EXPERIMENTS ON SPIRODISTICHIOUS SHOOT APICES. I

By

MARY SNOW

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The shoot apex of Rhoeo discolor, a spirodistichous species, is described in detail. The mean divergence angle between successive leaf centres is 152°-6. Each new leaf covers only a small arc when first visible, and its flanks then extend round the apex until they meet in the later part of the plastochron. The new leaf is asymmetric, its half which is anodic in the direction of the genetic spiral being the shorter transversely and covering a mean arc of 166°-5 when the flanks meet. Thus the centre of a new leaf does not lie directly over the meeting-point of the flanks of the previous leaf, but above its anodic half.

Experiments were made in order to discover the causes on which the divergence angle depends. As a preliminary some stem apices of Rhoeo were exposed and marked with transverse streaks of albumen and charcoal. But after several days the streaks had not been bent by the growth of the apex in the way which would be expected on Hirmer's theory of spiral growth.

In the main experiments the central part of $P_1$, the youngest leaf, was cut out completely. It was necessary first to cut down $P_2$ and the older leaves of the bud nearly to their bases. The main results were that $I_1$, the next leaf to arise, was displaced towards the missing centre of $P_1$, and that the angle $I_1-I_2$ was larger than the normal, and sometimes exceeded 180° (see figure 6). In some other experiments the central part of $P_2$ was removed as well as that of $P_1$. In these also the angle $I_1-I_2$ increased, and in one of them the genetic spiral reversed permanently, but the displacement of $I_1$ towards $P_1$ was usually less.

It is concluded that the position of the centre of each new leaf depends on a balance between inhibiting influences exerted on the stem apex by existing leaf centres. The position of a new leaf $n$ depends mainly on the inhibitions coming from the centres of the two youngest leaves, $n-1$ and $n-2$, and to a lesser degree on those from the centres of $n-3$ and possibly $n-4$. The strength of the inhibition thus decreases with the age of the leaf from which it comes and also with the distance from the inhibiting centre.

The asymmetries of the leaves that arose after the operations are reported and discussed in comparison with those of the normal leaves. Many of the facts can be explained if it is supposed that the same influences from existing leaves which tend to inhibit the formation of leaf centres
promote the extension of leaf flanks round the apex. But the asymmetry of \( I_1 \) in most of the experiments is at present not explained on this hypothesis.

The localization and determination of leaves in *Rhoeo* is further discussed and compared with the corresponding processes in *Lupinus albus* and other dicotyledons. It is concluded that in spirodistichous monocotyledons the localization of leaves, depending on physiological inhibitions, is different from what it is in dicotyledons, in which it was previously concluded to be a space-filling process. The process of determination is also shown to be different in *Rhoeo*, since a rather small central part of a leaf is determined first, and from it the determination extends by induction round the apex. In both these respects the experiments on *Rhoeo*, unlike those on dicotyledons, give good support to Richards's theory of phyllotaxis, which, however, was intended to apply to all groups.

**INTRODUCTION**

The phyllotaxis of monocotyledons has received less attention than that of dicotyledons and no experimental work has been done on them. The majority of monocotyledons have straight distichous phyllotaxis, and most of those which have spiral phyllotaxis have systems of the kind which is called spirodistichous, and not Fibonacci spirals. Spirodistichous systems, according to Hirmer (1922), occur in species belonging to the families Liliaceae, Juncaceae, Bromeliaceae, Araceae, Commelinaceae and Hydrocharitaceae; they are usually derived from distichy in ontogeny, the first leaf of the seedling being opposite the cotyledon, and the change to spirodistichy may occur at the second leaf or later. When this happens the leaves are laid down with a divergence angle of less than 180° but considerably greater than the Fibonacci angle of 137°.5 which is closely approached by most dicotyledons with spiral phyllotaxis. In consequence of this decrease of the divergence angle the two orthostichies become helices instead of straight lines. If the angle falls very much below 180° the two helices are no longer apparent to the eye.

The biological value of spirodistichy may well be that it exposes the leaves more fully to light than does straight distichy; for most spirodistichous types have short internodes, at least during a large part of their growth, and so would receive much less light if their distichy were straight.

A significant feature in which spirodistichous systems differ from the spiral systems of dicotyledons is that each young leaf covers an arc of more than 180° before the next leaf arises, not only in the young seedling, but also later. Indeed, to judge from the drawings given by Hirmer (1922) in many spirodistichous species each leaf encircles the whole apex before the next leaf arises. Thus the change in divergence angle in spirodistichous systems does not depend on a change in the arc covered by each young leaf, whereas in the seedlings of dicotyledons the changes in the divergence angle regularly do depend on changes in the arcs of the leaves. The divergence angles in spirodistichous plants vary considerably from one species to another. It has also been claimed that the angle varies considerably within a species or in a single plant, but it will be shown that this variation is not always so great as is supposed. Another feature in which the spirodistichous systems of monocotyledons differ from most spiral systems of dicotyledons is in the asymmetry of the leaves. This asymmetry is not always obvious in the blade of the mature leaf but can usually be seen in transections through the bud, where it appears that the morphological 'median' strand of the leaf divides the leaf into two lateral parts which differ in tangential extension and sometimes in radial thickness.
ON SPIRODISTICHOUS SHOOT APICES. I

From these facts it is clear that the hypothesis of the first available space cannot easily be applied to spirodistichous plants. According to this hypothesis ‘each leaf arises in the first space that becomes both wide enough and far enough below the growing point’ (Snow, M. & R. 1931, p. 16 and 1933, p. 360). This hypothesis is based on the theory of van Iterson (1907) and has been supported by various experiments (Snow, M. & R. 1931, pp. 33, 35). Van Iterson’s theory was in turn based on Hofmeister’s observation (1868) that each leaf arises in the largest gap between the previous leaves. But van Iterson expressly stated that his theory could not be applied to plants with asymmetric leaf bases since he had worked it out only for plants in which the bases of the youngest leaf primordia were circular in outline.

Schumann (1892,) however, did attempt to apply Hofmeister’s rule to plants with spirodistichous phyllotaxis. He maintained that the greatest available space in plants with sheathing leaf bases was to be found immediately above the point where the edges of the sheath of the youngest leaf met (p. 34). Where the leaves were symmetric this point lay opposite to the centre of the youngest leaf and distichous phyllotaxis resulted. But when the leaves were asymmetric this point was not opposite to the morphological centre of the youngest leaf, and spirodistichous phyllotaxis resulted (p. 42). The asymmetry of the leaves was thus taken by Schumann to be the determining factor in the phyllotaxis and was considered to be a basic inherited character. This theory meets with the difficulty that an asymmetry of either the one sense or the other is supposed to be inherited, though it is not determined by heredity of which sense that asymmetry will be. A further and more serious difficulty is that in many spirodistichous plants, and probably in all, the centre of each new leaf does not lie immediately above the point where the edges of the previous leaf meet, but slightly to one side of this point, as can be seen from Hirmer’s figures (1922) illustrating a wide range of types. Moreover Schumann himself according to Weisse (1932, pp. 340–341) later abandoned his attempt to explain spirodistichous phyllotaxis in accordance with Hofmeister’s rule.

The theory of Hirmer must next be considered. According to Hirmer spirodistichy is derived from distichy in ontogenesis through the shifting of the plane of symmetry of the apex by unequal growth on each side of the plane (pp. 17–19 and figure 46). The plane of symmetry here referred to is the median plane of the youngest leaf. In consequence of this asymmetric growth a sector is inserted in the apex in such a way that the centre of the next leaf which is about to arise is displaced to one side of the median plane of the previous leaf and a new plane of symmetry is established. This process is repeated each time that a leaf is formed.

The terms ‘anodic’ and ‘kathodic’ are used by Hirmer, and by Troll (1937) following him, with reference to the direction in which this shift of the leaf centre is supposed to have taken place. The anodic side of the leaf on Hirmer’s terminology is the side towards which the centre is supposed to have shifted; and this is in the opposite direction to that of the genetic spiral. But since this shift of the leaf is only assumed and has not been proved to occur, it seems to the writer better to use the terms anodic and kathodic with reference to the direction of the genetic spiral, as this is the accepted convention for other phyllotactic systems. The side of each leaf which Hirmer calls ‘anodic’ is thus in the present terminology ‘kathodic’, since it lies next to the centre of the next lower, that is older, leaf. The symmetry
of the leaf bases is considered by Hirmer to support his theory; for he claims that the side of the leaf termed ‘kathodic’ by him (‘anodic’ by the writer) is the larger, since it occupies the region in which the apex has grown most strongly, and is the side which has been, so to speak, left behind by the displacement of the leaf centre. In support of this contention he illustrates bud sections of many spirodistichous plants. In some of these plants, e.g. *Cordiline rubra*, *Richardia podophyllum* and *Tillandsia stricta*, this side does indeed appear to be the thicker radially in cross-section; but the figures do not provide evidence that it is the longer in tangential extension, as would be expected if the increase of growth was in the tangential direction as he postulates; for few of the sections illustrated pass through the critical level at which the meeting-point of the edges of the leaf can be seen, and these few are reproduced on too small a scale to allow of accurate measurements. Moreover in *Pollia condensata*, which is spirodistichous, Hirmer admits that the sides of the leaf are equal in size, and it will be shown in the present paper that in *Rhoeo discolor* the difference in the tangential extensions of the flanks is actually the opposite.

Hirmer has produced no evidence for his theory that a sector is inserted in the apex apart from this claim concerning leaf asymmetry which is unconvincing for the reasons given. Yet this theory has been included by Troll in his *Vergleichende Morphologie* (1937) as if it were well established, and a similar process is considered by Hirmer and by Troll to account for the spiral phyllotaxis of dicotyledons also.

Some observations on marked apices made to test Hirmer’s theory will be briefly reported before the main experiments. Since the results of these marking experiments were negative, and since the study of spirodistichy by observation alone had failed to provide a satisfactory basis for it, it seemed to the writer that operations on the apices were needed for the purpose, and the results of such experiments will be reported and discussed in the present paper.

*Rhoeo discolor* was the species chosen for investigation because it was found to be the least inconvenient species to dissect and to withstand the operations well. A further advantage is that the whole species shows very little genetic variation.

**The normal apex and phyllotaxis of *Rhoeo discolor***

The majority of the plants used in the experiments were young cuttings of *R. discolor* struck from basal buds in early spring; seedlings were also used after 12 to 14 leaves had been formed. Since the internodes elongate very little the apices of the operated plants were fairly close to ground level. The stem is completely encircled by the sheathing bases of the leaves which form closed tubes for a short distance above their insertions.

In order to determine the divergence angle the apices with seven or eight of the youngest leaves were embedded in collodion and sectioned by hand or with a microtome, and the sections were drawn under a projection apparatus. The angles were measured on the drawings. The centres of the leaves were located by the positions of their median conducting strands, which in *Rhoeo* are differentiated at an early stage. The median conducting strand was usually visible even in the youngest leaf. The centre of the axis was more difficult to determine and was judged by eye as accurately as possible. In order to allow for errors in determining the centre of the axis each divergence angle was measured in at least three
Figure 1. A to E are transections through the apical region of a normal plant of *Rhoeo discolor* from above downwards. In this and all subsequent figures vascular and procambial strands are shown with broken lines and the xylem regions of the central strands are shown black. The leaves and their axillary buds are shown alternately clear and stippled to guide the eye. The boundary between leaf and axis at the insertion level of a leaf is shown with long broken lines, and the region immediately beneath an axillary bud is enclosed within a dotted line. (Magn. A, × 58; B, C, D and E, × 52.)
sections taken from different levels and the average was found. This method could not always be applied to the youngest leaf, the central conducting strand of which was sometimes seen in only two sections so that two measurements had to suffice. The same procedure was usually adopted in the experiments reported below. Fourteen different plants (cuttings) were used for measurements of the divergence angle, and the total number of divergence angles measured was 76. The mean value of these angles was 152°±6; the extremes were 142°-2 and 161°-7. The standard deviation was 3°-7 and the standard error was 0°-42. This indicated that the variation of the divergence angles in this species is by no means so great as it is often stated to be in spirodistichous plants. For comparison the standard deviation of the divergence angle of *Lupinus albus* with Fibonacci phyllotaxis was found to be 2°-8 (Snow, M. & R. 1931). Transections of the apical region of a normal plant of *Rhoeo* are shown in figure 1. Four lateral strands were visible in the youngest primordium before the end of its first plastochron. Other strands were added later and these appeared to differentiate acropetally, new strands being inserted between older ones, so that large and small strands usually alternated. The median vascular strand was found to run nearly straight downwards for at least four internodes before uniting with the lateral strand of another leaf. The direction of differentiation of the central strand when it first appeared was not determined, but its subsequent differentiation within the leaf was seen to be acropetal, as it kept pace with the upward growth of the leaf.

Each leaf subtends an axillary bud, and the area from which the bud will develop is clearly visible in the axil of the second youngest leaf as a small group of cells with dense contents. The bud is seen as a definite protuberance in the axil of the fifth or sixth leaf, and it then becomes quite clear that it does not lie in the median plane of the leaf, but that its centre lies on a radius a few degrees anodic to that of the median strand. Its relationship to the median strand enabled the latter to be identified in a few leaves of the operated plants in which the median strand was scarcely larger than the lateral strands. The cells lying immediately beneath the insertion of an axillary bud were distinguished from the surrounding tissues by their dense contents. In the drawings these groups of cells with dense contents are enclosed within dotted lines.

As transections do not give a satisfactory representation of the shape and course of development of the youngest leaf, an attempt was made to draw the apex and the youngest leaf as seen in surface view from above through the dissecting microscope at different stages of the plastochron. The drawings were made free-hand and are reproduced in figure 2. The direction of the genetic spiral, from each leaf to the next younger, was clockwise in the four apices shown in figure 2, and the terms anodic and kathodic will be used with reference to this spiral. The same terminology will be used as in previous papers (Snow, M. & R. 1931, 1933, 1935): the leaf primordia visible at the time of operation, will be called *P₁*, *P₂*, *P₃*, etc., *P₁* being the youngest; those arising after the operation will be called *I₁*, *I₂*, *I₃*, etc., *I₁* being the first to arise. In figure 2, though no operation has been made, the youngest primordium will be referred to as *P₁*. Each drawing in figure 2 is accompanied by an outline drawing of a longitudinal section of the apex at the same stage of the plastochron. In figure 2, *A₂*, *B₂* and *C₂* these sections pass through the median plane of *P₁*, in *D₂* the section passes through the region which is about to give rise to *I₁*. The longitudinal sections were cut under the dissecting microscope from apices prepared in the
Figure 2. $A_1$, $B_1$, $C_1$ and $D_1$ are free-hand drawings of the apex viewed from above at different stages of the plastochron. The source of light was obliquely above the apex, and the arrows indicate the horizontal component of its direction. Horizontal and slightly oblique surfaces are illuminated; surfaces approaching the vertical are shaded. $A_2$, $B_2$, $C_2$ and $D_2$ are longitudinal sections through the plane $m$ to $l$ shown on the corresponding drawings, ×130. The base of $P_2$ which has been cut down is included in figures $A_1$ and $A_2$ only. The points in which the lines $n-n$, $a-a$, etc., cut the line $m$-l in the drawings $A$ to $D$ are indicated with corresponding letters in the sections $A_2$ to $D_2$. $n$ = summit of $P_1$; $o$ = summit of apex; $p$ = flanks or presumptive area of flanks of $P_1$; $i$ = foliar buttress of $I_1$; $q$ = cut surface of $P_2$. In $A_1$ and $A_2$, $P_1$ is small. In $B_1$ and $B_2$, $P_1$ is small-medium, the shaded lines represent cell rows in the region from which the flanks of $P_1$ will arise. In $C_1$ and $C_2$, $P_1$ is medium; the hood is beginning to arch over the apex. In $D_1$ and $D_2$, $P_1$ is very large. The arrow marked $r$ indicates the meeting-point of the edges of the flanks. The broken line shows the contour of the apex beneath the hood.
usual way as if for operations (p. 139) to ensure that the stage of the plastochron was the same as that shown in surface view and that the cut passed through the correct plane. They were drawn under the projection apparatus.

When $P_1$ is first visible as a protuberance it subtends an arc of about $90^\circ$, and by the end of the first plastochron it has encircled the whole apex, and its central region has by then made a hood which arches over the apex and partly conceals it, as is shown in figure 2D. Those parts of the leaf which extend round the apex as distinct from the original central part will be called ‘flanks’. For convenience the anodic and kathodic parts of the leaf which lie between the centre and the meeting-points of the flanks will be called the anodic and kathodic ‘halves’ though they are slightly unequal in size; they may be considered as morphological halves. A half of a leaf is thus more than a flank, as it comprises half of the central region as well as one flank.

Figure 2A shows $P_1$ at a fairly early stage of its development. The flanks of the leaf have extended until it covers an arc of nearly $180^\circ$, and the apex appears as an approximately circular dome. In figure 2B, the arc is slightly greater than $180^\circ$, and the region into which the flanks will extend is differentiated from the rest of the apex as an annular region extending for nearly $180^\circ$ round the apex. In this region curved cell rows are clearly visible. $P_1$ is slightly asymmetric, its anodic half being rather the taller and rising up more steeply than the kathodic half. In figure 2C, $P_1$ has developed considerably further, and its central part has formed a hood which arches over the apex and partly conceals it. Incidentally, the growth rate of the hood relative to that of the flanks showed some variation, for in some halves the flanks had already met round the apex when the hood had scarcely begun to arch over. In figure 2D a later stage is shown in which the flanks have met round the apex. The point in which they meet is clearly not opposite the centre of $P_1$, so that $P_1$ is asymmetric, its kathodic flank being the longer.

At a later stage the edges of the flanks unite and form a short tube as shown in figure 1D, leaf 4; above this tubular region the edges of the flanks continue to extend tangentially and overlap as shown in figure 1D, leaf 5, the anodic flank being the outer. It should therefore be noted that the overlapping of the flanks takes place only in the part above the basal tube.

A further point of interest seen in the dissections was the change that took place in the shape of the apex during the plastochron. Thus in figure 2A, $B_1$ and $C_1$, the apex appears as an approximately circular dome, but in figure 2D it is clearly elongated along a diameter passing through the centre of $P_1$. It is also ovate in outline, being broader towards the centre of $P_1$ than in the opposite direction. It is also slightly asymmetric, as the foliar buttress from which the next leaf will arise has begun to appear. For the apex rises steeply from the base to the top of this buttress on the anodic side from $P_1$ and then becomes less steep, whereas on the kathodic side from $P_1$ it follows a more gradual curve as shown in figure 2D.

It cannot be said with certainty at which stage one plastochron ends and the next begins. The elevation of the foliar buttress is no doubt part of a leaf-forming process, but whether the radial extension of the apex which precedes it is also associated with the formation of the next leaf is uncertain. The convention will here be adopted of considering the start of a plastochron to be the first visible uprising of a new leaf, however small, but not of a foliar buttress.
ON SPIRODISTICHOUS SHOOT APICES. I

It has already been noted that $P_1$ is asymmetric, its kathodic flank being the longer. The angle subtended by the smaller half of a leaf at the centre of the apex is a measure of the degree of asymmetry of the leaf. In the normal plant the smaller half was always the anodic half, but this was not always so in the operated plants. The arcs covered by the anodic half-leaves of normal plants were measured on the drawings; in the older leaves which had already formed tubes at their bases the meeting-point of these halves could only be recognized directly above the tubes.

A total of 46 angles were measured on 14 plants and the mean value was $166°\pm 5$. The extremes were $171°$ and $162°$, the standard deviation was $2°\pm 3$, and the standard error was $0°\pm 30$. This asymmetry is also visible in the blade of the mature leaf of which the anodic half is usually slightly narrower than the kathodic. The asymmetry of the leaves can often be seen not only in the length, or more strictly transverse extension, of the halves but also in their radial thickness, since the anodic half-leaf is often slightly thicker than the kathodic as can be seen in leaf 5, figure 1.

To sum up, the asymmetry of the leaves is shown in the following features: the anodic half-leaf is regularly the shorter in extension round the apex, and is also the outer in overlap in the upper parts of the leaf; in some leaves the anodic flank can also be seen to be the thicker radially, and at an early stage of development of $P_1$ it appears to be the more protuberant.

Since the mean of an anodic half-leaf is $166°\pm 5$, and the mean divergence angle is only $152°\pm 6$, it follows that the centre of a new leaf is not directly over the meeting point of the flanks of the previous leaf, although that is the lowest point in the boundary line round the apex, but closer by $13°\pm 9$ to the centre of that leaf.

THE EXPERIMENTS

(1) Methods and terminology

The operations were made under a Leitz Greenough microscope, usually at a magnification of $\times 75$. In order to expose the apex it was necessary to split the sheaths of the older leaves and bend them back, but the younger leaves were too brittle to be bent back and had to be cut off a short way above their insertions. By this means it was often possible to leave six or seven of the older leaves attached to the plant for photosynthesis. As the plants bled strongly it was found best to leave them unwatered for at least 2 days before the operation. When the operation had been made the apex was protected with cotton-wool until the bases of the cut-down leaves had grown up and covered it. As the exposed apices were liable to be damaged by insects and mites, derris powder was applied to the bases of the cut-down leaves close round the apex. This precaution did no harm and was usually, though not always, effective.

The stage of the plastochron was recorded for each experiment at the time of operation. The plastochron was divided into seven stages in terms of the size of $P_1$; the stages are given in table 1, p. 140.

After the operations the plants were left to grow for periods varying from 4 to 8 weeks, according to the temperatures. The axillary buds grew out strongly and were continually removed, the removal of the young leaves being sufficient, as in other species, to cause
them to grow out even when the stem apex was undamaged. When the apices had grown
even enough they were pickled in spirit, embedded in collodion and sectioned by hand. A few
leaves present before the operation were included with the pickled apex.

<table>
<thead>
<tr>
<th>size of $P_1$</th>
<th>arc covered by $P_1$, and its stage of development</th>
</tr>
</thead>
<tbody>
<tr>
<td>very small</td>
<td>90°; just visible</td>
</tr>
<tr>
<td>small</td>
<td>90° to 180° (figure 2A)</td>
</tr>
<tr>
<td>small-medium</td>
<td>over 180° (figure 2B)</td>
</tr>
<tr>
<td>medium</td>
<td>nearly 360° (figure 2C), hood arching over</td>
</tr>
<tr>
<td>medium-large</td>
<td>360°</td>
</tr>
<tr>
<td>large</td>
<td>hood further grown</td>
</tr>
<tr>
<td>very large</td>
<td>apex now extended in plane of $P_1$, and sometimes foliar buttress of $I_1$, visible</td>
</tr>
</tbody>
</table>

(2) Preliminary observations on marked apices

In order to test Hirmer's theory that a sector is inserted in the apex in such a way as to
displace the centre of $I_1$, some preliminary marking experiments were made before the
main experiments were undertaken. Since the theory postulates that a sector of increased
growth is inserted in the apex and displaces sideways a newly determined leaf centre, it
follows that the tissues must be displaced at both sides of the inserted sector and also in
the neighbouring regions.* An attempt was therefore made to discover whether actually
the tissues are so displaced. Egg albumen mixed with charcoal was used for marking the
apex. It was applied with a single hair of a paint brush so as to form a fine streak across
the apex and the cut-down bases of the youngest leaves, or else deposited in a straight
row of dots. If the streak became curved in the course of subsequent growth, or if any of
the dots shifted so that they no longer formed a straight line, this was taken to indicate
a displacement of the underlying tissues. These observations were made under the dissecting
microscope and recorded by free-hand drawings. On Hirmer's theory the point at which
the centre of $I_1$ is determined is displaced from a position opposite the centre of $P_1$ to
the position which it occupies when $I_1$ becomes visible. Since in Rhoeo the divergence angle is
152°-6 a displacement of 27°-4 should occur in the antidromic direction, that is, the opposite
to that of the genetic spiral. A streak or a row of dots extending across the apex along the
diameter which passes through the centre of $P_1$ should therefore develop an antidromic
curve in the region of the apex which is at 180° from the centre of $P_1$.

In six of these experiments the streak or row of dots of egg albumen and charcoal lay
either approximately along the diameter passing through the centre of $P_1$, or else along
the closely neighbouring diameter passing through the meeting-point of the flanks of $P_1$.
The latter diameter was sometimes preferred because the meeting-point of the flanks
could be determined more accurately than the centre of $P_1$, and a displacement in the
same direction along this diameter was to be expected. Actually in three of the above
experiments a slight antidromic displacement occurred in the part of the apex adjacent
to the meeting-point of the flanks of $P_1$. This displacement was seen at the time when $I_1$
first became visible and was estimated at about 15°, but during the subsequent growth of

* Hirmer (1922, pp. 17, 18) and Troll (1937, vol. 1, pp. 421, 422) imply that their sectors of increased growth
inserted in the apex expand more in one tangential direction than in the other. But this is mechanically
impossible, unless the neighbouring tissues of the apex offer more resistance on one side of each sector than
on the other, which is not suggested by these authors, nor to be expected.
ON SPIRODISTICHIOUS SHOOT APICES. I

I, a displacement in the opposite direction was noted, the line of marks tending to become straight again. In two other experiments no displacement was seen near the meeting-point of the flanks of P1. In the last experiment a slight homodromic displacement occurred in the part of the apex near the meeting-point of the flanks of P1.

In another five experiments the streak was placed in the plane at right angles to the median plane of P1, or near it. The ends of these streaks were farther from the position of Hirmer's supposed inserted sector, so that they would not be expected to be displaced so much by that sector, but some slight displacement might be expected. Actually, of the ten portions of these five streaks which rested on the leaf-forming zone of the apex, nine remained straight until I, had arisen, and the tenth, which was between the centres of P1 and I, was found to be slightly displaced towards the centre of I when I, had just arisen, in the opposite direction to that anticipated by Hirmer's theory.

These results do not support Hirmer's theory. For even in the three apices out of eleven in which the tissues were found to be displaced in the direction to be expected on that theory the displacements were not large enough, and in two others the displacement was in the opposite direction. The marking experiments were therefore discontinued, and operations on the stem apex or youngest leaves were undertaken instead.

(3) The nature of the operations and classification of results

Two kinds of operations were made on Rhoeo. In the first the apex was split in a longitudinal median plane and the two halves were left to regenerate new apices. The cuts were made through the median plane of P1 or at right angles to that plane. These operations were chosen as it was considered that splitting the apex would profoundly disturb the phyllotaxis system and that the positions of the first few leaves on the regenerated apices might provide evidence of the factors which determine the phyllotaxis of a normal plant. The results of these operations suggested that in this species, contrary to what was found previously with Lupinus albus (Snow, M. & R. 1931, 1933 and 1947), the centres of the youngest leaves inhibit the formation of a new leaf centre, and that the intensity of this inhibition decreases with the age of the inhibiting leaf. Accordingly, in order to test this hypothesis more directly, a second series of experiments was carried out in which the centre of P1 was removed or destroyed at an early stage of the plastochron. For on the hypothesis of inhibition a displacement of one or more of the subsequent leaves would be expected to follow, the inhibition due to the centre of P1 having been removed, or at least reduced. As the results of this second series of experiments were on the whole simpler and easier to interpret than those in which the apex was split, they alone will be described here and the others will be reserved for a later paper.

In these experiments it was thought desirable to remove only the central part of P1 leaving some portion of its flanks on the apex, as it seemed possible that if the whole visible part of P1 were removed at an early stage in the plastochron the leaf might fail to develop at all; the amount of space available for I1 would thereby be increased and any displacement of its centre might be attributed to this factor. For this reason when the operation was made at a very early stage in the plastochron the central part of P1 was first isolated by two cuts forming a V pointing towards the centre of the apex and the part of P1 lying within the V was then removed. The parts of the flanks lying outside the
MARY SNOW ON EXPERIMENTS

Table 2. The removals of the centre of $P_1$.

<table>
<thead>
<tr>
<th>nos. of experiments</th>
<th>size of $P_1$ at time of operation</th>
<th>$P_2-I_1$ (normal)</th>
<th>$I_1-I_2$</th>
<th>$I_2-I_3$</th>
<th>$I_3-I_4$</th>
<th>$I_4-I_5$</th>
<th>$P_3-I_1$ (normal)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>very small</td>
<td>285-5</td>
<td>19-8$k$</td>
<td>180-0</td>
<td>151-5</td>
<td>149-5</td>
<td>457-0</td>
</tr>
<tr>
<td>2</td>
<td>small</td>
<td>305-0</td>
<td>0-3$k$</td>
<td>171-0</td>
<td>144-7</td>
<td>160-0</td>
<td>457-0</td>
</tr>
<tr>
<td>3</td>
<td>small-medium</td>
<td>296-0</td>
<td>9-7$k$</td>
<td>185-3</td>
<td>140-0</td>
<td>—</td>
<td>457-0</td>
</tr>
<tr>
<td>4</td>
<td>medium</td>
<td>294-5</td>
<td>10-8$k$</td>
<td>174-0</td>
<td>135-3</td>
<td>156-7</td>
<td>457-0</td>
</tr>
<tr>
<td>5</td>
<td>medium</td>
<td>283-5</td>
<td>11-8$k$</td>
<td>179-3</td>
<td>122-0</td>
<td>—</td>
<td>457-0</td>
</tr>
<tr>
<td>6</td>
<td>small-medium</td>
<td>289-0</td>
<td>16-3$k$</td>
<td>167-0</td>
<td>142-0</td>
<td>—</td>
<td>457-0</td>
</tr>
<tr>
<td>7</td>
<td>small-medium</td>
<td>281-7</td>
<td>13-6$k$</td>
<td>196-0</td>
<td>113-0</td>
<td>172-0</td>
<td>457-0</td>
</tr>
<tr>
<td>8</td>
<td>medium</td>
<td>279-5</td>
<td>25-8$k$</td>
<td>194-5</td>
<td>126-0</td>
<td>157-7</td>
<td>457-0</td>
</tr>
</tbody>
</table>

Group I, in which the centre of $P_2$ was left intact

| 11                  | very small                        | 457-0              | 0-9$k$    | 173-5     | 135-3     | 159-0     | —                  |
| 12                  | large                             | —                  | —         | 187-4     | 139-0*    | 166-0*    | 154-0*             |

Group II, in which the centre of $P_2$ was also removed

| 9                   | very small                        | 455-7              | 2-2$k$    | 185-3     | 170-0     | 151-0     | 157-3             |
| 10                  | very small                        | 446-0              | 11-9$k$   | 181-7     | 167-0     | 155-0     | 157-0             |

Group III, in which the centres of $P_1$ and $P_2$ were both removed but $P_1$ regenerated a new centre

<table>
<thead>
<tr>
<th>nos. of experiments</th>
<th>$I_1$</th>
<th>$I_2$</th>
<th>$I_3$</th>
<th>$I_4$</th>
<th>$I_5$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>183</td>
<td>177</td>
<td>180</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>176</td>
<td>172</td>
<td>180</td>
<td>167</td>
<td>—</td>
</tr>
<tr>
<td>3</td>
<td>170</td>
<td>174</td>
<td>167</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>4</td>
<td>178</td>
<td>171</td>
<td>175</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>5</td>
<td>180</td>
<td>170</td>
<td>175</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>6</td>
<td>171</td>
<td>172</td>
<td>168-5</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>7</td>
<td>202</td>
<td>170</td>
<td>180</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>8</td>
<td>200</td>
<td>158</td>
<td>168</td>
<td>161</td>
<td>171</td>
</tr>
</tbody>
</table>

Group II

| 11                  | —     | 170   | 178   | 174   | —     |
| 12                  | —     | 164   | 190   | 175   | 170   |

Group III

| 9                   | 170   | 173   | 173   | 169   | —     |
| 10                  | 175   | 176   | 174   | 170   | —     |

Note. All divergence angles are measured in the original direction of the genetic spiral except the last three angles marked with asterisks in no. 12.

Table 3. The asymmetry of the subsequent leaves.

<table>
<thead>
<tr>
<th>nos. of experiments</th>
<th>$I_1$</th>
<th>$I_2$</th>
<th>$I_3$</th>
<th>$I_4$</th>
<th>$I_5$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>183</td>
<td>177</td>
<td>180</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>176</td>
<td>172</td>
<td>180</td>
<td>167</td>
<td>—</td>
</tr>
<tr>
<td>3</td>
<td>170</td>
<td>174</td>
<td>167</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>4</td>
<td>178</td>
<td>171</td>
<td>175</td>
<td>—</td>
<td>—</td>
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<tr>
<td>5</td>
<td>180</td>
<td>170</td>
<td>175</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>6</td>
<td>171</td>
<td>172</td>
<td>168-5</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>7</td>
<td>202</td>
<td>170</td>
<td>180</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>8</td>
<td>200</td>
<td>158</td>
<td>168</td>
<td>161</td>
<td>171</td>
</tr>
</tbody>
</table>

Group II

| 11                  | —     | 170   | 178   | 174   | —     |
| 12                  | —     | 164   | 190   | 175   | 170   |

Group III

| 9                   | 170   | 173   | 173   | 169   | —     |
| 10                  | 175   | 176   | 174   | 170   | —     |

Note. In no. 12 the measured halves of the leaves are those which are anodic in the new direction of the reversed genetic spiral.

V were thus left on the apex. When the operation was made at a later stage and $P_1$ subtended about 180° or more, its centre could be removed by a single tangential cut which still left parts of its flanks on the apex. Finally in one experiment in which $P_1$ was very small the centre was destroyed by a puncture.
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In order to expose the apex it was unfortunately necessary to remove the hood of \( P_2 \) which arched over it. The amount of \( P_2 \) which was removed varied considerably in different experiments. Accordingly since there is reason to suppose that the central part of the base of \( P_2 \) affects the position in which \( I_1 \) will arise, four of the twelve experiments reported were excluded from the main group, since in them the central part of the base of \( P_2 \) was either severely damaged so that it possessed no median vascular strand or had been completely removed. These four experiments are, however, included in tables 2 and 3, and will be described separately since they presented several points of interest. In the eight experiments included in the main group, group I, \( P_2 \) had formed a basal sheath with a central vascular strand and in some had also formed a small blade, or two small blades, one from each flank. In three of these eight the flanks of \( P_2 \) had been broken by the cut that had removed the centre of \( P_1 \), but the central part of \( P_2 \) was intact. These eight experiments constituting group I will be described first.

(4) The development of \( P_1 \) when its centre was removed alone

When the centre of \( P_1 \) was removed early in the plastochron while it subtended an arc of less than 360°, its flanks continued to extend round the apex until they met. The other edges of the flanks of \( P_1 \) which abutted on the wound were found to have reunited at the base when the apices were sectioned. The zone in which the two halves were united was low and did not usually reach above the level of the growing-point. The manner in which the reunion took place is uncertain, as the material was not sectioned until after three or more weeks; but examination of the apex with the dissecting microscope a few days after the operation often revealed a strip of tissue beginning to grow up from the tissue of the apex immediately above the wound, that is, on the apical side of the wound. It is thought that this strip of tissue, which will be called the 'reuniting zone', formed a bridge between the halves of \( P_1 \). It was usually narrow, showed the wound scar on its outer face and lacked a median vascular strand, as seen in figures 4 and 5, nos. 6, 7 and 8. There was, however, one experiment, no. 4, figure 3, in which the wound scar was seen on the inner face of the uniting zone also. Here it seems that this zone must have been formed from tissues internal to the wound and not from the undamaged tissue above it.

Concerning the nature of this reuniting zone the most probable interpretation is considered to be that it was formed by an extension of the flanks towards the original centre of \( P_1 \) through tissue lying to the apical side of the wound or internally to it. This possibility is supported by the fact that at a higher level each of the flanks usually formed a small and roughly symmetric blade; for this suggests that each flank had been partly reorganized to form a symmetric whole, though in the experiments of group I only one of these structures showed a thickened central region and enlarged median strand (experiment no. 8, figure 5). The reorganization of the flanks was thus usually incomplete, but may have been sufficient to enable each flank to extend round the apex towards the original position of the centre of \( P_1 \). For such an extension, though in the abnormal direction relative to the centre of \( P_1 \), would have been away from the centre of the reorganized flanks, and so in the normal direction relative to those new centres. Again in no. 3, figure 4, the uniting zone was unusually thick radially and unusually high; it also had a median vascular strand and a large axillary bud. In this experiment, therefore, it seems probable that the centre of
Figure 3. A and B are transections of no. 2 from above downwards. The centre of $P_1$ was destroyed by a prick. In $B$, $P_2$ was united with $P_3$ at $a$ and $b$. C and D are transections of no. 4 from above downwards. The centre of $P_1$ was removed. The flanks of $P_2$ have developed abnormally following injury. In $D$, the central part of $P_1$ is joined to $P_3$. The meeting-point of the edges of the flanks of $P_2$ is marked $m$. (Magn. $A$ and $C$, ×27; $B$ and $D$, ×18.) In this and subsequent drawings of experiments the wound scars are shown with a thick black line. The spiral at the top left-hand side of each upper section shows the original direction of the genetic spiral. $P_1a$ and $P_1k$ are the anodic and kathodic flanks of $P_1$ respectively. $P_1$ and alternate leaves are stippled as also in subsequent figures.
Figure 4. A and B are transections of no. 6 at different levels. The centre of \( P_1 \) was removed. The central part of \( P_2 \) is joined to \( P_3 \). C, D and E are transections of no. 3 at different levels. The centre of \( P_1 \) was removed. The adjacent faces of \( P_1 \), \( P_2 \), \( P_3 \) and \( P_4 \) were united on each side of a wound passing through them shown in C. F is a transection of \( P_1 \) in no. 3 at a higher level showing the leaf in two halves with no trace of a central vascular strand. (Magn. A and D, \( \times 33 \); B, \( \times 28 \); C, \( \times 20 \); E, \( \times 31 \); F, \( \times 17 \).)
Figure 5. A and B are transections of no. 8 from above downwards. The centre of $P_1$ was removed. A new centre has probably been regenerated in the kathodic flank at $P'_1$. The anodic flank has united with $P_2$ near the wound. C, D and E are transections of no. 7 from above downwards. The centre of $P_1$ was removed. E is part of a transection showing the reuniting zone of $P_1$ just above its insertion. (Magn. \(A \times 28; B \text{ and } E, \times 15; C, \times 31; D, \times 22\))
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$P_1$ was not completely removed, the cut being either too shallow, or not reaching close enough to the apex so that the base of $P_1$ was able to grow up for a short distance. This peculiarity of no. 3 is significant for the interpretation of the subsequent phyllotaxis, as will be pointed out below.

It needs to be mentioned that in several experiments, nos. 3, 4, 6 and 8, the outer face of $P_1$ was joined to $P_2$ in the region of the wound, and in no. 3, $P_2$ was in turn united with the older leaves. These unions, which often occurred where deep wounds had been made, do not seem to have affected the subsequent phyllotaxis. In four of these eight experiments an axillary bud had developed above the reuniting zone.

(5) The position of $I_1$

In the eight experiments of group I in which $P_1$'s centre was removed and the basal part of $P_2$ was intact, the position of $I_1$ was located by its angle from the centre of $P_2$, since its angle from the missing centre of $P_1$ could not be measured. The mean normal angle from $P_2$ to $I_1$ in the direction of the genetic spiral may be taken as twice the mean of the single divergence angle already measured—that is $305^{\circ}\cdot5$, and its standard deviation will be $0^{\circ}\cdot423 \times \sqrt{2} = 0^{\circ}\cdot6$.

The divergence angles $P_2I_1$ of the experiments are given in table 2. They varied from $305^{\circ}$ to $285^{\circ}\cdot5$, with mean value $291^{\circ}\cdot8$. The standard deviation was $7^{\circ}\cdot9$, and the standard error was $2^{\circ}\cdot80$. The experiments thus led to a decrease in the angle from the original position of the centre of $P_1$ to the centre of $I_1$. The difference between the mean angle of the normals and the experiments was $13^{\circ}\cdot5$, and the standard deviation of the difference of the means was $2^{\circ}\cdot86$. The difference may therefore be considered significant. Examples of these experiments are shown in figures 3, 4 and 5, nos. 2, 3, 4, 6, 7 and 8.

This displacement of $I_1$ towards the missing centre of $P_1$ is to be expected if the centres of $P_2$ and $P_1$ act as centres of inhibition in determining the position of $I_1$. For the removal of the centre of $P_1$ would reduce the inhibition acting on $I_1$ from that direction, and consequently $I_1$ would be displaced towards the missing centre of $P_1$ by the inhibition from $P_2$ (see the diagram, figure 6). The variation of this displacement in different experiments may have been due to variations in the amount of the centre of $P_1$ that was removed and in the level to which the centre of $P_2$ was cut down. There is little doubt that the experiments would have given more consistent results and showed a greater displacement of $I_1$ had it been possible to leave $P_2$ intact. But this was impossible as already explained, since the hood of $P_2$, concealed $P_1$ and was too brittle to be bent back. It is probable that the lack of displacement of $I_1$ in experiment no. 2 was due to the injuries inflicted on $P_2$ at the time of operation (see figure 3B). For the central part of $P_2$ in experiment 2 was less thick than normal, but as its central vascular strand was present it was considered best to include the experiment in this group rather than with those experiments in which $P_2$'s centre was removed completely, or so much of it that no central strand was present.

It was thought probable that the displacement of $I_1$ would be greatest early in the plastochron, and that towards the end of the plastochron little or no displacement would occur, since the centre of $I_1$ would by then probably be determined, in its normal position. For this reason all the operations but one were made fairly early in the plastochron, not later than the stage with $P_1$ medium. Within this range from $P_1$ very small to $P_1$ medium
the displacement of \( I_1 \) (column 4, table 2) shows no relation with the state of the plastochron (column 2, table 2). If any such correlation exists it has been obscured by other variable factors in these experiments. It may be concluded that up to the stage with ‘P1 medium’, \( I_1 \) is undetermined, since it can be displaced by an operation which does not touch its presumptive area. The fact that the displacement does not exceed 25° in these experiments may be due in part to the cutting down of \( P_2 \) as suggested above; it is also possible that after the centre of \( P_1 \) was removed, some of its influence still persisted in the apex as a residual inhibition at the time when \( I_1 \) was determined.

![Figure 6](http://rstb.royalsocietypublishing.org/)

**Figure 6.** A diagram showing the changes in mean angular positions of \( I_1 \) and \( I_2 \) after the operations of group I. The lines marked \( P_2, P_1, I_1 \) and \( I_2 \) show the normal angular positions of these leaves and those marked \( I_1', I_2' \) the mean angular positions after the operations.

(6) The position of \( I_2 \)

The position of \( I_2 \) must now be considered. The angle \( I_1-I_2 \) is recorded in table 2. It varied from 167° to 196° measured in the original direction of the genetic spiral, the mean value being 181°±0. Since the normal divergence angle is 152°±6 with standard deviation 3°±7, it is clear that this angle is considerably greater than the normal. The mean angles and the positions of \( I_1 \) and \( I_2 \) in the experiments and in a normal plant are shown diagrammatically in figure 6. This increase of angle would be expected on the inhibition theory; for the position of \( I_2 \) would be determined mainly by the inhibition from \( I_1 \), since the centre of \( P_1 \) had been removed and consequently \( P_1 \) did not inhibit \( I_2 \) at all strongly. Any residual inhibition coming from \( P_2 \) would also tend to increase the angle \( I_1-I_2 \) (see figure 2). Thus the displacement of \( I_2 \) is to be explained as due mainly to the same cause as the displacement of \( I_1 \), that is, to the removal of the centre of \( P_1 \) and the consequent diminution of the inhibition from \( P_1 \). The variation of this displacement may also be related to variations in the inhibition from the remaining parts of \( P_1 \), and in the residual inhibition from \( P_2 \).

In no. 3 (figure 4 C, D, E and F) an unusually slight displacement of \( I_1 \) (9°±7) is associated with a large angle \( I_1-I_2 \) (185°±3). From this it would seem that the strength of the inhibition due to \( P_1 \) may have changed during the interval between the determination of \( I_1 \) and \( I_2 \), since otherwise a small displacement of \( I_1 \) would be expected to be associated with a relatively small angle \( I_1-I_2 \). This experiment has already been referred to (pp. 143, 147) as one in which the uniting zone of \( P_1 \) was thick and showed a median vascular strand though the upper part of the leaf had made two separate blades, and this was thought to be due
to an incomplete removal of the centre of $P_1$ which continued to grow for a short while after the operation. If this explanation of the uniting zone is correct, it will also account for the unusual angles. For if the centre of $P_1$ was still growing and exerting some of its inhibiting effect when $I_1$ was determined, only a slight displacement of $I_2$ towards $P_1$ would be expected; and if the centre of $P_1$ had ceased to grow when $I_2$ was determined, then it would not inhibit $I_2$, and so would not oppose the increase in the angle $I_1-I_2$.

Actually the angle $I_1-I_2$ exceeded 180° in no. 3, and in the two remaining experiments, nos. 7 and 8, it was over 190°; it follows that in these three experiments $I_1$ was not the sole determining factor affecting the position of $I_2$. It is indeed possible that in no. 7 the inhibition due to $P_2$ was greater than in the others, since it was noted at the time of pickling that in no. 7 the central part of $P_2$ had grown strongly and had formed a small blade in spite of having been cut down at the time of operation. In no. 8 there is evidence that a new centre of $P_1$ had been regenerated in the kathodic half. This new centre may have been partly responsible for the large angle $I_1-I_2$, for it can be seen from figure 5 that had $I_3$ arisen opposite $I_1$, it would have been extremely close above the new centre of $P_1$. In no. 3 also it seems that $P_2$ must have exerted some influence, though less than in nos. 7 and 8.

The diminution of the angle $I_2-I_3$ can be understood as resulting from the increase of the angle $I_1-I_2$. For normally the centre of each new leaf partitions the larger angle between the two previous leaves, which is $360°-152°=208°$ (see figure 6). But in the experiments
since the angle $I_1 - I_2$ increased, the angle obtained by subtracting it from 360° decreased, and the centre of $I_3$ had to partition a smaller angle and so arose closer to $I_2$ than is normal. The next few angles also, so far as they could be measured, oscillated above and below the mean normal angle, while tending to return towards it, except in no. 1 (see table 2).

(8) Four further experiments in which the centres of $P_1$ and $P_2$ were both removed

The results of the four experiments forming groups II and III in which the centres of both $P_1$ and $P_2$ were removed are also recorded in table 2. The following points of interest may be noted. The two experiments of group III, nos. 9 and 10, figures 7 and 8, differ from those of group I not only in that the centre of $P_2$ was removed as well as that of $P_1$ but also in that $P_1$ appeared to have regenerated a new centre. Thus in no. 10 the kathodic flank of $P_1$ was considerably thicker than a normal flank in this region, and the vascular strand in the centre of this thickened zone was taken to be physiologically a new median strand. But as there was no axillary bud above it, this is not certain. Macroscopically $P_1$ was seen to have made two blades, of which the kathodic was considerably the larger and approximately symmetrical in the upper part.

In no. 9, figure 7, an entirely new leaf had been formed with its centre above the cut which had removed the centre of $P_1$. Since this leaf had no axillary bud, its median strand could not be identified with certainty, but it was taken to be the strand in the thickest part of the leaf marked $P_1$ in figure 7. Viewed macroscopically this new leaf had made an approximately symmetrical blade with a small kink at the top. It is probable that the flanks of the original $P_1$ dedifferentiated after the centre had been removed, since no trace of them was found when the apex was sectioned. This was the only experiment in which a single new leaf was regenerated after the centre of $P_1$ had been removed. This regeneration may have been facilitated by two conditions: first, $P_1$ was very young at the time of the operation; secondly, the centre of $P_2$ had been removed and its inhibiting influence on the formation of new leaf centres had consequently diminished.

The position of $I_1$ in this group was located by its angle from $P_3$, since the original centres of $P_1$ and $P_2$ were lacking. The normal angle $P_3 - I_1$ may be taken as three times the mean normal divergence angle or 457°. The angles are recorded in table 2. In this group in which $P_1$ had regenerated a new centre, $I_1$ showed a kathodic displacement of $2° - 2$ in no. 9 and $11° - 9$ in no. 10, and its centre was approximately opposite to the supposed median strand of the new $P_1$. It therefore seems probable that the new centre of $P_1$ exerted a repulsive effect on $I_1$. This effect, however, cannot have lasted as long as in a normal leaf, since the centre of $I_2$ was close above the centre of $P_1$, the angle $I_1 - I_2$ being $170°$ and $167°$ in the two experiments. The fact that $I_2$ occupies the smaller angle $P_1 - I_1$ in both these experiments raises the question whether any leaf other than the regenerated $P_1$ and $I_1$ was effective in determining $I_2$. It is suggested that $P_2$ was effective in doing so, since its centre lies on the same side of the apex as the larger angle between $P_1$ and $I_1$ (figure 7B, no. 9). $P_3$ would thus play the same part in these experiments in determining $I_2$ as did $P_2$ in three experiments of group I (nos. 3, 7 and 8) in determining $I_3$, for in both experiments a leaf arose in the smaller angle between the last two leaves, and the centre of a leaf four plastochrons older ($P_2$ or $P_3$) lay beneath the larger angle, while the centre of the leaf ($P_1$ or $P_2$) underlying the smaller angle had been removed. As this situation occurred in

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five experiments it is not unreasonable to suppose that the centre of the leaf underlying the larger angle was effective as a centre of inhibition. It is perhaps surprising that the centre of a leaf four plastochrons old should still inhibit effectively, but this question will be discussed later when the nature of the inhibition will be considered.

The question may be raised how it was that in the experiments of this group \( P_3 \) did not inhibit \( I_1 \), which was, in fact, displaced towards \( P_3 \), although it has been concluded that \( P_3 \) did inhibit \( I_2 \) slightly. From a cut-down leaf as old as \( P_3 \) only a slight degree of inhibition

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**Figure 7.** \( A, B \) and \( C \) are transections of no. 9 from above downwards. The centres of \( P_1 \) and \( P_2 \) were removed and \( P_1 \) regenerated a new centre at \( P'_1 \). In \( C \) the vascular strands in the centre of the stem are omitted, the shaded area is the moribund base of \( P_2 \) and \( P_2k \) is its kathodic flank. (Magn. \( A, \times 27; B, \times 19; C, \times 8. \))
would in any case be expected on the hypothesis adopted here. This slight inhibition from $P_3$ acting upon $I_1$ may have been outweighed by an inhibition from the regenerated centre of $P_1$ acting upon $I_1$ in the opposite sense (see figures 7, 10).

Since $I_2$ arose in the smaller angle between $P_1$ and $I_1$ in the two experiments, the direction of the genetic spiral was unchanged, though the angle $P_1 - I_1$ exceeded $180^\circ$ measured in the original direction of the spiral. The divergence angles tended to return towards the normal after oscillating above and below it.

![Figure 8. A and B are transections of no. 10 from above downwards. The centres of $P_1$ and of $P_2$ were removed. A new centre was regenerated in the kathodic flank of $P_1$ at $P'_1$. (Magn. $A, \times 32; B, \times 19.$)](http://rstb.royalsocietypublishing.org/)

There remain two experiments in which the centre of $P_2$ was removed, but $P_1$ did not regenerate a new centre—nos. 11 and 12. In no. 11 the angle $P_3 - I_1$ differed from the mean normal angle by only $0^\circ - 9$. The unchanged position of $I_1$ can be understood on the inhibition hypothesis, since on that hypothesis the inhibition from $P_2$ had been much reduced, so that it did not displace $I_1$ towards $P_1$ as it did in group I. Whether this is a general rule will appear from further experiments now in progress. In no. 12, figure 9, the position of $I_1$ in relation to its normal position could not be ascertained, since the centre of $P_3$ had been accidentally destroyed. The special interest of this experiment lies in the reversal of the spiral already mentioned on p. 149. A further point worth noting is that it is the only experiment in which the centre of $P_1$ was removed late in the plastochron when $P_1$ was large. The two halves of $P_1$ are united only at the base by a narrow strip of tissue which was dead at the time of pickling. The tendency of the two halves to reunite was probably less strong than when the operation was made earlier in the plastochron. The experiment of removing the centres both of $P_1$ and of $P_2$ is being repeated.
ON SPIRODISTICHOUS SHOOT APICES. I

(9) The asymmetry of \( I_1, I_2 \) and \( I_3 \)

In the description of the normal apex it was noted that the leaves were regularly asymmetric, the anodic flank being the shorter in extension round the apex. The mean angle subtended by the anodic half-leaf was 166°-5. The standard deviation was 2°-3 and the

Figure 9. A, B, C and D are transections of no. 12 from above downwards. The centres of \( P_1 \) and \( P_2 \) were removed. The meeting-point of the edges of the flanks of \( P_1 \) is marked \( m \). The vascular strands in the centre of the stem are omitted in \( D \). The sections shown in \( B, C \) and \( D \) are slightly oblique. \( E \) shows the direction of the genetic spiral before the operation. \( F \) shows its direction from \( I_1 \) onwards. (Magn. \( A, \times 36; B, \times 22; C, \times 20; D, \times 15 \).)
standard error 0°-30. Though these experiments were designed to investigate the causes of the phyllotaxis, it seemed probable that they might also throw light on the factors determining leaf asymmetry, since in monocotyledons asymmetric leaves are usually associated with spirodistichous phyllotaxis and symmetric leaves with distichy. Some relationship between the phyllotaxis and the symmetry of the leaves is therefore probable. With this object in view the angles subtended by the anodic halves of the leaves that arose after the operation were measured and are recorded in table 3. The term anodic is here applied to the halves of the leaves which are anodic in the original direction of the genetic spiral except in no. 12, in which the spiral was reversed at \( I_1 \), and the term anodic is applied in relation to the final direction of the genetic spiral.

The angles subtended by the anodic halves of \( I_1 \) in the experiments of group I were always greater than normal. They ranged from 170° to 202°. This is interpreted as the result of a differential growth of the flanks. For if the normal asymmetry of the leaf is due to the more rapid extension of the kathodic than the anodic flank, a differential change in their growth rates will bring about a corresponding change in their asymmetry. Also if either flank is promoted relatively to the other it will extend farther round the apex before

![Graph showing relation between angle \( I_1-I_2 \) and anodic halves of \( I_1 \) in experiments 1 to 8 represented by numbered dots. The dot \( N \) shows the relation between the normal means of the divergence angle and of the anodic half of a leaf.](image)
meeting the other flank and then will prevent it from extending any more. For at their extreme base the flanks of each leaf meet and unite, as already mentioned (p. 138), but do not overlap.

The greatest increase in the anodic arc of \( I_1 \) occurred in nos. 7 and 8, in which the angle \( I_1-I_2 \) also showed the greatest increase above the normal. These facts suggested the possibility that there might be some regular relationship between the increase in length of the anodic halves of \( I_1 \) and the increase in the divergence angle \( I_1-I_2 \). This relationship is shown on a graph (figure 10) in which the angle \( I_1-I_2 \) is shown on the ordinates and the angle subtended by the anodic half of \( I_1 \) on the abscissae. The graph shows clearly that the arc of the anodic half of \( I_1 \) increases as the angle \( I_1-I_2 \) increases except in no. 3, in which the anodic half is unduly small. This exception will be discussed below.

The increase in the angle \( I_1-I_2 \) has already been explained as the result of the removal of the centre of \( P_1 \) and the consequent decrease in the repulsion exerted by that leaf on the centres of \( I_1 \) and \( I_2 \). Variations in this angle were considered to be due to variations in the amount of the centre of \( P_1 \) that was removed and in the degree to which \( P_2 \) was cut down (see p. 148). Since the arc of the anodic half of \( I_1 \) varies directly with the angle \( I_1-I_2 \), there is reason to suppose that these same factors which caused the variations in the angle \( I_1-I_2 \) also caused those in the asymmetry of \( I_1 \).

This provisional conclusion, together with some other facts to be mentioned below concerning the present experiments, and also some evidence from other experiments to be reported in a later paper, have led the writer to consider the following possibility with regard to the relationship between phyllotaxis and leaf asymmetry in this species, both in normal plants and in the experiments. It may be that those conditions which inhibit the formation of a new leaf centre promote the extension of the flanks of a leaf round the apex. A new leaf centre would then in general arise on the same side of the apex as the shorter half of the previous leaf, as is found to be the rule in a normal apex. In terms of the inhibition theory it must be supposed that the influence exerted by the leaf centres on the subsequent leaves is such as to inhibit the formation of new leaf centres but to promote the extension of their flanks round the apex. This hypothesis seems at first rather arbitrary and improbable, but it agrees well with the facts concerning the normal plant and concerning \( I_1 \) and \( I_2 \) in the experiments. Thus in the experiments nos. 1 to 8 which form group I the removal of the centre of \( P_1 \) reduced the promoting effect normally received by the kathodic flank of \( I_1 \), so that the anodic flank, as described above, was able to extend farther before meeting the kathodic flank.

There remains to be considered experiment no. 3, figure 4, which was an exception to the relationship shown by the graph, figure 10, in that the arc of the anodic half of \( I \) was considerably smaller in relation to the angle \( I_1—I_2 \) than in any other experiment of group I. This arc was indeed only \( 170^\circ \), which is only \( 3^\circ-5 \) greater than the normal arc, whereas the angle \( I_1—I_2 \) was over \( 180^\circ \). Now in this experiment, though the angle \( I_1—I_2 \) is large, \( I_1 \) is only slightly displaced towards \( P_1 \), as was pointed out on p. 148, where both these facts were interpreted as resulting from an incomplete removal of the centre of \( P_1 \). The same explanation may account for the slightness of the change in the asymmetry of \( I_1 \). For if the centre of \( P_1 \) was still growing when the flanks of \( I_1 \) were extending round the apex a relatively long kathodic and short anodic flank would be expected in \( I_1 \) as in a normal leaf.
MARY SNOW ON EXPERIMENTS

In nos. 11 and 12 forming group II which are not included in the graph the asymmetry of \( I_x \) could not be measured satisfactorily, since in no. 12 the flanks of \( I_x \) had grown into the wound which may have affected their relative growth rates (figure 9), while in no. 11 the regeneration of the kathodic half of \( P_1 \) had interfered with the extension of the flanks of \( I_x \) which did not meet round the apex. These are the only two experiments in which there is definite evidence that developments near the wound had interfered with the flanks of \( I_x \). In nos. 9 and 10 forming group III the change in the asymmetry of \( I_x \) was similar to that in the experiments of group I, though rather less than in most of them. But it seems unprofitable to try to interpret the change in these two experiments, since the regeneration of a new centre of \( P_1 \), which probably took a considerable time, and the removal of \( P_2 \) made the conditions so complicated.

The arc of the anodic half of \( I_x \) also was longer than normal in the experiments of group I except in no. 8 (table 3, column 3), in which it was shorter than normal. In that experiment it seems that a new centre has been regenerated in the kathodic flank of \( P_1 \) (figures 5A, B), and this centre will, on the hypothesis proposed, have increased the extension of the kathodic half of \( I_x \) above it, which in turn will have interfered with the extension of its anodic flank.

In the remaining seven experiments of group I the increase in the anodic halves of \( I_x \) may be related to the large angle \( I_x-I_x \); for since \( I_x \) and \( I_x \) were more nearly opposite than in a normal plant the influence exerted by \( I_x \) on the two flanks of \( I_x \) was more nearly equal. It may be noted that the longer flank of \( I_x \) always lay on the opposite side of the apex from the centre of \( I_x \), which agrees well with the hypothesis that conditions which inhibit the formation of a leaf centre promote the extension of the flanks round the apex.

In no. 12, an experiment of group II in which the centres of \( P_1 \) and of \( P_2 \) were removed, the asymmetry of \( I_x \) is particularly significant. In this experiment the genetic spiral was reversed permanently at the angle \( I_x-I_x \) and the asymmetry of \( I_x \) was also reversed, so that here again the longer flank of \( I_x \) was on the opposite side of the apex from the centre of \( I_x \).

The asymmetry of \( I_x \), however, is difficult to reconcile with the hypothesis proposed above which therefore remains for the present only a possibility to be borne in mind. Since the asymmetry of \( I_x \) is at present not understood it will not be described here, but the main facts are recorded in table 3 and in the figures.

**Discussion and conclusions**

From the experiments on *Rhoeo discolor* reported above and from observations made on normal plants, information has been obtained with regard to three main questions. These questions concern the manner in which a leaf primordium is determined and develops, the factors locating the position in which a primordium is determined and the causes of the asymmetry of the primordium. They will now be discussed in turn.

As to the first question the evidence indicates that in *Rhoeo* the centre of a primordium or a small central region is determined first and that from this centre the flanks extend round the apex until they meet. For the fact that in *Rhoeo* the flanks of \( P_1 \) continued to extend round the apex after the centre of \( P_1 \) had been removed shows that once this extension has begun it does not depend on the presence of the centre. It might, indeed,
be suggested that the whole area occupied by $P_1$ had been determined to form a leaf before the centre was removed and was only gradually occupied by the flanks; but the results of some other experiments in which the apex was split do not support this suggestion. In these experiments, which will be more fully reported later, the split was made at right angles to the median plane of $P_1$. When the operation was made early in the plastochron at a stage when $P_1$ subtended less than 180° the whole visible part of the leaf was confined to one of the split halves, and the flanks of $P_1$ did not develop on the other half, as they would have been expected to do if they had been already determined. But they did continue to extend round the half-apex which carried the centre of $P_1$, extending through the tissue adjacent to the wound and above it. On the other hand, when the split was made later in the plastochron so that the flanks of $P_1$ were severed by the cut, then the flanks continued to extend round the half-apex remote from the leaf centre, but not round the half carrying that centre. The facts therefore indicate that the tips of the flanks of a leaf when once they are formed tend to extend round the apex or half-apex on which they are situated without needing any influence from the leaf centre for their further growth, and also that the flanks are determined later than the centre.

Thus the manner of initiation and development of a primordium in Rhoeo appears to differ from that which was found in the dicotyledon Lupinus albus previously investigated. For we concluded (1931, 1933) that in L. albus a leaf primordium was determined as a whole as soon as a space was available both wide enough and low enough for it. There was therefore a certain minimum area of the apex in which a primordium could be determined, and when a primordium was determined in it, this area constituted the primary area of the primordium (Snow, M. & R. 1933, p. 360). This primary area included the stipules as well as the central part of the leaf, though some extension of the stipules round the apex was found to take place subsequently. In Rhoeo, however, it appears that the primordium is not determined as a whole simultaneously but that its central part is determined first. It is possible that some part of this central region constitutes a primary area, but if so it is much smaller in relation to the total area subsequently occupied by the leaf than it is in Lupinus.

As to the factors locating the positions in which primordia are determined in Rhoeo, the present results indicate that each leaf centre inhibits the formation of new leaf centres in its neighbourhood and that this inhibition decreases with time and with distance. The clearest evidence in favour of this conclusion is to be found in the positions of $I_1$ and $I_2$ following the removal of $P_1$, for the centre of $I_1$ then arose closer to the original position of the centre of $P_1$ than it would normally have done and $I_2$ arose almost opposite to $I_1$. These changes cannot be explained in terms of any space-occupying process, similar to that which we found in Lupinus. For the centres of $I_1$ and $I_2$ usually did not fit into depressions in the changed boundary lines round the stem apices as can be seen in many of the figures, e.g. figs. 3D and 5D. Similarly, in a normal spirodistichous apex the leaf centres do not fit into any depressions, as was pointed out on p. 139. Moreover, the displacement of $I_2$ after removal of the centre of $P_1$ indicates that in a normal apex of Rhoeo the position of a new leaf $n$ is influenced by inhibition from leaf $n-2$, as well as leaf $n-1$. This inhibition from $n-2$ causes $n$ to arise farther from $n-2$ than it would otherwise have done, and so causes $n$ to deviate from the position opposite to the centre of $n-1$ in which it would otherwise have
arisen on account of the inhibition from \( n-1 \). Consequently when the centre of \( n-2 \) is removed, leaf \( n \) arises more nearly opposite to \( n-1 \). This, then, as the writer concludes, is in the main the explanation of the spirodistichy of *Rhoeo*.

There is evidence, however, that the position of the centre of leaf \( n \) is also affected by inhibitions from leaves \( n-3 \) and \( n-4 \). The inhibition from \( n-3 \) is shown when the angle \( I_1-I_2 \) exceeds 180°, indicating that \( I_2 \) is inhibited by \( P_2 \), which is \( n-3 \) in relation to \( I_2 \), and the inhibition from \( n-4 \) is shown by the position of \( I_3 \) which always arose on the side of the apex away from the centre of \( P_2 \), so long as that centre was intact; for this indicated that \( I_3 \) was inhibited by \( P_2 \). Thus \( n-3 \) reinforces \( n-1 \) and \( n-4 \) reinforces \( n-2 \) in their effects on \( n \), as can be seen from figure 1. It may be that these inhibitions from \( n-3 \) and \( n-4 \) would not be found in all spirodistichous species, since they do not seem to be necessary for spirodistichy. Other evidence was also reported for the conclusion that the position in which a leaf arises is determined by inhibitions from the four youngest leaves, their effectiveness diminishing with the age of the inhibiting leaf. It is probable, however, that in a normal plant in which all these four leaves are intact the effect of the older leaves \( n-3 \) and \( n-4 \) is relatively less than it was in the experiments, in which the centres of \( n-1 \) and sometimes of \( n-2 \) had been removed.

It is difficult to determine whether the diminution of inhibition with age of the inhibiting leaf depends for the most part directly on the age of that leaf, or on its distance from the apex which increases with age; but, since there is very little internodal extension between the youngest leaves, it is probable that the diminution cannot be accounted for by distance alone, but must in part depend directly on age.

As to the mechanism of this inhibition, the experiments provide no direct evidence, but it seems probable that an inhibiting substance is formed by the centres of the leaves and diffuses through the tissues of the apex. Whether it moves by simple diffusion or by some more complex process it is impossible to say, but it is clear that it must move upwards as well as transversely, since the four youngest leaves can all exert inhibitions on the new leaf arising at the apex. The results indicate also that in *Rhoeo* the central region of a leaf is the main source of inhibition, since on that basis it has been found possible to explain them consistently. They also suggest that the central conducting strand is the most effective part of that central region. For in three experiments, nos. 8, 9 and 10, in which \( P_1 \) regenerated a new central strand, the centre of \( I_1 \) was almost opposite to the new central strand, and so appeared to have been inhibited by the new strand. But this inhibition seems to have faded sooner than that from a normal leaf centre, since \( I_2 \) arose with its centre close to the new central strand of \( P_1 \). This rapid fading may be correlated with the absence of a bud from the axil of the new centre of \( P_1 \), which seems accordingly to have been imperfect in some way. On the other hand, the fact that in four other experiments, for instance, no. 4, figure 3, a bud did arise in the axil of a \( P_1 \) with its centre removed, may be explained by its having been already determined.

Finally, the problem of leaf asymmetry remains to be considered. As stated in the introduction, Schumann at first considered leaf asymmetry to be the determining factor of the phyllotaxis, but later abandoned this view. In Hirmer’s opinion (1922) the asymmetry and the phyllotaxis both result from the insertion of a sector in the apex, but reasons have been given for considering it improbable that such a process takes place, and in any case
it could not account for the fact that in *Rhoeo* the kathodic half (called by Hirmer 'anodic', see p. 133) is the longer tangentially, contrary to what Hirmer states to be the general rule.

Schoute (1913, pp. 297, 310) considered that leaf asymmetry was secondary and occurred when the space available for a primordium was itself asymmetric provided that the new primordium made contact with the underlying leaves. The new primordium then extended asymmetrically to fill the unequal gaps on each side of its centre. This may, indeed, perhaps account for the fact that in *Rhoeo* the anodic half is usually slightly the thicker radially, since it lies above the meeting-point of the edges of the previous leaf, where there is the most space available in a radial direction; but it cannot account for the greater length of the kathodic half in normal plants. The following results of the present experiments need also to be considered. When the centre of *P*₁ was removed, the anodic half of *I*₁ increased in length and in three experiments exceeded the kathodic, and this increase varied directly with the divergence angle \( \theta \), which also increased. Again in no. 9, figure 7, the centre of *I*₂ lay exactly over the meeting-point of the flanks of *I*₁, and yet *I*₂ was asymmetric, so that its asymmetry must have been due to something other than the space-filling process. Lastly, in no. 12, figure 9, in which the spiral reversed, *I*₂ was very asymmetric both in length of halves and in their radial thickness, and the longer flank was the thicker, contrary to what is found to be the rule in normal plants.

The facts reported concerning *I*₁ and *I*₂ were shown to agree in the main with the hypothesis proposed, that the factors which inhibit the formation of a leaf centre promote the extension of a leaf flank round the apex, improbable though this may at first appear. For in all the *I*₁ leaves except one, the longer flank lay on the side of the apex away from that on which the next leaf centre (*I*₂) was formed and thus on the more strongly inhibited side, as also it does in a normal plant. The exception was no. 3, in which it appeared that the centre of *P*₁ had been incompletely removed. The most convincing evidence in favour of the hypothesis proposed is the correlation of the increases in the angle \( \theta \) and in the arc of the anodic half of *I*₁ (see figure 10). The asymmetry of *I*₂ also was shown to support the hypothesis, but difficulties arose with regard to *I*₃ which cannot at present be resolved, so that the hypothesis must for the present remain provisional. In other spirodistichous species the sense of the leaf asymmetry still needs to be determined with certainty.

The differences between the processes of leaf determination in *Lupinus albus* and in *Rhoeo discolor* may now be briefly summarized as follows. In *Lupinus* the primary area of a leaf is determined as a whole and comprises the greater part of the area of the apex which the leaf will finally occupy. In *Rhoeo* the centre or a small central area is determined first, and the process of leaf formation extends gradually round the whole circumference of the apex. In *Lupinus* the position in which the next leaf will arise depends on the position of the first space large enough to accommodate its primary area which reaches a sufficient distance from the growing-point; and so it depends on the outlines of the insertions of the youngest primordia. In *Rhoeo* the position in which the next leaf centre will be formed depends on a balance between the physiological inhibitions exerted on the leaf-forming zone of the stem apex by the three or four youngest leaves.

It does not appear that in *Rhoeo* the next leaf centre is determined in the position which is farthest from the growing-point, neither in the experiments nor in normal plants (p. 139).
So in this respect also *Rhoeo* appears to differ from *Lupinus albus* and *Epilobium hirsutum*, in which species experiments led to the conclusion that the primary areas of leaves are determined in the available spaces that are lowest—that is, farthest from the growing-point (Snow, M. & R. 1931, 1933 and 1935). This is probably because in *Rhoeo* the physiological inhibitions proceeding from the young leaves may cause the lowest position to be unavailable for the next leaf centre. Moreover, since the youngest leaf subtends an arc of 360° before the next leaf arises the boundary line round the base of the stem apex is much less indented than in plants with smaller leaf arcs, and the differences of level are therefore less great than in the latter.

In view of the general similarity of the spirodistichous systems of monocotyledons, it seems probable that in the other species of monocotyledons with systems of this kind the process of leaf determination and the factors governing the positions of those leaves are similar to those in *Rhoeo*. But this raises the question how it is that in the young seedlings of several spirodistichous species drawn by Hirmer (1922), though not in *Rhoeo*, several leaves following the cotyledon arise in a straight distichy, and then the later leaves deviate gradually into spirodistichy. It may be that the inhibition from each of these early distichous leaves is weak and disappears before its second plastochron, so that the position of leaf \( n \) depends only on the inhibition from leaf \( n-1 \), opposite to which \( n \) arises. Or again, it may be that these early leaves scarcely inhibit at all, and that their positions depend on a space-filling process such as we found in *Lupinus albus*. For this process might be expected to place leaf \( n \) with its centre roughly over the meeting-point of the flanks of \( n-1 \), where the sheathing base of \( n-1 \) is thinnest; and since the distichous leaves are symmetric according to Hirmer, this position is opposite to the centre of \( n-1 \).

Since the present results show that in *Rhoeo* the placing of new leaves is governed by physiological inhibitions from older leaves, they agree in this respect with the theories of Schoute (1913) and of Richards (1948). Yet those theories were not proposed especially for spirodistichous monocotyledons, but generally for all systems of phyllotaxis. Indeed, it is mainly the much commoner spiral systems of dicotyledons which these authors have considered, and it was concluded previously (Snow, M. & R. 1931, p. 36; 1933, p. 396) that the results of experiments on *Lupinus albus*, a species with a typical Fibonacci spiral system, did not agree with Schoute’s theory but needed to be explained in terms of space-occupying factors, in agreement with the theory of van Iterson. The chief reason given for this was that according to Schoute a leaf centre is determined first, whereas the evidence from radial splits of \( I_1 \) in *Lupinus* was considered to show that in that species a leaf was determined as a whole (see Snow, M. & R. 1933, p. 397). This conclusion has indeed been criticized by Richards (1948), but it would take too long to discuss here in detail these criticisms, with most of which the writer cannot agree. It is hoped to discuss the question further when some further experiments now in progress are reported on leaf determination in dicotyledons.

Even the results of the experiments on *Rhoeo* do not agree with the theory of Schoute, since he supposed that each leaf centre was surrounded by a ‘dispersion area’ within which an inhibiting hormone completely prevented the formation of other leaf centres, and that the effect of this hormone ceased suddenly at the boundary of each such area. But it seems to the writer that the changes of leaf positions reported in *Rhoeo* cannot be
explained on this basis, but only on the basis of inhibitions that decrease gradually with the distances from their sources.

Wardlaw also (1949 a, b, c) has recently suggested a theory of leaf-determination and phyllotaxis in ferns according to which certain areas extending round the central parts of leaves already determined are made physiologically unavailable for the formation of other leaves, and he has based this theory on some valuable experiments on fern apices, which, however, are morphologically different from those of flowering plants.

The theory of Richards (1948) is much less rigid than that of Schoute, and is stated only in very general terms. Unlike Schoute he supposes that the inhibiting influences from existing leaves diminish continuously with distance. He claims that on theories such as his own, which he calls field theories, it is possible to explain the return of a spiral system to regularity after a disturbance. This is a very important claim, since the return to regularity after a disturbance and the attainment of regularity in seedlings are serious difficulties for a space-occupying theory such as that of van Iterson.

The present experiments on *Rhoeo* support very well Richards's idea of inhibitions diminishing continuously with distance, and they contain nothing contrary to his theory. Yet difficulties arise for this theory also if it is applied to dicotyledons, since Richards, like Schoute, supposes that the centre of a leaf, or at most a small central area, is determined first, whereas the evidence, as has been pointed out, still seems to the writer to show that in *Lupinus* a leaf is determined as a whole. Another difficulty is that on the theory of Richards the position of a new leaf should depend on inhibitions coming from all the leaves of the uppermost cycle at least. Yet in *Lupinus* the evidence has seemed to show that the position of a new leaf does not depend, or not appreciably, on the immediately previous leaf \( n-1 \), when leaf \( n \) does not make contact with that leaf, as normally it scarcely does. The position of \( n \) depends only on those leaves with which it does make effective contact. The evidence for this statement was summarized recently (Snow, M. & R. 1947, pp. 14, 15; 1948, pp. 271, 272) in a criticism of the so-called repulsion theories of phyllotaxis, and it seems to the writer to hold good in spite of criticisms made in correspondence by Richards.

Further experiments bearing on this point are also in progress.

A similar conclusion has been reached by Wardlaw (1949 a, pp. 173, 188; 1949c, pp. 106, 125) from experiments on fern apices. In these apices the visible leaves are not in contact at all, but Wardlaw has concluded that here also the position of a new leaf is affected only by the immediately adjacent leaves, and not by those remote from it (1949 a, p. 188). These fern apices having five leaves in the top cycle are very well suited for testing this point. He has also written that the position of a new leaf is determined by localized factors and not by factors affecting the meristem as a whole (1949 a, p. 177).

The writer concludes therefore that the process by which leaves are localized in spirodistichous monocotyledons is different from what it is in dicotyledons and ferns, and that the phyllotaxis of the first of these groups depends on physiological inhibitions such as are postulated by Richards, but that his theory cannot hold good for the other two groups, or not in its present form at least. The problem for the future seems to be whether in dealing with the dicotyledons and ferns it is possible in any way to secure the advantages claimed for the theory of Richards without coming into conflict with the experimental results.
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**References**


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