Andrew A. Benson

1917 – 2015

Andrew A. Benson (called Andy by his friends) died on January 16, 2015, in La Jolla, California; he was born in Modesto, California, on September 24, 1917. He graduated from Modesto High School in 1935 and studied chemistry at the University of California, Berkeley, obtaining a B.S. in 1939. He performed graduate work at the California Institute of Technology under Carl Niemann, receiving his doctorate in 1942, and then returned to Berkeley as an instructor in the Department of Chemistry. There, he was exposed to photosynthesis and radioisotope research by Samuel G. Ruben and Martin Kamen, two pioneers who had discovered ^{14}Carbon in 1940. His research came to a halt in 1942 with the onset of World War II. During that period Andy served in various functions in the civil service.

In 1946, Andy was appointed a research associate in the Radiation Laboratory at Berkeley in the photosynthesis group that was being assembled by Melvin Calvin. By feeding ^{14}C-labeled CO_2 to suspensions of the green alga *Scenedesmus*, he identified 3-phophoglyceric acid (PGA) as the first stable product of photosynthesis in joint work carried out with Calvin. For these studies, he designed the "lollipop," a flattened glass vessel that could be illuminated from both sides. After the introduction of $^{14}CO_2$, samples of the illuminated *Scenedesmus* suspension were removed after short exposure

Dee and Andy Benson at the dinner held at the La Jolla Country Club on September 24, 2014, commemorating his 97th birthday. SOURCE: BUCHANAN AND DOUCE, 2015.

times, collected in hot methanol, and analyzed by two-dimensional paper chromatography. The labeled compounds were localized on the chromatograms and identified by autoradiography. These techniques, introduced by Andy to the Calvin group, subsequently became the gold standard for ^{14}C-labeling experiments by laboratories worldwide.

In 1950, Andy chemically identified ribulose 1,5-bisphosphate as an essential component of the photosynthetic carbon reduction cycle. This 5-carbon sugar phosphate proved to be the long-sought missing link in the cycle that enables photosynthetic organisms to fix CO_2 and form 3-phosphoglycerate. Other intermediates of the carbon cycle, including sedoheptulose 7-phosphate (a 7-carbon sugar) and pentose monophosphates (5-carbon sugars), were identified by Andy in collaboration with other members of the Calvin group. The compounds identified in lollipop experiments served as the basis for formulating the carbon dioxide reduction cycle of photosynthesis. Although Calvin had proposed the original concept of a cycle, Andy was pivotal in bringing the idea to fruition. He developed techniques for degrading ^{14}C-labeled sugar phosphate intermediates to locate the ^{14}C-label in individual C-atoms, innovations central to deciphering the cycle. By late 1953, the photosynthetic carbon reduction cycle was more or less worked out, and evidence for the complete cycle was published the following year. Working in 1954 with Jacques Mayaudon, Andy showed independently of Samuel Wildman that the highly abundant "fraction I protein" of leaves catalyzed the incorporation of CO_2 into ribulose 1,-5-bisphosphate to yield 3-phosphoglycerate.

When Andy left Berkeley in 1955, he was appointed to the faculty at Pennsylvania State University and turned his attention to plant lipids. In 1957, he discovered the major membrane phospholipid phosphatidyl glycerol, and in 1961, the sulfolipid sulfoquinovosyl diglyceride. Both are essential to the formation and function of photosynthetic chloroplast membranes. In recognition of his outstanding contributions to the lipid field, the book *Lipids in Photosynthesis,* edited by Hajime Wada and Norio Murata, was dedicated to him in 2009 (Volume 30 in the series "Advances in Photosynthesis and Respiration," Springer, Dordrecht).

In 1962, Andy moved to the Marine Biology Research Division, Scripps Institution of Oceanography, in La Jolla, where he spent the remainder of his career, becoming emeritus in 1989. At Scripps he initially continued his research on plant lipids, but with time turned his attention to marine biology. With his coworkers he recognized the importance of calcitonin in calcium regulation in salmon, studied the role of arsenic in oceans, and identified previously unknown intermediates of arsenic metabolism in aquatic plants as well as the highest concentration of arsenic in kidneys of giant clams of the Great Barrier Reef, Australia. In 1992, he and Arthur Nonomura discovered the ability of methanol to stimulate the

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growth of crop plants. ^{13}C studies on this effect led to the detection of an unexpected glycoside, a lectin substrate, and a previously unrecognized plant pathway.

For 60 years, the work of Andrew Benson on the discovery of ribulose bisphosphate and the identification of intermediates involved in CO_2 fixation has been at the cutting edge of plant science. The breadth of his approach, the quality of his work, and the advances in understanding that his discoveries brought about are simply superb. He captivated the enthusiasm of all scientists studying photosynthetic organisms. Rather than work in the usual competitive manner, he encouraged others to become involved and take up his studies where he left off.

Key to Andy's success was his habit of working at the bench almost every day and his dissatisfaction with imprecise results. He always asked basic, essential questions as the starting point for new research endeavors, always approached scientific inquiries with enthusiasm, and expressed great satisfaction in his work. He was also known for his inspirational personality. He would listen carefully to the results and ideas of others, and then offer solid advice on additional experimental approaches. In this way, he introduced countless young and visiting scientists to plant biology, motivating them to perform at the highest level. He hosted numerous scientists in his laboratory, especially postdoctoral scholars.

In the eight years he spent in Berkeley, Andy was the key contributor in elucidating the essentials of the carbon reduction cycle. In recognition of his contributions to photosynthesis, this metabolic pathway is increasingly referred to as the "Calvin-Benson cycle." Many scientists and historians believe that the Nobel committee should have given the Nobel Prize to both Calvin and Benson. One of us (Govindjee) persuaded Benson to present details of his time with the Calvin group. This he later discreetly described in two personal retrospectives, "Following the Path of Carbon in Photosynthesis" and "Paving the Path" (Benson, 2002 a,b). His contributions were also described in a television series (Walker, 2012) and a popular book (Morton, 2007). The breadth and depth of his contributions to photosynthesis became better known in the scientific community when he made a video with one of us (BBB) in 2012. The video has been posted on YouTube (http://youtu.be/GfQQJ2vR_xE), and the transcript has been published (Buchanan and Wong, 2013). Filming of the video followed the publication of a special issue of Photosynthesis Research organized to commemorate Andy's 90th birthday in 2007 (Photosynthesis Research, Vol. 92; see also Buchanan et al., 2007). The special issue was presented to Andy at a memorable dinner held at the historic restaurant Le Procope in Paris that was organized to honor him on his 90th birthday (Lichtenthaler et al., 2008). Detailed information on his biography and research activities can also be found in an article honoring him on his 93rd birthday (Govindjee, 2010) and in an earlier oral history interview (Harkewicz, 2006).

Andy retained full mental vigor until the very end of his life. In his 96th year, he made a congratulatory video on behalf of one of us (BBB; see https://www.youtube.com/watch?v=c4jiYk-W_30). The following year he celebrated his last birthday, his 97th, with a dinner held at the La Jolla Country Club that was attended by his wife, Dee, and other family members, close friends, and former collaborators. Then, as throughout his life, he served as a model for all of us. A Celebration of Life ceremony was held for him on February 6, 2015, at the La Jolla Country Club.

Awards

Andy received numerous honors and awards during his career, including the Sugar Research Foundation Award, 1950; Ernest Orlando Lawrence Memorial Award of the Atomic Energy Commission, 1962; Phil.D. *honoris causa,* University of Oslo, Norway, 1965; fellow of AAAS, 1965; Stephen Hales Prize of ASPB, 1972; elected member of the National Academy of Sciences, 1973; elected fellow of the American Academy of Arts and Sciences, 1981; elected member of the Norwegian Society of Science and Letters, 1984; Supelco/AOCS Research Award, American Oil Chemists Society, 1987; and Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology, 2008. On the occasion of his 97th birthday, he was honored with the first Andrew A. Benson Award for "Conferring the Greatest Benefit on Mankind" for his recent work on the role of lectins in improving crop productivity. The award is sponsored by BRANDT iHammer.

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A more complete version of this obituary can be found in Lichtenthaler, H. K., Buchanan, B. B., Douce, R., and Govindjee (2015). Andrew A. Benson, 1917–2015. Photosynthesis Research. *doi 10.1007/s11120-015-0119-8.*

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