of the activity of a meristem common to main stem and branch, of which it is therefore a blend. In the same sense I interpret the raising of the leaves of Chenopodiaceæ (and others), and regard the *tissue connecting the raised leaf with the node above which it is raised as a blend of leaf-tissue and stem-tissue*.

This conclusion as to the participation of the leaf-tissue in the structure of the stem leads us to the various theories promulgated as to the phylogenetic origin of the stem, wholly or partially, from the "fusion" of the basal portions of leaves. References to these will be found in ČELAKOVSKY'S paper (17). But it may be pointed out that the view that I express here most closely conforms with POTONIÉ'S "pericaulome" theory (18). It is obvious that the theory of the participation of



leaf-tissue in the building up, at least of peripheral portions of the stem, would facilitate the comprehension of the distribution of vascular bundles in a number of types. In time the more central or the more peripheral bundles might disappear, but where the arrangement was found to be advantageous, or was the result of relatively recent change, traces of both sets of bundles might be preserved, and give rise either to amphivasal bundles or to several cylinders of bundles, each with its own cambium. Thus the peculiar mode of production of cambium in the Chenopodiaceæ might be a consequence of the leaf-displacement, but in such a case the same anomaly in the root would require explanation as a correlation.

One final point harmonising with the view that in the Chenopodiaceæ and, doubtless, other cases the stem is partly constituted of the basal portions of the displaced ("fused") leaves, is that when such displacement takes place the internode is shortened by the blending of leaf-base and stem, and it is worthy of note that the phanerogams most strongly suggesting fusion of leaf-base and stem are often those in which the internodes are short (*Salicornia*) or indistinguishable (various *Coniferæ*).

*Cyclic and Acyclic Phyllotaxis in Families.*

Change from cyclic to acyclic phyllotaxis or the converse does not always take place by the same method. Below is given a table showing the conceivable methods, the reverse ones being numbered alike in the two columns:—

Change from Cyclic to Acyclic.

(i) From an opposite arrangement by *gradual atrophy* of one leaf at each node, *e.g.*, certain *Gesneraceæ* according to GOEBEL (19).

(ii) *Sudden cessation* of the growing point to produce one of two leaves at each node (*oligomery*).

(iii) "*Fusion*" of two leaves in an opposite arrangement to produce one, *e.g.*, *Rhinanthus*, compare *Lysimachia*.

(iv) *Longitudinal displacement* of the leaves of one node along internodes, *e.g.*, *Chenopodiaceæ*, *Lysimachia*.

(v) *Elongation* of the original nodes.

Change from Acyclic to Cyclic.

(i) *Gradual evolution of one or more additional leaves* at a node; compare the evolution of interpetiolar stipules of *Rubiaceæ*.

(ii) *Sudden production* of additional leaf-primordia at a node (*pleiomery*).

(iii) "*Chorisis*" of a solitary leaf at a node to produce two or more; compare *Lysimachia*.

(iv) *Displacement of leaves* along the internodes.

(v) *Condensation* of certain *internodes*.

It is therefore evident that the precise morphological significance of the phyllotaxis requires to be investigated in each separate case, and that the terms "cyclic" and "acyclic" are often merely descriptive ones. In some cases it is

simple to guess at the explanation of any anomalies. For instance, *Clematis* is opposite-leaved, though the *Ranunculaceæ* are markedly alternate-leaved. Here we may assume that the acyclic arrangement is primitive, and suggest that, as the *Ranunculaceæ* are generally characterised by the possession of divided leaves, *Clematis* has acquired its opposite phyllotaxis by a process of chorisism or its physiological equivalent.

In some cases the graphic method put forward in this paper will enable us to form some conclusions, and some of the results of special enquiries instituted in this direction are given in the succeeding paragraphs.

As the *Chenopodiaceæ* seem to be derived from an ancestor with cyclic phyllotaxis, the question naturally arises as to whether the whole of the *Centrosperma* may not be cyclic in reality or in original design of their phyllotaxis. The evidence at present inclines in this direction, though further investigations into the longitudinal symmetry of the constituent families are required. The *Caryophyllaceæ*, almost without exception, are opposite-leaved, and the two leaves at a node develop at different times, while the one of the two branches at each node is "strengthened." In the *Amarantaceæ*, opposite and alternate phyllotaxis are about equally divided among the genera, but one alternate-leaved species of *Salvia*, as figured in ENGLER and PRANTL'S "Pflanzenfamilien," shows the chenopodiaceous type of phyllotaxis, in that the internodes are alternately longer and shorter; this character may therefore be common to alternately-leaved *Amarantaceæ*. In *Portulacaceæ*, *Aizoaceæ*, and *Nyctagineæ*, cyclic and acyclic types are both represented. *Cynocrambaceæ* and *Batidaceæ* are opposite-leaved, but the genus representing the former family has a unique type of leaf-arrangement higher up its axis. In the future, I hope to deal in detail with the *Centrosperma*.

The *Boraginaceæ*, closely as they agree with the *Labiata* in true design of inflorescence, construction of flower, and structure of fruit, are usually distinguished by their acyclic phyllotaxis. As they not only exhibit displacement of branches, but also of leaves, and seem to be opposite-leaved in fundamental design and ancestry, they are brought into closer connection with the *Labiata*.

Finally, a number of species showing both whorled and alternate leaves, and characterised by the *great irregularity of internode-curve*, seem to justify the hope that such irregularity will serve to indicate a species, genus, or family, in which the phyllotaxis fluctuates between cyclic and acyclic. Thus the investigation of one species or specimen—living or fossil—gives some clue to the general vegetative characters of a whole family (just as the construction of the internode-curve of a single axis may at once indicate the position of insertion of that axis). Such inherent irregularity of the internode-curve will be distinguishable from irregularity due to corresponding external change, because of the very frequency of the inconsistencies in the lengths of the successive internodes.

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21. Compare various papers by Miss E. SERGEANT and others.

## EXPLANATION OF THE CURVES.

In all the curves, save those of sympodial axes of *Myosotis*, *Petunia*, and *Ampelopsis*, the sub-curves printed plain are internode sub-curves, while the dotted sub-curves denote the displacements of the leaves; but the thicker plain lines in Curves 9 and 10 represent branch-displacements.

*Rhinanthus Crista-galli* (p. 61).(These curves are reduced to  $\frac{3}{4}$ .)

- Curve 1. Main stem of *Rhinanthus* IV.  
 „ 2. „ „ „ X.  
 „ 3*m.* „ „ „ XII.  
 „ 3 (I). Branch I of *Rhinanthus* XII.  
 „ 3 (II, III). Branch II (black) and Branch III (red) of *Rhinanthus* XII.  
 „ 3 (IV, IV'). „ IV „ „ IV' „ „ „  
 „ 3 (V, VI). „ V „ „ VI „ „ „  
 „ 3 (VII, VIII). „ VII „ „ VIII „ „ „  
 „ 4. Main stem of *Rhinanthus* III (largely alternate-leaved).

*Atriplex rosea* (p. 67).(These curves are reduced to  $\frac{1}{2}$ .)

- Curve 5*m.* Main stem of *Atriplex rosea*, Specimen I30.  
 „ 5 (I, II). Branch I (black) and Branch II (red) of *Atriplex rosea*, Specimen I30.  
 „ 5 (III, IV). „ III „ „ IV „ „ „ „ „  
 „ 6*m.* Secondary axis (*m*) of *Atriplex rosea*, Specimen 190.  
 „ 6 (I). First (lowest) Branch (tertiary axis 1) of the preceding axis *m*, *Atriplex rosea*, Specimen 190.  
 „ 6 (II). Second branch (tertiary axis 2) of axis *m*, *Atriplex rosea*, Specimen 190.  
 „ 6 (IV). Fourth „ „ 4 „ „ „ „  
 „ 6 (V). Fifth „ „ 5 „ „ „ „  
 „ 6 (VI). Sixth „ „ 6 „ „ „ „  
 „ 6 (VII). Seventh „ „ 7 „ „ „ „  
 „ 6 (*x*). Branch (tertiary axis) *x* of axis *m* „ „ „ „  
 „ 6 (*q*). Lowest branch (quaternary axis) of the tertiary axis 1, of *Atriplex rosea*, Specimen 190.

*Salicornia herbacea* (p. 69).

- Curve 7. Main stem of *Salicornia herbacea*.

*Atriplex hortensis* (p. 70).(These curves are reduced to  $\frac{1}{2}$ .)Curve 8*m*. Main stem of *Atriplex hortensis*, Specimen 14.

„	8 (IV).	Fourth branch on the main stem of <i>Atriplex hortensis</i> , Specimen 14.			
„	8 (V).	Fifth	„	„	„
„	8 (VI).	Sixth	„	„	„
„	8 (VII).	Seventh	„	„	„
„	8 (VIII).	Eighth	„	„	„
„	8 (IX).	Ninth	„	„	„
„	8 (X).	Tenth	„	„	„
„	8 (XI).	Eleventh	„	„	„
„	8 (XII).	Twelfth	„	„	„

*Symphytum officinale* (p. 71).(These curves are reduced to  $\frac{2}{3}$ .)

In these curves the thick plain line denotes the branch displacements; the thin plain black line the internode-segments; and the dotted line the leaf-displacements.

Curve 9 (I). Erect shoot I of *Symphytum officinale*.

„	9 (II).	„	II	„
„	9 (III).	„	III	„
„	9 (IV).	„	IV	„

*Anchusa* sp. (p. 72).(Explanation of the curves, which are reduced to  $\frac{2}{3}$ , as in *Symphytum*.)Curve 10 (I). Erect shoot I of *Anchusa*.

„	10 (II).	„	II	„
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*Lycopsis arvensis* (p. 76).(These curves are reduced to  $\frac{2}{3}$ .)Curve 11*m*. Main stem of *Lycopsis arvensis*.

„	11 (I).	Branch I	„	„
„	11 (I').	„ I'	„	„
„	11 (II).	„ II	„	„
„	11 (III).	„ III	„	„
„	11 (III').	„ III'	„	„
„	11 (V).	„ V	„	„

*Asperugo procumbens* (p. 77).Curve 12. Main stem of *Asperugo procumbens*.



*Myosotis sylvestris* (p. 78).(These curves are reduced to  $\frac{2}{3}$ .)

The mark  $\odot$  denotes where the leafless floriferous (sympodial) part of the axis commences. Thus, to the right hand of this, the measurements record the distances of flowers apart; whereas to the left hand the measurements are of interfoliar distances. The dotted line to the left of the mark  $\odot$  represents leaf-displacements, but to the right represents merely the alternate interfloral distances.

- Curve 13*m*. Relatively main stem (*m*) of *Myosotis sylvestris*, Specimen M16.  
 „ 13 (IV). Fourth branch on the stem *m* of „ „  
 „ 13 (V). Fifth „ „ „ „  
 „ 13 (VI). Sixth „ „ „ „  
 „ 13 (VII). Seventh „ „ „ „  
 „ 13 (VIII). Eighth „ „ „ „  
 „ 13 (IX). Ninth „ „ „ „  
 „ 13 (X). Tenth „ „ „ „  
 „ 14*m*. Relatively main stem (*m*) of *Myosotis sylvestris*, Specimen M18.

*Solanum Dulcamara* (p. 80).(These curves are reduced to  $\frac{2}{3}$ .)

- Curve 15*m*. Internode-curve of relatively main stem (*m*) of *Solanum Dulcamara*.  
 „ 15 (I-VII). Internode-curves of successive branches, I-VII, on stem *m* of *Solanum Dulcamara*.  
 „ 15 (X-XIII). Internode-curves of successive branches, X-XIII, on stem *m* of *Solanum Dulcamara*.

(The branches are numbered from below upwards.)

*Petunia hybrida* (p. 81).(These curves are reduced to  $\frac{2}{3}$ .)

In both curves the  $\times$ 's denote the points of insertion of flowers, as well as of the paired leaves. To the left of the first  $\times$  the axis is monopodial, to the right it is sympodial.

- Curve 16. Branch of *Petunia*.  
 „ 17. „ II of *Petunia*.

*Lysimachia vulgaris* (pp. 82-4).(These curves are reduced to  $\frac{2}{3}$ .)

- Curve 18*a, c*. Branches A (red) and C (black) of *Lysimachia* II  
 „ 18*b, d*. „ D ( „ ) „ B ( „ ) „

- Curve 19. Stem of *Lysimachia* III.  
 „ 20*a*. „ VIII, according to one interpretation.  
 „ 20*b*. Part of stem of *Lysimachia* VIII, according to another interpretation.  
 (This curve is continued from the point marked with a  $\times$  in  
 Curve 20*a*; the points marked *d* in the two correspond.)  
 „ 21. Stem of *Lysimachia* IX.  
 „ 22. „ XI.  
 „ 23. „ I.

*Oenothera biennis* (p. 91).

(This curve is reduced to  $\frac{2}{3}$ .)

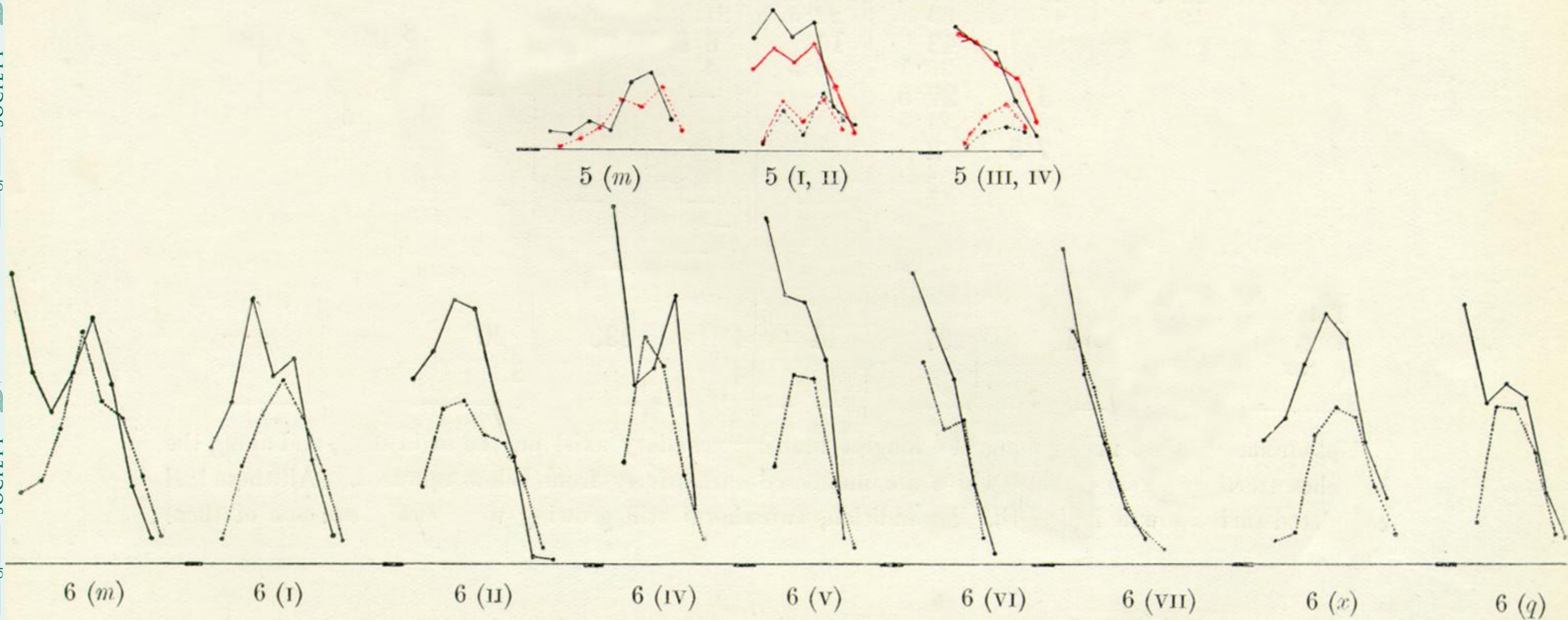
- Curve 24. Stem of *Oenothera* III.

*Ampelopsis hederacea* (p. 93).

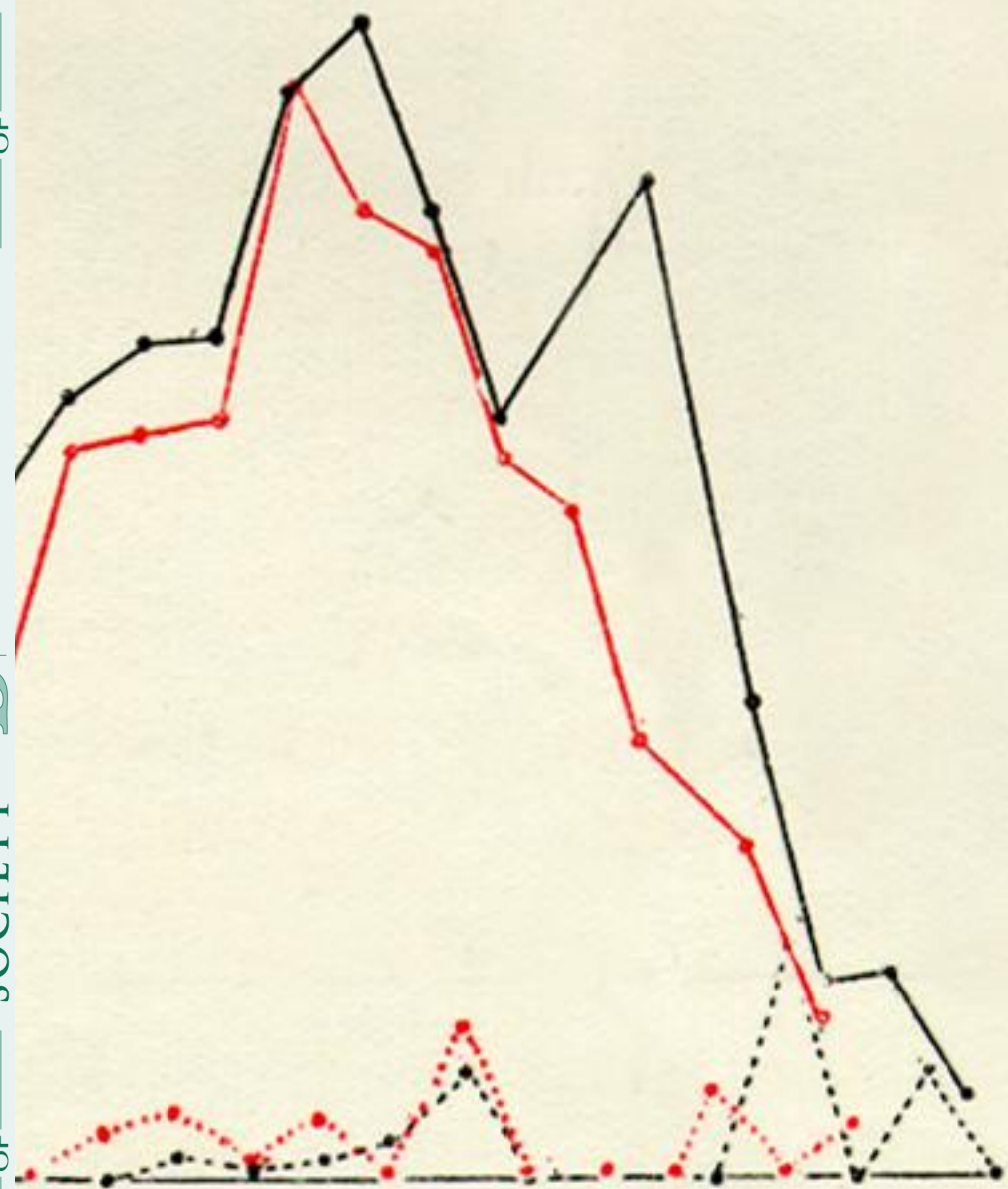
(These curves are reduced to  $\frac{2}{3}$ . The  $\times$ 's denote the points of insertion of tendrils.)

- Curve 25. General curve of interfoliar distances on the sympodial axis of  
*Ampelopsis* I.  
 „ 26. General curve of interfoliar distances of the sympodial axis of  
*Ampelopsis* II, analysed into three sub-curves. (The part not  
 analysed represents a monopodial portion.)

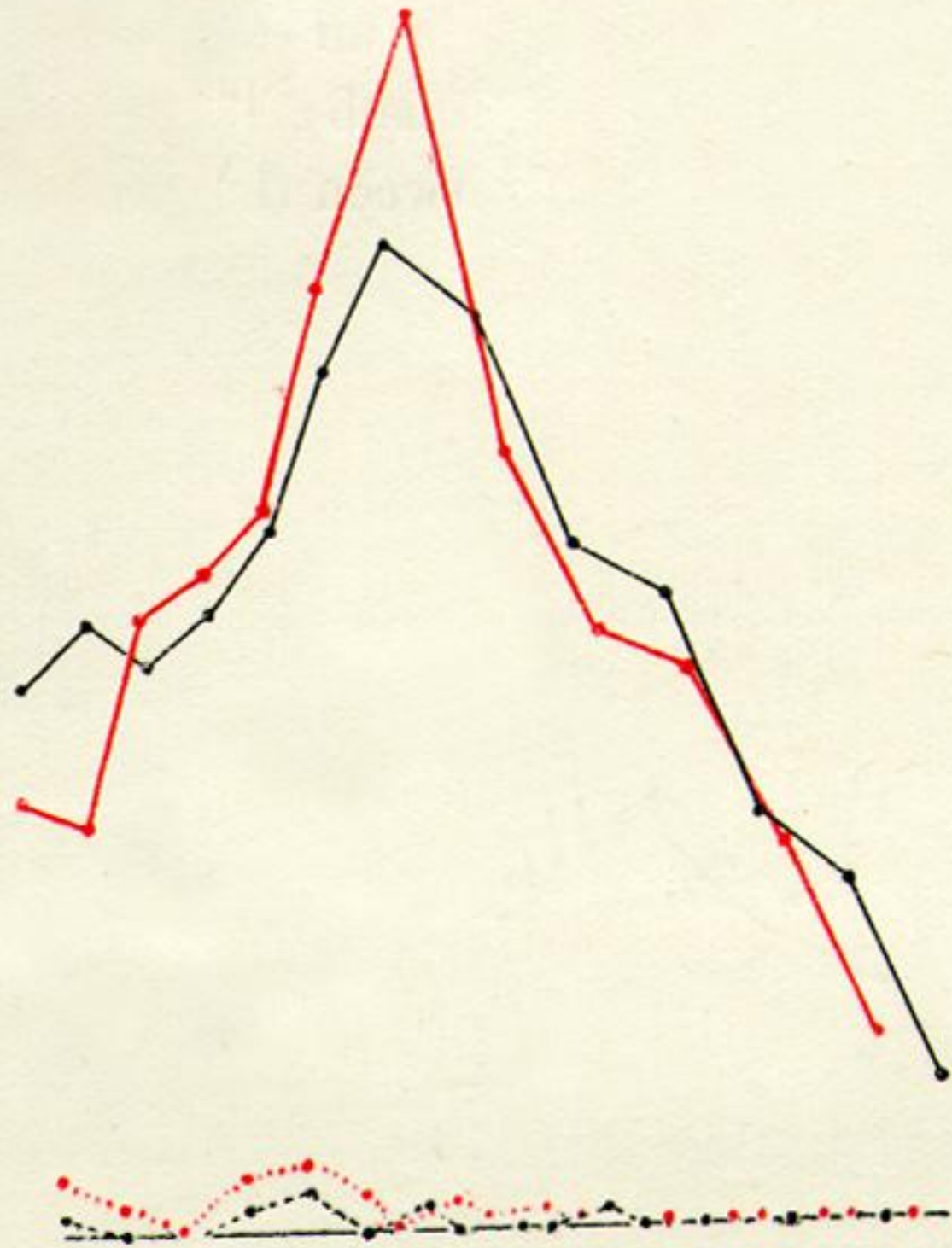








18 (a, c)



18 (b, d)