

NATIONAL ACADEMY OF SCIENCES

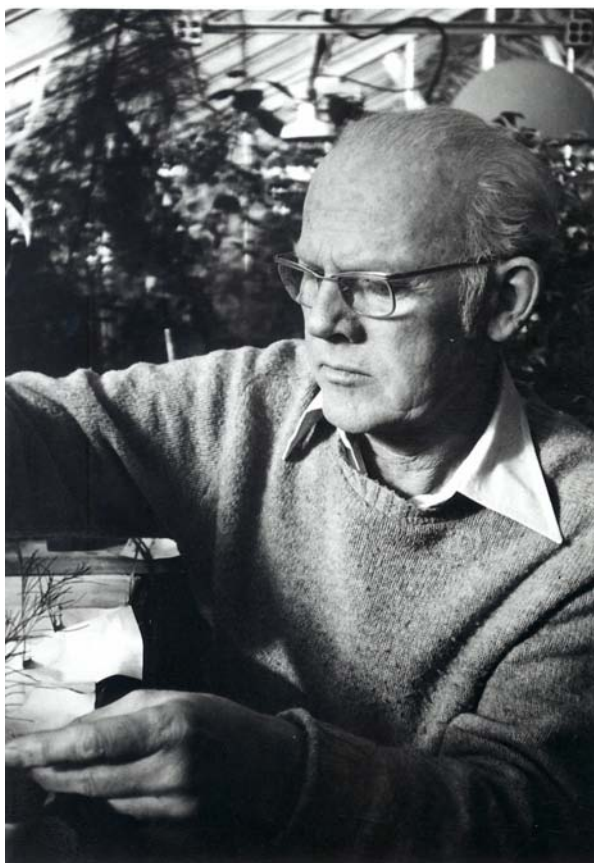
JOHN GORDON TORREY
1921–1993

A Biographical Memoir by
LEWIS FELDMAN AND ALISON BERRY

*Any opinions expressed in this memoir are those of the authors
and do not necessarily reflect the views of the
National Academy of Sciences.*

Biographical Memoir

COPYRIGHT 2007
NATIONAL ACADEMY OF SCIENCES
WASHINGTON, D.C.



John G. Torrey

JOHN GORDON TORREY

February 22, 1921–January 7, 1993

BY LEWIS FELDMAN AND ALISON BERRY

JOHN GORDON TORREY WAS A forthright, honest, highly principled man, and a groundbreaking plant scientist. All who associated with John, or “JGT” as he was called by his graduate students, valued greatly his opinions and wise counsel.

He was born in Philadelphia on February 22, 1921, the third of four children, and the second son of Edward and Elsie (Gordon) Torrey. He died January 7, 1993, in Greenfield, Massachusetts. Torrey graduated from Williams College (Williamstown, Massachusetts) in 1942 and shortly thereafter enlisted as an officer in the U.S. Army, serving for the duration of World War II in the Medical Administrative Corps in both the United States and Europe. As noted by Kenneth Thimann, John Torrey’s Ph.D. dissertation supervisor at Harvard, Torrey “came to Harvard while still in uniform and was the first graduate student to come into the Biology Department after World War II.” In 1947 while still a graduate student, he was awarded a traveling fellowship allowing him to spend a year (1948-1949) at Cambridge University in the Botany School. In 1949 in England he married Noreen Lea-Wilson whom he had met during his earlier military service in the United Kingdom. Also in 1949 when he returned to Harvard, Torrey submitted a thesis titled “Studies on the Physiology of Lateral Root Forma-

tion and Root Growth,” for which he was awarded a Ph.D. in biology in 1950. Thereafter roots would be at the center of his long and highly influential research career.

Torrey received assistant professor offers from Berkeley, Santa Barbara, and McGill. Thimann lobbied for McGill, but Torrey instead chose Berkeley and joined the Department of Botany in late 1949. There he became part of a young cadre of new faculty, including Leonard Machlis and Johannes Proskauer, who together rejuvenated the department and expanded its role from that of service to agriculture to include the broader discipline of plant science.

While at Berkeley, Torrey began to elaborate his research on roots, focusing mainly on their growth and development. His dissertation adviser, Professor Thimann, had played a central role in characterizing the structure and function of the plant growth regulator, auxin (indole-3-acetic acid), and Torrey built on this knowledge to provide definitive evidence for the involvement of auxin in lateral root initiation and outgrowth. Based on his previous tissue culture experience at Harvard with Professor Ralph Wetmore, Torrey incorporated sterile culture techniques into his studies of roots, allowing him to manipulate root growth and development. From these efforts came seminal papers that characterized the controls of patterning in roots, with special emphasis on vascular patterning. Torrey was able to show that patterning was regulated by the root apical meristem. His research papers and the reviews arising from this work serve as the foundation for much of contemporary experimental root biology.

While at Berkeley, Torrey taught, with Leonard Machlis, a plant physiology course that included a laboratory. As no suitable laboratory manual was then available, he and Machlis wrote *Plants in Action; a Laboratory Manual of Plant Physiology*, which not only became the standard text for plant

physiology laboratory classes throughout the United States but also served as a valuable laboratory reference.

In 1960 and now an associate professor at Berkeley, Torrey accepted an invitation to return to Harvard as a professor in the Department of Biology. There he expanded his studies of roots and began to focus on an aspect of root development that had earlier attracted his attention, namely, the fixation of atmospheric nitrogen (nitrogen fixation) in rootborne structures known as nodules. Torrey believed that his earlier work on lateral root development could provide a context for further discoveries of this scientifically interesting and economically important process. His initial studies of this phenomenon were with members of the pea family (legumes), in which nitrogen fixation occurs as a consequence of the association between the root and a bacterium belonging to the genus *Rhizobium*. Torrey was interested in the beginning stages of nodule initiation, and focused much of his early research on understanding the reprogramming of the root cortical cells allowing them to develop into nodules. During the early years following his return to Harvard, Torrey authored (in 1967) *Development in Flowering Plants*, in which he pointed the way to the challenges ahead for plant developmental biologists.

In the early 1970s Torrey moved his research activities to the Harvard Forest, in Petersham, Massachusetts, about 60 miles west of Cambridge. Coincident with this move was a redirection and refocusing of his research to include nitrogen fixation in root nodules of perennial, nonlegume plants, with initial emphasis on the genus *Comptonia* (Sweet Fern). This plant grew abundantly in and around the Harvard Forest, inhabiting open woodlands and clearings. Torrey and his group showed that the organism causing nodule formation in *Comptonia* and responsible for nitrogen fixation was neither a fungus, as was once believed, nor a mem-

ber of the bacterial group called Rhizobia, which carries out nitrogen fixation in root nodules of the pea family. Instead, the microsymbiont in *Comptonia* root nodules and those of related plant hosts, belonged to the genus *Frankia*, bacteria in the Actinomycete group, which are evolutionarily distant from the Rhizobia. A significant accomplishment stemming from these efforts was the discovery of how to grow *Frankia* in culture, outside the root nodule environment. These landmark discoveries formed the basis of the most productive period in Torrey's research career, in which more than 70 papers and one coedited volume (*Applications of Continuous and Steady-State Methods to Root Biology*) were published between 1978 and 1991, detailing various aspects of the development of the association between *omptonia* roots and *Frankia*.

In 1965 while still in Cambridge, Torrey assumed a major administrative role as the fifth director of the Maria Moors Cabot Foundation for Botanical Research. Using fair, balanced judgment he was instrumental in directing foundation funds to support a much needed updating of botanical facilities at Harvard, including the expansion of the University Herbaria and the establishment of the Controlled Environment Facility at the Harvard Forest. He also ensured that foundation funds were made available to junior faculty, and that the granting of these funds would involve a minimum of paperwork.

Later, in 1984, he continued his administrative duties through his appointment as the Charles Bullard Professor of Forestry and director of the Harvard Forest. He maintained these positions until 1990. As director he had great impact on activities at the forest, from initiating freshmen seminars (in those days a novelty at universities) to spearheading a consortium of scientists from several institutions that eventually led to the awarding of a large National Sci-

ence Foundation grant supporting the establishment of a Long Term Ecological Research site at the forest. The legacy of his efforts and his perspectives are today reflected in the expanded and varied ecological research activities at the forest.

Although located in Petersham, Torrey continued to teach classes, supervise graduate students, and meet with visiting scholars in Cambridge. He also established an association with the University of Massachusetts in nearby Amherst, and there offered his mentoring skills and served on doctoral dissertation theses.

He was a strong supporter of women in science and encouraged his female associates, both graduate students and visitors, to aim high. The legacy of this mentorship is today evident in the many successful academic careers of women who worked with John Torrey. "In a tough academic world," one former female graduate advisee noted, "he was truly a hero."

John Torrey was a recipient of many awards and appointments, including a Guggenheim Fellowship (1965-1966) and a Fulbright Senior Research Scholar Fellowship (1984). He was a member of the American Academy of Arts and Sciences, the Botanical Society of America, and the Society for Developmental Biology (president, 1963), among other organizations. He was elected to the National Academy of Sciences in 1981.

Torrey was known to his many associates worldwide for his interests in etchings, particularly those from Scotland, England, and New England, from the late 19th and early 20th centuries. In his retirement he had intended to explore "the interaction, interplay and influence of the group of British etchers on the Americans and vice versa." Whenever he traveled he would reserve some time to visit local antique and art establishments. In these adventures he was

usually, but not always, successful in acquiring a new etching or watercolor.

John Torrey was occasionally confused with the noted 19th-century American botanist of the same name, founder of the Torrey Botanical Club. Although there was no relation, he was mildly bemused by the confusion occasioned by the coincidence of both their names and occupations. His wry sense of humor was not often seen but could be noted occasionally, such as when Torrey drove past a graveyard and chuckled at the sign reading "One Way."

Reflecting on John Torrey, his Harvard colleagues recollected that he was "outspoken and, in his controlled way, passionate about what he thought was right and what he thought was wrong." On one occasion when a Harvard colleague off-handedly informed Torrey in his role as director of the Cabot Foundation that he (the colleague) would be spending funds differently from what was originally budgeted, Torrey noted firmly, "No, I don't think you should spend that money in a way that differed from your original intentions."

John and his wife, Noreen (Norah), were married for 43 years and had five daughters: Jennifer, Joanna, Susan, Sarah, and Carolyn.

John Torrey was a man of high ethics both in his science and in the way he lived his life. He treated everyone equally, with respect, dignity, and honesty, and he expected no less from others. At his passing his daughter Joanna penned, "We lay him to full rest, sorry that he is not here with us, hat in hand, to point up into the trees, or down to the earth, sharing his faith in that which grows."

Some information used in preparing this remembrance was obtained from the Memorial Minute of the Harvard University Faculty of Arts and Sciences, appearing in the November 7, 1996, edition of the *Harvard Gazette*.

SELECTED BIBLIOGRAPHY

1950

The induction of lateral roots by indoleacetic acid and root decapitation. *Am. J. Bot.* 37:257-264.

1951

Cambial formation in isolated pea roots following decapitation. *Am. J. Bot.* 38:596-604.

1957

Auxin control of vascular pattern formation in regenerating pea root meristems grown in vitro. *Am. J. Bot.* 44:859-870.

1958

Endogenous bud and root formation by isolated roots of convulvulus grown in vitro. *Plant Physiol.* 33:258-263.

1959

A chemical inhibitor of auxin-induced lateral root initiation in roots of *Pisum*. *Physiol. Plantarum* 12:873-887.

1972

On the initiation of organization in the root apex. In *The Dynamics of Meristem Cell Populations*, eds. M. W. Miller and C. C. Kuehnert, pp.1-10. New York: Plenum Press.

1975

With D. T. Clarkson, eds. *The Development and Function of Roots*. London: Academic Press.

1976

With L. J. Feldman. The isolation and culture in vitro of the quiescent center of *Zea mays*. *Am. J. Bot.* 63:345-355.

1978

With D. Callaham. Determinate development of nodule roots in actinomycete-induced root nodules of *Myrica gale*. *Canad. J. Bot.* 56: 1357-1364.

1979

With W. Newcomb, D. Callaham, and R. L. Petersen. Morphogenesis and fine structure of the actinomycetous endophyte of nitrogen-fixing root nodules of *Comptonia peregrina*. *Bot. Gaz.* 140:S22-S34.

1980

With D. Baker and W. Newcomb. Characterization of an ineffective actinorhizal microsymbiont, *Frankia* sp. EuII (Actinomycetales). *Canad. J. Microbiol.* 26:1072-1089.

1981

With J. D. Tjepkema, G. L. Turner, F. J. Bergersen, and A. H. Gibson. Dinitrogen fixation by cultures of *Frankia* sp. CpII demonstrated by $^{15}\text{N}_2$ incorporation. *Plant Physiol.* 68:983-984.

1985

With D. J. Marvel, G. Kuldau, A. Hirsch, E. Richards, and F. M. Ausubel. Conservation of nodulation genes between *Rhizobium meliloti* and a slow-growing *Rhizobium* strain that nodulates a nonlegume host. *Proc. Natl. Acad. Sci.* 82:5841-5845.

1986

With M. F. Lopez and P. Young. A comparison of carbon source utilization for growth and nitrogenase activity in two *Frankia* isolates. *Canad. J. Microbiol.* 32: 353-358.

With Z. Zhang and M. A. Murry. Culture conditions influencing growth and nitrogen fixation in *Frankia* sp. HFPCc13 isolated from *Casuarina*. *Plant Soil* 91:3-15.

1987

With D. J. Marvel and F. M. Ausubel. Rhizobium symbiotic genes required for nodulation of legume and nonlegume hosts. *Proc. Natl. Acad. Sci.* 84:1319-1323.

Endophyte sporulation in root nodules of actinorhizal plants. *Physiol. Plantarum* 70:279-288.

1989

With S. Racette. The isolation, culture and infectivity of a Frankia strain from *Gymnostoma papuanum* (Casuarinaceae). *Plant Soil* 118:165-170.

With S. Racette. Root nodule initiation in *Gymnostoma* (Casuarinaceae) and *Shepherdia* (Elaeagnaceae) induced by Frankia strain HFPGp11. *Canad. J. Bot.* 67: 2873-2879.

With L. J. Winship, eds. *Applications of Continuous and Steady-State Methods to Root Biology*. Dordrecht: Kluwer Academic.

With S. S. Tzeany. Spore germination and the life cycle of Frankia in vitro. *Canad. J. Microbiol.* 35:801-806.

1990

With S. Burleigh. Effectiveness of different Frankia cell types as inocula for the actinorhizal plant *Casuarina*. *Appl. Environ. Microbiol.* 56:2565-2567.

With S. R. Mansour and A. Dewedar. Isolation, culture, and behavior of Frankia strain HFPCg14 from root nodules of *Casuarina glauca*. *Bot. Gaz.* 151:490-496.

With W. Newcomb, S. Jackson, and S. Racette. Ultrastructure of infected cells in the actinorhizal root nodules of *Gymnostoma papuanum* (Casuarinaceae) prepared by high pressure freezing and chemical fixation. *Protoplasma* 157:172-181.

1991

With S. R. Mansour. Frankia spores of strain HFPCg14 as inoculum for seedlings of *Casuarina glauca*. *Canad. J. Bot.* 69:1251-1256.

