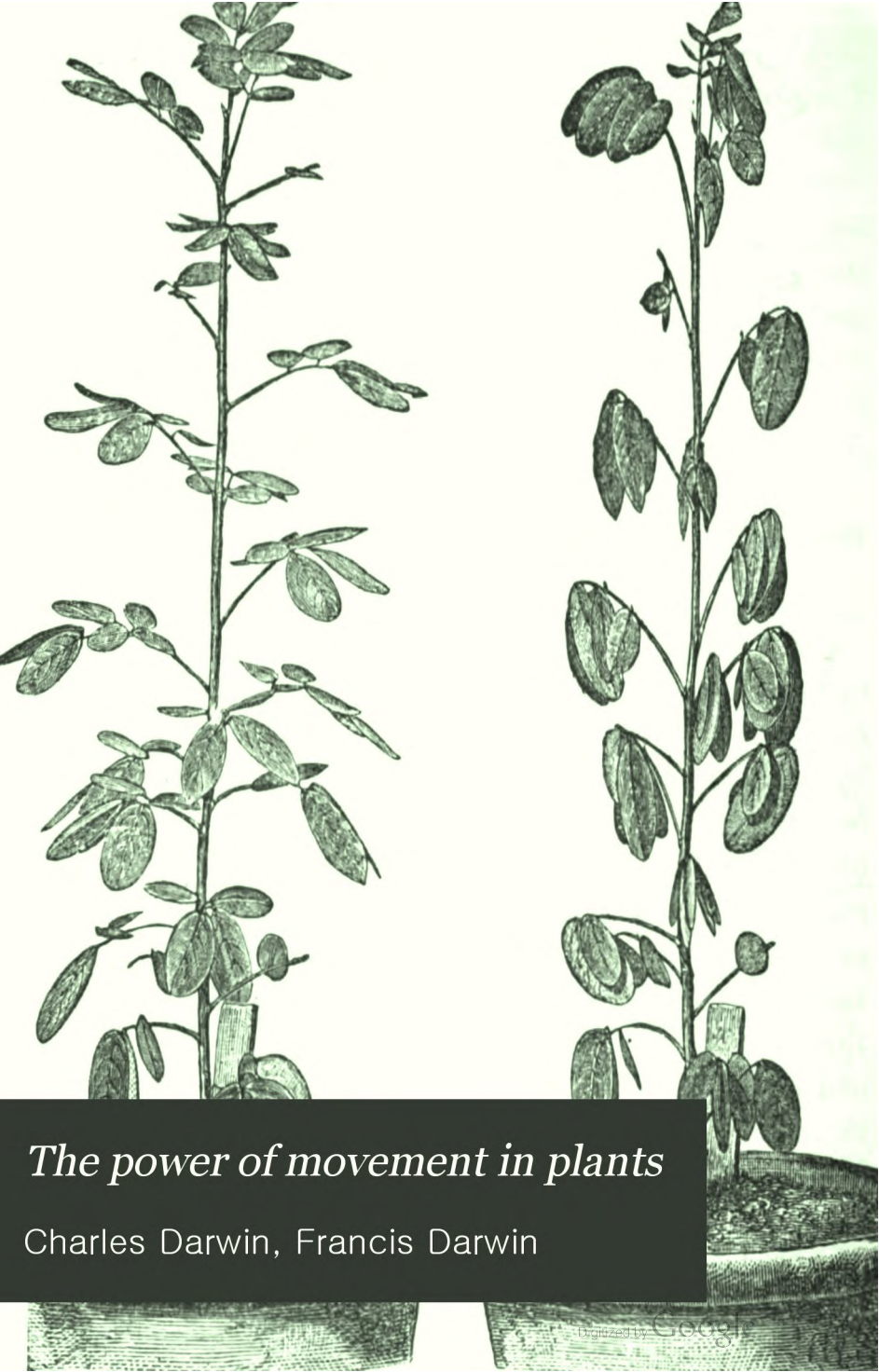




The power of movement in plants

Charles Darwin, Francis Darwin

THE
POWER OF MOVEMENT
IN
PLANTS.

THE
POWER OF MOVEMENT
IN
PLANTS.

By CHARLES DARWIN, LL.D., F.R.S.

ASSISTED BY
FRANCIS DARWIN.

WITH ILLUSTRATIONS.

NEW YORK:
D. APPLETON AND COMPANY,
1, 3, AND 5 BOND STREET.
1881.

CHAPTER IX.

SENSITIVENESS OF PLANTS TO LIGHT: ITS TRANSMITTED EFFECTS.

Uses of heliotropism—Insectivorous and climbing plants not heliotropic—Same organ heliotropic at one age and not at another—Extraordinary sensitiveness of some plants to light—The effects of light do not correspond with its intensity—Effects of previous illumination—Time required for the action of light—After-effects of light—Apogeotropism acts as soon as light fails—Accuracy with which plants bend to the light—This dependent on the illumination of one whole side of the part—Localised sensitiveness to light and its transmitted effects—Cotyledons of *Phalaris*, manner of bending—Results of the exclusion of light from their tips—Effects transmitted beneath the surface of the ground—Lateral illumination of the tip determines the direction of the curvature of the base—Cotyledons of *Avena*, curvature of basal part due to the illumination of upper part—Similar results with the hypocotyls of *Brassica* and *Beta*—Radicles of *Sinapis* apheliotropic, due to the sensitiveness of their tips—Concluding remarks and summary of chapter—Means by which circumnutation has been converted into heliotropism or apheliotropism.

No one can look at the plants growing on a bank or on the borders of a thick wood, and doubt that the young stems and leaves place themselves so that the leaves may be well illuminated. They are thus enabled to decompose carbonic acid. But the sheath-like cotyledons of some Gramineæ, for instance, those of *Phalaris*, are not green and contain very little starch; from which fact we may infer that they decompose little or no carbonic acid. Nevertheless, they are extremely heliotropic; and this probably serves them in another way, namely, as a guide from the buried seeds through fissures in the ground or through overlying masses of vegetation, into the light and air. This view

is strengthened by the fact that with *Phalaris* and *Avena* the first true leaf, which is bright green and no doubt decomposes carbonic acid, exhibits hardly a trace of heliotropism. The heliotropic movements of many other seedlings probably aid them in like manner in emerging from the ground; for apogeotropism by itself would blindly guide them upwards, against any overlying obstacle.

Heliotropism prevails so extensively among the higher plants, that there are extremely few, of which some part, either the stem, flower-peduncle, petiole, or leaf, does not bend towards a lateral light. *Drosera rotundifolia* is one of the few plants the leaves of which exhibit no trace of heliotropism. Nor could we see any in *Dionæa*, though the plants were not so carefully observed. Sir J. Hooker exposed the pitchers of *Sarracenia* for some time to a lateral light, but they did not bend towards it.* We can understand the reason why these insectivorous plants should not be heliotropic, as they do not live chiefly by decomposing carbonic acid; and it is much more important to them that their leaves should occupy the best position for capturing insects, than that they should be fully exposed to the light.

Tendrils, which consist of leaves or of other organs modified, and the stems of twining plants, are, as Mohl long ago remarked, rarely heliotropic; and here again we can see the reason why, for if they had moved towards a lateral light they would have been drawn away from their supports. But some tendrils are apheliotropic, for instance those of *Bignonia capreolata*

* According to F. Kurtz ('Verhändl. des Bot. Vereins der Provinz Brandenburg,' Bd. xx. 1878) the leaves or pitchers of *Darling-*

tonia Californica are strongly apheliotropic. We failed to detect this movement in a plant which we possessed for a short time.

and of *Smilax aspera*; and the stems of some plants which climb by rootlets, as those of the Ivy and *Tecoma radicans*, are likewise apheliotropic, and they thus find a support. The leaves, on the other hand, of most climbing plants are heliotropic; but we could detect no signs of any such movement in those of *Mutisia clematis*.

As heliotropism is so widely prevalent, and as twining plants are distributed throughout the whole vascular series, the apparent absence of any tendency in their stems to bend towards the light, seemed to us so remarkable a fact as to deserve further investigation, for it implies that heliotropism can be readily eliminated. When twining plants are exposed to a lateral light, their stems go on revolving or circumnutating about the same spot, without any evident deflection towards the light; but we thought that we might detect some trace of heliotropism by comparing the average rate at which the stems moved to and from the light during their successive revolutions.* Three young plants (about a foot in height) of *Ipomœa cœrulea* and four of *I. purpurea*, growing in separate pots, were placed on a bright day before a north-east window in a room otherwise darkened, with the tips of their revolving stems fronting the window. When the tip of each plant pointed directly from the window, and when again towards it, the times were recorded. This was continued from 6.45 A.M. till a little after 2 P.M. on June 17th. After a few observations we concluded that we could safely estimate the time

* Some erroneous statements are unfortunately given on this subject, in 'The Movements and Habits of Climbing Plants,' 1875, pp. 28, 32, 40, and 53. Conclusions were drawn from an insufficient

number of observations, for we did not then know at how unequal a rate the stems and tendrils of climbing plants sometimes travel in different parts of the same revolution.

taken by each semicircle, within a limit of error of at most 5 minutes. Although the rate of movement in different parts of the same revolution varied greatly, yet 22 semicircles to the light were completed, each on an average in 73.95 minutes; and 22 semicircles from the light each in 73.5 minutes. It may, therefore, be said that they travelled to and from the light at exactly the same average rate; though probably the accuracy of the result was in part accidental. In the evening the stems were not in the least deflected towards the window. Nevertheless, there appears to exist a vestige of heliotropism, for with 6 out of the 7 plants, the first semicircle from the light, described in the early morning after they had been subjected to darkness during the night and thus probably rendered more sensitive, required rather more time, and the first semicircle to the light considerably less time, than the average. Thus with all 7 plants, taken together, the mean time of the first semicircle in the morning from the light, was 76.8 minutes, instead of 73.5 minutes, which is the mean of all the semicircles during the day from the light; and the mean of the first semicircle to the light was only 63.1, instead of 73.95 minutes, which was the mean of all the semicircles during the day to the light.

Similar observations were made on *Wistaria Sinensis*, and the mean of 9 semicircles from the light was 117 minutes, and of 7 semicircles to the light 122 minutes, and this difference does not exceed the probable limit of error. During the three days of exposure, the shoot did not become at all bent towards the window before which it stood. In this case the first semicircle from the light in the early morning of each day, required rather *less* time for its performance than did the first semicircle to the light; and this result,

if not accidental, appears to indicate that the shoots retain a trace of an original apheliotropic tendency. With *Lonicera brachypoda* the semicircles from and to the light differed considerably in time; for 5 semicircles from the light required on a mean 202·4 minutes, and 4 to the light, 229·5 minutes; but the shoot moved very irregularly, and under these circumstances the observations were much too few.

It is remarkable that the same part on the same plant may be affected by light in a widely different manner at different ages, and as it appears at different seasons. The hypocotyledonous stems of *Ipomæa cærulea* and *purpurea* are extremely heliotropic, whilst the stems of older plants, only about a foot in height, are, as we have just seen, almost wholly insensible to light. Sachs states (and we have observed the same fact) that the hypocotyls of the Ivy (*Hedera helix*) are slightly heliotropic; whereas the stems of plants grown to a few inches in height become so strongly apheliotropic, that they bend at right angles away from the light. Nevertheless, some young plants which had behaved in this manner early in the summer again became distinctly heliotropic in the beginning of September; and the zigzag courses of their stems, as they slowly curved towards a north-east window, were traced during 10 days. The stems of very young plants of *Tropæolum majus* are highly heliotropic, whilst those of older plants, according to Sachs, are slightly apheliotropic. In all these cases the heliotropism of the very young stems serves to expose the cotyledons, or when the cotyledons are hypogean the first true leaves, fully to the light; and the loss of this power by the older stems, or their becoming apheliotropic, is connected with their habit of climbing.

Most seedling plants are strongly heliotropic, and

it is no doubt a great advantage to them in their struggle for life to expose their cotyledons to the light as quickly and as fully as possible, for the sake of obtaining carbon. It has been shown in the first chapter that the greater number of seedlings circumnutate largely and rapidly; and as heliotropism consists of modified circumnutation, we are tempted to look at the high development of these two powers in seedlings as intimately connected. Whether there are any plants which circumnutate slowly and to a small extent, and yet are highly heliotropic, we do not know; but there are several, and there is nothing surprising in this fact, which circumnutate largely and are not at all, or only slightly, heliotropic. Of such cases *Drosera rotundifolia* offers an excellent instance. The stolons of the strawberry circumnutate almost like the stems of climbing plants, and they are not at all affected by a moderate light; but when exposed late in the summer to a somewhat brighter light they were slightly heliotropic; in sunlight, according to De Vries, they are apheliotropic. Climbing plants circumnutate much more widely than any other plants, yet they are not at all heliotropic.

Although the stems of most seedling plants are strongly heliotropic, some few are but slightly heliotropic, without our being able to assign any reason. This is the case with the hypocotyl of *Cassia tora*, and we were struck with the same fact with some other seedlings, for instance, those of *Reseda odorata*. With respect to the degree of sensitiveness of the more sensitive kinds, it was shown in the last chapter that seedlings of several species, placed before a north-east window protected by several blinds, and exposed in the rear to the diffused light of the room, moved with unerring certainty towards the window, although

it was impossible to judge, excepting by the shadow cast by an upright pencil on a white card, on which side most light entered, so that the excess on one side must have been extremely small.

A pot with seedlings of *Phalaris Canariensis*, which had been raised in darkness, was placed in a completely darkened room, at 12 feet from a very small lamp. After 3 h. the cotyledons were doubtfully curved towards the light, and after 7 h. 40 m. from the first exposure, they were all plainly, though slightly, curved towards the lamp. Now, at this distance of 12 feet, the light was so obscure that we could not see the seedlings themselves, nor read the large Roman figures on the white face of a watch, nor see a pencil line on paper, but could just distinguish a line made with Indian ink. It is a more surprising fact that no visible shadow was cast by a pencil held upright on a white card; the seedlings, therefore, were acted on by a difference in the illumination of their two sides, which the human eye could not distinguish. On another occasion even a less degree of light acted, for some cotyledons of *Phalaris* became slightly curved towards the same lamp at a distance of 20 feet; at this distance we could not see a circular dot 2.29 mm. (.09 inch) in diameter made with Indian ink on white paper, though we could just see a dot 3.56 mm. (.14 inch) in diameter; yet a dot of the former size appears large when seen in the light.*

We next tried how small a beam of light would act; as this bears on light serving as a guide to seedlings whilst they emerge through fissured or encumbered ground. A pot with seedlings of *Phalaris* was covered

* Strasburger says ('Wirkung des Lichtes auf Schwärmsporen,' 1878, p. 52), that the spores of

Hæmatococcus moved to a light which only just sufficed to allow middle-sized type to be read.

by a tin-vessel, having on one side a circular hole 1.23 mm. in diameter (i.e. a little less than the $\frac{1}{40}$ th of an inch); and the box was placed in front of a paraffin lamp and on another occasion in front of a window; and both times the seedlings were manifestly bent after a few hours towards the little hole.

A more severe trial was now made; little tubes of very thin glass, closed at their upper ends and coated with black varnish, were slipped over the cotyledons of *Phalaris* (which had germinated in darkness) and just fitted them. Narrow stripes of the varnish had been previously scraped off one side, through which alone light could enter; and their dimensions were afterwards measured under the microscope. As a control experiment, similar unvarnished and transparent tubes were tried, and they did not prevent the cotyledons bending towards the light. Two cotyledons were placed before a south-west window, one of which was illuminated by a stripe in the varnish, only .004 inch (0.1 mm.) in breadth and .016 inch (0.4 mm.) in length; and the other by a stripe .008 inch in breadth and .06 inch in length. The seedlings were examined after an exposure of 7 h. 40 m., and were found to be manifestly bowed towards the light. Some other cotyledons were at the same time treated similarly, excepting that the little stripes were directed not to the sky, but in such a manner that they received only the diffused light from the room; and these cotyledons did not become at all bowed. Seven other cotyledons were illuminated through narrow, but comparatively long, cleared stripes in the varnish—namely, in breadth between .01 and .026 inch, and in length between .15 and .3 inch; and these all became bowed to the side, by which light entered through the stripes, whether these were directed towards the sky or to one side of

the room. That light passing through a hole only $\cdot 004$ inch in breadth by $\cdot 016$ in length, should induce curvature, seems to us a surprising fact.

Before we knew how extremely sensitive the cotyledons of *Phalaris* were to light, we endeavoured to trace their circumnutation in darkness by the aid of a small wax taper, held for a minute or two at each observation in nearly the same position, a little on the left side in front of the vertical glass on which the tracing was made. The seedlings were thus observed seventeen times in the course of the day, at intervals of from half to three-quarters of an hour; and late in the evening we were surprised to find that all the 29 cotyledons were greatly curved and pointed towards the vertical glass, a little to the left where the taper had been held. The tracings showed that they had travelled in zigzag lines. Thus, an exposure to a feeble light for a very short time at the above specified intervals, sufficed to induce well-marked heliotropism. An analogous case was observed with the hypocotyls of *Solanum lycopersicum*. We at first attributed this result to the after-effects of the light on each occasion; but since reading Wiesner's observations,* which will be referred to in the last chapter, we cannot doubt that an intermittent light is more efficacious than a continuous one, as plants are especially sensitive to any contrast in its amount.

The cotyledons of *Phalaris* bend much more slowly towards a very obscure light than towards a bright one. Thus, in the experiments with seedlings placed in a dark room at 12 feet from a very small lamp, they were just perceptibly and doubtfully curved towards it after 3 h., and only slightly, yet certainly, after 4 h.

* 'Sitz. der k. Akad. der Wissensch.' (Vienna), Jan. 1880, p. 12.

After 8 h. 40 m. the chords of their arcs were deflected from the perpendicular by an average angle of only 16° . Had the light been bright, they would have become much more curved in between 1 and 2 h. Several trials were made with seedlings placed at various distances from a small lamp in a dark room; but we will give only one trial. Six pots were placed at distances of 2, 4, 8, 12, 16, and 20 feet from the lamp, before which they were left for 4 h. As light decreases in a geometrical ratio, the seedlings in the 2nd pot received $\frac{1}{4}$ th, those in the 3rd pot $\frac{1}{16}$ th, those in the 4th $\frac{1}{36}$ th, those in the 5th $\frac{1}{64}$ th, and those in the 6th $\frac{1}{100}$ th of the light received by the seedlings in the first or nearest pot. Therefore it might have been expected that there would have been an immense difference in the degree of their heliotropic curvature in the several pots; and there was a well-marked difference between those which stood nearest and furthest from the lamp, but the difference in each successive pair of pots was extremely small. In order to avoid prejudice, we asked three persons, who knew nothing about the experiment, to arrange the pots in order according to the degree of curvature of the cotyledons. The first person arranged them in proper order, but doubted long between the 12 feet and 16 feet pots; yet these two received light in the proportion of 36 to 64. The second person also arranged them properly, but doubted between the 8 feet and 12 feet pots, which received light in the proportion of 16 to 36. The third person arranged them in wrong order, and doubted about four of the pots. This evidence shows conclusively how little the curvature of the seedlings differed in the successive pots, in comparison with the great difference in the amount of light which they received; and it should be noted that there was no

excess of superfluous light, for the cotyledons became but little and slowly curved even in the nearest pot. Close to the 6th pot, at the distance of 20 feet from the lamp, the light allowed us just to distinguish a dot 3.56 mm. (.14 inch) in diameter, made with Indian ink on white paper, but not a dot 2.29 mm. (.09 inch) in diameter.

The degree of curvature of the cotyledons of *Phalaris* within a given time, depends not merely on the amount of lateral light which they may then receive, but on that which they have previously received from above and on all sides. Analogous facts have been given with respect to the nyctitropic and periodic movements of plants. Of two pots containing seedlings of *Phalaris* which had germinated in darkness, one was still kept in the dark, and the other was exposed (Sept. 26th) to the light in a greenhouse during a cloudy day and on the following bright morning. On this morning (27th), at 10.30 A.M., both pots were placed in a box, blackened within and open in front, before a north-east window, protected by a linen and muslin blind and by a towel, so that but little light was admitted, though the sky was bright. Whenever the pots were looked at, this was done as quickly as possible, and the cotyledons were then held transversely with respect to the light, so that their curvature could not have been thus increased or diminished. After 50 m. the seedlings which had previously been kept in darkness, were perhaps, and after 70 m. were certainly, curved, though very slightly, towards the window. After 85 m. some of the seedlings, which had previously been illuminated, were perhaps a little affected, and after 100 m. some of the younger ones were certainly a little curved towards the light. At this time (i.e. after 100 m.) there was a plain difference

in the curvature of the seedlings in the two pots. After 2 h. 12 m. the chords of the arcs of four of the most strongly curved seedlings in each pot were measured, and the mean angle from the perpendicular of those which had previously been kept in darkness was 19° , and of those which had previously been illuminated only 7° . Nor did this difference diminish during two additional hours. As a check, the seedlings in both pots were then placed in complete darkness for two hours, in order that apogeotropism should act on them; and those in the one pot which were little curved became in this time almost completely upright, whilst the more curved ones in the other pot still remained plainly curved.

Two days afterwards the experiment was repeated, with the sole difference that even less light was admitted through the window, as it was protected by a linen and muslin blind and by two towels; the sky, moreover, was somewhat less bright. The result was the same as before, excepting that everything occurred rather slower. The seedlings which had been previously kept in darkness were not in the least curved after 54 m., but were so after 70 m. Those which had previously been illuminated were not at all affected until 130 m. had elapsed, and then only slightly. After 145 m. some of the seedlings in this latter pot were certainly curved towards the light; and there was now a plain difference between the two pots. After 3 h. 45 m. the chords of the arcs of 3 seedlings in each pot were measured, and the mean angle from the perpendicular was 16° for those in the pot which had previously been kept in darkness, and only 5° for those which had previously been illuminated.

The curvature of the cotyledons of *Phalaris* towards a lateral light is therefore certainly influenced by the

degree to which they have been previously illuminated. We shall presently see that the influence of light on their bending continues for a short time after the light has been extinguished. These facts, as well as that of the curvature not increasing or decreasing in nearly the same ratio with that of the amount of light which they receive, as shown in the trials with the plants before the lamp, all indicate that light acts on them as a stimulus, in somewhat the same manner as on the nervous system of animals, and not in a direct manner on the cells or cell-walls which by their contraction or expansion cause the curvature.

It has already been incidentally shown how slowly the cotyledons of *Phalaris* bend towards a very dim light; but when they were placed before a bright paraffin lamp their tips were all curved rectangularly towards it in 2 h. 20 m. The hypocotyls of *Solanum lycopersicum* had bent in the morning at right angles towards a north-east window. At 1 P.M. (Oct. 21st) the pot was turned round, so that the seedlings now pointed from the light, but by 5 P.M. they had reversed their curvature and again pointed to the light. They had thus passed through 180° in 4 h., having in the morning previously passed through about 90° . But the reversal of the first half of the curvature will have been aided by apogeotropism. Similar cases were observed with other seedlings, for instance, with those of *Sinapis alba*.

We attempted to ascertain in how short a time light acted on the cotyledons of *Phalaris*, but this was difficult on account of their rapid circumnutating movement; moreover, they differ much in sensibility, according to age; nevertheless, some of our observations are worth giving. Pots with seedlings were

placed under a microscope provided with an eye-piece micrometer, of which each division equalled $\frac{1}{500}$ th of an inch (0.051 mm.); and they were at first illuminated by light from a paraffin lamp passing through a solution of bichromate of potassium, which does not induce heliotropism. Thus the direction in which the cotyledons were circumnutating could be observed independently of any action from the light; and they could be made, by turning round the pots, to circumnutate transversely to the line in which the light would strike them, as soon as the solution was removed. The fact that the direction of the circumnutating movement might change at any moment, and thus the plant might bend either towards or from the lamp independently of the action of the light, gave an element of uncertainty to the results. After the solution had been removed, five seedlings which were circumnutating transversely to the line of light, began to move towards it, in 6, 4, $7\frac{1}{2}$, 6, and 9 minutes. In one of these cases, the apex of the cotyledon crossed five of the divisions of the micrometer (i.e. $\frac{1}{100}$ th of an inch, or 0.254 mm.) towards the light in 3 m. Of two seedlings which were moving directly from the light at the time when the solution was removed, one began to move towards it in 13 m., and the other in 15 m. This latter seedling was observed for more than an hour and continued to move towards the light; it crossed at one time 5 divisions of the micrometer (0.254 mm.) in 2 m. 30 s. In all these cases, the movement towards the light was extremely unequal in rate, and the cotyledons often remained almost stationary for some minutes, and two of them retrograded a little. Another seedling which was circumnutating transversely to the line of light, moved towards it in 4 m. after the solution was removed; it then remained

almost stationary for 10 m.; then crossed 5 divisions of the micrometer in 6 m.; and then 8 divisions in 11 m. This unequal rate of movement, interrupted by pauses, and at first with occasional retrogressions, accords well with our conclusion that heliotropism consists of modified circumnutation.

In order to observe how long the after-effects of light lasted, a pot with seedlings of *Phalaris*, which had germinated in darkness, was placed at 10.40 A.M. before a north-east window, being protected on all other sides from the light; and the movement of a cotyledon was traced on a horizontal glass. It circumnuted about the same space for the first 24 m., and during the next 1 h. 33 m. moved rapidly towards the light. The light was now (i.e. after 1 h. 57 m.) completely excluded, but the cotyledon continued bending in the same direction as before, certainly for more than 15 m., probably for about 27 m. The doubt arose from the necessity of not looking at the seedlings often, and thus exposing them, though momentarily, to the light. This same seedling was now kept in the dark, until 2.18 P.M., by which time it had reacquired through apogeotropism its original upright position, when it was again exposed to the light from a clouded sky. By 3 P.M. it had moved a very short distance towards the light, but during the next 45 m. travelled quickly towards it. After this exposure of 1 h. 27 m. to a rather dull sky, the light was again completely excluded, but the cotyledon continued to bend in the same direction as before for 14 m. within a very small limit of error. It was then placed in the dark, and it now moved backwards, so that after 1 h. 7 m. it stood close to where it had started from at 2.18 P.M. These observations show that the cotyledons of *Phalaris*, after being exposed to a lateral

light, continue to bend in the same direction for between a quarter and half an hour.

In the two experiments just given, the cotyledons moved backwards or from the window shortly after being subjected to darkness; and whilst tracing the circumnutation of various kinds of seedlings exposed to a lateral light, we repeatedly observed that late in the evening, as the light waned, they moved from it. This fact is shown in some of the diagrams given in the last chapter. We wished therefore to learn whether this was wholly due to apogeotropism, or whether an organ after bending towards the light tended from any other cause to bend from it, as soon as the light failed. Accordingly, two pots of seedling *Phalaris* and one pot of seedling *Brassica* were exposed for 8 h. before a paraffin lamp, by which time the cotyledons of the former and the hypocotyls of the latter were bent rectangularly towards the light. The pots were now quickly laid horizontally, so that the upper parts of the cotyledons and of the hypocotyls of 9 seedlings projected vertically upwards, as proved by a plumb-line. In this position they could not be acted on by apogeotropism, and if they possessed any tendency to straighten themselves or to bend in opposition to their former heliotropic curvature, this would be exhibited, for it would be opposed at first very slightly by apogeotropism. They were kept in the dark for 4 h., during which time they were twice looked at; but no uniform bending in opposition to their former heliotropic curvature could be detected. We have said *uniform* bending, because they circumnuted in their new position, and after 2 h. were inclined in different directions (between 4° and 11°) from the perpendicular. Their directions were also changed after two additional hours, and again on the following morning. We may

therefore conclude that the bending back of plants from a light, when this becomes obscure or is extinguished, is wholly due to apogeotropism.*

In our various experiments we were often struck with the accuracy with which seedlings pointed to a light although of small size. To test this, many seedlings of *Phalaris*, which had germinated in darkness in a very narrow box several feet in length, were placed in a darkened room near to and in front of a lamp having a small cylindrical wick. The cotyledons at the two ends and in the central part of the box, would therefore have to bend in widely different directions in order to point to the light. After they had become rectangularly bent, a long white thread was stretched by two persons, close over and parallel, first to one and then to another cotyledon; and the thread was found in almost every case actually to intersect the small circular wick of the now extinguished lamp. The deviation from accuracy never exceeded, as far as we could judge, a degree or two. This extreme accuracy seems at first surprising, but is not really so, for an upright cylindrical stem, whatever its position may be with respect to the light, would have exactly half its circumference illuminated and half in shadow; and as the difference in illumination of the two sides is the exciting cause of heliotropism, a cylinder would naturally bend with much accuracy towards the light. The cotyledons, however, of *Phalaris* are not cylindrical, but oval in section; and the longer axis was to the shorter axis (in the one which was measured) as 100 to 70. Nevertheless, no difference could be

* It appears from a reference in Wiesner ('Die Undulirende Nutation der Internodien,' p. 7), that H. Müller of Thurgau found that a stem which is bending

heliotropically is at the same time striving, through apogeotropism, to raise itself into a vertical position.

detected in the accuracy of their bending, whether they stood with their broad or narrow sides facing the light, or in any intermediate position; and so it was with the cotyledons of *Avena sativa*, which are likewise oval in section. Now, a little reflection will show that in whatever position the cotyledons may stand, there will be a line of greatest illumination, exactly fronting the light, and on each side of this line an equal amount of light will be received; but if the oval stands obliquely with respect to the light, this will be diffused over a wider surface on one side of the central line than on the other. We may therefore infer that the same amount of light, whether diffused over a wider surface or concentrated on a smaller surface, produces exactly the same effect; for the cotyledons in the long narrow box stood in all sorts of positions with reference to the light, yet all pointed truly towards it.

That the bending of the cotyledons to the light depends on the illumination of one whole side or on the obscuration of the whole opposite side, and not on a narrow longitudinal zone in the line of the light being affected, was shown by the effects of painting longitudinally with Indian ink one side of five cotyledons of *Phalaris*. These were then placed on a table near to a south-west window, and the painted half was directed either to the right or left. The result was that instead of bending in a direct line towards the window, they were deflected from the window and towards the unpainted side, by the following angles, 35°, 83°, 31°, 43°, and 39°. It should be remarked that it was hardly possible to paint one-half accurately, or to place all the seedlings which are oval in section in quite the same position relatively to the light; and this will account for the differences in the angles. Five coty-

ledons of *Avena* were also painted in the same manner, but with greater care; and they were laterally deflected from the line of the window, towards the unpainted side, by the following angles, 44° , 44° , 55° , 51° , and 57° . This deflection of the cotyledons from the window is intelligible, for the whole unpainted side must have received some light, whereas the opposite and painted side received none; but a narrow zone on the unpainted side directly in front of the window will have received most light, and all the hinder parts (half an oval in section) less and less light in varying degrees; and we may conclude that the angle of deflection is the resultant of the action of the light over the whole of the unpainted side.

It should have been premised that painting with Indian ink does not injure plants, at least within several hours; and it could injure them only by stopping respiration. To ascertain whether injury was thus soon caused, the upper halves of 8 cotyledons of *Avena* were thickly coated with transparent matter,—4 with gum, and 4 with gelatine; they were placed in the morning before a window, and by the evening they were normally bowed towards the light, although the coatings now consisted of dry crusts of gum and gelatine. Moreover, if the seedlings which were painted longitudinally with Indian ink had been injured on the painted side, the opposite side would have gone on growing, and they would consequently have become bowed towards the painted side; whereas the curvature was always, as we have seen, in the opposite direction, or towards the unpainted side which was exposed to the light. We witnessed the effects of injuring longitudinally one side of the cotyledons of *Avena* and *Phalaris*; for before we knew that grease was highly injurious to them, several were painted down one side

with a mixture of oil and lamp-black, and were then exposed before a window; others similarly treated were afterwards tried in darkness. These cotyledons soon became plainly bowed towards the blackened side, evidently owing to the grease on this side having checked their growth, whilst growth continued on the opposite side. But it deserves notice that the curvature differed from that caused by light, which ultimately becomes abrupt near the ground. These seedlings did not afterwards die, but were much injured and grew badly.

LOCALISED SENSITIVENESS TO LIGHT, AND ITS TRANSMITTED EFFECTS.

Phalaris Canariensis.—Whilst observing the accuracy with which the cotyledons of this plant became bent towards the light of a small lamp, we were impressed with the idea that the uppermost part determined the direction of the curvature of the lower part. When the cotyledons are exposed to a lateral light, the upper part bends first, and afterwards the bending gradually extends down to the base, and, as we shall presently see, even a little beneath the ground. This holds good with cotyledons from less than $\cdot 1$ inch (one was observed to act in this manner which was only $\cdot 03$ in height) to about $\cdot 5$ of an inch in height; but when they have grown to nearly an inch in height, the basal part, for a length of $\cdot 15$ to $\cdot 2$ of an inch above the ground, ceases to bend. As with young cotyledons the lower part goes on bending, after the upper part has become well arched towards a lateral light, the apex would ultimately point to the ground instead of to the light, did not the upper part reverse its curvature and straighten itself, as

soon as the upper convex surface of the bowed-down portion received more light than the lower concave surface. The position ultimately assumed by young and upright cotyledons, exposed to light entering obliquely from above through a window, is shown in the accompanying figure (Fig. 181); and here it may be seen that the whole upper part has become very nearly straight. When the cotyledons were exposed before a bright lamp, standing on the same level with them, the upper part, which was at first

Fig. 181.



Phalaris Canariensis: cotyledons after exposure in a box open on one side in front of a south-west window during 8 h. Curvature towards the light accurately traced. The short horizontal lines show the level of the ground.

greatly arched towards the light, became straight and strictly parallel with the surface of the soil in the pots; the basal part being now rectangularly bent. All this great amount of curvature, together with the subsequent straightening of the upper part, was often effected in a few hours.

After the uppermost part has become bowed a little to the light, its overhanging weight must tend to increase the curvature of the lower part; but any such effect was shown in several ways to be quite insignificant. When little caps of tin-foil (hereafter to be described) were placed on the summits of the cotyledons, though this must have added considerably to their weight, the rate or amount of bending was not thus increased. But the best evidence was afforded by placing pots with seedlings of *Phalaris* before a lamp in such a position, that the cotyledons were horizontally extended and projected at right angles to the line of light. In the course of 5½ h. they were directed towards the light with their bases bent at right angles; and this abrupt

curvature could not have been aided in the least by the weight of the upper part, which acted at right angles to the plane of curvature.

It will be shown that when the upper halves of the cotyledons of *Phalaris* and *Avena* were enclosed in little pipes of tin-foil or of blackened glass, in which case the upper part was mechanically prevented from bending, the lower and unenclosed part did not bend when exposed to a lateral light; and it occurred to us that this fact might be due, not to the exclusion of the light from the upper part, but to some necessity of the bending gradually travelling down the cotyledons, so that unless the upper part first became bent, the lower could not bend, however much it might be stimulated. It was necessary for our purpose to ascertain whether this notion was true, and it was proved false; for the lower halves of several cotyledons became bowed to the light, although their upper halves were enclosed in little glass tubes (not blackened), which prevented, as far as we could judge, their bending. Nevertheless, as the part within the tube might possibly bend a very little, fine rigid rods or flat splinters of thin glass were cemented with shellac to one side of the upper part of 15 cotyledons; and in six cases they were in addition tied on with threads. They were thus forced to remain quite straight. The result was that the lower halves of all became bowed to the light, but generally not in so great a degree as the corresponding part of the free seedlings in the same pots; and this may perhaps be accounted for by some slight degree of injury having been caused by a considerable surface having been smeared with shellac. It may be added, that when the cotyledons of *Phalaris* and *Avena* are acted on by apogeotropism, it is the upper part which begins first to bend; and when this part was rendered rigid in the manner just described, the upward curvature of the basal part was not thus prevented.

To test our belief that the upper part of the cotyledons of *Phalaris*, when exposed to a lateral light, regulates the bending of the lower part, many experiments were tried; but most of our first attempts proved useless from various causes not worth specifying. Seven cotyledons had their tips cut off for lengths varying between .1 and .16 of an inch, and these, when left exposed all day to a lateral light, remained upright. In another set of 7 cotyledons, the tips were cut off for a length of only about .05 of an inch (1.27 mm.) and these became bowed towards

a lateral light, but not nearly so much as the many other seedlings in the same pots. This latter case shows that cutting off the tips does not by itself injure the plants so seriously as to prevent heliotropism; but we thought at the time, that such injury might follow when a greater length was cut off, as in the first set of experiments. Therefore, no more trials of this kind were made, which we now regret; as we afterwards found that when the tips of three cotyledons were cut off for a length of $\cdot 2$ inch, and of four others for lengths of $\cdot 14$, $\cdot 12$, $\cdot 1$, and $\cdot 07$ inch, and they were extended horizontally, the amputation did not interfere in the least with their bending vertically upwards, through the action of apogeotropism, like unmutilated specimens. It is therefore extremely improbable that the amputation of the tips for lengths of from $\cdot 1$ to $\cdot 14$ inch, could from the injury thus caused have prevented the lower part from bending towards the light.

We next tried the effects of covering the upper part of the cotyledons of *Phalaris* with little caps which were impermeable to light; the whole lower part being left fully exposed before a south-west window or a bright paraffin lamp. Some of the caps were made of extremely thin tin-foil blackened within; these had the disadvantage of occasionally, though rarely, being too heavy, especially when twice folded. The basal edges could be pressed into close contact with the cotyledons; though this again required care to prevent injuring them. Nevertheless, any injury thus caused could be detected by removing the caps, and trying whether the cotyledons were then sensitive to light. Other caps were made of tubes of the thinnest glass, which when painted black served well, with the one great disadvantage that the lower ends could not be closed. But tubes were used which fitted the cotyledons almost closely, and black paper was placed on the soil round each, to check the upward reflection of light from the soil. Such tubes were in one respect far better than caps of tin-foil, as it was possible to cover at the same time some cotyledons with transparent and others with opaque tubes; and thus our experiments could be controlled. It should be kept in mind that young cotyledons were selected for trial, and that these when not interfered with become bowed down to the ground towards the light.

We will begin with the glass-tubes. The summits of nine cotyledons, differing somewhat in height, were enclosed for rather less than half their lengths in uncoloured or transparent

tubes; and these were then exposed before a south-west window on a bright day for 8 h. All of them became strongly curved towards the light, in the same degree as the many other free seedlings in the same pots; so that the glass-tubes certainly did not prevent the cotyledons from bending towards the light. Nineteen other cotyledons were, at the same time, similarly enclosed in tubes thickly painted with Indian ink. On five of them, the paint, to our surprise, contracted after exposure to the sunlight, and very narrow cracks were formed, through which a little light entered; and these five cases were rejected. Of the remaining 14 cotyledons, the lower halves of which had been fully exposed to the light for the whole time, 7 continued quite straight and upright; 1 was considerably bowed to the light, and 6 were slightly bowed, but with the exposed bases of most of them almost or quite straight. It is possible that some light may have been reflected upwards from the soil and entered the bases of these 7 tubes, as the sun shone brightly, though bits of blackened paper had been placed on the soil round them. Nevertheless, the 7 cotyledons which were slightly bowed, together with the 7 upright ones, presented a most remarkable contrast in appearance with the many other seedlings in the same pots to which nothing had been done. The blackened tubes were then removed from 10 of these seedlings, and they were now exposed before a lamp for 8 h.: 9 of them became greatly, and 1 moderately, curved towards the light, proving that the previous absence of any curvature in the basal part, or the presence of only a slight degree of curvature there, was due to the exclusion of light from the upper part.

Similar observations were made on 12 younger cotyledons with their upper halves enclosed within glass-tubes coated with black varnish, and with their lower halves fully exposed to bright sunshine. In these younger seedlings the sensitive zone seems to extend rather lower down, as was observed on some other occasions, for two became almost as much curved towards the light as the free seedlings; and the remaining ten were slightly curved, although the basal part of several of them, which normally becomes more curved than any other part, exhibited hardly a trace of curvature. These 12 seedlings taken together differed greatly in their degree of curvature from all the many other seedlings in the same pots.

Better evidence of the efficiency of the blackened tubes was incidentally afforded by some experiments hereafter to be given,

in which the upper halves of 14 cotyledons were enclosed in tubes from which an extremely narrow stripe of the black varnish had been scraped off. These cleared stripes were not directed towards the window, but obliquely to one side of the room, so that only a very little light could act on the upper halves of the cotyledons. These 14 seedlings remained during eight hours of exposure before a south-west window on a hazy day quite upright; whereas all the other many free seedlings in the same pots became greatly bowed towards the light.

We will now turn to the trials with caps made of very thin tin-foil. These were placed at different times on the summits of 24 cotyledons, and they extended down for a length of between $\cdot 15$ and $\cdot 2$ of an inch. The seedlings were exposed to a lateral light for periods varying between 6 h. 30 m. and 7 h. 45 m., which sufficed to cause all the other seedlings in the same pots to become almost rectangularly bent towards the light. They varied in height from only $\cdot 04$ to $1\cdot 15$ inch, but the greater number were about $\cdot 75$ inch. Of the 24 cotyledons with their summits thus protected, 3 became much bent, but not in the direction of the light, and as they did not straighten themselves through apogeotropism during the following night, either the caps were too heavy or the plants themselves were in a weak condition; and these three cases may be excluded. There are left for consideration 21 cotyledons; of these 17 remained all the time quite upright; the other 4 became slightly inclined to the light, but not in a degree comparable with that of the many free seedlings in the same pots. As the glass-tubes, when unpainted, did not prevent the cotyledons from becoming greatly bowed, it cannot be supposed that the caps of very thin tin-foil did so, except through the exclusion of the light. To prove that the plants had not been injured, the caps were removed from 6 of the upright seedlings, and these were exposed before a paraffin lamp for the same length of time as before, and they now all became greatly curved towards the light.

As caps between $\cdot 15$ and $\cdot 2$ of an inch in depth were thus proved to be highly efficient in preventing the cotyledons from bending towards the light, 8 other cotyledons were protected with caps between only $\cdot 06$ and $\cdot 12$ in depth. Of these, two remained vertical, one was considerably and five slightly curved towards the light, but far less so than the free seedlings in the same pots.

Another trial was made in a different manner, namely, by bandaging with strips of tin-foil, about $\cdot 2$ in breadth, the upper part, but not the actual summit, of eight moderately young seedlings a little over half an inch in height. The summits and the basal parts were thus left fully exposed to a lateral light during 8 h.; an upper intermediate zone being protected. With four of these seedlings the summits were exposed for a length of $\cdot 05$ inch, and in two of them this part became curved towards the light, but the whole lower part remained quite upright; whereas the entire length of the other two seedlings became slightly curved towards the light. The summits of the four other seedlings were exposed for a length of $\cdot 04$ inch, and of these one remained almost upright, whilst the other three became considerably curved towards the light. The many free seedlings in the same pots were all greatly curved towards the light.

From these several sets of experiments, including those with the glass-tubes, and those when the tips were cut off, we may infer that the exclusion of light from the upper part of the cotyledons of *Phalaris* prevents the lower part, though fully exposed to a lateral light, from becoming curved. The summit for a length of $\cdot 04$ or $\cdot 05$ of an inch, though it is itself sensitive and curves towards the light, has only a slight power of causing the lower part to bend. Nor has the exclusion of light from the summit for a length of $\cdot 1$ of an inch a strong influence on the curvature of the lower part. On the other hand, an exclusion for a length of between $\cdot 15$ and $\cdot 2$ of an inch, or of the whole upper half, plainly prevents the lower and fully illuminated part from becoming curved in the manner (see Fig. 181) which invariably occurs when a free cotyledon is exposed to a lateral light. With very young seedlings the sensitive zone seems to extend rather lower down relatively to their height than in older seedlings. We must therefore conclude that when seedlings are freely exposed to a lateral light some influence is transmitted from the upper to the lower part, causing the latter to bend.

This conclusion is supported by what may be seen to occur on a small scale, especially with young cotyledons, without any artificial exclusion of the light; for they bend beneath the earth where no light can enter. Seeds of *Phalaris* were covered with a layer one-fourth of an inch in thickness of very fine sand, consisting of extremely minute grains of siliceous sand coated with

oxide of iron. A layer of this sand, moistened to the same degree as that over the seeds, was spread over a glass-plate; and when the layer was $\cdot 05$ of an inch in thickness (carefully measured) no light from a bright sky could be seen to pass through it, unless it was viewed through a long blackened tube, and then a trace of light could be detected, but probably much too little to affect any plant. A layer $\cdot 1$ of an inch in thickness was quite impermeable to light, as judged by the eye aided by the tube. It may be worth adding that the layer, when dried, remained equally impermeable to light. This sand yielded to very slight pressure whilst kept moist, and in this state did not contract or crack in the least. In a first trial, cotyledons which had grown to a moderate height were exposed for 8 h. before a paraffin lamp, and they became greatly bowed. At their bases on the shaded side opposite to the light, well-defined, crescentic, open furrows were formed, which (measured under a microscope with a micrometer) were from $\cdot 02$ to $\cdot 03$ of an inch in breadth, and these had evidently been left by the bending of the buried bases of the cotyledons towards the light. On the side of the light the cotyledons were in close contact with the sand, which was a very little heaped up. By removing with a sharp knife the sand on one side of the cotyledons in the line of the light, the bent portion and the open furrows were found to extend down to a depth of about $\cdot 1$ of an inch, where no light could enter. The chords of the short buried arcs formed in four cases angles of 11° , 13° , 15° , and 18° , with the perpendicular. By the following morning these short bowed portions had straightened themselves through apogeotropism.

In the next trial much younger cotyledons were similarly treated, but were exposed to a rather obscure lateral light. After some hours, a bowed cotyledon, $\cdot 3$ inch in height, had an open furrow on the shaded side $\cdot 04$ inch in breadth; another cotyledon, only $\cdot 13$ inch in height, had left a furrow $\cdot 02$ inch in breadth. But the most curious case was that of a cotyledon which had just protruded above the ground and was only $\cdot 03$ inch in height, and this was found to be bowed in the direction of the light to a depth of $\cdot 2$ of an inch beneath the surface. From what we know of the impermeability of this sand to light, the upper illuminated part in these several cases must have determined the curvature of the lower buried portions. But an apparent cause of doubt may be suggested: as the cotyledons are continually circumnutating, they tend to form a minute

crack or furrow all round their bases, which would admit a little light on all sides; but this would not happen when they were illuminated laterally, for we know that they quickly bend towards a lateral light, and they then press so firmly against the sand on the illuminated side as to furrow it, and this would effectually exclude light on this side. Any light admitted on the opposite and shaded side, where an open furrow is formed, would tend to counteract the curvature towards the lamp or other source of the light. It may be added, that the use of fine moist sand, which yields easily to pressure, was indispensable in the above experiments; for seedlings raised in common soil, not kept especially damp, and exposed for 9 h. 30 m. to a strong lateral light, did not form an open furrow at their bases on the shaded side, and were not bowed beneath the surface.

Perhaps the most striking proof of the action of the upper on the lower part of the cotyledons of *Phalaris*, when laterally illuminated, was afforded by the blackened glass-tubes (before alluded to) with very narrow stripes of the varnish scraped off on one side, through which a little light was admitted. The breadth of these stripes or slits varied between $\cdot 01$ and $\cdot 02$ inch ($\cdot 25$ and $\cdot 51$ mm.). Cotyledons with their upper halves enclosed in such tubes were placed before a south-west window, in such a position, that the scraped stripes did not directly face the window, but obliquely to one side. The seedlings were left exposed for 8 h., before the close of which time the many free seedlings in the same pots had become greatly bowed towards the window. Under these circumstances, the whole lower halves of the cotyledons, which had their summits enclosed in the tubes, were fully exposed to the light of the sky, whilst their upper halves received exclusively or chiefly diffused light from the room, and this only through a very narrow slit on one side. Now, if the curvature of the lower part had been determined by the illumination of this part, all the cotyledons assuredly would have become curved towards the window; but this was far from being the case. Tubes of the kind just described were placed on several occasions over the upper halves of 27 cotyledons; 14 of them remained all the time quite vertical; so that sufficient diffused light did not enter through the narrow slits to produce any effect whatever; and they behaved in the same manner as if their upper halves had been enclosed in completely blackened tubes. The lower halves of the 13 other cotyledons became bowed

not directly in the line of the window, but obliquely towards it; one pointed at an angle of only 18° , but the remaining 12 at angles varying between 45° and 62° from the line of the window. At the commencement of the experiment, pins had been laid on the earth in the direction towards which the slits in the varnish faced; and in this direction alone a small amount of diffused light entered. At the close of the experiment, 7 of the bowed cotyledons pointed exactly in the line of the pins, and 6 of them in a line between that of the pins and that of the window. This intermediate position is intelligible, for any light from the sky which entered obliquely through the slits would be much more efficient than the diffused light which entered directly through them. After the 8 h. exposure, the contrast in appearance between these 13 cotyledons and the many other seedlings in the same pots, which were all (excepting the above 14 vertical ones) greatly bowed in straight and parallel lines towards the window, was extremely remarkable. It is therefore certain that a little weak light striking the upper halves of the cotyledons of *Phalaris*, is far more potent in determining the direction of the curvature of the lower halves, than the full illumination of the latter during the whole time of exposure.

In confirmation of the above results, the effect of thickly painting with Indian ink one side of the upper part of three cotyledons of *Phalaris*, for a length of $\cdot 2$ inch from their tips, may be worth giving. These were placed so that the unpainted surface was directed not towards the window, but a little to one side; and they all became bent towards the unpainted side, and from the line of the window by angles amounting to 31° , 35° , and 83° . The curvature in this direction extended down to their bases, although the whole lower part was fully exposed to the light from the window.

Finally, although there can be no doubt that the illumination of the upper part of the cotyledons of *Phalaris* greatly affects the power and manner of bending of the lower part, yet some observations seemed to render it probable that the simultaneous stimulation of the lower part by light greatly favours, or is almost necessary, for its well-marked curvature; but our experiments were not conclusive, owing to the difficulty of excluding light from the lower halves without mechanically preventing their curvature.

Avena sativa.—The cotyledons of this plant become quickly bowed towards a lateral light, exactly like those of *Phalaris*.

Experiments similar to the foregoing ones were tried, and we will give the results as briefly as possible. They are somewhat less conclusive than in the case of *Phalaris*, and this may possibly be accounted for by the sensitive zone varying in extension, in a species so long cultivated and variable as the common Oat. Cotyledons a little under three-quarters of an inch in height were selected for trial: six had their summits protected from light by tin-foil caps, $\cdot 25$ inch in depth, and two others by caps $\cdot 3$ inch in depth. Of these 8 cotyledons, five remained upright during 8 hours of exposure, although their lower parts were fully exposed to the light all the time; two were very slightly, and one considerably, bowed towards it. Caps only $\cdot 2$ or $\cdot 22$ inch in depth were placed over 4 other cotyledons, and now only one remained upright, one was slightly, and two considerably bowed to the light. In this and the following cases all the free seedlings in the same pots became greatly bowed to the light.

Our next trial was made with short lengths of thin and fairly transparent quills; for glass-tubes of sufficient diameter to go over the cotyledons would have been too heavy. Firstly, the summits of 13 cotyledons were enclosed in unpainted quills, and of these 11 became greatly and 2 slightly bowed to the light; so that the mere act of enclosure did not prevent the lower part from becoming bowed. Secondly, the summits of 11 cotyledons were enclosed in quills $\cdot 3$ inch in length, painted so as to be impermeable to light; of these, 7 did not become at all inclined towards the light, but 3 of them were slightly bent more or less transversely with respect to the line of light, and these might perhaps have been altogether excluded; one alone was slightly bowed towards the light. Painted quills, $\cdot 25$ inch in length, were placed over the summits of 4 other cotyledons; of these, one alone remained upright, a second was slightly bowed, and the two others as much bowed to the light as the free seedlings in the same pots. These two latter cases, considering that the caps were $\cdot 25$ in length, are inexplicable.

Lastly, the summits of 8 cotyledons were coated with flexible and highly transparent gold-beaters' skin, and all became as much bowed to the light as the free seedlings. The summits of 9 other cotyledons were similarly coated with gold-beaters' skin, which was then painted to a depth of between $\cdot 25$ and $\cdot 3$ inch, so as to be impermeable to light; of these 5 remained upright, and 4 were well bowed to the light, almost or quite as well as

the free seedlings. These latter four cases, as well as the two in the last paragraph, offer a strong exception to the rule that the illumination of the upper part determines the curvature of the lower part. Nevertheless, 5 of these 8 cotyledons remained quite upright, although their lower halves were fully illuminated all the time; and it would almost be a prodigy to find five free seedlings standing vertically after an exposure for several hours to a lateral light.

The cotyledons of *Avena*, like those of *Phalaris*, when growing in soft, damp, fine sand, leave an open crescentric furrow on the shaded side, after bending to a lateral light; and they become bowed beneath the surface at a depth to which, as we know, light cannot penetrate. The arcs of the chords of the buried bowed portions formed in two cases angles of 20° and 21° with the perpendicular. The open furrows on the shaded side were, in four cases, .008, .016, .024, and .024 of an inch in breadth.

Brassica oleracea (Common Red).—It will here be shown that the upper half of the hypocotyl of the cabbage, when illuminated by a lateral light, determines the curvature of the lower half. It is necessary to experimentise on young seedlings about half an inch or rather less in height, for when grown to an inch and upwards the basal part ceases to bend. We first tried painting the hypocotyls with Indian ink, or cutting off their summits for various lengths; but these experiments are not worth giving, though they confirm, as far as they can be trusted, the results of the following ones. These were made by folding gold-beaters' skin once round the upper halves of young hypocotyls, and painting it thickly with Indian ink or with black grease. As a control experiment, the same transparent skin, left unpainted, was folded round the upper halves of 12 hypocotyls; and these all became greatly curved to the light, excepting one, which was only moderately curved. Twenty other young hypocotyls had the skin round their upper halves painted, whilst their lower halves were left quite uncovered. These seedlings were then exposed, generally for between 7 and 8 h., in a box blackened within and open in front, either before a south-west window or a paraffin lamp. This exposure was amply sufficient, as was shown by the strongly-marked heliotropism of all the free seedlings in the same pots; nevertheless, some were left exposed to the light for a much longer time. Of the 20 hypocotyls thus treated, 14 remained quite upright, and 6 became slightly bowed to the light; but 2 of these latter cases were not really

exceptions, for on removing the skin the paint was found imperfect and was penetrated by many small transparent spaces on the side which faced the light. Moreover, in two other cases the painted skin did not extend quite halfway down the hypocotyl. Altogether there was a wonderful contrast in the several pots between these 20 hypocotyls and the other many free seedlings, which were all greatly bowed down to their bases in the direction of the light, some being almost prostrate on the ground.

The most successful trial on any one day (included in the above results) is worth describing in detail. Six young seedlings were selected, the hypocotyls of which were nearly $\cdot 45$ inch, excepting one, which was $\cdot 6$ inch in height, measured from the bases of their petioles to the ground. Their upper halves, judged as accurately as could be done by the eye, were folded once round with gold-beaters' skin, and this was painted thickly with Indian ink. They were exposed in an otherwise darkened room before a bright paraffin lamp, which stood on a level with the two pots containing the seedlings. They were first looked at after an interval of 5 h. 10 m., and five of the protected hypocotyls were found quite erect, the sixth being very slightly inclined to the light; whereas all the many free seedlings in the same two pots were greatly bowed to the light. They were again examined after a continuous exposure to the light of 20 h. 35 m.; and now the contrast between the two sets was wonderfully great; for the free seedlings had their hypocotyls extended almost horizontally in the direction of the light, and were curved down to the ground; whilst those with the upper halves protected by the painted skin, but with their lower halves fully-exposed to the light, still remained quite upright, with the exception of the one which retained the same slight inclination to the light which it had before. This latter seedling was found to have been rather badly painted, for on the side facing the light the red colour of the hypocotyl could be distinguished through the paint.

We next tried nine older seedlings, the hypocotyls of which varied between 1 and 1.6 inch in height. The gold-beaters' skin round their upper parts was painted with black grease to a depth of only $\cdot 3$ inch, that is, from less than a third to a fourth or fifth of their total heights. They were exposed to the light for 7 h. 15 m.; and the result showed that the whole of the sensitive zone, which determines the curvature of the lower

part, was not protected from the action of the light; for all 9 became curved towards it, 4 of them very slightly, 3 moderately, and 2 almost as much as the unprotected seedlings. Nevertheless, the whole 9 taken together differed plainly in their degree of curvature from the many free seedlings, and from some which were wrapped in unpainted skin, growing in the same two pots.

Seeds were covered with about a quarter of an inch of the fine sand described under *Phalaris*; and when the hypocotyls had grown to a height of between $\cdot 4$ and $\cdot 55$ inch, they were exposed during 9 h. before a paraffin lamp, their bases being at first closely surrounded by the damp sand. They all became bowed down to the ground, so that their upper parts lay near to and almost parallel to the surface of the soil. On the side of the light their bases were in close contact with the sand, which was here a very little heaped up; on the opposite or shaded side there were open, crescentic cracks or furrows, rather above $\cdot 01$ of an inch in width; but they were not so sharp and regular as those made by *Phalaris* and *Avena*, and therefore could not be so easily measured under the microscope. The hypocotyls were found, when the sand was removed on one side, to be curved to a depth beneath the surface in three cases of at least $\cdot 1$ inch, in a fourth case of $\cdot 11$, and in a fifth of $\cdot 15$ inch. The chords of the arcs of the short, buried, bowed portions formed angles of between 11° and 15° with the perpendicular. From what we have seen of the impermeability of this sand to light, the curvature of the hypocotyls certainly extended down to a depth where no light could enter; and the curvature must have been caused by an influence transmitted from the upper illuminated part.

The lower halves of five young hypocotyls were surrounded by unpainted gold-beaters' skin, and these, after an exposure of 8 h. before a paraffin lamp, all became as much bowed to the light as the free seedlings. The lower halves of 10 other young hypocotyls, similarly surrounded with the skin, were thickly painted with Indian ink; their upper and unprotected halves became well curved to the light, but their lower and protected halves remained vertical in all the cases excepting one, and on this the layer of paint was imperfect. This result seems to prove that the influence transmitted from the upper part is not sufficient to cause the lower part to bend, unless it be at the same time illuminated; but there remains the doubt, as in

the case of *Phalaris*, whether the skin covered with a rather thick crust of dry Indian ink did not mechanically prevent their curvature.

Beta vulgaris.—A few analogous experiments were tried on this plant, which is not very well adapted for the purpose, as the basal part of the hypocotyl, after it has grown to above half an inch in height, does not bend much on exposure to a lateral light. Four hypocotyls were surrounded close beneath their petioles with strips of thin tin-foil, .2 inch in breadth, and they remained upright all day before a paraffin lamp; two others were surrounded with strips .15 inch in breadth, and one of these remained upright, the other becoming bowed; the bandages in two other cases were only .1 inch in breadth, and both of these hypocotyls became bowed, though one only slightly, towards the light. The free seedlings in the same pots were all fairly well curved towards the light; and during the following night became nearly upright. The pots were now turned round and placed before a window, so that the opposite sides of the seedlings were exposed to the light, towards which all the unprotected hypocotyls became bent in the course of 7 h. Seven out of the 8 seedlings with bandages of tin-foil remained upright, but one which had a bandage only .1 inch in breadth, became curved to the light. On another occasion, the upper halves of 7 hypocotyls were surrounded with painted gold-beaters' skin; of these 4 remained upright, and 3 became a little curved to the light: at the same time 4 other seedlings surrounded with unpainted skin, as well as the free ones in the same pots, all became bowed towards the lamp, before which they had been exposed during 22 hours.

Radicles of Sinapis alba.—The radicles of some plants are indifferent, as far as curvature is concerned, to the action of light; whilst others bend towards and others from it.* Whether these movements are of any service to the plant is very doubtful, at least in the case of subterranean roots; they probably result from the radicles being sensitive to contact, moisture, and gravitation, and as a consequence to other irritants which are never naturally encountered. The radicles of *Sinapis alba*, when immersed in water and exposed to a lateral light, bend from it, or are apheliotropic. They become bent for a length of about 4 mm. from their tips. To ascertain whether this movement

* Sachs, 'Physiologie Végétale,' 1868, p. 44.

generally occurred, 41 radicles, which had germinated in damp sawdust, were immersed in water and exposed to a lateral light; and they all, with two doubtful exceptions, became curved from the light. At the same time the tips of 54 other radicles, similarly exposed, were just touched with nitrate of silver. They were blackened for a length of from .05 to .07 mm., and probably killed; but it should be observed that this did not check materially, if at all, the growth of the upper part; for several, which were measured, increased in the course of only 8-9 h. by 5 to 7 mm. in length. Of the 54 cauterised radicles one case was doubtful, 25 curved themselves from the light in the normal manner, and 28, or more than half, were not in the least apheliotropic. There was a considerable difference, which we cannot account for, in the results of the experiments tried towards the end of April and in the middle of September. Fifteen radicles (part of the above 54) were cauterised at the former period and were exposed to sunshine, of which 12 failed to be apheliotropic, 2 were still apheliotropic, and 1 was doubtful. In September, 39 cauterised radicles were exposed to a northern light, being kept at a proper temperature; and now 23 continued to be apheliotropic in the normal manner, and only 16 failed to bend from the light. Looking at the aggregate results at both periods, there can be no doubt that the destruction of the tip for less than a millimeter in length destroyed in more than half the cases their power of moving from the light. It is probable that if the tips had been cauterised for the length of a whole millimeter, all signs of apheliotropism would have disappeared. It may be suggested that although the application of caustic does not stop growth, yet enough may be absorbed to destroy the power of movement in the upper part; but this suggestion must be rejected, for we have seen and shall again see, that cauterising one side of the tip of various kinds of radicles actually excites movement. The conclusion seems inevitable that sensitiveness to light resides in the tip of the radicle of *Sinapis alba*; and that the tip when thus stimulated transmits some influence to the upper part, causing it to bend. The case in this respect is parallel with that of the radicles of several plants, the tips of which are sensitive to contact and to other irritants, and, as will be shown in the eleventh chapter, to gravitation.

CONCLUDING REMARKS AND SUMMARY OF CHAPTER.

We do not know whether it is a general rule with seedling plants that the illumination of the upper part determines the curvature of the lower part. But as this occurred in the four species examined by us, belonging to such distinct families as the Gramineæ, Cruciferæ, and Chenopodeæ, it is probably of common occurrence. It can hardly fail to be of service to seedlings, by aiding them to find the shortest path from the buried seed to the light, on nearly the same principle that the eyes of most of the lower crawling animals are seated at the anterior ends of their bodies. It is extremely doubtful whether with fully developed plants the illumination of one part ever affects the curvature of another part. The summits of 5 young plants of *Asparagus officinalis* (varying in height between 1.1 and 2.7 inches, and consisting of several short internodes) were covered with caps of tin-foil from 0.3 to 0.35 inch in depth; and the lower uncovered parts became as much curved towards a lateral light, as were the free seedlings in the same pots. Other seedlings of the same plant had their summits painted with Indian ink with the same negative result. Pieces of blackened paper were gummed to the edges and over the blades of some leaves on young plants of *Tropæolum majus* and *Ranunculus ficaria*; these were then placed in a box before a window, and the petioles of the protected leaves became curved towards the light, as much as those of the unprotected leaves.

The foregoing cases with respect to seedling plants have been fully described, not only because the transmission of any effect from light is a new physiological fact, but because we think it tends to modify somewhat the current views on heliotropic movements. Until

lately such movements were believed to result simply from increased growth on the shaded side. At present it is commonly admitted * that diminished light increases the turgescence of the cells, or the extensibility of the cell-walls, or of both together, on the shaded side, and that this is followed by increased growth. But Pfeffer has shown that a difference in the turgescence on the two sides of a pulvinus,—that is, an aggregate of small cells which have ceased to grow at an early age,—is excited by a difference in the amount of light received by the two sides; and that movement is thus caused without being followed by increased growth on the more turgescient side.† All observers apparently believe that light acts directly on the part which bends, but we have seen with the above described seedlings that this is not the case. Their lower halves were brightly illuminated for hours, and yet did not bend in the least towards the light, though this is the part which under ordinary circumstances bends the most. It is a still more striking fact, that the faint illumination of a narrow stripe on one side of the upper part of the cotyledons of *Phalaris* determined the direction of the curvature of the lower part; so that this latter part did not bend towards the bright light by which it had been fully illuminated,

* Emil Godlewski has given ('Bot. Zeitung,' 1879, Nos. 6-9) an excellent account (p. 120) of the present state of the question. See also Vines in 'Arbeiten des Bot. Inst. in Würzburg,' 1878, B. ii. pp. 114-147. Hugo de Vries has recently published a still more important article on this subject: 'Bot. Zeitung,' Dec. 19th and 26th, 1879.

† 'Die Periodischen Bewegungen der Blattorgane,' 1875, pp. 7,

63, 123, &c. Frank has also insisted ('Die Naturliche wä-gerechte Richtung von Pflanzentheilen,' 1870, p. 53) on the important part which the pulvini of the leaflets of compound leaves play in placing the leaflets in a proper position with respect to the light. This holds good, especially with the leaves of climbing plants, which are carried into all sorts of positions, ill-adapted for the action of the light.

but obliquely towards one side where only a little light entered. These results seem to imply the presence of some matter in the upper part which is acted on by light, and which transmits its effects to the lower part. It has been shown that this transmission is independent of the bending of the upper sensitive part. We have an analogous case of transmission in *Drosera*, for when a gland is irritated, the basal and not the upper or intermediate part of the tentacle bends. The flexible and sensitive filament of *Dionæa* likewise transmits a stimulus, without itself bending; as does the stem of *Mimosa*.

Light exerts a powerful influence on most vegetable tissues, and there can be no doubt that it generally tends to check their growth. But when the two sides of a plant are illuminated in a slightly different degree, it does not necessarily follow that the bending towards the illuminated side is caused by changes in the tissues of the same nature as those which lead to increased growth in darkness. We know at least that a part may bend from the light, and yet its growth may not be favoured by light. This is the case with the radicles of *Sinapis alba*, which are plainly apheliotropic; nevertheless, they grow quicker in darkness than in light.* So it is with many aerial roots, according to Wiesner;† but there are other opposed cases. It appears, therefore, that light does not determine the growth of apheliotropic parts in any uniform manner.

We should bear in mind that the power of bending to the light is highly beneficial to most plants. There

* Francis Darwin, 'Über das Wachsthum negativ heliotropischer Wurzeln': 'Arbeiten des Bot. Inst. in Würzburg,' B. ii.,

Heft iii., 1880, p. 521.

† 'Sitzb. der k. Akad. der Wissensch' (Vienna), 1880, p. 12.

is therefore no improbability in this power having been specially acquired. In several respects light seems to act on plants in nearly the same manner as it does on animals by means of the nervous system.* With seedlings the effect, as we have just seen, is transmitted from one part to another. An animal may be excited to move by a very small amount of light; and it has been shown that a difference in the illumination of the two sides of the cotyledons of *Phalaris*, which could not be distinguished by the human eye, sufficed to cause them to bend. It has also been shown that there is no close parallelism between the amount of light which acts on a plant and its degree of curvature; it was indeed hardly possible to perceive any difference in the curvature of some seedlings of *Phalaris* exposed to a light, which, though dim, was very much brighter than that to which others had been exposed. The retina, after being stimulated by a bright light, feels the effect for some time; and *Phalaris* continued to bend for nearly half an hour towards the side which had been illuminated. The retina cannot perceive a dim light after it has been exposed to a bright one; and plants which had been kept in the daylight during the previous day and morning, did not move so soon towards an obscure lateral light as did others which had been kept in complete darkness.

Even if light does act in such a manner on the growing parts of plants as always to excite in them a tendency to bend towards the more illuminated side—a supposition contradicted by the foregoing experiments on seedlings and by all apheliotropic

* Sachs has made some striking remarks to the same effect with respect to the various stimuli which excite movement in plants.

See his paper 'Ueber orthiotrope und plagiotrope Pflanzentheile,' 'Arb. des. Bot. Inst. in Würzburg,' 1879 B. ii. p. 282.

organs—yet the tendency differs greatly in different species, and is variable in degree in the individuals of the same species, as may be seen in almost any pot of seedlings of a long cultivated plant.* There is therefore a basis for the modification of this tendency to almost any beneficial extent. That it has been modified, we see in many cases: thus, it is of more importance for insectivorous plants to place their leaves in the best position for catching insects than to turn their leaves to the light, and they have no such power. If the stems of twining plants were to bend towards the light, they would often be drawn away from their supports; and as we have seen they do not thus bend. As the stems of most other plants are heliotropic, we may feel almost sure that twining plants, which are distributed throughout the whole vascular series, have lost a power that their non-climbing progenitors possessed. Moreover, with *Ipomœa*, and probably all other twiners, the stem of the young plant, before it begins to twine, is highly heliotropic, evidently in order to expose the cotyledons or the first true leaves fully to the light. With the Ivy the stems of seedlings are moderately heliotropic, whilst those of the same plants when grown a little older

* Strasburger has shown in his interesting work ('*Wirkung des Lichtes . . . auf Schwärmsporen*,' 1878), that the movement of the swarm-spores of various lowly organised plants to a lateral light is influenced by their stage of development, by the temperature to which they are subjected, by the degree of illumination under which they have been raised, and by other unknown causes; so that the swarm-spores of the same species may move across the field of the microscope either to or from

the light. Some individuals, moreover, appear to be indifferent to the light; and those of different species behave very differently. The brighter the light, the straighter is their course. They exhibit also for a short time the after-effects of light. In all these respects they resemble the higher plants. See, also, Stahl, '*Ueber den einfluss der Lichts auf die Bewegungs-erscheinungen der Schwärmsporen*' *Verh. d. phys.-med. Gesellschalt in Würzburg*, B. xii. 1878.

are apheliotropic. Some tendrils which consist of modified leaves—organs in all ordinary cases strongly diaheliotropic—have been rendered apheliotropic, and their tips crawl into any dark crevice.

Even in the case of ordinary heliotropic movements, it is hardly credible that they result directly from the action of the light, without any special adaptation. We may illustrate what we mean by the hygroscopic movements of plants: if the tissues on one side of an organ permit of rapid evaporation, they will dry quickly and contract, causing the part to bend to this side. Now the wonderfully complex movements of the pollinia of *Orchis pyramidalis*, by which they clasp the proboscis of a moth and afterwards change their position for the sake of depositing the pollen-masses on the double stigma—or again the twisting movements, by which certain seeds bury themselves in the ground*—follow from the manner of drying of the parts in question; yet no one will suppose that these results have been gained without special adaptation. Similarly, we are led to believe in adaptation when we see the hypocotyl of a seedling, which contains chlorophyll, bending to the light; for although it thus receives less light, being now shaded by its own cotyledons, it places them—the more important organs—in the best position to be fully illuminated. The hypocotyl may therefore be said to sacrifice itself for the good of the cotyledons, or rather of the whole plant. But if it be prevented from bending, as must sometimes occur with seedlings springing up in an entangled mass of vegetation, the cotyledons themselves bend so as to face the light; the one farthest off rising

* Francis Darwin, 'On the Hygroscopic Mechanism,' &c., 'Transactions Linn. Soc.,' series ii. vol. i. p. 149, 1876.

up, and that nearest to the light sinking down, or both twisting laterally.* We may, also, suspect that the extreme sensitiveness to light of the upper part of the sheath-like cotyledons of the Gramineæ, and their power of transmitting its effects to the lower part, are specialised arrangements for finding the shortest path to the light. With plants growing on a bank, or thrown prostrate by the wind, the manner in which the leaves move, even rotating on their own axes, so that their upper surfaces may be again directed to the light, is a striking phenomenon. Such facts are rendered more striking when we remember that too intense a light injures the chlorophyll, and that the leaflets of several Leguminosæ when thus exposed bend upwards and present their edges to the sun, thus escaping injury. On the other hand, the leaflets of *Averrhoa* and *Oxalis*, when similarly exposed, bend downwards.

It was shown in the last chapter that heliotropism is a modified form of circumnutation; and as every growing part of every plant circumnutates more or less, we can understand how it is that the power of bending to the light has been acquired by such a multitude of plants throughout the vegetable kingdom. The manner in which a circumnutating movement—that is, one consisting of a succession of irregular ellipses or loops—is gradually converted into a rectilinear course towards the light, has been already explained. First, we have a succession of ellipses with their longer axes directed towards the light, each of which

* Wiesner has made remarks to nearly the same effect with respect to leaves: 'Die undulirende Nutation der Internodien,' p. 6, ex-

tracted from B. lxxvii. (1878).
Sitzb. der k. Akad. der Wissensch.,
Wien.

is described nearer and nearer to its source ; then the loops are drawn out into a strongly pronounced zigzag line, with here and there a small loop still formed. At the same time that the movement towards the light is increased in extent and accelerated, that in the opposite direction is lessened and retarded, and at last stopped. The zigzag movement to either side is likewise gradually lessened, so that finally the course becomes rectilinear. Thus under the stimulus of a fairly bright light there is no useless expenditure of force.

As with plants every character is more or less variable, there seems to be no great difficulty in believing that their circumnutating movements may have been increased or modified in any beneficial manner by the preservation of varying individuals. The inheritance of habitual movements is a necessary contingent for this process of selection, or the survival of the fittest ; and we have seen good reason to believe that habitual movements are inherited by plants. In the case of twining species the circumnutating movements have been increased in amplitude and rendered more circular ; the stimulus being here an internal or innate one. With sleeping plants the movements have been increased in amplitude and often changed in direction ; and here the stimulus is the alternation of light and darkness, aided, however, by inheritance. In the case of heliotropism, the stimulus is the unequal illumination of the two sides of the plant, and this determines, as in the foregoing cases, the modification of the circumnutating movement in such a manner that the organ bends to the light. A plant which has been rendered heliotropic by the above means, might readily lose this tendency, judging from the cases already given, as soon as it became useless or

injurious. A species which has ceased to be heliotropic might also be rendered apheliotropic by the preservation of the individuals which tended to circumnutate (though the cause of this and most other variations is unknown) in a direction more or less opposed to that whence the light proceeded. In like manner a plant might be rendered diaheliotropic.

Please note that these transcriptions have been provided by the Darwin Correspondence Project for personal study only. They have not yet been proofread to the Project's publication standards. Many do not yet have footnotes and some contain transcription notes. We are thankful to the Darwin Correspondence Project be allowed access to these unprocessed letters.

Letter 7346 Darwin to Francis Darwin

18 October [1870]^{f1}

The Moat | Tunbridge

Oct 18.

My dear Frank

I enclose cheque for £115: ^{f2}I expected of course to have to aid you as you were so much longer than usual at Cambridge, but the above is rather more than I expected; & what is worse I do not see how you can hold out for this quarter with only £46.⁵⁰.—^{f3}But never, for God's sake, conceal debts from me, & tell me now, whether you owe any more: tell me this & think deliberately when you acknowledge the cheque to Down, where we return on Thursday morning. ^{f4}

As you have not kept accounts it is of course impossible for you know how you have overspent your income.— Let me urge you to make a point of conscience (& then I know it will be done, i.e. if I can persuade you that it is a duty) to keep accounts.— You cannot be sure about paying your debts if you do not, nor can you tell how to economise & spend your income to best advantage. I have never known a man who was too idle to attend to his affairs & accounts, who did not get into difficulties; & he who habitually is in money difficulties, very rarely keeps scrupulously honourable, & God forbid that this sh^d. ever be your fate.— If you once got into habit of attending to your money, & this implies keeping accounts, you w^d. feel it very little trouble. My father, ^{f5} who was the wisest man I ever knew, thought it the duty of every man, young & old, to keep an account of his money; & I very unwillingly obeyed him; for I was not always so bothersome an old fellow as I daresay I appear to you.—

We have been to Leith Hill & came here yesterday & have enjoyed ourselves; though mamma is not very well to day.

This is a wonderfully curious & pretty place. ^{f6}

Your affectionate Father | Ch. Darwin

Footnotes

^{f1} The year is established by the references to the Darwins' holiday at Leith Hill Place and Ightham Mote (see nn. 4 and 6, below).

^{f2} CD listed the amount for "F[rank]" under "Boys" in his account book (CD's Classed account books (Down House MS)).

^{f3} Francis had been at Trinity College, Cambridge since 1866; he graduated in 1870 (ODNB), taking third place in first class honours in the natural science tripos in December (The Times, 19 December 1870, p. 6).

Freshman Seminar 24p: Getting to Know Darwin
Fall 2012 Harvard College/Professor William (Ned) Friedman

F4 The Darwins returned to Down on Thursday 20 October 1870 ("Journal" (Appendix II)). No letter from Francis acknowledging the cheque has been found.

F5 Robert Waring Darwin.

F6 The Darwins were staying at Ightham Mote, a moated medieval manor house, which is in fact closer to Sevenoaks than to Tunbridge; they had left Down on 13 October, going first to Leith Hill Place ("Journal" (Appendix II)).

Letter 10517 Darwin to Francis Darwin

29 May 1876

Hopedene
Monday 30th

S My dear F.

You c^d. make aggregation less intense by using *much* weaker sol. of C. of Ammonia; or by putting minute splinters of glass on glands.

If your case of Teazle holds good it is a wonderful discovery. Try whether pure water or weak infusion of raw meat will bring out the protoplasmic masses.

The closest analogy seems to me that of an independent Amoeba or Foraminiferous animal &c which feeds by involving at any point of its gelatinous body particles of organic matter & then rejecting them— A mass of rotting insects would give such particles.— Perhaps this is your view. But I do not understand what you mean by a resinous secretion becoming slimy++, or about *living* insects being caught. I would work at this subject, if I were you, to the point of death.

If an Amoeba-like mass comes out of cells and catches dead particles & digest them it w^d. beat all to fits true digesting plants.

I never saw anything come out of quadrifids of Utricularia & I c^d. hardly have failed to see them, as I was on look out for secretion. It w^d be a grand discovery. Could you chop up or pound++ scraping from raw meat, or better ^{1/2} decayed wq meat & colour the particles first, & then you c^d see them in the protoplasmic masses; for surely you could hardly expect (unless there is a distinct hole)++ that they sh^d. be withdrawn within cells of glands.— The case is grand—

Are any orifices or orifice visible in cut-off summit of gland? For heaven sake report progress of your work.—

I see in last G. Chronicle another man denies that Dionaea profits by absorption & digestion, which he does not deny. It seems to me a monstrous++ conclusion++— But this subject ought to be investigated

|
Especially effects on seed-bearing— Teazles good. for this—

Yours affection^{ly}— | C. Darwin

No doubt marginal glands of Drosera answer to glands on serratures of other leaves. Probably glands w^d. be found on apices of spikes of Dionaea in bud-state.

Footnotes

Word++ indicates a place where a footnote will be added

Letter 11586 Charles Darwin to Francis Darwin

2 July [1878]

Down, | Beckenham, Kent. | Railway Station | Orpington. S.E.R.

July 2^d

My dear F.

Murie has written to me & you, asking me if you were away to look over your revise, which I have done & found nothing to correct & no criticism to make to you, except that one or two sentences might have been clearer. The whole++ strikes me as excellent & conclusive.— The revise is marked "25 copies": had you not better get more?—

I have sent cheque to a repeated bill from Griffin for 2.10.10— A thermometer has come from Kew, for which I have also paid,— I think 1.11.0.— There is a "*certificate*" with the thermometer.—

I will now go through your letter, but first will say that Bernard seems quite well, though temper not quite so placid as formerly. He has just started very happy & eager in "boobo" with Miss Dorcy & Bessy to the Station.

I think you certainly had better call on Semper; you can say that I asked you to do so to give my very kind remembrances. You know that he has lately returned from America—has travelled much in Philippines & Malay Arch.—has worked on same subjects as Balfour—is a first-rate man, & I liked him, but he is said to have bad temper & to think that everyone is depreciating him.— He dedicated a magnificent essay to me on eyes of a Mollusc,—++ Onchidium.—

I have written to Kew about Porliria: do++ the leaves look like silver under water? Can they shut up to check evaporation; something of this kind occurs (Duval-Jouve)++ with certain grapes: you could try (if you could get permission) by enclosing small branch in well wetted bottle with wet sponge.—

I am glad to hear that Sachs tries "fools experiments".

Do what you think fit about the £10 Telescope, & any other instrument; only do not waste money, as you know your honoured father hates this.

I go on maundering about the pulvinus, cushion or gland whichever you call it, & from what I have seen roughly in the petioles of the Cotyledons of oxalis, I conclude that a pulvinus *must* be developed from ordinary cells, which secrete water into the inter-cellular spaces on the concave side of a bending organ; & that a pulvinus is developed only when the bending has to be continued for a period++ after growth has ceased or nearly ceased.

The cotyledon of Oats bending towards light would, I think, do for observation, & I much wish that you w^d. try either there, or here whether by cutting thin sections about ^{1/10th} of inch above the soil of 2 or 3 cots:, you could measure under high power the diameter of the cells, & observe whether their diameter is the same all round. If you can ascertain their++ average diameter, then cut sections on the most bent part, at same height above soil as before, & see if cells on convave side++ of the stem where bent through heliotropism (or apogeotropism) are smaller than those on convex side.

Freshman Seminar 24p: Getting to Know Darwin
Fall 2012 Harvard College/Professor William (Ned) Friedman

I cannot remember whether such observations have been made, but I think that they are worth making. If there is++ no such action, as I imagine how++ the deuce can a pulvinus be developed in all sorts of Families?

I am trying a slight modification of your dodge; & putting night-light under large bell-glass, standing on little wooden bricks to let some air come in, & I have succeeded in keeping jar of water for many hours between 75⁰ & 80⁰ F;

I have thanked Murie & returned revise.

Footnotes

Word++ indicates a place where a footnote will be added

Letter 11628 Francis Darwin to Charles Darwin

24 July 1878

Botanisches Institut
Würzburg

July 24/78

My dear Father,

I have tried watering Porliera out of doors, I gave four small cans full in the day & next morning it was wide open though for several days before it had been shut. The pot-plant is very unhealthy I am afraid as its leaves are dropping off at the stalk.

I had a little talk to Sachs about heliotropism & he thinks it is no good to moulds to be heliotropic, he says that moulds which you find inside wallnuts or apples are highly heliotropic. He does not remember ever having seen a mould heliotropic in a state of nature but only when you bring them into unnatural conditions: he says potato underground stems are sensitive to light so that they won't grow or hardly at all in light, but he doesn't know whether they are heliotropic or not. I don't quite know what part he means I will talk some more. He says he agrees with Nägeli to a large extent in thinking that certain facts cannot be explained by saying that they are useful or not useful, but he thinks they exist as properties of plants like the power of assuming a certain form is of a crystal. If all plants were heliotropic & none apheliotropic, one might believe this. Stahl is working at the effects of light on the movements of swarm-spores, & he says he can make them heliotropic or apheliotropic as he likes, if puts some in bright sun & others in darkness & then put them both in diffused light, the sun-ones go to the darkest side & the dark ones to the lighter side.

July 25th Something or other stopped me finishing. I was rather seedy last night & didn't appear at the laboratory & this morning Sachs came all the way to see how I was, & drove me to the Labor in his drosky, & was very kind wanting to send me books & red-wine which is here the cure for all evils. I am all square this afternoon though rather too floppy to work. I will talk to Sachs about roots & geotropism. I was very glad to find that Sachs is dead against all the people that find the Descendenz theory in Ray Lamarck, Goethe &c. Sachs says that he believes some ferns of the family Marratiacea+e sleep, & some plants of the family in which Canna is. I think in my list I told you that Guaiacum officinale looks as if it ought to sleep but seemed to be ill, I thought it was a Leguminosa+e, but it is a Zygophyllacea+e & in a lecture Sachs said it slept. He says the pale joint in the leaf sheath of grasses is analogous with the movement organs of mimosa &c but he doesn't know whether they move. He thinks that we have worked at bloom to some extent from a wrong point of view & he believes that leaves want to keep dry in order that they may keep their stomata open to breathe. But why are they so idiotic as to have stomata which shut when they are wet. Perhaps they do that in order to keep their intercellular spaces from being water logged & then found they were stifling themselves & found it a better plan to keep the water off altogether. Or perhaps those leaves produced bloom whose stomata did not shut well in wet. He says that nerves have no bloom & also no stomata. He can give me two references to papers where the number of stomata on the upper & under side of lots of leaves is given, & by seeing about the bloom in these one might make out something. *T. resupinatum* ought to help us, where the stomata differ on the two sides.

Freshman Seminar 24p: Getting to Know Darwin
Fall 2012 Harvard College/Professor William (Ned) Friedman

The result:

ANNOTATIONS

`1.1 I have . . . the stalk.] *crossed pencil*
`1.00 next morning . . . shut.] *scored red crayon*; "Porliera" *added red crayon*
`2.1 I had . . . heliotropism 2.00] "Heliotropism" *added blue crayon*
`2.00 he says . . . heliotropic. 2.00] *double scored red crayon*
`2.00 he says . . . conditions: 2.00] "Theory" *added red crayon*
`2.00 they won't grow . . . crystal. 2.00] *crossed pencil*
`2.00 Stahl . . . lighter side. 2.00] *scored red crayon*
`3.00 Something . . . said it slept. 3.00] *crossed blue crayon*
`3.00 I think] *opening square bracket pencil*
`3.00 I think . . . to be ill, 3.00] "& Bloom" *added red crayon*
`3.00 Zygophyllacea+e . . . it slept. 3.00] *double scored blue crayon*
`3.00 He says . . . move 3.00] "Bloom" *added red crayon*
`3.00 He thinks . . . to breathe 3.00] "Bloom" *added blue crayon*
`3.00 But why . . . altogether 3.00] *double scored blue crayon*
`3.00 Or perhaps . . . something. 3.00] "M. Mer experiments about keeping leaves closed for week under wet" *added pencil*
`3.00 *T. resupinatum*. . . sides. 3.00] *double scored red crayon*

`Top of letter: "Bloom & General Theory"

Letter 12152 Darwin to Francis Darwin

12 July [1879]

Down, | Beckenham, Kent. | Railway Station | Orpington. S.E.R.

D July 12th

My dear F.

I am glad you have tried touching cells, for I sh^d. never have rested until hearing a result of some kind. Was the point kept in contact for some little time? It rejoices me that the Phys. (I forget name) has looked at Dipsacus; I have always thought that you ought to go with that subject.— W^d. it worth while to show him aggregated matter in Drosera in movement, ie in early stage of aggregation? I doubt whether you will succeed in Drosera by contact, as gland only sensitive part & seat of movement chiefly at base of filament.

I have tried in peat++ radicles of Pisum with caustic above & below. There was no difference between the 10 control & 10 touched *above* in their geotropism; but I hardly looked early enough. But of the 10 touched *below*, 3 curved in *opposition* to geotropism—2 or 3 were straight & 5 or 6 geotropic *in slight degree*; so contest wonderfully great.

I can see it will be impossible to try gold-beaten skin on mustard radicles.

It has pleased me that I think I fully understand cause of “Sachs' curvature” of radicles— too long to explain by letter.

I have finished long chapter on Sleeping Plants & sent it to M^r Norman to copy & diagrams to M^r Cooper.—

I am now looking over piles of notes on Heliotropism. By the way I am becoming frightened at changing so well-known a term as Heliotropism & cannot bring myself yet to write “Helism”. Or “Proshelism”. I am more perplexed than ever about life of D^r. D: Hen thinks it very dull, & wants it much shortened & otherwise arranged. Erasmus likes it. Your mother wants parts shortened.— I shall take it on Aug. 1st to Lakes & finish it there.

I am tired— Ever yours | C. Darwin

(What are your plans, if you have any, you degenerate Darwin.) Abbadabba flourishing & drumming

Footnotes

Word++ indicates a place where a footnote will be added