Andrew A. Benson

1917–2015

BIOGRAPHICAL *Memoirs*

A Biographical Memoir by
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Hartmut K. Lichtenthaler,
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NATIONAL ACADEMY OF SCIENCES

ANDREW ALM **BENSON**

September 24, 1917 –January 16, 2015

Elected to the NAS, 1973

By Bob B. Buchanan, Roland Douce, Govindjee, Hartmut K. Lichtenthaler, and Roger E. Summons

Andrew Alm Benson was one of the leading plant biochemists of the 20th century, known especially for his pioneering studies on photosynthesis (CO_2 assimilation, photosynthetic carbon reduction cycle) and plant lipids (phospholipid, phosphatidyl glycerol, and the sulfolipid, sulfoquinovosyl diglyceride). He was born on September 24, 1917, in Modesto California. His father was a physician, and his mother was a school teacher. 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. At Berkeley he became infatuated with chemistry and decided to do graduate work at the California Institute of Technology (Caltech) under Carl Niemann (NAS, 1952), one of the nation's leading carbohydrate chemists. An athletic person, Andrew was an avid climber in those days and proud of his conquests ranging from the walls of the Crellin Laboratory on the Caltech campus to peaks of the nearby San Gabriel and Sierra Nevada ranges.

Beginning his career at Berkeley: laying the foundation for the Calvin-Benson cycle

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 and Martin Kamen (NAS, 1962)—pioneers who two years earlier (1940) had discovered ^{14}C, that is, radiocarbon-14. Benson started his photosynthesis work with Ruben and Kamen using the isotope ^{11}C with its 'challenging-to-work-with' half-life of just 21 minutes. Later he turned to ^{14}C with its less energetic radioactivity but more manageable half-life of 5,730 years, when it became readily available. 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 U.S. Forest Service, where he was involved in fighting fires and aerial photogrammetry. He was later transferred to Stanford University and Caltech, 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 (NAS, 1954) had begun assembling. By feeding ^{14}C-labeled CO_2 to suspensions of the green algae, *Chlorella* and *Scenedesmus*, Benson identified 3-phosphoglyceric acid as the first stable product of photosynthesis in joint work with Calvin (Benson and Calvin, 1948; Calvin and Benson 1948). For these studies, Benson designed the "lollipop," a flattened glass vessel that could be illuminated from both sides (see Figure 12.37, Buchanan et al., 2000). After introducing $^{14}CO_2$, samples of the illuminated algal suspension were removed after short exposure times and collected in hot methanol, thereby stopping all enzymatic 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 paper chromatograms and visualized by autoradiography. In those days, and in the absence of the exquisitely sensitive instrumentation available today, compounds were initially, and tentatively, identified on the basis of their chromatographic behavior in different solvent systems propelled by a healthy charge of chemical intuition. These techniques, introduced by Benson to the Calvin group, subsequently became the gold standard for ^{14}C-labeling experiments by laboratories worldwide. Figure 1 shows Benson with an autoradiogram he developed in the 1950s.

Figure 1. Andrew Benson in his office in La Jolla in 2001. He is holding one of the early autoradiograms (from the 1950s) developed with a two-dimensional paper chromatogram. The film shows ^{14}C-labeled intermediates formed by Scenedesmus cells fed $^{14}CO_2$. (Source: Govindjee, 2010.)

Far-reaching early discoveries made in Calvin's laboratory

In 1951, 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 (Benson, 1951). 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-phosphoglyceric acid the compound Benson and Calvin had earlier identified as the first stable carbon product formed from CO_2. All previous attempts to identify a compound that accepted CO_2 and yielded PGA had been unsuccessful, thus attesting to the significance of Benson's discovery. Other intermediates of the carbon cycle, including sedoheptulose 7-phosphate (a 7-carbon sugar) and pentose monophosphates (5-carbon sugars) were identified by Benson in collaboration with other members of the Calvin group (Benson et al., 1951; Benson et al., 1952; Bassham and Calvin, 1957). James A. (Al) Bassham, a graduate student in chemistry, participated in much of this work. The compounds identified in lollipop experiments served as the basis for formulating the reductive cycle of CO_2 assimilation during photosynthesis. Although Calvin had proposed the original concept of a "cycle," Benson was pivotal in bringing the idea to fruition in its correct form. As a result of expertise gained in carbohydrate chemistry during his doctoral research at Caltech, 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 CO_2 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 scientist from Belgium, Benson showed that the highly abundant "fraction I protein" that Samuel Wildman had isolated catalyzed the incorporation of CO_2 into ribulose 1,5-bisphosphate to yield 3-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 the 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/oxygenase 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, more than 40 years after the original paper was written. 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 the names of both Benson and Calvin were included (Mayaudon et al., 1957). 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.

Transition to plant lipid research at Penn State

When Benson left Berkeley, he was appointed to the faculty at Pennsylvania State University (Penn State) where he drew on his earlier work in Calvin's laboratory on thioctic (lipoic) acid and turned his attention to plant lipids. His efforts were fruitful. In 1957, he and Benjii Maruo discovered the major membrane phospholipid, phosphatidyl glycerol; and in 1961, the sulfolipid, sulfoquinovosyl diglyceride. Both are essential for the formation and function of photosynthetic chloroplast membranes. In recognition of his outstanding contributions to the lipid field, two scientific books were dedicated to Benson. In 1987 the Proceedings of the 7th International Symposium on Plant Lipids held in Davis, California, in 1986 (*The Metabolism, Structure and Function of Plant Lipids* edited by Paul K. Stumpf, J. Brian Mudd, and W. David Nes), and in 2009 *Lipids in Photosynthesis*, a book edited by Hajime Wada and Norio Murata. A photograph of Benson attending the 1986 lipid meeting in Davis is shown in Figure 2.

Figure 2. 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.)

Move to marine biology at La Jolla

Benson left Penn State after six years and, following a brief appointment in the School of Medicine at the University of California at Los Angeles (UCLA), moved to the Marine Biology Research Division, Scripps Institution of Oceanography in La Jolla, where he spent the remainder of his career. He served as chairman of the Marine Biology Research Division from 1965 until 1969, as associate director of Scripps from 1966 to 1970, as director of Scripps's physiological research laboratory, from 1970 to 1976, and became emeritus in 1989.

At Scripps he initially continued his research on plant lipids, but later, turned his attention to marine biology. He and Géraud Milhaud recognized the importance of calcitonin in calcium regulation in salmon—a polypeptide they also studied as a model for aging in humans. During this period, he identified wax esters as a major marine nutritional energy source important for the survival of animals living in the sea and showing that as much as 70 percent of the dry weight of a copepod could be wax (Figure 3). The wax food-storage system provides animals such as copepods with a food reserve that can be controlled separately from its day-today fat metabolism.

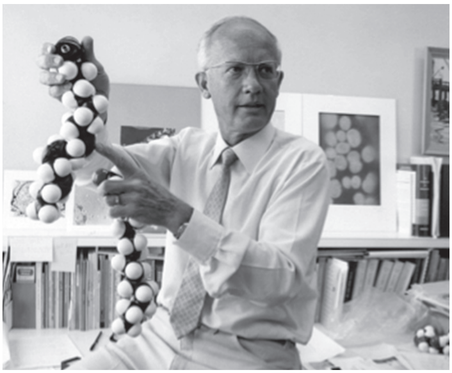

Figure 3. Andrew Benson holding a model of a wax molecule in his office in 1968. He and his collaborators found wax to be a major energy-rich food in the sea. This unpublished photograph was taken by a photographer from *Oceans Magazine.*

Benson went on to study the role of arsenic in oceans, using radioarsenic (^{74}As) as a tracer. He and Bob Cooney identified arsenate assimilation into arsenosugars and arsenolipids in unicellular marine algae using paper chromatography and autoradiography. Benson pointed to phosphate limitation as a possible factor in the entry of arsenic into the marine food chain via marine algae. He also showed that arsenic accumulated to high abundance in tissues of tropical marine invertebrates, including extraordinary concentrations in the kidneys of giant clams of the Great Barrier Reef, Australia. Absolute chemical characterization of these compounds was accomplished by the Western Australian chemists John S. Edmonds and Kevin A. Francesconi using NMR spectroscopy and X-ray crystallography, and their work ultimately revealed an array of very complex organo-arsenicals carrying dimethylarsinylribose moieties. Fortunately, for lovers of seafood, Edmonds and Francesconi also demonstrated that the most common stable arsenic compound to accumulate in marine animals was non-toxic arsenobetaine.

A picture of the boldness, breadth, and depth of his biochemical explorations was captured in Benson's radiochromatograms and stable isotope labeling experiments conducted over his career (Bassham, 2003; Benson, 2011; Nonomura et al., 2016). The isotopes, comprising ^{3}H, ^{11}C, ^{14}C, ^{80}Br, ^{45}Ca, ^{60}Co, ^{31}P, ^{32}P, ^{32}S, ^{35}S, ^{74}As and ^{125}I, were fed to algae, vascular plants, invertebrates and mammalian tissues in a variety of substrates both singly and doubly. He developed a 20-minute synthesis of ^{11}C-labeled phosgene that was to be used to understand the mechanism of its toxicity in experiments that were curtailed by Benson's conscription and Sam Ruben's untimely death by phosgene inhalation (Bassham, 2003; Benson, 2002a, 2002b, 2011; Gest, 2004).

Final years

Returning to plants, in 1992, he and Arthur Nonomura discovered the ability of methanol to stimulate the growth of crop plants (Nonomura and Benson, 1992). In 1997, Benson synthesized ^{13}C-labeled glycolic acid that led to ^{13}C-tracer investigations with his former postdoc, Roland Douce (NAS Foreign Associate, 1997), and other long-term colleagues in Grenoble. They administered these non-radioactive compounds to live cultured sycamore cells under a 400 MHz NMR spectrometer in the Center for Atomic Energy in Grenoble for the spectrum of the products to be evaluated. The metabolism of ^{13}C-labeled methanol in plants was studied in a similar way to reveal the production of ^{13}C-methyl-β-D-glucoside in vivo (Gout et al., 2000). Then, with Karl Biel, John Nishio and Nonomura, Benson tracked the glycoside to ninhydrin-N-linked-^{14}C-glycoside, later identifying it as a lectin substrate (Biel et al., 2010). 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).

> Key to Benson's success was his habit of working at the bench almost every day and his dissatisfaction with imprecise results.

Overview

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 occupied a key position in plant science. The breadth of his approach, the elegance and quality of his work, and the advances in understanding that his discoveries inspired, 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 a 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. For another of us (RES), it was a series of field trips to the Great Barrier Reef under Benson's leadership, and his discoveries concerning lipids in the marine realm, that inspired a career in the study of their chemical fossils.

Key to Benson's success was his habit of working at the bench almost every day and his dissatisfaction with imprecise results. Without exception he asked fundamental, 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 and overt generosity. He took enormous pleasure in open and vigorous 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 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, Roland Douce, France (function of the chloroplast envelope in photosynthesis); the late Shirley W. Jeffrey (NAS Foreign Associate, 2000), Australia (carotenoids and chlorophylls of marine algae); Roger E. Summons (Royal Society, 2008), United States (molecular fossils of microbes, plants and animals); and Joseph F. G. M. Wintermans, The Netherlands (biosynthesis of chloroplast glycerolipids). Endearing eccentricities were also part and parcel of Andrew's personal style. He was passionate about beautiful timbers, honey from exotic plants, postage stamps and the imperial system of weights and measures. It was impossible to win an argument with him about the merits of metrification.

In the eight years he spent in Berkeley, Benson was the key contributor in elucidating the essential intermediate metabolites of the photosynthetic 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 awarded the 1961 Nobel Prize to both Calvin and Benson. True to his character, Benson rose above the fray to the point of co-authoring, with Glenn T. Seaborg, the generous 1998 Biographical Memoir of Melvin Calvin (Seaborg and Benson, 1998) and speaking at Calvin's memorial service. 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 (Benson, 2002a; 2002b). His contributions were also described in a 2012 television program hosted by Timothy Walker (Walker, 2012) and in a popular book by Oliver Morton (Morton, 2008). Lastly, several of the original publications on carbon assimilation in photosynthesis and plant lipid research from Benson's laboratory were reviewed in a paper by HKL dedicated to him on his 90th birthday (Lichtenthaler, 2007). 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 (BBB) on July 27, 2012—nearly six decades after he left Berkeley. The video has been posted on You Tube (Buchanan, 2012) and the transcript has been published (Buchanan and Wong, 2013). The video was made after the publication of a special issue of *Photosynthesis Research* organized to commemorate Benson's 90th birthday in 2007. Twelve colleagues contributed articles to this issue that featured an editorial highlighting certain of his seminal contributions to his field (Buchanan et al., 2007). This special issue was presented to Benson at a memorable dinner at the historic Paris restaurant Le Procope 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 oral history interview (Harkewicz, 2006).

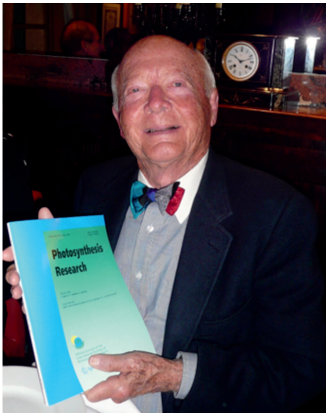

Figure 4. Andrew Benson at a dinner at the Le Procope restaurant in Paris celebrating his 90th birthday in 2007. He is holding the Special Issue of *Photosynthesis Research:* "A Tribute to Andrew A. Benson" commemorating his birthday. (Source: Lichtenthaler et al., 2008.)

Last years

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, link below). 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 Figure 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 (Nonomura et al., 2016). Benson is survived by his wife, Dee, two daughters, Claudia and Linnea, Dee's three children, Diane, Jim and Lisa, and eight grandchildren. Further words from Benson are at: https://youtu.be/c4jiYk-W_30.

Figure 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.)

Recognition

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; Member of the National Academy of Sciences, 1973; Senior Queen's Fellow in Oceanography, Australian National University and the Australian Institute of Marine Science, 1979; Fellow of the American Academy of Arts and Sciences, 1981; Member of the Norwegian Society of Science and Letters, 1984; Docteur, *honoris causa*, Université Pierre et Marie Curie, 1986; 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 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.

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