

WILLIAM H. WESTON

WILLIAM H. WESTON (1890–1978): TRIBUTE AND REMEMBRANCE

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The death of William ("Cap") Weston in 1978 brought to an end an era of unprecedented development in experimental mycology in the United States. For almost forty years, Weston and the vast array of students that he trained at Harvard University had been the leaders in a quiet revolution that changed forever the approach to the study of the fungi. The change they championed was from the traditional taxonomic and industrial approaches to one that stressed the biology of the fungi. Life cycles, sexuality, the alternation of generations, morphogenesis, the mechanisms employed to discharge gametes or spores, and all the quirks and peculiarities of that beautiful group of organisms became the center of attention in Weston's laboratory as a result of his ability to instill in students a profound love and respect for the fungi.

When Weston joined the faculty at Harvard University in 1921, he inherited a long tradition of research in mycology at Harvard that traced back to the noted American mycologist, W. G. Farlow, who had studied under Anton de Bary in Germany, and to Roland Thaxter, who had been Farlow's student and became the first curator of the Farlow Herbarium. These extraordinary mycologists were responsible for training a large number of scientists who later became important in the fields of mycology, plant pathology, genetics, and industrial microbiology. Among them was W. H. Weston, who went on to become perhaps the most renowned mycologist of his time in the United States. Admirers of Bessey, Whetzel, Alexopoulos, Dodge, Wolf, Couch, and of other noted mycologists who were Weston's contemporaries may disagree with me, but I hope they will forgive my bias when I say that if these gentlemen were alive today they would recognize Weston's great overall importance as a teacher of mycology.

It is a mystery to me why Weston's name is relatively unknown among my fellow plant pathologists. Perhaps this is due to the fact that Weston's major contributions in plant pathology came very early in his career while working in the Philippines for the US Department of Agriculture. Perhaps it is because our professional Society has never recognized his accomplishments while the Mycological Society of America long ago named Weston their first President and established a yearly Teaching Award in his honor. Or perhaps it is a reflection of today's declining interest in experimental mycology in an era of rapidly expanding molecular virology and bacteriology. Whatever the reason, I was pleased to accept the responsibility of writing this article in the hope of correcting, to some extent, that glaring gap in the background of readers interested in the historical aspects of our science.

THE EARLY YEARS

William Henry Weston was born in New York City in 1890, where he grew up, and he later attended Dartmouth College in New Hampshire. There, in addition to his academic achievements in the field of biology, he obtained recognition for his abilities as an agile, graceful skier. He became captain of the skiing team and thus acquired the nickname "Cap", which persisted during his entire life. Upon graduation from Dartmouth, he became a graduate student under Roland Thaxter, who had made the Farlow Herbarium at Harvard a center for mycological research in the United States. Weston received an A.M. in Botany in 1912 and the Ph.D. degree in 1915. Thaxter had a profound influence on Weston's development as a scientist. He often remarked about Thaxter's absolute attention to detail, which one can appreciate even today in Thaxter's superbillustrations of many different groups of fungi, particularly of the various members of the Laboulbeniales, fungi that are parasitic on insects. Although Weston often poked fun at Thaxter's rather imperial demeanor, he had the utmost respect for him as a scientist and inherited from him the ability to draw the best from his students. Although Thaxter often derided "practical" research, early in his career he had worked as the first plant pathologist at the Connecticut Agricultural Station and had been involved in what he called "squirt gun botany". In fact, Thaxter made important practical and scientific contributions to the field of plant pathology (14). Weston often remarked that Thaxter was merely posturing in his derisive references to applied research for, in fact, Thaxter had advised him to look for career opportunities in the US Department of Agriculture.

Weston's formal career began at Western Reserve University, where he

was instructor in Biology from 1915–1917. For the next four years he held various positions within the US Department of Agriculture, and two of these years were spent in the Philippines where he dealt with a wide range of diseases of tropical plants. During his entire career Cap made continuous references to his experiences in the tropics, which he loved. It is evident that his firsthand experience with tropical plant diseases and a recognition of their importance were highly influential in his development as a scientist. That he was able to advise many students in the field of plant pathology and instill an admiration and respect for the fungi that cause plant diseases was due entirely to his early experiences in the Philippines.

THE TROPICAL PLANT PATHOLOGIST

When he accepted an appointment with the USDA, the position carried the title "Plant Pathologist in Charge of Downy Mildew Investigations" as part of the Office of Cereal Investigations. Downy mildews of grasses are caused by various members of the genus Sclerospora and in the early 1900s were particularly destructive to sugar cane and maize in the Philippines. Because the Philippines were a US possession at the time, the USDA felt obligated to provide aid, but these diseases were not well known. Thus, young Weston was dispatched to the Philippines, where he spent the next two years working under fairly primitive conditions and attempting to understand the nature of these downy mildew pathogens and exploring their life cycles and epidemiology. A large series of meticulously detailed, interesting papers on different species of Sclerospora began to appear in 1919 in the Journal of Agricultural Research and several of them became classics. In particular, his description of nocturnal production of conidia by Sclerospora graminicola achieved almost instant renown, for he demonstrated that these spores were explosively discharged (5-8). Up to that time none of the Peronosporales were thought to possess such mechanisms for dispersal. As reported by Weston, in S. philippinensis and S. graminis each sporangium possesses a double wall that separates it from the tip of the sterigma. Initially these two walls are flat and tightly in contact with each other; as the sporangium grows and turgor increases, the membranes tend to bulge outward until adhesion of the two surfaces is broken and, with a sudden snap, both membranes bulge outward and the spore is catapulted away. Air currents then carry the spores to nearby maize plants. Although the sporangia are rather fragile and short-lived, Weston discovered that they are produced only at night, when the host surface is covered with dew, providing ideal conditions for germination and penetration.

Weston maintained a strong interest in the biology of different members of the genus *Sclerospora* throughout his life. There were descriptions of new Sclerosporas from Fiji, Australia, and the former Nyasaland (10, 11, 13, 15), as well as detailed descriptions of downy mildews of wheat, corn, and millet in the United States (9, 18), and he established *S. sorghi* as the correct etiologic agent of sorghum downy mildew (17). Later, he determined that a common malformation of the tassels of teosinte was caused by *Sclerospora* infection (16).

BACK TO HARVARD

Weston was appointed Assistant Professor of Botany at Harvard University in 1921, where he quickly attracted a large number of students with widely varying interests. Weston himself became a widely recognized expert in the aquatic Phycomycetes, which are mostly saprophytic, but his interest and direct involvement in tropical plant diseases continued unabated. For example, in 1924, he studied diseases of wild forage grasses and of coconut in Florida as a special investigator for the USDA. Later that year, he became interested in the sugarcane mosaic disease problems in Cuba and made a survey of the losses caused by this disease, sponsored by the Tropical Plant Research Foundation. He obtained leave of absence from Harvard in 1925 and traveled to Cuba as agricultural advisor for the Cuba Sugar Club and helped in the establishment of research programs aimed at controlling sugar cane mosaic. He traveled to Panama to study the fungi of Barro Colorado Island, and in 1935 he helped to search for a site appropriate for a biological research laboratory in the mountains of Puerto Rico.

Weston was fortunate in that, from the very beginning of his career at Harvard, he attracted many capable students who blossomed in an atmosphere where they were allowed absolute freedom to pursue their interests and to follow their best instincts as to the way to approach and solve scientific questions. Among the 54 students who obtained advanced degrees under his guidance, many became leaders in their own right and many, in turn, trained yet another generation of remarkable scientists. One need only mention the names of Ralph Emerson (Berkeley), Frederick Sparrow (Ann Arbor), John Raper (Chicago and Cambridge), Kenneth Raper (Madison), Alfred Sussman (Ann Arbor), etc to make this point. In the 30s, 40s, and 50s many of the leading mycologists at US Universities had been predoctoral, postdoctoral, or visiting scientists at Weston's laboratory. Even today, many remarkable discoveries in biology are being made by some of Weston's students. In a recent issue of Science, for example, Peter Mazur and colleagues at Oak Ridge describe the first successful attempt to preserve Drosophila embryos cryogenically (3). As a graduate student in Weston's laboratory in the early 50s, Mazur had worked on improving ways of preserving fungi, an interest that Cap fostered and Mazur developed into a lifetime career. Much earlier, Cap himself had developed a method to preserve fungal cultures by covering them with a layer of oil (1), a procedure that became standard practice for many years until lyophilization apparati became widely available.

Weston's influence upon impressionable graduate students is best expressed in the many prefaces to books written by his students. For example, Frederick Sparrow, in his book on *Aquatic Phycomycetes*, speaks of his "lasting indebtedness to Professor W. H. Weston, Jr. of Harvard University, who, by his stimulating guidance and his love for and profound knowledge of aquatic Phycomycetes, first aroused my interest in these most curious organisms".

The Teacher

For a scientist of his stature, Weston's list of publications, although full of interesting and important contributions to science, is remarkably short. This was by design. If he had been a co-author in all the papers published by all of the graduate students who did research in his laboratory and wrote their Ph.D. thesis under his tight scrutiny, as is commonly done today, his bibliography would have run into the hundreds of titles. Cap helped all his students write their first papers, but refused to add his name to the list of authors. He explained that he was proud of their publications but because he had not been personally involved in the laboratory work, he did not think it was appropriate to be listed as an author. "It is the duty of the Professor to help his students, but he must not build his career on their backs", he often said. A curious philosophy for our times, but a true expression of his generosity of spirit and his absolute dedication to the art of teaching.

To an incoming freshman at Harvard, as I was in the summer of 1945, Cap Weston presented a formidable, daunting figure. He was the epitomy of the Harvard Professor: A tall, gangly man with piercing blue eyes behind wire rimmed glasses, a clipped Boston accent and an incredible facility with the English language, who could easily convince any 17-yr old that life could not offer anything more interesting than to explore the biology of plants. An extremely friendly person, genuinely interested in students, he attracted large crowds to his lectures on cryptogamic botany. At the podium, he was in absolute control. He would start his lecture by disconnecting his hearing aid, warning students that questions would be entertained only at the end when he would "tune in again". He would then proceed to describe with beautiful precision and artful diagrams on the blackboard the vast world of algae, fungi, mosses, liverworts, etc that he loved and knew so well. In his hands, all these organisms became alive (he often complained that most textbooks, including Gaumann's Principles of Plant Infection, "did not contain a single live fungus"). There were no pyrotechnics, no gimmicks to attract the students' attention, just an infectious enthusiasm for the subject at hand. His sense of humor was legendary. The structures that some water molds use to parasitize

rotifers were labeled "lethal lollipops", his lecture on "Some Low Forms of Sex" referred to his description of the meeting of a *Fucus* egg and sperm cell. He would overwhelm students with his friendliness and, particularly in the laboratory sessions that accompanied all of his courses, he would sit with students and while helping them locate a particular structure under the microscope, he would manage to extract their personal histories and to uncover any problems they might have.

A kind, understanding person by nature, Cap nevertheless could be demanding and stern when students were not performing up to his high standards. All graduate students had to meet with him once a week to discuss research progress, and the pressure to denote this progress could be considerable. He was the most demanding when the time came to write the dissertation. An extremely lucid writer, he would scrutinize each sentence in the thesis until the meaning was absolutely clear. I have often stated that whatever facility I may have today as a scientific writer, I owe entirely to Cap Weston (4).

To his graduate students, Cap was not only a mentor but a true friend as well. During the Depression, for example, he helped students financially out of his own pocket. When a student had a personal problem, Cap was there to offer advice and help. Two personal experiences illustrate this facet of Cap's character. Sometime during my second year in graduate school, a fine of \$10 was levied on me for late payment of fees, which, I felt strongly, was incorrect. Being an obdurate person by nature, I refused to pay. Harvard kept sending me bills in the mail, which I would return dutifully with an explanation that I would not pay. Eventually, a note arrived indicating that unless the \$10 fine was paid by a certain date, "your connection with the University will be severed". The whole affair had become a "cause célèbre" in the Department, but I was surprised when, all of a sudden, the threatening notes from the Bursar stopped. Needless to say, Cap had paid the \$10 himself. When I inquired, he said, "My boy, it is admirable to take a stand on a matter of principle, but to ruin your graduate career for \$10 is sheer stupidity".

The second example involved a severe case of influenza that required me to remain bed-ridden in the room that I rented close to the Biological Laboratories. Being perennially short of funds, I refused to see a doctor and was determined to let the disease run its course. Late one evening, though, Cap Weston arrived with a thermometer and a thermos bottle. After taking my temperature, he proceeded to pour a glass of hot rum toddy, which, coupled with several aspirin tablets, he guaranteed would take care of the problem.

To the large number of graduate students who had joined Weston's laboratory immediately after the Second World War, no part of the day was more important than the coffee hour at Cap's outer office. Cap would preside

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over this daily function and inevitably the conversation was lively, interesting, and mostly about some startling new finding by one of his numerous students or about a recent article that someone in the crowd had brought along. The whole period was punctuated by his witty remarks and puns, which he spewed out continuously and sometimes required considerable mental contortions to decipher. As Charles Wilson points out in his description of these wonderful afternoon sessions (19), puns became so bad and so numerous that anyone adding one to the list had to pay a fine of \$0.15 (\$0.25 for those containing foreign words). Needless to say, Cap was the primary contributor to the pun fund. Cap's infectious good humor and frequent guffaws seemed to spread and reverberate throughout the entire building. The *esprit de corps* of his research group was built during those unforgettable afternoon sessions. Cap never missed an opportunity to teach and my nostalgic recollection of those coffee hours is that he taught us to laugh at ourselves.

Cap never took himself too seriously. A single instance of his inalterable good humor may be found in a short note in the journal *Phytopathology* by a certain Professor Aloysius T. McGinty (2) in which he berates W. H. Weston for erroneously attributing to an obscure pharmacist (M. Frechou) the first description of oospore germination in *Sclerospora* (12). He proceeds to decry Weston's "unseemly frivolity". McGinty, of course, was Cap's own creation and, to this day, I cannot imagine how *Phytopathology* published a note originating from some obscure laboratory in Ireland. Cap often chuckled about his ability to perpetrate this hoax with such relative ease.

One important bonus of life as a graduate student in Cap's group was the opportunity to meet distinguished visitors, including some of the most renowned mycologists of the time. For example, during my first year as a graduate student, Ralph Emerson arrived from Berkeley to work with Cap on *Allomyces*, the subject of Ralph's life-long research interests. Cap made no secret of the fact that Ralph was his favorite former student. They were very close and admired each other greatly. Ralph, like Cap, had dedicated his career to the teaching of mycology and had built a remarkably strong research group at Berkeley. Also like Cap, Ralph had an engaging personality, a great sense of humor, and a profound love of the fungi. I suspect that he emulated Cap in everything that he did, but he did it well. To a great extent, he succeeded because he coupled an extremely bright mind with a disarming sense of personal humility.

At regular intervals, Cap would be asked by different student groups to deliver his famous lecture on "How to Present a Scientific Paper", which was a beautifully conceived parody of the problems associated with delivering information to an audience. It was a list of how not to do it. During the course of the lecture, the lectern would fall off, the text sheets would scatter in all directions, and in the back of the room, the glass slides would crash to the floor as the projectionist screamed in horror. With sardonic wit he would underscore the dull, ponderous style of most speakers at scientific meetings. Cap would illustrate the various delivery styles ("And now to the A & P style—we have the goods but we do not deliver!"). Cap had orchestrated his lecture to the nth degree. I heard the lecture at least three times during my years at Harvard, and thought that it got better each time, as Cap kept adding more ingenious ways to poke fun at inarticulate, fumbling speakers. The lecture became famous nationwide and Cap often was asked to present it at other institutions. Imitators sprang up everywhere over the years, but I doubt that any of them matched Cap's style.

The War Years

The interest and expertise on tropical fungi that Cap Weston had acquired during the years in the Philippines and in his travels throughout Southeast Asia became important to the US Government when war broke out against Japan. He became a consultant to the Quartermaster Corps of the United States Army. He was the scientist in charge of investigations on fungal deterioration of Army material, such as tarpaulins, tents, leather, clothing, etc. He helped establish a laboratory in Panama where such materials could be tested under tropical conditions, and, after the war, he played a major role in the establishment of the Natick Laboratory of the Quartermaster Corps in Natick, Massachusetts. This laboratory became a world center for research on the biochemistry of cellulose degradation. He continued to be involved as a consultant to this laboratory even after his retirement from Harvard.

The Retirement Years

Cap retired in 1956 but continued to pursue his interest in teaching, this time at the elementary school level. He had a keen interest in utilizing children's natural curiosity about nature and science. His personality was ideally suited for television and for many years he was a familiar figure on the television screen as the leader of several programs designed to enliven the teaching of science for elementary school children in the Boston area. Later on he joined the Elementary Science Study of Educational Services, where he played a major role in improving the teaching of science in elementary schools.

In addition to his work for the Quartermaster Corps, he served as a consultant for various corporations and Government institutions. One such consultantship for the United Fruit Company in 1958 brought him for several days to the jungle outpost at Coto, Costa Rica, where I worked as a plant pathologist. He offered keen advice on possible means to control several banana diseases. A few forays to collect fungi in the tropical rain forest brought to the surface not only his wide knowledge of tropical fungi, but his love and appreciation of nature.

RECOGNITION

Weston received many honors throughout his life but I will list only a few. For example, in 1932 he became the first President of the Mycological Society of America and he was President of the New England Botanical Club from 1931 to 1933. He was a Fellow of the American Academy of Arts and Sciences and of the American Association for the Advancement of Science. He received honorary degrees as Doctor of Science from his alma mater, Dartmouth University, in 1956 and from McGill University in 1959. The US Department of the Army gave him a Civilian Distinguished Service Award and Medal in 1962 for his work with the Quartermaster Corps.

Weston was a frequent lecturer at many institutions in the United States and Canada. Special mention should be made of the Lowell Lectures in Boston, the Darwin Anniversary Address at Michigan State University, and the Ropes Memorial Lectures in Salem, Massachusetts. He was a Visiting Professor at Johns Hopkins University in 1937, at Louisiana State University in 1942, and at the University of California, at both Berkeley and Davis.

Cap Weston was primarily an outstanding teacher who, by dint of his personality and great intellect, managed to change the course of an important branch of science. He had a remarkable ability to influence and direct students, and he enjoyed the role of a protective father figure. His gracious, generous nature is remembered with affection by the many hundreds of students whose lives he touched and who had the good fortune to know him. He is survived by his wife, Lucile, of Wellesley; a son, Seth, of Dallas; and a daughter, Sabrina, of Arlington, MA.

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