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RALPH H. WETMORE

1892—1989

A Biographical Memoir by
JOHN G. TORREY

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Biographical Memoir

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April 27, 1892–April 28, 1989

BY JOHN G. TORREY

IN THE PERIOD immediately after World War II a renewed effort began in the botanical world on the nature and causes of plant morphogenesis. In the Department of Biology at Harvard University were assembled faculty members especially qualified to pursue collaboratively the problems of understanding plant development, using structural-analytical and biochemical-biophysical tools in new and revealing ways. On the physiological-biochemical side was K. V. Thimann with his interests and insights into plant hormones; on the structural-biophysical side was I. W. Bailey with his wide experience in structural-functional aspects of secondary growth in plants. In the middle and providing both the bridge and the cement was R. H. Wetmore with his understanding of the anatomical-cytological basis for meristematic activity.

Ralph H. Wetmore was born in Yarmouth, Nova Scotia, on April 27, 1892, of loyalist forebears who had moved from New England to Canada at the time of the American Revolution. His father was foreman of a wood-working plant in this maritime community, his mother an enthusiastic gardener and homemaker for the four children of which Ralph was the eldest.

After finishing the public school preparatory course for

college in Yarmouth, including the twelfth-year alternative to first-year college, Ralph at age sixteen began his teaching career at Pleasant Valley, near Yarmouth, in a one-room country school with twenty-six students of all grades, one through eleven. At age eighteen he took a year at Normal School to obtain his teacher's license, then taught in a public school in Milton, Nova Scotia, for four years.

During the war years 1914–18, Ralph was in and out of the army with physical disabilities. He enlisted on at least two different occasions but was rejected for overseas service with varicose veins on his legs and color-blindness. Most of the war he served in the divisional headquarters of the Canadian Army in Halifax, achieving the grade of sergeant.

Immediately after the armistice he entered Acadia University in Wolfville, Nova Scotia, late in the academic year of 1918, together with many other veterans anxious to pick up their life-work. He completed the undergraduate course in two and one-half years, receiving his B.Sc. with honors in biology in 1921. During this time his interests in botanical science were stimulated by the excitement created in the one-man botany department of Professor H. G. Perry, graduate of Harvard University. With Perry's encouragement Ralph applied for graduate study and entered Harvard in September 1921, working with Professor E. C. Jeffrey with whom Perry had taken his degree. In 1923 he married Marion G. Silver of Dayspring, Nova Scotia. He completed his Ph.D. in 1924, working in the field of evolutionary plant morphology and anatomy. His doctoral thesis was on the anatomy of dicotyledonous woody stems and the aerenchymatous system related to lenticels, published in 1926. During his graduate study he spent a summer in Labrador as botanist with a Canadian government expedition characterizing the flora around Lake Melville. After taking his doctorate, Ralph was awarded a National Research

Fellowship in the biological sciences at Harvard studying the cytogenetics and taxonomy of the genera *Aster* and *Solidago*, based largely on breeding experiments. In 1925 he returned to Acadia University to an appointment as assistant professor in biology, with the expectation that he might settle there and succeed Professor Perry who was nearing retirement.

In 1926 he received the offer of an assistant professor position in botany at Harvard by then-chairman, Professor Oakes Ames. Wetmore was persuaded by Professor Perry and the president of Acadia, Dr. Patterson, that his going to Harvard was not only an important and wise career choice but also that it would continue access of Acadia graduates to graduate study at Harvard. With some reluctance Ralph accepted the position. In 1926 he and his young family moved back to Cambridge, where he renewed what became a life-long association with the botanical sciences at Harvard University.

Immediately, Wetmore was drawn into full-time activity in teaching and departmental administration at which he was clearly adept. He taught the elementary course in botany with an enrollment of over a hundred students and was responsible for the laboratory of the botanical half of a large general course in biology offered for non-science concentrators. He was involved heavily in the planning of the Biological Laboratories building, at 16 Divinity Avenue, which was completed in 1930. He became chairman of botany in the new building and thereafter director of the Botanical Laboratories, serving until 1934 when the three separate departments of botany, zoology, and physiology were united into a single Department of Biology with one chairman and one director of the Biological Laboratories. Such a load diverted Wetmore's energies from research, except for summer studies in cytogenetics and cytotaxonomy, part of which

was conducted at his summer cottage in Nova Scotia. Some aspects of the work were taken up by his graduate student Delisle and the results of the study were published in 1939.

Upon relief from administrative chores, Ralph turned increasingly in his research to plant anatomy, the major topic of his doctoral research. His interests centered on the evidence that plant structure, especially wood anatomy, could bring to taxonomic relationships and evolutionary origins. In this line of work, Wetmore joined in collaboration with Professor I. W. Bailey of the Arnold Arboretum. Together, they assembled the wood collections necessary for the research.

Authenticated wood samples collected from around the world were placed in the Harvard University Herbaria; sections were prepared on slides for microscopic study. Further collaboration with Professor S. C. Record of Yale University led to large collections of wood samples at both universities. The collection at Harvard grew to over 25,000 specimens of wood covering 300 families of gymnosperms and angiosperms and over 35,000 microscope slides of wood sections, in addition to permanent mounts of pollen samples and flower parts, which together form the Bailey-Wetmore Wood Collection housed today in the Harvard University Herbaria building at 22 Divinity Avenue.

Research based on these collections led to new insights into both in the relationship between plant anatomy and taxonomy and in ideas as to evolutionary origins of the angiosperms.

Influenced by the activities and success in understanding systematic relationships among the woody dicots achieved by I. W. Bailey and his students, Ralph undertook a comparative study of the developmental anatomy of the herbaceous angiosperms. He soon found that too little was known concerning the development of the primary body of herba-

ceous plants to permit extensive or comprehensive comparative studies. He therefore began a series of studies in collaboration with his graduate students of the developmental processes in early embryogenesis of several plants including the woody gymnosperm *Pinus strobus*, the herbaceous flowering plant *Phlox drummondii*, and several species of the ferns and lower vascular plants, including the bracken fern, *Pteridium aquilinum*, and the fern *Phlebodium aureum* as well as studies in the lycopsids, *Lycopodium* and *Selaginella*. This research was extended to the anatomical analysis of continuing embryogenesis in the vegetative shoot apices and flowering apices of a number of the vascular plants, studies that paralleled comprehensive efforts of other plant anatomists active around the world, including K. Esau at Davis, California; A. S. Foster in Berkeley; R. A. Popham at Columbus, Ohio; E. C. Abbe at the University of Minnesota; and, in Europe, R. Buvat and L. Plantefol in France, F. A. L. Clowes in England, and others involved in similar research in the 1930s–1950s.

Careful and detailed anatomical studies of the shoot apex and of the origin of the cauline or stem-component of the shoot versus the foliar appendages—the leaves of the vegetative shoot apex or the floral parts produced by flowering apices—led naturally to speculation concerning the inherent independence of the meristem derivatives. Surgical operations on the shoot apex provided a novel, if drastic, approach to the problem. Wetmore and his students joined this approach, one pioneered by C. W. Wardlaw in Manchester, England, over the years of World War II and available in published form in the early 1940s. Over the period beginning in 1945 Wetmore's laboratory became one of the centers in the United States for research in the newly evolving field of experimental plant morphogenesis.

Using developments from tissue culture research pioneered

in France by R. J. Gautheret and evidence for the autonomy of cultured shoot and root apical meristems from work by P. R. White and others in the United States, Wetmore's group began to excise meristems and meristem parts and culture them in isolation in sterile nutrient culture. Close morphological and anatomical examinations of structures resulting from surgical manipulations led to new concepts of tissue and organ interaction. Attention focused on the role of the still incompletely defined plant hormones, especially auxin. In collaboration with Professor K. V. Thimann, a series of studies was made involving the role of auxins in leaf and shoot development of diverse taxonomic groups of plants.

Another related line of research was concerned with the physiological/biochemical control of vascular tissue differentiation in the shoot apex and its subtending tissues. Students in Wetmore's laboratory combined techniques of meristem culture and callus tissue culture deducing evidence for the chemical influences, especially hormonal, of the shoot on undifferentiated tissues. Further studies involved the development of isolated leaf primordia and the discovery of their early pluripotent capacity to form either buds or leaves and their later determination as leaves.

Wetmore served as an effective bridge between plant anatomy and plant physiology and was able, together with other faculty and with graduate students and postdoctoral fellows, to create a research atmosphere in which students were encouraged to reach across the gap and bridge it themselves.

Twelve years after his first marriage, Ralph's wife Marion died suddenly in 1935 from a hemolytic streptococcus infection. Ralph was left with two daughters, Katherine and Jean, then eight and five years of age. Ralph characteristically undertook the full responsibility for their upbringing.

In 1940 he married Olive (Hawkins) Smith, a tutor in English at Radcliffe College and together they raised the two girls and saw them each married and with children of their own, six grandchildren in all for the Wetmores. Olive continued in academic life at Radcliffe, serving in the department of English as tutor and later as acting dean of the college. Together Ralph and Olive created a home-away-from-home for the many students both undergraduate and graduate who had the good fortune to know them during their student lives in Cambridge. It was a long and happy marriage of mutual dedication to each other and to the academic life they both chose.

Ralph retired from teaching at Harvard and became professor emeritus in 1962 but continued active in research. He made the trips and visits to other research laboratories that he had foregone during his academic career. He traveled to Versailles in France to work with G. Morel and then for a period to Dartmouth in Hanover, New Hampshire, to conduct research with his former student A. DeMaggio. He also spent some time at the University of California at Davis, in the laboratory of E. Gifford. When back in Cambridge after retirement, Ralph devoted much of his time to the sorting and arranging of the large wood collection, spending half-days for a number of years, working on the wood collection, meeting colleagues and students, and keeping up with the world of plant development.

After giving up their home on Francis Avenue, just a block from the Biological Laboratories, Ralph and Olive moved to an apartment on Garden Street where they continued to host friends and students and colleagues. In 1982 Olive died and Ralph stayed on in Cambridge, active and independent and open to his many friends and family. At the ripe age of ninety-seven, he passed away at a nursing home near his daughter in Boxford. A memorial service

was held June 13, 1989, at Memorial Church, Harvard University, as a service of thanksgiving for the lives of Ralph and Olive Wetmore who had together influenced the lives of so many at Harvard.

Ralph participated in the national life of botanical and biological organizations in the United States. He had membership in many societies. He was a fellow of the American Association for the Advancement of Science and of the New York Academy of Science. He was an active member of the Botanical Society of America and served as its president in 1953; he was president of the Society for the Study of Development and Growth in 1948–49; and president of the New England Botanical Club, 1948–51. He held membership in the American Society of Naturalists, the American Society of Plant Physiologists, the Scandinavian Society of Plant Physiology, the International Association of Wood Anatomists, and the Torrey Botanical Club.

In 1932 Ralph was elected a fellow of the American Academy of Arts and Sciences and in 1954 a fellow in the National Academy of Sciences. He was awarded an honorary D.Sc. degree by his alma mater, Acadia University, in 1948. He received a Certificate of Merit by the Botanical Society of America on the occasion of its Golden Jubilee in 1964.

Over more than forty years of research and teaching and nearly fifty years of active scientific publication Ralph played important roles as quiet innovator, interpreter, and arbitrator in his chosen fields of science. He was one of the first among the developmental botanists to see the importance of organ and tissue culture methods and to apply them as tools useful in dissecting the intricacies of developmental processes—embryogenesis, cytodifferentiation, and meristem expression. Tissue and organ culture were introduced as laboratory experiments in his undergraduate courses and served as experimental approaches for many of his students

interested in plant morphogenesis. In a seminal review co-authored with C. W. Wardlaw of Manchester, England, Ralph fostered a better comprehension of the value and significance of surgical and *in vitro* cultural approaches to problems of plant development. His experiments with Rier on vascular tissue differentiation continue to provide the paradigm for studies on plant cytodifferentiation. Ralph's laboratory served as focal point in the United States for the development of experimental approaches to problems in plant morphology and anatomy.

His keen involvement in experimental research and interest in relationships between structure and function were carried on through his students, several generations of graduate students and postdoctoral associates, who went on to become distinguished teachers and researchers throughout the world.

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