



Minireview

Photosynthesis and the Charles F. Kettering Research Laboratory

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Abstract

A review of the establishment and subsequent demise of the Charles F. Kettering Research Laboratory (in Yellow Springs, Ohio) is presented here.

Historical summary

The research laboratory was established by the Charles F. Kettering Foundation, which was created in 1927 by Charles F. Kettering, who was a truly amazing man. Born on a farm near Loudonville, Ohio, he was curious about the things he saw, both mechanical and biological. At the age of eight he took his mother's brand new sewing machine apart and put it back together. Once while looking at the corn fields he wondered how one small grain of corn planted in the ground in the spring could grow into a stalk of corn weighing approximately 3000 times what the grain had weighed, and producing over 100 new grains on each ear of corn. His interest in mechanics led to his many achievements in the auto industry while with General Motors, including development of the self starter, storage batteries (Delco batteries) to activate the starter, tetraethyl lead to control gasoline combustion, methods to rapidly paint newly assembled autos and numerous other inventions. A picture of the amazing man is shown in Figure 1.

In addition to his interest in growth of corn, he was amazed that plants could capture the energy from the sun and this energy would be expressed in the gasoline used in autos. One of his goals was to convert the sun's energy into gasoline energy by eliminating plants as the middlemen. In all of his career activities he was never afraid to attack problems head on, and

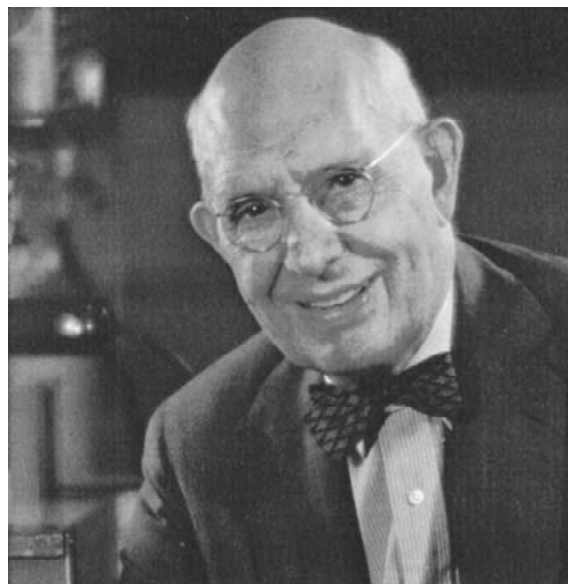


Figure 1. Charles F. Kettering.

in most cases he was successful. He wanted to do the same with the biological phenomena, which led to the creation of various laboratories dedicated to biological research. In 1930, he created a research laboratory dedicated to photosynthesis on the top floor of Antioch College in Yellow Springs, Ohio. The staff included Kettering, known to the group as Boss Kett, two physicists (Harry V. Knoll and V. H. Albers), two plant

physiologists (Odessa Inman and Clyde Eyster) and a chemist (Paul K. Rothemund). Working together, Knoll and Albers developed a method to measure the various forms of chlorophyll in chloroplasts, using a spectroscope and photographic plates as the measuring instruments. These measurements showing the existence of different spectral forms of chlorophyll *in vivo* preceded the outstanding research on this topic by C. Stacy French at the Carnegie Institute of Washington at Stanford. In 1948, Boss Kett established a second laboratory in the basement of his home in Dayton, with a staff of five chemists, three biologists and an instrumentation physicist. The Foundation then started awarding fellowships to several universities in his areas of interest.

Mr. Kettering's research interests and achievements continued to grow, and that led to the establishment of the Charles F. Kettering Research Laboratory adjacent to Antioch College in 1954 (see a photograph of this laboratory in Ke 2002). The initial research focused on photosynthesis and nitrogen fixation, both important biological energy conversion processes. Other research areas included magnetism, energy conversion processes and pulsed radiation. His wife, Olive, died of cancer, and knowing that cancer cells are sensitive to radiation, he developed equipment to produce pulsed X-rays, and tested it on various mammalian cell types to see if it could kill cancer cells preferentially. This interest in fighting cancer led to the formation of the Memorial Sloan-Kettering Hospital and Cancer Research Institute in New York.

My professional trail led to Yellow Springs in 1961, when I became director of the Kettering Research Lab. It is my understanding that I was nominated for that position by the late Martin Kamen, who had longstanding relationship with Mr. Kettering. I was in Stockholm, Sweden, at the time on a sabbatical leave at the Nobel Institute, and was offered the position during a meeting with Foundation officers in London. Photosynthesis research, which was the major part of my efforts up to that time, started with Sam Aronoff at Iowa State College in 1948. I was using carbon-14 to follow the plant sugars formed in the leaf, and followed sucrose as the major sugar translocating to the roots. My next research experience was with Henry Mahler at the University of Wisconsin, working on what was then called reduced *diphospho pyridine nucleotide* (DPNH; now reduced *nicotinamide adenine dinucleotide*, NADH)-cytochrome *c* reductase system. After one year there I went to work with the late Martin Kamen (1915–



Figure 2. Leo Vernon at his desk.

2002) in 1952 at Washington University in St. Louis. The focus there was bacterial cytochromes and the role they play in bacterial photosynthesis and electron transport. (Kamen's photograph appears in Govindjee and Gest 20002; also see Benson 2002). This led to the isolation of a cytochrome *c* from *Rhodospirillum rubrum*, followed by similar isolations from other bacteria (Vernon and Kamen 1954). We also studied the role of the cytochromes in photorespiration.

After a very rewarding two-year stay with Kamen I was offered and accepted a position in the chemistry department at Brigham Young University (BYU), where I stayed until my sabbatical leave to Sweden. The years at BYU were devoted to further work on bacterial cytochromes and the beginning of the preparation of subchloroplast fragments containing Photosystem 1 and Photosystem 2 (PS 1 and PS 2), using the nonionic detergent Triton X-100. To follow the electron transfer sequence in the two particle types we used ascorbate and 2,6-dichlorophenolindophenol for PS 1 and diphenylcarbazide for PS 2. Although I had many administrative duties, represented in Figure 2, I was able to continue and expand my research on subchloroplast fragments at the Kettering Laboratory.

The research interests of Boss Ket were photochemistry and energy transfer, and these were in harmony with my own interests as they related to photosynthesis. My first assignment was to build up a staff of scientists who were already established in their own field of research, and whose research was in the direction of: (1) chlorophyll photochemistry, (2) light-induced electron flow in chloroplasts and photosynthetic bacteria, (3) the role of cytochromes in the electron flow or (4) how the photosynthesis machine was organized into discrete photosystems. Accordingly the first appointments at the Lab were people who had proven accomplishments in these areas. This included Tony San Pietro for electron transfer reactions of PS I, Rod Clayton for photochemistry and electron transfer reactions in the reaction center complex of photosynthetic bacteria, Bacon Ke for techniques of measuring photochemical reactions of electron-transfer components in the plant chloroplast, and Gilbert Seely for photochemistry of isolated chlorophyll. A significant research program which was underway at the time was nitrogen fixation. All that was needed was to expand the research staff, since it was directed very well by Bill Bulen, who was working on the nitrogenase enzyme. The scientists listed above then recommended others to expand our research. In 1965, Marvin Lamborg joined the staff and later became Chairman of the Cellular Differentiation and Control Unit.

A major advantage to those working at the Lab was a very strong instrumentation staff directed by Bill Treharne, who had worked earlier with Boss Kett in the research laboratory he had built in the basement of his home in Dayton, Ohio. This group included Charlton McKibben and James Riley, and together they provided the unique instrumentation to measure the fast and elusive light-driven reactions in plant chloroplasts. Three patents were awarded to this group, two on wavelength independent direct reading radiometers and one on a linear reading thermometer. Hilton Mollenhauer also joined the staff and provided the electron microscopy unit that was needed as we looked at various cell parts. Ed Vause, vice president of the Kettering Foundation, was responsible for direction from the Board of the Foundation, and the administrative duties at the Lab were carried out by Justin Crawford and later by Millard (Cy) Smith. Funding from the Foundation was sufficient to increase the total staff from 25 in 1961 to well over 100 in 1970 when I left.

We were able to attract scientists from abroad to participate in the research, including Dan Raveed,

Noun Shavit and Joseph Neumann (Israel); Atusi Takamiya, Sakae Katoh, Teruo Ogawa and Tetsuo Hiyama (Japan); Harry Yamamoto (Hawaii); Peter Boger (Konstanz); Yung D. Kim and Sung Gue Lee (Korea) and Augusto Garcia (Argentina). In the late 1970s, several others came to work with Bacon Ke, including Kiyoshi Sugahara, Yasushi Yamamoto, Isamu Ikegami and Hiroshi Inoue (Japan); Zhou-xi Fang and Rong-zhou Lu (China); Aloysius Wild (Frankfurt); S. Sahu and Prasanna Mohanty (India); C. Gomez-Moreno (Spain); Sandor Demeter (Hungary) and V. A. Shuvalov and V. V. Klimov (USSR).

During my tenure at the Kettering Lab, a Scientific Advisory Committee was appointed, consisting of Phillip Handler, President of the US National Academy of Science, George Hammond, a renowned organic chemist from the California Institute of Technology, Paul Zamecnik, from Huntington Memorial Hospital of Harvard University, and Martin Kamen of the University of California, San Diego.

Research accomplishments

Anthony San Pietro

The first scientist to come to the lab was Tony San Pietro in 1962. His focus was on the electron transfer reactions initiated by light and leading to the formation by chloroplasts of reduced nicotinamide adenine dinucleotide phosphate (NADPH) in the presence of artificial electron donors, and this was coupled to the formation of ATP. This led to the identification of the iron-sulfur compound known as photosynthetic pyridine nucleotide reductase (PPNR), or ferredoxin. While at the Kettering Lab, San Pietro extended his research to include chromatophores of photosynthetic bacteria (B. Chance, A. San Pietro, M. Avron and W.W. Hildreth 1965). He built up a group including Clanton Black and a strong supporting staff. During his six years at the Kettering, Tony and his group published some 40 papers, and he organized three Symposia which attracted scientists from the US and around the world who were working on photosynthesis and the synthesis of protein during cellular differentiation. The first symposium was dedicated to C.B. van Niel for his pioneering research on bacterial photosynthesis, which was then extended to explain the role of water in plant photosynthesis. Figure 3 shows van Niel with some of the major participants, including the famous Robin Hill, who opened up



Figure 3. Robin Hill toasting Cornelis Benardus (Kees) van Niel. From left to right: Howard Gest, Hans Gaffron, C.B. van Niel, Robin Hill, Leo Vernon and Anthony San Pietro.

the field of photodriven electron transfer reactions in chloroplasts. This reaction is called the Hill Reaction, and he is shown paying tribute to van Niel (see Walker 2002 for the Hill reaction). The papers given in this symposium are recorded in the book 'Bacterial Photosynthesis,' edited by Howard Gest, Anthony San Pietro and myself, published by Antioch Press. The other symposia were on 'Non-Heme Iron Proteins; Role in Energy Conversion,' edited by San Pietro and a later one entitled 'Protein Synthesis,' co-edited by F. T. Kenney, Marvin Lamborg and Anthony San Pietro. After all this work, Tony moved to the University of Indiana at Bloomington, Indiana, where he is an Emeritus Distinguished Professor of Biochemistry. Clanton Black left after Tony did, and went to the University of Georgia and is a Research Professor in the Department of Biochemistry and Molecular Biology (see Black and Osmond, 2002, on CAM).

Rod Clayton

In early 1963, I was fortunate to be able to attract Rod Clayton from the Dartmouth Medical School to the Kettering Lab. As a biophysicist he was intensely interested in the photochemical reactions of the bacteriochlorophyll in photosynthetic bacteria. He had earlier shown that in the bacterium *Rb. spheroides*

there was a special form of bacteriochlorophyll (BChl) absorbing at 870 nm which was bleached reversibly by light. He believed this was the photoactive BChl in the reaction center (RC), and called this BChl P870. He initially found that the addition of the detergent Triton X-100 to the 'chromatophore' facilitated the photooxidative destruction of the antenna BChl and allowed the remaining P870 to be spectroscopically identified. He continued down this path at Cornell University in collaboration with a postdoctoral fellow, Dan Reed, leading to the isolation of the bacterial reaction center (Reed and Clayton 1968) (see Clayton, 2002, for his perspective).

At Yellow Springs he measured the fluorescence of RC, and also the light-induced shift in the absorption band of BChl. When Berger Mayne joined his staff they were able to measure the chemically-induced luminescence of chlorophyll in chloroplasts. As a chemical perturbation, Berger used the acid-base shift that had recently been described by Andre Jagendorf, and this was the chemical stimulation providing the energy for the observed delayed fluorescence (Mayne and Clayton 1966). (See Jagendorf, 2002, for a history of photophosphorylation.) As Rod said 'This opened another window into the pathways of electron flow.' As these data became known to the research world Rod was invited to many meetings as the main speaker, and he was attracted to Cornell University in 1966.

Bacon Ke

Another eminent scientist who joined us was Bacon Ke. Bacon had joined the Lab first in 1953, left for an industrial job in 1957, and then returned in 1963. The first task upon his return was to construct a kinetic spectrophotometer, used in conjunction with a commercial signal averager, to monitor small absorbance changes associated with photochemical changes in various electron carriers in photosynthetic systems (Ke et al. 1964). A number of studies with plant, algal and bacterial systems, as well as collaborations with other laboratory members, were carried out in the ensuing years, among them the interaction of cytochrome *c* in bacterial reaction centers (Ke et al. 1970), and determination of the precise extinction coefficient of P700 (Hiyama and Ke 1972). In 1968, with the help of R.H. Breeze, the Cary Spectrophotometer was adapted to measure circular dichroism (Ke et al. 1968). Continued development using the elasto-optic modulator eventually resulted in a versatile spectrophotometer capable of measuring changes in absorbance and fluorescence yield, as well as circular and linear dichroism (Ke et al. 1985).

In 1972, Tetsuo Hiyama and Bacon discovered 'P430,' which was subsequently shown to be the spectral species representing FeS-A/FeS-B in Photosystem I (Ke 2002). In the late 1970s, a number of visiting scientists joined Bacon (see the list given earlier) in the study of various aspects of Photosystems I and II: among them the study with S. Demeter from Hungary of electron tunneling in Photosystem I (Ke et al. 1979); the study of early photochemical reactions in photosystem I by the use of subnanosecond spectroscopy with V.A. Shuvalov from Pushchino (Shuvalov et al. 1979; independent measurements were made in Govindjee's research group in 1978, using picosecond spectroscopy); and the EPR study of the interaction of the primary electron acceptor pheophytin with the plastoquinone-iron complex in Photosystem II with V.V. Klimov, also from Pushchino (Klimov et al. 1980).

After Bacon retired in 1983, he went to Japan. While visiting in Japan in 1985 my wife and I had a wonderful dinner with Bacon and his wife, Keiko, who had taught our daughter how to play the piano while we were in Yellow Springs. Sakae Katoh was also at the dinner, and we reviewed our experiences at the Kettering Lab. While in Japan, Bacon wrote a photosynthesis book, published in 1991 in Chinese at the invitation of the Chinese Academy of Science. He then

returned to California, where he continued his work in photosynthesis. In 1993, H. Huzisige and Bacon coauthored a history article on photosynthesis research (Huzisige and Ke 1993). More recently, Bacon has prepared a comprehensive monograph entitled 'Photosynthesis: Photobiochemistry and Photobiophysics,' which was published in 2001 (Ke 2001). He also has an article in Part 1 of 'Celebration the Millennium,' called 'P430: a retrospective, 1971–2001' (see Ke 2002). This article contains a picture of my favorite building in Yellow Springs, The Charles F. Kettering research laboratory.

Gil Seely

The research program at the Lab was significantly expanded when Gil Seely joined the staff in 1962. He was a chemist with a background in porphyrin photochemistry, and experience with polymers. His research goal was to develop artificial systems, based on chlorophyll, which could perform energy-storing reactions similar to those of photosynthesis. Along the way he clarified the mechanisms of chlorophyll-sensitized reactions, and established their relation to polarographic redox potentials. Other areas of research concerned absorption and fluorescence spectroscopy of chlorophyll, including an oft-cited compilation of absorption spectral properties in solvents, in collaboration with one of my graduate students from Brigham Young University, Richard G. Jensen (Seely and Jensen 1965). Model system investigations included excited state energy transfer among chlorophylls on a polymer in solution, and properties of a heterogeneous system involving chlorophyll on plasticized polyethylene particles (Jensen et al. 1966). In view of the importance of the chemistry of chlorophyll, I asked Gil to co-edit the book 'The Chlorophylls' (Academic Press 1966). Gil stayed on at the Lab after I left, but eventually accepted a position at Arizona State University (Tempe), where he ultimately was able to demonstrate an energy-storing reaction in the particulate system.

Berger Mayne

Research involving chloroplast electron transport components and their interaction with the light absorbing pigments expanded when Berger Mayne joined our staff. Initially, he worked on the relation of delayed light emission to electron transport and photophosphorylation, studying the effect of chemical perturb-

ations on components of the system, as mentioned under discussion on Clayton. He found that the intensity of delayed light emission (3.7 ms delay) increased upon addition of electron acceptors such as ferricyanide or pyocyanine. As expected, it was inhibited by the addition of a phosphate acceptor system or uncouplers of photophosphorylation (Mayne 1968). These experiments showed that light emission was coupled to electron transport reactions and high energy intermediates. This agreed with earlier experiments done with R. Clayton (Mayne and Clayton 1966) relating delayed light emission to phosphorylation induced by a pH jump, as was done earlier by André Jagendorf and E. Uribe. Preillumination was required for the observed light emission. Similar experiments were done on delayed light emission and P700 content of isolated mesophyll and bundle sheath cells of selected C4 plant species. The observed values varied depending upon the carbon dioxide fixation pathway in the plants (Black and Mayne 1970).

Darrell Fleischman

A scientist who came to the laboratory to study photosynthesis extended his stay and his interests to show connections between photosynthesis and nitrogen fixation. Darrell Fleischman joined the Lab as a postdoctoral fellow working with Rod Clayton, studying the carotenoid red shift of illuminated photosynthetic bacteria. Berger Mayne and Rod Clayton found that in chloroplasts the delayed fluorescence was influenced by phosphorylation conditions, and it could be induced by an acid-base transition. Darrell found the same effect on bacterial 'chromatophores.' He showed that 'chromatophores' would emit light after addition of ferricyanide or dithionite to an illuminated chromatophore suspension, by adding dithionite and ferricyanide in succession to a dark-adapted suspension, or by injecting air into a pre-illuminated suspension of intact cells. This led to his demonstration that one phase of delayed fluorescence parallels P870⁺ decay, supporting the hypothesis that delayed fluorescence occurs when electrons return to the oxidized P870 from the primary acceptor, thus generating the excited singlet state. The chromatophore membrane potential provides a portion of the needed energy (Fleischman 1971). Darrell went into the nitrogen fixation field when an Indian scientist, N.S. Subba Rao, brought some stem nodules from a legume grown in India. Minocher Reporter looked at the electron microscope pictures and concluded that the nodules contained

photosynthetic bacteria. Surely enough they did. Subsequent work showed that light adsorbed by the bacteria drives nitrogen fixation in the nodules. Their photosynthetic system aids nodulation, and some bacterial strains live in the xylem of rice plants in Africa, where they fix nitrogen and stimulate plant growth. A review of recent work in this area has been published (Fleischman and Kramer 1998). Darrell stayed on at the lab when it was taken over by Wright State University, and made this connection between the fading photosynthesis program and the growing research program in nitrogen fixation.

Richard Dilley

In the spring of 1963, Richard Dilley joined me as a postdoctoral fellow and began work leading to new insights into electron transport-dependent and proton gradient energization-dependent thylakoid membrane conformational changes (Dilley and Vernon 1964). That work soon led to discovering that H⁺ ion accumulation (fitting into the emerging work by Peter Mitchell on the Chemiosmotic Hypothesis) along with K⁺ and Mg⁺ exchanges were the causal agents for the conformational changes and light-dependent volume changes (Dilley and Vernon 1965). Dick joined the lab as a Staff Scientist in 1966 and continued work on proton gradients and their relation to ATP formation, and thylakoid membrane structure using freeze fracture techniques. Some of the work involved collaboration with the late Noun Shavit (later a professor at the University of The Negev, Beer Sheva, Israel) who came to the Lab in 1967 to do postdoctoral work with Tony San Pietro (Shavit et al. 1968). In 1971, Dick joined the faculty at Purdue University, where he continued until his recent retirement (see Dilley, Part 3 of the history issues, forthcoming).

Charles Arntzen

While I was at the Kettering Lab we had good relations with universities in the area. Tony San Pietro and I had teaching appointments at Antioch College, and I had such appointments at Ohio State and Purdue Universities. Charles Arntzen, one of Fred Crane's students, got permission to complete his research work on a Purdue doctoral degree at the Kettering Lab, working with Dick Dilley. Charles worked on electron microscopic studies (in collaboration with Fred Crane) using freeze-fracturing methods in conjunction with digitonin fractionation of thylakoids to yield

fractions enriched in Photosystem I and Photosystem II. He identified the large (180A) particle as a PSII-associated particle which was enriched in the stacked grana membrane (Arntzen et al. 1969). Charles had an illustrious career; being invited to the National Academy of Sciences, became head of the MSU-DOE Plant Research Lab, joined DuPont for a while and became the President and CEO of Boyce Thompson Institute for Plant Research, which did genetic manipulation of plant cells to prepare transgenic proteins used in vaccines. He recently went to Arizona State University at Tempe, as a Distinguished Professor. (See Allen, 2002, for a photograph of Arntzen.)

Donald Keister and William Evans

Donald Keister came to the Lab in 1962 to work on the electron transport system and its role in the photophosphorylation process in *Rhodospirillum rubrum*. In collaboration with Tony San Pietro and Noun Shavit they studied the relationship of pH change and ATP formation. His work is summarized in two publications with Norma Jean Yike on the energy-linked reduction of NAD⁺ (Keister and Yike 1967) and the role of inorganic pyrophosphate as an energy source in photosynthetic bacteria (Keister and Yike 1967). When the focus of the lab shifted to nitrogen fixation, Don continued his cytochrome research on the soybean nitrogen-fixing symbiont *Rhizobium japonicum*. A similar transition was experienced by William Evans. He started in the Cell Differentiation group, working on chloroplast development in *Euglena*. He later shifted over to an investigation of the symbiotic infection of soybean by *Rhizobia*. He discovered that a *rhizobium* that had been isolated would form a photosynthetic system if it was grown on appropriate concentrations of appropriate carbon sources, under cyclic illumination in the presence of air.

Leo Vernon (author)

Although my main assignment at the Kettering Lab was an administrative one, with the help of a very competent research team I was able to continue my earlier work on the separation of the two photosystems of chloroplasts and the light-dependent electron transport reactions in the photosynthetic bacterium *Rhodospirillum rubrum*. I was blessed with the wonderful technical help of Elwood Shaw, Dorothy Limbach and Fern Lubbers along with the cooperation of other sci-

entists in the Lab: Bacon Ke, Tony San Pietro, Bill Treharne, Hilton Mollenhauer, Waldo Zaugg and visiting scientists Augusto Garcia, Teruo Ogawa, Harry Yamamoto and Dan Raveed. We continued my earlier work on the photoreduction of NADP by Photosystem I of chloroplasts in the presence of ascorbate and 2,6-dichlorophenolindophenol. We also developed a method to measure Photosystem 2 (PS 2) activity, using 1,5-diphenylcarbazide as an electron donor to the reaction center chlorophyll (Vernon and Shaw 1969). We also used the nonionic detergent Triton X-100 to isolate the photosystems without losing their photochemical activity (Vernon et al. 1966). Combining these techniques, we were able to isolate PS1 and PS2 from chloroplasts using the detergent Triton X-100 (Vernon and Shaw 1971) and determine the basic structure of these two systems (Vernon et al. 1971) (see Ogawa 2002).

William Bulen

During the 1960s, the nitrogen fixation program expanded under the direction of Bill Bulen, who hired James Corbin, William Newton, Barbara Burgess and others, including three of my former associates at Brigham Young University, Lamont Hadfield, Sigrid Klein and Gary Watt. The group intensively investigated the nature of the nitrogenase enzyme, explaining the roles of the molybdenum-iron protein (MoFe protein) and the iron protein (Fe protein) (Burgess et al. 1980).

Marvin Lamborg

In 1965, the cell differentiation program was started. Marvin Lamborg joined the group and later became Chairman of the Cellular Differentiation and Control Unit. This fit into the other programs, since for both photosynthesis and nitrogen fixation the functional cells need to differentiate into the specialized cells that carry out that particular process, and in some cases both processes proceed in the same cell. In nitrogen-fixing bacteria, ammonia inhibits the synthesis of the nitrogenase proteins. Marve and Alan Collmer showed that the locus of ammonia inhibition in *Klebsiella* occurs after transcription and before protein translation (Lamborg and Collmer 1976). Gerald Peters studied the physiology and structure of the symbiotic association of *Azolla* and *Anabena azolla*. Hilton Mollenhauer studied the structure and function of the Golgi apparatus in both plant and animal tissue, and Tom

Langan studied phosphorylation and dephosphorylation in histone proteins of chromatin. Don Keister showed that free living *Rhizobium* were capable of nitrogen fixation under micro-aerobic conditions.

Changes in laboratory programs

The programs in nitrogen fixation and cell differentiation continued in harmony with photosynthesis up to 1970, and then began to expand at the expense of the photosynthesis program. In 1968, it became apparent that the Kettering Foundation was gaining new interests. The composition of the Board of Trustees was changing. The son of Charles Kettering, Eugene Kettering, was Chairman of the Foundation Board until he died in 1969. His son, Charles Kettering II became the Vice President for Education and Robert Chollar became chairman of the Board. Chollar came from an industrial background and stressed mission-orientated research rather than academic research. This led to the advancement of nitrogen fixation as the major research activity of the Lab, since it seemed to have the greater possibility of yielding results that would directly benefit mankind and at the same time yield financial rewards to the Foundation. As new appointments were made to the Board the personal ties to Boss Kett disappeared and new interests were introduced, which led to other programs gaining support from the Foundation. The first of these was in the area of education, which led to the formation of IDEA, the Institute for the Development of Educational Activities. Then, in the 1980s, interest spread to the support of civic and community programs which would enhance community activities in the US and throughout the world. Seeing this coming, one of the Trustees told me in 1968 that it would be well for the Kettering Lab in Yellow Springs to be separately endowed with a portion of the funds of the Foundation, so that we could operate as a separate but stable research facility formally apart from the Foundation. With this in mind the key personnel of the Lab went to some 10 universities to explore the possibility of the Lab relocating to a university, which would provide research space and some faculty appointments for Lab personnel. Several universities were interested, but could not make the necessary commitment for the Lab to move to their location. Seeing what was coming for the Lab, I left my position as Director in 1970 to take a position as Research Director at Brigham Young University,

where I continued with a minor research program in a study of the two photosystems of chloroplasts.

The scientific interests of Boss Kett continue today at the Memorial Sloan-Kettering Cancer Center in New York, which is one of the leading centers for cancer research. I have not continued doing research on photosynthesis, but after leaving the administration at Brigham Young University I have become involved in the investigation of plant products as anticancer agents. This has led me to collaborate with Sydney Welt of the Memorial Sloan-Kettering Cancer Center, and I got a thrill the first time I walked into the building. There on the wall was a picture of Boss Kett, the same one we had at the Kettering Lab in Yellow Springs. I learned from Bill Treharne that there is now a Kettering Family Foundation, separate from the Charles F. Kettering Foundation. Charles F. Kettering III is President of the Kettering Family Foundation, which is carrying on some of the interests of Boss Kett which have been lost over the past 50 years. A museum is being built in Dayton, Ohio, which will have memorabilia of Boss Kett.

The Kettering Lab personnel have an annual picnic at Yellow Springs, which I was able to attend this year. It was great to see the former associates, but it saddened me to drive past the Kettering Lab building and see the sign on front: Antioch University Administrative Offices. The building was taken over by the Battelle Institute of Columbus, Ohio in 1984, then by the newly created Wright State University of Dayton, and finally given to Antioch University (it was Antioch College when I was there). Relating to this, an unbelievable event happened in Brazil in 1992. I was there, in Campinas, to give a lecture on plant thionins at a Pan-American symposium on toxins. At the banquet for the speakers, I was seated next to an American, Wayne Carmichael. I soon learned he was from Ohio, then that he was from Dayton, then that he was at Wright State University, then that he had laboratory space at the Kettering Laboratory in Yellow Springs, then finally that his office was in the office I had while in Yellow Springs. Amazing.

In spite of the sadness of seeing the demise of the Kettering program in photosynthesis research, I still appreciate the opportunity I had to be there and direct the very active, productive and well supported (by the Kettering Foundation) research program in the 1960s. And I am really proud and grateful for my association with the professional staff and support personnel who were there during my tenure. If you look at the professional staff and know where they are now, you will

realize that the Kettering Research Lab is represented in some of the top universities and research groups in the country. Our staff was invited to present talks on photosynthesis at various international meetings. Then also, the professional standing of the Kettering Lab allowed us to attract the world leaders in photosynthesis to the symposia we held in Yellow Springs. Look at the people in Figure 3, Howard Gest, Hans Gaffron, C.B. van Niel and Robin Hill. As Robin held aloft his toast to the symposium participants, I also toast the photosynthesis and nitrogen fixation research personnel from the Kettering Lab and around the world.

Acknowledgments

I want to thank all the research staff at the Kettering Lab for their contributions toward building it into a major research laboratory on photosynthesis and nitrogen fixation. Their contributions are summarized in this article. I also thank Justin Crawford and Millard (Cy)Smith, who served as administrative directors of the lab. This paper was edited by Govindjee.

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