NATIONAL ACADEMY OF SCIENCES

DANIEL I. ARNON
1910–1994

A Biographical Memoir by

BOB B. BUCHANAN

Biographical Memoirs, VOLUME 80

PUBLISHED 2001 BY
THE NATIONAL ACADEMY PRESS
WASHINGTON, D.C.

Photograph by Reinhard Bachofen, University of California at Berkeley, Summer 1988

Dan Arnon

DANIEL I. ARNON

November 14, 1910–December 20, 1994

BY BOB B. BUCHANAN

THE ELDEST OF FOUR children, Daniel Arnon was born in Warsaw, Poland, on November 14, 1910. The family lived in Warsaw, but spent summers on a farm where young Daniel first became intrigued by plants and agriculture. He was something of a child prodigy, being by far the youngest in his class. When he joined a private library, the young man amazed the librarian by often devouring four books a day. He also developed a lifelong love of sports and physical fitness. Soccer he especially enjoyed. He learned to swim so as to be able to scull on the Vistula River and tutored classmates in swimming, gymnastics, and mathematics to supplement the family income. His father was a food wholesaler who, in the aftermath of World War I, lost his business and became a purchasing agent.

As a result of witnessing the great famines following World War I, Arnon was attracted to the cause of scientific farming, which he had read about in the California novels of his hero Jack London. Convinced that there was no future for him in Poland, he saved his earnings and by age 18 secured his passage to New York. He worked there for a summer until he had money to buy a Greyhound bus ticket to California. As a student in Poland he had earlier applied by mail and been admitted to the University of California at Berkeley, but owing to a mix-up in the admissions office his matriculation was delayed. He thus attended a local college in Ontario (Chaffey Junior College of Agriculture, now Chaffey College), where he also worked in the orange orchards of southern California. After a year he transferred to Berkeley. Although the Great Depression was at its worst, he supported himself by taking odd jobs like gardening and in the summer by working on farms. At an early age Arnon became accustomed to hard work and maintained demanding work habits throughout his career. When the United States entered World War II, Arnon volunteered for the Army. He became a major in the Army Air Corps, where as we will see later he continued his work on plant nutrient culture. His military service later resulted in many picturesque anecdotes, and he maintained it had reinforced his inherent self-discipline—habits he faithfully maintained.

Except for military service during World War II Arnon spent his entire professional career at the University of California at Berkeley. He earned a bachelor’s degree in 1932 and went on to obtain a Ph.D. in 1936 under Professor Dennis R. Hoagland, a member of the Berkeley faculty who did pioneering work on the mineral nutrition of plants (Hoagland was elected to the National Academy of Sciences in 1934). Their research provided the basic formula for a nutrient solution (known as Hoagland’s solution) that continues to be used worldwide for the cultivation of plants.

ARNON THE PERSON AND THE SCIENTIST

Throughout his long career of groundbreaking research, Arnon held fast to simple principles that guided his research efforts. Repeating experiments was first on his agenda. Repetition is the mother of learning, he would remind those who tended to become weary of duplicating results. Design of simple experiments that yielded important new results was another important goal. New ideas and scientific advances were usually first presented at the weekly group meeting (the "kitchen seminar"), where dishes were prepared and tested before being served to the public. These sessions generated spirited discussions and served as an excellent forum for developing ideas and future experiments. Selected works from the current literature were also addressed. When a scientific paper was presented, the only rule was that the tenor of the discussion had to be on a level appropriate to the author's being present in the room. Otherwise, participants were encouraged to air their views and argue any position.

As in other endeavors, Arnon's energy and patience were boundless throughout these meetings, which often lasted for two hours or more. During this time, laboratory members had an opportunity to observe his dedication to ethics and scholarship in science. One could not leave these meetings without being impressed by the depth of Arnon's knowledge of the photosynthesis field—especially in the history of its development—and his conviction to upholding the highest scientific principles. In these sessions one also learned that Arnon was a debater at heart. He would play the devil's advocate with zest, not only to extend his own knowledge but also to air all possible objections in advance. In this way he was seldom unprepared when later challenges arose. But he never lost sight of the fact that truth was at stake. Once convinced of something he stalwartly defended it, whatever the cost to his reputation. Perhaps as a result of his rhetorical skills Arnon was lucid both as a speaker and a writer. These talents were undoubtedly an asset in enabling him to convey his research findings to the scientific community and the general public. In a little known contribution Arnon at mid-career served on a post-*Sputnik* national committee that developed the “Blue Series” high-school biology textbook for which he wrote four chapters on the evolution of life processes. Widely translated, it enjoyed national acclaim and use.

Arnon was recognized widely for his accomplishments. In addition to the National Academy of Sciences he was a member of the Royal Swedish Academy of Sciences, the Académie d’Agriculture de France, the Deutsche Akademie der Naturforscher Leopoldina, the Scandinavian Society of Plant Physiologists, and an honorary member of the Spanish Biochemical Society. Arnon was a fellow of the American Academy of Arts and Sciences and the American Association for the Advancement of Science. He served his profession as president and vice-president of the American Society of Plant Physiologists and was the leading force in establishing the *Annual Review of Plant Physiology and Plant Molecular Biology*. In the early 1950s he also led successful efforts to broaden the scope of the journal *Plant Physiology* to include emerging topics in plant biochemistry.

Arnon gave extensive service to the university, both as a faculty member and long-term department chair. He received the Berkeley Citation, the highest honor of the campus, “for distinguished achievement and for notable service to the University.” In addition to honorary lectureships his awards included the Newcomb Cleveland Prize (American Association for the Advancement of Science); a Charles F. Kettering research award (Kettering Foundation / National Academy of Sciences); the Finsen Medal (International Association of Photobiology); the Stephen Hales Prize, the Charles Reid Barnes Life Membership Award, and the Kettering Award in Photosynthesis (American Society of Plant Physiologists); Docteur honoris causa (Université de Bordeaux and Universidad de Sevilla); and the U.S. National Medal of Science “for fundamental research into the mechanisms of green plant utilization of light to produce chemical energy and oxygen and for contributions to our understanding of plant nutrition."

Arnon spent sabbatical periods in Europe with legendary figures, first as a Guggenheim fellow (with David Keilin in Cambridge and Hugo Theorell in Stockholm) and then as a Fulbright research scholar (with Otto Warburg in Berlin-Dahlem). These visits provided Arnon an opportunity to establish lifelong friendships with a number of other notable individuals, including Britton Chance, Robin Hill, Helmut Holzer, Henrik Lundegårdh, Roy Markham, and E. C. ("Bill") Slater. Later in his career Arnon spent a third sabbatical year in California with Cornelius B. Van Niel in Pacific Grove.

While his early work was done on limited budgets, much of Arnon's later research was accomplished in the post-*Sputnik* era, when funding was generous. He was particularly grateful for the excellent support he received from the National Institutes of Health (his first extramural grant), the U. S. Navy (funds for large equipment), and the Charles F. Kettering Foundation (post-retirement research support). During his prime Arnon thus had to spend relatively little time in raising support for the laboratory and was able to devote most of his attention to science. Arnon was shrewd when it came to money and without fail used time and circumstances to budgetary advantage. Until his retirement his laboratory was well financed: He took pride in stating that an experiment had never been postponed because of lack of funds.

Following his death Arnon's unspent funds formed the nucleus of an endowment that Berkeley's Department of Plant and Microbial Biology established to support a graduate fellowship and an annual lecture in his memory. As a part of this effort his papers have been placed in a permanent collection at the Bancroft Library on the Berkeley campus. It includes laboratory notebooks, slides, transparencies, and other research materials; manuscripts, preprints and publications; and grant applications and reprints. The archive is rich in resources that tell the story of photosynthesis at Berkeley, including the controversies surrounding Arnon's discoveries. The collection includes letters exchanged with many colleagues, including such well-known members of the Berkeley faculty as Melvin Calvin and Glenn Seaborg. In addition, members of the Arnon family have contributed a wealth of personal photographs, documents and other memorabilia that provide a fuller picture of the life of the man behind the scientist. (The website for the Arnon Papers is being constructed at the time of this writing. The material can be access using the Bancroft Library Finding Aids, http://www.oac.cdlib.org/dynaweb/ead/ead/berkeley.)

It is perhaps not surprising that Arnon's style of laboratory management was European, modeled to some extent after that of Warburg. Arnon believed in maintaining a core staff whose job was not only to carry out their own projects but also to instruct and guide incoming postdoctoral fellows and graduate students. In part because of this style and his high international visibility he tended to attract more postdoctoral scholars from Europe and Japan than from the United States. Another factor that discouraged American postdoctoral biochemists was Arnon's affiliation with the College of Agriculture, which at the time created a relative stigma that persisted until his election to the National Academy of Sciences in 1961.

Arnon had relatively few graduate students. While he encouraged them to join his laboratory, he was not presented with a steady supply of students because of the small size of his department. Arnon thought the ideal mix was one graduate student to perhaps three or four postdoctoral fellows. At its peak his laboratory consisted of no more than 20 members. Numerous students and postdoctoral scholars trained in the laboratory rose to positions of national and international leadership. Most kept in close contact with Arnon, as he remained fully active until his death. Arnon remained particularly close to Joseph-Marie (Jose) Bové (Bordeaux), Manuel Losada (Sevilla), Kunio Tagawa (Osaka), Achim Trebst (Bochum), and Robert Whatley (Oxford). Arnon also remained in contact with his long-time collaborator Harry Tsujimoto, who continued to live in San Francisco following his retirement from the university.

Arnon believed that small was virtuous. In 1961 he established the Department of Cell Physiology, where for many years the focus was restricted to his own interests—photosynthesis and nitrogen fixation—and he was the only Academic Senate faculty member. With time, new principal investigators joined the staff and the program broadened. In 1989 cell physiology became a part of the newly formed Department of Plant and Microbial Biology, which remained Arnon's academic home for the remainder of his life.

Typical of his European contemporaries, Arnon retained a certain formality and encouraged a quiet, professional atmosphere in the laboratory. He took science seriously. Nonetheless, the daily discussions he held with members of the laboratory were made engaging by his sagacious jokes and analogies. As a consequence, the vein was lighter than one would have suspected from Arnon's public demeanor. His attitude toward the laboratory began to change somewhat as his group became smaller and as he passed the official university retirement age of 68 (at which time he became a recalled professor, as he disliked the emeritus title). While his presence on campus did not noticeably change, he became more informal and relaxed in his daily routine and in his last decade he increasingly enjoyed vigorous discussions with colleagues and young academics alike.

His lifelong fondness for classical music also became more evident in later years, and he listened nightly to selected works, often of Beethoven.

Arnon died suddenly on December 20, 1994, at age 84. His five children survive him: Anne Arnon Hodge, Ruth Arnon Hanham, Stephen Arnon, Nancy Arnon Agnew, and Dennis Arnon. His wife, the former Lucile Soulé, preceded him in death by eight years. I was especially pleased that Arnon was able to work closely with fellow faculty member Anastasios Melis and me on a special volume of articles submitted by former students, postdoctoral scholars, and colleagues (*Photosynthesis Research*, November 1995, 46, no. 1-2). The volume was originally planned to commemorate Arnon's eighty-fifth birthday, but turned out to be a memorial as he died while the articles were in press. Much of the information contained in this write-up is taken from the articles published in that volume (see especially B. B. Buchanan, pp. 3-6 and B. B. Buchanan and K. Tagawa, pp. 27-35). The 1995 memorial volume was preceded by a special collection of invited articles published ten years earlier to honor Arnon on the occasion of his seventy-fifth birthday (*Physiologie Végétale* 73:707-875). The collection was presented to him at a gala celebration held on his birthday at the UC Berkeley Faculty Club when he received the Berkeley Citation.

OUR RELATIONSHIP

I first saw Daniel Arnon and learned of his work in two lectures he presented at Duke University in the spring of 1960. The lectures were part of a memorable series, "Recent Advances in Photosynthesis," organized by Aubrey Naylor of the Botany Department. As a second-year microbiology graduate student in the Duke Medical School, I had not known earlier of either Arnon or his research. What I remember is how impressed I was with his knowledge and contributions to photosynthesis. I also recall his effective and witty response to penetrating questions from the audience, including skeptical queries from James Franck, who by then had retired from the University of Chicago and was spending half of his time at Duke, where his wife, Herta Sponer, was a professor of physics. At the time I had no idea that I would meet much less become associated with Arnon, as I had every intention of continuing my microbiology career with heterotrophic bacteria.

The situation was, however, soon to change. After completing my Ph.D. at Duke in early 1962 I went to Berkeley for postdoctoral work on the biochemistry of anaerobic bacteria (clostridia) with Jesse C. Rabinowitz (Rabinowitz was elected to the National Academy of Sciences in 1981). Following the early work on *Clostridium pasteurianium* ferredoxin, Walter Lovenberg (also a new postdoctoral fellow in the laboratory) and I started a project on the chemistry of bacterial ferredoxin. In a relatively short period we obtained sufficient new information to contribute an abstract to the 1963 federation meeting in Atlantic City. Being without a job, I was chosen to make the oral presentation, my first at a national meeting, and was introduced by Robert Burris (Burris was elected to the National Academy of Sciences in 1961). Arnon was present at the same session in connection with Masateru Shin's contribution on the crystallization and characterization of chloroplast ferredoxin-NADP reductase. Arnon heard my presentation and afterward made several unsuccessful attempts to contact me at the meeting.

Back in Berkeley, Arnon tracked me down. We met in his office and, after introductory remarks, he offered me a tenure-track job as an assistant microbiologist in the California Agricultural Experiment Station. Having no plans at that point, I accepted his offer and joined the Department of Cell Physiology in September 1963. While both the name of the department and the title of my position have undergone change, I continue to hold this appointment.

Since our initial meeting in 1963 I remained associated with Arnon and spoke and visited with him almost daily—the last time at a laboratory Christmas party at our Berkeley home three days before his death. Arnon was in extraordinary spirits that evening and, in addition to telling an assortment of entertaining stories in his distinctive style, he participated in lively discussions of contemporary events, including the political changes underway in Washington. After the guests had left and Arnon had driven away, I commented to my wife, Melinda, on his seemingly excellent mental and physical condition and how much he reminded me of the man I had met for the first time more than 30 years earlier. I have since thought how fortunate it was to have arranged that party, as it provides a benchmark, however modest, for culminating our long-term association, in which he was first a mentor and then a colleague and friend.

THE PLANT NUTRITION YEARS (1936-50)

His graduate work with Hoagland brought Arnon international recognition and set the stage for his later becoming a major in the U.S. Army Air Corps in the course of his wartime military service. In that capacity, during 1943-46, he was commanding officer of a project designed to use nutrient culture for the production of food plants on Ascension Island—a 34-square-mile area of volcanic origin that served as a key refueling station in the South Atlantic theater for aircraft transporting war material into North Africa. The techniques developed on Ascension Island later served as a model for the extensive nutrient culture farms used to feed General Douglas MacArthur's occupation forces in Japan.

In the first part of his professional career Arnon (and collaborators) discovered the essentiality of molybdenum for the growth of all plants and of vanadium for the growth of green algae. These findings led to far-reaching developments in the study of nitrogen metabolism, in which both elements were shown to play critical roles. The molybdenum research later found agronomic application: The addition of a small amount of molybdenum to deficient soils restored fertility and dramatically increased crop yields in many regions of the world, especially Australia. In later life, well into his photosynthesis career, he jokingly referred to his nutrition years as “my first incarnation.”

THE PHOTOSYNTHESIS PERIOD (1951-78)

Arnon’s plant micronutrient work led him to photosynthesis, where in 1954 he discovered (and named) photosynthetic phosphorylation (photophosphorylation)—a finding that ranks in importance with the discovery of respiration in animals. He demonstrated that chloroplasts use the energy of sunlight to generate adenosine triphosphate (ATP), the universal energy carrier of living cells. Arnon discovered the cyclic type of photophosphorylation in which ATP is the sole product of energy conversion and the noncyclic type in which the formation of ATP is accompanied by the liberation of oxygen and the generation of reductant (reduced pyridine nucleotide, or NADPH). As a part of this research Arnon was the first to obtain complete photosynthesis outside the living cell—a feat comparable to that of Büchner’s cell-free fermentation. This discovery opened the door to a new epoch in photosynthesis and made possible the elucidation of the systems that regulate the assimilation of carbon dioxide and the paths of biosynthesis of major cellular products. As has occurred with other major advances, Arnon’s discoveries were for years either unaccepted or unappreciated by influential workers in the field.

When it became apparent that neither the photolysis of water nor the reduction of carbon dioxide was involved in cyclic photophosphorylation, Arnon developed the electron flow theory. Here, electrons emitted from photoexcited chlorophyll are transferred via a series of intermediate carriers back to chlorophyll in a stepwise cyclic transport linked to phosphorylation. This concept provided a framework for much of the later work in the field, including studies on nitrogen fixation and hydrogen evolution. Arnon's path-breaking work on photosynthesis was accomplished with chloroplasts isolated from spinach leaves. Following his lead, laboratories around the world adopted spinach as the experimental plant for research on photosynthesis.

A far-reaching discovery came in the year 1962, when Arnon showed that a red iron-sulfur protein, now known as ferredoxin, is a universal part of the photosynthetic apparatus. He found that ferredoxin, reduced by light, provides the electrons for generating the NADPH required for carbon dioxide assimilation. Arnon demonstrated that, in the presence of ferredoxin-NADP reductase, photoreduced ferredoxin provided the electrons for the reduction of NADP—a process itself found to be independent of light. He showed that ferredoxin is linked to the formation of ATP as a catalyst of both cyclic and noncyclic photophosphorylation. Moreover, in the presence of a bacterial hydrogenase (an enzyme missing in higher plants) ferredoxin photoreduced by chloroplasts provided the electrons for the production of hydrogen gas. This work laid the foundation for recently renewed efforts to use hydrogenase-containing green algae for the generation of hydrogen gas as an energy supply.

An extension of the noncyclic photophosphorylation experiments revealed that ferredoxin could also catalyze pseudocyclic photophosphorylation, a light-driven process in which oxygen rather than NADP serves as the acceptor in the transport of electrons from water. The use of monochromatic light to separate the cyclic, noncyclic, and pseudocyclic pathways proved to be a major asset in unraveling these processes. Agents that disrupted photophosphorylation were also useful.

During this period crystallization efforts were successfully extended to ferredoxins from a number of oxygenic and anoxygenic photosynthetic organisms. This research led to the discovery of novel ferredoxins and functionally related proteins from heterotrophic aerobic bacteria. In research stemming from the ferredoxin work Arnon and his colleagues discovered a new path of photosynthetic carbon dioxide assimilation in bacteria, the reductive carboxylic acid cycle (reverse citric acid cycle). This work uncovered the ferredoxin-linked mechanism of carbon dioxide fixation and gave insight into the evolution of photosynthesis. The finding of other novel autotrophic paths of carbon dioxide assimilation of carbon dioxide followed. Ferredoxin thus emerged as a central electron carrier that functioned broadly in plants and bacteria.

During the 1970s Arnon did extensive work with cytochromes of chloroplasts and cyanobacteria. This effort led to the discovery of an absorbance change at 550 nm that was later shown to be due to an acceptor of the oxygen-evolving photosystem (photosystem II). Cytochrome b-559 was examined in considerable detail during the decade. Three redox forms of cytochrome b-559 were identified, first in the chloroplasts and then in cyanobacteria—a system Arnon believed would be easy to dissect biochemically. Work in the laboratory during this period also extended our knowledge of cytochromes in photosynthetic bacteria. There is little doubt that the cytochrome efforts provided the stimulus for others to pursue subsequent work on these components and their role in electron transport.

The 1970s brought forth new evidence for the requirement for cyclic photophosphorylation in carbon dioxide assimilation by chloroplasts and an increase in our understanding of ferredoxin as a catalyst of photophosphorylation—a topic of continuing investigation in a number of laboratories. The identification of chloroplast membrane-bound iron-sulfur proteins at Berkeley and elsewhere soon followed and opened a new field of research that has increased greatly our understanding of electron transport in oxygenic photosynthesis.

SUMMING UP, MOVING FORWARD (1978-94)

Following his retirement in 1978 up to the time of his death Arnon continued to conduct research and write daily. During this time he spent considerable effort refining his unfashionable concept of three light reactions in photosynthesis. Arnon formulated this concept in the late 1960s, when he analyzed the effectiveness of photosystem II in promoting absorption changes in cytochrome b-559 and the C-550 component. The results led Arnon to abandon the Z-scheme, the widely accepted mechanism of photosynthetic electron transport that he himself had originally helped formulate. Arnon then proposed an alternative electron transport mechanism that involved not two but three light reactions. While eliciting spirited debate, his hypothesis still awaits wide acceptance. His last article, written shortly before his death, described these ideas in detail (1995).

In his last decade Arnon wrote four short articles chronicling his major discoveries, in his own words, “to set the historical research record straight for posterity.” The first article traced the history of the discovery of photophosphorylation, the second complete photosynthesis by isolated chloroplasts, and the third chloroplast ferredoxin. The fourth described the beginnings of the reductive carboxylic acid cycle and the long struggle before its acceptance by the scientific community. The popular highlight of the period was, however, Arnon's short 1982 article, reminiscent of his classic 1960 *Scientific American* contribution, in which in his inimitable style he extolled the wonders of photosynthesis (1982).

Arnon mentioned on several occasions that he hoped his program of jogging and swimming, together with a salubrious diet, would enable him to remain active well into his tenth decade. Had that happened he undoubtedly would have continued to add important knowledge to the field of photosynthesis. Nonetheless, his contributions remain monumental, reflecting the fact that he was able to work full-time until his death at 84. He improved the scientific basis of agriculture, and in the long term his work will increasingly find application in the production of food, and thus in the prevention of famine. In short, his boyhood dreams have been fulfilled.

SELECTED BIBLIOGRAPHY

As seen below, Arnon's research was typically accomplished with dedicated collaborators who in most cases spent several years in Berkeley and then moved to permanent positions elsewhere.

1939

With P. R. Stout. Molybdenum as an essential element for higher plants. *Plant Physiol.* 14:599-602.

1943

Mineral nutrition of plants. *Ann. Rev. Biochem.* 12:493-528.

1954

With M. B. Allen and F. R. Whatley. Photosynthetic phosphorylation, the conversion of light into phosphate bond energy by chloroplasts. 8th International Botanical Congress, Paris, Sec. 11, pp. 1-2.

With M. B. Allen and F. R. Whatley. Photosynthesis by isolated chloroplasts. *Nature (Lond.)* 174:394-96.

1955

The chloroplast as a complete photosynthetic unit. *Science* 122:9-16.

With M. B. Allen, J. B. Capindale, F. R. Whatley, and L. J. Durham. Photosynthesis by isolated chloroplasts. III. Evidence for complete photosynthesis. *J. Am. Chem. Soc.* 77:4149-55.

1957

With F. R. Whatley and M. B. Allen. Triphosphopyridine nucleotide as a catalyst of photosynthetic phosphorylation. *Nature (Lond.)* 180:182-85.

1958

With F. R. Whatley and M. B. Allen. Assimilatory power in photosynthesis. Photosynthetic phosphorylation by isolated chloroplasts is coupled to TPN reduction. *Science* 127:1026-34.

1959

Conversion of light into chemical energy in photosynthesis. *Nature* 184:10-21.

1960

The role of light in photosynthesis. *Sci. Am.* 203:105-18.

With M. Losada, A. V. Trebst, and S. Ogata. The equivalence of light and adenosine triphosphate in bacterial photosynthesis. *Nature* 186:753-60.

1961

With M. Losada, F. R. Whatley, H. Y. Tsujimoto, D. O. Hall, and A. A. Horton, Photosynthetic phosphorylation and molecular oxygen. *Proc. Natl. Acad. Sci. U. S. A.* 47:1314-34.

1962

With K. Tagawa. Ferredoxin as electron carriers in photosynthesis and in the biological production and consumption of hydrogen gas. *Nature* 195:537-43.

1963

With M. Shin and K. Tagawa. Crystallization of ferredoxin-TPN reductase and its role in the photosynthetic apparatus of chloroplasts. *Biochem. Z.* 338:84-96.

With K. Tagawa and H. Y. Tsujimoto. Role of chloroplast ferredoxin in the energy conversion process of photosynthesis. *Proc. Natl. Acad. Sci. U. S. A.* 49:567-72.

1964

With R. Bachofen and B. B. Buchanan. Ferredoxin as a reductant in pyruvate synthesis by a bacterial extract. *Proc. Natl. Acad. Sci. U. S. A.* 51:690-94.

1965

Ferredoxin and photosynthesis. *Science* 149:1460-69.

1966

With M. C. W. Evans and B. B. Buchanan. A new ferredoxin-dependent carbon reduction cycle in a photosynthetic bacterium. *Proc. Natl. Acad. Sci. U. S. A.* 55:928-34.

1975

With R. K. Chain. Regulation of ferredoxin-catalyzed photosynthetic phosphorylation. *Proc. Natl. Acad. Sci. U. S. A.* 72:4961-65.

1982

Sunlight, earth life. The grand design of photosynthesis. *Sciences* (October):22-27.

1984

The discovery of photosynthetic phosphorylation. *Trends Biochem. Sci.* 9:258-62.

1987

Photosynthetic CO_2 assimilation by chloroplasts: Assertion, refutation, discovery. *Trends Biochem. Sci.* 12:39-42.

1988

The discovery of ferredoxin: The photosynthetic path. *Trends Biochem. Sci.* 13:30-33.

1990

With B. B. Buchanan. A reverse Krebs cycle in photosynthesis: Consensus at last. *Photosynth. Res.* 24:47-53.

1995

Divergent pathways of photosynthestic electron transfer: The autonomous oxygenic and anoxygenic photosystems. *Photosynth. Res.* 46:47-71.