

Andrew A. Benson, 1917–2015

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Abstract On January 16, 2015, Professor Andrew Alm Benson, one of the leading plant biochemists of the twentieth century, died in La Jolla, California, at the age of 97; he was born on September 24, 1917. Benson was known especially for his pioneering studies on photosynthesis (CO₂ assimilation, carbon reduction cycle) and plant lipids (phospholipid phosphatidyl glycerol; and the sulfolipid, sulfoquinovosyl diglyceride). A photograph of Benson is shown in Fig. 1.

Keywords The path of carbon in photosynthesis · Calvin–Benson cycle · RuBP · Rubisco · Phosphoglycerate · PGA · Sulfolipid

Abbreviations

PGA Phosphoglyceric acid
RuBP Ribulose bis-phosphate
Rubisco Ribulose bis-phosphate carboxylase oxygenase

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; his father was a physician, and his mother was a schoolteacher. He graduated from Modesto High School in 1935 as Valedictorian of his class and went on to the University of California, Berkeley, where he studied chemistry, obtaining a B.S. in 1939. It was at Berkeley that he became infatuated with chemistry and decided to do graduate work at the California Institute of Technology (Cal Tech) under Carl Niemann, one of the nation's leading carbohydrate chemists.

After receiving his doctorate in 1942, Benson returned to Berkeley as an instructor in the Department of Chemistry. There, he was exposed to photosynthesis and radioisotope research by Samuel G. Ruben (1913–1943) and Martin Kamen (1913–2002)—two pioneers who two years earlier (1940) had discovered ¹⁴Carbon. Benson started his photosynthesis work with the short-lived ¹¹Carbon isotope but, when it became available in 1943, turned to ¹⁴CO₂ with a half-life of more than 5000 years (Benson 2011). His research came to a halt in 1942 with the onset of World War II. During that period Benson, a conscientious objector, served with the US Forest Service, where he was involved in fighting fires and aerial photogrammetry. He was later transferred to Stanford University and Cal Tech, where he carried out antimalarial drug research.

After resuming his career in 1946, Benson was appointed a Research Associate in the Radiation Laboratory at Berkeley in a photosynthesis group that Melvin Calvin (Nobel Laureate in Chemistry, 1961) had just begun assembling. By feeding ¹⁴C-labeled CO₂ to suspensions of the green alga *Scenedesmus*, Benson identified 3-phosphoglyceric acid (PGA) as the first stable product of photosynthesis in joint work carried out with Calvin. For these studies, Benson designed the “lollipop,” a flattened glass vessel that could be

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Fig. 1 Photograph of Andrew A. Benson. Source: Annual Review of Plant Biology, Vol. 53, 2002, published with permission

illuminated from both sides. After introducing $^{14}\text{CO}_2$, samples of the illuminated *Scenedesmus* suspension were removed after short exposure times and collected in hot methanol, thereby stopping all enzymatic carbon reactions. The samples were then analyzed by two-dimensional paper chromatography using solvents that had been developed for clear separation of the ^{14}C -labeled metabolites formed in the experiment. The labeled compounds were localized on the chromatograms and identified by autoradiography. These techniques, introduced by Benson to the Calvin group, subsequently became the gold standard for ^{14}C -labeling experiments by laboratories worldwide. Figure 2 shows Benson with a radiochromatogram.

In 1950, Benson, working on his own, detected and chemically identified ribulose 1,5-bisphosphate (originally named ribulose 1,5-diphosphate) as an essential component of the photosynthetic carbon reduction cycle. This 5-carbon sugar phosphate proved to be the long-sought missing link of the cycle that enables photosynthetic organisms to fix CO_2 and form 3-phosphoglycerate—the compound Benson and Calvin had earlier identified as the first stable carbon product formed from CO_2 . All previous attempts to identify the compound that accepts CO_2 and yields



Fig. 2 Andrew Benson in his office in La Jolla in 2001. He is holding one of the early radioautograms (from the 1950s) developed with a two-dimensional paper chromatogram. The film shows ^{14}C -labeled intermediates formed by *Scenedesmus* cells fed $^{14}\text{CO}_2$. (Source Govindjee 2010)

3-phosphoglycerate had been unsuccessful, thus attesting to the significance of Benson's discovery. Other intermediates of the carbon cycle, including sedoheptulose 7-phosphate (7-carbon sugar) and pentose monophosphates (5-carbon sugars), were identified by Benson in collaboration with other members of the Calvin group. James A. Bassham (1922–2012), a graduate student in chemistry, participated in much of this work. The compounds identified in lollipop experiments served as the basis for formulating the carbon dioxide reduction cycle of photosynthesis. Although Calvin (1911–1997) had proposed the original concept of a cycle, Benson was pivotal in bringing the idea to fruition. As a result of expertise gained in carbohydrate chemistry during his doctoral research at Cal Tech, Benson was able to develop techniques that the Calvin group adopted and applied 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 had been more or less worked out and evidence for the complete cycle was published the following year (Bassham et al. 1954).

Working with Jacques Mayaudon, a visiting professor from Belgium, Benson showed that the highly abundant “fraction I protein” that Samuel Wildman (1912–2004) had isolated catalyzed the incorporation of CO_2 into ribulose 1,5-bisphosphate to yield 3-phosphoglycerate (abbreviated PGA). Mayaudon and Benson described their discovery of this enzymatic activity in the draft of a manuscript they presented to Calvin shortly after completing the work in 1954. However, Calvin shelved the manuscript and it was not published until three years later with Mayaudon as sole author (Mayaudon 1957). Benson's name was left off. By then, Wildman had independently reported the CO_2 -fixing activity of the Fraction I protein that was called

carboxydismutase (the enzyme is now known as ribulose 1,5-bisphosphate carboxylase or Rubisco). Benson had also become fully occupied with other endeavors, and according to his letters and notes, he first became aware of the publication in 1997. At that time he also found out that Calvin had reported his and Mayaudon's results at the International Congress of Biochemistry held in Brussels in 1955, mentioning Mayaudon, but not Benson. However, in a second paper on the topic (Mayaudon et al. 1957) the names of both Benson and Calvin were included.

The picture is complicated by the fact that Calvin abruptly dismissed Benson in 1954, the same year that evidence for the complete cycle was published. When Benson left Berkeley, he was appointed to the faculty at Pennsylvania State University (Penn State) where he drew on his earlier work with Calvin on thioctic (lipoic) acid and turned his attention to plant lipids. His efforts were fruitful. In 1957, he and Benjii Maruo discovered and identified 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, two books were dedicated to Benson: (1) in 1987, *Proceedings of the 7th International Symposium on Plant Lipids* held in Davis, California ("The Metabolism, Structure and Function of Plant Lipids" edited by Paul K. Stumpf, J. Brian Mudd and W. David Nes, Plenum Press, New York), and (2) in 2009, "Lipids in Photosynthesis," edited by Hajime Wada and Norio Murata (Volume 30 in the series "Advances in Photosynthesis and Respiration," Springer, Dordrecht). A photograph of Benson attending the 1986 lipid meeting in Davis is shown in Fig. 3.

Benson left Penn State after 6 years and, following a brief appointment in the School of Medicine at the University of California at Los Angeles (UCLA), moved to the Marine



Fig. 3 Andrew Benson with William W. Thomson of the University of California, Riverside, at the 7th International Symposium on Plant Lipids. The meeting, held July 27–August 1, 1986 at the University of California, Davis, was organized by Paul Stumpf (1919–2007). Photograph by Hartmut K. Lichtenthaler

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. He and Géraud Milhaud recognized the importance of calcitonin in calcium regulation in salmon—a species they also studied as a model for aging in humans. During this period, he identified wax as a major marine nutritional energy source important to the survival of animals living in the sea. Benson went on to study 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 known to accumulate in animals in kidneys of giant clams of the Great Barrier Reef, Australia. Returning to plants, in 1992, he and Arthur Nonomura discovered the ability of methanol to stimulate the growth of crop plants. This finding led to Benson's ^{13}C -tracer investigations with his longtime friends in Grenoble that revealed an unexpected glycoside (Gout et al. 2000) later identified as a lectin substrate. This striking finding formed the basis for a previously unrecognized plant pathway that was described in a joint paper with Nonomura (Nonomura and Benson 2014).

For 60 years, the work of Andrew Benson on the discovery of ribulose bisphosphate and the identification of intermediates involved in CO_2 fixation have 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. One of us (RD) personally experienced Benson's generosity when, as postdoc, he discovered that the chloroplast envelope rather than the endoplasmic reticulum was the site of galactolipid synthesis. Benson refused to put his name on the paper, but when *Science* rejected it, he secretly wrote a strong recommendation letter to the editor. Fifteen days later the paper was accepted. He was a great communicator.

Key to Benson'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. His experiments were clean and his highly focused pursuits consistently led to decisive conclusions. He always approached scientific inquiries with enthusiasm and expressed great satisfaction in his work.

Benson was also known for his inspirational personality. He took enormous pleasure in open scientific discussions. 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 research, motivating them to perform at the highest level. He hosted numerous scientists in his laboratory, especially postdoctoral scholars, a number of whom went on to become leaders in their fields—for example, Joseph F.G.M. Wintermans, Netherlands (biosynthesis of chloroplast glycerolipids); Shirley W. Jeffrey, Australia (carotenoids and chlorophyll pigments of marine algae); Roger E. Summons, United States (the Precambrian age and the early evolution of life); Roland Douce, France (function of the chloroplast envelope in photosynthesis).

In the 8 years he spent in Berkeley, Benson was the key contributor in elucidating the essential intermediate metabolites of the carbon reduction cycle. In recognition of his contributions to our understanding of 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 1961 Nobel Prize to both Calvin and Benson. True to his character, Benson rose above the fray. Initially, he was reluctant to write about his experiences. One of us (Govindjee) spent considerable time persuading him to present his version of the events that took place during his time with the Calvin group. Benson later discreetly described certain details of this work in two personal retrospectives, “Following the path of carbon in photosynthesis” and “Paving the path” (Benson 2002a, b). His contributions were also described in a television series (Walker 2012) and a popular book (Morton 2009). Lastly, several of his original publications on carbon assimilation in photosynthesis and plant lipid research from Benson’s laboratory were reviewed in a paper dedicated to him on his 90th birthday (Lichtenthaler 2007, pp. 164 and 165). However, the breadth and depth of his contributions to photosynthesis were neither appreciated nor widely known in the scientific community until he made a video with one of us (Buchanan 2012)—nearly six decades after he left Berkeley. 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 the above-mentioned Special Issue of *Photosynthesis Research* organized to commemorate Benson’s 90th birthday in 2007 (*Photosynthesis Research* 2007, Vol 92). Twelve colleagues contributed articles to this issue that featured an editorial highlighting certain of his pathbreaking contributions to his field (Buchanan et al. 2007). The Special Issue was presented to Benson 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). Figure 4 shows a photograph of Benson accepting the Special Issue of *Photosynthesis Research*. Detailed information on his biography and research activities can also be found in an article honoring Benson on his 93rd birthday (Govindjee 2010) and in an earlier oral history interview (Harkewicz 2006).

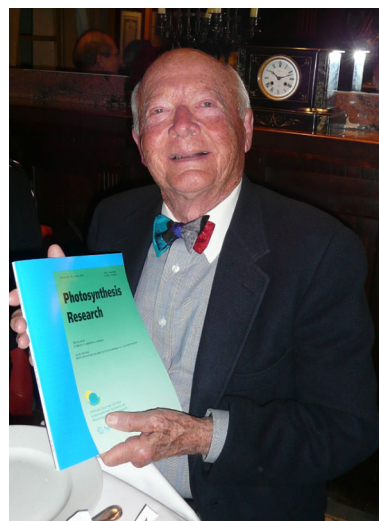


Fig. 4 Andrew Benson at a dinner at the Le Procope restaurant in Paris celebrating his 90th birthday in 2007. He is holding the Special Issue of *Photosynthesis Research*: “A Tribute to Andrew A. Benson” commemorating his birthday. (Source Lichtenthaler et al. 2008)

Benson 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, 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, other family members, close friends and former collaborators (see Fig. 5) (Buchanan and Douce 2015). 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. Benson is survived by his wife, Dee, two daughters, Claudia and Linnea, Dee’s three children, Diane, Jim and Lisa, and eight grandchildren.

Awards

Benson 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 (American Association of the Advancement of Science), 1965; Stephen Hales Prize of the American Society of Plant Biologists, 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; 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*



Fig. 5 Dee and Andrew Benson at the dinner held at the La Jolla Country Club on September 24, 2014 commemorating his 97th birthday. (Source Buchanan and Douce 2015)

the Greatest Benefit on Mankind” for his very last work on the modulation of ^{12}C -glycoconjugates in improving crop productivity. The award is sponsored by Brandt iHammer.

Acknowledgments The black-and-white photograph of Professor Benson was reprinted with permission from the *Annual Review of Plant Biology*, Vol. 53, 2002 by Annual Reviews. The authors thank Arthur Nonomura for providing key information on Andrew Benson’s life and contributions made in the latter part of his career and his assistance in editing the manuscript.

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