

On the Power possessed by Leaves of placing themselves at Right Angles to the Direction of Incident Light. By FRANCIS DARWIN, F.L.S.

[Read December 16, 1880.]

It is well known that certain organs of plants have the power of growing in oblique or horizontal directions. The rhizomes of many plants extend horizontally under ground, thus growing at right angles to the direction of gravitation instead of parallel to it, like ordinary geotropic or apogeotropic* stems and roots. When the obliquely-growing organ is above ground the case becomes more complex; for here it is not only growing obliquely with respect to the gravitation, but also with respect to the chief portion of incident light, namely that which comes from the zenith.

A seedling radish growing in open ground may illustrate the case. The hypocotyl grows vertically upwards, being both apogeotropic and heliotropic, and therefore growing parallel to the incident light which falls on it from above, and also to the line of gravitation. But the cotyledons place themselves in a nearly accurately horizontal position, at right angles both to the line of gravitation and to the light. It will be found, however, that it is the direction of the light, and not that of gravitation, which determines the position of the cotyledons; for if the seedling be placed (with due precautions) before an oblique lateral light its cotyledons adjust themselves so that their surfaces are once more at right angles to the direction of the light.

The following investigation is an attempt to arrive at a clearer conception of the nature of the power which leaves possess of thus placing themselves at right angles to the direction of incident light.

It will first be necessary to give, as an introduction to my own work, a short account of the state of knowledge on the subject.

The two chief theories which I shall have to consider are those of A. B. Frank and of De Vries. Frank† supposes that,

* Geotropic is used to mean *positively* geotropic, apogeotropic to mean *negatively* geotropic, in accordance with the terminology used in 'The Power of Movement in Plants,' by C. Darwin, assisted by F. Darwin, 1880, p. 5.

† 'Die natürliche wagerechte Richtung von Pflanzentheilen.' Leipzig, 1870.

besides the ordinary and well known forms of growth, geotropism and heliotropism, through which organs place themselves in the line of the earth's radius, or parallel to the incident light, as the case may be, there are special forms of growth, called transverse geotropism and transverse heliotropism. An organ which grows transverse-geotropically places itself horizontally; it has an inherent tendency to be horizontal, in the same way that the hypocotyl of a seedling has an inherent tendency to grow vertically upwards. In the same way a transversely heliotropic organ has an inherent tendency to place itself at right angles to, instead of parallel to, the direction of incident light. It may be said that this is no explanation at all; and this is true in a certain sense. But there is no reason why it should be more unsatisfactory than the accepted explanation of the vertical growth of stems and roots, namely that they have an inherent power of growing in these directions*. Another explanation of the facts is that given by De Vries, in his paper "On the Direction of Bilaterally Symmetrical Organs"†. The work in question is in great measure a criticism on Frank's views, and proposes a theory of an entirely opposite character. De Vries believes it to be quite unnecessary to assume the existence of special forms of growth as Frank has done, and that the old forms of growth, positive and negative geo- and heliotropism, can, under certain conditions, account for oblique or horizontal growth. He thinks that Frank has neglected a possible explanation of the phenomena in the combinations and antagonisms which occur among the ordinary heliotropic and geotropic forces. Thus an organ might be apheliotropic‡ and apogeotropic, and when exposed to a zenith-illumination might remain horizontal in consequence of the balance between the apheliotropic tendency to grow away from the zenith, and the equal and opposite apogeotropic tendency to grow towards it.

De Vries's work also shows the existence of two forms of growth, independent of gravitation and light, which, he believes,

* The essential part of Frank's doctrine is accepted by my father in 'The Power of Movement in Plants,' p. 438.

† 'Ueber einige Ursachen der Richtung bilateralsymmetrischer Pflanzentheile,' Arbeiten des bot. Instituts in Würzburg, Heft ii., 1872.

‡ Apheliotropism is a convenient term, used instead of negative heliotropism. When used without the prefix apo-, positive heliotropism is meant. See 'The Power of Movement in Plants,' *loc. cit.*

play an important part in the formation of the balance between opposite tendencies just alluded to, These forms of growth are *epinasty* and *hyponasty*. An organ is said to be epinastic, in De Vries's sense, when the longitudinal growth of the upper half exceeds the growth in length of the lower half; epinasty, if unopposed, will therefore result in the organ becoming convex above and curving downwards. Hyponasty is the reverse of epinasty; that is to say, the organ curves upwards, owing to the lower increasing more than the upper half in length.

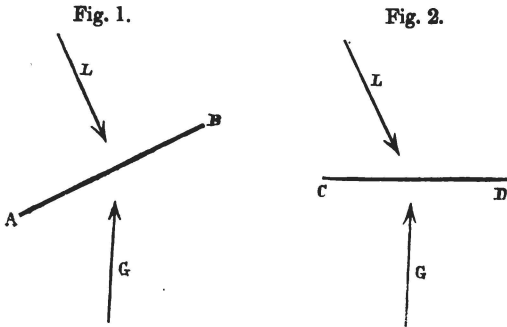
Frank subsequently replied to De Vries's criticism, and was again answered by De Vries. I shall not attempt to give any abstract of this discussion, though some points in it will be touched on later.

I have purposely given De Vries's theory in the simplest and crudest form, because this suffices to show the contrast between it and Frank's views; and this kind of exposition is enough to give an idea of the point from which I began my work. De Vries is careful to state that his views are only put forward as possible solutions of the problems. He points out the coexistence of a number of opposing growth-tendencies, and suggests how they *might* produce equilibrium. He does not intend his views to be applied to any special cases. He points out that a quantitative estimate of the opposing tendencies would be necessary before any special explanations could be possible.

The same principle which De Vries has formulated finds a prominent place in Sachs's paper, "Ueber orthotrope und plagiotrope Pflanzentheile"*. Thus, in explaining the power which *Marchantia* has of placing its thallus-lobes at right angles to incident light, he says (p. 239) that the plagiotropism (here equivalent to obliquity) of *Marchantia* may be regarded as a position resulting from negative geotropism, heliotropism (on the underside); and epinasty on the upper or light side. In the same way (p. 276), speaking more generally, he describes an organ as plagiotropic when it is negatively heliotropic, and at the same time negatively geotropic. The negative heliotropism seeks to bend it downwards, the negative geotropism upwards; thus, according to the specific sensitiveness to gravitation and light, and according to the intensity and direction of the latter, the organ will take up an oblique or horizontal position of equi-

* 'Arbeiten des bot. Instituts in Würzburg,' Bd. ii. Hft. ii., 1879.

brium. These extracts show that Sachs is, on the whole, in favour of an explanation in accordance with De Vries's views and opposed to that of Frank. There is, however, a feature in Sachs's views which does not occur in De Vries's; and this is the importance which Sachs attaches to the existence of specific sensitiveness to gravitation and light.



Diagrams illustrating different degrees of sensitiveness to light and gravitation.

If AB in fig. 1 represents an organ which places itself so that it is at right angles to the incident light, and if G represents the vertical direction in which gravity acts*, the specific sensitiveness to light is such that it requires the light to act with its greatest force, *i. e.* at right angles, in order to produce apheliotropic tendency strong enough to resist and balance the apogeotropic tendency; and the specific sensitiveness to gravitation is such that even when the organ is oblique, and when, therefore, the stimulus of gravitation must be feeble, the amount of apogeotropic action called into play is enough to balance the apheliotropism produced by the light.

The organ CD, shown in fig. 2, assumes a horizontal instead of an oblique position, because its specific sensitiveness to light and gravitation are different to those of AB: it is more sensitive to light and less so to gravitation; so that an amount of apheliotropism sufficient to balance the apogeotropism is produced by the weakened stimulus of oblique rays of light, and the necessary amount of apogeotropism is not produced until the organ is in

* The barbs of the arrows are made to represent the directions in which light and gravitation tend to cause the organ to bend; the stems of the arrows give the angles at which light and gravitation act.

the most favourable position for the action of gravity, *i. e.* horizontal.

I have dwelt on this view of specific sensitiveness, not only in order to give a clearer notion of Sachs's views, but because it leads on, as he himself states (p. 282), to the belief that light and gravitation act merely as stimuli ("Reize") on the organs of plants, the nature of the resulting behaviour of the plant being determined by the inner nature of the organ—as, for example, the uniform stimulus of gravitation is translated by a stem into a command to grow upwards, by a root into a command to grow downwards. And this theory of gravitation and light acting as stimuli is so necessary to the views which I hold on the subject, that I am glad to be able to give it the support of Sachs's opinion.

The Object of the present Research is, by observation of such organs as place themselves at right angles to the direction of the incident light, to determine whether the "Transversal-Heliotropismus" theory of Frank, or the balancement theories of De Vries and Sachs, is most in accordance with the facts.

It should be clearly understood that, in speaking of Frank's theory, I do not include his ideas about polarity, by means of which he seeks to explain transverse heliotropism and geotropism. I refer merely to the belief that a special form of heliotropism exists, in accordance with which an organ places itself at right angles to the light instead of parallel to it; and this I take to be the essential and important part of Frank's views.

Plan of Research.—The method which I have employed is essentially the same as that which has been employed in Sachs's laboratory for the study of ordinary heliotropism. The apparatus used for this purpose by Müller of Thurgau ('Flora,' 1876) consisted of a cylinder rotating slowly about its longitudinal axis, on which the seedlings under observation were grown. The cylinder was placed at a window; and the plants were protected from all illumination except such as fell on them in a direction parallel to the axis of rotation. The cylinder rotated so slowly* that no centrifugal effect was produced on the plants; but rapidly enough to destroy all geotropic action. The seedlings were therefore entirely free to obey the stimulus of light; and their heliotropic curvature was not liable to be influenced by gravitation, as is the case under ordinary circumstances. The principle on which the stimulus of gravitation can be avoided has

* One revolution in 20 in my experiments.

been fully discussed by Sachs in his paper, "Ueber Ausschliessung der geotropischen und heliotropischen Krümmungen"*. The history of the subject is there given; and a quotation from Sachs's 'Experimental Physiologie' (1865) shows that the principle of slow rotation was fully understood by him at that time. He points out (p. 107†) "that before any curvature, and before a perceptible amount of growth could occur" . . . the plant "would be in a reversed position." Thus any tendency to curvature which had been generated in the first position would be destroyed in the second position, and the plant would have no geotropic tendency of any kind.

Sachs is acquainted with John Hunter's experiments only as quoted by Dutrochet, and has not been able to see the original paper. And as Dutrochet quite misrepresents Hunter's meaning, it may be worth while to show that Hunter had a clear conception of the principle of slow rotation. He describes the means by which a basket of earth containing germinating beans was made to rotate, and goes on to say that the root of a bean had met with a small stone in its course, and had been turned by it into the direction of the axis of rotation, and had then *gone on in a straight line in that direction*. "Here, as there was no fixed inducement to grow in any one direction, the bean grew in a straight line in that direction given it by chance"‡.

The above quotation has a merely antiquarian interest, the method of slow rotation as it exists in modern physiological research, and especially the ingenious application of it to the study of heliotropism, is entirely due to Sachs.

In describing the application of the principle of slow rotation to the study of plagiotropic organs, I shall employ Sachs's term *Klinostat* to designate the instrument by which plants are kept in slow rotation. And I shall employ this term to signify an apparatus either for the avoidance of geotropism alone, or of both heliotropism and geotropism§.

Fundamental Experiment.—If a plant whose leaves have the

* Arbeiten, Würzburg, Bd. ii. Heft ii. p. 209.

† Quoted by Sachs in his Arbeiten.

‡ Quoted from Hunter 'On the Blood' (1794), in the Catalogue of the Physiological Series of Comparative Anatomy in the Museum of the Roy. Coll. of Surgeons, vol. v. 1840, p. 12.

§ For the detailed description of the klinostat used in my experiments see Appendix.

power of placing themselves at right angles to incident light is growing normally in the open air and lighted from above, its leaves will be horizontal. Let the plant be now made to rotate on a klinostat so that the axis of rotation coincides with the axis of the plant. Also let the direction of the incident rays of light be parallel to the axis of rotation, so that the morphologically upper side of the leaves is illuminated by rays striking them at right angles, just as they were when the plant grew on the ground. Then, if the normal horizontal position is the result of a balance between geotropism (positive or negative) and any other force—epinasty, hyponasty, positive or negative heliotropism—it is clear that, geotropism being destroyed by the rotation, the balance cannot be maintained.

If, on the other hand, the horizontal position of leaves is due to transverse heliotropism (or diaheliotropism*), there is no reason why the leaves should not remain at right angles to the incident light. The stimulus which determines the position of the leaves is still the same, since the light is still at right angles to the surface of the leaf. Experiments planned after this type have been carried out on several plants with various results, as will be shown in detail.

Definition of Terms.

Light parallel to axis.—In describing the fundamental experiment I spoke of the direction of the light as parallel to the axis of the klinostat. In the actual experiments the klinostat stood close to a window, so that at any given moment the light struck the plants on the klinostat obliquely; but as the plant was in continuous rotation about an axis perpendicular to the panes of glass in the window, it is obvious that the light would be practically parallel to the axis.

Let x and y , fig. 3, be the cotyledons of a seedling plant (with hypocotyl h) growing in a box of earth, B , which is fixed to the end of the spindle of the klinostat kk . Let the arrow 1 in fig. 3 represent the direction of the light striking the leaf x ; now let the klinostat rotate through half a turn, so that x is downwards, fig. 4, and now the arrow 2 will represent the direction of the light; so that x will be equally exposed to light in the direction of the two arrows 1 and 2 in fig. 4, the resultant being

* This term has been proposed, in 'The Power of Movement in Plants,' as more convenient.

Fig. 3.

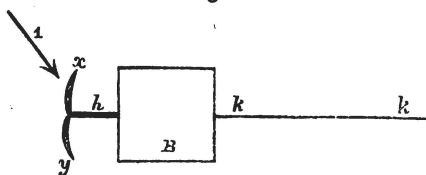


Fig. 4.

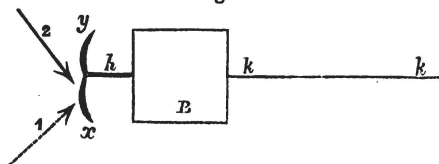


Diagram illustrating the rotation of a plant on the klinostat.

$k k$, the spindle of the klinostat; B , the box in which the seedling grows; h , the hypocotyl of seedling; x and y , its cotyledons.

Fig. 4 represents the change which occurs after the klinostat has rotated through half a turn. The arrows show the direction of light (see text).

In this and all subsequent drawings where $k k$ and B occur, the plane of the paper represents a vertical plane; the plane of the table on which the klinostat stands would therefore be at right angles to the plane of the paper.

equivalent to illumination parallel to the axis of rotation. In the greater number of experiments the klinostat was placed close to a (north) window, outside which a large (92 × 92 centims.) oblique mirror was fixed, so as to reflect as much light as possible horizontally into the room. When seedling radishes or cabbages, which are highly sensitive to lateral light, are placed on the klinostat in the position shown in figs. 3 and 4, the hypocotyls continue to grow parallel to the axis of rotation, showing that the efficient light is practically parallel to that axis. And in this sense I shall use the expression "*light parallel to axis of rotation.*"

Zenith position.—The position shown in figs. 3 and 4 is therefore equivalent to what would be illumination from above if the plant were growing in the normal position. I shall therefore call this position (when the axis of the plant is parallel both to the axis of rotation and to the incident light) the "*zenith position.*" If the under surfaces of the leaves are illuminated while the axis of the plant is parallel to the axis of rotation and to the light, the plant is said to be in the *nadir* position.

Lateral position.—The position shown in fig. 5, in which the spindle of the klinostat is still parallel to the incident light, but the axis of the plant is perpendicular to the axis of rotation, is equivalent to a strictly lateral illumination if the plant were not on the klinostat, and is called the “*lateral position.*”

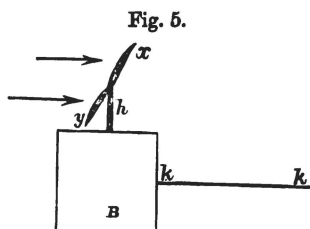


Diagram illustrating the “lateral position.”

k k, spindle of klinostat; *B*, box; *h*, hypocotyl; *x, y*, cotyledons; the arrows give the direction of incident light.

The other possible positions are when the axis of the plant is either parallel or perpendicular to the axis of rotation, and the axis of rotation is perpendicular to the incident light. These are the positions in which, as Sachs has shown, geotropic and helio-
tropic curvatures are both excluded.

Fig. 6.

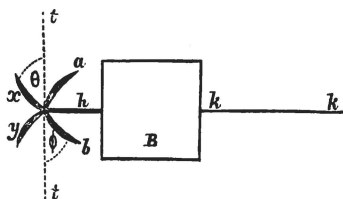


Diagram illustrative of the terms “transverse plane” &c.

k k, *B*, *h*, as in fig. 5; *t t*, the transverse plane; *a, b*, cotyledons making an angle ϕ behind the plane *t t*; *x, y*, cotyledons making an angle θ in front of *t t*.

Transverse plane is the plane at right angles to the axis of the plant. In fig. 6, if *h* is the hypocotyl of a seedling plant, *t t* is the transverse plane. If the cotyledons are bent back towards the stem of the plant as shown at *a* and *b*, then they are said to be *behind* the transverse plane. The cotyledons *x* and *y* are *in front* of the transverse plane. All angles in front of the trans-

verse plane are written with a + sign, those behind it with a - sign. When the plant is growing the right way up, not in the klinostat, I have given the angles as above and below the horizon, which in this case of course coincides with the transverse plane.

Diaheliotropic plane.—The expression diaheliotropism has been used by my father (*op. cit.* p. 438) as a more convenient term than any equivalent of the German "*Transversal-Heliotropismus*," to mean the power possessed by leaves of placing themselves "more or less transversely to the light." In accordance with this terminology, I shall call the plane at right angles to the incident light the *diaheliotropic plane*; and leaves in this plane may be said to be in the *diaheliotropic position*.

Upper and lower.—These terms applied to leaves mean, of course, the morphologically upper and lower sides.

Normal and inverse positions.—When the plant is not on the klinostat, but growing naturally, it is said to be in the normal position when the axis of the plant is vertical and the stem above the root. If the plant is upside down with its axis vertical, it is said to be in the *inverse position*.

Experiments with Ranunculus Ficaria.

These plants were especially well adapted for my experiments, being excessively common, and obtainable at an early period of the year, when many plants refuse to flourish properly. Moreover they grow healthily indoors under the conditions to which it was necessary to subject them. The method which I adopted consisted in wrapping the roots in damp cotton-wool, and covering this with an envelope of sheet india-rubber. Under these conditions the plants remained perfectly healthy, and put out numerous young leaves. The roots of the plant could then be tied on to a large pin; and this could then be fixed in various positions into a cork disk attached to the klinostat; and thus the plant could be illuminated from above, or below, or laterally, as might be desired. In other experiments, not made on the klinostat, the plants were fixed to the cork lining of the cover of a jar which was partly filled with water. They were thus cultivated in damp air, in the manner employed by Sachs in his experiments on bean-roots. In other cases the plants were grown with their roots in vessels of water. Lastly, other plants were simply grown in flower-pots.

Frank*, in his 'Wagerechte Richtung von Pflanzentheilen,' pp. 45, 46, speaks of the leaves of *R. Ficaria*, in common with a number of other radical leaves, as tending to place themselves at right angles to the light when laterally illuminated; the leaves which point away from the light rising up, while those directed towards it sink, so that both approach the diaheliotropic plane.

It was necessary to convince myself that plants indoors placed close to a window receive enough light to cause the leaves to be approximately at right angles to the incident light.

Experiment 1.—

TABLE I.

Date.	Leaf i.	Leaf ii.
	Lamina	Lamina
March 27, 9.20 A.M.	+15 ^o †	+15 ^o
March 28, 2.30 P.M.	+30	+20
March 30	- 6	+50
April 2	-30	+40

A plant whose leaves i. and ii. were both 15° above the horizon was placed, March 27th, so that the underside of i. was towards the light; its position was close to a window, so that the illumination was oblique from above. It will be seen that i. ultimately curved downwards and ii. upwards, the movement in both cases being such as to improve the illumination—that is, to make the leaves more nearly at right angles to the light.

Experiment 2.—April 17th, 4 P.M. A plant, whose leaves were pressing epinastically against the ground, was dug up; and on being freed from the resistance of the soil, the leaves, as is usually the case, sprung back so as to point vertically downwards‡. The plant was then fixed on the klinostat in the "zenith position" (see p. 427); so that the leaves pointed directly away from the light§.

* The fact of the leaves of *R. Ficaria* being apogeotropic in the dark, which Frank mentions (p. 46), I also confirmed. The rising of the leaves occurs long before the leaves are etiolated; so that the experiment is not open to the objection that the plant was in too abnormal circumstances.

† + means in front of the transverse plane, which in this case is equivalent to above the horizon.

‡ *R. Ficaria* exhibits this movement in the same way as *Pinguicula*, *Plantago*, &c.

§ It should be noted that when the plant is in the zenith position, as in this case, the transverse plane coincides with the diaheliotropic plane, so that ±0° means at right angles to the light.

TABLE II.*

Date.	Leaf i.		Leaf ii.		Leaf iii.	
	Lamina.	Petiole.	Lamina.	Petiole.	Lamina.	Petiole.
April 17, } 4 P.M.	-90° ca	-90° ca	-90° ca
April 19, } 8.25 A.M.	+10	+20°	-25	+10°	-20	-20°
April 20, } 8.45 A.M.	± 0	+20	± 0	+15	-12	-22

Thus two of the three leaves had gained the diaheliotropic plane" (that is, became at right angles to the light, see p. 429), and the third leaf (iii.) was only 12° behind that plane.

This experiment proves that the leaves are able to place themselves at right angles to the light without the aid of apogeotropism †. If when the plant is not on the klinostat, but growing in the normal position, the horizontal position is the result of apheliotropism balanced by apogeotropism, then in the above experiment (Exp. 1) the leaves ought to have remained in the position -90° into which epinasty had brought them—that is, the petiole and lamina pointing away from the light.

But it may be objected that epinastically bent leaves tend to recover a normal position independently of the direction of light. The following experiment shows that this is not the case.

Experiment 3.—A plant, whose leaves were bent epinastically backwards, was pinned (April 6th, 3.8 P.M.) inside a tin box; so that the plant was in complete darkness. The positions of the leaves having been noted, the box was fixed to the klinostat so that the axis of the plant was parallel to the axis of rotation.

TABLE III.

Date.	Leaf i.		Leaf ii.		Leaf iii.	
	Lamina.	Petiole.	Lamina.	Petiole.	Lamina.	Petiole.
April 6, } 3.8 P.M.	-50°	-50°	-80°	-80°	-80°	-30°
April 9, } 11.30 A.M.	-85	-50	-95	-70	-90	-35

* Where the measurements were for any reason taken somewhat roughly, *ca.*, abbreviation for "circa" = "about," is added, as in the upper line of Table II.

† *R. Ficaria* sometimes exhibits well-marked sleep movements of the younger leaves, which rise far above the horizon at night. These movements were well

It will be seen that, instead of diminishing, the epinastic curvature increased in all three cases. The tin box was then removed from the klinostat, and placed so that the plant was in the normal position; in a few days leaves i. and ii. (iii. was not noted) were well above the horizon, showing that their behaviour during the rotating was not due to cessation of growth.

It has now been proved that the antagonism of apogeotropism and apheliotropism is not necessary to the plant. But it may be said that, as the leaves are undoubtedly strongly epinastic, the balance may be due to the equality of epinasty on one side, and apogeotropism aided by positive heliotropism on the other. The following experiment disproves this view.

Experiment 4.—A plant was dug up on April 29th, 9.27 A.M., with a large ball of earth attached, so that the leaves were unable to bend backwards. The plant was placed in the dark until the leaves had become somewhat raised above the horizon; it was then placed on the klinostat in the zenith position, so that the leaves were pointing towards the light (April 29th).

TABLE IV.

Date.	Leaf i.	Leaf ii.	Leaf iii.	Leaf iv.
April 29, } 9.27 A.M. }	Lamina +90 ^o <i>chd</i> *	Lamina +24 ^o	Lamina +45 ^o	Lamina +45 ^o
April 30, } 8.30 A.M. }	+45	-23	+20	- 7
May 30, } 3.30 P.M. }	+25	- 5	+ 5	{ twisted sideways.

This (though not a very complete experiment) shows clearly enough that the leaves are not heliotropic, since they all at first curve away from the light; by glancing down any one of the columns headed "Lamina," it will be seen that all the angles become smaller, and in some cases the sign changes. In other

executed when the plant was on the klinostat, showing the existence of power of curving forward. It need hardly be said that I took care not to be deceived by the sleep-movements in estimating the movements with regard to the direction of incident light.

* *chd* means that the organ measured was so much curved that it was only possible to measure the angle made by the chord of its arc with the transverse plane.

words, they bend backwards away from the source of light and towards the diaheliotropic plane (see p. 429). Leaf ii. was 23° behind the diaheliotropic plane on April 30th; but by May 4th this angle had again diminished to -5° .

In the foregoing experiments all the leaves on a given plant have behaved in a similar manner. In the following experiment we have experiments 1 and 3 repeated on a single plant.

Experiment 5.—A plant having been subject to lateral illumination, was placed April 7th, 11.30 A.M., in the zenith position.

TABLE V.

Date.	Leaf i.		Leaf ii.	
	Lamina.	Petiole.	Lamina.	Petiole.
April 7, } 11.30 A.M. } ...	+52°	+52°	-15°	± 0°ca
April 9, } 11 A.M. } ...	+23	+55	-10	-10
April 9, } 11.10 A.M.* } .	+18	+50	- 5	- 5
April 14, } 8.15 A.M. } .	+20	+35	± 0	± 0

It will be seen that on April 9th leaf i., which had been far in front of the diaheliotropic† plane, had begun to move back towards it, and leaf ii. had begun to move from behind the transverse plane also towards it. The plant had to be removed and refixed on the klinostat, so that both leaves were brought 5° nearer the transverse plane. By April 14th the lamina of i. was at about the same angle ($+20^\circ$), though the petiole had bent backwards. Both lamina and petiole of ii. had reached and remained in the diaheliotropic plane.

Experiment 6.—Another similar experiment may be given. A plant which had been exposed for some days to a lateral illumination was (April 2nd, 3.45 P.M.) placed in the zenith position.

* The plant was removed at 11 A.M. April 9, and replaced not exactly in the same position.

† When a plant is in the zenith position, the diaheliotropic plane coincides with the transverse plane.

TABLE VI.

Date.	Leaf i.		Leaf ii.	
	Lamina.	Petiole.	Lamina.	Petiole.
April 2, 3.45 P.M. }	-80°	-25°	+60°	+45° <i>chd</i>
April 5, 4.30 P.M. }	-20	*- 8 <i>chd</i>	+15	+30 <i>chd</i>
April 6, 10.20 A.M. }	-10	- 7 <i>chd</i>	+ 6	+30

* For explanation of *chd*, see note to Table IV.

This experiment shows that one leaf may approach the diaheliotropic plane by moving away from the light, while another on the same plant may do the same by moving towards it. It shows once more that the leaves of *Ranunculus Ficaria* place themselves at right angles to the light when freed from the stimulus of gravitation.

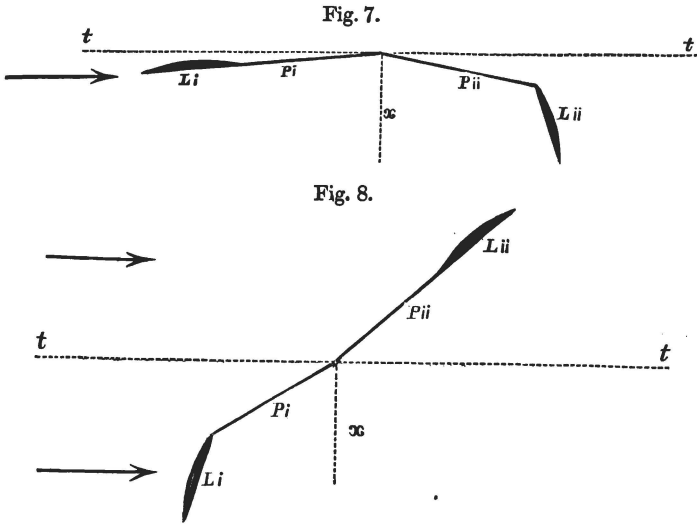
The following experiments show the power possessed by the leaves of adapting themselves to lateral illumination.

Experiment 7.—A plant was placed (March 25th) in the lateral position on the klinostat before a south-west window, where it was shaded as far as possible from direct sunlight in the evening. Leaf i. pointed (*i. e.* the axis of the petiole and of the midrib was directed) nearly towards the window ; ii. pointed away from the window.

TABLE VII.

Date.	Leaf i.		Leaf ii.	
	Lamina.	Petiole.	Lamina.	Petiole.
March 25, 3 P.M. }	- 3°	- 3°	-60° <i>ca</i>	-10°
March 27, 6.15 P.M. }	-45°	+45
March 28, 9.55 A.M. }	-80°	-30°	+42°	+42

Thus leaf i. bent epinastically downwards until the lamina was -80°, which, when the plant is in the *lateral* position, is nearly at right angles to the light. The lamina of leaf ii. moved through more than 100° in its attempt to reach the diaheliotropic plane.



Diagrams illustrating Experiment 7.

Fig. 7 shows the position of the leaves on March 25; fig. 8 on March 28: tt , the transverse plane; x , the axis of the plant; Pi and Pii the petioles of leaves $i.$ and $ii.$; Li and Lii the laminae. The arrows give the direction of the light.

These movements are shown in the diagrams: fig. 7 represents the position of the leaves on March 25th; fig. 8 on March 28th.

Another similar experiment gave somewhat different results. In this case it was the leaf pointing towards the light (corresponding to Li in fig. 7), which failed to place itself exactly in the diaheliotropic plane, though it moved in the right direction.

Experiment 8.—A plant had been grown a short time in the dark, and was not etiolated; the two youngest leaves ($i.$ being the older) had grown up highly inclined above the horizon. It was then (April 2nd) placed on the klinostat in the lateral position with the morphologically under surface of $i.$ facing the light. It will be seen that both leaves began to curve in the epinastic direction, $i.$ curving towards the light and $ii.$ away from it. The positions which the leaves ultimately assumed at the end of the five days during which the experiment lasted are not in the diaheliotropic plane; to reach this, $i.$ would have to move from -15° to -90° , and $ii.$ from $+52^\circ$ to $+90^\circ$. It is unfortunate that the experiment was not continued longer, as the leaves would possibly have become more truly at right angles to the light. It

TABLE VIII.

Date.	Leaf i.		Leaf ii.	
	Lamina.	Petiole.	Lamina.	Petiole.
April 2, 10.52 A.M. }	+90*	+80	+70	+80
April 3, 9.30 A.M. }	+ 5	+63	+57	+74
April 5, 4.25 P.M. }	-12	+22 <i>chd</i>	+25	+40
April 7, 11.21 A.M. }	-15	+20 <i>chd</i>	+52	+52

The angles here given were measured by stopping the klinostat when the plant was in the normal position, and measuring the angles above (+) and below (-) the transverse plane, *tt*. The axis of rotation and the direction of the light being parallel to *tt*, the leaves will be at right angles to the light when leaf i. is at -90° , and leaf ii. at $+90^\circ$.

should be noted that in the case of i. it cannot be the absence of apogeotropism which caused the failure to reach the diaheliotropic plane, since epinasty unopposed by apogeotropism would tend to bring it more easily into that position than if gravitation were acting on it. It is also clear that ii. could not have remained in its final position if it were dependent on apogeotropism; and it is therefore certain that some other force arrested the epinasty of ii. This experiment ought to be compared with the result of absolutely lateral, *i. e.* not oblique, illumination on a plant of *Ranunculus Ficaria* growing under the influence of gravitation in the normal position; but this unfortunately was not done. The results of experiments 7 and 8 show clearly that a leaf can move either in the epinastic or hyponastic directions, and that these movements are produced and checked by the stimulus of light, and without the stimulus of gravitation, in such a way that a plant *tends* to place its leaves at right angles to the light, though it may not perfectly succeed in doing so.

Experiment 9.—These observations show the effect of illuminating the under surfaces of the leaves.

TABLE IX.

Date.	Leaf i.	Leaf ii.
	Lamina.	Lamina.
April 2, 11 A.M.	- 45	- 35
April 5, 4.30 P.M.	-110	-120
April 7	- 90	- 80

On April 2nd, the leaves being 45° and 35° behind the transverse plane, the plant was fixed on the klinostat in the nadir position (p. 427). On April 5th the leaves had curled round in consequence of continuous epinasty, so that the upper surfaces were, as shown in fig. 9, partly illuminated. What was the meaning of the subsequent movement which occurred on April 7th I cannot say; but as it occurred on both leaves, it is perhaps worth giving: the consequence was that the leaves pointed towards the light.

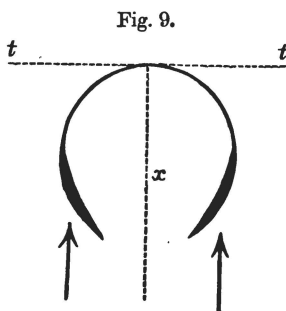


Diagram illustrating the position of the leaves on April 5th, Table IX. The arrows show the direction of the incident light.

Experiments with Beans (Vicia Faba).

A very young plant was transplanted (May 17th) from the open ground and kept under a bell-glass in the greenhouse for a couple of days, during which time it was subjected to a rather dull light from above. On May 19th (10.30 A.M.) two of the leaves were 38° and 41° above the horizon, and the plant was placed on the klinostat in the zenith position. On May 21st, 8.26 A.M., one leaf was $+16^\circ$, the other -2° . The experiment having been made to observe the "sleep" movement of the bean on the klinostat, was not continued any longer. There was evidence of power of bending in front of the transverse plane independently of apogeotropism; that is to say, the plants performed their sleep movements while on the klinostat.

The same experiment was repeated in the autumn. On Oct. 27th, 9.20 A.M., a plant 15 centim. high was removed from a shady part of a cool greenhouse and fixed on the klinostat in the zenith position. The two leaves next below the bud were chosen for observation, i. (the younger leaf) being at $+62^\circ$, ii. at $+15^\circ$. On Oct. 29th, 9.20 A.M., leaf ii. was -15° , on the same day in the evening (6.50 P.M.) at $+12^\circ$, the change being due to "sleep movement,"

and showing the existence of a power of moving towards the front of the transverse plane. On Nov. 4th it was -30° at noon, and it only rose to $+2^\circ$ by 11 P.M.; and on Nov. 6th it was still -25° at 12.50 P.M. Leaf i. was, on Nov. 6th, at 12.50 P.M. at -40° .

These facts show that the leaves of the bean are not able to remain at right angles to light while rotating on the klinostat; but the length of time required to drive back the leaves behind the diaheliotropic plane shows that there is a *tendency* to remain in that plane in spite of the absence of apogeotropism.

In another similar experiment the two leaves under observation were—i. at $+48^\circ$, ii. at $+57^\circ$; and the plant was then (Oct. 29th, 4.5 P.M.) placed in the zenith position at a north window which had no oblique mirror. On Nov. 8th, 10.13 A.M., it was found that the stem had become able to bend so that the leaves did not occupy the same positions with regard to the transverse plane in all parts of the revolution. The two extreme positions were—for leaf i. -8° and -20° , for ii. $+15^\circ$ and 20° . The stem was then tied to a new support, so that (i.) was at -8° , (ii.) at -5° . The same evening (Nov. 8th) the leaves rose to $+31^\circ$ and $+33^\circ$; and next day at 12.30 P.M. they were both at $+12^\circ$. They may therefore fairly be said to be still approximately in the diaheliotropic plane after eleven days on the klinostat. It should be remarked that experiments made at this time are not satisfactory, since the plants do not receive a normal amount of light.

Experiment with the Vegetable Marrow (Cucurbita ovifera).

On Nov. 1st, 10.11 A.M., a seedling whose hypocotyl was 7 centim. in length, was placed in the zenith position on the klinostat in the greenhouse. The cotyledons (called *left* and *right*) were both in front of the transverse plane, *left* $+15^\circ$, *right* $+45^\circ$. On Nov. 10th, 11.20 A.M., the cotyledons were curled backwards epinastically, the main part of the left cotyledon was $+35^\circ$, and the chord made by the right one was at $+20^\circ$. On Nov. 16th, 9.20 A.M., the left cotyledon was $+10^\circ$, the right $+13^\circ$. Thus after fifteen days on the klinostat the cotyledons were approximately at right angles to the light.

Experiment with the Plantain (Plantago media).

A plant growing in a box was placed in dull light for three or four days; and on July 2, 6.40 P.M., the angles made by the chords

from the base to the apex of three leaves were ^{i.} +70°, ^{ii.} +66°, ^{iii.} +34°; the plant was then placed on the klinostat in the zenith position at a north window. It remained in rotation till July 13, 10.30 A.M., when the leaves were at ^{i.} +25°, ^{ii.} +25°, ^{iii.} +30°, showing that ageotropism is not needed to keep the leaves even somewhat in front of the diaheliotropic plane.

Experiments with Cherries.

The plants used in these experiments were seedlings, having woody stems about 10 centim. high; the terminal buds developed into healthy green stems, and produced vigorous leaves in the course of the summer months, during which the experiments were carried on. The plants were grown in earth in the above-mentioned small wooden boxes, or in small flower-pots, which could easily be fitted on to the klinostat.

Some preliminary experiments were made on the behaviour of cherries growing, not on the klinostat, but in the normal position, to ascertain the way in which they react to light and gravity in various combinations*.

When lighted from above, the leaves of the seedling cherry-trees assume a position either a few degrees above or below the horizon. The young leaves are at first highly inclined (+60° or +70°), and bend epinastically down in the natural course of growth until they reach the horizontal position.

Experiment 1 (Table X).—The first experiment was made to find out whether the leaves of the cherry can adapt themselves to lateral illumination. A plant had two leaves opposite to each other, the lamina of leaf i. being 8° above, that of leaf ii. being 70° below the horizon.

TABLE X.

Date.	i. Lamina.	ii. Lamina.
May 20	+ 8	-70
May 24	-40	+53

It was then (May 20th) put close to a window, leaf i. pointing

* Seedling plants of oak and horse-chestnut were also tried, but were not found sufficiently sensitive to gravity or light to be useful plants for the experiments.

towards the light; and it will be seen that i. sunk and ii. rose, both therefore approaching the diaheliotropic plane.

When a cherry-plant is placed in the normal position in the dark, it behaves very differently from *Ranunculus Ficaria*, whose leaves bend apogeotropically upwards when released from the stimulus of vertical light which keeps them horizontal. Under similar conditions the leaves of the cherry remain almost in unaltered positions, and certainly exhibit no such well-marked rising as occurs in *R. Ficaria*, and, according to Frank, in other radicle leaves*.

Experiment 2 (Table XI.).—A plant whose leaves had been epinastically curved downward in a way to be presently described, was placed in a tall cylinder blackened inside, where the light was faint enough to cause seedling-cabbages growing in it to be “drawn up.” This was done on the morning of May 12th, after the angles given below had been measured. It will be seen that by the next evening there had been a considerable rise, owing to apogeotropism; and if the experiment had been on *R. Ficaria*, the apogeotropic movement would have been continued and the leaves would have become nearly vertical. But although the plant was now (May 13th, 6.45 P.M.) put in the dark until May 17th, the leaves did not become much raised above the horizon, and some went slightly below it.

TABLE XI.

Date.	Leaf i.	Leaf ii.	Leaf iii.	Leaf iv.	Leaf v.
May 12, 8.33 A.M.	-32°	-30°	-15°	-47°	-28°
Now (May 12th) placed in dull light.					
May 13, 6.45 P.M.	-27	-11	-4	-0	+27
Now (May 13th) placed in the dark.					
May 17, 10.20 A.M.	-0	+9	+7	-20	-7

In another experiment a plant growing out of doors, and having three approximately horizontal leaves, was placed in the dark in the afternoon of May 4th; it remained in the dark till the morning of May 7th; and the leaves exhibited no rising, but, on the contrary, sank to 12°, 28°, and 25° below the horizon.

* Frank does not mention the cherry; he says that the leaves of trees vary in their behaviour when placed in darkness.

(Experiments with the Klinostat.)

Experiment 3 (Table XII.).—The plant was grown in a small pot out of doors, and was a seedling with a woody stem 9 centim. high, with a bunch of eight leaves budding out at the top and other (older) leaves growing on the woody stem. On April 26th, 4 P.M., it was fixed in the zenith position at a north window, the large mirror being in front as above described. The angles in the following table were generally taken by removing the spindle of the klinostat with the plant attached, and measuring the angles at which the leaves stood when the plant was in the normal position.

TABLE XII.

Date.	i. Lamina.	ii. Lamina.	iii. Lamina.
April 26, 4 P.M. }	+ 3 ^o	+ 15 ^o	+ 18 ^o
April 26... }	After the above measurements were taken, it was placed in the zenith position.		
April 28, 8.20 A.M. }	- 14	- 13	+ 3
April 30, 8.40 A.M. }	- 21	- 25	- 7
May 4, 3.6 P.M. }	- 57	- 70	- 35

It is clear from this experiment that the leaves of the cherry are not able to remain even approximately at right angles to the light when on the klinostat; for it will be seen that all the three leaves curved strongly towards the stem. It appears that, in order to remain in the diaheliotropic plane, some force is wanted to oppose the tendency of the leaves to curve towards the stem. Therefore the cherry behaves in a markedly different manner from *Ranunculus Ficaria*; for the latter is able to keep its leaves in the diaheliotropic plane when grown on the klinostat, and without the assistance of apogeotropism to act as an opposing force.

Experiment 4 (Table XIII.).—The same plant was next, May 4th, 3.10 P.M., removed from the klinostat and placed in the normal position in the dark; and by the following morning (May 5th) the leaves had risen apogeotropically.

TABLE XIII.

Date.	i. Lamina.	ii. Lamina.	iii. Lamina.
May 5, 8.15 A.M. } ...	-20°	-30°	-20°
May 5, 8.15 A.M. } {	After above measurements, plant was fixed on klinostat and kept in the <i>dark</i> .		
May 7, 8.30 A.M. } ...	-50	-75	-30

It was then (May 5th) placed on the klinostat in the dark; and it will be seen that the leaves bent backwards towards the stem; and as this occurred in the dark as well as in the light, it proves that it is epinasty, and not apheliotropism, which causes the movement.

The experiment being continued, gave the same results as those in Experiment 3. When the plant was placed in the normal position, either in light or darkness, the leaves rose and approached the horizontal plane. When again placed on the klinostat in the light in the zenith position, the leaves bent epinastically, so as to become more nearly parallel to the stem, and could again be brought up through the action of apogeotropism by removing the plant from the klinostat and placing it in the normal position.

Other experiments were made with plants in the lateral position. The following may serve as an example.

Experiment 5 (Table XIV.).—The plant with which experiments 3 and 4 were made was placed for a few days (June 27th to 30th) at a window so as to be illuminated obliquely from above.

TABLE XIV.

Date.	i. Lamina.	ii. Lamina.	iii. Lamina.	iv. Lamina.
June 30, 8.47 A.M. } ...	+71°	+ 3°	-29°	+35°
June 30, 8.47 A.M. } {	After the above measurements, the plant was placed on the klinostat in lateral position, so that the same side of the plant was towards the light, as from the 27th to the 30th.			
July 1, 8.20 A.M. } ...	+60	-90	-80	- 8
July 2, 8.30 A.M. } ...	- 5	-90	-90	-25

Leaves Nos. i. and iv. are the ones which pointed away from the light; and if the plant had remained laterally illuminated in

the normal position and not on the klinostat, these two would have remained above the horizon; being, however, on the klinostat and freed from the influence of apogeotropism, they became epinastically bent like the leaf iii., which pointed towards the light, and whose original angle beneath the horizon was much increased; leaf ii. grew out parallel to the glass of the window—that is, halfway between those which pointed towards and those which pointed away from the light; its epinastic curvature was also large*.

Experiment 6 (Table XV.).—In another similar experiment, the leaf which was pointing away from the light, and which was above the horizon, remained in this position when the plant was placed on the klinostat, while the leaf which pointed to the light, and was below the horizon, became strongly curved. The following table gives the angles.

TABLE XV.

Date.	i. Lamina.	ii. Lamina.
May 17, 9.25 A.M....	+55°	- 11°
May 18, 10.30 A.M....	+55	- 65
May 19, 9.40 A.M....	+55	-118

The plant was fixed on the klinostat in the lateral position May 17th, 9.25 A.M., and the angles immediately taken. Leaf i. pointed away from the window, so that its upper surface was directed towards the light. It must not be supposed that the non-curvature of leaf i. resulted from any loss of epinastic power in its petiole; for after the observations recorded on May 19th the plant was removed from the klinostat, and on May 20th it was placed in the normal position, but in a reversed position as regards light; that is, leaf i. was made to point towards the light: under these circumstances it became curved, and was at 8° below the horizon on May 22nd, and 40° beneath it on May 24th.

It seems, therefore, that the stimulus of light was sufficient in

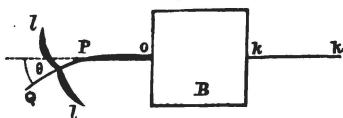
* It is hardly necessary to state that, in all cases where it was necessary, the heliotropic curvatures of the stem were prevented by tying it to a stick fixed in the pot.

this instance to keep the leaf in its previous position without the aid of apogeotropism, which in all the other experiments seemed to be needed as an antagonist to epinasty.

Sources of Error.—Before summing up the results of the experiments with cherries, it will be well to point out a source of error, which, however, does not vitiate the results given. On June 9th, after a cherry-plant had been rotating in the zenith position during my absence from home, since May 26th, it was noticed for the first time that the stem, which had grown much in my absence, was flexible, and bent with the weight of the leaves, so that it did not remain horizontal, but was constantly inclined at from 10° to 15° beneath the horizon in spite of the rotation of the klinostat. Thus the stem was always in the position shown in fig. 10, and consequently the leaves ll , arising from a flexible part of the stem, tended to bend apogeotropically towards the stem. If we make use of Sachs's method of estimating the strength of the geotropic stimulus as in some way proportional to the angle which the organ acted on makes with the line of gravity*, we shall see that the result of the flexibility of the stem is a small constant apogeotropic stimulus, tending to make the leaves bend backwards

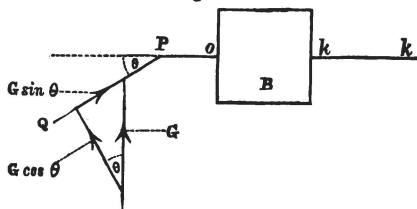
Diagrams illustrating the result of the flexibility of the stem.

Fig. 10.



kk , axis of klinostat; B, box in which plant grows; oPQ , the flexible stem making an angle θ below the horizon.

Fig. 11.



kk , axis of klinostat; B, box in which plant grows; oPQ , stem bent at P so as to make an angle θ below the horizon; G, the hypotenuse of the triangle, represents the force of gravity; $G \cos \theta$ and $G \sin \theta$ the resolved parts of G perpendicular and parallel to the stem PQ .

* 'Arbeiten,' Bd. ii. p. 240.

towards the stem of the plant (fig. 11). According to Sachs's diagram, let $o P Q$ be the stem of the cherry, which bends at the point P so as to make an angle θ beneath the horizon. Now, if the side G of the triangle represent the force of gravity, Sachs assumes that G may be resolved into its components $G \cos \theta$ acting at right angles to the stem $P Q$, and $G \sin \theta$ acting parallel to it. The arrows in the figure are drawn not in the direction in which gravitation acts, but to show in what direction the stem tends to move apogeotropically. Now the force $G \cos \theta$ acting at right angles to the stem will be constantly acting on different sides of the stem because of the rotation of the klinostat. But the force $G \sin \theta$ will act all the time parallel to the stem. If θ is a small angle, $G \sin \theta$ will be a small force. Consequently the plant will be in the same condition as if it were hung upside down (in the inverse position), only that, instead of the whole force of gravity, only a small part of the force will act on it; but the result will be a tendency in the leaves to bend backwards towards the stem; that is to say, this fraction of gravitation will assist epinasty. When I found out the flexibility of the stem, it occurred to me that the result which I had put down to epinasty might really be due to the weakened force of gravity acting on the leaves. I therefore repeated the experiment with plants whose stems were firmly tied to sticks stuck in the flower-pot, and found the results to be the same.

This precautionary experiment was in reality hardly needed; for I had observed the epinastic bending in several cases where there was certainly no flexibility of the stem.

In the case of large and heavy leaves, such as full-grown cherry-leaves, the influence of their weight on their position must be considered.

A plant whose leaves were at the following angles,

i.	ii.	iii.
-6°	$+11^{\circ}$	$+11^{\circ}$,

was put in the inverse position, so that the stem hung vertically down; and now the angles of the leaves were

i.	ii.	iii.
-30°	-45°	-50° .

This result is a consequence of the petiole being adapted to withstand the compression of its lower half when the plant is in the normal position; but the morphologically upper half

of the petiole not being adapted to withstand compression, yields when compressed by the plant being placed in the inverse position. When a cherry-plant is rotating on a klinostat, for instance in the zenith position (as shown in fig. 12), it is clear that there can be no tendency to curvature in the stem caused by the weight of the parts, since, owing to the rotation, there is no reason why the stem should curve in one direction more than another.

Fig. 12.

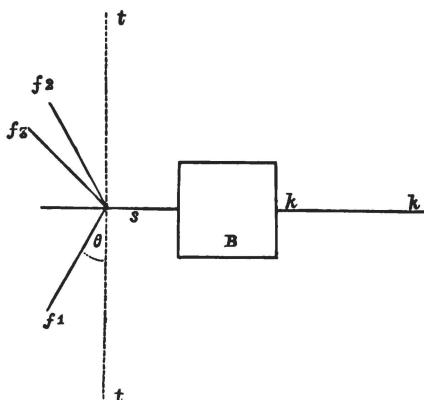


Diagram illustrating the effect of the weight of the leaves.

kk, axis of klinostat; *B*, box in which the stem of the plant grows; *tt*, the transverse plane; *f₁*, a leaf making an angle θ in front; *f₂*, the position *f₁* ought to occupy when the klinostat has made half a rotation; *f₃*, the position which it actually occupies, its weight having made it fall forwards.

The same thing would hold good with the petioles if they had symmetrical powers of resisting weight; but it has been seen that in the inverse position of the plant the compressing strain comes on the morphologically upper half of the petiole, which is normally subject to tension, and not compression. If, then, a leaf is slightly above the horizon when the plant is in the normal position, then, when the plant is placed on the klinostat, a leaf hanging down, such as *f₁*, will retain the original angle θ which it makes with the transverse plane, since the weight of the leaf is still compressing that half of the petiole which is able to bear compression. But when, owing to the rotation, the leaf assumes the position *f₂*, the weight of the leaf will be compressing that half of the petiole which is unable to resist it; consequently the leaf will fall forward into some such position as *f₃*. If the leaves were slightly below the

horizon in the normal position of the plant, the final result on the klinostat would be the same. The observation which fig. 12 represents was as follows. A leaf stood, in the normal position of the plant, 30° above the horizon or transverse plane; when the plant was placed on the klinostat, and the leaf was in the position of f_3 it was 45° in front of the transverse plane ($+45^\circ$); when it was in the position f_1 , it was again $+30^\circ$. It seems clear, therefore, that the weight of the leaf tends during half a rotation to bring the leaf in front of the transverse plane, while during the other half rotation it produces no alteration in the normal position. The whole effect, therefore, of the weight of the leaf is to bring the leaf in front of the transverse plane, a result which is exactly the opposite of the effect which the weight of the leaf has when the plant is in the normal position; for then the weight tends to bring the leaves below the horizon, which would be equivalent to behind the transverse plane. From this it follows that the epinastic curvature of cherry-leaves, when the plant is on the klinostat, is work done *against* the effect of the weight of the leaves, whereas in the normal position epinasty works in conjunction with the effect of the weight of the leaves.

These facts and considerations are given to show that the influence of the flexibility of the stem and unsymmetrical rigidity of the petioles have been taken into consideration as elements in the problem.

Besides the experiments given with various kinds of leaves, a number of experiments were made with the creeping stems of *Lysimachia Nummularia*; but as I was unable to arrive at a definite general result, I have not thought them worth publishing at present.

Conclusion.

The principle on which the facts above given are most explicable is that given by my father in his recently published book*; I mean the principle that the chief movements of plants are modifications of circumnutation.

In the parts of plants which are capable of movement the longitudinal tension is continually changing in such a way that a circumnutating movement is produced essentially the same as the revolving nutation of climbing-plants, though much less in amplitude. In the case of leaves, the movements are chiefly due to changes in the longitudinal tension of the

* 'The Power of Movement in Plants,' 1880.

upper and lower halves of the petiole ; so that the circumnutation of a leaf consists chiefly of alternate hypo- and epinastic movements ; a leaf, therefore, which appears to be stationary in the horizontal position is in reality constantly oscillating up and down. Circumnutation is regulated by stimuli ; it is only when an organ is in its normal position with regard to external forces (light, gravitation, &c.), that circumnutation remains in a state of equilibrium, and the oscillations are so equalized that the mean position of the organ remains the same. If the organ is displaced, the altered stimuli of the external forces act on the circumnutation and bring back the organ to the position of equilibrium. If a seedling plant is lighted from above, and therefore growing vertically upwards, its apex will be oscillating about the vertical line. If the illumination becomes lateral, the plant will bend heliotropically, owing to the exaggeration of the oscillations towards the light, and the diminution of those away from it. In the same way, if the hypocotyl is prevented from bending, the cotyledons adjust themselves to the lateral light by a similar kind of modified circumnutation. The change of position which occurs under these circumstances is a rising of one cotyledon and a sinking of the other. The rising is usually considered to be an apogeotropic, and the sinking an epinastic curvature. This is not necessarily the case. Both rise and fall are more properly to be defined as exaggerations of circumnutating movements in these two directions, due to the stimulus of light.

The above experiments (especially those with *Ranunculus Ficaria*) support this view, since they show that there are powers of movement residing in the petiole which are under the control of the light-stimulus, so that the leaves can bend either towards or from the source of light, in order to reach the diaheliotropic plane. Besides light, other stimuli can alter the circumnutation of leaves ; their movements are affected by gravitation and by the internal impulses which give rise to epinasty and hyponasty. We may have three forces acting on the leaves—the epinastic stimulus, and those of gravitation and light. If the sensitiveness to light is great, the leaf will be able to obey this stimulus in spite of disturbances, such as the loss of the gravitation-stimulus. This is what occurs with *R. Ficaria*, with *Plantago*, and the vegetable marrow (*Cucurbita ovifera*). But in the case of the cherry the light-stimulus is not strong enough ; the plant, when growing normally, trusts to the opposing forces of epinasty and apogeotropism to produce an approximate balance, the final

result being determined by the light-stimulus. Therefore, when the plant is on the klinostat, where the balance between epinasty and apogeotropism is destroyed, the light-stimulus is not strong enough to keep the leaves in the diaheliotropic plane.

The cases such as that of the bean seem to be intermediate between those of *R. Ficaria* and of the cherry. There is evidence that the leaves can remain for a considerable time approximately at right angles to the light without the help of gravitation; but ultimately they may be forced by epinasty to relinquish the diaheliotropic plane.

Thus the result of the experiments with the klinostat is, on the whole, to confirm the view published in 'The Movements of Plants'*, that the power which leaves have of placing themselves at right angles to the incident light is due to a specialized sensitiveness to light—diaheliotropism, which is able to regulate or govern the action of other external forces such as gravitation, or of internal forces such as epinasty.

APPENDIX on the Klinostat used in the above Experiments, made after the design of Horace Darwin.

The klinostat † used in my experiments differs in construction from that of Professor Sachs, which I had the advantage of seeing in action in his laboratory. The principle on which my klinostats are constructed is entirely due to my brother, Horace Darwin; and they have been found to answer so admirably that a detailed description of the instrument may not be out of place ‡.

The spindle of the klinostat (that is, the axis of rotation about which the plant turns) does not form an integral part of the clock which supplies the motive power, but is merely connected with the clock by a loop of silk passing round two pulleys, one on the

* Pp. 438-444.

† The klinostat used by John Hunter (*loc. cit.*) was made on the principle of a water-clock. The beans which were used in his experiment were placed in a basket filled with earth; this was attached to a straight rod serving as a spindle, which was supported at either end by a notch in the rim of a large tub filled with water, which flowed slowly out through a minute hole close to the bottom of the tub. The rotation was communicated by a piece of string wrapped round the basket; to the free end of the string a floating weight was fastened; and as the weight sank the basket rotated, at the rate of about one revolution in eight hours.

‡ The instruments were made by the Cambridge Scientific-Instrument Company, 18 Pantou Street, Cambridge.

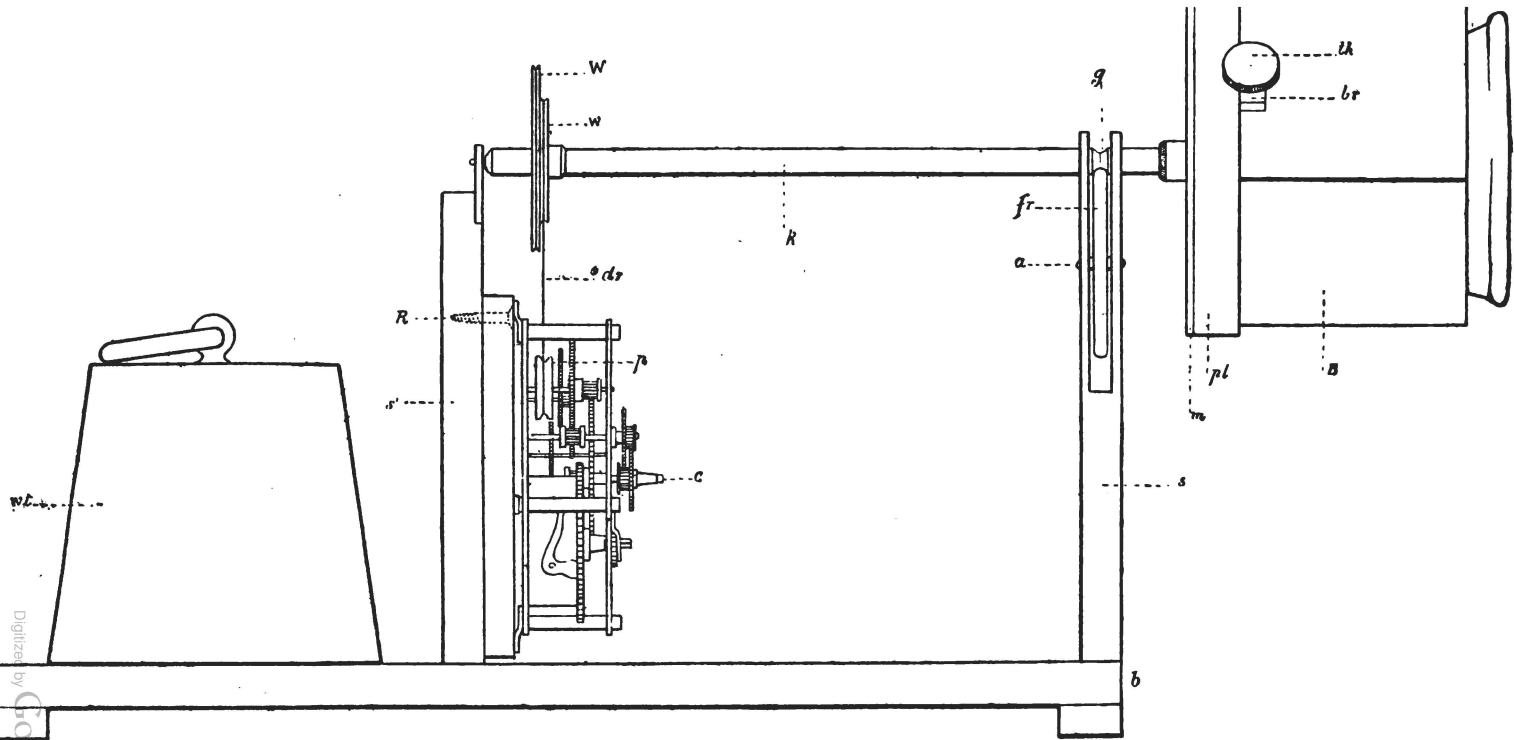


Fig. 13.—Diagram of the Klinostat, reduced, and exhibited in profile.

b *b*, the board on which the instrument stands; *wt*, weight used to counterbalance the weight of the plant; *s*, *s'*, the supports for the bearings; *k*, the spindle; *B*, the box in which the plant grows, or in which a flower-pot may be fixed, as here shown; *pl*, the wooden disk to which *B* is fixed; *m*, the metal plate shown in fig. 14 (*m*); *br*, one of two small blocks of brass between which *B* is fixed by means of a thumb-screw; *th*, thumb-screw; *W*, *w*, grooved pulleys fixed to the spindle; *p*, the pulley attached to the arbor of a wheel of the clock; *dr*, driving-cord passing round *p* and *W* or *w*; *c*, the clock; *R*, the screw on which the clock rotates in a vertical plane; *g*, a groove in *k* which rests on the friction-wheel; *fr*, the friction-wheel; *a*, its axle.

spindle of the klinostat, the other on the arbor of one of the clock-wheels. This principle has several advantages. The spindle can be instantly put out of gear by slackening the silk; the plant under observation can be at once removed without interfering with the clockwork. Another good point in the construction of the klinostat is that the plant is fixed to the free end of the spindle, which projects beyond the bearings, instead of in the middle; the shading* of the plants, which occurs if the plants are fixed to the middle of the spindle, can thus be avoided. As the plant is connected with the motive power by a spindle (*k*, fig. 13) only a centimeter in diameter, it can be covered with a properly constructed glass case, by which the air in its neighbourhood can be kept damp, while the clockwork will be in the dry air of the room. By means of a like arrangement I have kept the klinostat going for many weeks out of doors, the clockwork being in a box, the plant exposed to the open air. But the special advantage of my brother's design is the device by which the centre of gravity of the plant can be made to coincide with the axis of rotation of the machine, so that a very considerable weight can be easily driven by the clock. The box in which the plants are grown, or in which a flower-pot may be easily fixed, is shown at B (fig. 13). By means of a thumb-screw *th* the box can be attached to the wooden plate *pl*, which in its turn is fixed to the strong steel spindle (10 millim. diameter) *k'*, which forms the axis of rotation of the machine. The box is a cube, and can therefore be fixed in two positions, so that the axis of the plant may be either parallel or perpendicular to the axis of rotation (see fig. 17). The spindle *k* turns at one end in a hole in a piece of brass plate at the upper end of the wooden pillar or support *s'*. The other point of support of the spindle is supplied by the brass friction-roller *fr*, which turns in a simple slot in the wooden support *s*, the spindle being grooved at *g* to fit the wheel. The two supports *s* and *s'* are fixed, 25·5 centim. apart, in the wooden board *bb*, 40 centims. long. The board *bb* projects beyond the support *s* to give room for a heavy weight *wt*, which may be used to counterbalance the weight of the plant if required. The driving-force is supplied by a common American watch-action clock *c*, on one of whose smaller wheel-arbors a grooved pulley *p* is fixed. The pulley on the clock being then con-

* Sachs, *loc. cit.* p. 220.

nected with either of the grooved pulleys *W* or *w*, by means of a driving-belt of silk; the spindle of the klinostat can be kept in rotation, either at the rate of one revolution in 20 minutes, or of one revolution in half an hour.

Fig. 14.

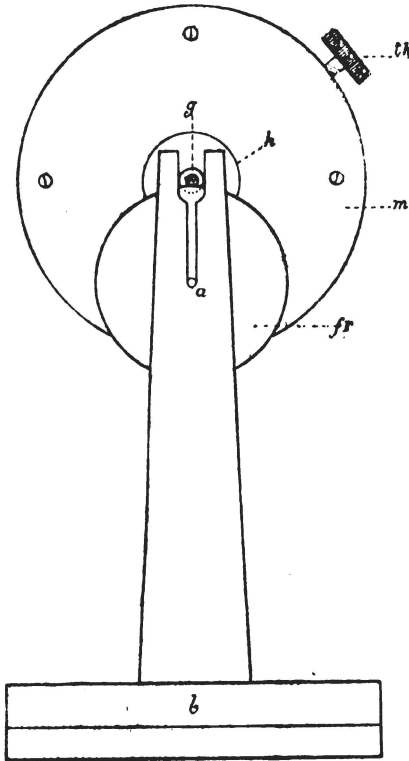


Fig. 14.—Elevation of the support, *s*, &c., in a plane at right angles to that of fig. 13, showing the mode of bearing on the friction-wheel. The spindle with its groove, *g*, is seen in section. Lettering as in fig. 13, with the exception of *h*, which is the edge of the hole in *m*, and within which is seen the disk (*d* in fig. 16) which serves to clamp the spindle in any eccentric position desired.

When a plant growing in the box is fixed on the klinostat, it hardly ever happens that the centre of gravity of the weight coincides with the axis of rotation, so that the clock has to work unequally in different parts of the rotation; and if this inequality in the distribution of the weight is at all large, the clock stops altogether. But the klinostat devised by my brother has an arrangement by which the position of the weight can be altered until its centre of gravity coincides with the axis of rotation.

Fig. 15.

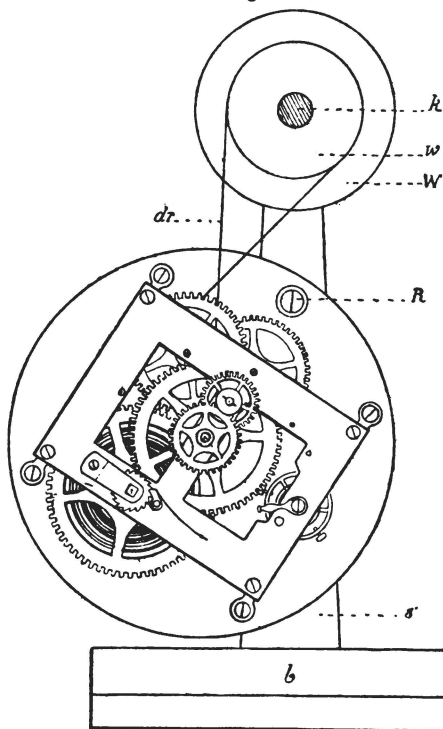
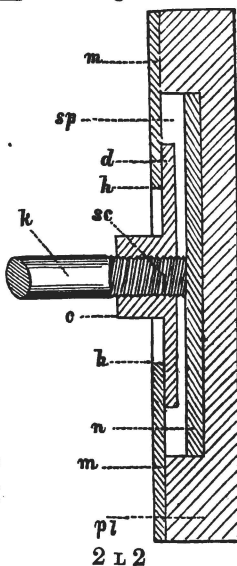


Fig. 15.—Elevation of the support, *s'*, &c. in the plane at right angles to fig. 13, to show the pulleys (*W*, *w*), the clock, and driving-cord. Lettering as in fig. 13.

This arrangement is shown in section in fig. 16. The end of the spindle *k* terminates in a screw *sc*, which passes through the boss *c* and the disk-shaped plate *d* to which *d* is united. As long as the end of the spindle does not press against the brass plate *n*, the disk (carrying with it the spindle) can slide about in any direction parallel to *n* in a cylindrical cavity *sp* sunk in the wooden plate *pl*, of which the floor is formed by a brass plate *n*, and the roof by the plate *m*. The latter plate is firmly attached at its circumference to the wooden disk *pl*, and is pierced in the centre by the hole *h h*. The edges of this hole (*h h*) will thus limit the amount of sliding

Fig. 16.



of the disk d in the space sp ; and 4 centim. is in practice found to be sufficient for the diameter of hh . If now the screw sc is made to project through the disk and press against n , the disk will be forced against the fixed plate m ; and by this means the spindle can be secured in an eccentric position; and thus the centre of gravity of the box and plant can be brought into the axis of rotation. This is practically managed in a simple manner. The screw is loosened just enough to allow the disk d to be moved by the application of a little force, and yet to support the weight of the box without allowing any slipping to occur. The plant is allowed to assume its natural position, which will be with the heaviest side downwards; the box is then lifted by a hand placed under it, so that the groove g no longer touches the friction-roller, and then the upper surface of the boss c (fig. 16) is struck gently with a hammer in a vertical direction. This displaces the disk d slightly in the right direction; the spindle is then replaced on the wheel, and its state of balance is again tested by giving it a slight rotation with the hand; if it still has a tendency to come to rest in a particular position, the vertical blows with the hammer must be repeated until, when the spindle is made to rotate, it has no marked tendency to come to rest in one position more than another.

Fig. 17.

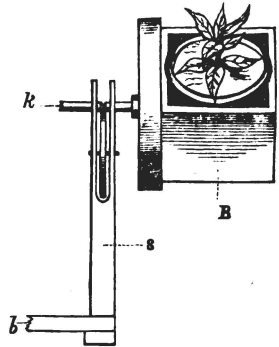


Fig. 17.—Elevation of part of the klinostat in the same plane as fig. 13, showing the arrangement by which a plant can be fixed so that its axis is perpendicular to the axis of rotation instead of parallel as in fig. 13. B, box with flower-pot and plant; k , spindle; b , portion of board on which instrument stands; s , the support.

A few small points connected with the practical working of the instrument may be mentioned. The clock is fixed to a wooden disk, and this is fixed to the support s' by a screw R passing through the disk at a point close to its circumference (see fig. 15). Thus the clock can rotate in a vertical plane, and can be fixed in any desired position by means of the screw. It is by this device that the driving-belt of silk passing round p and w or W can be rendered tighter or slacker with great ease; and a little experience soon shows the observer the necessary degree of tension. If the spindle has been removed from its bearings, it is useful to

know that before it is replaced and the driving-silk readjusted the clock should always be stopped, which may be done by inserting a heavy bit of wire into the balance-wheel, the other end of the wire resting on the board *bb*. If this is not done, two accidents may occur, either the silk may get entangled in the teeth of the wheels, or the clock may be forcibly stopped by touching one of the wheels in such a way that escapement becomes fixed; and this never happens when the balance-wheel is stopped as above described.

With this form of klinostat I have easily been able to keep a box of earth and a plant weighing 1000 grams in constant rotation with the certainty that it will not stop. By gearing a stronger clock to the driving-wheels *W* or *w*, a very much heavier weight could be easily driven.

On a Proliferous Condition of *Verbascum nigrum*, L.
By the Rev. GEORGE HENSLow, M.A., F.L.S., F.G.S.

[Read November 18, 1880.]

(PLATES XVI., XVII.)

THE specimen to be described * was received from Mr. Marshall of Ely, and agrees very closely in its malformations with a monstrous condition of *Lysimachia Ephemera*, L., described by Baillon (*Adansonia*, t. iii. p. 310, pl. iv.). As in the latter, there are differences between the malformed leaves on the lower and upper parts, respectively, of the inflorescence. Thus the terminal portion is much more diffuse than the lower part, while the central stem bears numerous tufts of undeveloped and malformed flowers, amongst which appear the elongated proliferous shoots proceeding from the centres of flowers and occupying the position of the axile placentas.

On the lower part of the stem there were very similar tufts of buds; but the flowers were often larger and mostly of a different character, as will be seen by comparing Plates XVI. and XVII., and as will be explained below.

* Leaving town just as the specimen arrived, and consequently being unable to examine it myself, I am indebted to Mrs. R. C. Barnard for the very careful examination as well as for the illustrations of the uppermost portion of the inflorescence and of the flowers borne by it. The lower part I placed in spirits, and examined on my return.