# *Remembering Melvin Calvin (1911–1997), a highly versatile scientist of the 20th century*

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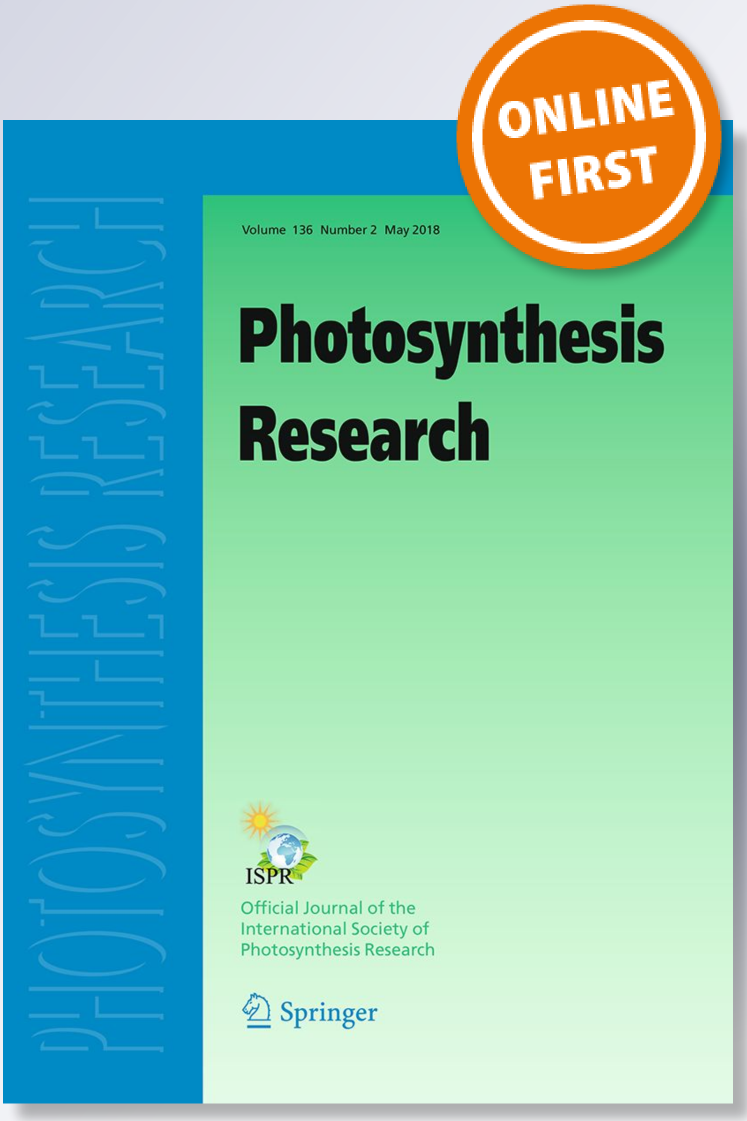


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HISTORY AND BIOGRAPHY

# Remembering Melvin Calvin (1911–1997), a highly versatile scientist of the 20th century

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**Abstract**
Melvin Calvin (1911–1997) was the recipient of the 1961 Nobel Prize in Chemistry for the discovery of the canonical photosynthetic carbon reduction cycle. We present here a very brief glimpse of this extraordinary American scientist, who in his time was a preeminent force in physical and organic chemistry. Besides natural photosynthesis, Calvin's prolific career included artificial photosynthesis, colors of organic substances, the origin of life, cancer, moon rocks, molecular basis of learning, and plant lipids & algal hydrocarbons as potential renewable sources of transport fuels.

**Keywords** American ingenuity · Andrew A. Benson · James A. Bassham · Carbon reduction cycle · Calvin Lab · Mr. Photosynthesis

*To this goal of understanding, all men—scientists and laymen alike—bring the humilities, which accompany recognition of beautiful and complex events. Each brings also the gift of his own experiences, which alone will allow insight into a profound phenomenon.*
—*Melvin Calvin (1969)*

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## Melvin Calvin: his life and work

Melvin Ellis Calvin was born in St. Paul, Minnesota, USA, on April 8, 1911. His father (Elias Calvin) was from Kalvaria, Lithuania, and his mother [Rose (neé Hervitz) Calvin] was from Georgia, Russia. Elias worked as a cigar maker and later as an automotive mechanic and Rose was a homemaker. In 1942, Melvin Calvin married Genevieve Jemtegaard, who passed away in 1987. They had two daughters (Elin Sowie and Karole Campbell) and a son, Noel (deceased), six grandchildren and two great grandchildren.

In this memoir, our accounts of Calvin and his family, students and colleagues, emphasize his wide breadth of research, his impact on many fields of science, and his personal nature. We introduce Melvin Calvin by showing his portrait from 1986 (Fig. 1).

In his youth, Melvin wanted to be a scientist, but his physics teacher thought that he "could never achieve that goal because he was too eager to reach conclusions". As a child, he loved to collect rocks, watch birds, and enjoyed looking at the "stuff" his parents had in their grocery store. He had honed this eagerness and other more scholarly traits to receive his doctorate in Chemistry, in 1935, from the University of Minnesota in Saint Paul. His thesis, under George Glockler, dealt with *electron affinity of halogens*.

Calvin worked from 1935–1937, with Michael Polanyi (https://en.wikipedia.org/wiki/Michael_Polanyi) at the University of Manchester, UK, with a keen interest in

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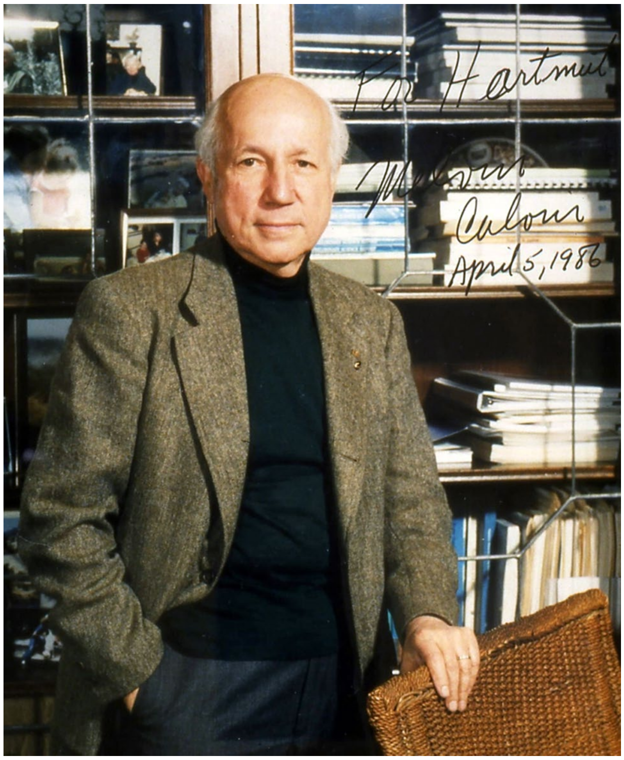


**Fig. 1** Photograph of Melvin Calvin in his retirement office at the University of California Berkeley; his autograph and presentation to one of us (HKL) lends provenance to the historical view of our marvelous colleague, leader and mentor. Archives of Hartmut Lichtenthaler

coordination catalysis. Following Polanyi's leadership, Calvin applied his signature interdisciplinary approach to science and became a leader in understanding the basics of the structure and behavior of organic molecules.

In 1937, Calvin joined the faculty at the invitation of Gilbert N. Lewis as an instructor at the University of California (UC) Berkeley; thereafter, on September 2, 1945, Ernest O. Lawrence, Director, UC Radiation Laboratory (UCRL), advised Calvin, "Now is the time to do something useful with radioactive carbon". This was so because in 1940, Martin Kamen and Sam Ruben had discovered, at the 60-inch Cyclotron at UC, long-lived radioactive $^{14}C$ (see Govindjee and Blankenship 2018; Kamen 1985). Right away, Calvin appointed Andrew (Andy) A. Benson to be the director of the photosynthesis laboratory to build it from the ground up and, upon which, Benson set into play the protocols for the discovery of the path of carbon fixation in photosynthesis. In these early years, together, they were interviewed and celebrated for their peaceful applications of radioactive isotopes; they had jointly authored their first publication on the path of carbon in photosynthesis (Benson and Calvin 1947). Figure 2a shows Calvin with Andy Benson and Jacques Mayaudon.[1]

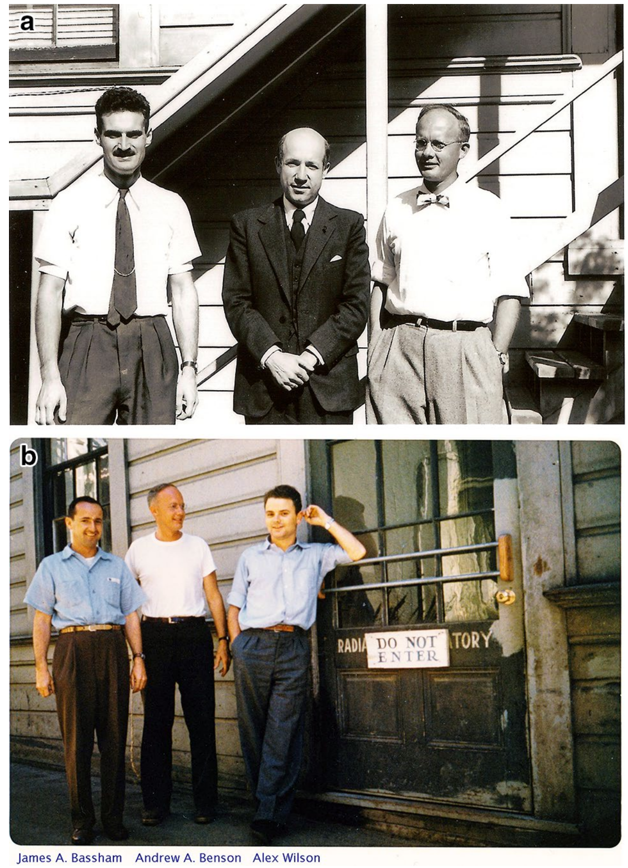


**Fig. 2** **a** Left to right: Jacques Mayaudon, Melvin Calvin and Andrew Benson (wearing a bowtie), behind their Lab at UC Berkeley, 1950s (see Fig. 7 (top left) in Benson 2002). **b** Left to right: James A. Bassham, Andrew A. Benson and Alex T. Wilson (Buchanan et al. 1952) at the front door of the Old Rad Lab, 1950s. For more on Wilson, see footnote 1. Archives of Arthur Nonomura

During the next several years, in close collaboration with Andy Benson, James A. (Al) Bassham, and many others, Calvin led the Old Radiation (Rad) Lab (ORL) to show that light acts on chlorophyll molecules rather than on carbon dioxide as had been thought previously; for more on this, see

[1] The late Alex T. Wilson, shown in Fig. 2a, was an international success. After co-authoring several papers for "The path of carbon in photosynthesis" series (see for example, Buchanan et al. 1952), and completing his post-doc with Calvin, Wilson returned to New Zealand, where he became foundation professor of Chemistry; established the science faculty as the inaugural Dean of the School of Science, *University of Waikato, Private Bag 3105, Hamilton, New Zealand 3240*. Wilson was a pioneer in the area of "global climate change" (see Wilson 1964); clearly, he carried Calvin's teachings to New Zealand.

footnote 2.[2] And they further changed the course of science as they proceeded to unravel the conversion of light energy into chemical energy in a process, they called 'the path of carbon in photosynthesis'. Calvin received the Nobel Prize for the first recognition of a photosynthetic carbon reduction cycle, most widely accepted by the name Calvin–Benson cycle (see Sharkey 2019); and we note that it is considered the cornerstone of the carbon reactions of photosynthesis (Buchanan 2016); for more on the cycle and integral contributions, see footnote 3.[3] We cannot sufficiently emphasize the importance of the hundreds of people that walked *The Path* with Calvin and, we salute all of them for their contributions to one of the greatest benefits for mankind.

Calvin served as Director of the Bio-Organic Chemistry group in the Lawrence Radiation Laboratory, starting in 1946; and after a year, he was promoted to be a full professor. He had first worked in the Cyclotron Building <https://chemistry.berkeley.edu/history>; then in 1958 in the Life Sciences Building. Finally, beginning in October 1963, his office was in a new circular building that was conceived by Melvin Calvin personally and designed by Michael Goodman. This, one of the smallest buildings on campus, was known informally as the "Roundhouse" or "Calvin Lab" although, the official name was the Laboratory of Chemical Biodynamics, Lawrence Berkeley Laboratory. It has now regained its eponymous title, *the Calvin Lab*.

Calvin had received many *prizes and honors* including the 1964 Humphrey Davy medal (of the Royal Society of London) as well as the 1978 Joseph Priestley medal (of the American Chemical Society) and the 1989 National Medal of Science (US President George Bush). In addition, he had been elected to the US National Academy of Sciences, the American Philosophical Society, the American Academy of Arts and Sciences, the Royal Society of London, the Royal Netherlands Academy of Sciences and Letters, and the Deutsche Akademie der Naturforscher Leopoldina (since 2008, the German Academy of Science). Calvin also received honorary D.Sc. degrees from the Michigan College of Mining and Technology, the University of Nottingham, Oxford University, and the Northwestern University.

In his lifetime, Calvin had published over 600 research articles. Surprisingly, in 2013, it came to light that some 20 vials of moon dust that had been returned to Earth after historic landings of Apollo 11 and 12, was found in storage by Berkeley Lab archivist Karen Nelson (Chao 2013). These rarest extraterrestrial samples were the source of Calvin's studies of carbon compounds in moon rocks and lunar soil! Such is the importance of carbon fixation that the very existence of any of the compounds that result from photosynthetic carbon reduction are *the* signs of life as we know it.

Among his many *books*, two are more familiar to most of us: *Theory of Organic Chemistry* (Branch and Calvin 1941) and *The Path of Carbon in Photosynthesis* (Bassham and Calvin 1957). With a nod toward the brand-new topic of radiation safety, Calvin assembled the first compendium of every synthesis with isotopic carbon, as well as, general principles for handling and measurement, into a guide for large-scale radiochemical and biological research (Calvin et al. 1949). This book included reference to Benson's electrometer, parts of which are shown in Fig. 3a; it was first utilized for the detection of background radiation.

We note that much of the group's early experiments were based on feeding $^{14}CO_2$ to microalgae in flattened glass vessels resembling the shape of lollipops, shown in face and side views in Fig. 3b. The tracer gas was bubbled into the culture at specified time intervals, at the end of which, the carbon reactions would be stopped by dropping the alga into hot methanol. The lollipop exhibited in Fig. 3b is one of the instruments that was actually utilized in the earliest runs and was limited to 5-min exposures or longer. By 1951, more sophisticated instrumentation was developed for leaf exposure. In his review, Sharkey (2019) pointed out that by 1954, a quenched flow apparatus, that we attribute to Bassham, enabled exposure times of less than one second and, furthermore, the concentration of $^{14}C$ was reduced to less than 15% by introduction of radioactive bicarbonate. This level of elegant science is rarely matched today.

Most importantly, beyond his research and books, Calvin's leadership and research directions had a major effect in the decisions of the U.S. Department of Energy (DOE) in initiating and supporting research towards *sunlight as a renewable energy source* that ranged from developing "artificial chloroplasts" to adapting photosynthesis for energy production. Calvin's lifelong interest was in "grow gasoline" projects, in which he had actively participated. The first isolate with hydrocarbons that could be 'cracked' to gasoline, diesel and aviation fuel was from *Botryococcus braunii*, whose 20% to 40% botryococcene hydrocarbons

[2] Already in 1931, Hans Kautsky, then working on chlorophyll a fluorescence kinetics, had postulated that the primary photosynthetic processes consisted of two light reactions, one that would reduce a primary electron acceptor followed by a second light reaction that would oxidize the primary electron acceptor (for details and original references, see Lichtenthaler 1992, and Govindjee 1995). Many others provided key experimental information with regard to the accessory pigments and the "loss of electrons" by chlorophylls in the reaction centers of their respective organisms (see for example, Blinks 1959, Duysens 1952, and Kok 1948; cf. Govindjee and Pulles 2016, Govindjee and Renger 1993, and Rabinowitch and Govindjee 1969).

[3] It is generally acknowledged that both Benson and Bassham made seminal contributions to elucidate the carbon fixation cycle (Fuller 1999; Govindjee 2010; Lichtenthaler et al. 2015; Buchanan et al. 2016; Nonomura et al. 2017), and all three shall be remembered as tall pillars of history (see Buchanan et al. 2016, on Benson; and Govindjee et al. 2016, on Bassham). We prefer their full acknowledgement by reference to the carbon fixation cycle as: "Calvin–Benson–Bassham cycle".

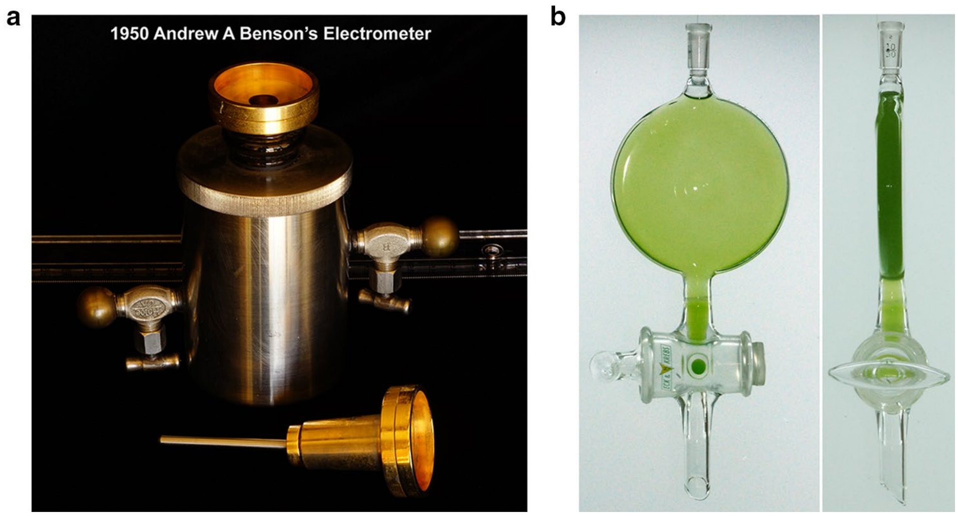


**Fig. 3** **a** One of the instruments used in the Old Radiation Lab at UC Berkeley: An electrometer that measured background radiation and rates of $^{14}CO_2$-gas flow (Calvin et al. 1949); gas flow-through detectors included gold-plated electrodes. From AN's personal archives; photograph by Arthur Nonomura. **b** Two views of a 3-inch glass "Lollipop" from the Calvin Lab, late 1940s and 1950s. The "lollipop" was a serious laboratory apparatus designed by Benson to feed $^{14}CO_2$ to microalgae by bubbling in the gas. When viewed from the side, the thin layer of this early model is revealed. In the face view, the lollipop's expansive light-gathering plane is seen. After a carefully measured time interval of exposure, with a quarter turn of the stopcock, the entire content was dropped quickly through its large bore into hot methanol to stop metabolism. The radiolabeled metabolites were concentrated, separated and analyzed. As quantities of radioactive isotopes became available, larger lollipops were constructed, up to 12-inches, each unveiling metabolite(s) of first recognition by Calvin's laboratory. From AN's personal archives; photograph by Arthur Nonomura

were observed to be sufficient to float the colonies on the water surface; and this was known informally as the Berkeley strain. Furthermore, these energy-rich hydrocarbons were so abundant that they were secreted and discernible as spherical droplets around the algal colony (see Fig. 4). In fact, one of us (AN) found that the wet biomass was ignitable, resulting in the legal and botanical name of the variety, *Showa*, that translated from Japanese, means "Brilliant Peace" (US Patent Plant 6,169; Nonomura 1988).

## Our reflections on Melvin Calvin

To start, we shall reflect on Melvin Calvin, the person he meant to us. He was once described "to be a veritable bouncing ball, full of energy and new ideas—perhaps a super ball!" (Loach 1997). He has been also called: "A scientist of exceptional curiosity". Further, Seaborg and Benson (1998) wrote, "He was widely known for his mental intensity, skill in asking questions, and impressive presentation of his research and ideas" [also see: Otvos et al. (2000), and Seaborg and Benson (2008), for further thoughts].

After Melvin Calvin had begun his academic life at UC Berkeley, he had risen rapidly as a young faculty member. He excelled in thinking about the dynamics of organic molecules including the porphyrins. This is important because chlorophyll is a porphyrin with magnesium at its center. By

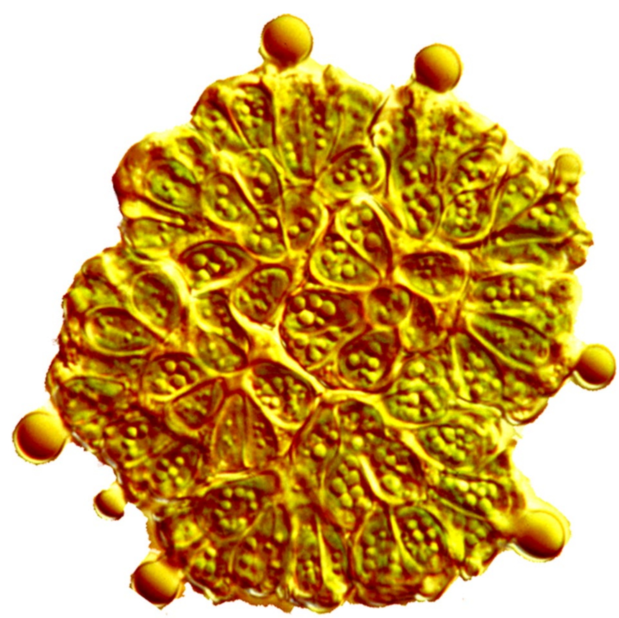

**Fig. 4** A photograph of a single colony of *Botryococcus*, a green alga, which may contain over a third of its dry weight in botryococcene hydrocarbons. We observe droplets that were shown earlier to be made of a hydrocarbon; also, the colonial matrix, between cells, was rich in hydrocarbons. From over 2000 isolates of *Botryococcus*, one shown here under phase contrast microphotography, was cultivated by Arthur Nonomura (1988) and the hydrocarbon chemistry and the content was analyzed by F.R. Wolf and J.A. Bassham (see Wolf et al. 1985)

the mid-1940s, an extraordinary opportunity had been presented to Calvin by Lawrence who had guided Calvin to head up a project using UCRLs supply of radioactive carbon to determine how it is metabolized in photosynthesis (see above). Within a few short months, Andy Benson had synthesized the world's supply of concentrated $^{14}CO_2$, and the rest is history. In a media blitz from 1949 to the 1950s, Calvin and Benson were featured in magazines such as *Colliers* and *Life*, earning the public nicknames of *Mr. Photosynthesis* for Calvin, and *The Atomic Man* for Benson. The pair shared fame in the popular press, becoming model scientists of the atomic era, and they were photogenic! Calvin was 34 years old when he had initiated the project to solve how $^{14}CO_2$, is "fixed" in photosynthesis; and, Benson was 6 years his junior. Just about the entire Bio-Organic group was in their 20s and 30s, eager to contribute to defining this previously unknown metabolic pathway. The great team of excited adventurers included research specialists from many different fields of the life sciences and chemistry—*even psychology*—and more, as the projects blossomed. Clearly, the young multidisciplinary scientists emulated their leader, Melvin Calvin, engaging in complex scientific investigations with unique and unmatched intensity of purpose. For the most part, largely independent yet obsessive self-starters were preferred—always on top of the field applying rigorous protocols, collaborating with great fervor, embracing a culture of trust—they were critical thinkers with an eye on the goal, as we have learned from many personal conversations with Andy Benson and Al Bassham (*cf.* Benson 2002; Bassham 2003). These early pioneers worked in an aging facility, the Old Radiation Lab (ORL), which everybody referred to in terms of endearment because, somehow, it provided exactly the surroundings that promoted open-ended creativity—they could construct and change their 'beloved' ORL at will. Calvin gave them wide latitude to improvise!

In today's world, the above-mentioned design for discovery and innovation is becoming popular in many tech startups, wherein smart young entrepreneurs are finding themselves working under similar circumstances; and, as well, major scientific breakthroughs are being borne from similar designs. This may not be coincidental because Calvin was hailed by Atomic Energy Commission (AEC), National Science Foundation (NSF), National Aeronautics and Space Administration (NASA), and other top institutions of science around the world for advice on management, design and execution of their future scientific advancements. *Thus, in our view of the 1950s, there was nothing like ORL in the world.* Calvin's novel management style of major science projects contributed to that extraordinary era known widely for its "American Ingenuity". It is no surprise, then, that Calvin had been labeled as *Mr. Photosynthesis* and yet his vast reservoir of knowledge that fed his curiosity, for just about everything, made him so much more than that as he worked across many disciplines. Our personal reminisces follow.

## Reminiscence by Hartmut Lichtenthaler

In January 1962, I came as a postdoctoral fellow to Melvin Calvin's Laboratory of Chemical Biodynamics at UC Berkeley. Just a few weeks earlier, in December 1961, Calvin had received the Nobel Prize in Stockholm. At that time, there was a special atmosphere of departure to new horizons in science in Calvin's laboratory in the Life Sciences Building and in his Donner laboratory as well. With the excellent equipment in his laboratories and with the then available new methods of investigation and modern instrumentation, the scientific world was wide-open for us, the young scientists. There was the feeling that we could start in almost any field of biology and chemistry and make substantial scientific progress. In contrast to the then poorly equipped European research laboratories (I had come from West Germany) that we had experienced before, we found in Berkeley very favorable working conditions so that we were determined to succeed and to try to make basic, essential and innovative contributions to science.

Calvin was the '*spiritus rector'* and driving force of this spirit. He encouraged all newly arrived international and domestic post-docs and guest scientists that in giving their best, they would succeed. He himself gave wonderful advice in which way to start their new research. This was further promoted by Calvin's senior scientists, all of them experienced top scientists, such as James Al Bassham, Kenneth (Ken) Sauer, Ning Pon and Roderic (Rod) B. Park in his photosynthesis laboratory as well as Edward (Ed) L Bennett and Richard Lemmon in his Donner laboratory. Along with his top technical assistant Martha Kirk, they all gave very valuable advice and very helpful practical hints for the daily laboratory work.

Calvin was a very open-minded scientist, a person with a very broad horizon and knowledge. He started his day very early, and discussions with him often took place at 7:00 A.M. in his office (Lichtenthaler 2015). He was extremely curious and had a great spirit to start unusual and unconventional research in order to achieve new and convincing experimental data to solve old questions and thus to contribute to the progress in science. In addition, he intensively promoted interdisciplinary research. In fact, during my time in his group between 1962 and 1964, we had chemists, biochemists, physical-chemists, plant physiologists, physicists, photobiologists, and for some time, also, a medical doctor in Calvin's laboratories. He was convinced and right that only discussion and cooperation between the different areas of science, which were floating apart, would bring essential new knowledge and progress. And this was one

**Fig. 5** A photograph of the "Calvin Lab" (The Melvin Calvin Laboratory) on the UC Berkeley campus—it stands as a reminder to the entire World about Calvin and his discoveries; it is '*the Roundhouse*" featuring a toroid exterior and wide-open interior with radiating benches that fostered integrative collaborations. The building now houses Simons Institute for Theory of Computation. See https://simons.berkeley.edu/about/calvin-lab

essential factor for his large success and his many science publications.

I have to mention another factor in this regard. Calvin very much promoted the open scientific discussion. Already in his large laboratory in the Life Sciences Building and even more in his newly constructed "Roundhouse"-Laboratory (see Fig. 5), there was a large black board next to the coffee machines, and it was visible from most lab benches. This was the place where two or three of lab members could discuss their research and certain problems with it with one another. Those researchers who just had any spare time, during their work, could join, listen and sometimes contribute to these discussions. These mostly interdisciplinary discussions were an essential stimulus for the ongoing research and they not only broadened the scientific knowledge of the participants but gave new directions to their research and could even lead to joint research efforts.

Another factor in Calvin's substantial progress and his many scientific contributions was the fact that he had opened his laboratory for guest scientists and post-docs from all over the world. I recall that during my time in Calvin's laboratory (1962 to 1964), international scientists came from: Canada, France, Germany, Great Britain (UK), Greece, The Netherlands, Poland, Switzerland, Yugoslavia, and also from Japan, Sri Lanka and Australia. These scientists brought not only new scientific questions but also new investigation techniques into Calvin`s laboratories, thus broadening the research and keeping it always topical on newly emerging questions.

Calvin was a great person and gave wonderful advice. By his personal example and enthusiastic engagement in science, he inspired and promoted many young scientists and numerous post-docs from all over the world to give their best to the progress of our knowledge in science. In fact, he was an excellent academic teacher. In addition, he intensively promoted national and international scientific cooperation. He encouraged all persons in his laboratory and far beyond to cooperate in joint interdisciplinary research as he was convinced that real progress in science could only be made by joint endeavors.

During my time in his laboratory and also later-on I had an excellent and very friendly relationship with Melvin Calvin. We both liked to quickly develop a new scientific idea and to discuss the possibilities for its execution. Before I left his laboratory in 1964, he gave me the valuable advice: "In your future research go always new ways, deal with the major topics of science, never work on side aspects which others have left over". I am thankful for this excellent advice!

In 1986, I gave a lecture in the Biology Department at UC Berkeley. Calvin had already retired but still kept an office and a laboratory in the chemistry facility. He had 2 h to meet me and to discuss his and my current research. He was still interested in his old idea to possibly replace regular fuel by isoprenoid compounds accumulated in the latex of milky sap plants, and he had a post-doc working on this topic. When I told him that we had strong evidence that chloroplasts would possess their own, mevalonate-independent pathway for isoprenoid biosynthesis (a pathway that years later turned out to be the DOXP/MEP pathway; see Lichtenthaler et al. 1997), he was very enthusiastic. At that time Calvin was already 75, but he still had his great and fresh pioneering spirit for new research like he had in the 1960s. When leaving, he gave me his newest photograph with the dedication "For Hartmut, Melvin Calvin, April 5, 1986" (see Fig. 1).

## Reminiscence by Arthur Nonomura

I had been working with James A. Bassham (Govindjee et al. 2016) and Fred R. Wolf to isolate *Botryococcus braunii* var. *showa* Nonomura as a source of biofuels. Together, we had achieved the first laboratory cultivation of 20–40% hydrocarbon content in a photosynthetic organism, when I had my first meeting with Melvin Calvin. It was an impromptu one-on-one call into his office by which we established a common ground in an instant: My father and he were the same age and both Calvin and I had parents who were immigrants. We could view science both as Americans and from a different standpoint, through the lens of our international heritage. Directly, and without hesitation, Calvin proceeded to describe the Carbon Reduction Cycle in fine detail and with such clarity that I became inspired by his dynamic notion of organic physical chemistry. Not only had he used the organic structures, he also *described his schemes drawn as if in space with arm, leg and body motions to emphasize reactions, interactions, and sequences of formation* as he spoke. At that very moment, I understood how Calvin had integrated all of the reactions and products that were elucidated by Benson's Protocol from 1946 (Nonomura et al. 2017, 2018), long before I was born! The "aha moment" had materialized when Calvin walked into ORL one fine morning to reveal that he had applied his keen knowledge of physical chemistry to *all* of the tracer metabolites that were identified in ORL to deduce a *cycle*. This elucidation came to the utter surprise of all of the scientists in the laboratory and, in due time, it shook scientists around the world. By doing so, Calvin, having had the integral support and pivotal contributions of Benson, Bassham and, in fact, all the other scientists who had passed through his laboratory, took the field in a completely different direction from the convention of the time—to the recognition of 3-PGA (3-phosphoglyceraldehyde) as the first product of ribulose bis phosphate-carbon dioxide fixation and to the very first isolation of what is now known as rubisco (**ri**bu**l**ose **bis** phosphate **c**arboxylase **o**xygenase) by Benson and Jacques Mayaudon (Lichtenthaler et al. 2015; also see Wildman 2002), in their canonical cycle (Buchanan et al. 2016; Nonomura et al. 2017; Sharkey 2019). *And the Roundhouse became the architectural metaphor to Calvin's cycle, a superstructure unit instrument of discovery.* (Thank goodness Bassham had walked me through the cycle a few weeks prior to Calvin! Now, I very much wanted to figure out how to use these metabolic pathways to accelerate primary productivity, but really how?)

Well, getting back to our first meeting, Calvin had asked many questions and so did I, and as I left, he kindly offered full access to his laboratory, instrumentation and library. This was truly an honor and although I felt like 15 min had passed, the staff asked what we had been talking about for over an hour. Indeed, in our respective fields, chemistry (Calvin) and botany (mine), we were having quite the jam session; and, Wow! I came away from our meeting feeling like I had a mind meld, given a rock-solid foundation for thinking on multiple approaches to improve photosynthesis.

Calvin was a brilliant physical chemist and yet he operated like a thoroughly innovative chief science officer. To an audience in a lecture hall, Calvin filled the room with excitement, vision, and controversy. In the laboratory, he assembled the best of the best and directed scientific investigations of the *first order* with open communication. Calvin was that rare *forward-thinking* scientist who could articulate his designs for the future that were markedly decades ahead of the time and maintained funding as a controller for success. I returned to the Life Sciences Building with high regard for Calvin as a gentleman and supreme scholar.

After collaboration in Calvin's lab, I moved to the University of California San Diego (UCSD) as Research Faculty with Ralph A. Lewin, who introduced me to Benson, one floor above us in the corner office at the top of Hubbs Hall. When I was at UCSD, Calvin fully supported publication of our discoveries in their series, *The Path of Carbon in Photosynthesis* (initiated by Calvin and Benson in 1948). My three decades of investigations with Benson, from agricultural fields to laboratory and back onto the farm, culminated in the first recognition of *a lectin cycle* in plants (Nonomura and Benson 2014). To do this, I built my own superstructure of discovery out of my 2000-acre farm.

Mechanisms for modulation of glycoregulation had been sought in the chloroplast and yet, by applying Calvin's maxim to, "go always new ways" (as HKL has put it), last year, I located key cytological functions in the vacuole (Nonomura et al. 2018). As a result, we have a powerful new tool of photosynthetic biochemistry to transfer to growers; and, as a first vehicle of instruction, two of us (GG and AN) are working with Dmitry Shevela and Karl Biel to produce educational posters similar to the Z-scheme (Shevela et al. 2017) that will tie recent findings on cytological functions to the carbon reactions of photosynthesis. (Note that a new poster on the Plant Lectin Cycle (https://doi.org/10.13140/RG.2.2.14328.39682) can be downloaded from http://www.life.illinois.edu/govindjee/.)

## Reminiscence by Govindjee Govindjee

While giving the Keynote (plenary) lecture "Perspectives" on June 1, 1968, in Freudenstadt, Germany, at the First International Photosynthesis Congress, Melvin Calvin (1969) had included the text "To this goal of understanding" (see the quote at the beginning of this Tribute) that has stayed in my mind since then. To me, it tells how he valued the work and thoughts of everyone attending this Conference. I was only one of hundreds in the audience, but I was so inspired by his lecture and words that I remember the moment even today. Many other colleagues were equally impressed by his humility and kindness (for example, see footnote 4[4]).

I knew Calvin's extraordinary research even in 1955, when I had applied for a Ph.D. at UC Berkeley (see Supplementary Material). I was admitted to the doctoral program in Botany to work with Calvin. However, I had opted to undertake research with Robert Emerson and Eugene Rabinowitch, at the University of Illinois at Urbana-Champaign (UIUC) (see Govindjee 2004, 2019). Although I never did

[4] Raghuveer (Raj) Prasad, of the Forestry Department (Canada), sent me his admiration of Calvin for his scholarship, leadership and contributions to photosynthesis. Prasad, working during 1963–1965 as a research biochemist at the College of Agriculture at UC Berkeley, recalls: "In 1963, while standing in line in a Bank on the campus, Calvin was standing behind me, and I offered my place to him to show respect: He was highly polite, and thanked me for the offer, but stayed behind. And, in 1964, when he was President of the American Society of Plant Physiology, I met him at the annual meeting and he was again very kind when we talked, which reflected his gentle modesty and scholarship".

any research in the area of the path of carbon in photosynthesis, I have, during my 38 years on the faculty at UIUC (1961–1999), taught this topic to both undergraduate and graduate students, with great enthusiasm [see e.g., Chapter 17 in Rabinowitch and Govindjee (1969, pp. 220–240); Berkowitz et al. 2007)]. I wrote in Rabinowitch and Govindjee (1969): *One likes the simplicity of Calvin's cycle—a single carboxylation and a single reduction!—but nature is not under obligation to be simple*.

For *history and evolution* of this area, see not only what Calvin (1989, 1992) wrote, but also what his two other major coworkers (Benson and Bassham) said (see: Bassham and Calvin 1957; Calvin and Bassham 1962; Benson 2002; Bassham 2003). Beautiful descriptions as well as photographs of Calvin may be viewed at the e-plaque at the California site (http://berkeleyplaques.org/e-plaque/melvin-calvin-biochemist/?cat=49). Appendix 1 lists some of the websites on Calvin for readers to get a good picture of this giant of a scientist. I also refer the readers to the excellent collection of material at UC Berkeley (https://oac.cdlib.org/findaid/ark:/13030/c8959p32/entire_text/). Prototypes of the lollipop laboratory glassware (ID: 2015-00007 *Benson, Andrew A.)*, autoradiograms, and a collection of papers in the Path of Carbon in Photosynthesis series (ID: 2015-00006) may be accessed from the Caltech Archives, Mail Code B215A-74, California Institute of Technology, Pasadena, California 91125 USA.

*From recollections of Calvin's daughter Elin Sowie*. I have had the privilege of interacting recently with Elin Sowie, one of the two daughters of Melvin Calvin; she wrote to me after reading our brief draft of our write-up on her father. She considered our write-up on her father to be a "lovely remembrance". She also told me that when she was a child, she was always fascinated, for some reason, by an outfit where her parents had rented frozen food lockers to store some food for their dinners. She also remembered that at least one of the pivotal ideas on the Carbon Reduction Cycle occurred to her father when he was caught in traffic (even then) on the Bay Bridge on his way to San Francisco. One further memory she had about her father was that he took her on walks around the neighborhood when she was small to collect thin slices of succulents that were growing along the street. She did not remember if Melvin had told her then specifically or if it was a later surmise on her part that the slices were for the purpose of examining the cells in cross section. In any case, it is a favorite memory of Elin; she also vividly remembers the picture of her father with the tanks full of the green alga *Chlorella* in the old laboratory (ORL) because it was one of the places that Elin loved best in that magical old building. *The above tells me how Melvin cared for his family and how he shared his academic life with them.*

**Fig. 6** A photograph of the 1961 celebration of Calvin's Nobel Prize. Melvin Calvin is 3rd from the left, standing between the two lights from the top, and with his hand folded over. Clockwise from Calvin, 3rd from him is Kenneth Sauer, a close faculty associate of Calvin, and 4th is his wife Genevieve Calvin. This photograph was provided by Vittal Yachandra of Berkeley. ©2010 The Regents of the University of California, through the Lawrence Berkeley National Laboratory, reproduced with permission

## In recognition of successful science

I am delighted to know that Elin is very happy that, together with Arthur Nonomura, and Hartmut Lichtenthaler, I am remembering Melvin Calvin more than 20 years after he left us. Figure 6, from the Lawrence Berkeley National Laboratory, shows a celebration of the 1961 Nobel Prize to Calvin, convened by Glenn T. Seaborg, who was at the time the 2nd Chancellor of UC Berkeley.

Seeman (2018) has mentioned that his interaction with Melvin Calvin was via Marilyn Taylor, a trusted administrative assistant, who was loved by the scientists, and the one who typed and proofread all of Calvin's manuscripts. "All questions, requests, and forms were sent to her, and Calvin's responses came promptly from her". *This was the experience of all we know.* What interested us most, however, is that Seeman was the one who designed the postage stamp issued by the US Postal Service (see Fig. 7). In addition, we value the following statement by Calvin to Seeman's daughter when she was in 7th grade; Calvin wrote: "I suppose the simplest way to answer is to tell you there is nothing, in my life at least, that surpasses the pleasure which a successful scientific activity gives. Everything else is peripheral to that".

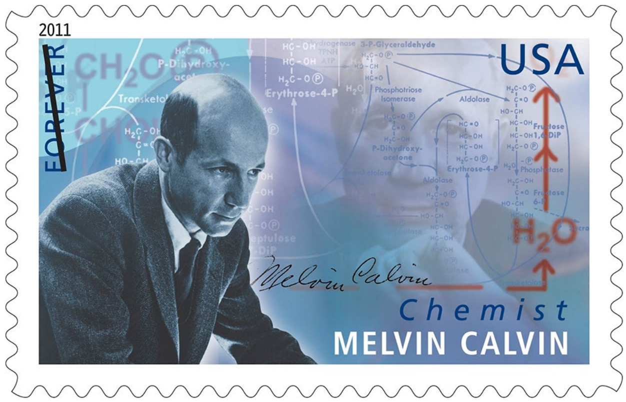


**Fig. 7** US Postal Service stamp of Melvin Calvin in its Nobel Laureate series

## Epilog

Long before you could display a three-dimensional model of a molecule on a monitor and even before desktop computers were imagined, Calvin could, in his mind's eye, envision complex organic molecules and their interactions. By the 1950s, Calvin had applied this talent many times over, resulting in orchestration of the numerous organic molecules of the metabolic pathway into the first recognition of the Carbon Reduction Cycle. How did he do it? To use a musical metaphor, Calvin had *perfect pitch* when it came to physical chemistry by which he conducted the dynamics. He understood every known detail of organic chemical structures to the extent that he could assemble macromolecules and store libraries in his memory. Calvin had immersed himself in his program 24/7 for over a decade, fitting each report from every scientist into the pathway. He was an intense chain-smoking human dynamo that worked hard and fast. He listened. He could be circumspect about something or someone that did not fit. On the other hand, with those he respected, he relaxed and nurtured their science. Often, Calvin would work in the background if there had been something, he could do to help his staff (see Fuller 1999, for an example of what he called, "Calvin's human side;" see footnote 5[5]). Perhaps he would make a telephone call or write a letter of recommendation or talk with the Dean on his colleagues' behalf. These things, he did without fanfare, possibly because he had already moved on to a new idea; and more likely, he wished to elevate his post-docs and faculty. He certainly was a strong leader and yet, he let science take its course by giving his investigators the freedom of creativity. At his peak, Calvin may have been collaborating with as many as 50 scientists in his laboratory, with weekly progress reports. With each and every discussion, he knew every detail. Had there been an inconsistency or a failed experiment, Calvin got on top of it *with* the scientist, contributing to solutions from every angle.

What Fuller (1999) has described was neither micromanagement nor interference by any measure. Calvin showed interest in everybody because he was curious about everything. His scientists were unfettered in another sense because they were not required to spend their valuable time writing grant proposals. Calvin obtained and provided the funding. Furthermore, he scheduled social events, often camping excursions, inviting all who would gather. In a way, each of Calvin's scientists were recipients of the currently trending "genius grants" to exceptional individuals such as from the MacArthur Fellows Program, the Breakthrough Prize, and others. Moreover, Calvin's geniuses have led successful careers and, thus, leaving a legacy of scientific innovation for generations to come. We refer the readers to Moses and Moses (2000) and Fuller (1999) for a complete picture of the background and the essence of Calvin's leadership; we have taken the liberty of drawing our ideas heavily from these sources.

To the thinking mind, the Carbon Reduction Cycle reflects the glory of Nature. And to a fertile imagination, it opens new portals into sustaining civilization. Indeed, the totality of Calvin continues to be truly relevant today—and celebrates, as well, that one giant leap for mankind (Neil Armstrong, from the surface of the moon, July 20, 1969).

We end this Tribute by showing three photographs that capture Calvin's life and career (a) an autoradiogram—where Benson played a major part—that led to the Nobel Prize (Fig. 8a); (b) his scientific communication skills—as a lecturer and wearing his necktie with a porphyrin ring design (Fig. 8b); and (c) his social communication skills by succinctly showing his work and that of his team to world leaders (Fig. 8c). We have included Calvin's selected papers in chronological order in the Supplementary Material. The two together provide us the real breadth of Melvin Calvin's contributions in a multitude of research areas—he was truly a giant of a scientist!

[5] Fuller (1999) wrote: "However, he [Calvin] already had submitted an abstract, co-authored collectively by me, Andy [Benson] and Rod Quayle, to be presented at the meeting. Well, none of us had been aware of such a submission! Pointing out the 'good exposure' for me, he asked if I could go in his place! Clearly, pressure for my independence was growing; I jumped at the chance. Then the very human side of Melvin emerged. "Clint", he asked, "doesn't your family live back East, and wouldn't you like to visit them on the way home?" I suggested that detouring to Providence, Rhode Island on my way from Florida to Berkeley would be a pretty expensive divergence. Reflecting, he suggested sending me, with all expenses paid, to Brookhaven National Laboratory (BNL) on Long Island; after my stay as a consultant there, I could visit my parents on my way home".

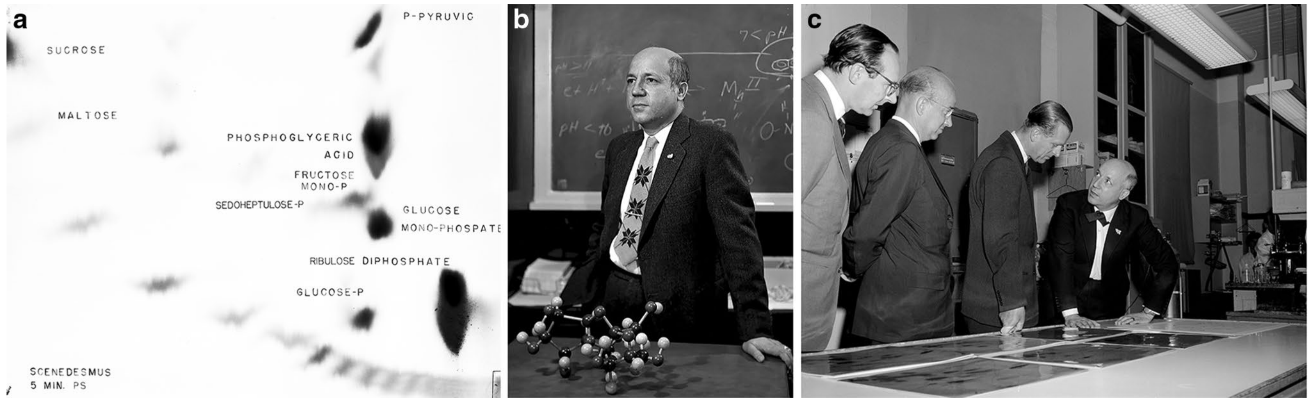


**Fig. 8** **a** X-ray films exposed to 2-Dimensional paper chromatography resulted in autoradiograms. In this plate, key metabolites were labeled with $^{14}CO_2$ within 5 min of photosynthesis, such as, ribulose bisphosphate, clearly identified in the lower right corner. There would never have been a Calvin–Benson cycle without these autoradiograms developed by Benson. This plate was a teaching autoradiogram by Benson, circa 1960, now in the personal archive of AN. High resolution scientific photography by AN. **b** Melvin Calvin lecturing wearing a special tie with stylized 'porphyrin rings', his mother made for him. ©2010 The Regents of the University of California, through the Lawrence Berkeley National Laboratory, reproduced with permission. **c** Visit of HRH Prince Philip, Duke of Edinburgh, in Calvin's laboratory in the Life Sciences Building, Berkeley, in March 1962. Calvin is showing to the Prince and other honored guests several autoradiograms that led to the photosynthetic carbon reduction cycle. ©2010 The Regents of the University of California, through the Lawrence Berkeley National Laboratory, reproduced with permission

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

## Appendix 1: Randomly selected web sites on Melvin Calvin

https://www.jewishvirtuallibrary.org/melvin-calvin
https://en.wikipedia.org/wiki/Melvin_Calvin
https://www.nobelprize.org/prizes/chemistry/1961/calvin/biographical/
https://www.berkeley.edu/news/media/releases/97legacy/calvin.html
https://www.britannica.com/biography/Melvin-Calvin
https://www.nndb.com/people/545/000100245/
https://www.chemistry.msu.edu/faculty-research/portraits/melvin-calvin/
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