DARWIN'S BIOLOGICAL WORK

SOME ASPECTS RECONSIDERED

CENTENARY ESSAYS BY

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Solanum rostratum Dun. Two flowers of the racemose inflorescence showing the asymmetry of the reproductive parts. The style curves downwards and always lies between the lower enlarged stamen and the main axis of the inflorescence so that adjacent flowers of the inflorescence are mirror images of each other. See note on p. ix.

LIST OF PLATES

PREFACE

On 24 May 1859, reviewing the papers which had been read before the Linnean Society of London in the preceding session, the President, Thomas Bell, is recorded in the history of the Society as having regretted that the session had passed without being marked 'by any of those striking discoveries which at once revolutionize, so to speak, the department of science on which they bear', or which 'shall produce a marked and permanent impress on the character of any branch of knowledge'. Nevertheless, one contribution was certainly 'to produce a marked and permanent impress', for, on 1 July 1858, the communications of Charles Darwin and Alfred Wallace *On the Tendency of Species to form Varieties* had been read to the Society. Few judgments can have proved so erroneous as that of Thomas Bell.

The story of the publication in the following year of *The Origin of Species* and of the controversy which ensued has often been told. It is less well known that feeling was intense even within the Linnean Society and several Fellows withdrew from it because Darwin was not summarily expelled. Yet, within ten years, the Council of the Linnean Society was more rigorous in its interpretation of 'Darwinism' than Darwin himself. This humble man, who, in diffidently sending specimen chapters of *The Origin of Species* to his publisher, requested that after perusal they be sent to a 'lady being excellent judge of style [who] is going to look out for errors for me', was indeed beginning to effect a revolution.

Yet we should not think of Darwin solely in relation to evolution and natural selection. He was in fact one of the foremost geologists of his day and his early papers made noteworthy contributions to that science. His work came to encompass the whole field of biology, but was never superficial. Several of his publications, for example *The Various Contrivances by which Orchids are fertilized by Insects*, have not yet been superseded. It is true, of course, that evolution came to be a unifying principle in all Darwin's scientific work, but such unifying principles are a great stimulus to biological progress.

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NOTE

Superior figures in the text refer to the Notes and References at the end of the book (p. 311).

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P. R. BELL

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*.**

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]

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, 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 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