On Geotropism and the Localization of the Sensitive Region¹.

BY

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With Plate XXIX.
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TWO well-known cases of localization of heliotropic and geotropic sensitiveness are described in the *Power of Movement in Plants*. In the case of heliotropism the method is simple and the conclusion clear. The seedlings of *Phalaris* are extremely sensitive to light, but when little caps of an opaque material are placed on the tips of the plants they no longer bend towards the light, or only do so in a very slight degree, as Rothert² has shown. Now since, in this experiment, the part which is capable of curvature is fully exposed to light, it follows that the power of perceiving light resides chiefly in the tip, which thus plays the part of a nerve-centre specialized so as to receive a stimulus and to transmit it to the motor apparatus.

In the case of the gravitation stimulus the case is not so simple: we cannot shelter part of a plant from gravitation as we can from light, and the only plan which at first suggested itself was the removal of the sensitive part by

¹ Paper read before the Botanical Section of the British Association, Dover, Sept. 1899.

² Cohn's *Beiträge*, Bd. vii, 1894.

amputation. The result was that the roots so treated lost nearly or completely their power of curving geotropically.

The conclusion drawn from this experiment, namely, that the root-tip is a sense-organ for gravitation, was much criticized, sometimes unjustly, but in one respect with justice. It was said that amputation might act as a shock and thus prevent curvature. It was this—the difficulty of distinguishing between the removal of the sense-organ, and the disturbing effect of the *operation* of removal—that made Rothert¹ (in his admirable summary of the question) despair of any solution. However, in August, 1894, Pfeffer² read a paper at the Oxford meeting of the British Association, in which he explained his well-known method, now generally associated with the name of his brilliant pupil Czapek³. The root is forced to grow into a little glass stocking, that is to say, a tube closed at one end and bent at right angles, so that while that part of the root which is capable of curvature is horizontal the tip is vertical. Under these circumstances no fresh curvature takes place; the sense-organ at the tip of the root is not stimulated, since it points vertically downwards: it is, as it were, satisfied with its position, and consequently transmits no influence to the bending region. This beautiful method has not been found applicable to other organs, and thus it happens that apogeotropic sensitiveness⁴ has not been localized as far as I know. Rothert⁵ and Czapek⁶ have indeed shown some reason to believe that in the case of *Avena* and *Phalaris* the tip is the percipient part; but neither method is, in my opinion, absolutely convincing.

¹ Flora, 1894, vol. lxxix.

² Annals of Botany, Sept. 1894, p. 317.

³ Czapek, Prings. Jahrb., 1895, p. 243.

⁴ In the case of diageotropic flowers, where the part which is horizontal takes no part in the curvature, there must be transmission of stimulus, as Vöchting (Bewegungen d. Blüten und Früchte) and Schwendener and Krabbe (Abhand. d. k. Preuss. Akad., Berlin, 1892) have shown. Czapek (Pringsheim's Jahrb., xxxii, 1898, p. 274) shows that diageotropic sensibility is to a great extent localized in the lamina of a *Tropaeolum* leaf.

⁵ Cohn's Beiträge, Bd. vii, Heft 1, 1894, p. 187 of reprint.

⁶ Pringsheim's Jahrb., 1898, p. 254.

Rothert's argument is as follows. When a heliotropically curving *Phalaris* is carefully watched, a certain relation between the form of the curvature and the distribution of growth-rate is found to exist. And since the same relation is found in a geotropically curving *Phalaris*, Rothert argues that this relation, being correlated with a certain localization of heliotropic irritability in one case, is probably correlated with similar localization of geotropic irritability in the other case. Whether or no the arguments are sound, the fact is as Rothert and Czapek suppose.

Let us first take the case of an apogeotropic organ in which the power of perceiving the gravitation-stimulus is not confined to one part of the organ, but distributed through all the growing parts, such an organ, in fact, as Sachs describes as typical. Imagine two such organs placed horizontally, one end being supported and the other projecting freely into the air. Let us further imagine that one specimen (*normal*) is fixed by its basal end, while the other (*inverted*) is fixed by its apical end. What will happen? The behaviour of both specimens will be the same, i.e. the free ends of both will bend up and will ultimately point vertically upwards.

An experiment of this sort was made with young dandelion stalks by Frank¹ in 1868, from a different point of view, namely, to show that the geotropic curvatures are not affected by the morphological position of the organ, that is, by whether the free end is morphologically the base or the apex. Noll² has made similar experiments with the flower stalks of *Aconitum* in his researches on the relation between epinasty and geotropism.

All this seems to have little bearing on the question before us, but its connexion is real enough. Imagine that precisely a similar experiment is made with organs in which only the apex is sensitive to gravity, while the basal part is not directly sensitive, but merely bends upwards when it receives a trans-

¹ Beiträge zur Pflanzenphysiologie: I. Ueber die durch die Schwerkraft verursachten Bewegungen von Pflanzentheilen, p. 80, 1868.

² Flora, 1893, p. 360.

mitted stimulus—in fact, imagine that our apogeotropic organ has the qualities which actually exist in roots. What will happen? The normal plant in which the apex is free will behave like the above described specimens—it will bend upwards, and when the sensitive apex is vertical it will cease to be stimulated, and will therefore cease to transmit a stimulus to the bending region.

Now take the other case in which the tip is fixed and the base free: the tip being horizontal is stimulated, and an influence is transmitted to the motor region, so that the basal end begins to rise. But now observe the difference between the two: the curvature of the normal specimen brings the tip nearer and nearer to, and finally into the vertical position, the position of equilibrium. But no amount of movement in the inverted specimen has any effect on the tip, which remains irritated because it remains horizontal. It is clear, therefore, that the motor part of the inverted specimen ought to continue curving *ad infinitum*.

I had concluded that this ought to take place with roots, and made many fruitless efforts to demonstrate the fact, but was foiled by the difficulty of fixing the root by its slippery tip and also by the difficulties caused by the weight of the cotyledons. It was only when I turned to grass seedlings that I succeeded. Rothert¹ has shown that in the seeds of the grasses *Setaria*, *Panicum*, and *Sorghum* the localization of the heliotropic sensitiveness is more definite than in *Avena* or *Phalaris*. The structure of these seedlings is remarkable from the presence of what may be called a hypocotyl—a relatively long stalk between the sheath-like cotyledon² and the grain. This hypocotyl is the part which bends, but according to Rothert it is not sensitive to light, while the cotyledon is sensitive to light but does not bend. These

¹ Cohn's Beiträge, loc. cit.

² I use the word cotyledon (in the sense in which it was employed in the Power of Movement) to mean the hollow sheath-like leaf-structure which precedes the true leaves. Rothert has adopted the term cotyledon in this sense, leaving on one side all questions as to the morphology of the part in question.

species having well-marked localization of light-sensitiveness seemed well suited for my purpose. My procedure is as follows: seedlings of *Setaria*, *Sorghum*, &c., are carefully removed from the sawdust in which they have germinated and placed immediately in water; the best are then selected, the roots are cut off, and each seedling is fixed by pushing its cotyledon into a capillary glass tube, which is supported horizontally in damp air; the seedlings are further supplied with water by means of a fine spray occasionally applied. They grow fairly well, but no doubt owing to the unnatural circumstances, they have not the full vigour and regular behaviour of properly rooted seedlings. A large number of experiments were made in this way, and though many cases occurred in which the seedlings either refused to grow or refused to geotrope, yet on the whole the result was abundantly convincing.

The result was precisely what was expected on the hypothesis that the cotyledon is the sense-organ for gravitation. The free end continued to curve in one direction for days, producing a series of coils like a tendril, or even tying itself in knots. Three or four complete circles is the most I have seen; but if the conditions were more favourable, I see no reason why more turns should not be made. The figures here given (Plate XXIX) are reproduced from accurate drawings kindly made for me by Miss Pertz while the experiments were in progress. The specimens were usually drawn when it was clear that growth, and therefore curvature, had ceased: they are not therefore any guide to the minimum time required for the production of spirals. In the figures the grains are shaded for the sake of distinctness; the limit of the cotyledon is marked by a transverse line in Figs. 1, 3, 4, 5 (*Sorghum* and *Setaria*); the cotyledon in Fig. 2 (*Phalaris*) extends to the grain. The roots were cut off to make the free end of the seedling lighter; adventitious roots, however, often appear as shown on the hypocotyls in Figs. 3 and 4. Fig. 2 shows the simplest case of curvature, Fig. 3 the most complex. Fig. 1 is interesting as showing that, when the cotyledon is only

some 10° – 20° from the vertical, the curvature is in the right direction. Figs. 3 and 4 show that the cotyledon has some power of geotropic movement, there is not therefore an absolute distinction between the motor and sensitive regions. It should be especially noted that the occurrence of prolonged curvature in the hypocotyl does not disprove the existence of some independent geotropic sensitiveness in that part, it merely proves that sensitiveness is overwhelmingly present in the cotyledon.

To those who wish to repeat the experiments, I recommend *Sorghum* seedlings, as they are larger and more vigorous than *Setaria*, and give a higher percentage of corkscrew-like specimens. *Phalaris* also gives the result with considerable certainty. Most of the experiments were made in the dark, but some heliotropic experiments were made. It being known that the heliotropic sensitiveness is, in the species used (*Setaria*, *Sorghum*, *Phalaris*), either quite or nearly confined to the cotyledon, it is clear that the same sort of continued curvature ought to be obtainable by one-sided illumination. For this purpose seedlings were fixed on a klinostat in such a way that they were heliotropically stimulated, though removed from the action of gravity.

Under these conditions they bent over to the light and continued curving just as in the case of the geotropically affected plants. But it is not easy to cultivate the seedlings on the klinostat, and probably on this account the heliotropic experiments did not give such good spirals as those obtained geotropically. Fair results were also obtained without a klinostat.

As a control, seedlings were also grown on a klinostat in a dark room; under these circumstances the seedlings should remain straight. In the first trials this was not the case, and this may possibly have been due to my having examined them too often with a light.

When the jar in which the seedlings were contained was wrapped in black cloth and the klinostat kept in the dark room, the curvatures were almost absent. But this question

needs further experimentation. Another point is worth mention, though here again more work is wanted. If a seedling is fixed by the tip in a vertical glass tube, the apex of the cotyledon being upwards, there seems no reason why curvature should occur, since the sensitive part, the cotyledon, is in the position of non-stimulation. But curvature does occur in this situation, and this may be due to two causes: (1) the tube can only be approximately vertical, and it is possible that the slight stimulus (which analogy suggests must accompany slight obliquity) *being continuous* may be enough to make the hypocotyl bend; (2) it is possible that a certain amount of geotropic sensibility may exist in the hypocotyl; if this were so, it would behave like an ordinary apogeotropic organ, and these are well known to curve up when fixed with all available accuracy, with the free end down¹. But this would only account for a movement through 180° , which would bring the free end vertically upwards. In many of my preliminary experiments the tubes were certainly not strictly vertical; and when especial care was directed to this point, the effect was small, as the following observations show. Seven *Sorghum* seedlings were fixed by their upwardly directed cotyledons, and after two days only gave an average deviation of about 30° from the vertical. The tubes holding the cotyledons were then fixed horizontally, and by the next day six out of the seven had curved through 180° more or less.

Theoretically the method here described is an ideal one for discovering in what position a geotropic organ is most strongly stimulated by gravitation. Sachs², as is well known, supposed that the horizontal is the position of maximum stimulation, a conclusion which has been controverted by Elfving³ and Czapek⁴. In 1888 Miss Bateson and I⁵ pointed out that as

¹ Frank, loc. cit., p. 80. Czapek, however, shows that if a geotropic organ is placed in gypsum, so that it cannot circumnutate, it is not geotropically stimulated when the apex is vertical.

² Arbeiten, i, p. 454; ii, p. 240.

³ Acta Soc. Sc. Fenn., 1880.

⁴ Czapek, Prings. Jahrb. xxvii, 1895; xxxii, 1898.

⁵ Annals of Botany, 1888, p. 65.

soon as a stem or root begins to curve the line of gravitation strikes it at a new angle, and therefore the stimulus is not constant. But with *Setaria* or *Sorghum* the sensitive part remains in one position, so that the stimulus is constant. I have made a number of experiments with grass seedlings at various angles, but I have not been able to come to a definite conclusion, although the result certainly favours the belief that a seedling fixed with the cotyledon pointing obliquely downward is more strongly stimulated than when it is in the opposite position ¹.

The method which I have described I hope to apply to a number of other plants, especially those in which sensitiveness to light is known to be only partially localized at the apex.

I have already tried it with leaves and with diageotropic flowers, but the results are not yet complete enough for publication.

¹ Miss Pertz has tested this point by means of the intermittent klinostat without being aware that Czapek had used this method. With grass-haulms she obtained results similar to Czapek, and there can be no doubt that his result is correct. See Miss Pertz's communication in the present number of the *Annals of Botany*, p. 620.

DESCRIPTION OF FIGURES IN PLATE XXIX.

Illustrating Mr. Darwin's paper on Geotropism.

Figs. 1 and 5. *Setaria* : seven days' exposure.

Figs. 3 and 4. *Sorghum* : six days' exposure.

Fig. 2. *Phalaris* : ten days' exposure.

For further details see p. 571.

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