

## Andrew A. Benson: personal recollections

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Received: 1 August 2015 / Accepted: 15 August 2015  
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**Abstract** Andrew A. Benson, one of the greatest and much loved scientists of our century, passed away on January 16, 2015; he was born on September 24, 1917. A grand celebration of his life was held on February 6, 2015, in California. Here, we present one of his photographs and key excerpts from what was said then, and soon thereafter.

**Keywords** Benson's protocol · Path of carbon · Photosynthesis · Radioisotope

The publication of these personal recollections coincides with what would have been Benson's 98th birthday. These recollections were read and edited by (1) **Gerald (Gerry) T. Edwards**, who wrote: I find this a unique tribute for publication in *Photosynthesis Research* which follows on the celebration of the life of Andrew A. Benson (referred by all as Andy) by scientists and family. It shows the enormous admiration for his personal attributes (his compassion, humility, support of others, spirit) among scientists, as a mentor, among family and friends, and the breadth and magnitude of his scientific contributions throughout his life. (2) **Thomas (Tom) D. Sharkey**, a member of the editorial board of *Photosynthesis Research* (PSRES), wrote: I have read the text—it reflects the spirit of the remarks... this will be a very nice addition to the literature on this very great man, Andy Benson. (3) **Eva-Mari Aro**, also a member of the editorial board of PRES wrote: I have read the manuscript and for me it was a great experience; this review gives an excellent opportunity for both established and young scientists to get to know Andy Benson, whose research was central in establishing the first steps of carbon assimilation in the Calvin-Benson cycle. And finally (4) **Bob Buchanan** wrote: This article on Andy Benson reads well and adds interesting information on his life and scientific contributions.

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### Abbreviations

PNAS Proceedings of the National Academy of Sciences, USA  
SIO Scripps Institution of Oceanography  
UCSD University of California, San Diego

Andrew (Andy) Alm Benson (1917–2015) was a giant in the field of photosynthesis. It was his research with a number of scientists, especially James A. (Al) Bassham and Melvin Calvin, that solved the path of carbon in photosynthesis. Much has been written on him (see e.g., Biel and Fomina 2015; Lichtenthaler et al. 2008, 2015a, b; Buchanan 2012; Buchanan and Douce 2015; Buchanan and Wong 2013; Buchanan et al. 2007; Govindjee 2010; Harkewicz 2006).

We begin this special tribute by showing a photograph of Andy (Fig. 1). He loved the ocean. Indeed, his office was on the top 4th floor, on the northwest corner of Hubbs Hall of Scripps Institution of Oceanography (SIO), University of California (UC), San Diego (SD). One of us (AN) and Andy had stepped out to the balcony overlooking UC's Natural Reserve System when this photo was taken. On this balcony, Andy and AN would demonstrate the optics of glass microbeads (see Nonomura and Benson 2012) for the refraction of otherwise lost sunlight up to the

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**Fig. 1** Andy Benson on the balcony outside his office; photo by one of us (AN)

phylloplane. In the picture, Andy is holding an issue of the Proceedings of the National Academy of Sciences (PNAS), USA. He read every word in the PNAS; when he was done reading, he would leave them outside his office to freely share with others. Students and colleagues might ask Andy any question, for example, about transmembrane transport; and, not only would Andy have an answer, he would discuss the chemistry of alkyl glycosides and symporters; then he would pull the supporting article in PNAS (Kaback et al. 2007) that he had read 3 months prior and hand over the issue. If you stood around a minute longer, Andy would proceed to connect the first article to others in older PNAS issues. Finally, Andy would ask if you knew where he

could find another Stetson, hat size 9, because such extremely large hats are rare. Only then would you realize his great brain capacity from which he powered his enlightened erudition. Andy gave us clarity of vision, lucid expression, brilliant peace—friendly accomplishments of the first order, engendered by his fond personal relations and classy apparel—and elegant thinking that will inspire future generations of young scientists to see well beyond the ocean’s horizon.

A grand *Celebration of Andy’s Life* was organized by his family and held on February 6, 2015, at the La Jolla Country Club, La Jolla, California; and with as many as ~200 friends and relatives present. Notably among those that came to remember Andy were most of his co-authors; many colleagues from UCSD, including Maarten Chrispeels, William Fenical, Ronald S. Burton, Francis C. Knowles, and Lanna Cheng; and the staff of SIO, which included Carole Mayo, Marie Mathers, Mario Aguilera, Samphos Chin, and many others.

[See a video that starts the celebration with all those gathered followed by James (Jim) Neri’s welcoming talk and his stories at [https://www.youtube.com/watch?v=q\\_knpzOWprI](https://www.youtube.com/watch?v=q_knpzOWprI)].

In this tribute, we remember Andy Benson by quoting a few excerpts from a video taken by one of us (AN), as well as remarks that were sent later.

## George Lorimer from College Park, Maryland

### On the shoulders of a giant of metabolic biology: an appreciation of Andy Benson

“In 1676, Robert Hooke, the English physicist, wrote a letter to Isaac Newton, praising his younger colleague for his accomplishments. In his reply to Hooke, Newton wrote the following: If I have seen further it is because I have stood on the shoulders of Giants.

The giants to whom Newton was clearly referring were the astrophysicists Copernicus and Galileo, both of whom lived 100 years before Newton. I don’t mean to compare myself with Newton; that would be utterly absurd. But I do want to develop this theme of standing on the shoulders of giants and seeing further in my tribute to Andy Benson.

I have spent a good part of my professional life studying a single protein, the enzyme that is now known by the acronym Rubisco [ribulose bis-phosphate carboxylase oxygenase]. This is the most abundant protein in the world. It’s the protein that catalyzes the first step in the photosynthetic fixation of carbon dioxide. Worldwide it converts about 200 billion tons of carbon dioxide to organic forms of carbon. So, essentially all the food we eat, all the clothes we wear, all the wood in the homes we live in, all the fuel

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in the cars we drive, essentially all of it has passed through this one enzyme either recently or back in the Pleistocene. Now I didn't discover Rubisco—that was done by Andy Benson some 65 years ago. Not only did Andy discover this very important enzyme, but he also discovered the molecule with which the carbon dioxide interacts; that was ribulose1,5-bisphosphate. This was the culmination of a series of brilliant experiments beginning in about 1947 in the Lawrence Radiation Laboratory at the UC Berkeley, where the newly discovered [by Martin Kamen and Sam Ruben] isotope of carbon, carbon-14, was employed.

But let me digress for a moment. When I was an undergraduate some 55 years ago, I studied from a textbook by E.E. Conn and P.K. Stumpf “*Outlines of Biochemistry*”. It was [then] a small book of only 390 small pages. In it there were perhaps a handful of biochemical pathways. I now teach biochemistry and the textbook, Nelson and Cox’s “*Principles of Biochemistry*” has grown enormously; it is now 1200 large pages long and instead of a handful of pathways there are now many, many pathways. Who was responsible for all of this? I am going to tell you that it was Andy Benson because he saw the power of using radioactive isotopes to map out metabolic pathways. We may fairly describe the procedure that Andy developed as *Benson’s Protocol*.

Let me generalize Benson’s Protocol. You start off with a radioactive substance *A*; that was  $^{14}\text{C}$ —labeled carbon dioxide in Andy’s case. Next you take your favorite biological object; that was a suspension of algal cells in Andy’s case, but it could be anything you choose, *E. coli*, yeast, lobster tails, salmon, beef hearts, or whatever. Then you expose your favorite biological object to the radioactive compound *A* for some period of time, 5 s, 5 min, 5 h, or whatever. After that period of time, you stop the reaction by breaking open the cells and now, instead of having just one radioactive compound, you have many radioactive compounds. The task in hand is then to identify all of these compounds *B*, *C*, *D*, *E*, *F* and *G* so that one can construct the chain of events that occurs within the cells. When Andy started doing this, nobody had employed radioisotopes in such an ambitious project as that undertaken by him. The development of Benson’s protocol led to the elucidation of the path of carbon in photosynthesis, now known as the Benson–Calvin cycle [also called the Calvin–Benson or Calvin–Benson–Bassham cycle by others]. But it is a mistake to think that Andy’s legacy is confined to path of photosynthesis in plants. Benson’s Protocol was subsequently and widely adopted, and in the golden age of metabolic biochemistry, all sorts of metabolic pathways were worked out; the pathways to fatty acids, to sterols, to terpenes, to purines and pyrimidines. If you look at all of these papers one can’t help concluding that these guys are just applying a variant of Benson’s Protocol, over and over

again. That’s why the textbooks of today are packed full of these pathways. I think Andy’s legacy can best be summarized in the words of Isaac Newton.

If today we can see further, it is because we stand on the shoulders of a generous and gentle giant, whose long and wonderful life we celebrate today, Andy Benson.

I want to conclude with a little anecdote that provides a perspective on another aspect of Andy Benson. He was enormously modest about his own accomplishments. When I got to know him a little better I noticed that whenever I tried to get him to elaborate on the events in the Calvin lab he would immediately change the subject. However, if you wanted to talk about the accomplishments of junior scientists, then Andy Benson was unfailingly enthusiastic and effusive in his praise for what the younger scientist had accomplished. I’ll give you a personal example. I didn’t meet Andy until about 30 years ago although he was one of my scientific heroes. I came to the UCSD to give a seminar on our work on Rubisco. Five minutes after the seminar started, I noticed a white haired gentleman slipping into the seminar room and sitting among the graduate students. When the seminar was over, he rose and made some very kind remarks about the work that I had done. I must have been about 42 years old at the time. You can imagine how I felt when one of my scientific heroes praises the work that I had done. It doesn’t get much better than that.

But this is not just a specific phenomenon. Similar stories have been told to me by Andy’s legion of admirers and friends the world over. Andy was always unfailingly generous to his colleagues and younger scientists.

I shall conclude with a toast to the spirit of Andy Benson: May there be many more like Andy Benson from whose broad shoulders the next generation of scientists can see further.”

The above text is a transcribed and slightly edited form of remarks that can be heard in a video at: <https://www.youtube.com/watch?v=H1ZdwbORROA>.

A prime example of the application of Benson’s Protocol is presented by Karl Biel, as follows.

### **Karl Y. Biel, from Pushchino, Russia**

#### **One of the greatest episodes of my life with Andrew A. Benson**

“In 1988, Professor Eduard A. Titlyanov (Institute of Marine Biology of the Russian Academy of Sciences, Vladivostok, Russia) organized a large expedition to the Seychelles on the Russian scientific board “Academician Aleksandr Nesmeyanov” at the invitation of the

Government of the Republic of Seychelles. Eduard Titlyanov assembled a high-level professional team of Russian and American scientists and Professor Andrew A. Benson was the leader of the Americans. The scientists "...had to elucidate the question of what the photosynthesizing organisms are that determine the high productivity of the coastal waters of the Seychelles Islands" (Titlyanov and Titlyanova 2007). In this expedition, I participated as the head of the "Laboratory for Biochemistry and Physiology of Photosynthesis." In our research, we had often utilized Andy's [ $^{14}\text{CO}_2/\text{H}^{14}\text{CO}_3$ ]-paper-chromatography.

During the above expedition, Andy socialized with members of all the research groups and the crew with much pleasure while his scientific interest was primarily on lipids and biochemistry and physiology of photosynthesis.

Every day, Andy participated not only in planning, but also in executing experiments; he also took time to discuss topics of interest.

One day Andy asked me, "What kind of "gross-book" is always on your lab desk?"

I said: "This is my "3-kilogram" copy of my second dissertation (Biel 1988), which I have to defend after this expedition at the Institute of Plant Physiology in Moscow, Russia. If you have an interest, you can read it. But there is only one small problem—my dissertation is written in Russian. Of course, I can share some information; even, I may try to translate some parts of it, but not all the 543 pages."

Andy said: "It is not a problem; I can read Russian; at least, I can try to read it."

It was hard to believe; however, I was very excited and responded, "WOW, it is great! But may I ask you something? If you really will understand the content and will positively accept my data, could you write a review of the dissertation to Academician of the Russian Academy of Sciences, Professor Andrei L. Kursanov, who is the Chairman of my Scientific Committee?" I guess it wasn't my winner joke because Andy accepted my "wish" seriously.

Andy told me strongly, "First of all, we'll see how tough you and your dissertation are."

In reality at that time I had not realized at all what a hard cognitive and amazing time I had created for myself. Over the next 3–4 days, every morning when I went to the Lab, I met Andy with my manuscript. As always, he was very friendly, polite and with a huge sense of humor, but he did not mention even one word about my "gross-book."

Then suddenly he told me: "Karl, it is time to ask you some questions."

During all of my life before and after this test, I had never received such intense critical scrutiny and being subjected to fundamentally very complicated questions

related to my research and biological sciences in general. And it was not just 2–3 h of questioning, it happened for more than a week in the mornings and the evenings, all the free time we had from our expedition work.

During the discussion of my work, I was amazed that Andy understood the entire text, tables and illustrations because Russian is a very difficult language even for some people who have grown up in Russia. He quizzed me so seriously and strongly that sometimes it seemed to me that this was his thesis, not mine. In the end Andy was satisfied with my answers and promised to send a review to A. L. Kursanov; and he kept the promise. Andy's letter is the best example of a review!

After such a deep and uncompromising analysis of my thesis, I realized what it meant to be a true scientist—really, a Scientist, with a capital letter—as was and always will be for me, Professor Andrew Alm Benson. His contribution to Plant Biology, Biochemistry, and science in general is hard to overestimate (see Biel et al. 2014; Biel and Fomina 2015).

Since that time in 1988, we have been friends and I have treasured close scientific (e.g., Nonomura et al. 2011) and social communications with him until, January 16, 2015, when Andy left us."

### Robert Cooney, from Honolulu, Hawaii

"I first met Andy in his office one late afternoon in 1977 where I had gone to discuss the possibility of doing a rotation in his laboratory. I was a first year graduate student in the chemistry department at UCSD, and had absolutely no clue what I was going to do with my life. The thing I remember most from our meeting was that as soon as I arrived, Andy started talking about "*The Green Flash*" and that perhaps one would be visible that evening as the sun went down. I am sure it was obvious to him that I had absolutely no idea what he was talking about and he quickly pulled a book from his desk and handed it to me describing the history and science of the green flash. I had never met anyone like Andy before (or since!) and left the meeting thinking that come what may, this was the laboratory for me! The breadth and depth of Andy's knowledge was beyond compare, yet it was his humility and humanity that endeared him to all that knew him. His positive outlook on life was infectious and his thirst for new knowledge unquenchable. Andy had theories on just about every aspect of our world imaginable, but was always thrilled to hear of something new. He made everyone he met feel as if he or she were the smartest and most important person in the world, despite the fact that one simultaneously felt inadequate in his presence. I was the last graduate student to get a Ph.D. under Andy's guidance, and while I can

never match his genius, I did learn from him many lessons that have served me well, such as always to look at the world with awe and constantly wonder how things work. I learned the importance of speaking your mind and never fearing the consequences of being outspoken in pursuit of what you believe. Andy believed that science was about the pursuit of truth and what was important was that we ultimately get it right. Along the way we may make mistakes, but the important thing is that we learn from them and figure it out.

As he once said, *“One result from an experiment is infinitely better than none.”*

I have often repeated that to statisticians, who don't seem to appreciate that fact. Andy was truly a pioneer in science, who remained excited every day throughout his entire life by all that lay over the next hill of discovery.

Two decades after my first meeting with Andy, my wife Kay and I were having dinner with Andy and Dee at Roy's Restaurant in Honolulu with a beautiful view of the ocean. As the sun sank into the sea on an incredibly clear day, we all saw the most amazing *green flash* ever. He was a rare individual that I feel privileged to have known and that has impacted my life in so many ways. I could never imagine a world without Andy Benson and feel his loss daily, but am comforted by the fact that so much of him lives on in all of us who knew him. His many scientific discoveries are important, yet they pale in comparison with the person that he was and the impact he had on so many. He made us all feel important.”

## Victor Vacquier, from La Jolla, California

### Remembering a fish tale

“I was in Costco [a wholesale store], where they had those glass case booths with clerks selling whole fish and shellfish kept fresh on beds of ice. And there was Andy. Oh, my gosh! There he was, bending this young man's ear. The clerk was about 25 years old. Andy had a poker he was using to show the young sales clerk the parts of the fish on display—the lateral lines, [etc.]. Then he flipped the fish over to show the guy the anal fin, proceeding to tell him about salmon reproduction and how they die at the end of spawning. Now, this guy didn't cry or anything, but Andy was really into it, just going on and on. Andy bought this fish, put it in his cart, they said their “goodbyes” to each other, and Andy left.

Then, I came out from hiding and sympathetically asked the young man, “I thought that old guy was going to talk your ear off.”

To which the clerk excitedly replied, “Yes, but I learned so much about fish that I never knew. I didn't know any of this stuff that he just told me. Do you know that guy?”

I said, “Yes, he is Dr. Andrew Benson, a professor at SIO.”

The clerk asked, “What does he do?”

I told him, “One of the things he does is to go to Alert Bay, on the west coast of British Columbia, and study salmon.”

The clerk asked, “Oh man, I wish that guy would come back.”

I added, “I'll tell you something else he did. He discovered what happens to carbon assimilation.

When the clerk picked his jaw up from the floor, he inquired, “You mean, he figured out photosynthesis?”

We refer the readers to listen to the full story by Victor Vacquier at: <https://www.youtube.com/watch?v=8m686bwSWRk>.

## Barry Holtz, from Bryan, Texas

“I always carry a piece of red cedar wood with me. My children for years had wondered why I had these little chips and planks of wood with me. They were everywhere: In the car, my briefcase, and in my pockets. This is a very powerful totem and it reminds me of those years in Alert Bay, chasing copepods and salmon; and doing great science with great people. I think that Alert Bay was one of those places that brought to Andy and his wife Dee great joy; and, I think, some peace and renewal.

There are a million stories to tell about Andy Benson, we all have them. I hope someday that we can compile these narratives. So, I was searching through my billion card index of Andy Benson-isms, trying to find the one for this occasion. Now, there's one that always bubbles up when I try to tell other folks about Andy. I know you all remember the white Mercedes, The Mighty Panzer Kampfwagen. Bear in mind, that I was brought to SIO not because I was a scientist. I was a hillbilly from the wilds of Pennsylvania; but I had a Mercedes of the same year, and I had tools. So, I am sure that Stu Patton and Andy conspired to get this post-doc out here who was a car mechanic and that was great by me. We kept The Mighty Panzer going, Dee [Benson], for how many years? Twenty-five or twenty-six. We even cut the back half off and put another

half on. There came a day when Dee said, “We’ve got to get Andy out of that car.” We did.

When we were post-docs at SIO, we often drove down to Mission Bay to this taqueria, a factory that made Mexican tacos. They were cheap and really good. Benson would pile us all in the car and we’d go sailing down Interstate 5!

One day, Ernie Marques, Rick Phleger and I were in the car and Andy says, “Aren’t you guys completely offended? I mean, totally offended by the sign at the side of the road? That cabinet maker’s sign over there.”

We were thinking, “Say what?”

Andy says, “The sign is slonch-wise!”

That’s a perfect Benson-ism, “Slonch.”

It’s a wonderful word he made up that’s really onomatopoeic.

For years, the sign on I-5 had been leaning 45° to the right. Andy was absolutely offended that a guy who made cabinets hadn’t ever squared up his sign, but there was an incredible lesson in the slonch-wise sign.

Andy said, “Did you see it?”

None of us could comment. The point was, we hadn’t seen it.

Andy said, “You’ve got to learn to see things. If you don’t record the data, you will never get to process it.”

All of us were sitting there with our jaws dropped to the floor when we realized that we were not looking [at the world] as scientists all that time.

“You can’t process the data if you haven’t recorded it. You can choose to process it when you want, but you have to see it.”

Andy Benson taught us to observe scientifically, probably on another plane, and widen the view from 45° to 180°.

Andy set a great example of how to embrace science and the great diversity of disciplines that science involves. His interests were incredibly broad and he taught each of us to love and respect the process of science. We’ve all become better scientists because of that and by the touch of Dee and Andy Benson.”

After a brief introduction by Jim Neri (see below), you can hear the talk by Barry Holtz at: <https://www.youtube.com/watch?v=jTbgiPIFIgQ>.

### John N. Nishio, from Chico, California

“Andy really cared about his colleagues as much as he did the science. I was an early career professor attending the 1993 Photosynthesis Conference in Nagoya, Japan, when an elderly gentleman came up to study my poster.

I glanced at his nametag, and gasped, “Are you the Andrew A. Benson of the Benson–Calvin Cycle?!”

Andy smiled, and quietly replied, “Yes.”

I was happy that such a scientist of high status was reading my little contribution.

After a while, he asked me if I had seen his poster; to which I replied, “No.”

He insisted that I go see his poster. I said I would, but wanted to be by my poster. Time passed and Andy came by again, jovially requesting to come by his poster.

I said, “Okay, I’ll try to make it.”

The next time he came around, Andy just grabbed my arm and pulled me to his poster because he wanted me to meet Arthur, his coauthor. I was amazed that a professor of Andy’s stature would take such personal interest. That meeting led to a visit with Andy at SIO, where he showed me how he did his magic. I will never forget how Andy greeted me at the dock behind his building. He was in his late 70s, and he jumped onto the dock by way of a pipe and then went bounding up the stairs to his laboratory. That energy and spirit was an inspiration. The next morning Andy had finished reviewing some of my ideas about metabolic pathways in our collaboration. Andy was so gracious about it—the consummate scientist—and onward we went to undertake years of work (e.g., Biel et al. 2010). Andy’s approach to science, his rigor and knowledge, remain an inspiration. He was from the Central Valley of California and he touched many of us with his down-to-earth values and caring spirit. I treasure the wisdom, kindness, and knowledge that he so willingly shared.”

### Govindjee, from Urbana, Illinois

“Andy was honored with the Lifetime Achievement Award at Champaign-Urbana, Illinois, and he could not make it to the ceremony. Upon my request, Andy sent me his signature apparel, a bow-tie, to wear. It was with great difficulty that I learned to tie it to wear it properly so that I could accept the award on his behalf (see Govindjee 2010 for several wonderful photographs of Andy; <http://www.life.illinois.edu/govindjee/honorsfrom.html>). I have added references to key papers and to videos in the Appendix which provide insights into Andy’s scientific career.”

We provide, below, a glimpse of what some of the family members said before we present the concluding remarks by one of us (AN).

### From Andy’s family

**James Neri**, Dee Benson’s son, was the master of ceremonies on February 6, 2015, and he recalled much about Andy when he was growing up. Jim’s recollections provide

us with a glimpse of Andy's human qualities: a positive, organized, but fun-loving and unique attitude to life. We cite here just a few quotes:

"Andy invited me to his lab and showed me how to make glass figures and I saw the many experiments he was working on. That was when I first understood what a great scientist he was.

He took me on an expedition in a Styrofoam canoe through the mangrove swamp he had helped create in Mission Bay to study how these amazing plants can survive in salt water.

Andy was a prolific letter-writer and would write to anyone he thought might listen; e.g., he wrote a letter to the city complaining that there was too much space between the 'L' and 'Y' in the word 'ONLY' stenciled in the road.

He kept everything that was not being used in cardboard boxes, carefully selected so each item would fit perfectly, and labeled them on all sides with the item and the date; and he knew where everything was.

Andy's rose garden was his pride and joy. I installed an automatic irrigation system for him and would often find him watering the roses the correct way, with a hose. He worked with radiation; dove in shark-filled waters; ate 30-year old dented tinned salmon; and would live to be 97."

To listen to Jim's talk, go to: <https://www.youtube.com/watch?v=0kFkDkanr7Q>, and see the Appendix.

**Diane**, Dee's daughter, recalled the fun they had meeting interesting people. She remembered that their house was a frequent gathering place, and her mom (Dee) and Andy made it comfortable for everyone. "There were lively conversations, laughter and a great range of topics were discussed."

The recollections of **Lisa and Greg Foster**, Dee's daughter and son-in-law, also provide us with a glimpse of Andy's personal qualities. We cite here just a few examples from what Lisa said:

"Andy taught our children how to make fresh black walnut ice cream with liquid nitrogen. When I was in high school, Andy brought me to his lab where he taught me how to clean parasites from plant leaves and measure the weight of one piece of my hair." See the Appendix for additional comments.

**Beverly Foster**, daughter of Lisa and Greg Foster, gave a beautiful account of her association with Grandpa Andy. Beverly said:

"I remember the day I knocked on the door to his study; he was playing tribal music. He had me come in and close my eyes. When I opened my eyes, he had a shirt for me. It was from the tribe. He told me they had come through the stereo to give it to me. Sometimes he would bring home dry ice; and we would use tongs to dip rubber bands in, throw them on the ground and watch them shatter. He

would take us to his lab and show us everything. He even had us pet a shark. He always wanted the best for us. Grandpa Andy wanted to watch us learn and grow." See Appendix for additional comments.

Remembrances by **Claudia Benson & Linnea Benson**, two of Andy's daughters (the third is the late Bonnie).

"We both remember spending weekends with our Dad in Yosemite, and sleeping outside under the stars; we were very proud that he knew the Russian letters, and that he took close up pictures of the sea lions. We vividly remember one incident when he had to run for his life after being chased by the sea lions. He was a brave man."

### Arthur Nonomura, from Powell, Ohio

Arthur began his concluding remarks by making special recognition of Dee Benson as the light of Andy's life.

"You are atop a mountain around a campfire on a chilly night with starlight above and, as Andy is putting another log on, he stokes the coals and bright flames illuminate your faces. You are radiant, smiling from cheek to cheek, warm and cozy."

Then Andy turns to you and inquires: Do you know that wood is made of sugars? Yes, long chains of sugars. When wood burns and you are seeing the light and feeling its warmth, you are sensing the release of the sun's energy that was stored in it.

Andy always explained things with amazing clarity. He studied the things that make up plants: light, air, water, and minerals. He knew the elements by heart, right down to their isotopes. When Andy looked deeply into the carbon molecules of plants, he made a discovery that shook the world. He handled concentrated radioactivity to track the "theory of everything" of plants; and he did this at a time in the 1950s, when only the bravest of the brave would dare handle manmade atomic materials.

Did you know that Andy walked around the circumference of the world? On an expedition to the Arctic, he walked a 10-m circle around North Pole. Also, he traveled to the end of the earth, Tierra del Fuego; and to Lizard Island, in the middle of the Great Barrier Reef, to find the biggest bean, about the size of a hockey puck, to feed the world.

Andy continued to carry forth science seeking the truth every day to the last, adding to his discoveries by rigorous research on arsenic, aging, waxes, cabbages and kelps.

In a word, what did Andy give to the world? Like hearing the sounds of the ocean in a seashell, from now on, in every product of plants—your amber waves of grain—and hereafter in that wood log aflame at the campfire, we all will see the great power of the sun; and we shall all

know the source of its warmth—in Andy’s precious smile.”

**Acknowledgments** The authors express their sincere gratitude to Dee Benson, her children and grandchildren for organizing the Celebration of Andy’s Life. It was a magnificent tribute to the personal character of Andrew A. Benson, the Scientist. We thank Robert Cooney and John Nishio for sending their tributes to Andy for inclusion in this historical article; James Neri for his contributions; and those of the entire Benson family. We are grateful to Eva-Mari Aro, Bob Buchanan, Gerry Edwards, and Tom Sharkey for reading this Tribute and for making suggestions before its publication.

## Appendix

This appendix provides additional personal insights from family and friends, and sources to Benson’s contributions in photosynthesis.

### Some quotes from Andy Benson

Stainless tableware shall be left in the detergent until a suitable moment arrives when hot water is available and then dry them into the drawer with a linen towel. Group! Unless you really appreciate a Linen Glass Cloth, please use the cotton towels.

### James (Jim) Neri added:

Here is a glimpse of Andy’s human qualities and a positive and fun-loving attitude to life.

- Andy had a whale’s *baculum* on his desk; when someone came he would ask for fun: “Do you know what this is?”
- He would write his initials A-A-B on everything in the freezer, such as ice cream cartons, and pre-mixed margaritas. Thus, my friends and I began referring to him simply as “AAB” and would delight in scooping vanilla “AAB-cream” and pre-mixed margarita “AAB-sauce” from their containers in the freezer he kept out back.
- He kept everything in the freezer. The more exotic the item the better: Mare’s Milk liquor, Wormwood honey, Macacauba wood from the Amazon— all graced his shelves and were trotted out to be sampled and admired. A story was told about each.
- When Andy turned 93, I garaged his 1973 BMW 3.0cs since he had had a couple of close calls, letting him know I’d bring it back for a visit any time he liked. After about a year or so, we were having coffee one morning and he looked right at me and said, “You can have that car.” So now, I will restore it in his honor.
- Andy would leave notes everywhere with very tiny chicken scratch writing that let you know how something could have been done better.

- NO one but Andrew Alm Benson knew how to wash dishes properly, especially [in] automatic dishwashers. I would often fumble with a glass until he snatched it from me and showed me how to wash it correctly.
- Andy had brought a pachinko machine home from Japan and hung it on the wall in the kitchen. We played Japanese pinball for hours, enjoying the racket it made.
- Andy had an aluminum bicycle that he would ride to work through thick traffic. It had saddlebags and he stated that it was the best bicycle ever made.
- He had a Hobie surfboard that he never rode—it used to hang from the ceiling in his office. I borrowed it to fish from ...
- Andy had carpet installed in his garage to protect the concrete from staining. Who else would do such a thing?
- Dee and Andy were gracious hosts and would feed whoever showed up, from world-renowned scientists to surf kids off the beach.

### Lisa Foster added:

The following adds much to what we have already learned about Andy’s human qualities.

- He took me to a Los Angeles private viewing of ‘Calypso’s Search for the Britannic’ where he introduced me to Jacques Cousteau.
- When Andy was head of a research laboratory at SIO, he took me to pet the dolphins and see the penguins up close.
- He left 3 × 5 cards in the bathroom with instructions on how to take a 3 min shower and the proper way to flush the toilet.
- When I was in high school, Andy received a Queen Elizabeth grant to lecture in Australia for 3 months. I was privileged to go with him and my mother for 1 month traveling from city to city, listening to him teach and meeting a host of amazing scientists and their families.
- When his grand-daughter, Beverly, was in grade school enrolled in a Spanish immersion program, Andy bought a Winnie the Pooh computer program and spent hours with her sitting on his lap in his office helping her to learn the language (the fun way).
- Andy always had the correct way to do things. On one visit, he told me that people tie their shoes wrong. They tie granny knots, when it should be a square knots; I told him that most people really don’t care. However, I have been tying my shoes with a square knot since.
- He always knew the best foods—Scrapple, tamales from Louisiana, and the monster oysters.
- Andy loved his kitchen, showed me his ceramic knife, and said to me that every chef should have one, I do now!

- He always had the best tools. Around 1998, I was helping cut a hole (for the TV in the living room) and commented on how nice his jig saw was, a Craftsman from the early 1960s. He just gave it to me. It's my favorite tool.

**Beverly Foster added:**

“When I was young I went to a Spanish speaking school in California. To help with my schooling I played a computer game. It was Winnie the Pooh, but it was all in Spanish. My grandfather Andy let me play on the computer in his study. I was always told that no one else was allowed in that study. But I used to sit on his lap and play that game with him. He would ask me what it was saying and I would tell him. He was always so impressed by how much Spanish I knew.

On special occasions, holidays and family gatherings we would bond over our love for dove bars.

He used to tell me that he was not able to come visit us because we lived in the edge of the earth and he was afraid he would fall off.

He treated me with much love and kindness. I grew up with him as my Grandpa Andy. I am so thankful for that.

**Govindjee listed the following for the benefit of all the readers:**

- (1) References to the story of Benson in the discovery of the path of carbon in photosynthesis are: Benson (2002, 2010); also see Bassham (2003).
- (2) A complete historical discussion of “The path of carbon in photosynthesis during 1937–1954” is presented by Nickelsen (2015) in chapter 6 (pp. 201–250).
- (3) A conversation with Andy Benson by Govindjee and others (video recorded by John Nishio) for the historians amongst us; it is very slow (about a minute) to connect, but it relates to Benson having shown that fraction 1 protein of Sam Wildman was the same as Rubisco (also see Wildman 2002): [http://www.life.illinois.edu/govindjee/index\\_files/Andy%20Benson\\_Asilomar\\_2002.mpg](http://www.life.illinois.edu/govindjee/index_files/Andy%20Benson_Asilomar_2002.mpg)
- (4) A Tribute to Andrew A. Benson was published on his 90th birthday in *Photosynthesis Research*, Volume 92, Issue 2, May 2007, pp. 143–271; it had 13 papers on several topics related to both photosynthesis and respiration. Authors included, in alphabetical order: Claude Alban, Jan M. Anderson, Christoph Benning, Maryse A. Block, Jacques Bourguignon, Bob B. Buchanan, Claus Buschmann, Francis X. Cunningham Jr., Roland Douce, Elisabeth Gantt, S. W. Jeffrey, Jacques Joyard, Hartmut K. Lichtenthaler, Norio Murata, Fabrice Rébeillé, Norbert Rolland, Achim Trebst, Hajime Wada, and David Alan Walker (see Buchanan et al. (2007) and the papers that follow).
- (5) British Broadcasting Corporation (BBC) has produced a movie that includes Benson's work. (See T. Walker (2012) Botany: a blooming history: photosynthesis. <http://www.bbc.co.uk/programmes/p011lymf>)
- (6) A highly popular video, produced by Bob Buchanan, on Andrew A. Benson's 95th birthday, has been seen, as of August, 15, 2015, by over 3500 viewers. It is available at: [https://www.youtube.com/watch?v=GfQQJ2vR\\_xE](https://www.youtube.com/watch?v=GfQQJ2vR_xE)

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