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ROBERT H. WHITTAKER

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A Biographical Memoir by

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AND GENE E. LIKENS

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Biographical Memoir

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ROBERT H. WHITTAKER

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BY WALTER E. WESTMAN, ROBERT K. PEET, AND
GENE E. LIKENS

ROBERT HARDING WHITTAKER was one of the preeminent community ecologists of the twentieth century. By studying the interactions of plant populations at the biogeochemical, species, and community levels, he made contributions to basic knowledge in several subdisciplines of biology.

He developed new approaches for the analysis of plant communities and provided exemplary insight into the patterns of composition, productivity, and diversity of land plants. He brought clarity to such disparate fields as the classification and ordination of plant communities, plant succession, allelochemistry, evolution and measurement of species diversity, niche theory, and the systematics of kingdoms of organisms. In several influential monographs he detailed the vegetational patterns of various montane regions of the United States, and—during the last six years of his life—extended his research to Mediterranean- and arid-climate regions of the United States, Israel, Australia, and South Africa.

Whittaker's most cited work is his undergraduate textbook, *Communities and Ecosystems* (1970,3; second edition, 1975,3), which not only introduced thousands of students throughout the world to ecology but also provided a succinct summary of a highly diverse literature and new insights useful to professional ecologists.

EDUCATION AND EARLY LIFE

Robert H. Whittaker, the youngest of three children, was born on December 27, 1920, in Wichita, Kansas, to Clive Charles and Adeline Harding Whittaker. His mother encouraged Whittaker's abiding interest in languages, while his father stimulated an early interest in natural history.

Whittaker entered Washburn Municipal College (now University) in Topeka, Kansas, in 1938. He received a Bachelor of Arts degree in biology and languages in 1942 but postponed his plans to pursue graduate work in ecology to enlist in the Army. He was stationed in the United States and in England until 1946 as an Army-Air Force weather observer and forecaster. Upon his return to civilian life in 1946, he entered graduate school at the University of Illinois, where he completed his Ph.D. two-and-a-half years later.

When Whittaker applied for graduate standing in the Department of Botany at Illinois, his application was denied because of insufficient background in botany, but he was admitted to the Zoology Department and awarded a fellowship. In February 1946, he began his graduate studies under the direction of Victor Shelford, who retired from active teaching that summer. Charles Kendeigh replaced Shelford as Whittaker's adviser in September, and though Whittaker worked with him and acknowledged his debt, Whittaker was also heavily influenced by the University of Illinois botanist Arthur G. Vestal, whom Whittaker called his "second adviser."

SCIENTIFIC WORK

The Continuum of Plant Species Distribution

Whittaker was particularly taken by classroom lectures in which Vestal questioned rigid Clementsian notions of plant association and discussed Gleason's opposing idea of individ-

ualistic species distributions. From later conversations it was apparent that Whittaker keenly appreciated Vestal's influence in shaping his own theoretical approach and, in his later years at Cornell, was pleased to play a similar role for the graduate students of others.

Whittaker's doctoral dissertation (1948,1) examined patterns of plant species change along an altitudinal gradient in the Great Smoky Mountains of Tennessee. In seeking to understand underlying patterns of species change, he plotted plant species' distributions along axes of environmental change. He then was able to show that the ecological importance of plant species (as measured by density or cover) rose and fell in a Gaussian fashion along key environmental gradients, with each species showing an individualistic distribution.

Though Whittaker had hypothesized the occurrence of groups of coadapted species with parallel distributions, what emerged from his work was a validation of Gleason's hypothesis and rejection of his own: Most species were distributed independently along environmental gradients.

The significance of this work was obvious. It supported the "continuum" concept of species distribution and extended the statistical basis for gradient analysis in general. W. H. Camp wrote Whittaker that his manuscript was "probably the most important ecological paper of the present century" and that his method would revolutionize the field.¹

Plant and Insect Population Patterns, and Element Cycling

In 1948, Whittaker was appointed instructor in the Department of Zoology at Washington State College (now University) in Pullman, Washington. While at Washington State

¹ Despite this assessment, Whittaker's doctoral dissertation was not published until eight years later (1956,1). By that time—along with J. T. Curtis and the Wisconsin school—he had developed a series of detailed gradient analyses, but it took another ten to fifteen years before his thesis was widely accepted.

he began field work on the vegetation of the Klamath region and Siskiyou Mountains of Oregon and California, including a comparative study of vegetation on serpentine and quartz-diorite soils.

Returning to the original focus of his dissertation work, Whittaker completed a manuscript on foliage insects in the Great Smokies, building on his vegetation analysis there. At the same time he conducted a uniquely thorough study of copepod communities of small ponds in the Columbia basin.

Whittaker left Washington State in 1951 to become a senior scientist in the Hanford Laboratories Aquatic Biology Unit, Department of Radiological Sciences, in Richland, Washington. Quick to see the value of radioactive tracers for unraveling complex ecological problems, he studied in detail the movement of radioactive phosphorus in aquarium microcosms. His results were important to understanding the fate of radionuclides in the environment and for evaluating the movement and storage of nutrients in ecosystems. At Hanford (and later at Brookhaven National Laboratory with George Woodwell), he also contributed to the first large-scale study of the effect of chronic gamma radiation on the structure and function of forest ecosystems.

While at the Hanford Laboratories, Bob met Clara Caroline Buehl, and the two were married on New Year's Day, 1953. Although Clara had an M.S. in biology, her role in the marriage soon became that of wife and mother rather than scientific collaborator. The Whittakers raised three sons: John Charles, Paul Louis, and Carl Robert.

Dimension Analysis and the Classification of the Kingdoms

In 1954, Whittaker was hired as an instructor in the Department of Biology of Brooklyn College, the City University of New York, where he would remain for ten years. During the summers he returned to the Great Smoky Mountains,

where he initiated a major effort to obtain measurements of the biomass and productivity of the forest communities along an elevational gradient.

Because he was interested in the entire production of plants above ground, he began to develop methods for measuring productivity of shrubs and herbs and other parts of trees in addition to trunks. He used a volumetric measurement based on growth rings and succeeded, through laborious calculations, in obtaining productivity estimates for the major plant communities in the mountain range. His efforts provided a basis for the subsequent development of the dimension analysis methodology still widely in use.

Throughout his career—in addition to conducting model studies of a variety of ecological systems—he also maintained an interest in the problem of classification and speciation. In 1957 he proposed a new classification for the kingdoms of organisms based on the evolution of trophic structures and nutritional energy sources (1957,1). Later updated (1969,4), this system of classification eventually was accepted widely and used in biology textbooks.

Desert and Forest: Structure and Function

From 1963 to 1965, Whittaker and W. A. Niering published a series of studies of the Arizona Saguaro cactus desert—among the first studies of a desert community to emphasize functional rather than structural attributes. For this work the authors received the Ecological Society of America's 1966 Mercer Award for the best paper published in the preceding two years by a young ecologist.

In 1964 another colleague and future collaborator, George M. Woodwell, persuaded Whittaker to take a year's leave from Brooklyn College to work with him at Brookhaven National Laboratory in New York State. The two developed a profound respect and fondness for each other, and

throughout the 1960s the team of Whittaker and Woodwell was one of the most productive and influential in plant ecology. Together they produced eight papers on the surface area, biomass, production and nutrient flow, and effects of gamma radiation on structure and diversity of forested ecosystems in the Brookhaven oak-pine forest and surrounding vegetation.

Just before leaving Brookhaven in 1966, Whittaker had initiated studies—with Gene E. Likens and F. Herbert Bormann—on the biomass, productivity, and nutrient content of the Hubbard Brook Experimental Forest in New Hampshire. These subsequently led to two major monographs about this northern hardwood forest ecosystem (1970,1; 1974,3). With Likens, Whittaker also compiled the widely cited summary tables of plant production, biomass, and associated characteristics for ecosystems of the world.

Species Diversity, Ordination Methods

In 1966 Whittaker decided to accept the offer of a professorship at the new Irvine campus of the University of California. He took up this new post with great enthusiasm and anticipation but was dismayed by the rapid pace of urbanization around Irvine. In September 1968 he accepted an invitation to move to Cornell University as professor of biology in the Section of Ecology and Systematics, where his last years were marked by a significant expansion and solidification of his reputation.

Once again pursuing his early interest in species diversity, Whittaker was stimulated in part by the attention G. E. Hutchinson, R. H. MacArthur, and their students had given to the topic. His concise paper in *Science* (1965,3) remains a classic review of the field. When general theories to explain patterns of plant species diversity did not emerge, Whittaker emphasized factors influencing local patterns, based on pe-

cularities of site history and environment. In association with Hugh Gauch, Jr., and others he also explored techniques for ordinating species data—techniques that helped computerize earlier gradient analyses he had developed along with J. T. Curtis and the Wisconsin school.

TEACHER, DIPLOMAT, HONORED RESEARCHER

At Irvine and Cornell, Whittaker had the opportunity to supervise graduate students for the Ph.D. for the first time. Of the twelve he trained, eight went on to complete their dissertations under his supervision.

Through personal diplomacy, furthermore, he built bridges between American and European ecologists, calming the waters he himself had troubled with his challenges to phytosociological theories and methods of classification. His reviews of classification and ordination studies and his global studies of diversity and productivity helped inspire North American ecologists to increase contacts and collaboration with ecologists beyond their borders.

In his later years Robert Whittaker reaped the rewards of a prolific intellectual career. He enjoyed a solid reputation among his peers, who elected him vice president of the Ecological Society of America in 1971. He was elected to the National Academy of Sciences in 1974 and named Cornell's Charles A. Alexander Professor of Biological Sciences in 1976. Elected to the American Academy of Arts and Sciences in 1979, he also held honorary memberships in the British Ecological Society and the Swedish Phytogeographical Society. At the time of his death he was president of the American Society of Naturalists.

HEALTH PROBLEMS

In 1974 Whittaker's wife contracted cancer. Clara's struggle with the disease lasted three years, and at Christmas

time in 1977, she finally succumbed. Though her prolonged illness upset Whittaker greatly, he remained stoically silent, and many of his students and colleagues were not aware of the events that were troubling him. Turning to his traditional values for support, he increased the intensity with which he pursued his work.

Following Clara's death, Whittaker developed a close friendship with his doctoral student, Linda Olsvig. In October 1979 the two were married, and Linda, taking an active interest in his research, accompanied Whittaker into the field on visits to Israel and South Africa. There were no children from this marriage.

Four months after his second marriage Whittaker complained of hip pain. X-rays revealed cancer in hip and lungs, but he set himself to complete as much of his work as possible. His health failed in September and he died on October 20, 1980. Shortly before his death, the Ecological Society of America honored him with its highest award, that of Eminent Ecologist.

IN CONCLUSION

Difficult as it to assess which of Whittaker's many contributions to the science of ecology will prove most profound or long lasting, one hallmark stands out. Demonstrating the continuity of species' response to environmental gradients, he challenged the classificatory approach to vegetation structure. Though Whittaker credited Ramensky, Gleason, Curtis, and McIntosh with much, it was his own theory, method, and empirical evidence that solidified gradient analysis into a scientifically accepted approach.

IN THE PREPARATION OF THIS MEMOIR, the authors often referred to a short biography by W. E. Westman and R. K. Peet published shortly after Whittaker's death, "Robert H. Whittaker

(1920–1980)—The Man and His Work,” *Vegetatio* 48(1982):97–122. A memorial volume has been published by Whittaker’s students and colleagues: R. K. Peet, ed., *Plant Community Ecology. Papers in Honor of Robert H. Whittaker* (Dordrecht: Junk, 1985). In 1975 Robert Whittaker supplied the National Academy with an autobiographical note, which remains on file with the Archives of the National Academy of Sciences in Washington, D.C.

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