



NATIONAL ACADEMY OF SCIENCES



WILLIAM A.
ARNOLD

1904-2001

A Biographical Memoir by
GOVINDJEE
AND NUPUR SRIVASTAVA

© 2014 National Academy of Sciences
*Any opinions expressed in this memoir are those of
the authors and do not necessarily reflect the views
of the National Academy of Sciences.*

Photo courtesy of the family of William Arnold. ☰



WILLIAM ARCHIBALD ARNOLD

December 6, 1904 – October 26, 2001

BY GOVINDJEE AND NUPUR SRIVASTAVA

WILLIAM ARNOLD—BILL, to all who knew him—was a plant physiologist, physicist, and biologist all in one and a researcher of the highest order in each field. His achievements read like a march of scientific progress. He discovered what came to be called the photosynthetic unit, with Robert Emerson, in 1932. He made the first reliable measurements, in his 1935 Harvard Ph.D. dissertation, of the minimum quantum requirement for the evolution of an oxygen molecule. In 1951, together with J. Robert Oppenheimer, he made critical suggestions on the mechanism of excitation energy transfer in photosynthesis. With Bernard Strehler in that same year he discovered delayed light emission (DLE) in photosynthetic

A handwritten signature in black ink that reads "W. A. Arnold".

organisms. He made the first measurements of excitation energy migration by depolarization of fluorescence, with Eleanor Meek in 1956. He discovered thermoluminescence in chloroplasts, with Helen Sherwood in 1957. He elucidated the primary photochemical reactions at the photosynthetic reaction center down to 1K with Rod Clayton in 1960. Bill discovered the presence of electroluminescence, also in chloroplasts, with Jim Azzi in 1971. As this list suggests, Bill Arnold was one of the founding fathers of our understanding of the physical basis for photosynthesis.

Bill was a scientist for almost all of his long life and considered himself “lucky” to be one, as he stated in his autobiography. He believed that discoveries are made because we follow our “scientific curiosities” (Arnold, 1991). His scientific life was passionately devoted to performing experiments; he carried them out carefully, and they were always elegantly designed. The methodological sections of his papers are clear and provide details in the simplest possible terms. Bill once told one of us (Govindjee) that “scientists should be asked to write on stones; then, they will publish less.” He always believed in precision, simplicity, and, above all, brevity. His shortest published sentence was “It does.”

In a tribute to Bill, Jean Lavorel, a French scientist who visited him in March 1957, called him “a giant

and pioneer of biophysics of photosynthesis.” Of Bill’s personality, Lavorel wrote:

The man is straight, plain, even-tempered, attentive and nice. [He] is utterly methodical but resourceful and imaginative. During...discussion, he would listen intensely, but interrupt as soon as matters got vague or obscure; in his turn, he would speak in a quiet manner and explain things very clearly. I have been deeply impressed by his modesty and his capacity to pay attention to the work of other people—even younger than him. [He] once said whimsically, that in his opinion, the most important technological modern contributions to science were the photomultiplier and the black adhesive tape!

[A] remarkable point in [his 1991] article was its simple title: “Experiments.” It was presumably difficult to express more directly that [his] whole scientific life...has been passionately devoted to doing experiments. Carefully designed the methodological sections in his publications are a model of precision and strictness and aimed at answering questions, sometimes of apparent naïve simplicity. By so doing, he has opened the way to several important fields in the biophysics of photosynthesis, in which many of us have had the opportunity to work and contribute. (Lavorel, 1996, p. 31-34)

Barnett's work was on terrestrial magnetism, and his experiments had to be done from 11 p.m. till 6 a.m. to avoid interference from city streetcars. Bill worked all night on them.

Personal History

Bill was born in Douglas, Wyoming, on December 6, 1904, the first of four children of William A. Arnold and Nellie Agnes O'Brien Arnold. The elder Arnold owned a lumber yard and a contracting business. Around 1910 the family moved to Pleasant Hill, Oregon, where Bill started grammar school. His favorite subject was arithmetic, and he later claimed to have read every book in the school library. His interest in physics began when a neighbor gave him a high school physics book when he was in the eighth grade. In 1920, due to his father's ill health, the family moved to the San Fernando Valley in Southern California, where they bought a small ranch and raised chickens. Bill attended the nearest high school, in Van Nuys. There he made friends with some classmates who had built radio receivers, and with their help he, too, soon had a "radio shack."

Bill's high school algebra teacher had a second job at the Mount Wilson Observatory, and she stimulated Bill's interest in astronomy and arranged several trips for him and his classmates to the observatory. His chemistry teacher took them to the California Institute of Technology (Cal Tech) for Friday night lectures, and after attending the lectures, Bill became eager to go to college there. Bill graduated from high school in 1923 and enrolled at Cal Tech. His father helped him financially through the first year, and Bill held several jobs—including working in restaurants and a position

with Edison General Electric. In 1926 he got a job as a research assistant under Dr. S. J. Barnett, head of the Physics Department at UCLA, who was doing research at Cal Tech. Barnett's work was on terrestrial magnetism, and his experiments had to be done from 11 p.m. till 6 a.m. to avoid interference from city streetcars. Bill worked all night on them. Despite the demands of work and study, he managed to woo and win the hand of Jean Irving Tompkins, whom he married on September 11, 1929.

The Photosynthetic Unit

In 1930, while still an undergraduate, he started to work with Robert Emerson in a plant physiology laboratory. The work involved novel experiments on the effects of flashing light, obtained from neon lamps, on photosynthesis in algae, which Bill found very exciting. He and Emerson used cell suspensions of *Chlorella*—a green alga, a favorite of Nobel Laureate Otto Warburg, under whom Emerson had done his doctoral thesis. They exposed these cells to brief flashes of light and found that under the most optimal conditions, only one molecule of oxygen was produced for every 2,400 molecules of chlorophyll (the green pigment that carries out photosynthesis) present. This was the beginning of a series of experiments that led to the concept of what we know today as the "photosynthetic unit," a cluster of



Arnold as a young man. Photo courtesy of the family of William Arnold.

chlorophyll molecules that act as what we call “antenna” serving a “reaction center.” After Bill graduated with a B.S. degree, Emerson procured an appointment for him in the Biology Division at Cal Tech as a research assistant, hired to continue the photosynthesis experiments. At this time the two men collaborated on two classic papers published in the *Journal of General Physiology*. They wrote: “We need only suppose that for every 2,480 molecules of chlorophyll there is present in the cell one unit capable of reducing one molecule of carbon dioxide each time it is suitably activated by light.” They must have really meant “for the oxidation of water molecules to give one oxygen molecule” since they had measured oxygen, not carbon dioxide (Emerson and Arnold, 1932a and 1932b).

Kinetics and the Efficiency of Photosynthesis

Emerson was instrumental in helping Bill get admitted to Harvard to work for his Ph.D. with William J. Crozier. In 1932 Bill and Jean moved to Massachusetts. Bill completed his doctorate in general physiology in 1935. His thesis work involved the first study on the kinetics of photosynthesis (Arnold, 1933a, 1935) and the effect of ultraviolet light on the process (Arnold, 1933b); on the efficiency of photosynthesis, which he found to be 35 percent (a finding that he did not publish until 1949); and on the photosynthesis unit, which was then called the chlorophyll unit (Arnold and Kohn, 1934). The 35

percent efficiency of photosynthesis translates into a minimum number of 8-10 photons to release one oxygen molecule. This was almost twice the number that had been published by Otto Warburg, who believed that the evolution of one oxygen molecule (requiring extraction of 4 electrons from 2 molecules of water) must require only 4 photons, in agreement with Einstein’s law of photochemical efficiency. Obviously, Warburg did not know that there are two light reactions and two photosystems in photosynthesis (see below). It was much later that Warburg was proven wrong and Bill and, later still, Emerson proven right (see Nickelsen and Govindjee, 2011; Govindjee, 1999; R. Govindjee et al., 1968). In his Ph.D. research Bill was able to test the assumptions in his and Emerson’s original work at Cal Tech and showed the generality of the photosynthetic unit in various phyla of plants. Jack Myers (1994) wrote a beautiful description of this experiment (also see Govindjee and Björn, 2012):

The 1932 papers of Emerson and Arnold were great ones, both conceptually and experimentally. The results were so far out of synch with the thinking of the times that it took many years for them to become a cozy part of the dogma of photosynthesis.

Emerson and Bill were also far ahead of their time in using repetitive light flashes, with appropriate dark times, to allow for the recovery of photosynthetic intermediates, and in their ability to use the technique



Giants of Photosynthesis: Left to Right: William Arnold, C. Stacy French, Hans Gaffron, Eugene Rabinowitch, and Robin Hill. Photo courtesy of the family of William Arnold.

of manometry to average data over hundreds of light flashes to accurately obtain the small number of oxygen molecules evolved per thousands of chlorophyll molecules present.

After receiving his doctorate, Bill worked as a Sheldon Fellow in 1935-1936 at UC Berkeley, where he studied quantum mechanics under Oppenheimer (see Knox, 1996); here, he also carefully investigated the maximum quantum yield (or its inverse, the minimum quantum requirement) of oxygenic photosynthesis. As part of his thesis Bill had perfected the technique of calorimetry to measure the efficiency of photosynthesis. His findings, of 8 - 10 photons per oxygen, were later

placed on a firm basis by the extensive work of Emerson (see Emerson and Lewis, 1943; Emerson and Chalmers, 1955; Emerson, 1958) using manometry, as was used by Warburg himself. It was Bill who had later produced the first recording Warburg manometry system to get out of the drudgery of measuring pressure changes manually (see Arnold et al., 1951). Emerson, however, did not adopt the system, as he felt he could make more precise measurements using his cathetometers, which were read manually.

In 1936 Bill and Jean moved to Pacific Grove, California, to work with Cornelis Van Niel on a General Education Board Fellowship. He also attended the world-famous microbiology course given by Van Niel, where it is said that the professor would lecture for hours without break. Here Bill worked with Van Niel for the first time on purple photosynthetic bacteria. The two scientists established a quantitative method for measuring bacteriochlorophyll from photosynthetic bacteria (Van Niel and Arnold, 1938). In the meantime, Bill and Jean's first child, Elizabeth Irving, was born on May 16, 1937.

Wartime Research

In 1938 Bill was awarded a Rockefeller Fellowship and went to Copenhagen, Denmark, to work at Neils Bohr's Institute for Theoretical Physics. There he studied the use of radioactive tracers in biology under Georg

Hevesy and Hilde Levi. It is a little-known fact that Bill was the one who suggested using the term “fission” to describe what happened in the experiment by Otto Frisch showing that uranium atoms will split into two parts and release a large amount of energy when hit by neutrons. (The idea for the word may have come from Bill’s knowledge of bacteria dividing in two by a different kind of fission.)

The Arnold family returned to Pacific Grove in September 1939, only days after the outbreak of World War II. On July 25, 1940, their second daughter, Helen, was born. Bill later wrote, “...1941 proved to be the high point of my university career.” He was made assistant professor of biophysics in June 1941 at the Stanford University branch in Pacific Grove. With the American entry into the war, however, his biophysics course was interrupted. The National Defense Research Committee ordered him, in 1942, to help do research on anti-aircraft fire. Reluctantly, the family left Pacific Grove for Fort Monroe, Virginia. Bill was later transferred to the Eastman Kodak Company in Rochester, New York, where he worked on rangefinders and stayed until 1944. That September he was “loaned” to Eastman Kodak’s operation in Oak Ridge, Tennessee, to work on the electromagnetic separation of uranium 235.

Discovery of Light Emission by Plants

Around 1947 Bill became a member of the biology division of the newly formed Oak Ridge National Laboratory (ORNL) and returned to his research on photosynthesis. The division included 70 scientists and technicians, and Bill was among the most highly respected of them. He was hired to staff the initial research units in biochemistry, cytogenetics, physiology, and radiology, and was considered a pioneer in the division. (Eventually he became one of the few Oak Ridge scientists to join the National Academy of Sciences, when he was elected in 1962.)

Not long after Bill joined ORNL, a symposium on photosynthesis was organized in Chicago as part of the meeting of the American Society of Plant Physiology. This meeting was in response to the argument between Warburg and Emerson over the number of quanta required per oxygen molecule during photosynthesis. Almost 60 years later Malkin and Fork (1996, p. 43-44) recalled the dispute, mentioning Bill and the methods he had followed for the calorimetric measurements of the quantum requirement of photosynthesis:

As with so many of the measurements done by Arnold, his early use of the calorimetric method in 1936-37 to determine the quantum yield of photosynthesis was ahead of his times. Herman Spoehr, who headed Carnegie Institution’s Department of Plant Biology predicted in 1926...that small heat differences

between photosynthetically active and inactive leaves could be used to quantify photosynthetic efficiency. Arnold adapted for biological use [1911] Callendar's "radio balance" that was developed to measure heat emission from radioactive materials. This apparatus was based on the measurement of temperature change of a small amount of irradiated sample resting in a silver cup, by the thermoelectric effect, through use of a network of thermocouple junctions, communicating to the main body of the apparatus. It essentially acted as a null instrument, opposing the temperature changes by passing an electric current through one of the thermocouples and cooling the sample by the resulting Peltier effect. Arnold was able to measure the small heat difference between a photosynthetically active and an inactive sample, with a measurement time of about a minute. *Chlorella pyrenoidosa*, *Chlorella vulgaris*, *Scenedesmus* sp., and an avocado leaf were used as samples. To inactivate his samples Arnold pre-exposed them to ultra-violet light. While the results varied quite a bit between the different experiments, Arnold found that the maximum efficiency of light energy storage, using a wavelength [of] about 660 nm, was around 28% in *Chlorella pyrenoidosa*. This number is equivalent to a quantum requirement of 9.2, sufficiently close to the theoretical value of 8 quanta, which is the minimum requirement for two photochemical systems acting in series. Unfortunately, it seems that Arnold was not sufficiently sure that he obtained the right result, since he was himself influenced by the vigor by which Warburg insisted upon quantum requirements of 4 and even less. Therefore, the publication of

his article was deferred for twelve (!) years, when finally Hans Gaffron convinced Arnold to publish the results. (Arnold, 1949)

During an attempt to show that illuminated chloroplasts produce adenine triphosphate (ATP)—the carrier for energy transfer within cells—Bill and ORNL colleague Bernard Strehler discovered delayed light emission in 1951. Much later Bill described in a revealing manner what had preceded the discovery:

Strehler came to the Lab; he had a brand new PhD, a tremendous amount of energy, and lots of ideas about everything. One day he appeared at the lab door and said "Arnold, how would you like to make one of the fundamental discoveries in plant physiology?" My answer was "OK. If it won't take too long." (Arnold, 1986)

Strehler (1996, p. 17), in a dedication to Bill, wrote:

It is evident that my scientific career would have been almost barren were it not for the gifts that fate gave me in the form of fellow scientists, Arnold, in particular. I am grateful to him for showing me improved methods of thinking and for testing ideas. I have my own hypothesis regarding his vigor at his longevity. I noticed in 1951 or so that he kept relighting his pipe very frequently and that he tamped tobacco into that pipe at odd intervals. I suspect that his pipe was usually devoid of tobacco

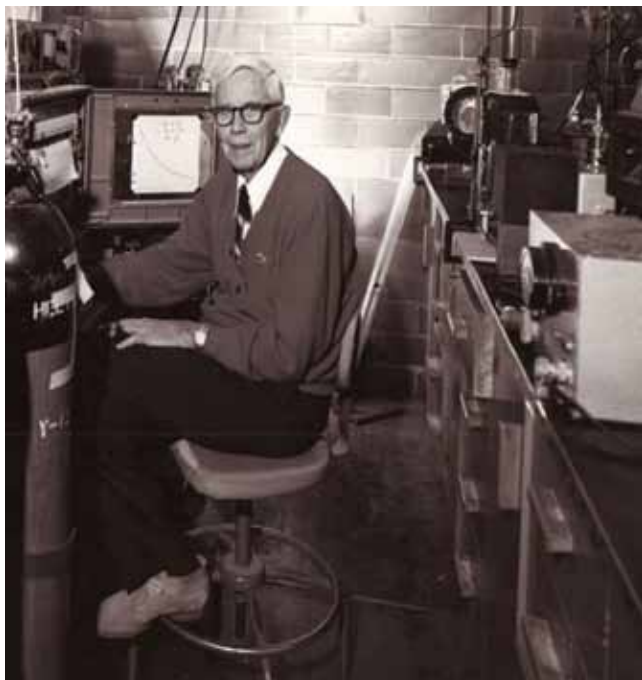
and that the lighting and tamping were social formalities without harmful physiological consequences.

As was determined in the late 1950s and early '60s, photosynthesis requires two photosystems (I and II). Photosystem II oxidizes water to oxygen and reduces plastoquinone (a molecule involved in plant photosynthesis) to plastoquinol. Photosystem I, on the other hand, oxidizes plastoquinol and reduces the pyridine nucleotide NADP (nicotinamide adenine dinucleotide phosphate) (see the evolution of this concept in Govindjee and Björn, 2012). Bill and Strehler made a series of findings concerning Photosystem II and delayed light (see Arnold, 1991). Arnold and his collaborators learned that a) the action spectrum for the production of delayed light is the same as that for Photosystem II; b) the emission spectrum of delayed light is the same as that of the fluorescence (Arnold and Davidson, 1954); c) there are two kinds of delayed light—recombination light has a lifetime of 2-3 microseconds (ms) and does not depend on temperature, while the main fraction of the delayed light from almost 10 ms to a few hours seems to be due to the formation of excited chlorophyll by the reversal of early steps in photosynthesis; and d) a plot of the logarithm of the delayed light intensity versus the logarithm of the time in the dark shows a number of different components. DLE has been used at length to probe quite effectively the action of Photosystem II in plants and

algae. The extensive use of DLE has been reviewed by Lavorel (1975), Jursinic (1986), and many others. Jursinic et al. (1978) showed that all DLE, which reflects a reversal of charges in Photosystem II, is not the same; it is insensitive to membrane potential a few microseconds after the exciting light is turned off, but after milliseconds it is sensitive to membrane potential in the presence a proton gradient.

Bill and Sherwood (1957) discovered another phenomenon of light emission: the afterglow in photosynthetic samples. Here, a sample is illuminated either by continuous light or by flashes of light, then immediately cooled to the temperature of liquid nitrogen, then slowly heated in darkness. During this process an afterglow called thermoluminescence (TL) is emitted. This phenomenon is one of Bill's fundamental discoveries; it is the thermally stimulated light emission from pre-illuminated photosynthetic material. TL is characteristic of a wide range of materials—for example, semiconductors, minerals, inorganic and organic crystals, and complex biological systems such as the photosynthetic apparatus—that share the common ability of storing radiant energy in thermally stabilized trap states.

TL later proved to be a phenomenon common to all photosynthetic organisms: photosynthetic bacteria, cyanobacteria, algae, and higher plants. With the basic idea of delayed DLE in mind, Bill tried to make glow



Arnold in his lab at Oak Ridge. Photo courtesy Oak Ridge National Laboratories

curves from chloroplasts. He performed experiments using various combinations of filters and photomultipliers with different spectral sensitivity. This led to his discovery that TL originated from the “light energy converting photosynthetic apparatus” and that chlorophyll was involved in the absorption and emission of light in the glow curves.

In 1965 Bill proposed a picture of the light reaction in photosynthesis in which free electrons and holes

play an essential part, but no evidence of this was found. By postulating temperature-dependent equilibria between two or more electron carriers in Photosystem II, acting as traps for electrons or holes, Govindjee, with Arnold and DeVault, provided the current theory for TL (see DeVault et al., 1983, and DeVault and Govindjee, 1990; also Rutherford et al, 1984, and Rose et al, 2008). The phenomenon of TL for the understanding of photosynthesis, particularly of Photosystem II and the Oxygen Evolving Clock of Bessel Kok and Pierre Joliot, has now been exploited in many laboratories (see reviews by Sane and Rutherford, 1986; Vass and Inoue, 1992; Vass and Govindjee, 1996; Ducruet, 2003; and Vass, 2005).

Finally, by chance Bill discovered the existence of electroluminescence in photosynthetic samples, this time working with Jim Azzi, when they attempted to modify or displace some putative precursor of luminescence through electrolysis by applying voltage to a chloroplast suspension using electrodes. The most remarkable aspect of this work was the frequency doubling of the luminescence stimulation signal with respect to an alternating applied voltage (Arnold and Azzi, 1971).

Eli Greenbaum, an ORNL corporate fellow who has conducted research on photosynthesis for many years, said, “Bill discovered the electronic nature of energy transfer in photosynthesis.” For his work, Bill received the Charles F. Kettering Award, in 1963, from

the American Society of Plant Physiologists, which cited him for “his application of rigorous principles of physics to a biological phenomenon.” Bill held the position of Assistant Director at ORNL, during 1950, but he didn’t like the administrative details, and, thus, he resigned from the position and devoted full time to experiments. Jack Myers remembers:

I stopped in whenever I could. Just talking to Bill always recharged me. I admired the physicist approach in him. His habit was to think long and deeply before doing an experiment. In contrast, living with the greater complexity and lower predictability of biology, I was more likely to dash off and do an experiment just to see what could happen and then polish it off after seeing the first results. We touched briefly on a minor matter, the effect of UV on chloroplasts, but I cannot now remember what the point of disagreement was. The early days of Oak Ridge were not Bill’s best days.

Robert Pearlstein, who had joined William Arnold’s laboratory as a post-doc fellow, and considered Arnold to be a very generous and kind person, mentioned his sense of humor (Pearlstein, 1996, p. 9):

Bill Arnold’s distinguished contributions to science were already familiar to me when we first met in 1963 in Albert Szent-Györgyi’s lab at the Marine Biological Laboratory in Woods Hole.

Bill introduced me to his special brand of humor shortly before welcoming me to the Oak Ridge National Laboratory three years later.

Bill retired in 1970, at age 66. But retirement did not slow down his scientific work at all—his lifelong passion for science remained undiminished, and he became a consultant. In testimony of his value in that role, the authors would like to cite a letter that the 1961 Nobel Chemistry Laureate Melvin Calvin wrote on July 28, 1977, to Dr. S.F. Carson, deputy director of the Biology Division of Oak Ridge National Laboratory:

As you must know, we here in the Biodynamics photosynthesis laboratory have been following Bill Arnold’s work on the biophysics of photosynthesis since the early days but even more so in the last few years as he has, with his characteristic originality, discovered two entirely new effects of electric fields on the behavior of the quantum conversion apparatus in green plants. The observation of these effects is bound to have a substantial impact on our understanding of the basic mechanisms of the quantum conversion of light into chemical energy in green plants. Obviously, such understanding will lead more quickly to the construction of useful devices for solar energy capture than any we have today. It would be a sad action and wasteful of our limited resources if Bill Arnold were not retained, at the very least as a working consultant at Oak Ridge National Laboratory.



Bill Arnold, handing a flower to his daughter Helen, after delivering a lecture on photosynthesis at Oak Ridge High School. Others in the photo are students and a teacher. Photo courtesy of the family of William Arnold.

On a personal note: When Don DeVault and one of us (Govindjee) sent Bill the second draft of a paper explaining the mechanism of thermoluminescence in plants and inviting him to collaborate and co-author it, Bill wrote only three lines: “I think the latest draft of the paper is fine. I will be delighted to be a co-author; you must be sure that [it] is not too long.” This was the greatest honor Govindjee felt he had ever received, as

he had been unable to publish his work (Govindjee and Rabinowitch, 1960) on the Emerson Enhancement Effect with Robert Emerson due to Emerson’s untimely death in 1959.

Bill’s granddaughter Lucinda (Cindy) Choules vividly remembers him:

My grandfather Dr. William A. Arnold was a brilliant mathematician; to him math was just a fun game to play. It is this amazing math aptitude and love for math, which, I believe, first got him interested in the sciences. He had a highly inventive mind full of scientific questions. Grandpa Bill was a quiet, but very funny man; when you got to know him, it wasn’t so much what he said but how he said it. He treated everyone as an equal, and even at a time when female scientists were scarce. He chose to mentor, encourage, and treat as colleagues a number of very talented female scientists. He saw the world a little bit differently than other people; I believe that it was because of this that he made many discoveries in science, during his career.

He was always kind, and in good health even in his 90s. He drove his car until he was about 93. He also climbed the stairs down to his lab, at home every day until he was about 95 years old. He was an active person with an active mind who never stopped learning. I loved him very much and miss him terribly still today.

Bill's wife, Jean, died November 17, 1997. They had been married 68 years. Bill died on October 26, 2001, at the age of 96. In keeping with his wishes, his body was cremated and the ashes were buried next to Jean's at Oak Ridge Memorial Park.

Bill is survived by two daughters, Helen Holbrook Arnold Herron and her husband, David K. Herron, of Indianapolis, and Elizabeth Irving Arnold of Seguin, Texas; a sister, Dorothy Habib of Seagrove Beach, Florida; as well as five grandchildren and three great-grandchildren. In addition to his wife and his parents, Arnold was preceded in death by two brothers, James M. and Joseph H. Arnold.

Bill's daughter Helen recollected of her father's life:

Maybe claiming everything interested Bill is an overstatement. Spelling did not, but his lapses in that area were covered up by his handwriting, which was so bad that no one could make out all the letters anyway. (And yet he could always make a neat, accurate drawing of an instrument he wanted built in the shop, with all the measurements legible.) Foreign language requirements were a trial, perhaps because all those words needed to be spelled. Music eluded him, although he enjoyed the lyrics. Jean was of great help to him because she could spell, write, punctuate and type. She was a language major and tutored him to pass the German and French exams, plus helping with translations in later years. Cornelis (Kees) Van Niel was a friend



Arnold (right) with James Franck, 1926 Nobel laureate in physics. Photo courtesy of the family of William Arnold.

and teacher. A few other close friends and co-workers were Stan Carson, Edward (Andy) Anderson, and Betty Blagg (who became Mrs. Anderson). No one had any money, but they all liked to talk science and tell stories. Bill was lucky to be one of those people who find the natural world wonderful and the exploration of it the most exciting thing they can do. As young scientists they gathered to talk about experiments, spin theories, and throw out ideas. They were interested in so many things and had so many ideas that they did not hoard them or feel threatened by criticism. They collaborated on projects and encouraged others to do experiments they did not have time for. Bill continued to love his research but did not allow lab work to crowd out time with the family. He was a comfortable companion because of his good-natured tolerance for people

and his enthusiasm for understanding things. He welcomed and answered simply any questions Elizabeth or I might ask, especially concerning science or math. Bill's sense of humor and easy way with people reflected his self-confidence and his enjoyment of life, friends and science. (Herron, 1996)

To one of us (Govindjee), Bill was a fabulous person for whom he had the highest respect and esteem. He is remembered as a peaceful and thoughtful scholar, unhurried and unaffected by the competitiveness of society. His avocation was reading. He was interested in mathematics, astronomy, physics, chemistry, biology, and geology. He liked watching television, particularly news programs, science-related programs, and science fiction. For a great many years he was concerned with the problems of population and food production. Jim Azzi, co-discoverer of electroluminescence, gave Govindjee some quotations from Bill to cite: "He wished he understood everything that he knew," and "Science is basically mathematics (he meant thermodynamics) on one side and experimentation on the other."

Acknowledgements

We are indebted to many whose cooperation made this tribute to Bill Arnold a reality. In alphabetical order, they include: Elizabeth Irving Arnold; James "Jim" R. Azzi; Walter Betsch; Lucinda "Cindy" Choules; Maarten Chrispeels; Mary Anne Davidson; Elias "Eli" Greenbaum; Dorothy A. Habib; Helen Arnold Herron; Jean Lavorel; Jack Lewis, of Oak Ridge National Laboratory (ORNL); David Mauzerall; Jack Myers; Robert and Linda Pearlstein; Amy L. Rothrock, of ORNL; Lianne and William Russel; Bernard Strehler; Imre Vass; and Tony Ziselberger, of NAS. In addition, we thank the Freedom of Information Act Office of the U.S. Department of Energy, Oak Ridge Operations Office, for providing one of us (Govindjee) with the entire file on William Arnold. In addition we thank Helen Arnold Herron for many photographs, Bill's death certificate, and his passport, and we thank Cindy Choules for additional photographs.

AWARDS AND HONORS

-
- 1935 Sheldon Fellow
- 1936 General Education Board Fellow
- 1938 Rockefeller Fellow
- 1962 Member, U.S. National Academy of Sciences
- 1963 Charles F. Kettering Award
- 1975 American Society of Plant Physiologists—Charles Reid Barnes Life Membership Award
- Member, American Physical Society
- Member, American Society of Plant Physiologists
- Member, Sigma Xi
- Member, American Association for the Advancement of Science
- Member, American Institute of Biological Sciences

REFERENCES

-
- Arnold, W. A. 1933a. The effect of ultraviolet on photosynthesis. *J. Gen. Physiol.* 17:135-143
- Arnold, W. A. 1933b. The order of the Blackman reaction in photosynthesis. *J. Gen. Physiol.* 17:145-149.
- Arnold, W. A. 1935. Kinetics of photosynthesis in *Chlorella*. *Cold Spring Harb. Symp. Quant. Biol.* 3:124-127.
- Arnold, W. A. 1949. A calorimetric determination of the quantum yield in photosynthesis. In *Photosynthesis in Plants*. Eds. J. Frank and W. E. Loomis. pp. 273-276. Ames, IA: Iowa State Press.
- Arnold, W. A. 1986. Delayed light, glow curves and the effects of electric fields. In *Light Emission by Plants and Bacteria*. Eds. Govindjee, J. Amesz, and D. C. Fork. pp. 29-34. Orlando: Academic Press.
- Arnold, W. A. 1991. Experiments. *Photosynth. Res.* 27:73-82.
- Arnold, W. A., and J. Azzi. 1971. The mechanism of delayed light production by photosynthetic organism and new effect of electric fields on chloroplasts. *Photochem. Photobiol.* 14:233-240.
- Arnold, W. A., and H. I. Kohn. 1934. The chlorophyll unit in photosynthesis. *J. Gen. Physiol.* 18:109-112.
- Arnold, W. A., and H. K. Sherwood. 1957. Are chloroplast semiconductors? *Proc. Nat. Acad. Sci. U.S.A.* 43:1105-1114.
- Arnold, W. A., E. W. Burdette, and J. B. Davidson. 1951. A recording Warburg apparatus. *Science* 114: 364-367.
- DeVault, D., and Govindjee. 1990. Photosynthetic glow peaks and their relationship with the free energy changes. *Photosynth. Res.* 24:175-181
- DeVault, D., Govindjee, and W. A. Arnold. 1983. Energetics of photosynthetic glow peaks. *Proc. Nat. Acad. Sci. U.S.A.* 80:983-987.

REFERENCES

- Ducruet, J.-M. 2003. Chlorophyll thermoluminescence of leaf discs: simple instruments and progress in signal interpretation open the way to new ecophysiological indicators. *J. Exptl. Bot.* 54: 2419-2430
- Emerson, R. 1958. The quantum yield of photosynthesis. *Ann. Rev. Plant Physiol.* 9:1-24
- Emerson, R., and W. A. Arnold. 1932a. A separation of the reactions of photosynthesis by means of intermittent light. *J. Gen. Physiol.* 15:391-420.
- Emerson, R., and W. A. Arnold. 1932b. The photochemical reactions in photosynthesis. *J. Gen. Physiol.* 16:191-205.
- Emerson, R., and R. Chalmers. 1955. Transient changes in cellular gas exchange and the problem of maximum efficiency of photosynthesis. *Plant Physiol.* 30:504-529.
- Emerson, R., and C. M. Lewis. 1943. The dependence of quantum yield of *Chlorella* photosynthesis on wavelength of light. *Am. J. Bot.* 30:165-178.
- Govindjee. 1999. On the requirement of minimum number of four versus eight quanta of light for the evolution of one molecule of oxygen in photosynthesis: A historical note. *Photosynth. Res.* 59:249-254.
- Govindjee, and L. O. Björn. 2012. Dissecting oxygenic photosynthesis: The evolution of the "Z"-scheme for thylakoid reactions. In: *Photosynthesis: Overviews on Recent Progress and Future Perspective*. Eds. S. Itoh, P. Mohanty, and K. N. Guruprasad. pp. 1-27. New Delhi, India: I.K. Publishers.
- Govindjee, and E. Rabinowitch. 1960. Action spectrum of the second Emerson effect. *Biophysic. J.* 1:73-89.
- Govindjee, R., E. Rabinowitch, and Govindjee. 1968. Maximum quantum yield and action spectra of photosynthesis and fluorescence in *Chlorella*. *Biochim. Biophys. Acta* 162:530-544.
- Herron, H. A. 1996. About Bill Arnold, my father. *Photosynth. Res.* 48:3-7.

REFERENCES

- Jursinic, P. A. 1986. Delayed fluorescence: current concepts and status. In *Light emission by plant and bacteria*. Eds. Govindjee, J. Amez, and D. C. Fork. pp. 291-328. New York: Academic Press.
- Jursinic, P. A., Govindjee, and C. A. Wraight. 1978. Membrane potential and microsecond to millisecond delayed light emission after a single excitation flash in isolated chloroplasts. *Photochem Photobiol* 27:61-71.
- Knox, R. S. 1996. Electronic excitation transfer in the photosynthetic unit: Reflections on the work of William Arnold. *Photosynth. Res.* 48:35-39.
- Lavorel, J. 1975. Luminescence. In *Bioenergetics of Photosynthesis*. Ed. Govindjee. pp. 223-317. New York: Academic Press.
- Lavorel, J. 1996. The importance of being lucky: A tribute to William Arnold. *Photosynth. Res.* 48:31-34.
- Malkin, S., and D. C. Fork. 1996. Bill Arnold and calorimetric measurements of the quantum requirement of photosynthesis—once again ahead of his time. *Photosynth. Res.* 48:41-46.
- Myers, J. 1994. The 1932 experiments. *Photosynth. Res.* 40:303-310
- Nickelsen, K., and Govindjee. 2011. *The Maximum Quantum Yield Controversy: Otto Warburg and the Midwest Gang*. Bern Studies in the History and Philosophy of Science, Bern: University of Bern, Switzerland; Institute für Philosophie.
- Pearlstein, R. M. 1996. Bill Arnold: scientist, philosopher, friend. *Photosynth. Res.* 48:9-10.
- Rose, S., Minagawa, J., Seufferheld, M., Padden, S., Svensson, B., Kolling, D. R. J., Crofts, A. R., Govindjee. 2008. D1-arginine257 mutants (R257E, K, and Q) of *Chlamydomonas reinhardtii* have a lowered Q_b redox potential: analysis of thermoluminescence and fluorescence measurements. *Photosynth. Res.* 98:449-468.

REFERENCES

- Rutherford, A. W., Govindjee, and Y. Inoue. 1984. Charge accumulation and photochemistry in leaves studied by thermoluminescence and delayed light emission. *Proc. Natl. Acad. Sci. U.S.A.* 81:1107-1111.
- Sane, P. V., and A. W. Rutherford. 1986. Thermoluminescence from photosynthetic membranes. In *Light Emission by Plants and Bacteria*. Eds. Govindjee, J. Ames, and D. C. Fork. pp. 291-329. Orlando: Academic Press.
- Strehler, B. L. 1996. Halcyon days with Bill Arnold. *Photosynth. Res.* 48:11-18.
- Van Niel, C. B., and W. A. Arnold. 1938. The quantitative estimation of bacteriochlorophyll. *Enzymol.* 5:244-50.
- Vass, I. 2005. The history of photosynthetic thermoluminescence. In *Discoveries in photosynthesis. Advances in Photosynthesis and Respiration, vol. 20*. Eds. Govindjee, J. T. Beatty, H. Gest, J. F. Allen. pp. 665-680. Dordrecht: Springer.
- Vass, I., and Govindjee. 1996. Thermoluminescence from the photosynthetic apparatus. *Photosynth. Res.* 48:117-126.
- Vass I., and Y. Inoue 1992. Thermoluminescence in the study of Photosystem II. In *The photosystems: structure, function and molecular biology*. Ed. J. Barber. pp. 259-294. Amsterdam: Elsevier.

SELECTED BIBLIOGRAPHY

- 1932
- With R. Emerson. A separation of the reactions of photosynthesis by means of intermittent light. *J. Gen. Physiol.* 15:391-420.
- With R. Emerson. The photochemical reaction in photosynthesis. *J. Gen. Physiol.* 16:191-205.
- 1933
- The effect of ultraviolet light on photosynthesis. *J. Gen. Physiol.* 17:135-143.
- 1934
- The chlorophyll unit in photosynthesis. *J. Gen. Physiol.* 18:109-112.
- With C. P. Winsor. On the theoretical significance of Talbot's law. *J. Gen. Physiol.* 18:97-101.
- 1938
- With C. B. Van Niel. The quantitative estimation of bacteriochlorophyll. *Enzymol.* 5:244-250.
- 1939
- With O. R. Frisch and H. Levi. Thin mica windows. *Rev. Sci. Instr.* 10:197.
- 1949
- A calorimetric determination of the quantum yield in photosynthesis. In *Photosynthesis in Plants*. Eds. J. Frank and W. E. Loomis. pp. 273-276. Ames, IA: Iowa State Press.
- 1950
- With J. R. Oppenheimer. Internal conversion in the photosynthetic mechanism of blue-green algae. *J. Gen. Physiol.* 34:627-645.
- 1951
- With B. L. Strehler. Light production by green plants. *J. Gen. Physiol.* 34:809-820.

SELECTED BIBLIOGRAPHY

- 1954
With J. B. Davidson. The identity of the fluorescent and delayed light emission spectra in *Chlorella*. *J. Gen. Physiol.* 37:677-684.
- 1956
With E. S. Meek. The polarization of fluorescence and energy transfer in grana. *Arch. Biochem. Biophys.* 60:82-90.
- 1957
With H. K. Sherwood. Are chloroplast semiconductors? *Proc. Nat. Acad. Sci. U.S.A.* 44:1-4.
- 1960
With R. Clayton. The first step in photosynthesis: evidence for its electronic nature. *Proc. Nat. Acad. Sci. U.S.A.* 46:769-774.
- 1965
An electron-hole picture of photosynthesis. *J. Phys. Chem.* 69:788-791.
- 1966
Light reaction in green plant photosynthesis: A method of study. *Science* 154:1046-1049.
- 1971
With J. Azzi. The mechanism of delayed light production by photosynthetic organism and new effect of electric fields on chloroplasts. *Photochem. Photobiol.* 14:233-240.
- 1974
With S. Perdue and J. Azzi. Photochemical activity of single chloroplast recorded by the use of nuclear track emulsion. *Science* 185:59-61.
- 1976
Path of electrons in photosynthesis. *Proc. Nat. Acad. Sci. U.S.A.* 73:4502-4505.

SELECTED BIBLIOGRAPHY

- 1977
Delayed light in photosynthesis. *Ann. Rev. Biophys. Bioeng.* 6:1-6.
With J. Azzi. Two effects of electrical fields on chloroplasts. *Plant Physiol.* 60:449-451.
- 1983
With D. Devault and Govindjee. Energetics of photosynthetic glow peaks. *Proc. Nat. Acad. Sci. U.S.A.* 80:983-987.
- 1985
Delayed light, glow curves, and the effects of electric fields. In: *Light Emission by Plants and Bacteria*. Eds. Govindjee, J. Amesz, and D. Fork. pp. 29-34. New York: Academic Press.
- 1991
Experiments. *Photosynth. Res.* 27:73-82.

Published since 1877, *Biographical Memoirs* are brief biographies of deceased National Academy of Sciences members, written by those who knew them or their work. These biographies provide personal and scholarly views of America's most distinguished researchers and a biographical history of U.S. science. *Biographical Memoirs* are freely available online at www.nasonline.org/memoirs.