

Celebrating Andrew Alm Benson's 93rd birthday

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Abstract We celebrate Andy Benson's 93rd birthday on September 24, 2010 through this Editorial. This short account about Andy Benson should serve as a prelude to the short article that Andy has written for the entire photosynthesis community, which gives a glimpse of why he left the field of the "path of carbon in photosynthesis," when he had already discovered, together with Melvin Calvin, James Alan Bassham, and others, most of the major steps in what we now call the Calvin–Benson cycle.

Keywords James A. Bassham · Carl B. Benson · Emma C. Alm Benson · Dee Benson · Calvin-Benson cycle · Melvin Calvin · Martin Kamen · Lifetime Achievement Award of the Rebeiz Foundation · Robert A. Millikan · Samuel Ruben · University of California at Berkeley · University of California, San Diego

Introduction

Andy Benson's 90th birthday was celebrated wonderfully well by a special issue¹ of Photosynthesis Research (Buchanan BB, Douce R, Lichtenthaler HK, editors; Photosynth Res 92(2): 143–271) and a dinner on October 24, 2007, at the historic *Le Procope* restaurant in Paris [Lichtenthaler HK, Buchanan BB, Douce R (2008) Photosynth Res 96: 181–183]. It is my personal pleasure to

celebrate, after 3 years, the 93rd birthday of my dear friend Andy Benson on September 24, 2010. (It is 3 years because that is the time it took me to convince Andy to give me his story on why he left Berkeley in 1954.) Andy is not only one of the most extraordinary scientists I have associated with, but a person with great humor, talent, and a fantastic memory of details of experiments that he did 50–60 years ago. He is my model of a scientist and a great human being. On behalf of the entire photosynthesis community, I wish him many more years of good life. In this brief tribute to Andy, I present a short biography and his contributions, his honors, and some selected photographs that we took in 2001 when Rajni (my wife) and I visited him and his wife Dee in San Diego, California. This account should serve as a prelude to the short article that Andy has written for the entire photosynthesis community, which gives a glimpse of why he left the field of the "path of carbon in photosynthesis," when he had already discovered all of the steps in what we now call the Calvin–Benson cycle. (See A. A. Benson, this issue.)

Biography and his contributions

Andrew Alm Benson was born in Modesto, California on September 24, 1917. His father Carl B. Benson was a medical doctor, and his mother, Emma C. Alm Benson, was a schoolteacher. Andy attended elementary school in Escalon and Modesto. He graduated from Modesto High School in 1935 where he was Valedictorian of his class. He

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¹ Among those who honored Andy at that time were: Jan Anderson, Christoph Benning, Bob Buchanan, C. Buschmann, Roland Douce, Elisabeth Gantt, S.W. Jeffrey, Hartmut K. Lichtenthaler, Achim Trebst, H. Wada, Norio Murata and David Alan Walker.

has been in the Hall of Fame of his school since 1983. After high school, Andy studied Chemistry at the University of California Berkeley (UC Berkeley), obtaining a B.S. degree in 1939. This was followed by graduate work at the California Institute of Technology (Caltech) in Chemistry and Neurobiology. I was thrilled to know that he had Linus Pauling (Nobel Laureate in Chemistry, 1954) among his many distinguished professors there. For his doctoral thesis (1942) with Robert A. Millikan, Andy worked on the synthesis of fluorinated analogs of thyroxin II.

Andy's professional life began with his appointment as an Instructor in the Department of Chemistry at the University of California, Berkeley. Here, he was first exposed to photosynthesis research by two pioneers (Samuel G. Ruben and Martin Kamen). He initially studied plant photosynthesis using short-lived C-11 in collaboration with Ruben and also used S-35 in those studies (Ruben and Kamen had discovered C-14 in 1940). With the world's supply of long-lived C-14 in his hand, Andy was the first to begin investigations on the path of carbon in photosynthesis. With Ruben, he also began studies on the mechanism of the biochemical toxicity of phosgene that he had synthesized from radioactive C-11-labeled CO₂.

For some period of time, Andy left photosynthesis research as he was drafted in 1943 for Civilian Public Service in Nevada where his work included fighting forest fires, aerial photogrammetry, and related fieldwork. He was transferred to anti-malarial drug research, as a Research Associate, in the Department of Chemistry, Stanford University, where he worked on drug synthesis; this was followed by continued anti-malarial research at Caltech.

When World War II ended, Andy returned to the University of California, Berkeley, as a Research Associate and Assistant Director of the Radiation Laboratory with Melvin Calvin (Nobel Laureate in Chemistry, 1961). Again using C-14-labeled CO₂, in 1947, Andy discovered and identified the first product of photosynthesis, phosphoglyceric acid, with Melvin Calvin. In 1950, Andy discovered and chemically identified ribulose 1,5-bisphosphate and other intermediates in the *path of carbon in the photosynthesis cycle* (the Calvin–Benson cycle²; in view of crucial and enormous contributions of Andy Benson, it must not be called the Calvin cycle as it has been depicted in most of the text books and elsewhere). After completing most of the important work, Andy was “dismissed” from the laboratory in 1954. (This is the story I had invited him to write 3 years ago, and it is the story I have edited; it follows my introductory remarks in this Guest Editorial; in my personal opinion, Andy would have shared the Nobel Prize if

he were allowed to stay and continue his work on carbon dioxide fixation in the Calvin lab).

After Andy left Calvin's lab, he was appointed first as an Associate Professor and then a Professor in the Department of Agricultural and Biological Chemistry at Pennsylvania (Penn) State University. While there, he worked on Lipid Metabolism, discovering two major membrane lipids. With Bunji Maruo, in 1957, he discovered and identified the major membrane phospholipid on Earth—phosphatidyl glycerol, an important membrane component of bacteria and of all algae and green leaves. In 1961, he discovered and identified the sulfolipid of plants, effective replacement of membrane phospholipids, and probably the best detergent molecule in Nature. (He is the discoverer of *phosphatidylglycerol*, a phospholipid, and *sulfoquinovosyl diglyceride*, a sulfolipid.) Volume 30 (Lipids in Photosynthesis, edited by H. Wada and N. Murata) of my series “Advances in Photosynthesis and Respiration” (Springer, Dordrecht) was dedicated to him for his discoveries in the field of chloroplast lipids. The volume opens with the following words:

“This book is dedicated to one of the leading plant biologists of the twentieth century

Andrew Alm Benson

Who made major breakthroughs

In understanding the carbon fixation cycle, known as the Calvin–Benson cycle
and

For his discoveries in the structure and the function of chloroplast lipids
(*phosphatidylglycerol and sulfolipids, among others*)”

In 1961, Andy was appointed Professor-in-Residence in the laboratory of Nuclear Medicine and Radiation Biology, Departments of Biophysics and of Physiological Chemistry, School of Medicine, and University of California at Los Angeles (UCLA). Here, he studied “hot atom” chemical reactions for 1 year. In 1962, he transferred to the Department of Marine Biology at Scripps Institution of Oceanography at the University of California, San Diego, in La Jolla, California (UCSD) where he remains to this day.

At the UCSD Scripps Institution of Oceanography, Andy was a Professor of Biology. His research on lipid metabolism continued. In 1968, Andy utilized spawning salmon as a model for the study of degenerative process of aging humans and with Gérard Milhaud, he recognized the importance of calcitonin in calcium regulation in the salmon. In 1970, with Judd C. Nevenzel and Richard F. Lee, he recognized wax as a major marine nutritional energy source and its role in providing for survival of marine animals (as “Nature's Starvation Insurance”). In 1979, Andy studied the intermediates of arsenic metabolism in aquatic plants and the unique arsenolipid produced by these

² Wolosiuk RA, Buchanan BB (2010) Photosynthesis: carbon reactions. In: Taiz L Zeiger E (eds) Plant physiology, 5th ed. Sinauer Associates, Inc., Sunderland, MA, pp. 199–242.

plants. In 1981, he discovered the highest concentration of arsenic, known to accumulate in living organisms, in the kidney of the giant clams of the Great Barrier Reef, Australia. The following year, Andy suggested the application of benzylidene ascorbate for the successful treatment of human tumors. With continuing support for expeditions and funds from Robert O. Peterson foundation, Andy studied coral metabolism, Pacific salmon aging, and the production and function of calcitonin in salmon and other fishes. During this period, specific coral lipids were recognized as an important medium for energy transfer in the coral reef ecosystem. Other areas included: studies of mangrove physiology and metabolism.

During 1962–1988, at the Scripps Institution of Oceanography, Andy was involved with several administrative activities as well. These included: 1965–1969, Chairman, Marine Biology Research Division; 1965–1988, Trustee, Foundation for Ocean Research, San Diego; 1966–1970, Associate Director for Biology, Scripps Institution of Oceanography; 1966–1988, Vice President, Board of Trustees, Foundation for Ocean Research; 1970–1971, Chairman, Department of Marine Biology, and Chairman, Research Council. Zoological Society of San Diego, San Diego Zoo; 1970–1977, Director, Physiological Research Laboratory; 1977–1988: Member, Council of Advisors, The Cousteau Society; 1980–1988, Board of Trustees, Laboratory for Comparative Biochemistry, San Diego.

Since 1989, he has been Professor Emeritus at the Scripps Institution of Oceanography. In 1992, Andy was the co-discoverer of methanol stimulation of plant growth and productivity of agricultural crops. It was during this period that Andy discovered growth-stimulating effects of methanol on algae and higher plants. (Since 1990, he has been a member of the advisory board of the Marine Biotechnology Institute Co, Ltd. Tokyo.) He is in his office (and a small lab) everyday including weekends. It is here that I chat with him on the telephone quite regularly and often we laugh a lot when Andy cannot find the manuscript that I want him to look at or send it to me. The problem of finding files became an issue after he purchased a new computer.

Honors and awards

Andy has received many awards—too many to list. I have made my choice for the following.

- Sugar Research Foundation Award for 1950, co-recipient with Melvin Calvin: for elucidation of the sequence of intermediates for sucrose synthesis in plants.
- In 1962, just 1 year after Melvin Calvin received the Nobel Prize in Chemistry, Andy received one of the Ernest Orlando Lawrence Memorial awards for his contributions in developing atomic energy; it was presented to him by Glenn Seaborg of the US Atomic Energy Commission. The ceremony took place at the National Science Foundation building in Washington, DC.

The award reads (Time, May 4, 1962):
 “**Andrew A. Benson**, 44, of UCLA’s Lab of Nuclear Medicine and Radiation Biology, pioneered the use of Carbon-14 as a radioactive tracer in biochemistry. Since then he has been a leader in the use of radioactive isotopes to study photosynthesis, the process by which plants use sunlight to convert CO₂ to food.”
- Honorary doctorate, University of Oslo, 1965: for developments in lipid biochemistry and photosynthesis.
- Fellow, American Association for the Advancement of Science, 1965.
- Stephen Hales Award, 1972, American Society of Plant Physiologists (now Biologists).
- Member United States (US) National Academy of Sciences, 1973.
- Fellow American Academy of Arts and Sciences, 1981.
- Elected member, Royal Norwegian Society of Sciences and Letters, 1984.
- Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology, 2008, presented in October, 2009 [Andy was unable to attend, but the award was accepted by the author (Govindjee) who also introduced the life and work of Benson].

The award reads:
 “2008 Lifetime Achievement Award
Professor Andrew A. Benson
 For his scientific achievements and original research in the field of Photosynthetic Carbon Fixation and Chloroplast Lipids”

See details and photographs of this ceremony at:
<http://www.vlppb.org/LTAAwardBensonCeremonyFinal%20112909a.htm>

A pictorial tribute to Andy Benson

To start with, I show two photographs of Andy that are almost 35 years apart. Figure 1 is a 1939 photograph of Andy Benson working in a laboratory at the University of



Fig. 1 Undergraduate Andy Benson measuring the rate of oxidation, by oxygen, of a compound he had made for Glenn Seaborg (in G.N. Lewis laboratory). Photo, May 10, 1939. *Source:* Andy Benson



Fig. 2 Andy Benson holding giant bean pods (*Entada scandens*) that were found growing and hanging high in trees in Lizard Island. Photo by Clanton Black, 1973. *Source:* Andy Benson

California, Berkeley, whereas Fig. 2 is a 1973 photograph of Andy holding giant pods of *Entada scandens*.

Although I had been in contact with Andy Benson earlier and had admired his research, it was only in 2001 that I got to know him better. At the 12th International Congress of Photosynthesis in Brisbane, Australia, I shared the same platform with him. He spoke about the history of the path of carbon fixation in photosynthesis, and I talked



Fig. 3 Andy Benson, wearing a bowtie, and the author (Govindjee) at a dinner in Brisbane, Australia. In the background is Christa Critchley, organizer of the 12th International Congress on Photosynthesis. Photo, 2001. *Source:* Govindjee

about the role that my first doctoral professor Robert Emerson had played in the elucidation of the light reactions of photosynthesis. Figure 3 shows our picture at a dinner in Brisbane. Andy has always been forthright and very open in all his discussions. I learned a great deal from him at that conference.

Later in 2001, together with Howard Gest, I went to San Diego/La Jolla, California to learn firsthand the personal discoveries Andy had made during his stay at the University of California, Berkeley, first in the laboratories of Sam Ruben and Martin Kamen (discoverers of C-14) and then in the laboratory of Melvin Calvin. We worked together on getting him to write his perspective of these discoveries. Rajni (my wife) scanned all his slides that were later used in his personal perspective published in 2002, where his detailed technical story was included (See A. A. Benson (2002) *Photosynth Res* 73:29–49). Figure 4 shows Andy at his computer in his office at the Scripps Institution of Oceanography. We were surprised to find that Andy had retained not only all his books, but also his original pictures of chromatograms and chemicals from his time with Martin Kamen, Samuel Ruben, and Melvin Calvin. In Fig. 5, Andy is holding the 2-D radiogram showing the dark spots for the intermediates in the Calvin–Benson cycle; we can see spots for all the sugars as well as phosphoglyceric acid (the 3-carbon intermediate) and ribulose diphosphate that he isolated and chemically identified as the universal “acceptor” for carbon dioxide.

Figure 6 shows several so-called lollipops (that Andy had stashed away in his lab) that were used during the 1950s to hold the suspensions of algae fed radioactive C-14 carbon dioxide and exposed to light before the algae were

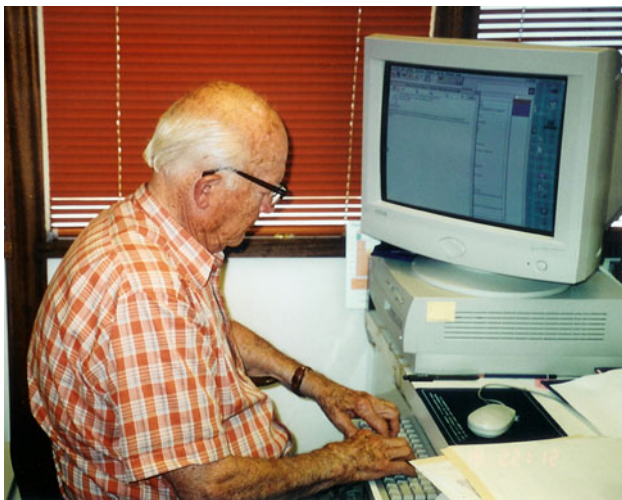


Fig. 4 Andy Benson in his office at the Scripps Institute of Oceanography. Photo, 2001. *Source:* Govindjee

killed for the analysis of the products. There was a surprise in my eyes when I saw the desiccator that had Sam Ruben's name on it (Fig. 7). Andy showed us the aspirator that

Martin Kamen used in his research (Fig. 8). I then had a course in the details of some of the intricate experiments that were performed in those early days (Fig. 9). I was fascinated and did understand it then. However, I would prefer not to be quizzed on it today!

Next, we saw that one of Andy's filing cabinets still had bottles of old chemicals from the 1950s (Fig. 10). All this told me the passion with which Andy must have worked then and it is remarkable that he continues to cherish his research and discoveries even 50 years later.

Rajni and I went to the University of California, Berkeley, to feel the air of that place. All we could find is the old door of the Calvin lab. Figure 11 is a picture of that door.

As mentioned above, the Rebeiz Foundation for Basic Research at Champaign, Illinois, honored Andy in 2009, by selecting him for its prestigious (2008) Lifetime Achievement Award. Unfortunately, he could not attend the ceremony for health reasons. I was one of the speakers who presented his credentials, and even accepted the Award on his behalf—but not that easy—I learned how to wear a bow



Fig. 5 Andy Benson holding one of the early (1950s) 2-D paper radiograms of $^{14}\text{CO}_2$ fed *Scenedesmus* cells. It shows the 3-carbon acid, the phosphoglyceric acid (the first product of carboxylation); ribulose di phosphate (ribulose bis phosphate), the 5-carbon

intermediate (that is the one that is carboxylated); sedoheptulose (the 7-carbon intermediate) and all the sugars (glucose, sucrose); polyglycosides are seen below "sucrose." Photo, 2001. *Source:* Govindjee



Fig. 6 A photograph of several glass “lollipops” used for putting algal suspensions to which $^{14}\text{CO}_2$ was injected and then after illumination, the suspension was let out, by opening the stopcock, into boiling methanol. Photo, 2001. *Source:* Govindjee



Fig. 7 A photograph of several items from the days Andy Benson had worked with Sam Ruben and Martin Kamen, discoverers of C-14. In the desiccator, marked “S. Ruben,” there still was a chlorophyll sample that Sam Ruben had left to dry in the 1940s. The round container with black top had a vial that contained the first radioactive hydrogen (tritium) that belonged to Ruben. In the back is a copy of Martin Kamen’s famous book “Radiant Science, Dark Politics.” In the photograph, there is also an empty can that had contained Makre fillet that Andy used for lunch! Photo, 2001. *Source:* Govindjee

tie (trademark of Andy), and I did that with Andy’s own tie that was mailed to me several days in advance. Figure 12 shows my photograph (courtesy of the Rebeiz Foundation) with Andy’s bow tie in place. Figures 13 and 14 show the audience that had gathered at the Rebeiz Foundation premises, raising their Champagne glasses to congratulate Andy Benson and to wish him and his wife Dee Benson (Fig. 15) a good life ahead. Cheers!

Some personal tidbits

I could not resist ending this celebration without telling a few fun things.



Fig. 8 Andy Benson holding an aspirator, with a vacuum gauge at the top; this instrument was used by Martin Kamen during 1940s and he used this to aspirate reactive gases. Photo, 2001. *Source:* Govindjee



Fig. 9 Andy Benson explaining to Govindjee the intricacies of experiments, using a tube from his Berkeley days with Ruben and Kamen. This thin-walled aluminum tube was made by Sam Ruben in 1938. Photo, 2001. *Source:* Govindjee

- We did have fun when we visited Andy in 2001 in San Diego. We enjoyed sitting in two of his vintage cars (one a Mercedes Benz and the other a BMW): neither had seat belts, and one did not have seats in the back; thus, we sat on old telephone directories.
- One day Andy came to pick us from our hotel; to our surprise, he was walking up to our floor, when we were coming down by the elevator.
- When Rajni and I visited Andy and Dee’s home in San Diego/La Jolla, I discovered that he had not opened his T-shirt given at the last party for Melvin Calvin; it was in its original plastic cover. I succeeded in persuading him to open it and wear it. And, he did. Rajni took our photograph when he laughed after



Fig. 10 Chemicals from Andy Benson's days in the 1950s at UC Berkeley. All the chemicals were still in original containers and they were kept in a cardboard box inside a filing cabinet. Photo, 2001. Source: Govindjee



Fig. 11 A photograph of the door, marked 117, from the ORL (Old Radiation Lab), Photo, 2001, at University of California, Berkeley. Source: Govindjee



Fig. 12 The author (Govindjee) is getting ready to accept the Lifetime Achievement Award of the Rebeiz Foundation on behalf of Andy Benson, since he could not attend the ceremony (October, 2009). Photo, taken in Champaign, Illinois, courtesy of Tino Rebeiz. (Note: The bowtie was obtained by Govindjee from Andy Benson)



Fig. 13 Some of the audience gathered at the Rebeiz Foundation of Basic Biology in Champaign, Illinois in October, 2009, congratulating Andy Benson on his receiving the Lifetime Achievement Award. Photo, courtesy of Tino Rebeiz (<http://www.vlpbp.org/LTAAwardBensonCeremonyFinal%20112909a.htm>)

I covered Calvin's name on the T-shirt by my hand. There was humor in the air [Govindjee and D. Krogmann (2005) In: Discoveries in Photosynthesis, Volume 20, Advances in Photosynthesis and Respiration, pp 63–105, see Fig. 7(b)].

- One day I asked Andy “what is your secret of long life?” He said “Well, I eat, for lunch, canned sardines, made in Norway.” Recently, he told me that everyday, he takes liquid ‘Qunol’ (Coenzyme Q₁₀) and cactus to control the Type 2 Diabetes.



Fig. 14 Carole and Tino Rebeiz, in the center of the photo, and others, congratulating Andy Benson on his receiving the Lifetime Achievement Award (October, 2009). Photo, courtesy of Tino Rebeiz. See: <http://www.vlpbp.org/LTAAwardBensonCeremonyFinal%20112909a.htm>



Fig. 15 Dee Benson and Andy Benson at their home in La Jolla, California. Photo, 2001. *Source:* Govindjee

Acknowledgments I thank many who helped lead me to the completion of this manuscript. The list is long, but it includes: Andy Benson, Dee Benson, Bob Buchanan, Howard Gest, Rajni Govindjee, Carole Mayo, and Tino Rebeiz. I also remain grateful to a 2001 National Science Foundation Grant (SES 00-92507), given to Govindjee and Howard Gest that made our trip to San Diego possible. The writing of this article was made possible because of the ever-present support of the University of Illinois at Urbana-Champaign.