

HISTORY AND BIOGRAPHY

Remembering James Alan Bassham (1922–2012)

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Abstract James Alan Bassham, known to many as Al, was born on November 26, 1922, in Sacramento, California (CA), USA. He died on November 19, 2012, in El Cerrito, CA. To celebrate his life at his 3rd death anniversary, we present here a brief biography, comments on his discoveries, but most importantly, remembrances from family and friends; we remember this wonderful and modest person who had played a major pivotal role in the discoveries that led to what he would like to call the P(hotosynthetic)

C(arbon) R(education) cycle, known to many as the Calvin Cycle, the Calvin–Benson Cycle, or the Calvin–Benson–Bassham Cycle. Based on a personal request by Bassham himself to one of us (Govindjee), we refrain from including his name in the cycle—in recognition of his many students and associates he would have liked to honor.

Keywords Andrew Benson · Melvin Calvin · Carbon fixation in plants and algae · Martin Kamen · Lawrence Radiation Laboratory · Samuel Ruben

This manuscript was read and edited by **Bob B. Buchanan**, who made the following comments: “The article is a tribute to a scientist who, starting as a graduate student, made lasting contributions to research leading to the elucidation of the Calvin–Benson cycle. One gains insight into the special role James Alan (Al) Bassham played in the work as well as into the admiration he received from his friends and colleagues. The article deserves a place in the history of photosynthesis”.

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Introduction

James Alan (Al) Bassham was born on November 26, 1922 in Sacramento, California, USA, and passed away on November 19, 2012, in El Cerrito, California. His parents were James Calvin Bassham and Helen Alma Bassham (see “**Early life**” section). Figure 1 shows an informal photograph of Al Bassham, taken in 1971.

Al was a resident of El Cerrito, California. He was a biologist and a biochemist of the highest order; along with Andrew (Andy) Benson and others in the Bio-Organic Chemistry Group, headed by Melvin Calvin, in the Lawrence Radiation Laboratory (LBL) at the University of California, Berkeley (UCB), Al played a key major role in the discoveries for which Calvin later received the 1961 Nobel Prize in Chemistry (http://www.nobelprize.org/nobel_prizes/chemistry/laureates/1961/calvin-bio.html). The Prize recognized the elucidation of the *Path of Carbon in Photosynthesis* (see Bassham (2003) as well as Benson (2002a, b) for their perspectives and the contributions of others). Melvin Calvin died on January 8, 1997 (see Loach 1997), and Andy Benson died on January 16, 2015 (see Lichtenthaler et al. 2015).





Fig. 1 An informal portrait of James Al Bassham (c. 1971). From Bassham family archives

This cycle is known mostly as the Calvin cycle or the Calvin–Benson cycle,¹ but to recognize Al's work, it has also been referred to as Calvin–Benson–Bassham cycle; he was a modest person and he preferred to call this cycle Photosynthetic Carbon Reduction (PCR) cycle; this abbreviation, however, is strictly used, in biology and biochemistry, for *Polymerase Chain Reaction* technology in molecular biology for targeted amplification of DNA sequences (see https://en.wikipedia.org/wiki/Polymerase_chain_reaction).

Bassham received both his BS and PhD in Chemistry in 1945 and 1949, respectively, from the University of California (UC) Berkeley. His PhD thesis dealt with key experiments on carbon reduction during photosynthesis, work he did in the Bio-Organic Chemistry Group of what used to be the Lawrence Radiation Laboratory, at the University of California Berkeley; it is now Lawrence Berkeley National laboratory, University of California (or for short Berkeley Lab). This work was done under the leadership of Melvin Calvin, but initially with the help of Andrew Alm Benson, amongst others (see Benson 2002a, b; Bassham 2003). Al continued this work as Associate Director of this group.

In addition to the work on the basic carbon reduction cycle of photosynthesis, Bassham conducted research on the biosynthetic paths leading from this cycle to the thermodynamics and kinetics of the path of carbon and the factors that control the flow of material and energy in this metabolic network. Two major techniques were crucial: (1)

discovery of radiocarbon-14 by Martin Kamen and Samuel Ruben at LBL, UCB (see Kamen 1963; Gest 2004), and (2) the availability of chromatographic techniques (see Benson 2002a, b; Bassham 2003). Bassham coauthored “The Path of Carbon in Photosynthesis” (see Calvin and Bassham 1962), which appeared soon after the 1961 Award of the Nobel Prize to Melvin Calvin.

Early life

James Alan (Al) Bassham grew up in a small mountain town called Trinity Center in Shasta County, Northern California. There he developed a lifelong fondness for mountains, hiking, and wildflowers. In illustration of the rural remoteness of his childhood, Al recalled that when, rarely, an automobile was heard in the distance on the state highway (then a mountain road), the locals would go up onto the mountain with a picnic to watch it approach. His early education was in a one-room schoolhouse, ably taught by his mother Helen Alma Bassham (née Baker), a gentle-natured elementary school teacher who kindled his interest in painting and music. Al's father, James Calvin Bassham, had been an officer and instructor in the Army Corps of Engineers during World War I, and then, during the Great Depression (1930s), worked variously as a forester, a fire spotter, a mining engineer, foreman for gold mining and gold dredging operations, an assayer, a land surveyor, and a snow-season lineman for telephone lines in the mountainous Shasta area.

Al had great respect for his father's mechanical skills and cleverness as an engineer (Fig. 2a). For instance he told the family that his father once purchased a house, but not its property, and moved the two-story structure by himself to an adjacent lot. An inherited do-it-yourself resourcefulness translated into the great facility Al showed later, in the Calvin Lab, where he and other members routinely designed and built their own apparatus. As a teenager, Al boarded in Redding, CA, to attend Shasta Union High School, which is still standing. As recalled by two of us (H.B. and S.B.), he credited his interest in science to an outstanding high school chemistry teacher, Walter L. Dimmick, who inspired him to pursue his studies and helped him to get a scholarship at UC Berkeley. He joined his high school's marching band, playing the French horn (Fig. 2b); later, in 1941 as a University of California Berkeley undergraduate, he would play the same brass in the Cal Marching Band. During his undergraduate years, Al moonlighted as a surveyor during the construction of new piers along the San Francisco Bay waterfront between Alameda and Oakland, siting locations for piles to be driven. According to his family, Al learned his surveying skills working alongside his second cousin, Jim Hall, who

¹ This carbon fixation pathway has also been referred to, in the literature, as “reductive pentose pathway” cycle; carbon reduction cycle, C-3 pathway; Bassham–Benson–Calvin cycle, and Benson–Bassham–Calvin cycle (BBC cycle). One of us (Govindjee) who has had extensive conversations with both Andy Benson and Al Bassham, would have preferred to call it Calvin–Benson–Bassham cycle, but all things considered, “Calvin–Benson cycle” is now used (see e.g., Buchanan et al. 2015).



Fig. 2 Childhood and upbringing. **a** Al Bassham with his father Jim (c. 1923). **b** Al playing French horn in his high school marching band (c. 1939). From Bassham family archives

126 had helped him get the job. During this time, Al was
127 awarded a Phi Beta Kappa Key and inducted into one of the
128 oldest established college honor societies.

129 Al's undergraduate career was interrupted during World
130 War II. News of the attack on Pearl Harbor (Hawaii) on
131 December 7, 1941, precipitated the call for a blackout of
132 lights along the west coast of the US, so Al studied for a
133 German exam by flashlight in his apartment's closet; later
134 he wryly recalled it occurring to him at the time that he
135 was perhaps studying the wrong language! He joined the
136 Navy Reserve Officers' Training Corps (one of the coun-
137 try's original six Navy ROTC's, headed on the UC
138 Berkeley Campus by Admiral Chester William Nimitz). Al
139 attended midshipmen school courses at MIT (Mas-
140 sachusetts Institute of Technology) and at Harvard
141 University, both located in Cambridge, MA, and served for
142 3 years in the US Navy in the Pacific Arena as a young
143 radar officer, radar being at the time a new and top secret
144 technology (Fig. 3a). Al received a letter from UC
145 Berkeley while he was at sea, informing him that he had
146 earned enough transferred credits from MIT and Harvard
147 to graduate, and so, though he hadn't intended to be
148 through with his undergraduate studies, he received his
149 diploma in the middle of the Pacific Ocean in 1945. He
150 occasionally spoke to his family of certain striking mem-
151 ories from this time, such as of a monsoon weathered at
152 sea, with waves that could be felt bending the transport
153 ship as they passed beneath, of the sound of kamikaze
154 fighter planes crashing in the fog into the waters around
155 the fleet, and of the captain who ordered there be no cel-
156 ebration in the fleet at the announcement of the Pacific
157 War's end, which thwarted the old officer's hopes for
158 attaining the rank of admiral. This order was obeyed only
159 on the flagship itself, where Al was serving as a young
160 radar lieutenant—he could see the flares and fireworks

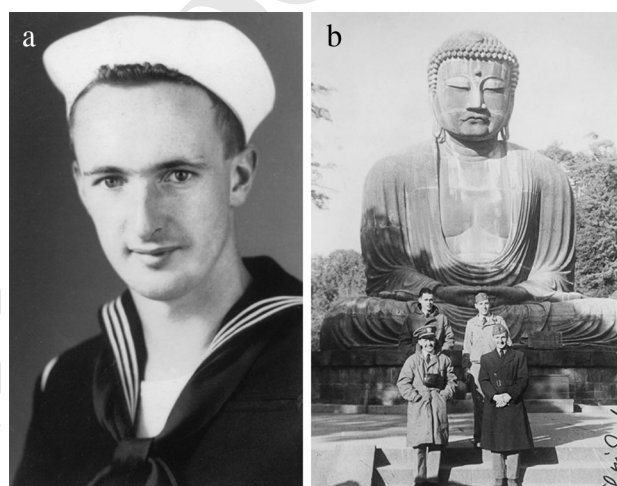


Fig. 3 Interruption of science career by World War II. **a** Al in active duty in the US Navy, ~1943. **b** Lieutenant James Alan Bassham (front, right) in Kamakura, Japan, after the War (1945). From Bassham family archives

going off from the surrounding ships whose captains were
turning a blind eye.

After the war, Al served for a short time in Japan
(Fig. 3b), where he gained a great appreciation for the
culture and especially for the gardens. When Al eventually
built a home for his family in 1964, he made a small
ornamental stream and pond in the yard, complete with
arched wooden bridge and landscaping inspired by the
gardens he had seen in Japan. Al remained in the navel
reserves until 1968, when he retired with the rank of
captain.

When Bassham returned to UC Berkeley in 1946, Dean
Wendell Latimer invited him to work towards his PhD. At
this point, he chose (and was chosen by) Melvin Calvin in
the Bio-Organic Chemistry Group of the Lawrence



Fig. 4 Early days at the Old Radiation Laboratory (ORL). **a** Left to right: Al Bassham as a graduate student, Andy Benson, Alex Wilson in the early 1950s (courtesy of Arthur Nonomura). **b** Front row, left to right: Andy Benson, Al Bassham, Malcolm Thain, J. Rodney Quayle. Back row, left to right: Robert Norris, Hans Kornberg, Alice Holtham,

Jacques Mayudon, Clinton Fuller. Photo taken by Melvin Calvin (c. 1953). **c** On Mt. Whitney (c. 1949). Left to right: Dick Lemmon, William Siri, Andy Benson, Al Bassham and Bert Tolbert. **d** Al entertaining on the piano at an academic get-together; **b**, **c** and **d** are from Bassham family archives

176 Radiation Laboratory to study photosynthesis, in particu-
 177 lar carbon reduction during photosynthesis. Al joined the
 178 photosynthesis subgroup, which included Andy Benson,
 179 in the Old Radiation Laboratory (ORL) (Fig. 4a, b), an
 180 old wooden building where E.O. Lawrence had carried
 181 out early cyclotron work. Al received his PhD in Chem-
 182 istry from UC Berkeley in 1949. He told his family that
 183 he felt he'd been fortunate to work with this wonderful
 184 group under the leadership of Melvin Calvin, who
 185 excelled at putting together teams of cross-disciplinary
 186 researchers. The research team was both varied and
 187 cohesive, inspiring great intellectual foment and long
 188 lasting friendships. The dedicated young researchers let
 189 off steam with rock climbing, ski trips, and other highly
 190 social activities and get-togethers (Fig. 4c, d)—it was a
 191 close-knit group.

Discoveries on the path of carbon in photosynthesis

The best presentation of Bassham's discoveries is in his personal retrospective (see Bassham 2003).

My first awareness of the idea of using radioactive carbon dioxide in research on photosynthesis came while attending a freshman chemistry laboratory section at the University of California, Berkeley in 1940. Sam Ruben, a young member of the chemistry faculty, was our section leader. One morning, instead of the usual discussion of the scheduled laboratory experiment, he told us about his research. I was intrigued with the idea of using radiocarbon as a tool of study of photosynthesis. I never dreamed that I might someday have the chance to participate in this exciting work.

207 This exciting work has been summarized by Bassham and
 208 Calvin (1957), Calvin and Bassham (1962), and most
 209 thoroughly by Bassham (1979, 2003).

210 As we now know, Al did his work beautifully and made
 211 major key discoveries, with Andrew Benson, that led to the
 212 final picture of the carbon reduction cycle of photosyn-
 213 thesis. Figure 5a shows a photograph of the three major



Fig. 5 Photographs from the ^{14}C laboratory. **a** Path of carbon pioneers; left to right: Al Bassham, Andy Benson and Melvin Calvin (courtesy of Karl Biel; see Biel and Fomina 2015). **b** Al marking spots on a chromatogram (c. 1961). **c** Al with graduate students Kazuko Aoyagi and Steve Ruzin, looking over a steady-state photosynthesis apparatus (1984); both **b** and **c**, courtesy of Lawrence Berkeley Lab

scientists: Bassham, Benson (standing) and Calvin; Fig. 5b shows Al with one of the chromatograms, and Fig. 5c shows Al with two student researchers. Chronologically, in the earliest papers: (1) Benson and Bassham (1948) dealt with malic acid, not quite in the main pathway; this was followed by detailed and thorough papers by Bassham et al. (1950, 1954); (2) Benson et al. (1950) provided the detailed techniques that led to the solution of problems related to future discoveries; this was soon followed by the discovery of the 7-carbon sugar in the pathway (sedoheptulose 1,7 bis phosphate) (see Benson et al. 1951). All this and more was summarized wonderfully by Benson et al. (1952). For a Tribute to Benson, see Lichtenthaler et al. (2015); also see Nonomura et al. (2015) for tributes written after Benson's death.

In the opinion of us (Govindjee), a major contribution of Al Bassham was to explore and provide basic information on the dynamics and the kinetics of the intermediates. This was first shown when (a) as light was turned off, the concentration of ribulose bis phosphate (RuBP, the 5-C sugar) instantly decreased and that of phosphoglyceric acid (PGA, the 3-C intermediate) increased; and (b) when $[\text{CO}_2]$ was lowered, concentration of RuBP increased and that of PGA decreased—both being consistent with the proposed cycle (Bassham et al. 1956; also see Bassham and Kirk 1960, 1962; and discussion in chapter 8 in Rabinowitch and Govindjee, 1969).

Bassham (2003) wrote: “These changes provide a compelling argument for two conclusions (1) Cofactors generated by light are required for the formation of RuBP, but not for its utilization in a subsequent reaction; (2) Light-generated cofactors are required for transformation of 3PGA to sugars but not for the reaction which forms 3PGA”. Further, Bassham and Krause (1969) dealt thoroughly with the thermodynamics and the energetics of the photosynthesis process.

Personal and family life

Al Bassham met his future wife, Leslie Alberta Groetzing, at the lab in 1956 (Fig. 6a). They married in 1958, and left immediately for Great Britain and Oxford, where Al had the pleasure of working with Sir Hans Krebs. Leslie and Al's first son, Eric, was born during this year abroad in Oxford (Fig. 6b); succeeding children, Glen, Helen, and Frank, were born after their return to California and UC Berkeley. During a well-deserved 1 year visiting professorship in Honolulu, HI in 1968–1969, Leslie and Al had a fifth child (Susan).

Al's young family occasionally visited him at work, to see the flat glass flasks (the “Lollipops”) of algal cultures in gem-like colors. His office, where he had cultivated a

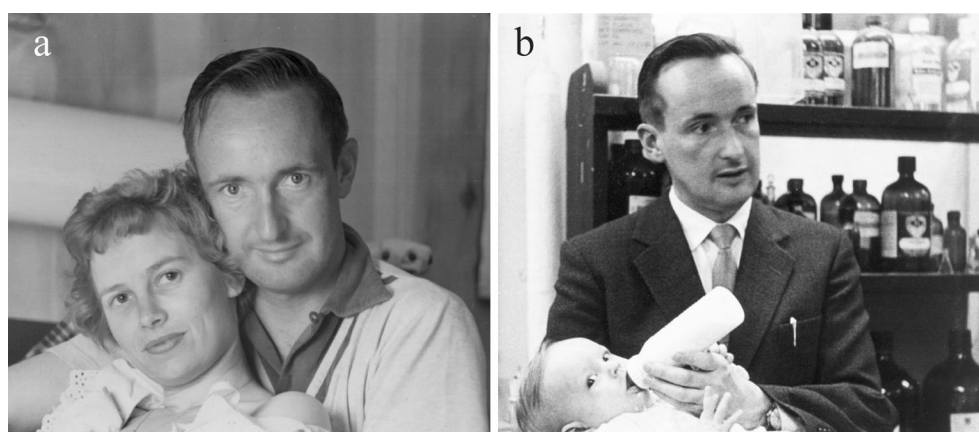


Fig. 6 Balance of career and life. **a** Leslie and Al, who met in the lab and were married in 1958. **b** Al with their first child (Eric), who was born in Oxford in 1959; during this period, Al was working in the lab of Sir Hans Krebs. From Bassham family archives

split-leaf philodendron to jungle proportions, was in a glassed-in corner on an upper level of the “new” round Calvin Lab (then called the Radiation Laboratory). His family remembers his travels to international conferences in tales and curiosities brought from afar (such as, carved wooden bears with Soviet Sickles from the USSR, a rug from Turkey, a noren from Japan). He formed lifelong, loyal friendships with his early colleagues, meeting weekly for years after retirement (1985) with the “Wednesday Lunch Group” in the old Calvin Lab. When, during the 1960s, there was a depressing pall of teargas hanging over the campus, he is remembered at that time returning home to say (comically, per Dr. Seuss), “Poor dad, dad is sad, what a bad day dad had.” In general, though, he was never prone to complaints, but was instead inclined to droll or dry humor, both at home and in the company of colleagues.

When not at work, he spent most of his time with family—pursuing home projects—building, gardening, hiking, camping, and picnicking. For a time he served as Parks & Recreation Commissioner for the City of El Cerrito, during which time he battled banks of poison oak to which he was miraculously immune, carving hiking trails throughout Hillside Park above the old quarry. He began jogging during his lunch hour on the UC Campus during his forties. He continued to run into his early seventies after his retirement, winning first place at least once in his age group in the annual El Cerrito “Hillside Races,” although he drolly and typically quipped, “Since I was practically the only one competing in my age group, it would have been disgraceful not to win.” He memorized Gilbert and Sullivan songs, played guitar and piano, and loved classical music—and when music composition computer programs became available, he toyed with them as well. Watercolor painting and photography were other hobbies he pursued. He loved maps and cartography, mountains and seaside and

was an avid supporter of nature and wild area conservation. He is very much missed by his family.

Comments by others, arranged alphabetically by last name

We provide below comments, with minor editing, received from many scientists after Al Bassham’s death. We also refer the reader to what R. Clint Fuller wrote about the leadership of Al Bassham in Calvin’s lab (see Fuller 1999).

Kazuko Aoyagi (*Businesses Development at Celerion Inc., Princeton, New Jersey, USA*)

How blessed was I to be one of his last graduate students! In 1981, I came to the US as a Fulbright exchange student from Japan with a young daughter. Doing research on top of the course work, in English, while taking care of my young daughter was challenging, but Al made me feel very welcome. He was a great mentor to me.

We were on the mission to probe plant genetic codes to improve productivity and crop yields. There are two types of plants: C-3 plants, which initially make a three-carbon compound during photosynthesis, and include wheat and many other important agricultural crops; and C-4 plants, which initially make a four-carbon compound during photosynthesis, and include corn and other tropical grasses. The plant growth rate is determined by net photosynthesis and, in general, the net photosynthesis of C-3 plants is only about 60 % of the net rate of C-4 plants due to loss of carbon by photorespiration. Al assigned me the project of studying the key enzyme pyruvate orthophosphate dikinase, or PPDK, which makes the 4-carbon compound these plants use to fix CO₂. I purified PPDK from corn and developed an antibody to PPDK, allowing us to detect a

very small amount of PPDK in a wide range of C-3 plants, which was undetectable by conventional enzyme assay. The day I confirmed this result in my 'negative' control C-3 plant samples our strategy completely changed. Being a great biochemist, Al was open-minded. Instead of ignoring the low signal as mere background noise, he was willing to pursue these findings, even though his proposal had already been submitted for funding. We revised our game plan from genetic engineering C-3 plants by inserting the missing C-4 PPDK gene in order to increase productivity, to understanding the role of PPDK in C-3 plants. The new journey was exciting for both of us. During my 4 years at the Chem Bio, or Round House, I had the great pleasure of meeting Melvin Calvin, who served on my PhD committee.

One of my favorite memories outside the lab was running (jogging) with Al, during lunchtime, on the Strawberry Canyon Fire Trail, which runs behind the Round House toward Lawrence Berkeley National Laboratory, with more than a thousand-foot climb with a stunning view of the East Bay. Al's stamina was amazing. I had a hard time keeping up with him, while he was able to tell jokes. (Later, this inspired me to train for cross-country races. I placed 3rd as a Masters runner in the Pacific Association of USA Track & Field cross-country championship in 1995 and 1996.) My training with Al prepared me to join the prestigious lab of Nam-Hai Chua at the Rockefeller University in New York City, where I continued to work in plant molecular biology.

Thirty-four years later, I find myself working in a different field, but I am truly grateful to have had the opportunity to work with Al Bassham.

Mina Bissell (*Life Sciences Division, Lawrence Berkeley National Laboratory, University of California, USA*)

I remember Al as one of the most thoughtful and gentle souls I have ever met—a wonderful gentleman, astute scientist and friend. If the truth has to be known, he saved my career. I interviewed for a job with Al and Melvin Calvin at the Laboratory of Chemical Biodynamics for a staff scientist position when I was still a postdoctoral fellow doing glucose metabolism. By the time I finished my work and got the offer in writing, I was 5 months pregnant with my second child. When I walked through the door of the Laboratory to start my job, Melvin was coming down the steps; he took a look at me and said "who are you? We don't allow pregnant women in the lab". I went home in tears. Then Al called and said, "Mina, never mind. You are working with me. This will pass, you can come and occupy your office, but wait to go to the lab after the baby is born." My office was next to Al's and since this pattern of almost being fired by Melvin continued for a few years, Al was

right there to calm down all of us! It was quite a scene. Al admired the fact that Melvin and I ultimately became good friends. But the only reason I did not leave earlier as had many others was because of AL!

It is many people's and my conviction that the Calvin cycle should be called the Calvin–Benson–Bassham Cycle, as some experts had called it already years ago. Al had contributed so much to that story, as well as to my early work, which took off from the techniques he had helped develop to study the path of carbon in photosynthesis. A significant contribution was related not to photosynthesis, but to virus-transformed cells (see Bissell et al. 1976). I miss him.

Werner Kaiser (*Institute of Plant Molecular Physiology and Biophysics, Universität Würzburg, Germany*)

I came to Al's lab as a postdoc, funded by Deutsche Forschungsgemeinschaft. Three of us (my wife with our 2 year-old son, and myself) arrived in January 1977 in Berkeley. Everything was new, and even the smell of Berkeley was exciting. Al and his wife Leslie had arranged a big two-room apartment in a motel for us, and the freezer was filled with food and all goods required for a 2 year old child. We were extremely grateful for so much help and kindness.

As I had no specific research plan, Al and I decided to take maximum profit out of the technical possibilities of the lab, and specifically out of the 2D-paper electrophoresis for metabolite separation. While the method was not new anymore at that time, its perfect arrangement in Al's lab proved to be extremely useful for me. And as Al's lab was also famous for its 'intact spinach chloroplasts', I focused on regulation of chloroplast carbon metabolism, which also gave a good fit with John Paul's work [see his statement below]. After 18 months, we had worked out how light-induced changes in the concentrations of major stroma metabolites regulate ADP-glucose formation and starch synthesis. In addition, using low H₂O₂ concentrations as an oxidant and dithiothreitol (DTT) as a reducing agent, we could nicely demonstrate counter-regulation of oxidative and reductive pentose phosphate cycle. A total of 5 papers from 18 months of work was not a bad result, and I guess Al was as satisfied as I was.

While hard work was certainly important, Al encouraged us to explore the wonderful landscapes and historical sites of California and the South West. Further, very often after work, Al's "troop" met at a small pub located close to Campus, the "Cheshire Cat" (which still exists, as I saw recently). As a native German I was convinced that only German beer was the real stuff—but I had to admit that 'Anchor Steam beer' could easily stand the comparison.

In 1978, our daughter Sophia was born, and we were proud to have a native US citizen in our small family. When in Fall of 1978 we had to go back to Germany, we were sure that we would miss for a long time Al, his crew, as well as Berkeley and California.

Sir Hans Kornberg (*Department of Biology, Boston University, Boston, Massachusetts, USA*)

Sixty-one years have passed since I first encountered Al Bassham. In 1954, I was so fortunate as to hold a Fellowship awarded by the (New York-based) Commonwealth Fund, which enabled selected people from the UK to undertake research for 2 years in the USA. One of the valuable features of these awards was the requirement that the holder travel extensively through the United States between years 1 and 2, and write an essay on some aspect of American life not connected with one's research. I chose to investigate American regional cooking and, setting off from Yale, ate my way across 40 states.

However, I wished to utilize this opportunity also to learn something to benefit my chosen career and had therefore sought permission from Melvin Calvin (whom I had met briefly on a previous occasion) to spend some weeks in his laboratory, at the University of California, Berkeley, in order to learn the exciting techniques that had been developed, particularly by Andy Benson and Al Bassham, for the use of radioactive tracers in tracing metabolic pathways. Permission having been readily granted, I was duly welcomed to the Old Radiation Laboratory and placed under the benign tutelage of, particularly, Rod Quayle and Al Bassham. I cannot overemphasize the debt I owe to these ever-patient, ever-helpful colleagues who taught me the techniques that, later on, I applied to elucidate the glyoxylate cycle and that critically determined my subsequent academic career.

But it was not only in the laboratory that I learned to value Al's friendship. He was determined that, as a newcomer to California, I should see something of the natural beauties of the State, and therefore, on several occasions, took me for camping trips to Yosemite and the foothills of the Sierra Nevada. I remember fondly these glorious excursions, enriched by Al's knowledgeable commentaries and his warm companionship.

A year after I had returned to England (and to a temporary position in the laboratory of Sir Hans Krebs, in the University of Oxford), Al and his wife Leslie decided to spend a sabbatical period in that laboratory; this enabled me to renew our friendship and also to introduce them to my wife, Monica. It turned out that both Leslie and Monica were in the early stages of pregnancy—so, in order to vacation together before family responsibilities imposed restrictions on movement, we set off to explore the

Rhineland and the Netherlands—a memorably delightful trip, which we vicariously re-lived when Monica and I visited the Basshams many years later.

Although it is now over half a century since Al and I last met (and Monica died 26 years ago), I shall always remember and treasure Al as a gifted scientist, a caring teacher and, above all, a good companion and a very good friend.

Vivian Moses (*Department of Microbiology, Queen Mary & Westfield College, London, UK*)

From October 1956, the time I first became a member of the Bio-Organic Chemistry Group [at UC Berkeley] a year after Andy Benson had left, it was clear that Al Bassham was the rock on which photosynthesis research was based even though that particular year he spent in Oxford, UK. Melvin Calvin was, of course the Group's leader, a participant in most of the discussion and the source of many (often provocative) ideas and initiatives. But not all of them: one Friday afternoon, before going out for a beer, Duncan Shaw and I were musing on a blackboard on the possible workings of a *Dephlogisticated Soot Cycle*, in which the first enzyme was to be carbon dioxide polymerase. Calvin happened by and was highly intrigued: "Hold it", he said as, embarrassed, we began to erase our scribbles: "There may be something in it." Ten minutes later, Al, by then having his beer in La Val's, was highly amused.

But when it came to experimentation, there was nobody to beat Al, ably supported in particular by Martha Kirk. He had been in on the path of carbon project almost from the beginning and saw it through to beyond the end. It was partly from Al that I learned the skills of interpreting our chromatograms and the radioautograms that came from them. He was very good at spotting what those spots might mean and how the whole system hung together.

Although my own primary interests in time drifted away from photosynthesis, it was always a pleasure to chat with Al, whose office was diametrically opposite to my own on the third floor of the Round House. And after I left Berkeley in 1971 to return to my roots in London (UK), I never failed to meet with him and chew the fat on my many subsequent visits to Berkeley, always an enjoyable and stimulating encounter.

Like all his surviving colleagues, in 2012 I lost a good friend, one who for the remainder of my own life will generate warm feelings and happy memories of our collective scientific endeavors, discussions and thinking.

Arthur Nonomura (*BRANDT iHammer, Powell, Ohio, USA*)

When the Old Radiation Lab, ORL, was in its last days, and while the Chemical Bio-dynamics Laboratory

(Roundhouse) completed construction, James A. Bassham and others temporarily moved their offices to the Life Sciences Building, LSB; and they had closer relations with botanists, microbiologists and zoologists from the upper floors, thus, expanding the interdisciplinary discourse of the leaders of *The Path* for decades, thereafter. Melvin Calvin had embarked on a project to “grow gasoline” and while he was looking at Euphorbiaceae, Bassham, having cultured algae for the “lollipop” experiments, had been looking among phycologists in LSB, where John A. West, Paul Silva, and G. F. Papenfuss worked with the world’s most active group of botanists specializing in marine algae. When I had just completed graduation requirements, Al Bassham tapped on my shoulder to find an alga that would produce hydrocarbons equivalent to light sweet crude oil. Fred R. Wolf, one of his post-doctoral lipid chemists, came all the way down the hill from the Roundhouse to LSB and rooted me out to guide me back up the hill; Bassham explained the biochemistry and organization of the project with such clarity, that Fred and I knew exactly how to reach our goal by working in synchrony. For the next months, I worked with them to select “Showa” out of 2000 isolates.

It was not unusual to work with colleagues day and night; but the sophisticated protocols, intensity of purpose, broad scope of approach and depth of comprehension of subjects—all modeled from Bassham’s character—were of a stratospherically higher plane. When the first gas crunch hit home in Berkeley, we were elevated even higher! As a result, it wasn’t long before Fred Wolf unveiled a gas chromatograph of one of the isolates containing 30–40 % dry weight renewable hydrocarbon. With Bassham’s tacit approval, I filed the patent and assigned it to UC Berkeley. Come the biofuels revolution of 2010, the patent marked that we were 30 years ahead of our time.

Al Bassham’s talent was elucidation of the exact truth. Add to that, he was a great communicator; in a single sentence he would capture the essence of the complexities of an entire thesis. His lectures shed light on biochemical pathways in which the flow of energy was set in motion by his speech alone. In the same way that he nurtured my development, Al Bassham elevated colleagues and students to full potential.

John Paul (Cameron Winery, Dundee, Oregon, USA)

Most people who knew Al probably remember the brilliant mind that he possessed as a research scientist. But when I think of Al Bassham the image of a wonderful teacher and lecturer comes to mind. He was the guy who could distill a complex notion into a series of simple, understandable truths.

At the last conference that I attended with him (the Society of Plant Physiology in Blacksburg, VA, in 1978)

Al was selected to give a keynote address. I am sure that everyone thought he was going to rehash or tell a tangential story of the Nobel winning work that he performed with Andy Benson and Melvin Calvin. (And I must admit that he didn’t tell me what he was going to talk about.) So it came as a surprise when he strode up to the podium and proceeded to introduce the new line of research that he and I had been working on, admittedly a far cry from the earth-shaking stuff that had won the 1961 Nobel Prize for Calvin! The project that we were doing involved the determination of pool sizes for various plant metabolites and the insertion of those concentrations into free energy equations. The results of those calculations allowed us to predict exactly where regulatory enzymes would be located.

Al and I had been wrestling with this concept for months but when he stood up there at the lectern, it suddenly looked brilliant and amazingly simple. The end result was that when I later gave my paper setting forth the data on that project, it was to a standing-room audience due entirely to his flawless and enthusiastic presentation of the topic.

Kenneth (Ken) Sauer (Department of Chemistry, University of California Berkeley, California, USA)

James A. (Al) Bassham was a good friend and colleague from the time when I arrived in 1960 at the Calvin Lab at UC Berkeley and the Lawrence Berkeley Lab. During the earlier period from 1947 to 1953, Al had joined a group that included Andy Benson, Nate Tolbert and others working under the direction of Melvin Calvin. Their research objective was to apply the recently discovered radioactive carbon-14 isotope to the investigation of biochemical reaction pathways of carbon. In particular, they used ^{14}C in the form of CO_2 to investigate its role in the photosynthetic uptake and incorporation into carbohydrates, proteins and other essential biological carbon-containing compounds. The outstanding success of these studies led to the award of the Nobel Prize to Melvin Calvin in 1961. Meanwhile Benson, Tolbert and others had left Berkeley to pursue their scientific careers elsewhere, and Al Bassham became the senior researcher in the lab at Berkeley. He was joined in their ongoing investigations by more than a dozen students, postdocs, visiting scientists and career associates, including Martha Kirk, Vicky Lynch, Vivian Moses [see above], Ning Pon and Rod Park. The team under Bassham’s direction developed methodologies and sophisticated instrumentation that are world-renowned. In addition to the discovery of the participation of a large assortment of biochemical intermediates, their kinetic studies led to detailed maps of the photosynthetic carbon-fixation pathways and light-to-chemical energy conversion.



Fig. 7 The authors. **a** Helen Bassham and Govindjee at the University of California, Berkeley; photo by Rajni Govindjee, June 16, 2015. **b** Susan Bassham, with Al Bassham in 2002; from Bassham family archives

My arrival in 1960 found a highly stimulating and friendly environment in California. My growing family and I were welcomed by Al and his family, together with Martha Kirk and others, to visit and explore the delights of the Sierra Nevada. For us, it was the beginning of a lifelong experience of intellectual and social enrichment.

Bert M. Tolbert (Department of Chemistry and Biochemistry, University of Colorado, Boulder, Colorado, USA)

*James A Bassham, Friend and Colleague, 1946 on—*Al Bassham wanted to work on photosynthesis, the problem of how plants convert CO₂ into living plant material. So he joined the Bio-Organic Group with Melvin Calvin and started working on the use of the new tool, Carbon 14. I remember that Al's training in radar and electronics was a welcome ability. As a graduate student he worked directly with Melvin Calvin and was thus the first member of a group of distinguished scientists that solved the initial process of how plants use carbon dioxide.

Al Bassham and I were about the same age and we had diverging experience during World War II—he as a Naval Officer and I as a Chemist with the Manhattan Project. In Berkeley, Al's work, directed by Calvin, was quite separate from my work. Our social and recreational lives had much in common and we both loved the mountains and had many trips together. It was with great pleasure to me when he asked me to be Best Man at his wedding.

Al Bassham served in the photosynthesis group as an informal group leader along with Andrew A. Benson. They were responsible for developing the apparatus to grow algae used in the experiments, feeding highly radioactive CO₂ to the algae for just the correct length of time, and stopping the reaction very quickly to give a mixture of labeled products to be analyzed by techniques which they

and others in the lab had developed. Andy and Al also taught their experimental methods to the many visiting distinguished scientists and colleagues, methods such as counting radioactivity and chromatography of photosynthetic intermediates. After Andy Benson left the group, Al Bassham was assigned general responsibility for the group operation under Professor Calvin's direction. Until the time Al retired in 1985, he worked and published many papers on details of these photosynthesis reactions.

I moved to the University of Colorado in 1957 and then spent the summer of 1958 with Melvin Calvin's Bio-Organic Group, attending group meetings, including Al's studies of the carbon fixation reaction. In 1959, Al and Leslie were able to attend my wedding to Anne Grace Zweifler, a former member of Calvin's photosynthesis research group.

The authors

We end this tribute by showing photographs of the authors: Govindjee and Helen Bassham (Al's daughter) on June 16, 2015, when the two discussed the publication of this article (Fig. 7a), and Susan Bassham, with her father (Al Bassham) when she received her PhD from the University of Oregon, in 2002 (Fig. 7b).

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References

- Bassham JA (1979) The reductive pentose phosphate cycle and its regulation. In: Gibbs M, Latzko E (eds) *Photosynthesis II. Photosynthetic carbon metabolism and related processes*. Encyclopedia of plant physiology, new series, vol 6. Springer, Berlin, pp 9–28
- Bassham JA (2003) Mapping the carbon reduction cycle: a personal retrospective. *Photosynth Res* 76:35–52
- Bassham JA, Calvin M (1957) The path of carbon in photosynthesis. Prentice-Hall, Englewood Cliffs
- Bassham JA, Kirk M (1960) Dynamics of the photosynthesis of carbon compounds. 1. Carboxylation reactions. *Biochim Biophys Acta* 43:447–464
- Bassham JA, Kirk M (1962) The effect of oxygen on the reduction of CO₂ to glycolic acid and other products during photosynthesis by *Chlorella*. *Biochem Biophys Res Commun* 9:376–380
- Bassham JA, Krause GH (1969) Free energy changes and metabolic regulation in steady-state photosynthetic carbon reduction. *Biochim Biophys Acta* 189:207–221
- Bassham JA, Benson AA, Calvin M (1950) The path of carbon in photosynthesis. VIII. The role of malic acid. *J Biol Chem* 185:781–787
- Bassham JA, Benson AA, Kay LD, Harris AZ, Wilson AT, Calvin M (1954) The path of carbon in photosynthesis. XXI. The cyclic regeneration of carbon dioxide acceptor. *J Am Chem Soc* 76:1760–1770
- Bassham JA, Shibata K, Steenberg K, Bourdon J, Calvin M (1956) Photosynthetic cycle and respiration: light and dark transients. *J Am Chem Soc* 78:4120–4124
- Benson AA (2002a) Following the path of carbon in photosynthesis: a personal story. *Photosynth Res* 73:29–49
- Benson AA (2002b) Paving the path. *Annu Rev Plant Biol* 53:1–25
- Benson AA, Bassham JA (1948) Chemical degradation of isotopic succinic and malic acids. *J Am Chem Soc* 70:3939–3940
- Benson AA, Bassham JA, Calvin M, Goodale TC, Haas VA, Stepka W (1950) The path of carbon in photosynthesis. V. Paper chromatography and radioautography of the products. *J Am Chem Soc* 72:1710–1718
- Benson AA, Bassham JA, Calvin M (1951) Sedoheptulose in photosynthesis by plants. *J Am Chem Soc* 73:2970
- Benson AA, Bassham JA, Calvin M, Hall AG, Hirsch HE, Kawaguchi S, Lynch V, Tolbert NE (1952) The path of carbon in photosynthesis. XV. Ribulose and sedoheptulose. *J Biol Chem* 196:703–715
- Biel K, Fomina I (2015) Benson–Bassham–Calvin cycle: contribution to the organic life on our planet. *Photosynthetica* 53:161–167
- Bissell MJ, Rambeck WA, White RC, Bassham JA (1976) Glycerol phosphate shuttle in virus-transformed cells in culture. *Science* 191:856–858
- Buchanan B, Gruissem W, Jones R (2015) *Biochemistry and Molecular Biology of Plants*, 2nd edn. Wiley, New York
- Calvin M, Bassham JA (1962) *The photosynthesis of carbon compounds*. WA Benjamin, New York
- Fuller RC (1999) Forty years of microbial photosynthesis research: where it came from and what it led to. *Photosynth Res* 62:1–29
- Gest H (2004) Samuel Ruben's contributions to research in photosynthesis and bacterial metabolism with radioactive carbon. *Photosynth Res* 80:77–83
- Kamen MD (1963) The early history of C-14. *J Chem Educ* 40:232–242
- Lichtenthaler HK, Buchanan BB, Douce R, Govindjee (2015) Andrew A. Benson, 1917–2015. *Photosynth Res* 124:131–135
- Loach PA (1997) Obituary: a remembrance of Melvin Calvin. *Photosynth Res* 54:1–3
- Nonomura A, Lorimer G, Holtz B, Vacquier V, Biel KY, Govindjee (2015) Andrew A. Benson: personal recollections. *Photosynth Res*. doi:10.1007/s11120-015-0186-x
- Rabinowitch E, Govindjee (1969) *Photosynthesis*. John Wiley; it is available at: <http://www.life.illinois.edu/govindjee/photosynBook.html>; its pdf can be downloaded free from: <http://www.life.illinois.edu/govindjee/g/Books.html>