Photosynthesis Research **73:** 1–6, 2002.

Editorial

Celebrating the millennium – historical highlights of photosynthesis research

> 'Glorious Apollo is the parent of us all. Animal heat is solar heat; A blush is a stray sunbeam; Life is bottled sunshine, and Death the silent-footed butler who draws out the cork',
>
> – Wynwood Reade, Martyrdom of Man, 1924

Early roots of photosynthesis research

The English clergyman Stephen Hales published a remarkable book in 1727 entitled 'Vegetable Staticks.' This classic summarized pioneering studies on plant physiology that included experiments aimed at explaining how the sun affects plants. Hales concluded that

> one of the great uses of leaves is what has been long suspected by many, viz., to perform in some measure the same office for the support of the vegetable life, that the lungs of animals do, for the support of animal life; Plants very probably drawing thro' their leaves some part of their nourishment from the air....And may not light also, by freely entering the expanded surfaces of leaves and flowers, contribute much to ennobling principles of vegetables.

In 1772, 45 years after 'Vegetable Staticks' appeared, Joseph Priestley reported the first experiments showing the production of 'dephlogisticated air' (oxygen gas) by plants, and the interdependence of animal and plant life mediated by gases. Priestley and others, however, were unable to reproducibly demonstrate oxygen production by plants because they were unaware of the requirement for light in photosynthesis. The puzzle was solved in 1779 by the Dutch physician Jan Ingen-Housz, who documented the requirement for light and determined that leaves were the primary sites of oxygen formation.

After Ingen-Housz, a century elapsed before another major root of photosynthesis research emerged, from the laboratory of Theodor Englemann. Using the pigmented organism '*Bacterium photometricum*' (a mixture of *Chromatium* species), Englemann observed (in 1883) accumulations of the motile cells at specific wavelengths of a dispersed spectrum, including a wavelength 'band' in the infrared. This photosensory response suggested that the bacteria were photosynthetic, but Engelmann's tests for oxygen production gave negative results. This posed a dilemma because, in 1883, the definition of photosynthesis included oxygen production as a major feature. In 1888, Engelmann published another study in which he erroneously claimed that he was able to detect oxygen formation, thus satisfying the accepted definition of photosynthesis.

The situation was finally clarified by Hans Molisch, a plant physiologist and microbiologist. His landmark monograph of 1907 detailed the properties in pure cultures of a number of species of nonsulfur purple bacteria and described the photoheterotrophic growth mode. Moreover, Molisch provided strong evidence showing that purple bacteria do not produce molecular oxygen. Because photosynthesis in 1907 was still defined as biological CO_2 reduction accompanied by O_2 formation, leading investigators were puzzled by Molisch's results and conclusions. Decades later, some still questioned whether the nonsulfur purple bacteria were photosynthetic. This illustrates the misleading power of immature definitions (see Howard Gest, this issue).

Engelmann (1881–1882), however, was the first to demonstrate an action spectrum of oxygenic photosynthesis using algal filaments. His microscopic observations revealed that aerobic bacteria accumulated around the filaments at red and blue wavelengths of a spectrum, showing the participation of chlorophyll in oxygenic photosynthesis. This was also the first evidence for bacterial chemotaxis (in this instance, aerotaxis).

We refer the reader to the classical book 'Photosynthesis' by Eugene Rabinowitch (Interscience Pub-

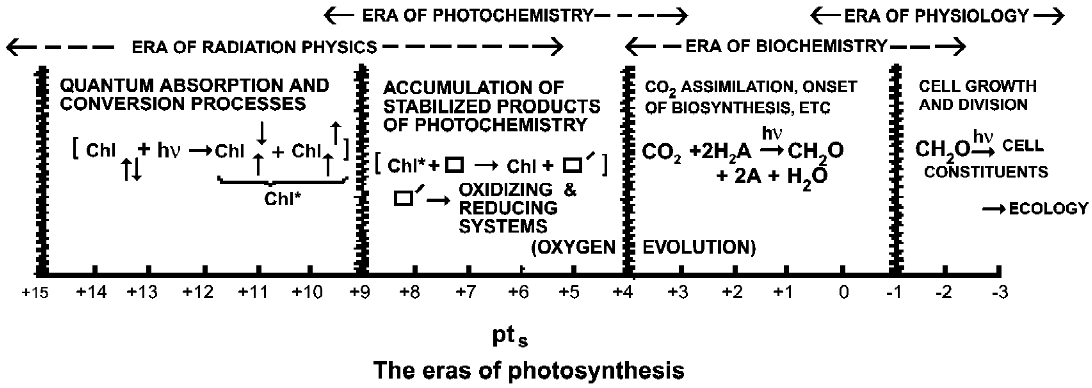

Figure 1. The eras of photosynthesis, according to Martin Kamen (Primary Processes in Photosynthesis. Academic Press, New York, 1963). The term logarithm of the reciprocal of time, expressed in seconds (pts), was suggested by David Gutsche, for which Kamen thanks him.

lishers, New York, 1945) for further information on the early history of photosynthesis.

Into the 20th century and the new millennium

The development of cell biochemistry in connection with research on heterotrophic metabolism during the first several decades of the 20th century paved the way for new insights into photosynthetic processes. Seen through the 'historical lenses' of fermentation and aerobic respiration research, elucidation of photosynthesis in its various ramifications presented new and complex challenges. Biosynthesis of sugars from CO_2 and water via the (Melvin) *Calvin*–(Andrew) *Benson*–(James Al) *Bassham* cycle of 'dark' reactions requires light dependent production of reducing power (NADPH) and ATP. Benson presents, in this issue, a personal story of the discovery of this cycle. He brings before us the early work of Samuel Ruben and Martin Kamen, co-discoverers of C-14, that later led to the path of carbon in photosynthesis. David Walker presents an essay on the discovery (during 1937–1940) of the Hill reaction in chloroplasts that clearly showed the biochemical separation of 'light reactions' from the 'dark reactions.'

The pioneering work of Robert Emerson and coworkers, beginning in 1957 with the discovery of the Enhancement effect, and the crucial experiments of Bessel Kok, Louis N.M. Duysens and Jan Amesz in 1961 on the antagonistic effect of 'light 1' and 'light 2' on the redox state of electron carriers, led to acceptance of the 'Z'-scheme proposed in 1960 by Robert (Robin) Hill and Fay Bendall. By 1963, the concept of the requirement of the two light reactions and two pigment systems for the production of the reducing power (NADPH) in oxygenic photosynthesis became an established fact. This was evident when 'photosynthetikers' met at the Airlie House in Warrenton, Virginia, for a conference on 'Photosynthetic Mechanisms of Green Plants.' Jack Myers, in this issue, discusses his views on the history of this milestone in photosynthesis research. Clearly, the controversy between Otto Warburg and Robert Emerson on the minimum quantum requirement of oxygen evolution was solved in favor of Emerson: a minimum of 8–12 photons per oxygen.

The synthesis of ATP in light by chloroplasts (photophosphorylation) was discovered by Daniel Arnon, Mary Belle Allen and F.R. Whatley in 1954. In the same year, Albert Frenkel observed photophosphorylation by intracytoplasmic membranes of photosynthetic bacteria. André Jagendorf summarizes, in this issue, the history of research on the mechanism of photophosphorylation.

The generation of ATP and NADP(H), in turn, depends on extremely fast reactions of photochemistry and radiation physics. Martin Kamen (1963) noted that the time scale spanning the 'eras' from quantum absorption to photosynthetic cell growth encompasses 19 orders of magnitude. Thus, 'the passage through all these eras requires learning the languages of radiation physics, solid state physics, photochemistry of condensed systems, quantum chemistry, biochemistry, enzymology, plant physiology and descriptive biology.' Thirteen years after Kamen made these remarks, the first map of photosynthesis genes was described, and the languages of molecular biology and genetics had to be added to the list.

Figure 2. A recent photograph of Kamen with his first doctoral student (Howard Gest).

Figure 3. The two editors in San Diego, California, where the final planning and the organization of the special issues of *Photosynthesis Research* celebrating the last millennium took place.

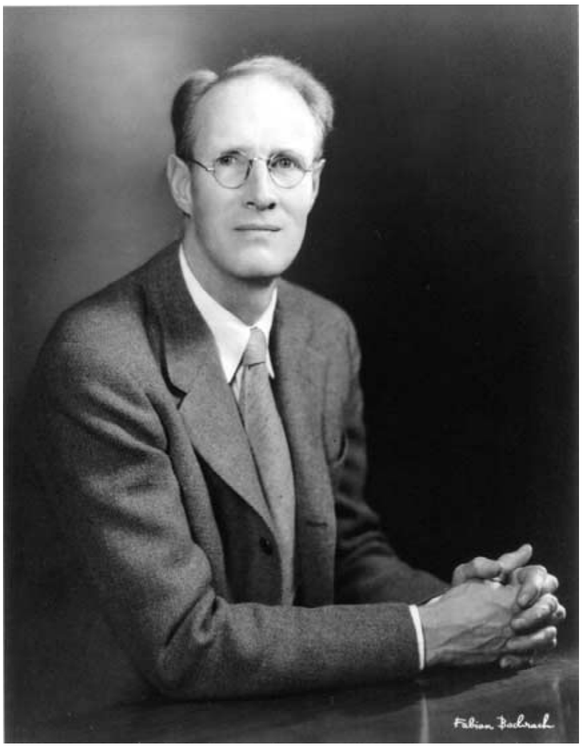

Figure 4. Robert Emerson (1903–1959), to whom we dedicate this historical issue.

The eras of photosynthesis, according to Kamen (Primary Processes in Photosynthesis. Academic Press, New York, 1963) are shown in Figure 1. Figure 2 shows a recent photograph of Kamen with his first doctoral student (HG).

Progress since 1963 has been spectacular, yielding many new insights into the several 'eras.' Noteworthy are advances in knowledge of structure and function of reaction centers, regulation of expression of photosynthesis genes, and evolutionary relations of diverse photosynthesis systems. Barry Marrs, in this issue, describes his unique personal experiences with the beginnings of the molecular genetics of anoxygenic photosynthesizers. Also in this issue, Ralph Lewin describes the history of the discovery of Prochlorophyta, now suggested to be related to cyanobacteria. We have taken the liberty of reproducing, in the appendix, one of his many poems for fun and frolic. Other historical and personal minireviews, included in this issue, will provide much food for thought for future research in these and related areas.

Part 1 of the special issues on the historical highlights presents, in addition to the perspectives mentioned above, eight historical and personal minireviews on anoxygenic photosynthesis by Roderick K. Clayton (reaction centers) the late Jan Amesz and Sieglinde Neerken (excitation energy trapping), André Vermeglio (two-electron gate on the acceptor side); Gerhart Drews and Robert A. Niederman (membrane biogenesis), Sam Kaplan (genes and their expression in *Rhodobacter sphaeroides* 2.4.1), J. Thomas Beatty (natural selection and evolution), and Paul Ludden (on nitrogen fixation). These are followed by 20 historical and personal reviews on oxygenic photosynthesis: Robert M. Pearlstein (theory of excitation energy transfer), Steve Brody (earliest measurements on the lifetime of chlorophyll *a* fluorescence), Mamoru Mimuro (visualization of excitation energy transfer), John Allen (control of 'state changes' by the redox state of plastoquinone), Robert J. Porra (on the determination of chlorophyll concentrations), Jan Anderson (on the localization of Photosystems I and II on different parts of the thylakoid membrane), René Delosme and Pierre Joliot (on the period 4 oscillation in chlorophyll fluorescence), Peter Homann (on the roles of chloride and calcium in Photosystem II), Alan Stemler (on the role of bicarbonate on the donor side of Photosystem II), Jack van Rensen (on the role of bicarbonate on the acceptor side of Photosystem II), Nathan Nelson and Adam Ben-Shem (on Photosystem I), Bacon Ke (on P430, electron acceptor of Photosystem I), Bob Buchanan and coauthors (on the ferredoxin/thioredoxin system), Ulrich Heber (on the Mehler reaction), André Jagendorf (already mentioned, on photophosphorylation), Sam Wildman (Fraction I protein and Rubisco), Marshall D. Hatch (on C-4 pathway), Archie Portis and Michael E. Salvucci (on Rubisco activase), Hans Heldt (on metabolite transport), Pierre Bennoun (on chlororespiration), Sergey V. Shestakov (on molecular genetics of cyanobacteria), and Jean-David Rochaix (on the genomes of the green alga *Chlamydomonas*). Finally, we have added a section on 'Photosynthesis Research' in some key laboratories and in certain countries. Yaroslav Kouchkovsky discusses the achievements of the 'Photosynthesis Laboratory' at Gif-sur-Yvette, in France. Govindjee and David Krogmann have provided in this issue a valuable list of historical articles (perspectives, notes), quotes and Nobel and Kettering awards, related to photosynthesis research.

In 1993, Hirose Huzisige and Bacon Ke described the 'Dynamics of the history of photosynthesis research' in chart form, together with a valuable compendium of references to the original literature (Photosynthesis Research 38: 185–209). We (Govindjee and

David W. Krogmann; and Howard Gest and Robert E. Blankenship) have taken a somewhat different approach to the Time Line. We are developing separate Time Lines for oxygenic and anoxygenic photosynthesis. In Part 2 of the special issues on the historical highlights of photosynthesis research, we plan to present these Time Lines. When the true common denominators of oxygenic and anoxygenic photosynthesis were finally recognized, research in the two areas began to complement each other in mutually beneficial ways. This can be expected to continue as research on the molecular details of structure and function advances in the new millennium. In addition, Part 2 will contain an almost equal number of historical and personal minireviews on several aspects of past research. We anticipate that this format will lead to a greater appetite for minireviews, and we encourage readers of this journal to contribute relevant articles to the Historical Corner of *Photosynthesis Research*, which deals with stories of discoveries and the people involved.

Figure 3 shows the two editors in San Diego, California, where the final planning and the organization of the special issues of *Photosynthesis Research* celebrating the last millennium took place.

We dedicate Part 1 of the special issues to Robert Emerson (Figure 4). Govindjee and his wife Rajni Govindjee were Emerson's last PhD students before his death on February 4, 1959. His research provided the main basis for establishing the 'light reactions' of photosynthesis, beginning with the concept of the 'photosynthetic unit' (antenna and reaction centers), the minimum quantum requirement of oxygen evolution to be 8–12, and the discovery of the Emerson Enhancement effect, that led to the recognition of two light reactions and the concept of the two photosystem schemes of oxygenic photosynthesis (see E. Rabinowitch 1961; Robert Emerson. National Academy of Sciences (USA) Biographical Memoirs XXXV: 112–131).

Acknowledgments

Govindjee and Howard Gest thank the National Science Foundation (Grant SES 00-92507) for funds to travel to the Scripps Oceanographic Institute, University of California, San Diego, to plan and edit the current historical minireviews. Further, this grant provided us the opportunity to learn first-hand the history of the discovery of the path of carbon in photosynthesis from Professor Andrew Benson. We thank Professor David Knaff, Editor-in-Chief of *Photosynthesis Research*, and Ir. Dr Jacco Flipsen, Publishing Manager, and Ms Ellen Girmscheid, Production Editor, Kluwer Academic Publishers, for their outstanding help in bringing out this special issue.

We are particularly indebted to Dr Vani Shanker for copy editing and checking the texts of all the manuscripts. We also thank Ms Mijin Park, who provided all the initial organization, and Ms Jill Lynch, who has scanned and organized the photographs and figures used in this issue. Finally, we thank Drs David Krogmann and Colin Wraight for reading this manuscript, and Dr Ralph A. Lewin for permission to reproduce his 1987 poem.

Appendix

The following is a poem that we like; it is not necessarily the way it might have happened.

In the beginning

In the beginning the earth was all wet;
We hadn't got life–or ecology–yet.
There were lava and rocks–quite a lot of them both–
And oceans of nutrient Oparin broth.
But then there arose, at the edge of the sea,
Where sugars and organic acids were free,
A sort of a blob in a kind of a coat–
The earliest protero-prokaryote.
It grew and divided: it flourished and fed;
From puddle to puddle it rapidly spread
Until it depleted the ocean's store
And nary an acid was found any more.

Now, if one considered that terrible trend,
One might have predicted that that was the end–
But no! In some sunny wee lochan or slough
Appeared a new creature–we cannot say how.
By some strange transition that nobody knows,
A photosynthetical alga arose.
It grew and it flourished where nothing had been
Till much of the land was a blue shade of green
And bubbles of oxygen started to rise
Throughout the world's oceans, and filled up the skies;
While, off in the antediluvian mists,
Arose a few species with heterocysts
Which, by a procedure which no-one can tell,
Fixed gaseous nitrogen into the cell.

As the gases turned on and the gases turned off,
There emerged a respiring young heterotroph.
It grew in its turn, and it lived and it throve,
Creating fine structure, genetics and love,
And using its enzymes and oxygen-2,
Produced such fine creatures as *coli* and you.

This, then is the story of life's evolution
From Oparin broth to the final solution.
So, prokaryologists, dinna forget:
We've come a long way since the world was all wet.

We owe a great deal–you can see from these notes–
To photosynthetical prokaryotes.

(*Source:* The Biology of the Algae and Diverse Other Verses by Ralph Lewin (1987), The Boxwood Press, 183 Ocean View Blvd, Pacific Grove, CA 93950, USA).

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