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HARRY ALFRED BORTHWICK

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A Biographical Memoir by

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H A Borthwick

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BY STERLING B. HENDRICKS

HARRY BORTHWICK was born in Otsego, Minnesota, a small village about thirty miles from Minneapolis. His mother, Frances, was the aunt of Hubert Humphrey, who became Vice-President of the United States, and the sister of Harry B. Humphrey, a leading phytopathologist. It was the latter who influenced Harry to enter the School of Agriculture of the University of Minnesota in 1917. When his parents moved to San Jose, California, in 1919, Harry transferred to Stanford University, where he majored in botany. After receiving a B.A. degree in 1921, he continued in graduate school with research interest in plant morphology, leading in 1924 to an M.S. degree. Harry became a research assistant in the Division of Botany of the Agriculture School of the University of California at Davis in 1922, shortly before his marriage to Myrtis Hall.

At Davis, Harry was first an assistant to and later a close associate of E. C. Robbins, a botany teacher and author of a well-known textbook in that field, who was engaged in research on crop plants. Harry continued working toward a doctorate at Stanford, devoting his attention mainly to the reproduction and development of both higher and lower plants. The position at Davis also required attention to basic and applied aspects of vegetable crop plants. These endeavors fashioned the pattern of his later scientific efforts. The main themes were: A wide knowledge of the functioning of plants of all types, with close attention to minute details of form and development and concern for ways to turn the more basic work to practical use in agriculture. Harry and Katherine Esau divided the work at Davis on the development of the vegetable crops of California—asparagus, beans, sugar beets, and carrots, among others.

One of the first undertakings at Davis was the study of the development of lettuce from ovum fertilization to seed maturity. This classic work, often referred to over the course of the last fifty years, also served as a background for later work on seed germination. In the early 1930s, Harry worked on thresher injury to beans and on carrot seed development. The latter study was undertaken with L. T. Emsweller, who left Davis in 1935 to take charge of work in floriculture at the U.S. Department of Agriculture station in Beltsville, Maryland.

Shortly after Emsweller went to Beltsville, the Congress passed what was known as the Bankhead–Jones Act, providing for research in depth in several aspects of agriculture. One of the most fundamental discoveries in biology had been made in 1920 in the Department of Agriculture by H. A. Allard and W. W. Garner. This was photoperiodism, or dependence of plants and animals on the length of day. In 1936 a decision was made to establish under the Bankhead–Jones Act a small group to look further into the nature of photoperiodism and its significance in agriculture. Because the photoperiodic response in plants partly regulates flowering, it was thought that progress might best result from attention to the morphological aspects involved in plants changing from vegetative to reproductive growth and to the underlying physiology. Emsweller recommended Harry Borthwick to undertake the work. Marion W. Parker, who was then teaching plant physiology at the nearby University of Maryland, was invited to join the effort.

Borthwick and Parker foresaw that an understanding of photoperiodism would probably require growing plants under closely controlled environmental conditions in order not to confound responses to light with temperature and other changes. Such controlled conditions, which are now commonplace, had not previously been obtained except in a very limited way at the Boyce–Thompson Institute. They decided that a.c. carbon arc lamps, developed for treatment of tuberculosis, were the only available type giving the required high light intensities. Growth rooms were constructed with such lamps as light sources, but the plants grown in them were poorly developed compared to those from the field. Because the rare-earth loaded carbons gave radiation that was relatively more intense in the blue parts of the spectrum than in the red, Borthwick and Parker experimented with supplementary radiation from incandescent filament lamps to enhance the red. The resulting growth of the selected plants was entirely satisfactory and of low variability. The high requirement for red light anticipated what later became known as the high energy reaction for plant growth, the exact nature of which is still much debated.

On H. A. Allard's recommendation, a soybean and cocklebur variety sensitive to light and requiring short days for flowering was selected. Barley *var. Wintex* was chosen as a long-day plant. The findings by others that the leaf was the receptor organ for the effective light and that transport of the stimulus to the terminal of the plant required phloem continuity were soon verified. A major discovery at this juncture was the effectiveness of short irradiations near the middle of long nights in preventing flowering response. In the 1940s, the tendency of those interested in control of flowering was to attempt detection of florigen, a hypothetical hormone. Parker and Borthwick considered this a poor approach, offering little opportunity for examination by experiment. They were more inclined to conduct quantitative studies of the involvement of light in the flowering process. This would require measurement of action spectra. Wanting advice on methods and instrumentation for such an undertaking, they sought me out as one who might be interested. We soon began an informal cooperation that would endure for the next twenty-five years and unfold a whole new area of knowledge about plants.

Action spectra for short-day plants were obtained in 1945. These indicated the presence of a blue pigment related to phycocyamin of the blue-green algae as the receptor for light. Long-day plants were found to have the same action spectra but with the opposite flowering response. With this finding of universality in control of flowering, attention was turned to other responses to light. One of these was etiolation of plants growing in darkness. When examined, with cooperation of F. W. Went, who was visiting Beltsville, it, too, had the action spectrum for flowering control. Many students of plant growth at the time were little inclined to believe such findings, but some came to Beltsville on their own volition to observe. Harry's awareness, open mindedness, and coúrtesy encouraged an informality of approach and devotion to finding the meaning of things.

The most basic finding, however, came from close at hand in an unexpected way. For more than a century, many seeds were known to require light for germination. Eben and Vivian Toole, who worked with seeds in a laboratory adjacent to the room where the action spectra were measured, proposed examining the promotion of lettuce seed germination. The flowering-action spectrum again was found. But, most important, the potentiated action of red light, which required a day for display, was found to be immediately reversible by a short exposure to far-red radiation. This indicated that the photoresponsive pigment was photoreversible and thus had at least two forms, only one of which was biologically effective. When attention was returned to flowering and etiolation, their potentiations were also seen to be photoreversible. The action spectra, moreover, were closely the same for all responses.

Harry had throughout these years paid close attention to the agricultural implications of the findings. These were chiefly applicable to the control of weeds and, through plant breeding, to many crops such as soybeans. With H. M. Cathey, who had succeeded Emsweller in floricultural work at Beltsville, Harry studied the control of flowering of poinsettia and chrysanthemum, which came into wide use in flower production. With A. A. Piringer and R. J. Downs, he studied the effect of light on woody perennials (trees and shrubs). These studies clearly emphasized the high energy action of far-red radiation, which had first been sensed in the development of lighting for growth rooms. The main response was control of the dormancy of buds by moderate periods of radiation. This is one of the many aspects of photoperiodism. The years were fruitful ones, with rewards wherever attention turned.

The reversibility of photoresponsiveness was the keystone to progress about photoperiodism in the molecular sense. Through its use the product of molecular absorbancies of the receptive pigment and the quantum efficiency for conversion could be measured after the method used by Otto Warburg in work on cytochrome oxidase. In this way the pigment was established as deeply colored and present only in minute amounts in both albino and green plants long before it was seen. It, moreover, was probably a protein.

Although the work on photoperiodism was steadfastly supported for fifty years in the U.S. Department of Agriculture, the many pressures of limited funds militated against enlarging the effort when promising paths of investigation arose. Harry, foreseeing the possibility that great rewards might result from biochemical applications, used his limited funds to induce H. W. Siegelman to join the group. In a few years it became obvious that the receptive pigment could only be detected in vivo by its photoreversibility. But, would reversibility work in vitro to serve for assay in an attempted isolation?

Again, nearby cooperation was at hand. Karl Norris, an engineer working in the field of agricultural marketing, had developed spectroscopic methods for measuring the quality of apples. The method involved measuring minute absorbancies at two frequencies in optically dense media. With Norris and his associate, Warren Butler, the method, when applied reversibly, immediately indicated the presence of the pigment in etiolated maize tissue, both before and after grinding. With the assay perfected, isolation of the pigment was finally achieved.

With the pigment, by then known as phytochrome, identified, Harry again looked toward finding some clue to its actions. He knowingly left the inviting molecular approaches to others of suitable interest and training. One unexpected clue to the method of action was quick display of response, rather than the long delayed ones that had previously been studied. This was demonstrated by J. C. Fondeville, who had come from France to work temporarily in Beltsville. He had been studying the diurnal movement of mimosa leaflets as an example of photoperiodism or biological rhythm, a favorite topic of P. Bert in Bordeaux more than a century earlier and of Charles Darwin and his son, Francis, in their *Power of Movement in Plants.* It was soon established that the leaflet closure upon placing mimosa plants in darkness could be prevented by changing the phytochrome from the far-red to the red-absorbing form. The response was displayed within ten minutes and was photoreversible. This established the role of phytochrome in the control of turgor with most likely action on a controlling membrane. Others soon turned their attention to this inviting approach and are now elaborating it in many promising directions. Harry by then (1969) had retired, fully aware that in this long and often lonely journey others now stood on the threshold of opportunity to look even deeper and perhaps in the end to find out more about differentiation in flowering, which is still elusive.

In 1972, in his last publication, Borthwick looked back over thirty-five years of research on photoperiodism in plants. Although fully aware of the measurement of time by plants, he had never accepted what others have called "the biological clock," or endogenous rhythm. These were meaningless words to him—words that did more to obscure than to enlighten, and little to advance, experimentation. Also, he had rejected "florigen," the postulate flowering hormone, as more of the imagination than of fact. Instead, the course he had charted into the core of photoperiodism consisted of a sound mixing of biological understanding and physical experimentation.

Honors came to Harry Borthwick in his later years. He was elected to the National Academy of Sciences in 1961. He was President of the American Society of Plant Physiologists for a term and the recipient of its highest honor, the biennial Stephen Hales Award, and of a life membership. He received the Hoblitzelle Award for distinguished service to agriculture, the Joachem–Hafiz award from Switzerland, and the Distinguished Service Award from the U.S. Department of Agriculture. His greatest pleasure and deepest recognition, however, came from his many associates in research. They knew and honored him for his unselfish dedication to a central effort.

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KEY TO ABBREVIATIONS

Am. J. Bot. = American Journal of Botany
Am. Nat. = American Naturalist
Ann. Bot. = Annali di Botanica
Annu. Rev. Plant Physiol. = Annual Review of Plant Physiology
Bot. Gaz. = Botanical Gazette
Florists' Rev. = Florists' Review
Plant Physiol. = Plant Physiology
Proc. Am. Soc. Hortic. Sci. = Proceedings of the American Society for Horticultural Science
Proc. Int. Seed Test. Assoc. = Proceedings of the International Seed Testing Association
Proc. Natl. Acad. Sci. USA = Proceedings of the National Academy of Sciences of the United States of America
Proc. Plant Propag. Soc. = Proceedings of the Plant Propagators Society
U.S. Dep. Agric. Misc. Publ. = U.S. Department of Agriculture Miscellaneous Publication

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