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A THEORY OF THE REGULATION OF PHYLLOTAXIS BASED ON *LUPINUS ALBUS*

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A theory is proposed to account for the exact regulation of phyllotaxis systems. It is consistent with a space-filling or packing interpretation of phyllotaxis, and is based on evidence showing that, at least in *Lupinus albus*, each leaf base is determined over a primary area which covers a constant arc of the circumference of the apex, and then extends further secondarily before its turn comes to act as a contact member for younger leaf bases above. The theory is that the secondary extension of a leaf base varies as the divergence angle between its two contact leaves below, and that this gradually regulates a disturbed system. Evidence of this correlation is offered, and its cause and imperfections are discussed.

To test the theory, a first diagram is constructed showing a regular phyllotaxis system with contacts 2 and 3 and with divergence 137°, as in *L. albus*, and with the leaf bases represented by circles as if on the surface of an unrolled cylinder. An inner circle represents the primary area of each leaf base and an outer circle its area when later it acts as a contact member for younger leaves. Two further diagrams are then constructed which at the base are similar to the last, but higher up show a leaf that has been displaced 20° laterally in either direction by splitting vertically its presumptive area, as was done in the experiments on *L. albus*. From this level onwards the diagrams are continued in accordance with space-filling principles, by inserting the constant primary area of each leaf base in its turn into the lowest available space between the older ones and then surrounding it with a concentric zone of secondary extension proportional in width to the divergence of its contact leaves below. The diagrams return towards the previous regular arrangement about as quickly as the comparable actual apices, and finally become more regular than a normal apex. It is therefore claimed that the theory provides an escape from the chief difficulty confronting a space-filling interpretation of phyllotaxis.

The changes of phyllotaxis in the more severely disturbed apices are described and interpreted, including several changes to spirals with four leaves in a turn. The shapes and development of the leaf bases are discussed in relation to regulation in this and other species.

I. Introduction and statement of the theory

By various lines of evidence, chiefly experimental, we have been led to adopt (1931, 1952) a space-filling or packing theory of phyllotaxis, which has seemed to us to follow naturally from the valuable work of van Iterson (1907). In brief, this theory is that each new leaf is determined in the first space on the growing apical cone that attains a necessary minimum size and minimum distance below the extreme tip. But the serious difficulty has remained that it has not been clear how a theory of this kind can account for the *exact* regulation of phyllotaxis systems to their usual fairly high accuracy, or for the fact that they return to regularity after a disturbance, natural or experimental, which is not enough to upset them completely. This difficulty has been emphasized recently by Schuepp (1959) and by van Iterson himself (1960), and we are indebted to Dr F. W. Richards for demonstrating to us with diagrams some years ago that on a packing theory of phyllotaxis any small disturbance will be propagated, and not eliminated from the system.

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But the method of demonstration implied that each leaf base, when once formed, was supposed to remain constant in size relatively to the surface of the apex or axis at its insertion, and so to cover a constant arc of the circumference. Actually it does not do so; it continues to extend laterally during several plastochrons, at least in *Lupinus albus*, the species which we have chiefly studied, and probably in most species. This lateral extension is a secondary process, and can be distinguished, as we have shown previously (1933, 1959) from the primary determination of the leaf base over a constant arc of the circumference. But yet on a packing theory it must affect the positions in which the still younger leaf bases will be determined, since some of it will have taken place before they are determined.

We had for a long time suspected that the regulation of the phyllotaxis after a disturbance depended on changes in the secondary extensions of the leaves, in many species at least, and this suspicion was strengthened when we found (1959) that in *Lupinus albus* the amounts of secondary extension of the leaf bases are indeed susceptible to regulation. For the extensions of the youngest leaves are partially inhibited by the next older leaves, since they can be increased by cutting down these older leaves. If therefore, this is one factor regulating the secondary extensions, there may be others also, and it becomes possible to consider and test various ways in which, after a disturbance, the phyllotaxis may be regulated through changes in the secondary extensions of the bases of the young leaves. In the present paper, after describing the normal secondary extension of the leaf bases, we shall consider the following possible explanation of the regulation of phyllotaxis.

(1) After a disturbance the secondary extensions of the young leaf bases vary directly as the divergence angles between the centres of the two older leaves with which they make contact below.

(2) As a result of this variation the phyllotaxis returns gradually to regularity, if the disturbance is not too big.

As evidence for the first point we offer a graph showing the relation between the total arcs covered by various leaves arising after the operations in some of our recent experiments on apices of *Lupinus albus*, and the divergence angles between their contact leaves. These arcs and divergence angles are well suited for revealing any such correlation since both varied widely after the disturbances caused by the operations. To support the second point we offer diagrams showing that if the secondary extensions of leaf bases, represented as circles, vary with the divergences of their contact leaves, the phyllotaxis does indeed return gradually to regularity after a disturbance.

A very different kind of theory has recently been proposed by van Iterson (1960) to explain the exact regulation of phyllotaxic systems, which he considers to be unexplained on existing theories of phyllotaxis. It is based on a comparison with ‘crispations’, which are patterns of stationary elevations and depressions caused by vibrations in the surfaces of liquids contained within boundaries. Clearly if it should turn out that exact regulation *can* after all be explained on the basis of a packing theory of phyllotaxis, as will here be maintained, the reason for proposing the crispation theory would disappear, though naturally it still might be correct. It is probably too soon to make much further comment, since van Iterson’s present statement of his crispation theory is said to be preliminary; but we find it difficult to understand how a crispation theory could be combined with a packing or space-filling theory of phyllotaxis such as seems to us to follow naturally upon van Iterson's own earlier and very valuable work on phyllotaxis (1907). It is also difficult to understand how a crispation theory could be reconciled with many of the results of operations on plant apices, especially those in which a cut at one side of the apex has changed the positions of several subsequent leaves all around it without entirely upsetting the whole phyllotaxis system. Perhaps the full statement of the crispation theory will answer such questions.

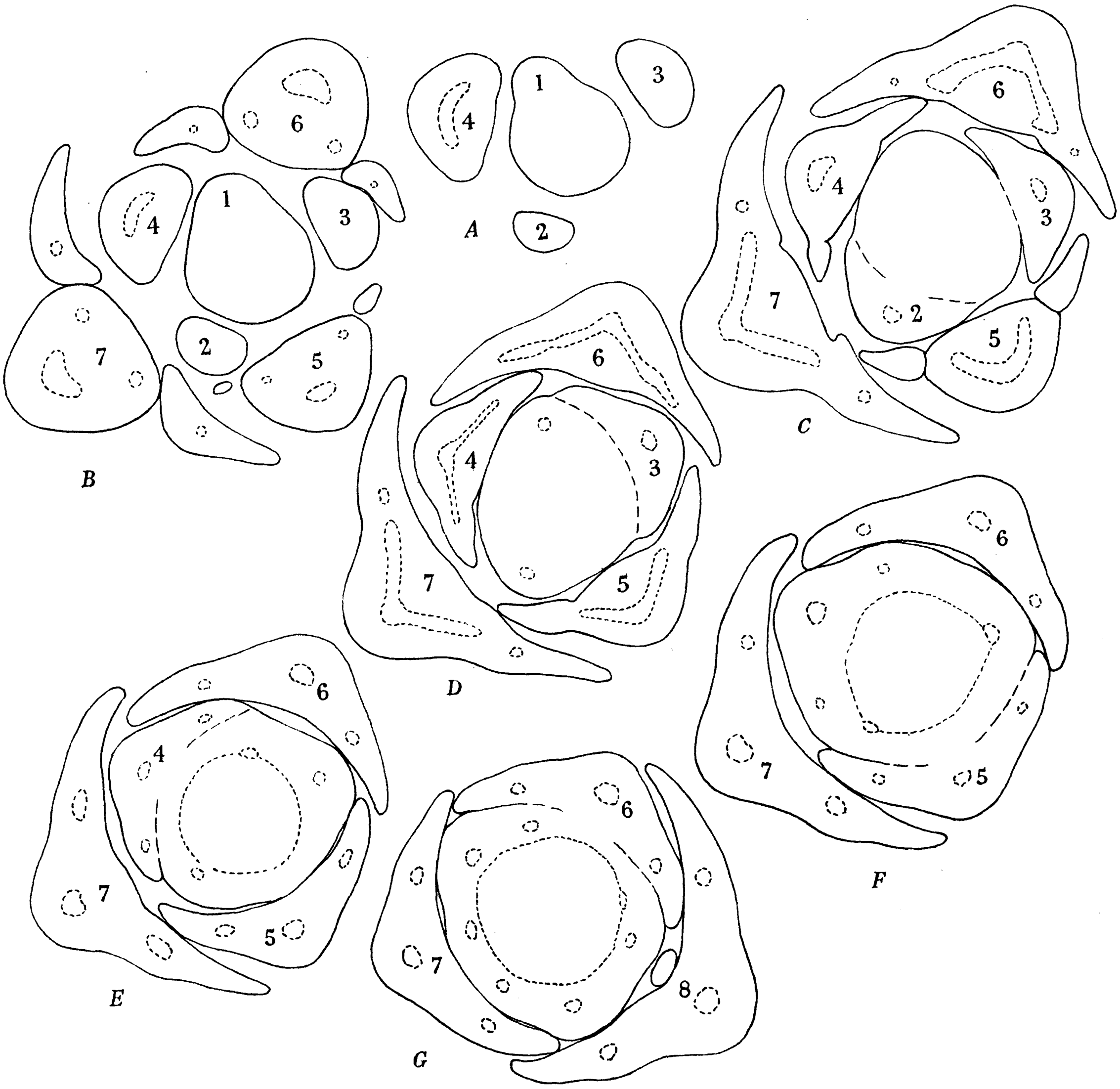

Figure 1. Normal apical buds of *Lupinus albus*. *A* to *F* transections through insertions of leaves 1 to 5 in one apex at late plastochron: *G* through insertion of leaf 6 in another apex. (Magn. *A*, *C*, ×82; *B*, ×88; *D*, ×75; *E*, *F*, ×65; *G*, ×45.)

II. The secondary extension of the leaf bases in normal lupin buds

The mean arcs covered by the leaf bases from the second to the thirteenth below the apex in normal intact lupin apical buds comparable with those operated upon are given in table 1, and examples of the successive leaves or leaf bases from the first to the seventh are shown in figure 1. The arcs were measured at the insertions of the leaves and the buds were taken at stages corresponding with the earlier or later stages of the period of experiment, but little or no difference was found in the arcs at these different stages of growth of the whole seedling, except in those of the older leaves, from the eighth or ninth below the apex downwards. For measuring these older leaves usually only the stages corresponding with the end of the experimental period could be used, since at earlier stages these leaves were usually too close to the base of the plant, being amongst the first formed eight or nine leaves of the seedling, which have arcs differing from those of the leaves formed later. All the apical buds of table 1 in which the arcs of leaves 2 and 3 were measured had been embedded in paraffin and microtomed. Some of the others and all those operated upon, to be described below, were embedded in collodion and sectioned free-hand, as usual.

TABLE 1. MEAN ARCS COVERED BY SUCCESSIVE LEAVES IN APICAL BUDS OF NORMAL LUPIN SEEDLINGS

number of leaf below apex	2	3	4	5	6	7	8	9	10	11	12	13
mean arc in degrees	115	129	136	140	145	145	154	158	160	162	161	162
number of leaves measured	(9)	(9)	(14)	(13)	(15)	(14)	(10)	(6)	(6)	(5)	(5)	(5)

It can be seen in table 1 that the arcs increase fairly rapidly until the fourth leaf below the apex, but from then onwards they increase more slowly, and scarcely at all after the tenth leaf.

No mean arc is given for the first leaf, since its arc cannot be measured at early plastochron when it first becomes visible. But the following single arcs of first leaves at late plastochron stages were measured in degrees, 79, 80, 90, 92, 95, 95, 96, 102. These measurements tend to a limit at about 100°, and in agreement with this the smallest arc of a second leaf measured was also 100°. The primary arc over which a leaf is determined we found experimentally to be 90° in this race of lupin (1959), but this arc need not be the same as that of the visible leaf at any particular stage. The measurements indicate that a little before the end of its first plastochron the youngest leaf fully covers its determined primary area, and then it begins to extend secondarily. The check and recovery in the secondary extension from leaves 6 to 8, if genuine, is unexplained.

Since the lateral edges of a leaf extend only transversely in this species at least, and do not turn and run up towards the apex, it seems that their long continuing extension must be made possible by some slight incipient internodal elongation of the axis. This would gradually raise each leaf base to a higher level in relation to its contact leaves, and so enable it to extend further laterally above them.

III. EVIDENCE THAT THE SECONDARY EXTENSIONS OF LEAF BASES VARY WITH THE DIVERGENCE OF THEIR CONTACT LEAVES BELOW

The evidence to be presented in this section consists of measurements made on drawings of sections of forty apical buds of *Lupinus albus* in which we have split vertically the presumptive area of I_1, the next leaf due to arise, or more often of I_2, the next again. They were left to grow for about 15 days. The chief phyllotactic changes will be described in detail for their own interest in §6, but here they need to be summarized briefly, in order that what follows may be intelligible. In sixteen of these apices leaves were formed by both halves of the split presumptive area, which will be called *N*, whether I_2 or I_1. The two leaves formed by this area will be called *Nk* and *Na*, being at the kathodic and anodic sides of the cut in relation to the genetic spiral, and other subsequent leaves will be called $N+1$, $N+2$, and so on. All but one of the pairs of leaves, *Nk* and *Na*, were united above the wound. In fourteen more apices only *Na* was formed and in ten more *Nk* only. We have described already (1959) the leaves *Na* or *Nk*, as evidence for the constancy of the primary leaf arc, in sixteen of these apices in which they abutted on one side of the wound.

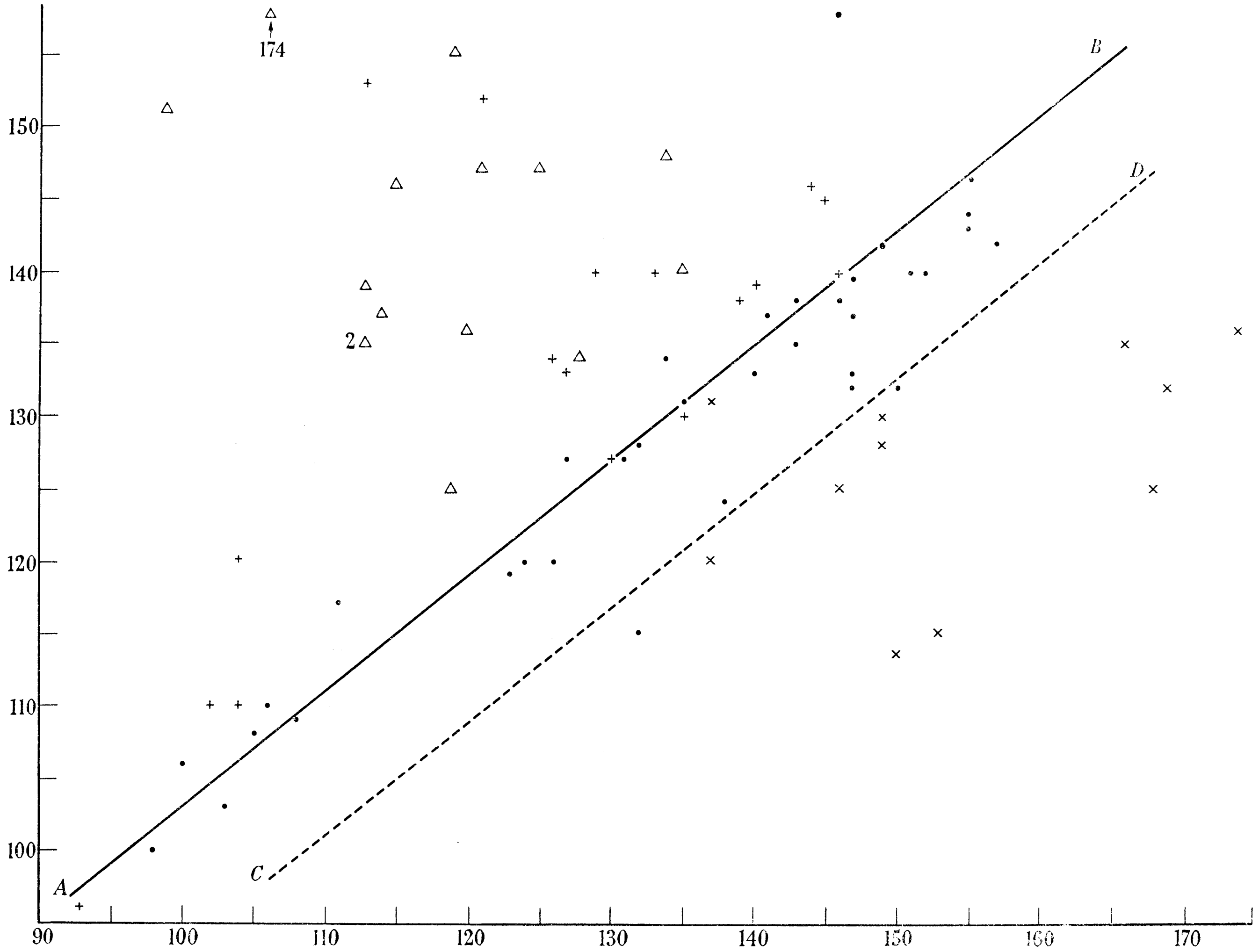

FIGURE 2. Relation of secondary arcs in degrees covered by various young leaves (ordinates) to angles between centres of their contact leaves (abscissae) after splitting of I_2 or I_1 in *L. albus*. The points referring to these leaves have symbols which indicate the overlap or separation of the edges of their contact leaves, as follows: △, overlap 20° or more; +, overlap 10° or more, but less than 20°; ●, overlap or separation less than 10°; ×, separation 10° or more. 2△ marks two coincident points.

The forty apices include some in which the leaves older than the split I_1 or I_2 were cut down rather low, and some in which they were cut down slightly, for the purpose of the previous paper (1959). But this difference of treatment affects chiefly the arcs of the first few leaves that arise after the operation, of which few are included in the evidence to be presented here: consequently it is not likely to have made much difference to any correlation between arcs and divergences, and actually it did not seem to have done so.

The evidence indicating that the secondary extension of a leaf base varies with the divergence angle between the centres of its contact leaves is presented graphically in figure 2. Since the primary arc over which a leaf is determined has been found to be constant at any one stage of development of the plant, as explained above and previously (1933, 1959), the variations of the total arcs covered later by the leaf bases are due to the variations of their secondary extensions. The measurements of these total arcs represented in the graph were made on the leaves from $N+2$ onwards in the forty apices operated upon, since these leaves made contact below with others that had been, or could have been, displaced directly or indirectly by the operation. In age they ranged from the fifth below the apex to the tenth, or once the eleventh. At these stages of development the secondary extension has greatly slowed down or nearly ceased, as table 1 shows, so that the leaf arcs are comparable enough for the present purpose. All the leaves included in the graph made either contacts 2 and 3 below, as is normal, or contacts 3 and 4. The contacts here intended are not necessarily those found at sectioning, when the leaves had extended secondarily, but those which measurements on the sections showed to be the original contacts. The following groups of leaves were omitted, as being not comparable in their arcs:

(1) Leaves that made contact with two others that were nearly simultaneous, or, at the other extreme, with two others differing in age by two plastochrons instead of one, since such leaves were situated in depressions of unusual shape.

(2) Leaves that made contact with the wound or with leaves of abnormal shape, or that were situated in depressions that from any other cause were of abnormal shape.

(3) Leaves that in extending laterally had been blocked at one edge by the edge of another leaf at the same level.

(4) Leaves of which the original contacts were uncertain.

The graph indicates that the arcs of the leaves, and therefore their secondary extensions, are indeed positively correlated with the divergence angles between their contact leaves below, and the line *AB* marks what appears to be the general trend of distribution of most of the points. It therefore seems reasonable to suggest an explanation of regulation based on such a correlation. However, there are several points rather far above the line of general trend, indicating leaves with arcs unusually big in relation to the angles between their contact leaves and several rather far below the line; and this suggests that some second factor is complicating the results. Moreover, the distribution of these aberrant points appears to follow very roughly a trend different from that marked by the line *AB*, running downwards from left to right; and this suggests that the second factor also is partially correlated with the angles between the contact leaves, but acts in the opposite sense on the arcs of the leaves between them.

A study of the leaves marked by these aberrant points has indicated what this second factor may be, and the question is of some interest. The leaf bases in *Lupinus albus* begin to extend transversely from the very earliest stage, as table 1 shows. In a normal apex the edges of two successive leaves are at first separated, and in their second and third plastochrons, when they are determining the position of the leaf between them, their edges are still separated by 15° (see table 1). But in their fourth and fifth plastochrons they reach the same angular position, and then they begin to overlap. The leaves with which those included in the graph made contact had ended their most rapid transverse extension, but yet they varied greatly in size, having been formed on disturbed apices, and the divergence angles between their centres also varied. Both these variables naturally affected the overlaps of the contact leaves, which must have tended to vary in the same sense as their sizes and arcs and in the opposite sense to the divergence angles between them. It seems that the variations in the overlap of the contact leaves were the second factor affecting the arcs of the leaves between them, as the following evidence will show.

These overlaps or separations have been measured between the contact leaves of all the leaves included in the graph, and their amounts are indicated by symbols centred on the points marking the leaves. Different symbols indicate leaves situated between contact leaves overlapping by 20° or more, between those overlapping by 10° or more, but less than 20°, and between those separated by 10° or more. When the contact leaves neither overlap nor are separated by as much as 10°, the leaves between them are indicated by black circles only. If now separation is considered as a negative overlap, the distribution of the different kinds of symbol on the graph is roughly similar to that of the more widely scattered points themselves, and indicates a progressive diminution of overlap in a direction on the graph that falls from high above the line *AB* on the left to rather far below it on the right. Thus big overlaps of the edges of contact leaves are found to lead to leaves between them that have abnormally large arcs in relation to the divergence angles between the centres of those contact leaves, and separations of the edges of contact leaves to lead to leaves with abnormally small relative arcs.

This can also be shown quantitatively by listing the mean overlaps of the contact leaves of all the leaves in the graph divided into groups with arcs at successive distances from above the line *AB* to below it, separations being again taken as negative overlaps. These mean overlaps are 24·8° for twenty-six leaves 6° or more above *AB*, 8·1° for fourteen leaves less than 6° above *AB*, or on it, 1·0° for twenty-one leaves less than 6° below *AB*, and −14·9° for sixteen leaves 6° or more below *AB*. These overlaps and separations of contact leaves were, of course, measured at the end of the period of experiment. Earlier, when these leaves were determining the position of the new leaf between them, their overlaps will have been less or negative, but the order of these quantities in the four groups at different heights on the graph will presumably have been the same.

The effects of the varying overlaps of the contact leaves on the leaf arcs and also those of the varying divergence angles between the contact leaves can be understood if one supposes that the secondary lateral extension of a young leaf base is impeded when its lateral parts reach the central parts of the bases of its contact leaves, which are the parts that reach highest up the apex, since then they are delayed until the necessary space is made available for them above those central parts by the elongation of the axis (see figure 3*A*, *B*). Consequently secondary extension varies with divergence angle between centres of contact leaves, as the line *AB* on the graph indicates. But in *Lupinus albus* the upper contours of each side of a leaf base very early become concave upwards, as is also shown in figure 3*A*, *B*. By observing in the solid we have seen these concave upper contours developing in a leaf as early as the beginning of its second plastochron, and they result from the secondary lateral extension, which in turn is connected with the stipule formation. Consequently in this species a leaf developing between two contact leaves extends laterally without much hindrance over the flatter lateral parts of those leaves unless or until its edges reach their higher and steeper central parts. But then it is more impeded, since its own morphological shape and orientation normally keep the extension of its edges to the transverse direction round the apex, and prevent them from running upwards towards the growing point.

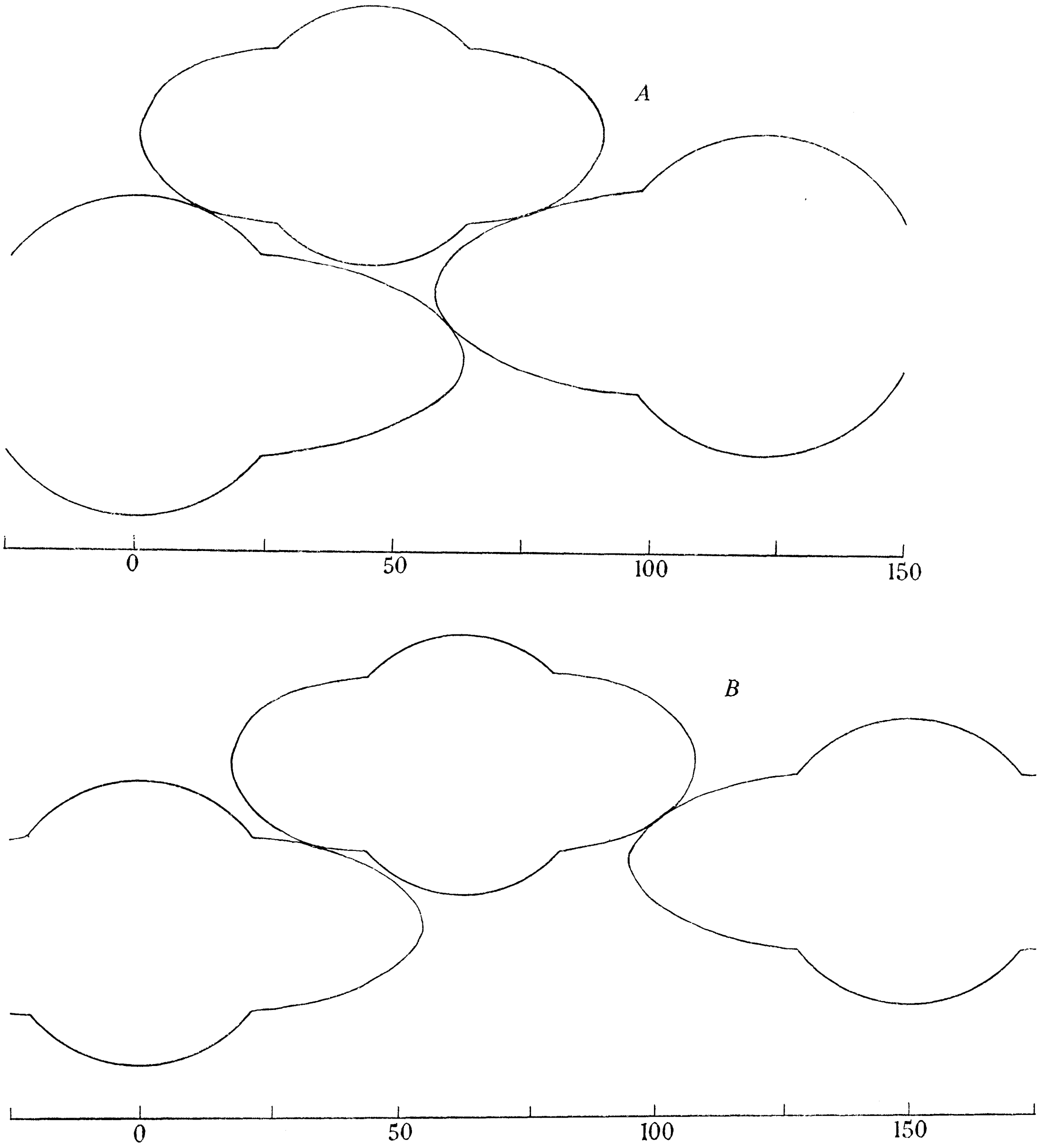

Figure 3. Diagrams showing *A* high position of a leaf between contact leaves that overlap, and *B* low position between contact leaves with edges separated. In *A* the contact leaves have been drawn larger than in *B*, and with their centres closer. The leaf between them has the normal primary arc of 90°. The base lines show the angles in degrees. The leaf bases are shown as if on the surface of an unrolled cylinder.

But the more the lateral parts of the contact leaves overlap, the higher in relation to their central parts will have been the position in which the leaf between them was first determined, and the more easily will the edges of that leaf extend over their central parts (see figure 3*A*). Similarly, the less the contact leaves overlap, the lower will be the position of the leaf between them, and the more will its lateral extension be impeded. Finally, if the edges of the contact leaves remain separated, the position of the leaf between them will be lower still, since its central part will have been determined as if sinking a little into the open gap; so then its lateral extension will be more impeded still (see figure 3*B*).

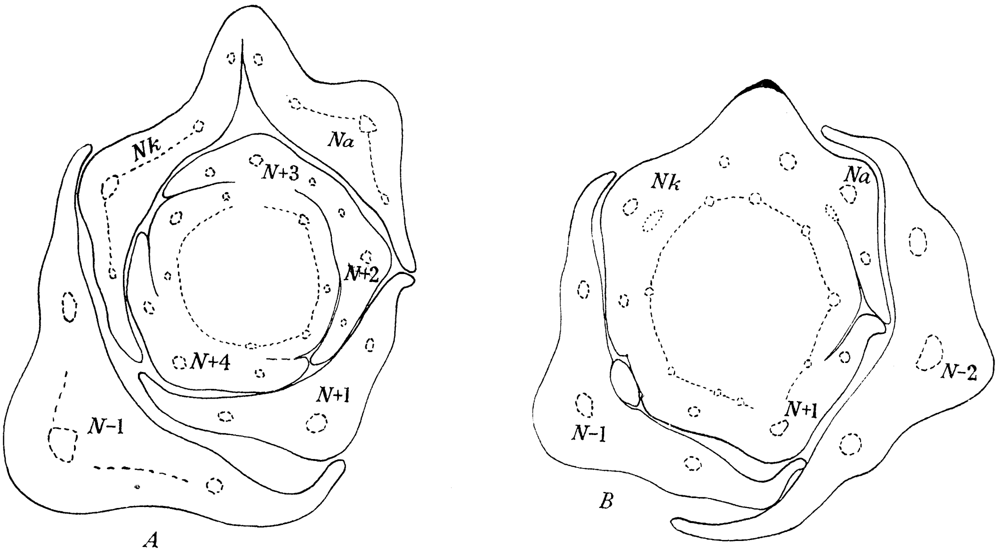

FIGURE 4. *A* and *B*. Sections of an apex, no. 38, in which the I_2 area, here called *N*, was split. *Nk* and *Na* are united above the wound. The arc of $N+4$ is discussed in the text. The wound scar is shown black in *B*. (Magn. *A*, × 37; *B*, × 32.)

A piece of evidence strongly supporting this interpretation is provided by one leaf, $N+4$ in figure 4*A*, that was between contact leaves with edges separated by 16°. This leaf would at first be expected to have a very small arc in relation to the divergence angle of its contact leaves, which was 142°; but actually its arc was 139° and quite close to the line *AB* on the graph. It was found that the gap between the edges of the contact leaves was filled up by an axillary bud belonging to a still older leaf below (figure 4*B*). Such buds are normally not formed at this stage of development of a lupin seedling unless it is near to flowering, but occasionally one or two buds are formed in the axils of leaves formed just before or after an operation. It therefore seems very probable that the leaf in question had a relative arc of about average size because it had been prevented from occupying a specially low position by the exceptional axillary bud between the edges of its contact leaves. It was indeed situated unusually high for the leaf in this gap, as will be made clear when the phyllotaxis is described in described in §6. This leaf was omitted from the graph (figure 2) as being in a depression of unusual shape.

Several of the leaves that did occupy specially low positions were still so small at the end of the period of experiment, that it seems probable that they had been unable to recover from the check to their lateral extension caused by the central parts of their contact leaves, and unable therefore to begin again to extend laterally even when the elongation of the axis provided the space necessary for extension above the contact leaves.

On the basis of the theory of the regulation of phyllotaxis to be proposed here it must be expected that in *Lupinus albus* the leaves with exceptionally large or small relative secondary arcs will interrupt and delay the regulation. It will be shown in the next section that regulation is indeed often interrupted in this species, and that some of the interruptions can be traced back to the exceptionally large relative arc of a certain leaf formed after the operation. In species in which the leaf bases do not develop the re-entrant or concave upwards shape described above for *Lupinus*, the leaves with exceptional relative arcs would not be expected, nor the resulting interruptions of regulation. It would therefore be of great interest to find whether such other species regulate their phyllotaxis more smoothly and rapidly than *Lupinus albus*.

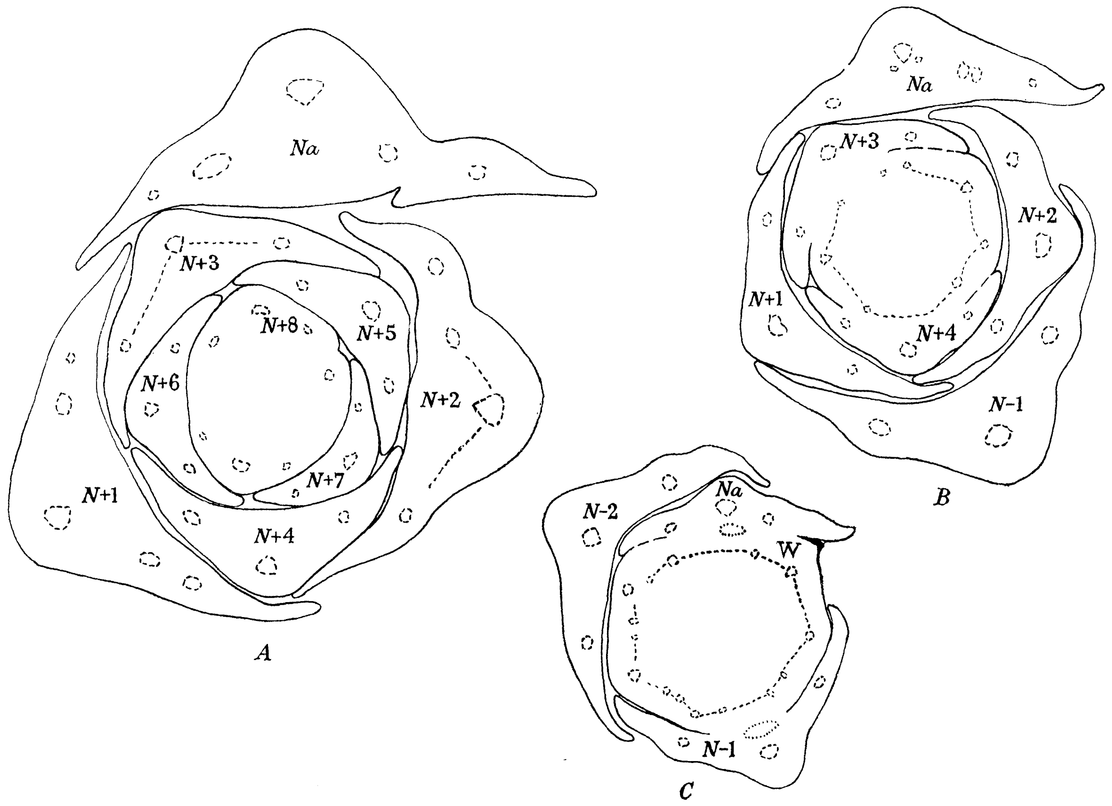

FIGURE 5. Sections of and apex, no. 101, which regulated its phyllotaxis after the I_1 area had been split. A leaf, *Na*, has arisen abutting on the anodic side of the wound. In this and subsequent figures a thick black line represents the wound scar, here marked *W*. (Magn. *A*, × 51; *B*, × 31; *C*, × 20.)

IV. EXAMPLES OF REGULATION OF PHYLLOTAXIS IN THE APICES OPERATED UPON

As convenient examples of returns to regularity we have taken eleven apices in which, after the splitting of the I_1 or I_2 area, a new leaf arose at the anodic side of the wound only, with its base abutting on the side of the wound, and in which the phyllotaxis remained spiral with three leaves in a turn and showed no special peculiarities. An example is shown in figure 5, apex no. 101. The new leaf at the side of the wound was a displaced I_1 or I_2, whichever of these presumptive areas was split, but here it will be convenient to give the name N to the split area, whether I_1 or I_2, and to call a new leaf at the anodic side of it Na. Measurements of the divergence angles in these eleven apices, from the angle $N-1$, Na onwards, are given in table 2. The first angle of the series is always very big, since Na is displaced in the anodic direction from its normal position. The second angle, Na, $N+1$ is always made very small by the displacement of Na, since $N+1$, which was not in contact with Na when determined, arose very close to its normal position. The third angle $N+1$, $N+2$, is always very small, and then the mean angles settle down to the normal mean of 137° or very close to it, apart from an isolated increase of 5° in the mean for the seventh angle, $N+5$, $N+6$. This angle was larger than the normal 137° in seven out of eight of the apices of table 2 in which it could be measured, and it provides a useful test of the theory proposed in the previous section, since it shows that regulation has somewhere been interrupted, and the cause needs to be looked for.

Table 2. Divergence angles in eleven apices with leaf N displaced to anodic side of wound (Na), in degrees

numbers of apices	split leaf area	$\angle N-1, Na$	$Na, N+1$	$N+1, 2$	$N+2, 3$	$N+3, 4$	$N+4, 5$	$N+5, 6$	$N+6, 7$	$N+7, 8$	$N+8, 9$
39	I_1	164	104	160	133	—	—	—	—	—	—
41	I_1	175	105	147	145	124	151	141	—	—	—
43	I_2	175	113	150	126	140	134	—	—	—	—
45	I_1	152	126	147	134	142	138	141	—	—	—
52	I_2	164	104	157	142	127	144	143	134	136	—
59	I_2	172	102	155	146	136	142	—	—	—	—
60	I_2	166	111	149	140	138	135	144	143	136	134
88	I_1	152	121	144	135	141	130	139	139	134	—
90	I_1	150	121	149	140	137	138	145	134	139	—
91	I_1	152	120	146	134	140	133	137	142	136	—
101	I_1	154	119	147	127	147	131	145	132	133	141
	mean	161	113	150	137	137	138	142	137	136	137

In all the apices of table 2 the large angle $N+5$, $N+6$ came directly above leaf $N+3$ (see figure 5) and in seven of the eight apices in which this angle could be measured, the leaf $N+3$ covered an arc that was very big in relation to the divergence angle in which it was situated. This is shown most clearly on a graph like figure 2 by the distances of points representing the arcs of the $N+3$ leaves above the line of general trend AB, the mean value of these distances in the eight apices being 17·5°. These large relative arcs indicate that the $N+3$ leaves must have been situated at levels that were high in relation to their contact leaves, below, and the $N+3$ leaves must therefore have tended to separate widely the leaves $N+5$ and $N+6$, which were above them on each side; and this accounts for the large angle between $N+5$ and $N+6$. The high insertion levels of the $N+3$ leaves can in their turn nearly all be explained as due to large overlaps of the edges of their contact leaves or in one instance to abnormally thickened edges of their contact leaves. The mean overlap of their contact leaves in the relevant eight apices was 13°. Thus the sequence of irregularities support the provisional conclusions reached in the previous section, that deviations from a normal correlation of secondary leaf arc with divergence angle of contact leaves are commonly caused in this species by abnormal overlapping of the edges of the contact leaves, and that when this happens it must interrupt the regulation of the phyllotaxis.

Two other striking examples of a leaf with large relative arc underlying a large divergence angle were found in two apices of other groups, nos. 66 and 100, figures 12 and 15. In no. 100 the leaf $N+4$ had a very big relative arc which came 49° above the line AB in the graph (figure 1) and the divergence of $N+6$ and $N+7$, which were above $N+4$ on each side was also big, 145°. In no. 66 $N+4$ had a relative arc that came 59° above the line AB, the highest point of any in the graph, and the divergence of the leaves above $N+4$, which also were $N+6$ and $N+7$, was bigger still, 148°.

Although the means of the successive angles in table 2 quickly approach the normal 137°, the angles in each apex approach it much more slowly. If we take an angle deviating from 137° by more than 5° to indicate that an apex has not settled down after the operation, such a deviation is found as late as the sixth or seventh angle of the series in six of the eleven apices. Naturally even after that angle it is not certain that the apices had quite returned to normal, but in three of them a further three or four angles were measured and did not deviate by more than 5°. This makes it rather probable that these three apices had indeed settled down after the sixth or seventh angle, since in previous measurements of fifty-two divergence angles in normal apices, admittedly of a different race of *Lupinus albus*, we found the probable error of a single angle to be 1·88° (1931, p. 5). In many of the other apices the series of angles measured was too short to show when, if at all, they settled down completely.

V. Construction of diagrams to test the theory of regulation

In order to test whether returns to regularity, such as those found in the apices operated upon, can be understood as resulting from the correlation of secondary leaf extension with divergence angle between contact leaves, we have constructed diagrams in which the primary leaf areas are represented as circles on the surface of an unrolled cylinder, as was done by van Iterson (1907). But we have made a change by adding to each primary leaf area a concentric zone of secondary extension. We have taken the arc covered by a primary area to be 90°, in agreement with our most recent estimate (Snow & Snow 1959), and in a diagram of a normal apex (figure 6) we have added a zone of secondary extension 16° wide, so that the total arc becomes 90°+32° = 122°. This is the mean of the total arcs of the critical second and third leaves below the apex (table 1), with which the leaf about to arise will make contact, and on which its position will depend according to the theory here adopted. Actually the bases of the young leaves extend gradually, and they are not circular, but transversely extended, even as early as in the last part of their first plastochron, and concave upwards on each side, as already stated, from the beginning of their second plastochron, so that their shapes are difficult to specify exactly. Thus two rather drastic simplifying assumptions have been made, but it seemed too difficult to construct diagrams with progressively changing sizes and shapes of leaves. Also in many species the leaf bases are much more nearly circular than in *Lupinus albus*, and our purpose was to test whether in general on a packing theory the phyllotaxis would return to regularity after a disturbance, rather than to limit the test to this one species.

The divergence angles were taken as 137°, and were plotted along the abscissae at the scale of 25° to one inch. The differences in level between successive leaves were found by calculation to be numerically equivalent to 30·97°, and were plotted along the ordinates at the same scale, at which their value was 1·239 in. In this way a regular diagram was constructed in which the primary area of each leaf was shown in contact with the zones of secondary extensions of the leaves 2 and 3 plastochrons older. The parts of these zones which would have run over the bases of older leaves were omitted, since they would have made no difference. The positions of the centres of the leaf bases are the same as in a diagram made with circles of a fixed diameter of 106°, half way between 90° and 122°.

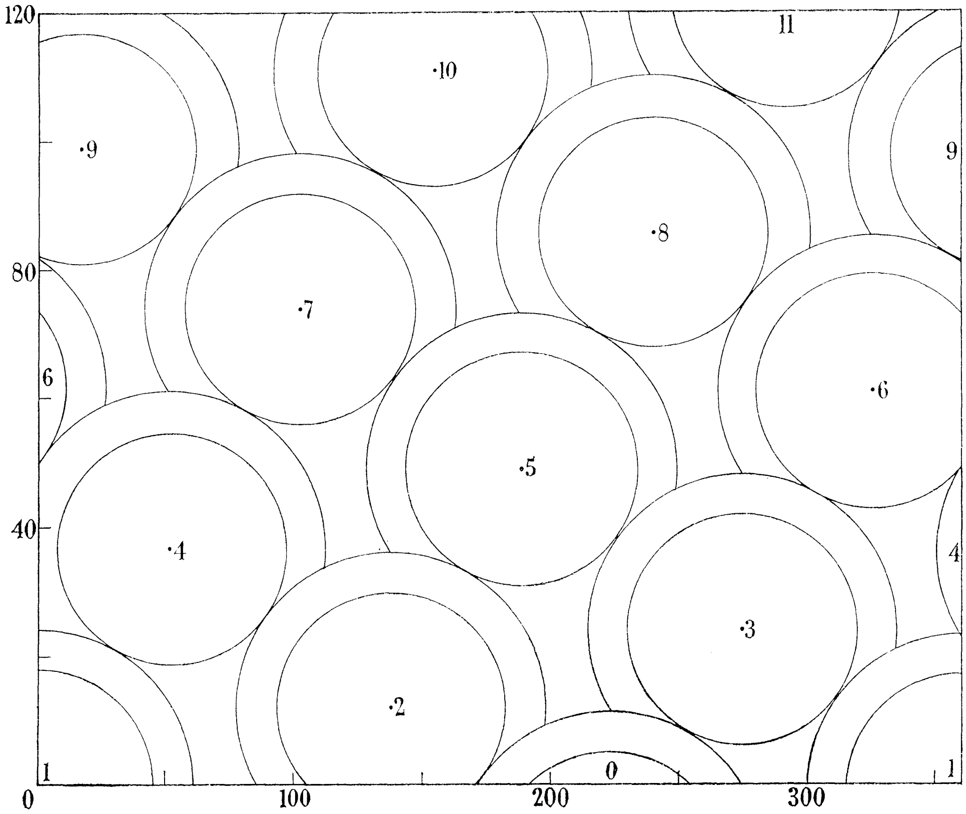

FIGURE 6. A diagram of a regular spiral phyllotaxis system with contacts 2 and 3 and divergence angle 137°, and with each leaf base represented by two concentric circles on an unrolled cylinder. The inner circle marks the primary determined area, and the outer circle a zone of secondary extension. The diagram is further explained in the text. Abscissae, angles in degrees; ordinates, vertical distances in $\frac{1}{10}$ in. Reduced to $\frac{1}{3}$.

In the same way we constructed the lower regular part of a diagram of a disturbed apex with a leaf *Na* at the anodic side of the wound (figure 7), but above the level of the split leaf area *N* we proceeded differently. Apart from the leaves *Na* and *N*+2, which reached the wound on each side, each leaf above the level of the split area was fitted in its turn as a circular primary area with diameter 90° into the lowest available space between two older leaves, so as to make contact with them. Also each leaf, when thus fitted into its space, was given a concentric zone of secondary extension having a width proportional to the divergence angle between the centres of its contact leaves below. These contact leaves in the apices represented were always contacts 2 and 3, except for the leaves *Na*

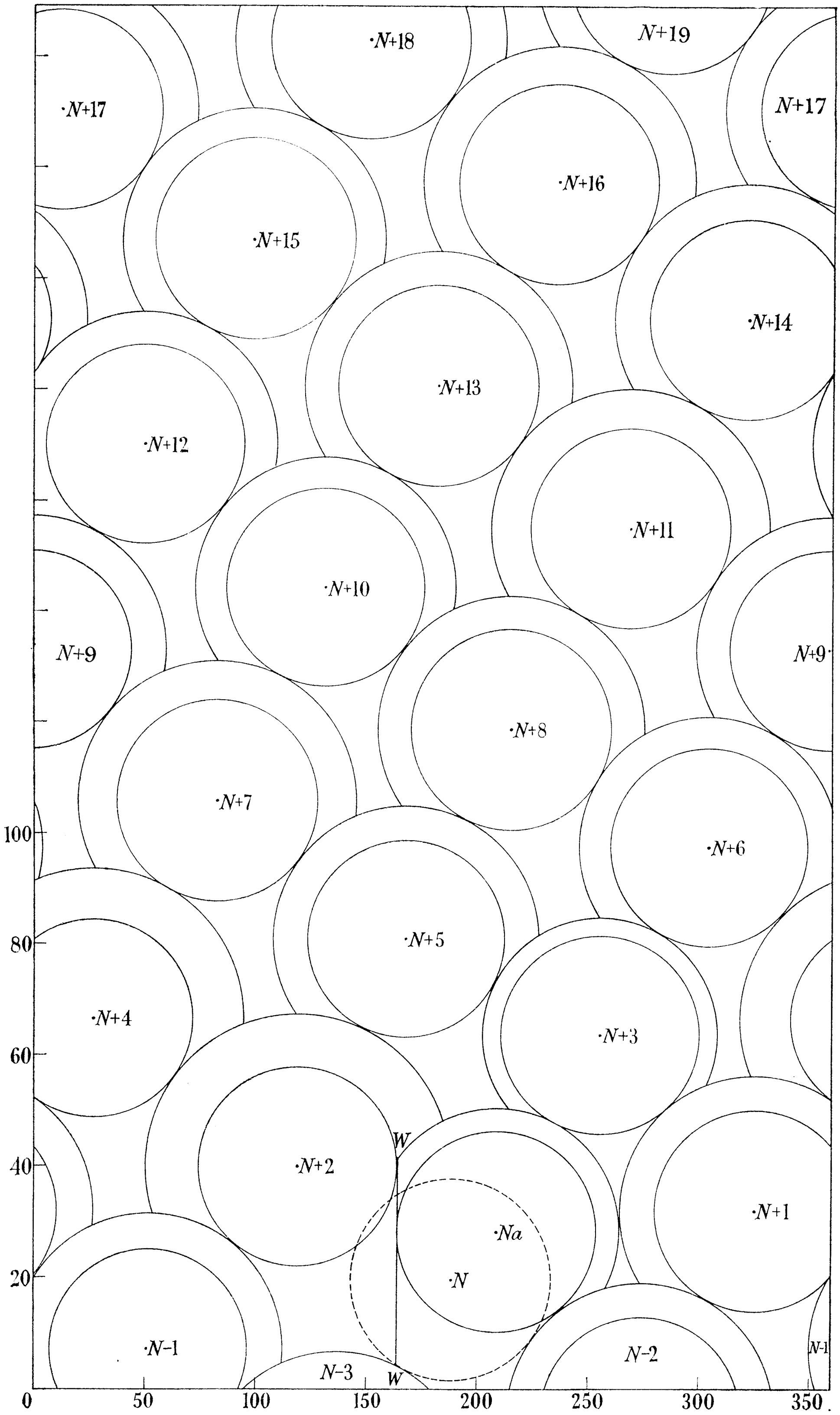

FIGURE 7. A diagram similar below to figure 6, but showing higher up the consequences of displacing one leaf, *Na*, in the anodic direction by splitting its presumptive area, *N*, as in operations on *L. albus*. *Na* is displaced 20°. The area *N* is marked with a dotted circle, and the wound splitting it with the vertical line *WW*. The zones of secondary extension of the successive leaf bases are made to vary in width with the divergence angles between their contact leaves. Further explanation in the text. Reduced to $\frac{1}{3}$.

TABLE 3. RESULTS FROM DIAGRAM OF ANODIC DISPLACEMENT OF LEAF *N*

number of leaf	divergence angle of contact leaves in degrees (normal 137)	total arc allotted in degrees (normal 122)	divergence angle to next leaf in degrees (normal 137)	rise to next leaf in units equal to 2·5° (normal 12·39)
$N-1$	137·0	122·0	157·0	20·8
Na	—*	101·0*	117·0	3·8
$N+1$	137·0	122·0	153·5	8·0
$N+2$	—*	114·0*	136·0	24·0
$N+3$	117·0	106·0	131·0	3·0
$N+4$	153·5	135·5	141·5	14·5
$N+5$	136·0	121·0	136·5	16·5
$N+6$	131·0	117·0	138·0	8·25
$N+7$	141·5	125·5	132·5	13·5
$N+8$	136·5	121·5	143·0	14·5
$N+9$	138·0	123·0	132·5	11·25
$N+10$	132·5	118·0	138·0	10·75
$N+11$	143·0	126·5	138·5	15·0
$N+12$	132·5	118·0	132·5	10·75
$N+13$	138·0	122·5	140·0	12·0
$N+14$	138·5	123·0	136·5	14·5
$N+15$	132·5	118·0	137·5	10·25
$N+16$	140·0	124·0	136·0	13·0
$N+17$	136·5	121·5	138·5	13·0
$N+18$	137·5	122·0	135·5	12·0
$N+19$	136·0	121·0	137·0	12·0
$N+20$	138·5	123·0	138·5	13·2
$N+21$	135·5	121·0	135·5	12·2
$N+22$	137·0	122·0	137·5	12·0
$N+23$	138·5	123·0	136·5	13·25
$N+24$	135·5	121·0	137·0	12·0
$N+25$	137·5	122·0	136·5	12·25
$N+26$	136·5	121·5	138·0	12·75

* See text.

and $N+2$ which touched the wound. Thus the diagram implies that each leaf is determined over a constant primary area, but is then surrounded with a variable zone of secondary extension before its turn comes to act as a contact member, and so to take part in determining the position of a younger leaf. The correlation of the total leaf arc, and hence of the secondary leaf extension, with the divergence angle within which the leaf arises is taken in the diagrams of the disturbed system (figure 7) according to the sloping line *AB* drawn on the graph (figure 2): but the absolute values for the arcs have all been reduced, since those shown on the graph are measurements of leaves from the fifth to the tenth below the apex, whereas what is needed for the diagram is the mean of the arcs of the second and third leaves, on which the position of the next leaf to arise will depend, as already explained. The mean of these two arcs was found to be 122·5° in normal apices (table 1), and accordingly the line *CD* has been drawn on the graph parallel to *AB* but lower, passing through the point representing a leaf arc of 122°, made up of 90° primary and 32° secondary, and a divergence of contact leaves of the normal 137°. Then, for making the diagram, the values for the leaf arcs appropriate to the various divergence angles have been read off along the line *CD*.

The leaves *Na* and $N+2$, which touched the wound at different levels, needed special treatment. Leaf *Na* was placed with its primary area of 90° touching the anodic side of the wound, and with its centre displaced 20° in the anodic direction, this being not far from the mean displacement in the apices of this group which was 24°. The vertical wound was placed in the angular position corresponding with this position of *Na*, that is to say, $45° - 20° = 25°$ kathodic from the normal position of the centre of *N*. Leaf *Na* made contact on its other side with $N-2$ below. But the secondary extension of *Na* could not be made proportional to any angle between two contact leaves, since *Na* was in the space between one contact leaf and the vertical wound. So instead its zone of secondary extension was made 11° wide, less than the normal 16°, this being close to the mean width actually found in the comparable *Na* leaves, which was 12·3°. On one side the secondary extension is completely blocked by the wound, so that *Na* is asymmetric and its total arc is only $90° + 11°$ instead of $90° + 22°$, as the diagram shows.

The wound was also made to reach up a little above the split presumptive area *N*, which is shown as a dotted circle, high enough for the primary area of leaf $N+2$ to make contact with the kathodic side of the upper part of the wound, as actually it was found to do in the apices of this group. Correspondingly leaf $N+2$ was placed with its centre 45° kathodic from the wound and in contact with $N-1$ below on its other side. Since $N+2$ was nearly in a position of contact with $N-1$ and *Na*, instead of $N-1$ and the wound, it was given a zone of secondary extension proportional in width to the angle $N-1$, *Na*. This zone was 24° wide, but on one side, as the diagram shows, the wound completely blocks the secondary extension of $N+2$ at the level of its centre, like that of *Na*, so that its total arc at this level is 114° instead of 138° although at a higher level it extends laterally above the wound. This representation agrees roughly with the observed position and size of $N+2$ in most of the apices (see figure 5).

Table 3 gives in columns 4 and 5 the successive divergence angles and differences of level or rises from one leaf to the next measured on the diagram, starting from leaf $N-1$, and these result from developing the diagram according to the rules stated. It also gives in column 3 the total arcs allotted to each successive leaf in constructing the diagram, and these, which are made up of primary arc and secondary extension, have been obtained from the graph (figure 1) in the way already explained. But since these total arcs depend on the divergences of the contact leaves (column 2), which have been measured on the diagram, they also result, though indirectly, from the development of the diagram. The chief results of this diagram are also summarized in tables 5 and 6, row 1. It can be seen that the divergence angles return towards the normal 137° nearly as rapidly as in the actual apices of table 2, and that the successive rises to the next leaf and total arcs also return towards the normal. Figures 7 and 8 do not include the leaves higher than $N+18$ in the diagrams.

In the actual apices of this group the series of angles measured was much shorter, not more than ten at the most (table 2). It was concluded that some of these apices had probably settled down or returned to normal regularity after the sixth or seventh angle of the series, which was the last that deviated by more than 5°. But this was because account was taken of the natural variability of the divergence angles of normal lupin apices, indicated by the probable error of 1·88° which we found previously (1931). The diagram should become much more exactly regular, if self-regulating in principle, since it is subject only to the errors of drawing; and this indeed it does, as tables 3 to 6 show, though naturally only after a large number of angles.

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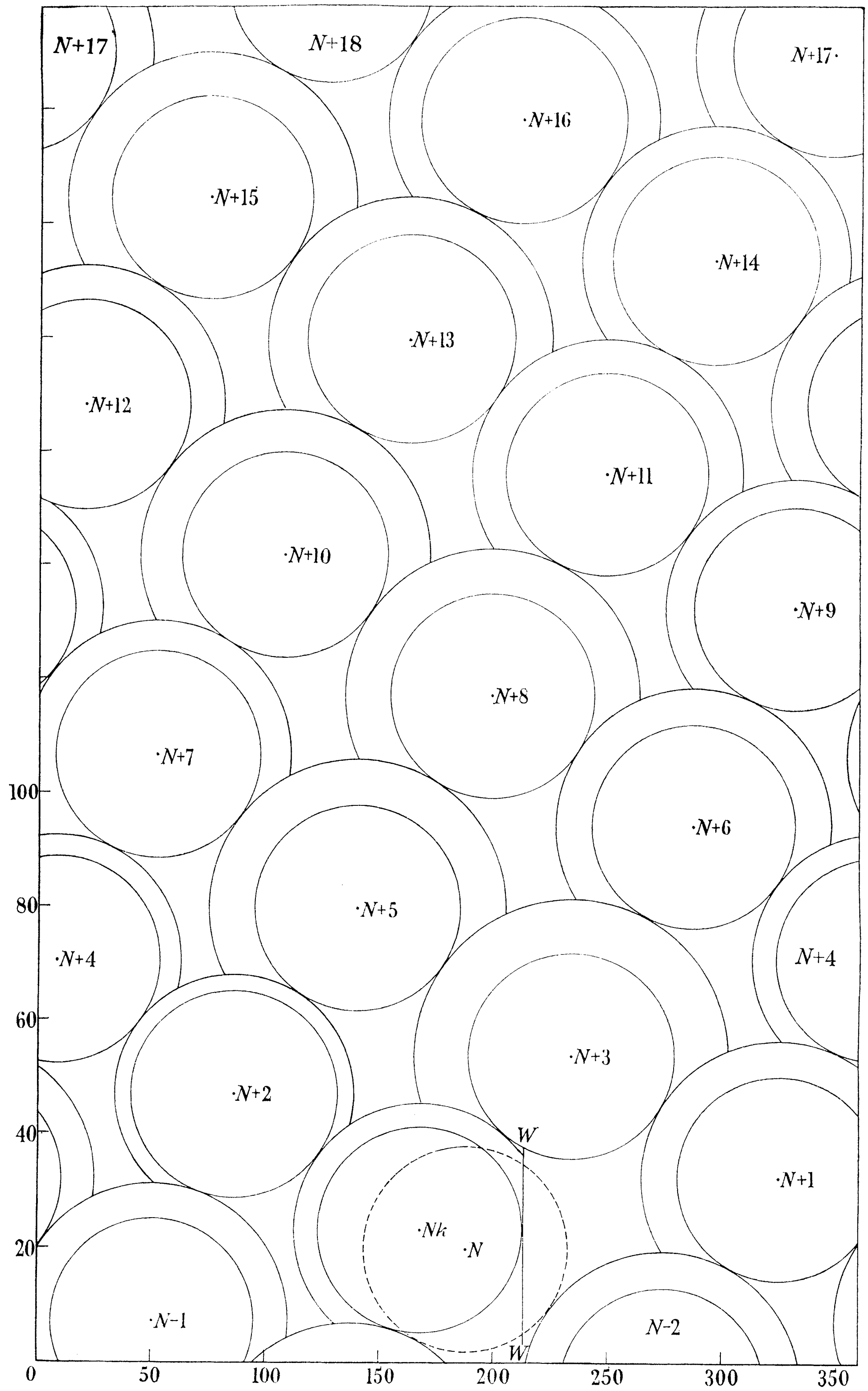


FIGURE 8. A diagram similar to figure 7, except that the displaced leaf, here called *Nk*, has been displaced in the kathodic direction. Further explanation in the text. Reduced to $\frac{1}{3}$.

Another diagram, figure 8, was constructed on the same principles to represent a disturbed system with a new leaf, Nk, in contact with the kathodic side of the wound. This result was obtained in three apices only, since the primary area of Nk usually lay partly above the wound. Nk was shown displaced 20° in the kathodic direction from the normal angular position of leaf N, and it was given an extension of 11°, like Na in figure 7. The wound also was placed in the corresponding angular position, 25° anodic from the normal centre of N, but in this diagram no leaf except Nk needed special treatment, since no younger leaf made contact with the other side of the wound.

TABLE 4. RESULTS FROM DIAGRAM OF KATHODIC DISPLACEMENT OF LEAF N

number of leaf	divergence angle of contact leaves in degrees (normal 137)	total arc allotted in degrees (normal 122)	divergence angle to next leaf in degrees (normal 137)	rise to next leaf in units equal to 2·5° (normal 12·39)
$N-1$	137·0	122·0	117·0	15·8
Nk	—*	101·0*	157·0	8·8
$N+1$	137·0	122·0	122·0	15·0
$N+2$	117·0	106·0	148·0	6·75
$N+3$	157·0	138·0	134·0	17·0
$N+4$	122·0	110·0	132·0	9·0
$N+5$	148·0	131·0	147·0	9·5
$N+6$	134·0	119·5	127·0	12·25
$N+7$	132·0	118·0	147·0	10·6
$N+8$	147·0	130·0	132·5	15·25
$N+9$	127·0	114·0	137·0	9·5
$N+10$	147·0	130·0	141·5	14·4
$N+11$	132·5	118·0	132·5	12·0
$N+12$	137·0	122·0	142·5	11·7
$N+13$	141·5	115·5	133·0	14·0
$N+14$	132·5	118·0	139·0	10·75
$N+15$	142·5	126·0	136·5	13·75
$N+16$	133·0	118·5	136·0	11·8
$N+17$	139·0	123·5	138·5	12·5
$N+18$	136·5	121·5	135·0	12·6
$N+19$	136·0	121·0	137·5	12·0
$N+20$	138·5	123·0	137·5	13·0
$N+21$	135·0	120·0	136·0	12·0
$N+22$	137·5	122·5	138·0	12·4

* See text.

Table 4 gives the measurements made on this diagram corresponding with those made on the previous one, and the total leaf arcs allotted. The chief results are also summarized in tables 5 and 6, row 2. It can be seen that the divergence angles, the rises to the next leaf, and the leaf arcs all returned towards the normal about as rapidly as in the previous diagram.

The result is very different if a diagram of a disturbance of phyllotaxis is made on similar principles but with the leaf bases represented as of fixed size. For then, as Dr Richards first pointed out to us, the disturbance is not eliminated but increases until it completely upsets the system.

There may be other varying factors besides the divergence of the contact leaves which regulate spiral phyllotaxis; and such factors may differ in comparative strength in different species. But here we claim to have provided evidence that at least this one factor can modify the secondary extension of the leaf bases in *Lupinus albus*, and to have shown that in so doing it can regulate spiral phyllotaxis after a disturbance, even on the basis of a packing theory. A packing theory, therefore, can no longer be excluded as incompatible with regulation.

Table 5. Rates of regulation of divergence angles in diagrams

direction of displacement	serial numbers of last angles deviating from normal 137° by following amounts: 5° or more	2° or more	more than 1°	number of angles measured
anodic	10	15	23	28
kathodic	14	19	20	24

Table 6. Rates of regulation of rises from one leaf to the next in diagrams

direction of displacement	serial numbers of last rise differing from normal 12·39 units by following amounts: 4 or more	2 or more	1 or more	number of rises measured
anodic	8	17	17	28
kathodic	5	12	17	24

VI. The phyllotaxis after the operations

The various phyllotaxis systems that followed the splitting of the presumptive area of I_1 or I_2, here called N, in the forty apices of the present experiments are summarized in table 7, with some other relevant facts. The origins of these systems will here be briefly described and interpreted, and some points of special interest arising from them will be discussed in the next section. The descriptions will be made largely in terms of the resulting genetic spirals, but this will be only for convenience, and will not imply that these spirals are causally significant.

The most interesting group is the first group of 16 apices, the 'doubles' as they may be called, in which two N leaves arose, Nk at the kathodic side of the wound and Na at the anodic side, the two being nearly always joined together above it. For in the first eight apices of this group, as listed in table 7, a genetic spiral was developed with four leaves in each turn of 360°, a rather unusual system quite unknown in normal lupins. It ran in the opposite direction to that of the previous genetic spiral, and an example is shown in figure 9, apex no. 51. The divergence angles in these apices are given in table 8.

The development of this system can be understood as resulting mainly from a delay in the formation of the leaves Nk and Na, which were usually at a higher level than $N+1$, and sometimes at the same level, as table 7*A* shows, but never lower. Similar delays in the formation of Nk and Na, or of Nk when formed alone, were often found in our previous similar experiments, and were interpreted on a spatial basis and explained with the help of diagrams (1933, p. 388, and figure 17, p. 374; and figure 10). In brief, the explanation is that when the presumptive area N has been split, the necessary spaces for the formation of leaves adjacent to the wound first become available at levels considerably higher than that of the split presumptive areas, so that the leaves formed in them are delayed and may even arise later than $N+1$. Even when this happens, it is simplest still to give the name $N+1$ to the leaf which is in or near to the normal angular position of that leaf.

TABLE 7. PHYLLOTAXIS AFTER SPLITTING OF PRESUMPTIVE AREA OF LEAF N (I_1 OR I_2)

A. Sixteen apices with two N *leaves* Na *and* Nk *one on each side of the wound*

protocol numbers of apices	split presumptive area	phyllotaxis after operation	level of *Na* and *Nk* in relation to $N+1$
50	I_2	$N-1$, $N+1$, *Na*, and *Nk* form a single cycle leading to a reversed genetic spiral with four leaves in a turn	higher
51	I_2	as in no. 50	higher
57	I_2	as in no. 50	higher
92	I_2	as in no. 50	higher
95	I_2	as in no. 50	equal
44	I_2	as in no. 50	equal
46	I_1	as in no. 50	equal
49	I_1	as in no. 50	equal
66	I_1	the same cycle of 4 leaves led to a reversed genetic spiral, which had 4 leaves in a turn as far as $N+3$, but then changed to 3 leaves in a turn	higher
54	I_2	the same cycle of 4 leaves led to a reversed genetic spiral, which reversed again later and continued in the original direction with 3 leaves in a turn	higher
56	I_2	as in no. 54	higher
35	I_2	the same 4 leaves formed a single cycle, but no regular spiral system followed	higher
38	I_2	as in no. 35	equal
97	I_2	as in no. 35	higher
94	I_1	as in no. 35	higher
93	I_1	*Na* was inserted higher than *Nk* and $N+1$, though united with them; at $N+2$ a spiral starts in the original direction with 4 leaves in a turn	higher

Note: *Na* and *Nk* were at the same level or nearly so except in no. 93. They were united above the wound except in no. 49 in which they were separate.

B. Fourteen apices with Na *only*

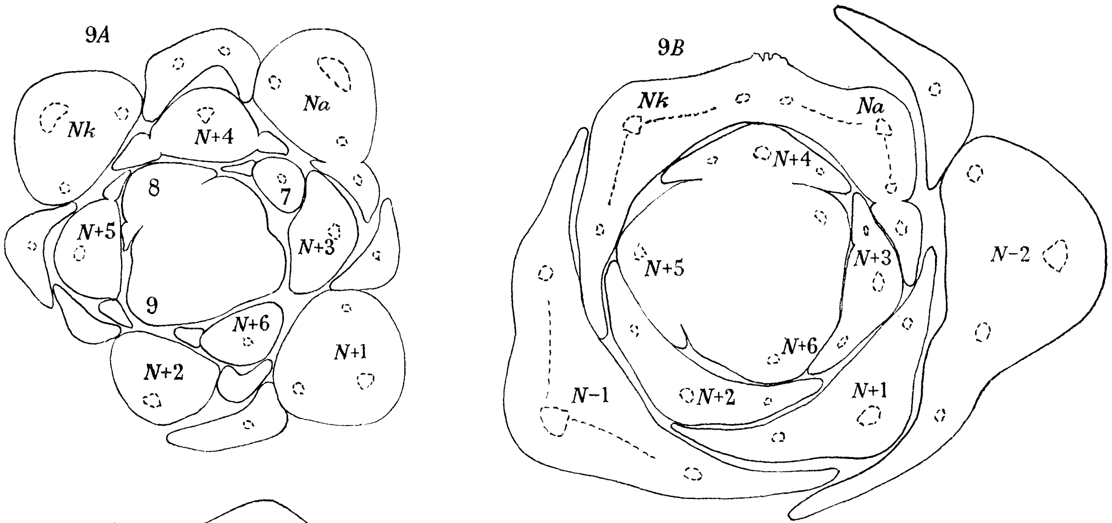
protocol numbers of apices	split presumptive area	position of *Na*	phyllotaxis after operation
eleven apices numbered as in table 2	as in table 2	abutting on side of wound	genetic spiral continued
60	I_2	abutting on side of wound but adhering to surface of apex above its base	genetic spiral continued
85	I_1	partly above wound	genetic spiral continued
98	I_2	partly above wound	genetic spiral continued

Note: All the genetic spirals had three leaves in a turn.

C. Ten apices with Nk *only*

protocol numbers of apices	split presumptive area	position of *Nk*	phyllotaxis after operation
76	I_1	abutting on side of wound	genetic spiral continued
82	I_1	abutting on side of wound	genetic spiral continued
78	I_2	partly above wound	genetic spiral continued
83	I_2	partly above wound and joined to bract beyond it	genetic spiral continued
77	I_1	as in no. 83	genetic spiral continued
79	I_1	as in no. 83	genetic spiral continued
100	I_2	as in no. 83	$N+1$ arose before *Nk* and nearly opposite to it: the genetic spiral was reversed
61	I_2	partly above wound	as in no. 100
53	I_2	partly above wound and joined to $N+2$ beyond it	at first as in no. 100 but genetic spiral followed in the original direction
47	I_2	as in no. 53	as in no. 53

Notes. (1) All the genetic spirals had 3 leaves in a turn.
(2) In nos. 53 and 47 *Nk* and $N+2$ were united though at different levels and overlapping.



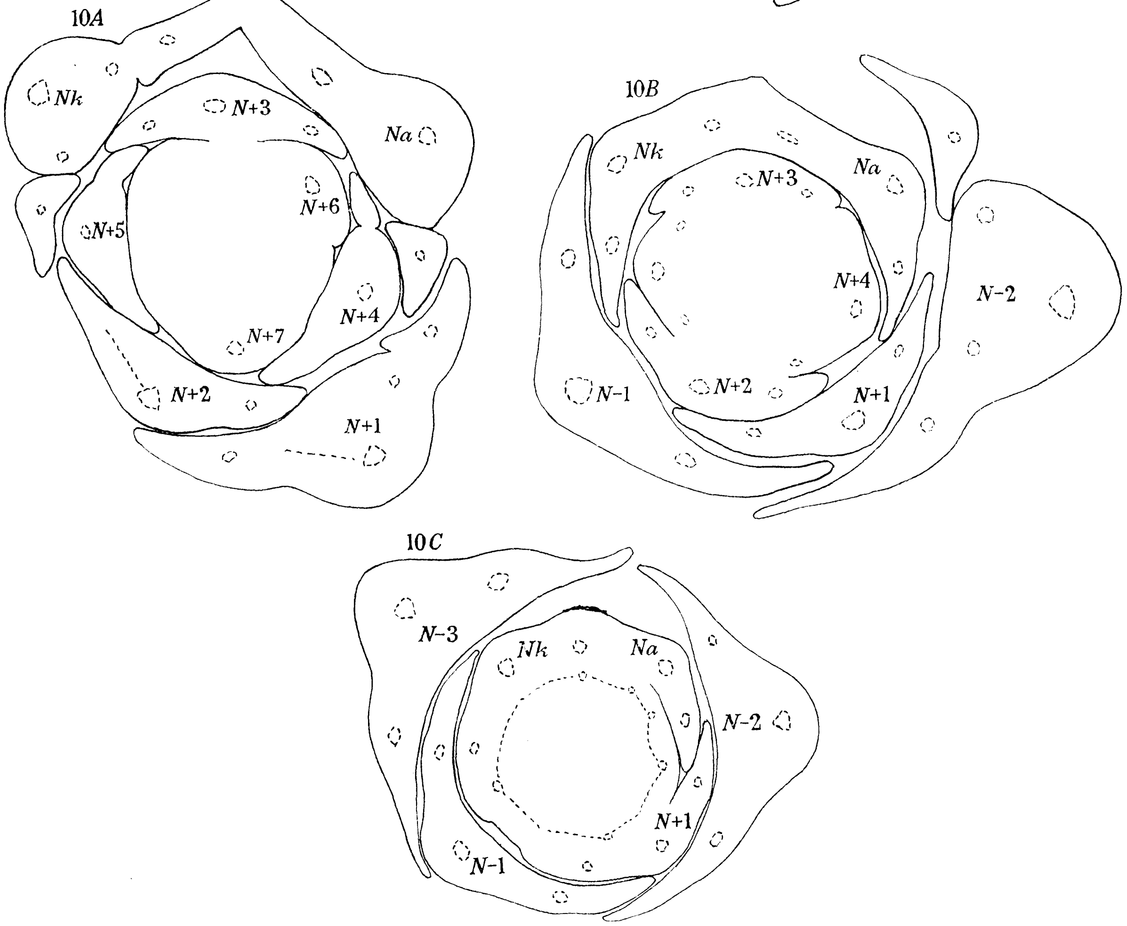


FIGURE 9. *A* and *B*. An apex, no. 51, in which the I_2 area was split, *Nk* and *Na* both developed, and a genetic spiral with four leaves in each turn followed in the reverse direction. (Magn. *A*, × 60; *B*, × 53.)

FIGURE 10. *A*, *B* and *C*. An apex, no. 54, in which I_2 was split, *Nk* and *Na* developed, and there followed first a reversed four-in-turn genetic spiral and then a three-in-turn spiral in the original direction. (Magn. *A*, × 60; *B*, × 57; *C*, × 36.)

As a result of these changes of levels, the leaves $N-1$, $N+1$, Na, Nk, in that order, formed a single cycle of four leaves in the direction opposite to the original genetic spiral. By the expression 'a single cycle' will be meant here something which differs from a single turn of a genetic spiral only by allowing simultaneous, or nearly simultaneous, as well as successive leaves. This first cycle of four leaves resulted in a cycle of four gaps which were at successively higher levels as figure 9 shows, so that the leaves which filled these gaps formed a genuine turn of a genetic spiral, which then continued, still in the reverse direction, with four leaves in each turn. In some of these eight apices there were occasional united leaves at stages later than the first cycle of four, but in spite of these it seems reasonable to consider their phyllotaxis as spiral, especially as united leaves may not be exactly at the same level.

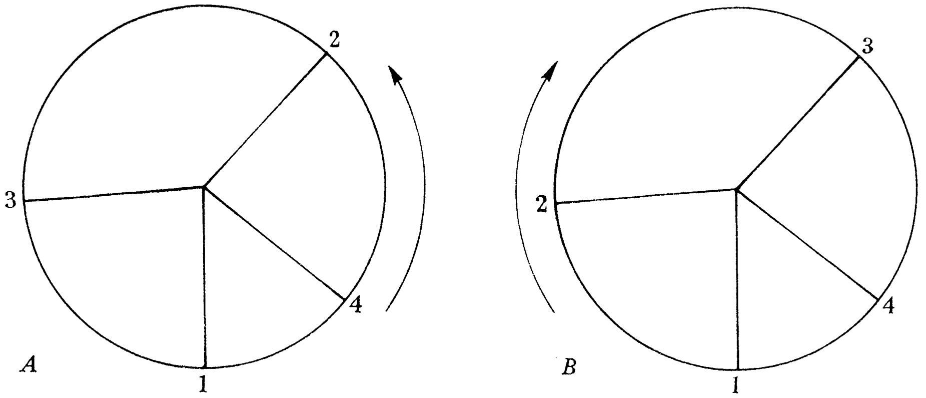


FIGURE 11. *A*, *B*. Diagrams showing how a three-in-turn genetic spiral can change to a reversed four-in-turn spiral by interchanging the levels of two successive leaves.

The diagrams, figure 11 *A* and *B*, show how a four-in-turn spiral could develop from a three-in-turn spiral in the opposite direction, simply by a change in the relative levels of two successive leaves, those marked 2 and 3. In the present eight apices the four-in-turn spirals did not develop quite in this simple way, although there was a change which brought Nk and Na to a higher level than $N+1$, or at least to an equal level, and the genetic spiral was reversed. The difference was that, besides the change shown in figure 11, two leaves, Nk and Na, were formed instead of one leaf N. From this it might be expected that there would be *five* leaves in the first reversed cycle in these apices. But this was not so, since Nk and Na reached far beyond the normal boundaries of leaf N, and Nk in so doing filled the gap which $N+2$ would otherwise have occupied (see figure 9). Consequently $N+2$ was displaced to the next gap, at the further side of $N-1$, and so was removed from the first cycle of leaves starting from $N-1$. The approaches to regularity in the four-in-turn spirals will be discussed in the next section.

Two other apices of this group, nos. 54, figure 10, and 56, developed at first similarly to those already described, making reversed four-in-turn spirals, but later they reversed again and returned to three-in-turn spirals in the original direction. They seem to have done this by interchanging the levels of two successive leaves and so making the change shown in the diagram, figure 11, but in the reverse direction, from *B* to *A*. It also seems probable that the two leaves with their levels interchanged were $N+3$ and $N+4$, but unfortunately this cannot be seen with certainty, since in both apices the sections were rather oblique and also the blade of $N+3$ had grown up at an unusual angle, leaning inwards towards the apex, perhaps as a result of pressing against the collar formed by the united N leaves. An interchange of the levels of $N+3$ and $N+4$ could readily be understood, since the angle *Na*, *Nk*, within which $N+4$ was situated in the previous eight apices, was exceptionally large in the present two (108° and 112°) and much exceeded the angle $N+1$, *Na* (85° and 75°) in which $N+3$ was situated in the previous eight, so that in the present two the position for a leaf within the angle *Na*, *Nk* is likely to have become available the sooner.

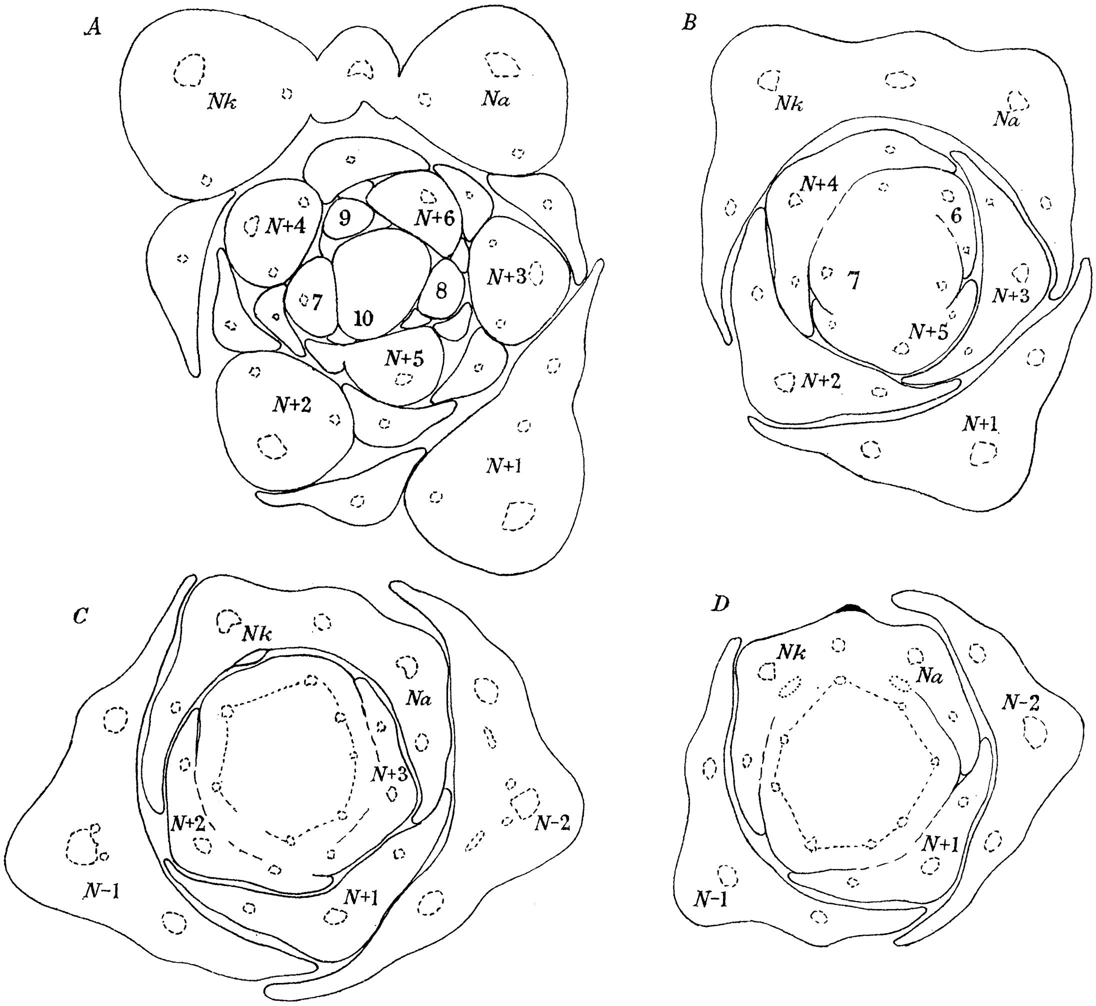


FIGURE 12. *A*, *B*, *C* and *D*. An apex, no. 66, which, when I_1 had been split, formed at first a reversed four-in-turn genetic spiral, and then changed to a three-in-turn spiral. (Magn. *A*, × 50; *B*, × 43; *C*, × 31; *D*, × 27.)

Another apex, no. 66, figure 12, also developed at first in the same way, forming a reversed four-in-turn genetic spiral, but after $N+3$ it changed to a three-in-turn spiral, and did so quite differently from nos. 54 and 56, without reversing a second time. This change was clearly due to the large size of $N+4$, which filled not only its usual gap between *Na* and *Nk*, but also the next gap between *Nk* and $N+2$, in which indeed its morphological centre was formed (compare figures 9 and 12). Consequently the number of leaves in the turn of the spiral ending with $N+4$ was only three instead of four, and the spiral continued in the same direction but with three leaves in each turn, the leaves arising successively in the available gaps.

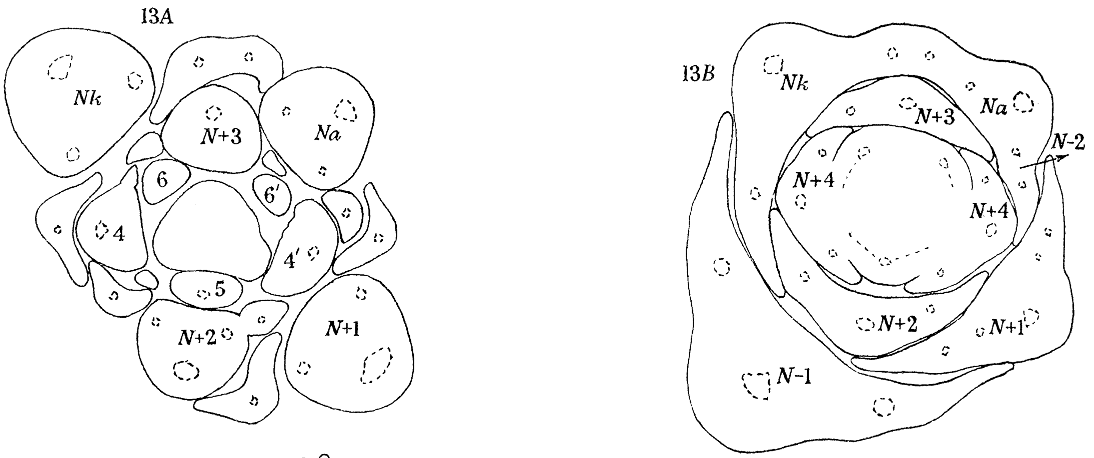
The explanation of the unusual position of the centre of $N+4$ in this apex is probably that the divergence angle *Nk*, $N+2$ was much greater than the angle *Nk*, *Na*, exceeding it by 33°, and that this made the space between *Nk* and $N+2$ available sooner than that between *Nk* and *Na*, although $N+2$ was at a higher level than the N leaves. The very large arc of $N+4$ can be understood as an extreme example of the principle proposed in §3, that the higher the level at which a leaf arises in relation to its contact leaves, the less will its secondary extension be impeded by them. For the morphological centre of $N+4$ was at so small an angular distance from that of *Nk*, only 27°, that even its primary area must have reached laterally beyond the highest point of *Nk*, and so was free to extend secondarily quite unimpeded into the gap beyond it.

The next four apices of table 7*A* also formed the usual reversed cycle of four leaves as a result of the operation, but they did not go on to develop any spiral system. In two of them, no. 94, figure 13, and no. 97, the positions of the gaps between the leaves of the first cycle were such that $N+2$ and $N+3$ were nearly opposite, and the system continued to be nearly bilaterally symmetric about that plane. It was of a kind which we described previously in *Epilobium hirsutum* and called an oscillating decussation (1935). It is of some interest that this sytem is possible and can continue in the normally spiral lupin, although it has no genetic spiral and no regular parastichies. It can readily be understood on the basis of a packing theory or other spatial theory. The other two apices of these four, nos. 35 and 38, became irregular.

It may be noted that in no. 38, figure 4, $N+4$ occupies the position between *Nk* and $N+1$ which in the other fifteen apices of this group was occupied by $N+2$, an older leaf. This confirms that in no. 38 the leaf in this position was delayed and inserted higher than usual, as was suggested when its large arc was discussed in §3.

Only the last apex, no. 93, figure 14, developed differently from the others from the start, one difference being that the centres of *Nk* and *Na* are very close together, and consequently the edge of *Nk* has not, as in the others, displaced $N+2$ to the further side of $N-1$. At $N+2$ there starts what may reasonably be considered a four-in-turn genetic spiral in the original direction, although $N+3$ and $N+4$ are really at about the same level: and this spiral continues with fair regularity to the youngest leaf, $N+10$. But it is difficult to interpret the positions of the early leaves up to $N+4$, since the cut has caused the parts of *Nk* and *Na* to grow radially outwards in an unusual way, and the axis also has bulged out in the same direction and become elliptic in transection (figure 14*C*). This increased radial growth near the wound had already been observed in the solid at 2 days after the operation, and it seems to have disturbed the positions of the N leaves, which were afterwards involved in it, and of $N+3$ above them. It was also observed in the solid that *Nk* and $N+1$ had arisen at 3 days after the operation, but *Na* between them had not, although in the sections *Nk* and *Na* appear to be at the same level: and this also makes interpretation difficult.

Of the six apices with united *Nk* and *Na* reported in our previous paper (1933) two, nos. 30, figure 19, and 31, developed reversed four-in-turn spirals, as is now clear, in



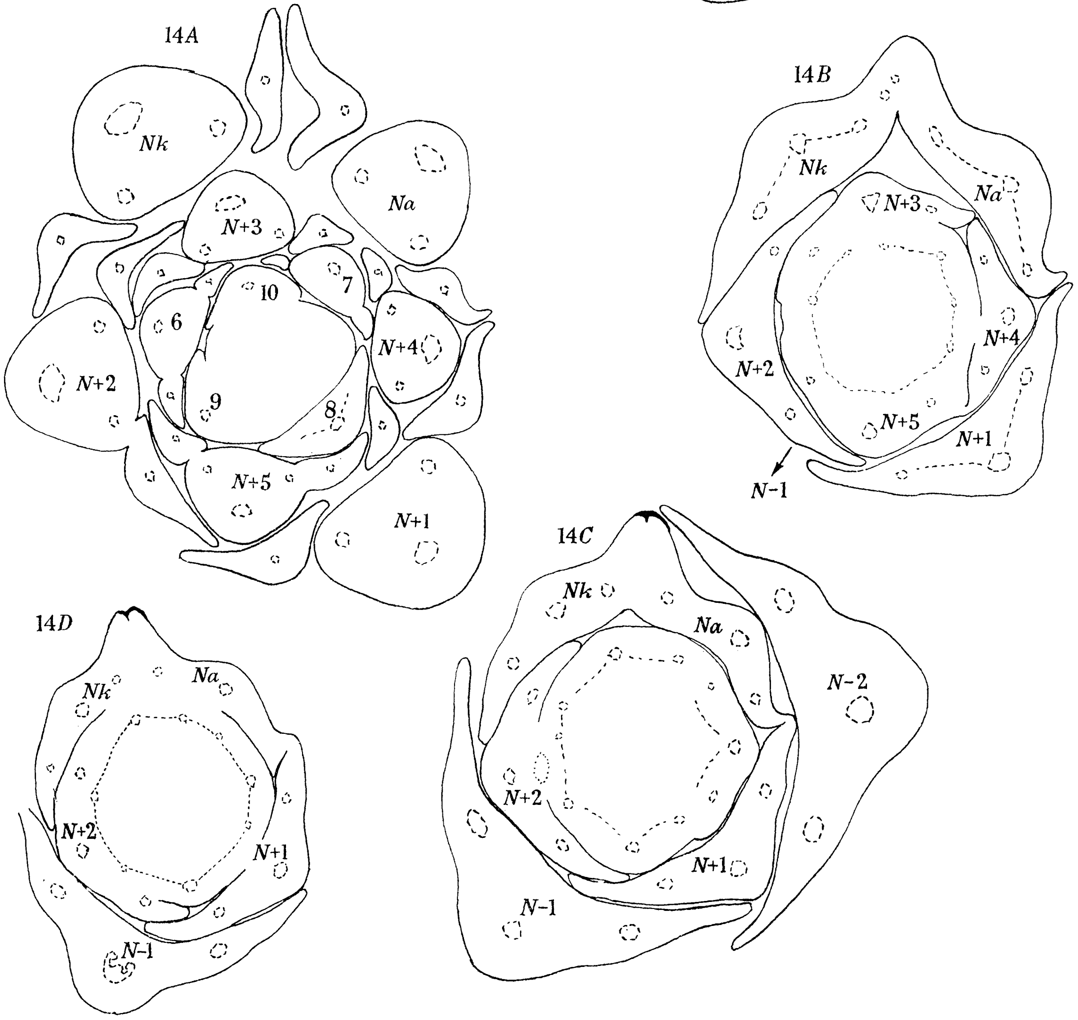


FIGURE 13. *A* and *B*. An apex, no. 94, with I_1 split, in which the phyllotaxis became bilaterally symmetric. (Magn. *A*, ×51; *B*, ×45.)

FIGURE 14. *A*, *B*, *C* and *D*. An apex, no. 93, with I_1 split, which formed a four-in-turn genetic spiral in the original direction. (Magn. *A*, ×51; *B*, ×36; *C*, ×33; *D*, ×27.)

just the same way as the first eight reported here. A third, no. 29, figure 18, was at first similar, but then one leaf, I_4, occupied two consecutive gaps, and the spiral became a three-in-turn in the same direction. In lupin seedlings of the race used for the earlier experiments four-in-turn spirals must have been less likely to persist, since the primary leaf arc was much bigger, as already mentioned, and too big for them to be stable.

All these transitions from three to four-in-turn spirals and the reverse are transitions between contact numbers of the Fibonacci series and contact numbers of the series beginning 1, 3, 4, 7. Camefort (1956, p. 173) has maintained that such transitions from one series to another can only be explained as due to the creation or destruction of supposed leaf generating centres in the apex. But those reported here have now been readily explained on space-filling principles, apart from apex no. 93 which was made obscure by abnormal growth.

The second group of apices of table 7, those with a leaf at the anodic side of the wound only, was the least disturbed in its phyllotaxis. In all of them the genetic spiral simply continued in the same direction, though for some time with irregular divergence angles. The angles in the first eleven of these apices, in which *Na* abutted on the side of the wound, were given in table 2, and have been discussed, and one of them was illustrated in figure 5. These eleven apices were chosen as a starting point for the diagrams of phyllotactic regulation proposed because they were fairly similar to each other, and their phyllotaxis systems were considerably disturbed, but not completely upset.

Also in the third group of apices in table 7, those with a leaf *Nk* at the kathodic side of the wound only, the genetic spiral continued without being completely upset in six of the ten apices, as the table shows, though for some time with irregular angles. But these apices were less uniform than those with *Na* only, since *Nk* usually extended above the wound, and on the far side of it was sometimes joined to a bract, such as is shown in figure 15, no. 100. Such bracts may alternatively be considered as being parts of the side of *Nk* that have extended secondarily above the wound, have enlarged in the free space on the far side of it, have grown up separately from *Nk* except near the base, and have formed an additional conducting strand. If allowed to grow out, such bracts would appear as additional stipules.

In the last four apices with *Nk* only, *Nk* arose at a higher level than $N+1$, probably because it was delayed through having to occupy an abnormally high position, as in the apices with both *Nk* and *Na*. In no. 100, figure 15, the inversion of sequence is not shown clearly in the sections, which are slightly oblique, but at 2 days after the operation it had been observed in the solid that $N+1$ had arisen, though *Nk* was not seen. These two leaves are so large that together, including the bract united with *Nk*, they nearly surround the apex, leaving two main depressions in the contour line, one on each side of the apex, where their edges approach or meet. The position of the next leaf, $N+2$, is of interest for it has arisen in the depression between $N+1$ and *Nk* on the same side of the apex as its normal position, although here it is within the slightly smaller of the two angles between the morphological centres of $N+1$ and *Nk* (174° as against 186°), *Nk* having been displaced by the wound in the kathodic direction even beyond a position opposite to $N+1$. $N+3$ has then arisen a little later in the depression on the other side of the apex.

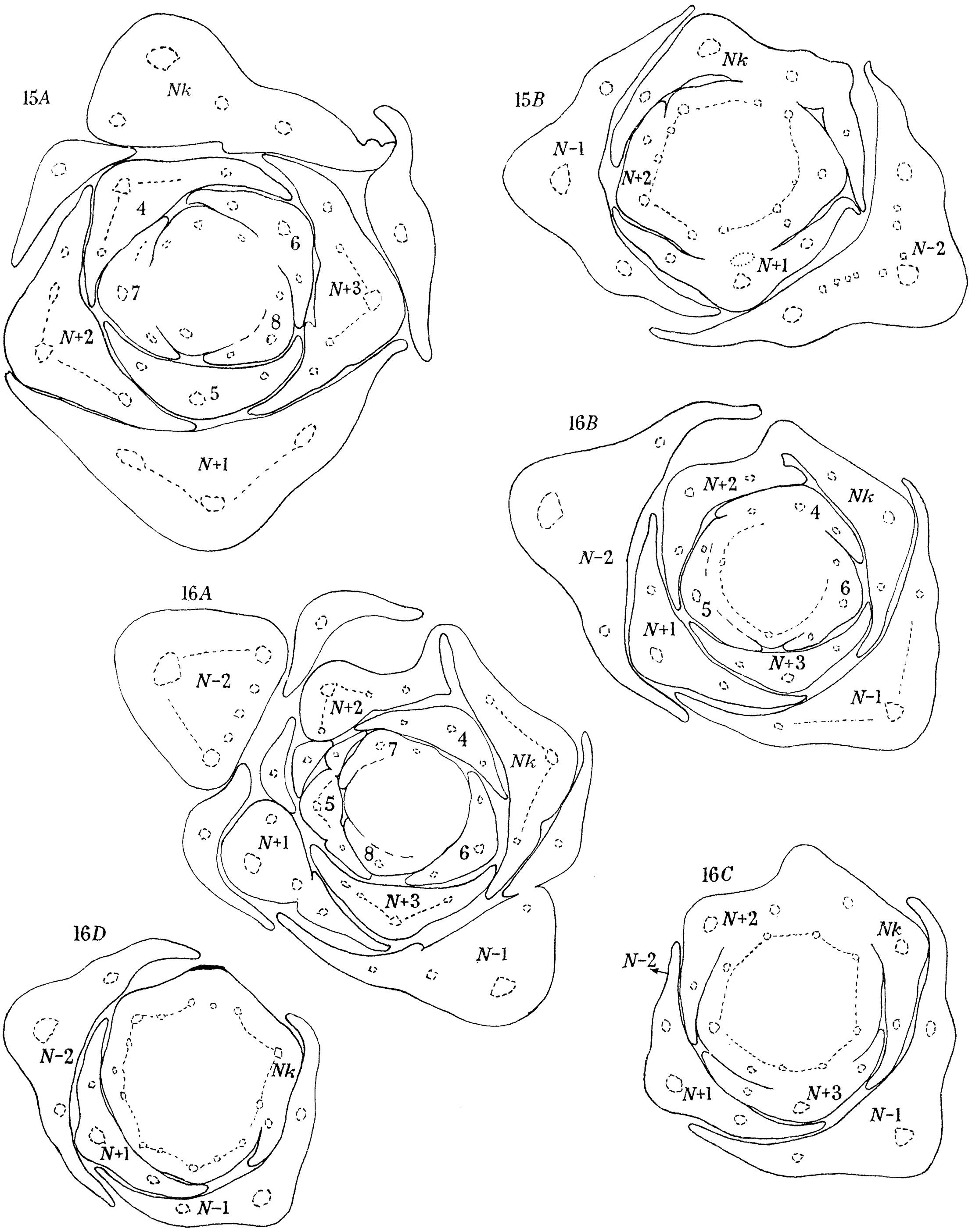


FIGURE 15. *A* and *B*. An apex, no. 100, in which, when I_2 had been split, a new leaf, *Nk*, arose at the kathodic side of the wound. The apex formed a reversed three-in-turn genetic spiral. (Magn. *A*, × 47; *B*, × 27.)

FIGURE 16. *A*, *B*, *C* and *D*. Another apex, no. 47, in which a leaf, *Nk*, arose at the kathodic side of the wound. The apex formed a genetic spiral in the original direction. (Magn. *A*, *B*, × 32; *C*, × 35; *D*, × 25.)

The explanation is clearly that within the smaller angle between the morphological centres of $N+1$ and Nk there is an open gap between their edges, whereas on the other side of the apex their edges meet, so that space for leaf formation became sooner available within the smaller angle. We have discussed similar situations previously (1931, p. 9). $N+2$ and $N+3$ converge towards $N+1$, since $N+1$ is inserted lower than Nk, instead of converging towards the other side of the apex, as the corresponding leaves would normally have done, and in so doing they establish a reversed three-in-turn genetic spiral which continues. In no. 61 the course of development was similar, but the special interest of no. 100 was lacking, since the position of $N+2$, though on the same side of the apex as in no. 100, was both within the larger angle between the centres of $N+1$ and Nk, and also above the larger gap between their edges. The genetic spiral was reversed, as in no. 100.

In nos. 47, figure 16, and 53, the development was again at first similar, but the positions of $N+2$ and $N+3$, which again converged towards $N+1$, were interchanged as compared with their positions in the two previous apices, so that the genetic spiral which they established was in the original direction. This interchange of positions can be readily understood in no. 47 (figure 16), since Nk had been displaced very far by the wound, even beyond the position opposite to $N+1$ so that the side of the apex on which $N+2$ arose was that on which the angle between the morphological centres of Nk and $N+1$ had become considerably the greater (191°), and so also was the distance between their edges. Nk and $N+2$ were united above the wound, though at different levels and overlapping.

In no. 53, on the other hand, the angle between the centres of Nk and $N+1$ was slightly smaller on the side of the apex on which $N+2$ arose than on the other side (175° as against 185°). The separations of their edges were not very different on the two sides of the apex, but it is not possible to compare them exactly, since Nk was again united with $N+2$, though at a different level, as in no. 47, but in a manner that made it impossible to locate its boundary exactly.

Unions between leaves at considerably different levels and overlapping are peculiar and exceptional. Those in the two apices just mentioned and one other were above the wound, and were probably somehow facilitated by it: but one was found elsewhere, between Na and $N+1$ in no. 93, figure 14*D*, and is unexplained. In the unions between overlapping leaves the united faces are commonly found to be similar, being both ventral or both dorsal. How this comes about deserves to be specially studied.

Imperfect leaves such as were sometimes formed previously (1933) from the split presumptive area were not found after the present operations, which were made either on I_1 at early plastochron, or on I_2. Those found previously were considered to result from operations made on I_1 at middle or late plastochron, when that area was partially determined (1933, pp. 365, 373, 397).

VII. The regulation of the spirals with four leaves in a turn, and the conditions in which leaves unite

Table 8 shows the successive divergence angles in the first eight apices of table 7, which all developed reversed four-in-turn spirals in the same manner. Since Na and Nk were at approximately the same level, as already explained, the spiral proper starts with the third angle of the series, Nk, $N+2$. By comparing these angles with those in the three-in-turn spirals given in table 2, it can be seen that in the four-in-turn spirals both the mean values and the angles of the separate apices approach regularity much more slowly if at all.

Table 8. Divergence angles in eight apices that formed four-in-turn spirals, in degrees

numbers of apices	$N-1, N+1$	$N+1, Na$	Na, Nk	$Nk, N+2$	$N+2, 3$	$N+3, 4$	$N+4, 5$	$N+5, 6$	$N+6, 7$	$N+7, 8$	$N+8, 9$
44	87	121	82	102	123	95	83	117	102	—	—
46	83	112	94	102	103	98	88	106	110	—	—
49	90	98	112	87	105	106	88	106	97	112	—
50	89	90	104	109	93	122	76	103	—	—	—
51	93	93	84	117	108	93	90	109	109	—	—
57	87	90	98	115	92	97	90	—	—	—	—
92	80	93	85	123	103	112	80	104	107	103	77
95	87	105	84	111	111	93	90	110	104	100	90
mean	87	100	93	108	105	102	86	108	105	105	83

Spirals with four leaves in a turn normally have contact numbers that are consecutive members of the summation series 1, 3, 4, 7, 11, etc., and the four-in-turn spirals induced in the lupin seedlings conform to rule in making contacts 3 and 4, when they are fully established. The ideal divergence angle for systems with contacts belonging to this series is 99·5°. Measurements on natural four-in-turn spirals are rather scarce, but Fujita (1939) has recorded the frequencies of different values of varying divergence angles, grouped at intervals of 1°, in *Cunninghamia lanceolata* with contact numbers 4 and 7. His measurements show that angles of 99° or 100° are much the most frequent, and that angles deviating from the ideal angle of 99·5° by amounts greater than 3·5° are very uncommon. The variation is not more than he has recorded for three-in-turn spirals in other species with contact numbers 5 and 8, and less than for three-in-turn spirals with lower contact numbers. Thus there appears to be no special difficulty about regulation in natural spirals with four leaves in a turn. In the lupin apices, however, the induced four-in-turn spirals had angles which continued to vary widely on both sides of 99·5°, and it seems to us that these apices failed to regulate accurately because their primary leaf arcs of 90° were too big in relation to so small a divergence angle.

Another point of interest concerns the unions between leaves that are at about the same level, and the maximum distance between their centres which allows such unions. Apart from unions just above the wound, which seem to be facilitated by it, the present apices provided seven unions between leaves at about the same level, and the divergence angles between their morphological centres were 66, 78, 80, 88, 90, 92, 93 degrees. On the other hand, five pairs of leaves at the same level, which met edge to edge without uniting, had centres diverging by angles of 93, 94, 100, 100, 103 degrees. These facts indicate that the leaves cannot unite if their centres diverge by much more than 90°, and they support our previous conclusion that lupin leaves unite only when their primary areas partially coincide (1933, p. 399), since in the present race of lupins we have estimated the arc of the primary area to be 90° approximately (1959). But in the race of lupins used for the earlier experiments the arc of the primary area was much larger and was estimated first at 124° (1933, p. 397), and later at 122° (1955). In conformity with this larger primary arc we find that in the earlier experiments the divergences of the centres of ten pairs of united leaves, excluding again unions above the wound, were 93, 95, 99, 101, 103, 105, 106, 107, 107, 110 degrees. These figures indicate a much higher maximum divergence of leaf centres allowing unions.

Leaves, however, that meet just above the wound must be able to unite by their secondary extensions, since in the present apices the divergences of the centres of the united *Nk* and *Na* often exceeded considerably the primary arc of 90°, and in two apices, nos. 54 and 56, were as high as 108° and 112°. The wounds always open out and broaden during the early days after the operation, and it may be that when the edges of the adjacent leaves are extending secondarily above the now sloping upper contours of the broadened wound, they are enabled to unite by the contact which they make with it. Several observations have indeed indicated that adjacent wounds do facilitate unions between leaves or between leaf and axis.

VIII. The development of the leaf base in relation to regulation in *L. albus* and in other plants

The simple idea from which the theory of regulation here proposed developed is that if in a system which is being built up from the base one puts larger building units into the larger gaps between the previous ones, one will tend to keep the upper contour even. Since we had found that in *L. albus* the primary leaf area covers a constant arc (1933, 1959), this area could not provide the variability of building units needed; but it seemed that the secondary extension of the leaf base might do so, being variable, as we had found, and influenced by certain factors (1955, 1959). The measurements in the present paper showing that the secondary extension of a leaf base does vary with the divergence angle between its contact leaves were indeed measurements of its lateral extension round the apex only, but it seems probable that the further a leaf base can extend laterally the further it extends towards the apical summit also. For if this were not so, some of the many transverse sections would surely have revealed that it was not, by showing that the leaf bases covering large arcs laterally were relatively thin in a direction at right angles, and those covering small arcs relatively thick. But actually this was seldom, if ever, seen to be so, and it is in accordance with this that in the diagrams, figures 6 to 8, the leaf bases are made constant in shape, being represented as circular primary areas surrounded with concentric zones of secondary extension.

Since therefore the evidence indicates that the lateral extension of the leaf bases is limited in *L. albus* by the contact leaves on each side, and that in correlation with this limitation their extension towards the summit of the apex is also limited, it seems that their *shape* must be in some degree fixed and invariable. Yet it is not absolutely fixed, since in exceptional conditions the leaf bases can become very asymmetric, especially when they extend transversely above the apical end of a wound and expand into a free space beyond it. Moreover, it seems that the rather fixed morphological shape of a leaf base must be orientated in the correct way in relation to the apical cone of the stem. For, as already pointed out, the lateral parts of a leaf base appear to be delayed in their extension by having to wait for more space to become available above the contact leaves; and they cannot turn and extend towards the apical summit, in this species at least, although the median part of the same leaf base has already reached a higher level on the apical cone.

However, in many monocotyledons the leaf bases seem to be much more plastic, and in *Rhoeo discolor*, for example, an edge of a leaf base progressing laterally by secondary extension can turn and grow towards the apical summit when it meets an obstacle, and so pass over it (Snow, M. 1955). But in such a species with spiro-distichous phyllotaxis the method of regulation may be very different.

The idea underlying the present theory of regulation gained some support from the results of operations on apices of *Epilobium hirsutum*, a species having whorled phyllotaxis with pairs of opposite leaves (Snow & Snow 1935, p. 80). For some of the apices disturbed by the operations returned to regular decussation by forming successively at different levels two nearly opposite leaves, of which the lower was not only the larger absolutely, as being the older, but also covered a larger arc. These two were followed by a pair of leaves in the plane at right angles that were at the same level and also nearly opposite, instead of converging towards the lower of the two previous leaves; and this can be understood on space-filling principles as being due, at least in part, to the larger arc of that leaf. The regulating effect of this larger arc will have been increased if, as in *L. albus*, in correlation with it the base of the larger leaf extended more rapidly towards the apical summit also.

The apices of various Labiatae returned much more frequently to regular decussate phyllotaxis after being disturbed by operations (Snow, R. 1942, p. 116), and they most often did so in a rather similar way. In these apices, in which the decussate phyllotaxis is much more firmly stabilized, the sections often showed clearly that the lower leaf base of the unequal pair, covering the larger arc, had also extended much more rapidly towards the apical summit, so that its upper contour was just level with that of the smaller leaf base (1942, figures 9, 10, 11). This levelling of the upper contours was indeed so striking that it seems probable that some special factor was here at work in addition to the larger relative size of the lower leaf base, perhaps an incipient formation of a node tending to bring the two leaves to the same level. This suggestion resembles the idea underlying Schoute's (1938) theory of 'early binding whorls' which he applied to such phyllotaxis systems as these. His basic idea may indeed be sound, even if, as one of us has maintained (Snow, R. 1942), the elaborate theory of whorl formation which he built upon it is untenable.

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