On Epinasty and Hyponasty.

BY

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With Woodcuts 7 and 8.

THE analysis of the conditions which determine the position assumed by dorsiventral members in the course of their growth is a problem which, though it has engaged the attention of many observers, cannot as yet be regarded as completely solved.

In giving a brief historical outline of these observations, noting the gradual growth of knowledge on the subject, the first which need be considered are those of Frank[1]. As the result of a long series of experiments he came to the conclusion that dorsiventral members possess a peculiar form of irritability to the directive influence of light and of gravity, in virtue of which they place their flat surfaces perpendicularly to the direction of incidence of the rays of light or of the action of gravity, in such wise that the normally superior surface of the member is turned to the light, in the one case, and is uppermost in the other. To these phenomena Frank gave the names Transverse Heliotropism and Geotropism respectively,—names which are now commonly replaced by the less cumbrous terms Diaheliotropism and Diageotropism, suggested by Darwin.

[1] Frank: Die natürliche wagerechte Richtung von Pflanzentheilen, etc., Leipzig, 1870. For a full discussion of this subject see Vines, Lectures on the Physiology of Plants, Cambridge, 1886, Lectures 17 and 18. I purposely omit all reference to observations on the *torsions* of these members, as my own researches only refer to these incidentally.

[Annals of Botany, Vol. III. No. XI. August, 1889.]

It must be pointed out, however, that whilst it appears from Frank's observations that all dorsiventral members are diaheliotropic, it is not equally clear that they are all diageotropic; in fact, this appears to be rather the exception than the rule. Frank, for instance, states that, in most cases, members which are more or less horizontal under normal conditions and when exposed to light, grow erect in darkness in consequence, as he suggests, of negative geotropism. He cites, as examples of this, the creeping shoots of *Lysimachia nummularia*, *Polygonum aviculare*, *Atriplex latifolia*, and other plants, radical leaves, and the thallus of *Marchantia*.

The next paper to be noticed is that of De Vries[1], which consists largely of a criticism of Frank's theory of diaheliotropism and diageotropism. The main contribution which he makes towards a knowledge of the subject is the fact that the growth of the two opposed sides of dorsiventral members is unequal, and that this unequal growth is apparently due entirely to inherent conditions. When the growth of the upper surface is the more active, De Vries terms the member *epinastic*; when that of the lower, *hyponastic*. He observed that, as a rule, leaves are hyponastic at first, becoming epinastic in the latter part of their period of growth.

De Vries' contention, as against Frank, is that the assumption of peculiar forms of heliotropic and geotropic irritability in the case of dorsiventral members, is unnecessary and unwarranted by the facts. He endeavours to show that the various positions assumed by dorsiventral members can be accounted for as being due to various combinations of epinasty, hyponasty, negative or positive heliotropism or geotropism, the weight and balancing of the parts; discarding altogether the idea of diaheliotropism and diageotropism.

In his important paper on orthotropic and plagiotropic members, Sachs[2] touches upon this subject, and his views

[1] De Vries: Ueb. einige Ursachen der Richtung bilateralsymmetrischer Pflanzentheile, Arb. d. bot. Inst. in Würzburg, I, 1874.

[2] Sachs: Ueb. orthotrope und plagiotrope Pflanzentheile, Arb. d. bot. Inst. in Würzburg, II, 1879.

may be gathered from what he says with reference to the thallus of *Marchantia.* The plagiotropism of the thallus of *Marchantia* is, he says, to be ascribed to (negative) geotropism, to positive heliotropism (of the under side), and to the epinasty of the upper side. In the earlier part of his paper he speaks of the negative heliotropism of the thallus, but he explains that this apparent negative heliotropism is in fact the hyponasty of De Vries. Sachs' conclusions, therefore, go to confirm De Vries' dissent from Frank's theory of diaheliotropism.

Wiesner's[1] conclusions may next be briefly stated. He is of opinion that the ultimate position of dorsiventral leaves is the resultant of the opposing forces, negative heliotropism and negative geotropism : the leaf, which at first tends to rise by negative geotropism, is brought into the most favourable light-position by negative heliotropism, and is retained in that position because these conditions of illumination are those which most strongly resist negatively geotropic curvature.

The next paper on the subject, that by F. Darwin[2], is one which marks a distinct advance. By experiments with the clinostat he ascertained that dorsiventral leaves tend to place their normally upper surfaces at right angles to the incident rays of light. The importance of these observations is, that they go far to invalidate De Vries' argument against Frank, inasmuch as they show that the position in question is assumed by dorsiventral leaves under conditions in which gravity, whether as regards geotropic stimulation or the balancing of the parts, is inoperative. The conclusion 'that the power which leaves have of placing themselves at right angles to the incident light is due to a specialised sensitiveness to light—diaheliotropism—which is able to regulate or govern the action of other external forces, such as gravitation, or of internal

[1] Wiesner : Die heliotropischen Erscheinungen im Pflanzenreiche, Denkschr. d. Math.-Naturwiss. Klasse d. K. Akad. d. Wiss. Wien XXXIX, Part 2, p. 58, 1880.

[2] F. Darwin : On the power possessed by leaves of placing themselves at right angles to the direction of incident light. Journal Linnean Society, XVIII, London, 1881. See also 'Movements of Plants,' 1880.

forces, such as epinasty,' is strongly in favour of Frank's views. F. Darwin also confirms Frank's statement that radical leaves are negatively geotropic (apogeotropic), at least in the case of *Ranunculus Ficaria,* and notes also that radical leaves under normal conditions are epinastically pressed against the ground.

Another paper which must be noticed, but which can hardly be regarded as contributing much to the elucidation of the subject, is that of Detmer[1]. From observations on the effect of darkness and light on the expansion of leaves, Detmer came to the conclusion that epinasty is not, as De Vries thought, spontaneous, but is induced by the action of light; that it is what he terms 'a paratonic nutation-phenomenon.' He therefore suggests that the word 'photo-epinasty' should be substituted for 'epinasty.' It may be pointed out that he omits to refer at all to hyponasty; but of course if epinasty is not spontaneous, it is impossible to avoid the inference that the same is true of hyponasty, and the assumption of 'photo-hyponasty' is therefore inevitable, though Detmer does not carry out his views to this logical conclusion.

Vöchting[2] has made some interesting observations on the assumption of the fixed light-position by the leaves of certain Malvaceae, and comes to the somewhat ambiguous conclusion that the hypothesis upon which Frank bases his idea of transverse heliotropism is incorrect, though, as far as the facts go, Frank is on the whole right. With regard to the lamina, Vöchting considers that the effect of light is to bring it into that position in which it receives the maximum of incident rays. With regard to the petiole, it is stated to be negatively geotropic, positively heliotropic, and persistently epinastic in its basal portion.

Finally, there is an important paper by Krabbe[3] in which he arrives at the general conclusion that the light-position of leaves cannot be explained by ascribing it to simple combina-

[1] Detmer: Ueb. Photoepinastie der Blätter, Bot. Zeitg. 1882.

[2] Vöchting: Ueb. die Lichtstellung der Laubblätter. Bot. Zeitg., 1888.

[3] Krabbe: Zur Kenntniss der fixen Lichtlage der Laubblätter. Pringsheim's Jahrb. f. wiss. Bot. XX, Heft 2, 1889.

tions of directive forces, such as heliotropism, epinasty, etc., but is, on the contrary, the expression of a special heliotropic property. He shows that the weight of the leaves does not in any way affect their movements, and ascertains, by clinostat-experiments in darkness on *Phaseolus*, *Dahlia*, *Fuchsia*, and other plants, that when leaves are unaffected by any external directive influences, they exhibit well-marked longitudinal epinasty. It is not necessary to go into all the details of the paper, as they deal chiefly with torsions, a part of the subject into which I do not propose to enter at present. It need only be noted that he considers the leaves of *Dahlia* to be negatively geotropic.

Coming now to my own observations, I must premise that the general method of experiment was arranged, and many of the experiments made, before I was aware of the publication of Krabbe's paper. The object in view was to ascertain (1) whether epinasty and hyponasty are spontaneous movements, or are induced by light or other causes as stated by Detmer; and (2) whether the curvatures of dorsiventral members which, as pointed out in the foregoing historical sketch, have been hitherto ascribed to negative geotropism, are or are not due to this cause. I may at once give the conclusions to which I have been led: (1) Epinasty, and also hyponasty, are not induced, but are spontaneous movements; (2) dorsiventral members, so far as my experiments go, are not negatively geotropic, the movements hitherto ascribed to negative geotropism being due to hyponasty, and altogether independent of the action of gravitation.

The first series of experiments were extremely simple. Detmer based his theory of photo-epinasty on the observations that (1) the cotyledons of seedlings of *Cucurbita* remained closed up, with their upper surfaces in contact, when kept in continuous darkness for ten days, but they at once began to separate when, at this age, the plants were exposed for three to five hours to bright diffuse light; and (2) that the laminae of the primordial leaves of *Phaseolus*, kept in continuous darkness for fourteen days, presented a folded or crumpled appearance, in consequence of hyponastic growth; but after an exposure for three to five hours to bright diffuse light the laminae began to flatten out and to become smooth. In both cases the exposure to light was followed by epinastic growth of the laminae. With the view of testing the accuracy of these statements with regard to the cotyledons of *Cucurbita*, I kept a large number of seedlings of both *C. ovifera* and *C. Pepo* in darkness for twenty days (June 10–30), and I found that in a large majority of cases the cotyledons separated more or less widely, the separation becoming first apparent about the sixth day. They were, however, exposed to feeble light for a few moments, not more frequently than once in twenty-four hours, for the purposes of observation, but this exposure can hardly be taken into account. Similar observations on the primordial leaves of *Phaseolus* proved the accuracy of Detmer's statement that the laminae do not become fully expanded in darkness.

These observations of mine suffice to prove that, in the case of *Cucurbita*, epinastic growth can take place in darkness, and thus, on the matter of fact, Detmer's theory is shown to be untenable. It is open to the further criticism that the phenomena which he describes are capable of another and a simpler explanation. Light certainly promotes the epinastic growth of the leaves in question, but there is no evidence that it initiates this growth; the effect of light is not '*paratonic*,' as Detmer would have it to be, but it is '*phototonic*.' The epinastic growth of the laminae, when exposed to light, is well marked, not because light induces photo-epinasty, but because the leaves are in the epinastic stage of their growth; so that when, under the influence of light, they regain the phototonic condition and resume their growth, that growth is necessarily epinastic.

The second series of experiments were made on plants other than those which Detmer observed, and had as their object the determination of the growth-movements of dorsiventral members when removed either from the directive influence of light alone; or, by means of the clinostat, from that of both light and gravity. The general method of experimentation was the following. Plants were placed in darkness in the normal position, and the effect of these conditions upon the position of the leaves or other dorsiventral members was carefully noted at intervals of generally twenty-four hours. Other similar plants were rotated on the clinostat in darkness, and the effect observed as in the former case. By comparing the behaviour of the members in the two cases, it was possible to draw some conclusions as to the influence of gravitation upon the growth of the members under observation. All the plants were grown in pots ; and, when on the clinostat, were so placed that the long axis of the plant coincided with that of the machine.

It will be convenient to arrange my observations according to the results which I obtained ; that is, in accordance with the more striking epinastic or hyponastic growth.

1. Observations on Epinastic Members.

These observations were all made on dorsiventral foliage-leaves. The following is a typical case. A seedling of *Helianthus annuus*, about 40 cm. high, with four whorls of leaves (generally three leaves in each whorl in the plants used), in addition to the cotyledons and the apical bud, had been grown under normal conditions and fully exposed to light. Hence, at the beginning of the experiment, the leaves were approximately horizontal. The effect of being kept for twenty-four hours in darkness in the normal position was that the leaves of the upper whorls, especially the second and third, showed a strongly marked downward curvature. In the younger leaves this curvature extended throughout the whole length of the leaf from the apex to the insertion ; in the older, but still growing leaves, the curvature was confined to the petiole. The oldest leaves, having ceased to grow showed no change in position.

The remarkable difference in the appearance of the plant, before and after being kept in darkness is shown in the accompanying figures.

The curvature in question is not due to flaccidity of the tissues, for the leaves are fully turgid after their sojourn in darkness, and when an attempt is made to lift them up into the horizontal position they spring back into the recurved

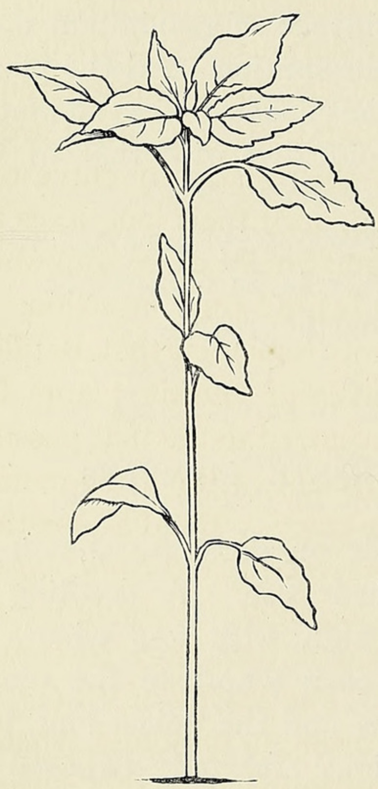

FIG. 7. Normal plant of *Helianthus annuus.*

FIG. 8. Same plant after twenty-four hours in darkness.

position with considerable force. Moreover, the leaves show the same curvature, and in the same time, when (*a*) the plant is rotated on the clinostat in darkness, and (*b*) when the plant is placed upside down in darkness.

On being again exposed to light, the recurved leaves regain the horizontal light-position within twenty-four hours.

Precisely similar results were obtained on repeating these experiments with *Helianthus dentatus*, *H. tuberosus*, *H. pubescens*, *Dahlia variabilis*, *Fuchsia serratifolia*, and *Urtica urens*. The leaves of *Mirabilis Jalapa* behaved in a similar manner, but the curvature was slower and less marked than in the other cases. My observations as to the position assumed in darkness by the leaves of *Dahlia* and *Fuchsia* precisely agree with those of Krabbe, who used these plants in his experiments.

I made more prolonged observations (four days) on *Helianthus dentatus* on the clinostat in darkness. At their first development in the apical bud, the leaves, under these circumstances, are perfectly straight, so that their long axes are in a line with that of the stem; then they gradually curve outwards, throughout their whole length, until their long axes are at right angles to that of the stem, and finally curve backwards till their apices touch the internode behind their insertion.

In making these observations I was reminded that Batalin[1] had observed that the growing leaves of certain plants fall, whilst others rise, at night; and it occurred to me that possibly the former would react under experiment in the same manner as those which I had already observed. Batalin mentions *Impatiens parviflora*, *Polygonum Convolvulus*, and *Sida Napaea*, as plants whose young leaves fall at night. I made experiments with the two former, and found that they reacted in much the same way as *Helianthus*. The leaves of *P. Convolvulus* show this peculiarity when growing in darkness, whether on the clinostat or in the normal position, that, as they become longitudinally recurved, the lamina becomes revolute, curving inwards on both sides towards the under surface of the midrib.

There can be no doubt that these curvatures of the leaves are due to epinasty; either, as in most of the cases, to longitudinal epinasty alone, or, as in the case of *Polygonum Convolvulus*, to both longitudinal and transverse epinasty.

Nor can there be any doubt, in view of the conditions of

[1] Batalin: Ueb. die Ursachen der periodischen Bewegungen der Blumen- und Laubblätter. Flora, 1873.

the experiments, that the epinasty was spontaneous. These observations, taken in conjunction with those on the seedlings of *Cucurbita*, seem to prove conclusively the falsity of Detmer's theory of photo-epinasty.

If any further evidence is required, it is afforded by my observations on *Primula officinalis*, which has proved itself to be most instructive. If a plant be taken which has been growing fully exposed to light, it will be seen that the older radical leaves are more or less nearly horizontal; those next in age, obliquely ascending; and the youngest very nearly, but not quite, vertical. On being placed in darkness in the normal position, the first change to be noticed is that the younger leaves become quite vertical, whilst the older leaves, though still growing, remain horizontal. About the fourth day in darkness it will be observed that the lamina of the youngest leaves is being developed in a revolute manner, whilst, at the same time, they curve outwards throughout their whole length: at the same time the older, but still growing leaves, instead of being horizontal, have become arched, their apices being firmly pressed against the soil. About this time (sixth day) growth ceases, and the positions remain unchanged.

Exactly the same phenomena are exhibited when the plant, instead of being placed in the normal position, is rotated on the clinostat.

The natural interpretation is, that the movement of the youngest leaves into line with the long axis of the plant when first placed in darkness is due to hyponasty, whilst the subsequent curvature outwards, away from this line, is due to epinasty. In other words, the leaves of *Primula* are hyponastic at their first development, becoming subsequently epinastic, at the time when the expansion of the lamina begins, and remaining so until growth ceases.

Somewhat similar results to those recorded of *Primula* were obtained with *Vicia Faba*. At their first development the long axis of the leaf is nearly parallel to that of the stem, the lamina of each leaflet being longitudinally infolded; in other words, the leaf is hyponastic. This position is retained in darkness, both when the plant is in the normal position and when it is rotated on the clinostat. Under normal conditions, the leaves, as they develope, become epinastic ; the petiole sinks, and the laminae of the leaflets flatten out. Leaves in this stage of development show epinastic curvature in darkness, both in the normal position and on the clinostat; but I have never succeeded in observing, in darkness, that transition from the hyponastic to the epinastic growth which is so marked in *Primula*, as the leaves of *Vicia* are apparently incapable of growth for more than a very short period under these circumstances.

2. Observations on Hyponastic Members.

In describing the foregoing observations on *Primula* and *Vicia*, I have assumed, without explanation, that the rising up of the youngest leaves of the former in darkness, and the position taken up by the leaves of the latter at their first development, are due to hyponasty. The only other possible supposition is that gravitation is the active cause. But, inasmuch as these phenomena are equally apparent when the plants are rotated on the clinostat in darkness, it is clear that they cannot be due to gravitation. They are, in fact, spontaneous, and can only be ascribed to the more rapid growth of the lower side of the leaf, that is, to hyponasty.

Still more convincing evidence of the spontaneous nature of hyponasty is, however, forthcoming. As the assumption that dorsiventral leaves are negatively geotropic seems to rest chiefly upon observations made upon radical leaves, I did not content myself with observing only *Primula*, but extended my observations to two other plants, *Plantago media* and *Taraxacum Dens-Leonis*, with the following results.

Plantago media. A plant which had been growing fully exposed to light, the leaves of which were, consequently, expanded horizontally, was kept in darkness in the normal position for seventy-two hours. The young leaves gradually rose up from the horizontal position, the youngest ones becoming erect. At the same time the rising leaves became strongly involute, the lateral margins of the lamina being curved inwards towards the upper surface of the midrib. The older leaves showed marked epinasty.

A similar plant was, at the same time, rotated on the clinostat in darkness for seventy-two hours. The leaves of this plant behaved in precisely the same manner as those of the plant in the normal position.

The leaves of a plant which have risen in consequence of having been kept in darkness, return to the horizontal position in two or three days when exposed to light.

Taraxacum Dens-Leonis. The leaves of this plant behave in a quite similar manner to those of *Plantago*, except that the transverse hyponasty is less marked.

The change of position of the young radical leaves of these plants in the normal position in darkness was described by Frank, and was attributed by him to negative geotropism,—an explanation which seems to have been hitherto accepted without question. The clinostat-experiments, however, prove that this explanation is not in accordance with fact. The movements can only be due to hyponasty, both longitudinal and transverse. These leaves present the peculiarity that the change from the hyponastic to the epinastic phase of growth takes place at a relatively late stage in their development.

Remembering Batalin's observation, to which reference was made above, that certain growing leaves rise at night, such as those of *Chenopodium*, Cabbage, *Polygonum aviculare*, *Stellaria*, *Linum*, etc., I made some observations on two of the plants mentioned by him, namely *P. aviculare* and *Linum usitatissimum.* I found that, when placed in darkness for twenty-four hours, in the normal position, the previously horizontal younger leaves of these plants rose up hyponastically, becoming erect, and that the same effect followed in darkness when the plant was rotated on the clinostat.

A more important observation was made with *Marchantia.* A plant growing in a pot was placed in the normal position in the dark chamber exposed to weak diffuse light entering through a side-window, a mirror being placed behind the plant so as to equalise the illumination on the two sides. Another plant was rotated on the clinostat under the same conditions of illumination. The position of the plant on the clinostat was such that the flat surface of the thallus was at right angles to the long axis of the machine, and that the direction of the incident rays of light was perpendicular to the long axis of the machine, and parallel to the flat surface of the thallus. The same window and mirror illuminated both plants. Exposure to light was considered necessary in view of the probably long duration of the experiment; but it is evident that, under the conditions of the experiment, no heliotropic effect could be induced.

The experiment commenced on July 29, and continued until August 9. In three days the ends of many of the branches of the thallus commenced to curve away from the surface of the soil in both the plant in the normal position and that on the clinostat, and this position was retained and became more marked throughout the duration of the experiment.

It is on this observation and those which precede it that I base the conclusion that the curvatures of dorsiventral members which have hitherto been ascribed to negative geotropism are not due to this cause, but are the expression of an inherent more active growth of the lower side, that is, of hyponasty.

The results which I have obtained establish conclusively that epinasty and hyponasty are important factors in determining the position assumed by growing dorsiventral members; and that therefore no observations on the action of gravity or of light on such members are conclusive unless the hyponastic or epinastic state of the member has been previously ascertained and duly taken into account.

With this I conclude the account of my principal observations, and it only remains to briefly discuss the various forces which determine, in the plants which I have observed, the position assumed by the dorsiventral members under normal conditions, and to mention one or two experiments on geotropism which I have made by the way.

Taking first the case of the epinastic members, it may be assumed that there are three forces at work; their own epinasty, the action of light, and the action of gravitation. The tendency of epinasty, in the case of leaves, is to bring the lamina into the vertical plane, the apex being directed downwards.

When an epinastically recurved leaf is exposed to vertical light of sufficient intensity, the effect is to raise the lamina into the horizontal plane so that its upper surface is at right angles to the direction of the incident rays. From this I conclude that the lamina is diaheliotropic. Doubtless the influence of gravitation promotes the assumption of the horizontal position; but it is clear that this is mainly due to the action of light, since gravitation is incapable of preventing epinastic curvature in darkness when the plant is in the normal position.

With regard to the influence of gravitation in determining the position of epinastic dorsiventral members, I inferred from my observations which prove that hyponastic members are not negatively heliotropic, that this is true also of epinastic members; in fact, that no dorsiventral member is negatively geotropic. Though I do not claim to have fully investigated the matter, I have made some observations on epinastic members which tend to prove, not only that they are not negatively geotropic, but that they are diageotropic. The following case will explain the mode of experimentation. A young plant of *Helianthus annuus*, growing in a pot, its stem being firmly secured to a stick to prevent geotropic curvature, was placed in darkness with its long axis horizontal. In this position of the stem, the two youngest leaves were situated, the one on the upper surface, the other on the lower surface of the horizontal stem, the apex of the former pointing vertically upwards, that of the latter vertically downwards. The phyllotaxis of *Helianthus* being opposite and decussate, the two leaves of the next whorl were situated one on each side of the horizontal stem, their surfaces being now vertical. By the fourth day of the experiment the following changes in position had been effected. Of the youngest pair of leaves, the upper had recurved so that its upper surface had come to be nearly horizontal; the lower had only slightly changed its position, having risen somewhat out of the vertical plane in the acropetal direction. The two leaves of the second whorl both exhibited marked epinastic curvature, and their petioles had undergone torsion through nearly a right angle, so that, in both, the upper surface of the lamina was directed upwards, though it was not flat on account of the epinastic curvature. Similar results were obtained with *H. pubescens* and with *Dahlia variabilis.*

It must be borne in mind, in the interpretation of these facts, that the leaves were strongly epinastic, and there can be no doubt that the changes in position were due partly to this cause and partly to the action of gravitation. If, now, an explanation be attempted on the assumption that the leaves are negatively geotropic, it will be found to be impossible. Taking first the youngest pair of leaves, the upper leaf, being vertical, is in the position of stable equilibrium as regards negative geotropism; hence its curvature into the horizontal plane must be due to epinasty acting powerfully in opposition to negative geotropism. With regard to the lower leaf, inasmuch as it could hardly have been absolutely vertical, it is probable, on the theory of its negative geotropism, that gravitation tended to raise it into precisely the opposite position to that in which it was originally placed, and this effect was to some extent realized in the observed change of position. In this case, then, negative geotropism succeeded in overcoming epinasty. But this conclusion is in direct contradiction to that arrived at with regard to the upper leaf. Inasmuch as the two leaves belonged to the same whorl, they must have been in the same epinastic stage of growth; hence, it is impossible to assume that in the one case epinasty overcame negative geotropism, whilst in the other negative geotropism overcame epinasty.

The explanation which I would offer as a substitute is based on the assumption that the leaves are diageotropic; that is to say, that their reaction to the action of gravitation is to place themselves in the horizontal plane with their morphologically upper surfaces facing the zenith. From this point of view, the change in position of the upper youngest leaf is ascribed to epinasty acting together with diageotropism; and the change in position of the lower youngest leaf to diageotropism acting in opposition to epinasty. It may be objected with reference to this last statement, that it is inconsistent with the fact which I have brought prominently forward, that the young leaves of *Helianthus* show marked epinastic recurvature in darkness, which can only be explained on the assumption that here epinasty has overcome diageotropism. This objection is, however, without weight. The two statements are found to be perfectly consistent when it is remembered that the effect of gravitation depends upon the angle at which it acts. Now, in the case of a plant in the normal position, the effect of diageotropism on the horizontal leaf is at its minimum, increasing as the leaf-surface forms a larger angle with the horizontal, and attaining its maximum when the leaf points vertically downwards. Hence a leaf, under such conditions, sinks below the horizontal because epinasty is more powerful than diageotropism in that position, and continues to do so until a position of equilibrium is reached. In the special case now under consideration, the leaf, pointing vertically downwards, is in that position in which diageotropism exerts its greatest influence, an influence, as it appears, sufficiently strong to prevent epinastic curvature and even to raise the lamina somewhat towards the horizontal position. The phenomena presented by the two youngest leaves can, therefore, be explained more satisfactorily on the theory of diageotropism than on that of negative geotropism. The phenomena presented by the leaves of the second whorl, cannot be at all explained on the theory of negative geotropism, but only on that of diageotropism; this is sufficiently obvious to render any detailed discussion unnecessary.

I may note, in passing, that Krabbe assumes that the leaf of *Dahlia* is negatively geotropic, and he does so for the following reason. He observed that the leaf does not exhibit epinastic curvature when in the normal position and exposed to light, whereas it does exhibit this curvature when exposed to light on the clinostat. From this he concludes that the heliotropic effect of light is insufficient, by itself, to counteract epinasty; and that the horizontal position of the leaf under normal conditions is due to the combined influence of light and of gravitation in opposition to epinasty, the latter, as he suggests, producing a negatively geotropic effect. The facts do not, however, justify this conclusion. They may be accounted for on the assumption that the light to which Krabbe exposed the plant in his clinostat-experiments was not sufficiently intense to induce the full heliotropic effect. But apart from this assumption, his observations only prove that gravitation has some effect, though the facts give no indication of the nature of the effect. In accordance with what I have stated above, I believe the effect of gravitation in *Dahlia* to be diageotropic, and I would point out that Krabbe's observation can be explained quite satisfactorily from this point of view.

With regard to hyponastic members, it may be assumed that here also there are three forces which determine their position: their own hyponasty; the action of light; the action of gravitation. The tendency of hyponasty is to raise the member so that its long axis approaches the vertical. The effect of light is, as in epinastic members also, to bring and retain the member in the horizontal position—that is, it is, I believe, diaheliotropic. The effect of gravitation is, as I have clearly proved, certainly not to produce negatively geotropic curvature, but is probably diageotropic.

I have made some experiments on hyponastic members, similar to those on epinastic members described above, with the object of ascertaining whether or not they are diageotropic. A normal plant of *Plantago media*, growing in a pot, was placed in darkness with its long axis horizontal. Of the numerous leaves, the seven youngest showed themselves to be hyponastic by rising away from the surface of the soil; the remaining leaves simply showed well-marked epinastic curvature and nothing more. The seven youngest leaves not only rose hyponastically, but they gradually assumed different positions according to their relation to the centre or axis of the plant. On the second day of the experiment—that is, after forty-eight hours in the horizontal position in darkness—their relative positions were as follows, the numbers used indicating the relative age of the leaves, No. 1. being the youngest. Leaf 1, inserted vertically below the axis, showed strong hyponastic curvature so that it curved completely over the growing-point; leaf 6, inserted almost directly beneath leaf 1, had curved upwards so that its upper surface was nearly horizontal; leaves 2, 5, and 7, were inserted above the axis, leaf 2 nearly vertically above it, leaf 5 obliquely on the left side, leaf 7 obliquely on the right side; these three leaves were slightly raised from the soil, but showed no other change of position; leaves 3 and 4 were inserted laterally on the axis, almost opposite each other, and showed, in addition to hyponastic curvature, torsion through nearly 90°, so that a part of their upper surfaces faced the zenith. On continuing the observation twenty-four hours longer, the only change observable was that leaf 6 had risen slightly above the horizontal, and that the youngest leaves began to be involute in consequence of transverse hyponasty. As I have already proved that the young leaves of *Plantago* are not negatively geotropic, it is useless to attempt an explanation of these phenomena based on the assumption of negative geotropism: it is only necessary to ascertain whether or not they are explicable on the assumption of diageotropism. Taking first the leaves inserted below the axis, the position of leaf 1 can be satisfactorily accounted for by supposing that, at this early age, hyponasty is so powerful that it altogether neutralises diageotropism: in accordance with this, the position of leaf 6 is due to diminished force of hyponasty, a consequence of its being older than leaf 1, which can only so far counteract diageotropism as to raise the lamina slightly above the horizontal. Coming next to the leaves inserted above the axis, leaves 2, 5, and 7, the explanation becomes more difficult. In the case of leaf 2, hyponasty must be strong, and yet the only effect is the raising of the leaf slightly from the surface of the soil, when it might have been expected to cause the leaf to curve over downwards in the same way as it caused leaf 1 to curve over upwards. I believe the cause of the different hyponastic effect in these two leaves, of nearly the same age, is their relative position. The tendency of the hyponastic growth of leaf 2 was to bring the morphologically superior surface of the leaf into such a position that it would face downwards. Now this tendency is in direct opposition to the most striking effect of diageotropism, which is to bring the morphologically upper surface of the leaf in such a position that it faces the zenith. Hence the hyponasty of leaf 2, strong as it undoubtedly must have been, was insufficient to counteract diageotropism to any considerable extent in this position; and, as torsion seems to have been physically impossible, no change of position took place. If this explanation is adequate in the case of leaf 2, it must apply also to leaves 5 and 7, in which, as they were older, hyponasty was less powerful. In the two lateral leaves, Nos. 3 and 4, both hyponasty and diageotropism produced their full effects, the one in curvature, the other in torsion. Similar results were obtained with *Taraxacum Dens-Leonis*.

It may be urged, in criticism of these views, that I have assumed diaheliotropism without adducing any evidence in support of the assumption. In reply I would submit that my observations do afford definite evidence on this important point. It appears to me to be quite impossible to explain the return to the horizontal, when exposed to sufficiently intense light, of members which have become curved either epinastically or hyponastically in consequence of having been kept in darkness, in any other way than by attributing it to the influence of the light on their diaheliotropic irritability. It is true that gravitation co-operates in inducing this return to the horizontal, but the fact that hyponastic or epinastic curvature takes place in darkness when the plant is in the normal position proves that gravitation alone cannot determine the assumption and maintenance of the horizontal position.

My observations lead me to the conclusion that the forces which are active during growth under normal conditions in determining the position of dorsiventral members, are their own inherent hyponasty or epinasty; the action of light producing a diaheliotropic effect; the action of gravitation producing a diageotropic effect. The ultimate position assumed is, I believe, a fixed light-position, the influence of light being the most powerful factor. Light can, as F. Darwin's experiments prove, overcome epinasty or hyponasty; and these can overcome the influence of gravitation, as I have shown, except when in so doing they would bring the morphologically upper surface of the member to face downwards, a possibility which is not often realised in plants growing in the normal position.

The conclusions at which I have arrived with regard to growing members appear to me to be equally applicable to motile foliage-leaves. So far as I am aware no explanation has as yet been offered of the differences in the nyctitropic movements of leaves; of why it is that some motile leaves rise, and others fall at night. These differences may be explained on the assumption that motile leaves, like growing leaves, may be either epinastic or hyponastic; that is to say, they may be in a state of epinastic or hyponastic tension, though the tension is not associated with actual growth. Motile leaves which fall at night do so, apparently, because their epinastic tension is no longer counteracted by diaheliotropism; similarly, leaves which rise at night do so because their hyponastic tension is no longer counteracted by diaheliotropism. The former behave like, for instance, the growing leaves of *Helianthus* when placed in darkness; the latter, like the younger leaves of *Plantago*. This view is simply a natural consequence of the remarkable similarity between the nyctitropic movements of growing leaves, as described by Batalin, and those of motile leaves; it can hardly be doubted that an explanation which holds good in the one case is correct in the other.

So far I have dealt exclusively with dorsiventral members which, when fully exposed to light of sufficient intensity, place their upper surface at right angles to the incident rays; to members, that is, which are diaheliotropic. But it must not be overlooked that there are dorsiventral members which take up a different light-position, presenting their margin to the incident rays, and which have hence been described as paraheliotropic. This phenomenon is presented both by young growing leaves and by mature motile leaves. So far as I am aware, no observations have been made on growing leaves of this kind with the view of ascertaining whether they are epinastic or hyponastic, and I have not had time this season to make any experiments with them. But some inferences can be drawn as to the conditions of paraheliotropism in mature motile leaves, at least in those cases, which seem to be relatively few, in which the paraheliotropic movement is not effected by means of torsion. For example, Darwin[1] has pointed out that the leaflets of *Robinia* fall at night, whereas when exposed to bright sunlight they rise above the horizontal. In accordance with what has been said above in explanation of nyctitropic movements, that of the leaflets of *Robinia* may be ascribed to epinasty. The assumption of the paraheliotropic position is, therefore, effected in opposition to the inherent epinasty of the leaflets.

In *Averrhoa bilimbi* the leaflets fall downwards at night until they are vertical, and are therefore probably epinastic like those of *Robinia*. But they likewise sink on exposure to bright light into an obliquely descending position, so that the effect of the inherent epinasty of the leaflets is modified to only a slight extent.

This kind of reaction to light cannot, I think, be satisfactorily explained otherwise than on the assumption of a special paraheliotropic irritability.

There remains to be considered yet another class of move-

[1] Darwin: Movements of Plants, p. 445.

ments which are affected by light, those, namely, of highly sensitive members such as the leaves of the Sensitive Plant (*Mimosa pudica*) and the perianth-leaves of many flowers. It is well known that the leaflets of *Mimosa* close on being placed in darkness, and open on being again exposed to light, and that many flowers close in darkness, or on diminution of the intensity of the light, re-opening when again exposed to light or when the intensity of the light is increased, whereas others close in light and open in darkness. In the attempt to analyse these phenomena, it must be first pointed out that the effect of light is quite different in this case from that in the cases previously discussed. In those cases it was directive or heliotropic; in these it is dependent, not upon the direction, but upon the intensity of the incident light. This is made clear by the fact that exactly the same movements can be induced by other means; in the leaflets of *Mimosa*, by a touch, in the perianth-leaves of flowers by variations of temperature. In the next place, it may be inferred from the observations described above, that the position assumed in darkness by a dorsiventral member is that which results from the conditions of tension inherent in the member. Hence the leaflets of *Mimosa*, and the perianth-leaves of flowers which close in darkness, are hyponastic; whereas the perianth-leaves of flowers which open in darkness are epinastic. The opening of the former, when exposed to sufficiently intense light, is due to the induction of epinastic tension; the closing of the latter, under the same circumstances, is due to the induction of hyponastic tension.

The movements of these leaves under the influence of light afford instances of true photo-epinasty and photo-hyponasty, as distinguished from those cases (*Cucurbita, Phaseolus*) to which Detmer applied this explanation; the essential difference being that, in these cases, light induces a tension which is precisely the opposite of that inherent in the leaf, whereas in Detmer's cases light merely rendered possible, by inducing phototonus, the external manifestation by growth of the conditions of tension inherent in the leaf.

I am conscious that the number of plants which I have observed is small; but, as they represent diverse groups, and as the forms of the members are various, the results obtained may be considered to be of wide application. I hope, however, to resume and extend my observations next spring.