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THE MOVEMENT OF PLANTS IN RESPONSE TO LIGHT

The Power of Movement in Plants[1] is not one of Charles Darwin's better known books, nor is it one of his most readable. The gradual development of a grand theme and the sustained excitement of *The Origin of Species* are lacking, and all but the most persevering reader would to-day be discouraged by the lengthy descriptions of experiments and their results. Nevertheless, at its publication in 1880, *The Power of Movement* excited considerable interest and *The Times*, despite its previous antipathies, took the occasion to eulogize its author and his work.[2]

One of the investigations reported upon in *The Power of Movement* concerned the movements of plants in response to differences in illumination, a phenomenon then referred to as *heliotropism** since its occurrence in nature was frequently related to movements of the sun. It was in this field that Darwin made significant discoveries which affected the whole development of the subject and which contributed ultimately to the discovery of plant growth substances and the opening of a new and vigorous chapter of plant physiology. It is the purpose of this essay to trace the understanding of the part played by light in causing the movement of plants, to show Darwin's work in relation to that of his contemporaries, and to discuss the developments that have followed from his investigations. We shall, as Darwin, confine ourselves here to the reactions of the higher plants, although the effects of light on the lower, such as the fungi and the algae, are no less interesting and pose problems no less perplexing. By concentrating upon a familiar

* Those movements of plants in which the direction of the movement has a definite relation to the direction of the agent causing it are referred to as *tropisms*.

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and apparently circumscribed biological problem we shall, too, be the better able to appreciate the significance of the changes of outlook that have occurred in half a century of research.

THE RECOGNITION OF LIGHT AS A CAUSE OF PLANT MOVEMENT

The movements of shoots, leaves and flowers in relation to light must have been amongst the earliest observations of civilized man. Theophrastus, writing in the third century B.C., was familiar with the turning of leaves towards the sun,[3] and Varro in the first century B.C. records similar phenomena and also the existence of flowers which follow the course of the sun throughout the day.[4] Pliny, a century later, describes how the leaflets of *Trifolium* (clover) close together at the approach of a storm.[5] In later years Acosta, writing of medicinal plants, mentions the conspicuous folding together of the leaflets and leaves of *Tamarindus indica* L. (tamarind) at evening and their opening at dawn.[6] Other plants, all members of the Leguminosae, among them species of *Acacia*, *Sesbania sesban* (L.) Merr. and *Cassia absus* L., whose leaves show these 'sleep' movements are described by Alpinus in the sixteenth century.[7]

The first general discussion of movements of this kind and speculation as to their cause is not to be found until the end of the seventeenth century. By this time it had already been shown that the opening of the flowers of *Anemone* could be brought on by heat in the absence of light.[8] In Oxford, a Dr Sharrock, 'very knowing in vegetables and all pertaining therunto', had grown plants before an open window and, by reversing them after an interval of time, caused their stems to assume S-shaped curves, or bend to any position which his friends cared to indicate.[9] These experiments were known to John Ray, the illustrious British botanist, and he was led to regard the bending of stems towards the light as being caused, not by a difference in illumination of the two sides of the stem, but by a difference in temperature. The more strongly illuminated side is that closer to the fresher air; it follows, he argued, that its temperature will be lower and its growth consequently slower than that of the shaded.[10]

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Light as a Cause of Plant Movement

The reluctance shown by Ray to ascribe heliotropic curvature to a direct effect of light upon the plant persisted throughout the eighteenth century, possibly because light had not been one of the Aristotelian elements which played so important a role in medieval philosophy. Even Stephen Hales, for example, who occupies an honoured place in the history of botany for his experiments in the ascent of sap, attributed this curvature to a greater loss of water by evaporation from the illuminated side of a stem than from the shaded,[11] causing shrinkage of the former. Linnaeus, aware of the movements of flowers[12] and leaves[13] in relation to light, observed that the 'sleep' movements of leaves at dusk were not caused by a fall in temperature, since they also took place in the more or less constant temperature of a conservatory,[14] but he was at a loss for an alternative explanation. The Genevan naturalist Bonnet,[15] in the middle of the eighteenth century, appears to have been the first to carry out extensive experiments on the nature of plant movements, although, of course, by modern standards these experiments are extremely confused. His conclusions were that movements were principally determined by warmth and moisture, particularly the latter, and in arriving at this position, which his experiments hardly justify, he was clearly elaborating the earlier views of the French Academician Dodart.[16] From Bonnet's own experiments, Duhamel,[17] a more penetrating observer, appears to have concluded that heliotropic curvatures were, in fact, dependent upon light alone, but his explanation of the manner in which these curvatures were caused had no greater validity than Bonnet's. He envisaged the existence of 'vapours' within the plant, the quantity and flow of which could be influenced by external factors, and it was to these that the movements of the plant could be ascribed.

These early attempts to explain the behaviour of plants in light, though imperfect, were, nevertheless, the beginnings of an attempt to link observable phenomena with tangible causes. Refined methods of experimentation, together with advances in the physical sciences, led to much more rapid advances in the nineteenth century. Although it would be illegitimate to attempt to divide the history of science into centuries, it is true that here the difference in outlook between the eighteenth and nineteenth is profound. Whereas before the turn of the century methods were crude and thinking confused,

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from the beginning of the nineteenth century to the present there can be traced the steady development of fruitful ideas and profitable experimentation. In the study of the effects of light on vegetation, the reluctance to consider light itself as an active factor, so conspicuous in Ray and Bonnet, disappeared with the eighteenth century.

De Candolle, one of the first in the nineteenth century to experiment on the effects of illumination, and, incidentally, the first to use the term 'heliotropism', regarded the bending of unequally illuminated stems as part of the general phenomenon of 'etiolation'.[18] A plant grown in darkness lacks chlorophyll and its stems are usually extremely elongated. (It is now known that these two effects, although commonly associated, are not necessarily related.) According to de Candolle, to put his view in modern terms, in an unequally illuminated stem the metabolism on the illuminated side is more intense; as a consequence, the illuminated cells mature faster and extend less than the shaded and a curvature results. The shaded side can, in fact, be regarded as partially etiolated. This theory, although it explained curvature towards light (now referred to as *positive phototropism*), would not account for curvature away from light (*negative phototropism*), such as is seen in those roots which react at all to light, and in certain stems, such as underground rhizomes.

Shortly after its publication, Dutrochet challenged the theory, on other grounds, as the result of an ingenious experiment.[19] Taking a stem of *Medicago sativa* L. (lucerne) which had bent towards the light, he split it into two longitudinally, perpendicular to the plane of bending. The side adjacent to the light curved still more, while that away from it straightened, whereas, argued Dutrochet, if elongation of the shaded side was, as maintained by de Candolle, the cause of curvature, the reverse result should have been obtained. Dutrochet consequently concluded that light was affecting only the illuminated side and that it was the shaded that was passively involved. His theory to account for phototropic bending supposed a contraction of the contents of the illuminated cells, leading to a contraction of the cells themselves, arising from metabolic changes attributable to light, and a difference in the sizes of the cells in different regions of the plant. In the stem, for example, he envisaged a diminution in the sizes of the cells from the outside towards the

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centre. The contraction of the larger cells was greater than that of the smaller and, in unilateral illumination, curvature towards the illuminated side was inevitable. In roots the gradation in cell size was supposed to be reversed, and consequently the curvature. But there was no anatomical support for this view and, ingenious though Dutrochet's theories were, they had to be discarded. In fact, as a result of careful measurements, it had become clear by the middle of the nineteenth century that unilateral illumination caused a difference in the growth of the two sides of the stem. Curvature was, in consequence, confined to the extending regions, a fact which had been demonstrated unwittingly by Sharrock two centuries earlier. De Candolle's interpretation of the manner in which light acted upon the stem was, in essence, generally accepted at this time, even by Sachs, although his view changed radically later. It was, nevertheless, also clear, largely as a result of the work of Sachs and his students, that the question was more complex than imagined by de Candolle. Etiolation had, in fact, several different aspects, only one of which was the effect of light on the extension of individual cells.

By 1874 the writings of Sachs[20] were turning attention to the possibility of a direct effect of light on the extensibility of the cell wall, or of changes in the protoplasm of the cell which might affect the properties of the wall. In the growing region of a stem, he suggested, light promoted the growth in thickness of the cell walls and consequently the extension of the cells by the absorption of water was impeded. Sachs's student, de Vries, later maintained that in phototropic curvature there was, apart from any effect upon the cell wall, an actual increase in turgor on the shaded side contributing to its greater extension.[21] There was, too, a new element entering Sachs's writings at this time, for he had noticed that the more nearly perpendicular was the direction of light entering the cells of a normally upright stem to the longitudinal axis of those cells (and consequently of the stem), the greater was its phototropic effect. This, he pointed out, was quite similar to the effect of gravity, in that both agents cause the longitudinal axes of the cells they act upon to come into alignment with their own line of action. In addition, Francis Darwin, Charles's third son, and his assistant in all his botanical experiments towards the end of his life, working in

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Sachs's laboratory in 1881 had shown that the roots of *Sinapis alba* L. (white mustard) grew slower in the light than in the dark.[22] But these roots were indisputably negatively phototropic and, according to Candollian ideas, should have shown the reverse behaviour to account for the receding curvature.* The behaviour of stems and roots in relation to light thus appeared the precise reverse of that in relation to gravity and Sachs, developing an idea of Frank,[25] came to regard phototropism and geotropism as similar phenomena, differing only in the nature of the initial stimulus.[26]

It is to the credit of Wiesner, working in Vienna at this time, that he was the first to investigate the relation between the amount of light falling on a shoot and the subsequent curvature.[27] He was also the first to show that in the absence of oxygen no curvature occurred at all,[28] indicating that the bending process required a supply of energy from within the plant in addition to any received from the light. The mechanical cause of the bending he considered to be changes in turgescence of the cells in the growing region, probably brought about by light, coupled with an increase in the extensibility of the cell walls. Wiesner's quantitative approach was later developed extensively by the school of F. F. A. C. Went at Utrecht.

Pfeffer must also be mentioned here for, although he himself did little directly concerned with phototropism, it is to him that the elaboration of the Darwins' experiments is largely due. Having earlier worked with Sachs at Würzburg, he studied, amongst other physiological problems, those concerned with the periodic movements of leaves, such as those of *Desmodium gyrans* DC. (telegraph plant) and other members of the Leguminosae. At this time he attributed the phototropic responses of higher plants to changes in the turgescence of the cells, due to osmotic effects. He did not share with Sachs his later view of the all-importance of the direction of the light, nor did he deny, as did Sachs, the possibility of one and the same structure displaying both positive and negative phototropism according to the intensity of the light, a property first

* A suggestion that the tissues of the root, being translucent, acted as a lens, so that the light was concentrated on the shaded side, was later shown to be correct.[23] Even so, this concentration of light is sharply limited and the total illumination of the shaded side is less than that of the illuminated.[24]

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demonstrated in *Lepidium sativum* L. (cress) by Müller.[29] Later, in 1887, he settled at Leipzig and founded the school which was to have such a profound influence on the study of plant movements. Influenced, as we shall see, by Darwin, he, more than any of his contemporaries, now developed the view that tropisms were manifestations of Irritability, a fundamental property of living matter of all kinds. The property of Irritability, which encompasses those processes by which living matter reacts to disturbances in such a way as to maintain its equilibrium, was well known as a philosophical notion,[30] but for Pfeffer became one of the bases of physiology. In the enlarged edition of his *Pflanzenphysiologie* of 1897,[31] Pfeffer formulated the principles of Irritability with a clarity and precision which, even though the value of the concept is now questioned, are conspicuous in the writings of the period.

That phototropism, along with geotropism, was a response of this kind was envisaged by Dutrochet as long ago as 1824,[32] but subsequently ignored by him and overlooked until noticed by Pfeffer. By 1880 it had become general to regard tropic responses to light as a manifestation of Irritability; even Sachs who, like de Candolle, at first saw the response to light as due to physical changes forced on to the plant by the external agent, came to accept the notion without demur. Wiesner, however, remained a conspicuous exception.

The Originality of Darwin's Work

We are now in a position to consider Darwin's contribution to the study of phototropism. *The Power of Movement in Plants* was the result of some five years' experimenting, in which Charles was assisted by Francis Darwin, just down from Cambridge.* It was, in Darwin's own words, 'a tough piece of work' which followed directly from *The Movements and Habits of Climbing Plants*. It is clear from the preface and footnotes that Darwin was familiar with the work of Sachs at Würzburg, with the current theories of growth of cells and with the experiments of Wiesner in Vienna. These, however, are mentioned only incidentally; Darwin's whole approach to the problem of movement was different from that of the Conti-

* The writing of the book appears to have been entirely the work of Charles Darwin.[33]

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nental workers and his inspiration lay elsewhere. Whereas Sachs, Wiesner and Pfeffer were seeking to explain the behaviour of plants in terms of physical and chemical causes, Darwin turned to plant movements as yet a further demonstration of the interrelatedness of living plants and their common origin. Although he accepted fully that growth curvatures were an expression of Irritability, for him it was sufficient to demonstrate that these phenomena had advantageous consequences. He envisaged the response as having become linked to the stimulus in the course of evolution, so producing an organism better fitted in the struggle for existence.

It will be recalled how in his study of climbing plants Darwin had demonstrated that the apices of these plants, when not in contact with a support, described remarkable sweeping movements. 'In accordance with the principles of evolution', wrote Darwin in 1881, 'it was impossible for climbing plants having been developed in so many widely different groups unless all kinds of plants possess some slight power of movement of an analogous kind'.[34] His experiments do, in fact, reveal that growing stems, roots and leaves show in general irregular rotatory movements (*circumnutation*). That the striking movements of the stems of climbing plants were a development of this common property was and still is an acceptable hypothesis. Darwin, however, made a further claim, namely that the movements associated with light and gravity were also modified forms of circumnutation, a generalization that was not adequately supported by his evidence, as Francis Darwin was forced to admit in later years.* It was, nevertheless, probably Darwin's preoccupation with the property of circumnutation that led him to pay close attention to the apices of stems and roots in his experiments on phototropism, although Ciesielski's demonstration[36] some years earlier that the roots of *Pisum* would turn downwards in the normal way only if their tips were intact may also have been in his mind.

Darwin used as material for his research either young seedlings, where the absence of a mature stem simplifies observation, or germinating seeds of cereals and grasses. In the latter plants, belonging to the family Gramineae of the Monocotyledons, the stem, unlike that of most Dicotyledons, shows little elongation until flowering. That which passes for a stem in the vegetative state

* According to Blackman.[35]

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consists principally of a tube formed of sheathing leaf bases. This peculiarity is reflected even in the embryo, and the growing point of the young stem is contained within a tubular structure called the *coleoptile*. As the seed of a cereal or grass germinates, the coleoptile behaves like a stem and its summit, solid and pointed, is pushed up through the soil to the surface (fig. 1). At this stage the first normal leaf, formed from the enclosed growing point, soon ruptures the coleoptile and leaves it a withered remnant at its base. In its actively growing stem-like phase, the coleoptile shows the phototropic responses of a stem and it forms, as Darwin found, a very convenient experimental object, since it is easily obtained and consists of little more than a tapering hollow cylinder of tissue, uncomplicated at its tip by rudimentary leaves or branches. Moreover, the way in which it grows can be easily seen; there is initially an increase in the number of cells forming the coleoptile, but after it has reached approximately 1 cm. in length, all subsequent growth is exclusively by cell elongation, only the mature cells at the base remaining unchanged.[37] The coleoptile is not circular in transverse section, but oval, with one broad side adjacent to the seed. In critical phototropic experiments it is necessary to know the orientation of the coleoptile in relation to the light, because the broad side will absorb significantly more radiation than the narrow.

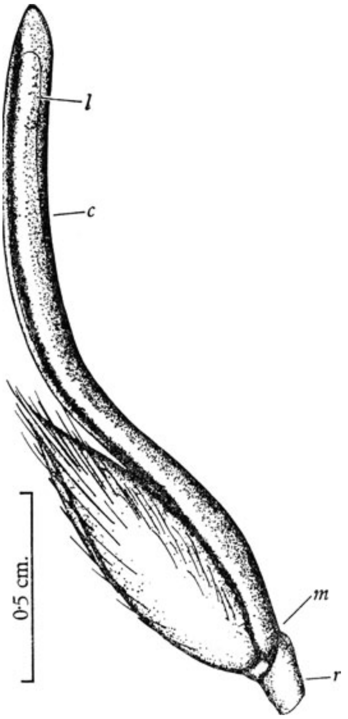

Fig. 1. The germinating seed of *Avena sativa*, the glumes (husk) removed. *c*, coleoptile; *l*, first leaf enclosed within the coleoptile; *m*, mesocotyl; *r*, coleorhiza containing first root. The coleoptile has become erect through the action of light and gravity. Note the flat side adjacent to the seed.

The Darwins' first experiments on phototropism were concerned

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with the effect of unilateral illumination on the circumnutation of seedlings and coleoptiles. They demonstrated that the movement towards the source of the light was superimposed upon the circumnutation, suppressing the latter completely when the light was strong. They also tried the effect of blackening one half of a coleoptile longitudinally and placing it so that one of the vertical boundaries of the blackened area was in the middle of the illuminated side, the other boundary, diametrically opposite, forming the mid-line of the shaded side. In these circumstances the plane of the curvature of the coleoptile was deflected by approximately 45° from the window. This result clearly throws doubt on Sachs's directional theory for, according to Sachs, the curvature of such an organ should be such as to bring its axis into alignment with the radiation, which here must have been principally from the window. Darwin was either unaware of this latter theory of Sachs or chose not to comment upon it, using this experiment solely to show that light acts over the whole stem and not just along a narrow longitudinal strip adjacent to the source.

The first observations which suggested that the response to light was not entirely local, but in part transmitted, were made upon the coleoptiles of *Phalaris canariensis* L. (canary grass).[38] The Darwins were struck with the way in which these coleoptiles (as other coleoptiles and seedlings), when exposed to light, bent first at the tip, the bending then travelling down the coleoptile for some 2 cm. in such a way that the alignment of the tip in relation to the light remained unchanged. They demonstrated that the mechanical transmission of the bending was not an essential part of the phenomenon, for, where the upper parts of the coleoptiles were constrained within narrow glass tubes, the bending continued to appear in the free part below.

Two further experiments led them to the view that the upper part of the coleoptile determined the bending of the lower. In the first, approximately 1·5 to 4·0 mm. were cut from the tips of coleoptiles; with the smaller decapitations there was diminished sensitivity to light, but removal of 2·5 to 4·0 mm. destroyed the sensitivity altogether. In the second, to combat the reasonable objection that wounding from the amputation might have interfered with the sensitivity, the apex was shielded from light by blackened tubes or caps of thin tinfoil. These experiments led to the conclusion

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