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Review

Discoveries in oxygenic photosynthesis (1727–2003): a perspective*

Dedicated to the memories of Martin Kamen (1920–2002) and William A. Arnold (1904–2001)

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'Science and art belong to the whole world and before them
vanish the barriers of nationality.'
– Goethe, 1813

Abstract

We present historic discoveries and important observations, related to oxygenic photosynthesis, from 1727 to 2003. The decision to include certain discoveries while omitting others has been difficult. We are aware that ours is an incomplete timeline. In part, this is because the function of this list is to complement, not duplicate, the listing of discoveries in the other papers in these history issues of *Photosynthesis Research*. In addition, no one can know everything that is in the extensive literature in the field. Furthermore, any judgement about significance presupposes a point of view. This history begins with the observation of the English clergyman Stephen Hales (1677–1761) that plants derive nourishment from the air; it includes the definitive experiments in the 1960–1965 period establishing the two-photosystem and two-light reaction scheme of oxygenic photosynthesis; and includes the near-atomic resolution of the structures of the reaction centers of these two Photosystems, I and II, obtained in 2001–2002 by a team in Berlin, Germany, coordinated by Horst Witt and Wolfgang Saenger. Readers are directed to historical papers in Govindjee and Gest [(2002a) Photosynth Res 73: 1–308], in Govindjee, J. Thomas Beatty and Howard Gest [(2003a) Photosynth Res 76: 1–462], and to other papers in this issue for a more complete picture. Several photographs are provided here. Their selection is based partly on their availability to the authors (see Figures 1–15). Readers may view other photographs in Part 1 (Volume 73, Photosynth Res, 2002), Part 2 (Volume 76, Photosynth Res, 2003) and Part 3 (Volume 80, Photosynth Res, 2004) of the history issues of *Photosynthesis Research*. Photographs of most of the Nobel-laureates are included in Govindjee, Thomas Beatty and John Allen, this issue. For a complementary time line of anoxygenic photosynthesis, see H. Gest and R. Blankenship (this issue).

'Science is built of facts, as a house is built of stones: but an accumulation
of facts is no more science than a heap of stones is a house.'
– Henri Poincaré, 1905

Introduction

In oxygenic photosynthesis, organisms release oxygen upon illumination. The overall equation of oxygenic photosynthesis is as follows:

$$CO_2 + H_2O + \sim 10\text{–}12 \text{ quanta of light} \longrightarrow O_2 + \{CH_2O\} + \text{loss as heat and fluorescence.}$$

The process occurs in two major stages: (1) Electrons are transferred from water to $NADP^+$, utilizing light

*Choice of first names used in this paper is arbitrary: authors have used formal first names, nicknames, or just initials, depending on their availability, or their own preferences.

absorbed by several pigment protein complexes. Electron and hydrogen atom (or proton) carriers are located in thylakoid membranes [see Menke (1990) for the term 'thylakoid']. The end result is the release of O_2 and production of reduced $NADP^+$ (NADPH) and, in addition, ATP is formed. ATP and NADPH are then utilized, in the stroma matrix, to convert CO_2 to carbohydrate $\{CH_2O\}$ in a series of reactions catalyzed by water-soluble enzymes. Oxygenic photosynthesis occurs in plants (angiosperms, gymnosperms, pteridophytes, and bryophytes), in green algae, and other multipigmented algae (e.g., red algae, brown algae, yellow algae, diatoms), and in prokaryotes (cyanobacteria, and prochlorophytes). (See John Whitmarsh and Govindjee 1999.) Determination of the concentration of chlorophyll *a* (and *b*) is central for all quantitative measurements of oxygenic photosynthetic activities. Since their publication, the equations of Arnon (1949) have been a fixture in most laboratories. However, Robert J. Porra has pointed out quantitative errors and provided improved formulae for chlorophyll estimation [see Porra (2002) for further history and details]. Measuring oxygen itself has progressed from counting bubbles, through spectroscopic changes induced by oxygen binding, to manometry, to simple and inexpensive polarographic electrodes. Readers are encouraged to consult Martin Kamen (1963), that has inspired many in the field of photosynthesis, Blankenship (2002) for a summary of photosynthesis and an account of how different photosynthetic organisms fit in the evolutionary scheme of life, and Ke (2001) for the development of specific details and ideas on the pathways that lead to the production of NADPH and ATP.

Andy Benson wrote in 1977

> The history of science is never written by the scientists involved in making discoveries. That would be too painful, too embarrassing, to reveal the mistakes and disappointments along the way. Each discovery yields such a simple answer or concept that it should have been obvious, simple, and straightforward to prove.

However, there is another side to the coin: only those who have done the work know what took place at the time their work was done, and why. No one else can come close to their first-hand descriptions. For earlier historical accounts, see Rabinowitch (1945), Huzisige and Ke (1993), Wild and Ball (1997) and Govindjee (2000). Readers may consult Huzisige and Ke (1993) for full references to papers published until 1993.

The historical timeline of discoveries in chlorophyll *a* fluorescence will be covered elsewhere (Govindjee 2004). Further, the early history of an important topic, not covered here, dealing with how plants protect themselves in excess light, is discussed by Demmig-Adams (2003) and by Adir et al. (2003).

History of the structure of chloroplasts is fully discussed by Staehelin (2003). History of the X-ray structures of Photosystems II and I are presented, respectively, by Horst Witt (this issue), and by Petra Fromme and Paul Mathis (this issue).

In addition to the listing provided in this paper, readers are encouraged to consult papers in Govindjee and Gest (2002a), Govindjee et al. (2003a) and the papers in this issue. To give just a few examples, see Belyaeva (2003) for chlorophyll biosynthesis, Bennoun (2002) for chlororespiration, Borisov (2003) for discoveries in biophysics of photosynthesis, de Kouchkovsky (2002) for research at CNRS in Gif-sur-Yvette, Delosme and Joliot (2002) for photoacoustics, Grossman (2003) for complementary chromatic adaptation, Heber (2002) for Mehler reaction, Joliot and Joliot (2003) for excitation energy transfer among Photosystem II units, Klimov (2003) for the history of the discovery of pheophytin as electron acceptor of Photosystem II, Krasnovsky (2003) for discoveries in photochemistry in Russia, Kuang et al. (2003) for discoveries in China, Larkum (2003) for contributions of Lundegardh, Lewin (2002) for the discovery of Prochlorophyta, Papageorgiou (2003) for discoveries in Greece, Pearlstein (2002) for a 1960 theory on excitation energy transfer, Raghavendra et al. (2003) for discoveries in India, and Vernon (2003) for discoveries at the Kettering Research Laboratory.

For ease in separating the eras of the history of oxygenic photosynthesis, we have arbitrarily grouped discoveries and developments into five separate time periods, lettered, in chronological order, A–E.

> 'The tragedy of science – the slaying of a beautiful hypothesis by an ugly fact.'
> – T.H. Huxley, 1893

A. 1727–1905: from Stephen Hales to Frederick Frost Blackman

1727: Hales, air and light

The English clergyman and naturalist Stephen Hales (1677–1761; see Hales 1727; Figure 1a) pioneered

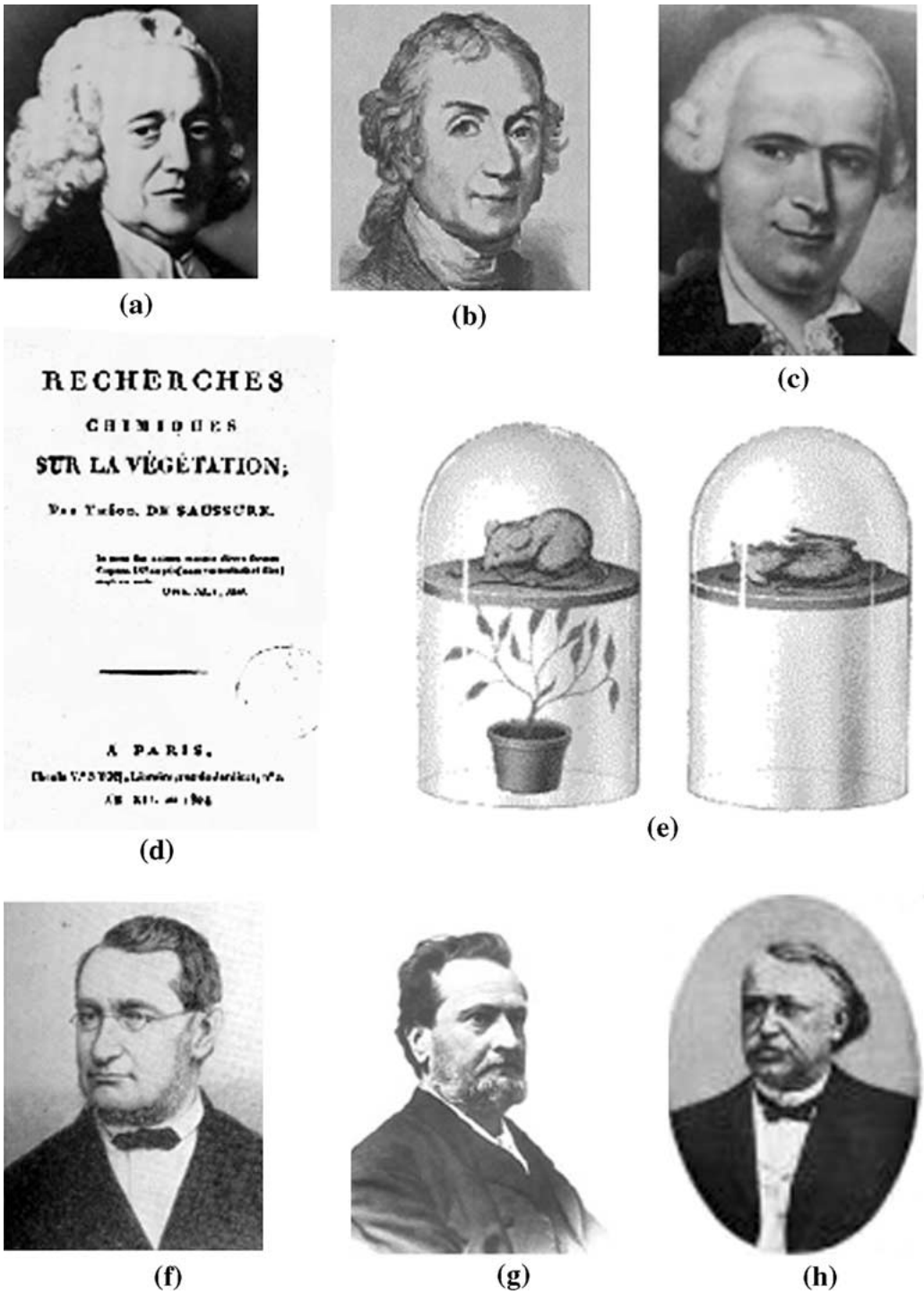

Figure 1. (a) Stephen Hales; (b) Joseph Priestley; and (c) Jan Ingen-Housz; (d) Cover of T. de Saussure's thesis; (e) Priestley's mouse experiment; (f) Robert Mayer; (g) Julius von Sachs; and (h) Theodor Engelmann.

techniques that involved the measurement of water vapor given off by plants. Hales observed a decrease of ~15% in the volume of air above the surface of water when he grew a plant in a closed atmosphere. He concluded that air was 'being imbibed into the substance of the plant.' Hales could not really account for his observation. He thought that plants produced some substance that combined with air, and this caused the volume of the atmosphere to decrease. From our perspective, it was simply that he had called attention to air being a possible participant in the life of a plant. He suggested that plants derive nourishment from the atmosphere through leaves. He noted 'may not light also, by freely entering surfaces of leaves and flowers contribute much to ennobling principles of vegetation.'

1754: Bonnet and oxygen bubbles

Charles Bonnet (1720–1793; see Bonnet 1754), who was born in Switzerland, noted in 1754 that submerged, illuminated leaves produce bubbles. The gas filling the bubbles was later shown to be oxygen. This method is regularly used in schools around the world as a way of measuring rates of photosynthesis.

1772: Priestley, Scheele, Lavoisier and oxygen

Joseph Priestley (1733–1804), a non-conformist English minister, chemist, and philosopher, discovered, during 1771–1772, that plants can 'purify' air that had been 'injured' by the burning of a candle (see Priestley 1772; Figure 1b). He noticed that in an enclosed space a burning candle extinguishes itself, and a mouse suffocates. In a classic experiment, he found that an illuminated sprig of mint produced the 'dephlogisticated air' that sustained the life of a mouse (Figure 1e), and the burning of a candle. In 1775, he discovered that this 'good air' was also evolved from mercuric oxide when heated with focussed light. A free thinker, Priestley, in later life, found a haven from persecution in England by moving to Pennsylvania, USA. The discovery of oxygen as 'fire-air' is also credited to the Swedish apothecary Karl (Carl) Wilhelm Scheele (1742–1786; see Scheele 1781), who delayed publication but communicated his findings to Antoine Lavoisier (1743–1794), a French tax collector and father of modern chemistry. Lavoisier weighed reactants and products of combustion, which he proposed as a reaction with oxygen. The term 'oxygen' was first used in print by Lavoisier in 1785–1786, to describe a *principe oxygène* (acidifying principle). Lavoisier was beheaded under a trumped-up charge in 1794 (see Lane 2002). [For further discussions on the contributions of Priestley, see Hill (1972), and Gest (2000).]

1779–1796: Ingen-Housz, light and CO_2

A Dutch physician Jan Ingen-Housz (1730–1799) (Figure 1c), who was the son of a leather merchant, but was mentored by the British physician John Pringle, demonstrated that a plant in Priestley's experiment was dependent on the sunlight reaching its green parts (see Ingen-Housz 1779, 1796). (Antoine Laurent Lavoisier (mentioned above) worked on the composition of air and water; he developed the concepts of oxidation and respiration, and showed that 'fixed air' is composed of carbon and oxygen.)

It was Jan Ingen-Housz (1796) who proposed clearly that CO_2 was the source of carbon in the plant. He used the terms carbonic acid for CO_2 (fixed air) and oxygen for 'dephlogisticated air.' It was Lavoisier, however, who had developed the 'new' terminology. Perhaps it was first used in print by Erasmus Darwin (1731–1802) (grandfather of Charles Darwin).

1782: Senebier and CO_2

Jean Senebier (1742–1809), a Swiss scientist and a Swiss pastor from Geneva, established that so-called 'fixed air' (CO_2) was indeed essential to photosynthesis. In 1782, he showed that while carbon dioxide is absorbed by the plant from the air, combustion-supporting oxygen was released (see Senebier 1783, 1788).

1804: de Saussure and water

Nicolas Theodore de Saussure (1767–1845; see de Saussure 1804), a Swiss scientist, son of the scientist Horace-Benedict de Saussure (1740–1799; Horace-Benedict was the first to climb Mont Blanc in 1787), suggested that water participates in photosynthesis as a reactant. Further, he wrote *'l'acide carbonique, est elle essentielle pour la vegetation?'* ('Is CO_2 essential to plants?'). In 1804, he referred briefly to an experiment in which he 'placed *raquettes* of the cactus *Opuntia* in CO_2 enriched atmospheres and found that CO_2 and oxygen were absorbed simultaneously.' Figure 1d shows the title page of de Saussure's

publication. With the benefit of contemporary knowledge, his results implied that respiration occurred as usual but that both respiratory CO_2 and external CO_2 were being taken up as a consequence of Crassulacean Acid Metabolism (CAM; see '1956: Walker,' below). He was a pioneer in establishing the field of 'phytochemistry.' He was named professor of minerology and geology at the Geneva Academy.

1813: Heyne and CAM

In a letter to the British Linnaean Society from India, Benjamin Heyne, an English physician, reported diurnal changes in the acidity of Crassulacean leaves. He wrote

> The leaves of the *Cotyledon calycina*, the plant called by Mr Salisbury *Bryophyllum calycinum*, which on the whole have an herbaceous taste, are in the morning as acid as sorrel, if not more so. As the day advances, they lose their acidity, and are tasteless about noon; and become almost bitterish towards evening." [See Black and Osmond (2003) and Raghavendra et al. (2003), for further comments on the history of CAM.]

1818: Pelletier, Caventou and chlorophyll

Two French scientists Pierre Joseph Pelletier (1788–1842) and Joseph Bienaimé Caventou (1795–1877) named the green plant pigment *chlorophyll* ('green leaf') (Pelletier and Caventou 1818).

1837: von Mohl and chloroplast

A German botanist Hugo von Mohl (1805–1872) discovered chloroplasts in plant cells; he provided the first definitive description of what he called '*Chlorophyllkörnern*' (chlorophyll granules) in green plant cells (see Staehelin 2003).

1845: Mayer and the conversion of light energy to chemical energy

Julius Robert Mayer (1814–1878; see Mayer 1845; Figure 1f), of Heilbronn, Germany, a physician, proposed 'the law of conservation of energy,' known also as the First Law of Thermodynamics. He clearly stated that 'plants convert light energy into chemical energy' during photosynthesis. This established the ingredients for the complete equation of oxygenic photosynthesis, as we know it today. As an aside: J.P. Joule (1818–1890) had made unkind remarks on Mayer's numerical value of the mechanical equivalent of heat. Mayer attempted suicide and was confined for a period in a mental institution. It was J. Tyndall (1820–1893) who lectured on Mayer's work and brought recognition to his work.

1860: Boussingault and the photosynthetic quotient

Jean Baptiste Boussingault (1802–1887; see Boussingault 1864) determined the ratio of oxygen evolved to carbon dioxide taken up (the photosynthetic quotient) to be close to 1.0.

1862–1884: Sachs and starch

Julius von Sachs (1832–1897; see Sachs 1892, pp. 313, 319, 324, 332, 344, 354 and 388; Figure 1g), an innovative German plant physiologist, botanist, and author of several standard textbooks, showed that starch grains, produced in leaves, are the first visible product of photosynthetic activity (Sachs 1862, 1864; see p. 360 in Sachs 1892). He is also given the credit for proving that chlorophyll is involved in photosynthesis. Sachs, born in Breslau, had worked with J.E. Purkinje (1817–1869) in Prague in his early career and had published on growth of plants (Sachs 1853). Much later, Hans Molisch (1856–1937) made pictures in starch within a leaf by illuminating through a photographic negative. See Walker (1992) for a starch picture of 'Innocence' by Pierre Paul Prudhon (1758–1823), and R. Hangarter and H. Gest (this issue) for further details.

1864: von Baeyer and the now defunct formaldehyde hypothesis

A. von Baeyer (1835–1917; von Baeyer 1864) proposed that formaldehyde was the product of photosynthesis, and that several formaldehyde molecules were condensed to form sugars. E.C.C. Baly (1871–1948) promoted this idea further, but it was shown later to be in error as formaldehyde was never found to be an intermediate.

1874–1877: Timiriazeff and red light

A Russian physiologist Climent Arkad'evitch Timiryazev, also known as Timiriazeff or Timirjazeff (1843–1920; see Timiriazeff 1877), established the red maximum of the absorption spectrum of chlorophyll

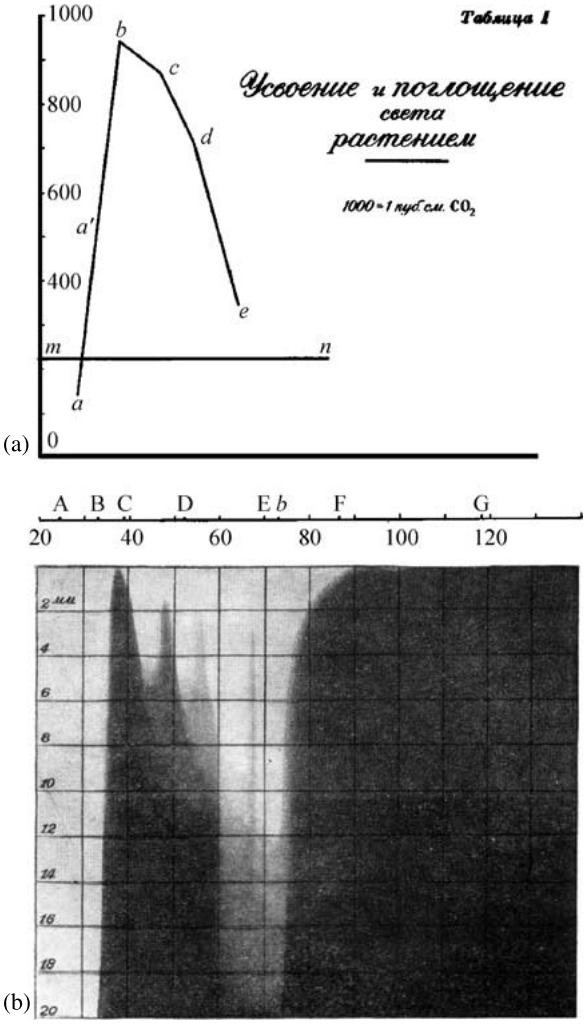

Figure 2. Climent Timiriazeff's Experiment. (a): The action spectrum of carbon dioxide assimilation by green leaves (in the red region). (b): The absorption spectrum of chlorophyll solutions. The ordinate of the upper curve is the rate of CO_2 fixation in cm^3. The abscissae of both the upper and lower curves are marked arbitrarily in millimeters. The wavelengths are marked by A (761 nm), B (687 nm), C (656 nm), D (589 nm), E (527 nm), F (486 nm) and G (431 nm), the Fraunhofer lines. The ordinate of the lower curve is the absorbance in arbitrary units (mm). The figures are from Timiriazeff (1874 and 1875). Figures and legends were provided by A.A. Krasnovsky Jr (see Appendix A).

and showed that red light absorbed by chlorophyll is the most efficient for photosynthesis (Figure 2; and Appendix A). On the basis of this experiment, Timiriazeff claimed that chlorophyll is an optical and chemical photosensitizer of photosynthesis. He proposed that light absorption by chlorophyll causes its chemical transformation (now known to be oxidation), which induces further reactions leading to photosynthesis. For details see Appendix A and Krasnovsky (2003).

1882: The Soret band

Jacques Louis Soret (1827–1890; see Soret 1883) discovered an intense absorption band in the blue region of the spectrum of porphyrins and their derivatives. It became known as the 'Soret' band.

1883: Engelmann, the site of photosynthesis and its action spectrum

Theodor W. Engelmann (1843–1909; Figure 1h), a German botanist, who spent much time in the Netherlands (Engelmann 1882, 1883, 1884; Kamen 1986), recognized that photosynthesis occurs in long spiral shaped chloroplasts of *Spirogyra* cells. Further, he showed that aerophilic bacteria accumulate above illuminated chloroplasts in the blue and red regions of the spectrum, establishing the role of chlorophyll in oxygen evolution by algae.

1893: Barnes, MacMillan and the term 'photosynthesis'

To eliminate confusion with processes in animals, the American botanist Charles R. Barnes (1858–1910) suggested that 'carbon assimilation' by plants should be named 'photosyntax'; an alternative word 'photosynthesis,' favored by C. MacMillan, was also considered, but rejected by Barnes at that time. Barnes favored photosyntax until 1896. However, by 1898, photosynthesis became the accepted word. [For a more complete story, see Gest (2002).]

In the same year (1893), H.T. Brown and J.H. Morris suggested that most leaves contain glucose, presumably as a product of photosynthesis. Later in 1943, James H. Smith (1895–1969), at the Carnegie Institution of Washington at Stanford, established that the major products of photosynthesis were disaccharides (sucrose); see Figure 3a for a photograph of Smith (extreme left, top row) with others at the Carnegie Institute of Washington, at Stanford. Figure 3b shows a 1972 photograph of other contemporary scientists (*vide infra*).

1903: Tswett and chromatography

A Russian botanist Mikhail Semenovich Tswett (1872–1919), born in Asti, Italy, invented the technique of chromatography in 1903. He separated for the

Figure 3. (a): James H.C. Smith and others in the mid-1960s at the Division of Plant Biology, Carnegie Institute of Washington (CIW), Stanford, California. *Top row* – Smith (first from left); C. Stacy French (third from left); Olle Björkman (fourth from left). *Middle row* – William Vidaver (center, with folded hands on his knees). *Next row down*: Yaroslav Kouchkovsky (first from left; with glasses, white shirt and tie); and David C. Fork (second from left), among others. Photo, courtesy of CIW. (b): Past dignitaries of photosynthesis research, gathered at Gatlinburg in 1971. *Left to right*: William Arnold; C. Stacy French; Hans Gaffron; Eugene Rabinowitch; Robert Hill and Lawrence R. Blinks. Photo courtesy of Oak Ridge National Laboratory.

first time plant pigments (chlorophylls and carotenoids) by passing their solutions through glass columns packed with finely divided calcium carbonate (see Tswett 1906). (Chromatography comes from Greek 'chroma,' meaning color, and 'graphein,' to write.) [See Krasnovsky (2003) and Albertsson (2003) for photographs and further information on Tswett.]

1905: Blackman, light-dependent and light-independent reactions

Frederick Frost Blackman (1866–1947; Figure 4a), an English plant physiologist at Cambridge, carried out quantitative experiments on the rates of photosynthesis under different light intensities, temperatures and CO_2 concentrations in *Elodea*, an aquatic plant. Together with G.L.C. Matthaei, Blackman proposed

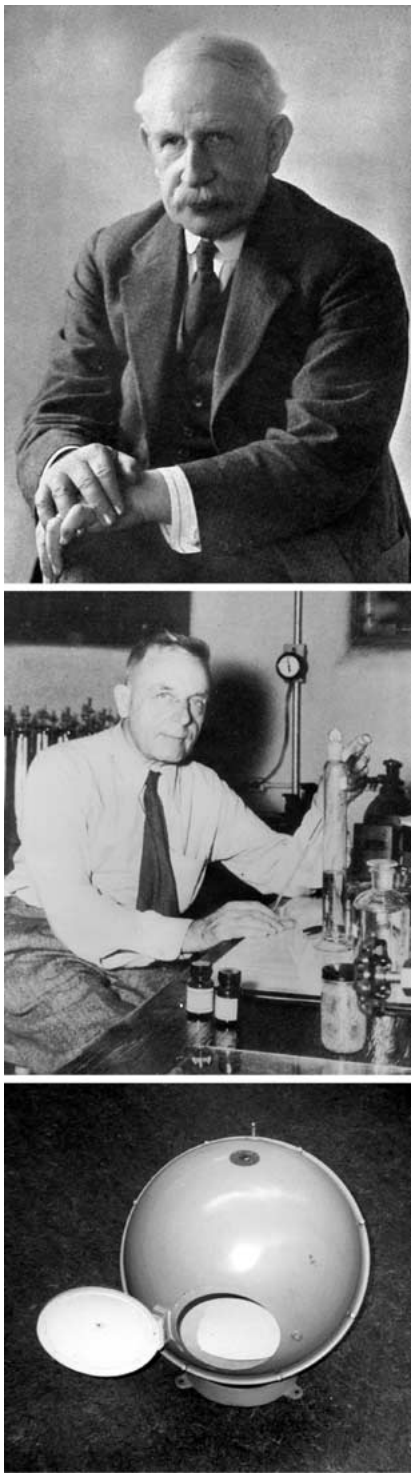

Figure 4. Top: Frederick Frost Blackmann. *Middle*: Otto Warburg, while he visited the 'Photosynthesis Laboratory' at the University of Illinois, Urbana, Illinois, during the late 1940s, after World War II. Photo courtesy of Clint Fuller. *Bottom*: Warburg's integrating sphere, used to measure the quantum yield of oxygen evolution. Photo courtesy of Elfriede K. Pistorius.

the 'law of the limiting factor,' by which the slowest step, or factor in shortest supply, limits the overall rate of photosynthesis. At low light intensity and high CO_2 concentrations, there was no temperature effect. On the other hand, in strong light and limiting CO_2 concentrations, increasing temperature increased the rate of photosynthesis (see Blackman 1905; Blackman and Matthaei 1905). The concept of light-limited and dark-limited photosynthesis was born. However, it was later (in 1924) that O. Warburg (1883–1970; Figure 4b) and T. Uyesugi explained the result of Blackman as showing that photosynthesis has two classes of reactions: light and dark reactions. Warburg called the dark reaction the 'Blackman reaction.'

1905: Mereschkowsky and chloroplasts as descendents of bacteria

C. Mereschkowsky (1905; see Martin and Kowallik 1999) suggested that chloroplasts (then called 'chromatophores') were descended from cyanobacteria (then called 'blue-green algae') and reported that he had been able to show that chloroplasts synthesize protein.

'It is a good morning exercise for a research scientist to discard a pet hypothesis every day before breakfast.'
–Konrad Lorenz, 1966

B. 1913–1954: from Richard Willstätter to Daniel Arnon and Bob Whatley

1913: Willstätter, Stoll and the chemistry of chlorophyll

Richard Willstätter (1872–1942), of Germany, with A. Stoll (1887–1971), of Switzerland, provided the first detailed chemical investigations on chlorophyll, including its chemical structure (see Willstätter 1915). It was suggested that chlorophyll plays an active role in photosynthesis. Willstätter was awarded a Nobel Prize in Chemistry in 1915 (see Govindjee and Krogmann 2002). Willstätter's photograph appears in Govindjee et al. (this issue) and in a paper by Porra (2002). Later, Willstätter suggested the concept, now known to be erroneous, that water and CO_2 combine to form H_2CO_3, and that the latter is converted into oxygen and carbohydrate during photosynthesis. This was the 'precursor' of the erroneous 'photolyte' theory of O. Warburg. (Robert Emerson asked Willstätter to be his doctoral advisor, but was directed by Willstätter to choose Warburg.)

1918: Osterhout and the induction of photosynthesis

Photosynthetic induction (delays in the onset of photosynthesis following abrupt illumination after darkness) was first observed by W.J.V. Osterhout (1871–1964; see Osterhout 1918a, b) and A.R.C. Hass in experiments with *Ulva* at Woods Hole, Massachusetts, in 1918. [See L.R. Blinks (1974) for a biography of Osterhout; we have heard that it was Osterhout's lectures at Harvard that influenced Robert Emerson to study photosynthesis.]

1922–1923: Warburg, Negelein and the minimum quantum requirement of photosynthesis

Otto H. Warburg (1883–1970) (see Figure 4c) for a photograph of an integrating sphere used by Warburg; also see Homann 2002), together with E. Negelein, both from Germany, reported the minimum quantum requirement (i.e., minimum number of photons) to be 3–4 per oxygen molecule evolved during the overall process of photosynthesis (see Warburg and Negelein 1922). This was later shown to be in error by a factor of 2–3 [see Govindjee (1999a) for a historical article]. Warburg received the 1931 Nobel Prize in Physiology and Medicine for his discoveries concerning respiration.

1923–1930: Thunberg, Wurmser and photosynthesis as a redox reaction

In 1923, T. Thunberg (1873–1952) proposed, as one of several hypotheses, that photosynthesis is a redox system in which CO_2 is reduced and water is oxidized (see Thunberg 1923). During 1925–1930, René Wurmser (1890–1993) had also advanced the concept of photosynthesis as a redox reaction (see Wurmser 1921, 1930). This was followed by the well-formulated papers of Cornelis B. van Niel that proposed oxygenic photosynthesis as a special case of a more general light-driven transfer of hydrogen from a donor to CO_2 (see Gest and Blankenship, this issue). Wurmser's photograph appears in Joliot (1996), and that of van Niel in Govindjee et al. (2003b).

Spoehr and McGee (1924) stated that the 'first step' of photosynthesis is absorption of CO_2 by leaves! (We have known for a long time that the first step is the absorption of light.)

1930: Hans Fischer and structure of chlorophyll

Hans Fischer (1881–1945), of Germany, received the Nobel Prize in Chemistry in 1930 for his investigations on chlorophylls and hemes. He solved the complete chemical structure of chlorophyll in the 1940s.

1931: van Niel and photosynthesis as a redox reaction; Keita Shibata's book

Cornelis B. van Niel (1897–1985) [see his photograph in Govindjee et al. (2003a, b)], a Dutch American microbiologist, developed comparative biochemical arguments comparing anoxygenic photosynthetic bacteria with oxygenic plants. Accordingly, photosynthesis was the transfer of hydrogen atoms from H_2A to CO_2 (i.e., an oxidation reduction reaction) (see Van Niel 1931, 1941):

$$CO_2 + 2H_2A \longrightarrow CH_2O + H_2O + 2A$$

(also see Gest and Blankenship, this issue).

In plants, H_2A was H_2O. The concept of 'photolysis' of H_2O was reinforced.

Keita Shibata (1877–1949) was largely responsible for the initiation of modern research in photosynthesis, plant biology, and biochemistry in Japan (see Shibata's excellent 1931 monograph 'Carbon and Nitrogen Assimilation'; reproduction of the original text and its 1975 English translation, by Howard Gest and Robert Togasaki, is available from the Japan Science Press).

1932: Emerson, Arnold and the 'unit of photosynthesis'

Robert Emerson (1903–1959) and William Arnold (1904–2001), two American biophysicists, using suspensions of the green alga *Chlorella*, and repetitive brief and intense light flashes, deduced that only one out of several hundreds of cooperating chlorophyll molecules is directly involved in photochemistry. In these experiments, the concept of the 'photosynthetic unit' was born: that is, several hundred antenna pigment molecules serving a single reaction center chlorophyll, a 'photoenzyme' [see the classical papers of Emerson and Arnold (1932a, b)]. This work was done at the Kerckhoff Laboratory of Biological Sciences at the California Institute of Technology ('Caltech'), Pasadena, California (Figure 5). [See Govindjee et al. (1996) for a special issue honoring Arnold.] In addition, the 'Blackman reaction' was shown to last several milliseconds in darkness. [See photographs of Emerson in Figure 6a and in Govindjee and Gest (2002b), of Arnold in Figure 3b and in Myers (2002); for further discussions, see Clayton (2002); Borisov (2003); Delosme (2003).]

Figure 5. William Kerckhoff Laboratories of the Biological Sciences at Cal Tech, Pasadena, California, where the 1932 experiments on the 'Photosynthetic Unit' were performed by Robert Emerson and William Arnold. Photo by Govindjee, taken in 1995.

1935: Dastur, Mehta and the two photochemical stages of photosynthesis

Dastur and Mehta (1935) wrote 'If the photosynthetic process takes place in more than one photochemical stage it is probable that for one stage a particular wavelength of light is more efficient than the other.'

1935–1941: Yakushiji, Scarisbrick and Hill discover cytochrome f

Yakushiji (1935) was the first to observe cytochrome *f* in leaves, but thought it was cytochrome *c*. Although cytochrome *f* was discovered during 1939–1940 by R. Scarisbrick and Robin Hill, its publication was delayed by World War II (see Scarisbrick 1947; Hill 1965 for further details).

Figure 6. (a) A photograph, taken at the Division of Plant Biology, Carnegie Institute of Washington (CIW), Stanford, California (date, somewhere between 1938 and 1943), showing Charleton M. Lewis (back row, first from left); Hans Spoehr (back row, fourth from left), Robert Emerson (back row, fifth from left), Harold Strain (front row, sixth from left), among others. Photo is a courtesy of CIW. (b) Robin Hill (first from left), C. Stacy French (fourth from left), and James H. C. Smith (sixth from left), among other contemporaries, circa early 1950s. Photo was provided by the late Hans Gaffron family, via Peter Homann. (c) Jack Myers (*extreme right*) with Maria Ghirardi. Photo taken by Govindjee in 1992.

Davenport and Hill (1952) described a detailed procedure, based partly on the earlier observations, for the solubilization and purification of cytochrome *f*. [See D. S. Bendall (this issue) for a history of cytochrome *f*.]

1936: Gaffron, Wohl and the concept of excitation energy transfer

Hans Gaffron (1902–1979), with K. Wohl (in 1936), explained the 1932 Emerson and Arnold experiments by implying that most chlorophyll molecules act in transferring excitation energy, ultimately to the 'photoenzyme' (now called the reaction center). Thus, the concepts of 'antenna' and 'reaction center' emerged under other designations. Gaffron and Wohl explained that if this did not happen, photosynthesis would take a much longer time to begin than it does under low light intensities. [See Figure 3b for a photograph of Gaffron with others; also see Homann (2003).]

1937: Rabinowitch, Weiss and oxidation of chlorophyll a in vitro

Eugene Rabinowitch and J. Weiss (1937) provided evidence that chlorophyll *a* can be oxidized by light and by ferric compounds. A photograph of Rabinowitch can be seen in Figure 3b.

1937: Pirson and the role of manganese

André Pirson, of Germany, showed that manganese is essential for oxygenic photosynthesis (see Pirson 1994).

1937–1938: Karrer and Kuhn receive Nobel Prizes for carotenoids

Paul Karrer (1889–1971; see Karrer 1934), a Swiss chemist, was awarded in 1937 the Nobel Prize for work on the chemistry of carotenoids and of vitamins A and C, and Richard Kuhn (1900–1967; see

Kuhn 1935), an Austrian chemist, was awarded a Nobel Prize in 1938 for further work on carotenoids and vitamins. Owing to the political conditions at the time, Kuhn was prevented from accepting the prize. In 1949, he received the gold medal and the diploma. [See Govindjee (1999b) for a historical account of carotenoids in photosynthesis; photographs are shown in Govindjee et al. (this issue).]

1937–1939: Hill and his reaction

Robert (Robin) Hill (1899–1991), in Cambridge, England, demonstrated that oxidation of water to oxygen and carbon dioxide fixation into carbohydrates are separate processes. This conclusion was reached since Hill obtained oxygen evolution by chloroplast suspensions when artificial electron acceptors (e.g., ferric oxalate; ferricyanide), other than CO_2, were used (Hill 1937, 1939). This reaction, which Hill called 'the chloroplast reaction,' became better known as the 'Hill reaction.' This latter term was first used in print by French and Anson (1941). [See photographs: of Hill in Figure 6b, in Anderson (2002), in Walker (2002a), and D.S. Bendall (this issue); of French in Figure 3b, in Figure 6b and in Myers (2002).]

1938: Blinks, Skow and recording of oxygen evolution

Lawrence R. Blinks (1900–1989; Figure 3b) and R.K. Skow made continuous records of photosynthetic induction in oxygen evolution from *Ricinus* leaves and of pH changes associated with the onset of photosynthesis in water lily.

1938: Smith demonstrates that pigments are bound to proteins

Emil Smith (1938) demonstrated that chlorophyll was bound to proteins. For an early discussion, see Govindjee (1989).

1939–1941: Ruben, Kamen and the discovery of carbon-14

In 1939, Sam Ruben (1913–1943), Martin Kamen (1913–2002), W.Z. Hassid (1897–1974) and Don DeVault (1915–1990) of the USA, published the first experiments on tracing the path of carbon in algae by using radioactive $^{11}CO_2$ (half life, 20 min), but the results were not conclusive (see Ruben et al. 1939; and discussion in Benson 2002). Ruben and Kamen (1941) discovered the long-lived form of carbon, ^{14}C. [See Benson (2002) for their photographs, and for Benson's experiments on the first use of $^{14}CO_2$ in deciphering the path of carbon in photosynthesis; also see Gest (this issue).]

1940: McAlister, Myers, photosynthesis and chlorophyll fluorescence

E.D. McAlister (1901–1980) and Myers (1940) showed an inverse relationship between CO_2 uptake and fluorescence emission during photosynthetic induction. [The 1931 work of Hans Kautsky and A. Hirsch on fluorescence was largely qualitative; for a historical review, see Govindjee (1995).] [See Appendix B for an e-mail from Myers to Govindjee (2002); and Figure 6c for a photograph of Myers; another appears in Myers (2002).]

1941: Ruben, Kamen and the source of oxygen in photosynthesis

Using $H_2{}^{18}O$ tracer experiments, Sam Ruben, M. Randall (1898–1950), Kamen and Hyde (1941) concluded that O_2 evolved in photosynthesis originates from water. Vinogradov and Teiss (1941; also see their 1947 paper) reached a similar conclusion; they found that the isotopic composition of photosynthetic oxygen produced under normal conditions is similar to that in water oxygen, but different from oxygen in CO_2 and in atmospheric oxygen.

1941–1943: Emerson, Lewis, the minimum quantum requirement and the red drop in photosynthesis

Robert Emerson (1903–1959) and Charleton M. Lewis (1905–1996; Emerson and Lewis 1941, 1942, 1943; see Appendix C for an obituary of Lewis), working at the Carnegie Institute of Washington, Stanford, California, obtained a value of 10–12 for the minimum number of quanta per oxygen molecule released in photosynthesis. (See Figure 6a for photographs of Emerson and Lewis, with others, at the Carnegie Institution of Washington, where this work was done.) This followed a 1935 measurement in W. Arnold's PhD thesis at Harvard University, and of Farrington Daniels (1889–1972) and coworkers at the University of Wisconsin, Madison, Wisconsin, in the late 1930s. [Arnold's photograph appears in Figure 3b and in Myers (2002), p. 27.]

We show in Figure 4b a photograph of Warburg, when he visited Emerson's laboratory at the University of Illinois at Urbana, after World War II. Despite this 'collaboration,' there was no resolution of the controversy between Warburg and Emerson concerning the minimum quantum requirement of oxygen production: this value lay between 2.8 and 4 quanta per oxygen molecule according to Warburg, and between 10 and 12 quanta per oxygen molecule according to Emerson.

Emerson and Lewis (1943) discovered the 'red drop' in the maximum quantum yield of photosynthesis on the longer wavelength side of 680 nm in the green alga *Chlorella pyrenoidosa*. This anomaly was not understood until 1957 when Emerson discovered the so-called *enhancement* effect in photosynthesis.

1943: Dutton, Manning, Duggar and energy transfer from fucoxanthol to chlorophyll

Dutton et al. (1943) were the first to demonstrate that light energy absorbed by accessory pigments (e.g., fucoxanthol) was indeed transferred to chlorophyll *a*. This was shown by watching chlorophyll *a* fluorescence when light was absorbed by fucoxanthol in a diatom. (See 1952 listing of Duysens; Dutton 1997; Govindjee 1999b; Brody 2002; Mimuro 2002.)

1944: Warburg, Lüttgens and the role of chloride in photosynthesis

O. Warburg and W. Lüttgens discovered the requirement of chloride in the Hill reaction of chloroplasts [see Homann (2002) for details and photographs].

1946: Meirion Thomas and CAM

Welsh plant physiologist Meirion Thomas (1894–1977) independently rediscovered the simultaneous dark uptake of CO_2 and O_2 by Crassulacean leaves first observed by de Saussure (1804). Subsequent work by others during this period further defined what Thomas had called 'crassulacean acid metabolism' (CAM). [See Black and Osmond (2003) for a detailed history and a photograph of Thomas.]

1947: Wildman and fraction I protein

Sam Wildman, in 1947, isolated a protein from leaves that is present in large quantities (see Wildman 2002). Wildman's 'fraction I protein' proved to be an enzyme, later termed 'carboxydismutase,' and now known as ribulose-1,5-bisphosphate carboxylase-oxygenase, or 'Rubisco' (see R.J. Ellis, this issue). Photographs of Wildman appear in Benson (2002), Wildman (2002) and Wildman et al. (this issue); also see Thornber et al. (1965) for an isolation method of purified fraction I protein.

1948: Krasnovsky reaction in chlorophyll a in vitro

Krasnovsky (1948) discovered that in the presence of appropriate chemical reagents, chlorophyll *a* in solution can be reversibly reduced in light [see Borisov (2003) and Krasnovsky (2003) for further details].

1948–1954: Calvin, Benson, Bassham and the discovery of the photosynthetic carbon reduction cycle

Using $^{14}CO_2$ as a tracer, Andrew Benson, Melvin Calvin (1912–1997) and James A. Bassham and coworkers found that (1) phosphoglyceraldehyde (a triose phosphate) was the first stable product of CO_2 reduction; (2) ribulose bisphosphate, a 5-C sugar, was the acceptor of CO_2; and (3) that there was a cycle to regenerate the acceptor. Their experiments elaborated the complex major pathway of CO_2 reduction by green plants, which included a 7-carbon sugar (see Calvin et al. 1950; the perspectives of Calvin 1989; Benson 2002; Bassham 2003). Melvin Calvin was awarded the 1961 Nobel Prize in Chemistry for this achievement (Figure 7a). Figure 7b shows a recent photograph of Benson, who did most of the early pioneering work.

1951: Strehler, Arnold and the discovery of delayed light emission in plants

Bernard Strehler (1925–2001; Figure 7c) and William Arnold observed 'delayed light emission' while investigating the possible synthesis of ATP by plants (Strehler and Arnold 1951). Delayed light emission has been related to the reversal of Photosystem II reactions (see Lavorel 1975). [A photograph of Arnold appears in Myers (2002).]

1951–1952: Vishniac and Ochoa, Tolmach and Arnon and NADP reduction

In 1951, three independent papers by Wolf Vishniac (1922–1973) and S. Ochoa, N.G. Tolmach, and Dan Arnon (1910–1994) demonstrated the photochemical

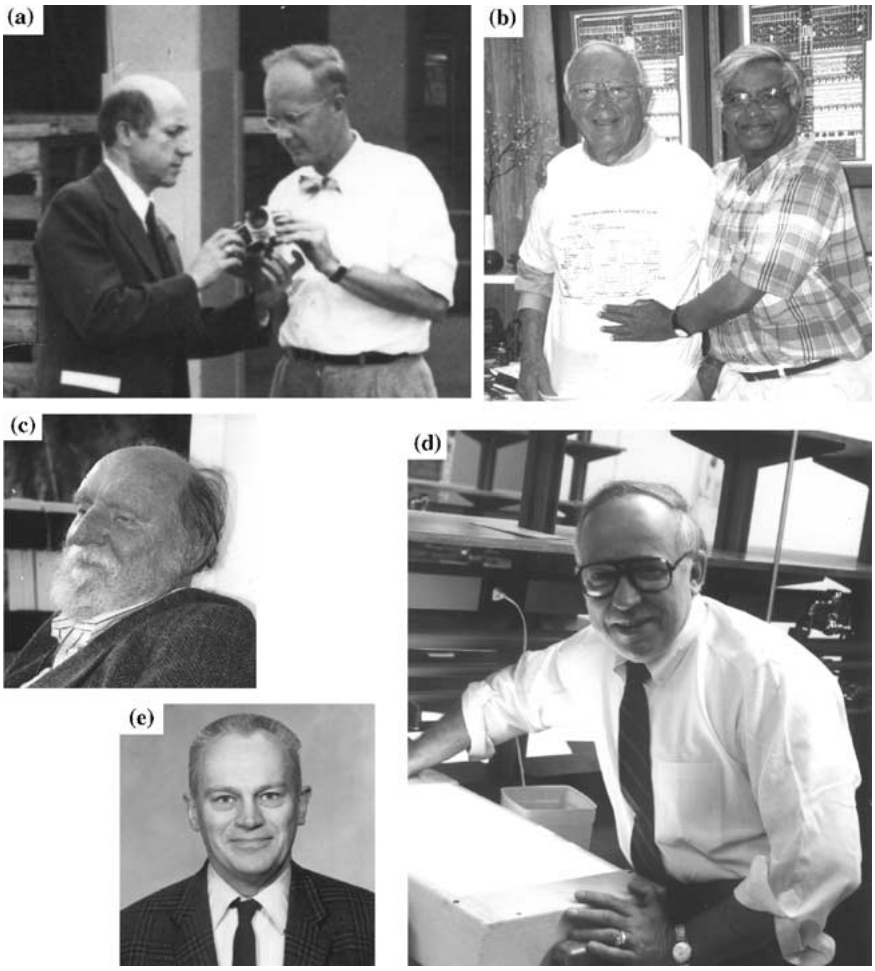

Figure 7. (a) Melvin Calvin (*left*) and Andrew Benson (*right*) examining a camera. Photo was provided by the late Calvin to Govindjee in 1988. (b) Andrew Benson, wearing the Calvin–Benson–Bassham cycle T-shirt (*left*) with Govindjee, who was jokingly hiding Calvin's signature on the shirt. Photo taken in August 2001 by Rajni Govindjee. (c) The late Bernard Strehler. Photo taken in 1995 by Govindjee. (d) Dave Krogmann in about 1964. Photo was provided by Krogmann. (e) Fred Crane. Photo was provided by D. Krogmann.

reduction of pyridine nucleotide ($NADP^+$, then called 'TPN') in catalytic amounts which drove the reductive carboxylation of pyruvic acid to malic acid. A photograph of Ochoa is in Govindjee et al. (this issue).

1952: French, Young, Duysens and the energy transfer from accessory pigments to chlorophyll a

C. Stacy French and Victoria M.K. Young (1952) demonstrated excitation energy transfer from phycoerythrin and phycocyanin to chlorophyll *a*.

Duysens reported, in his 1952 doctoral thesis, the existence of a portion of chlorophyll *a* in red algae that was inactive in fluorescence (see a photograph of Duysens and of the cover of his thesis in Govindjee et al. 2003b). Following earlier measurements by E.C. Wassink (1904–1981) (see Appendix D for an obituary of Wassink) and coworkers, and of Dutton et al. (1943), Duysens showed and quantitatively calculated the efficiency of excitation energy transfer from various accessory pigments (chlorophyll *b*; phycocyanin; phycoerythrin; fucoxanthin) to chlorophyll *a*.

Further, in the same thesis, L.N.M. Duysens had also described the powerful tool of difference absorption spectroscopy to understand the effects caused by illumination of photosynthetic cells. (Duysens was also the discoverer of a small absorbance decrease that he had thought to be due to a small portion of bacteriochlorophyll, that he called 'P' (later to be named

Figure 8. (a) A photograph taken in the middle 1950s. *Left to right*: Robert Emerson, Kenneth Thimann, Daniel Arnon, unidentified, and Dean Burk. Photo from the collection of the late Hans Gaffron family, provided via Peter Homann. (b) A 2002 photograph of Bob Buchanan (*center*) and two of the daughters of the late Daniel Arnon, in front of one of the homes of Arnon in Berkeley. Photo taken by Govindjee. (c) Coworkers of Robert (Bob) Emerson when the Emerson Enhancement effect, in photosynthesis, was discovered: Carl N. Cederstrand (*left*), and Ruth (Shortie) V. Chalmers (*center*), with Emerson (*right*). Photo taken in 1957 by Govindjee. (d) Govindjee standing in front of the door of 157 Natural History Building, University of Illinois, Urbana, Illinois, that led to Emerson's laboratory during 1943–1959. Photo taken in 1999 by Robert Clegg. (e) A photograph of Rajni Govindjee (*right*), Iris Martin (*center*) and Govindjee (*left*), who worked with George Hoch, in the summer of 1962, at Martin Marietta Labs. in Baltimore, Maryland, when they discovered Emerson enhancement effect in NADP reduction in chloroplasts. Photo was taken in 1999 by Amy Whitmarsh. (f) Robin Hill (*right*) and Achim Trebst (*left*). Photograph from the late Hans Gaffron collection, obtained via Peter Homann.

P870). (See Clayton 1963, 2002; Reed and Clayton 1968; Parson 2003.)

1952–1962: Metmyoglobin (methaemoglobin) reducing factor of Hill; diaphorase of Avron and Jagendorf; PPNR of San Pietro and Lang; and ferredoxin of Tagawa and Arnon

Mordhay Avron (1931–1991) and André Jagendorf described in 1956 the purification and characterization of a $TPNH_2$ diaphorase from spinach leaves which would become known as $NADP^+$ ferredoxin oxidoreductase (see Shin, this issue). In the same year, San Pietro and Lang (1956) discovered the ability of isolated chloroplasts to catalyze the light driven accumulation of NADPH and began the work of purification of the soluble protein catalyst which was called PPNR (photosynthetic pyridine nuceleotide reductase) that would become known as ferredoxin (Tagawa and Arnon 1962). Davenport (1960) established the identity of 'ferredoxin' with the methaemoglobin-reducing factor that he had earlier described with Robin Hill and Bob Whatley (Davenport et al. 1952) in their attempt to isolate the natural electron acceptor of the chloroplast.

1954: Arnon, Allen, Whatley and the discovery of photophosphorylation in chloroplasts, and of photosynthesis in chloroplasts

Daniel Arnon (1910–1994), Mary Belle Allen (1922–1973) and F.R. Whatley published the first demonstration of direct, light-driven synthesis of ATP, by isolated chloroplasts (Arnon et al. 1954a, b). See also '1958: Allen, Whatley and Arnon and 'non-cyclic' and 'cyclic' photophosphorylation.' [See a photograph of Arnon, with his contemporaries, in Figure 8a; and of his two daughters and Bob Buchanan, in front of Arnon's home, in Figure 8b; his portrait appears in Porra (2002).] Albert Frenkel, also in 1954, observed, for the first time, photophosphorylation by membrane fragments of photosynthetic bacteria [Jagendorf 2002; see time line on anoxygenic photosynthesis by Howard Gest and Robert Blankenship (this issue)].

Arnon (1954a; also see Allen et al. 1955) next published a demonstration of photosynthetic carbon dioxide fixation by isolated chloroplasts; the yield was very low. This was followed by a clear demonstration of the process by Jensen and Bassham (1966) and by David Walker. [See Walker (2003) for a history of CO_2 fixation by intact chloroplasts.]

1954: Duysens and the observation of 515 nm absorbance change

Duysens (1954) discovered an absorbance change at 515 nm; this was later used to measure changes in membrane potential in plants and bacteria, and became known as the 'carotenoid band shift' (see a historical account in Govindjee 1999b).

1954: Quayle et al. and carboxylase activity

Quayle et al. (1954) observed enzymatic carboxylation of ribulose bisphosphate in crude extracts from *Chlorella*.

'Science is spectral analysis.
Art is photosynthesis.'
– Karl Kraus (1894–1936)

C. 1956–1964: from Bessel Kok to Keith Boardman

1956–1957: Kok and the discovery of P700, reaction center of Photosystem I

Bessel Kok (1918–1978; see Kok 1956), while in Wageningen, in The Netherlands, discovered a light-induced absorbance decrease that had its highest long-wavelength value at 700 nm (labeled as P700) in several photosynthetic organisms. This is ascribed to oxidation of what we now call 'reaction center chlorophyll of Photosystem I,' or P700. A portrait of Kok appears in Myers (2002). Figures 9a–c show photographs of Kok with his contemporaries.

1956: Smith names pigment-protein complexes 'holochromes'

James H.C. Smith (1895–1969) and V.M.K. Young (in 1956) postulated that pigments *in vivo* are bound to proteins, and called them 'holochromes' (from Greek 'holos' for whole, and chroma for color). Figure 9a shows Smith, in a group photograph, wearing a bow tie. There were hints of this idea in the early work of Lubimenko (see Lubimenko 1910; Lubimenko and Brilliant 1924), who claimed that green and yellow pigments are included into protein-pigment complexes.

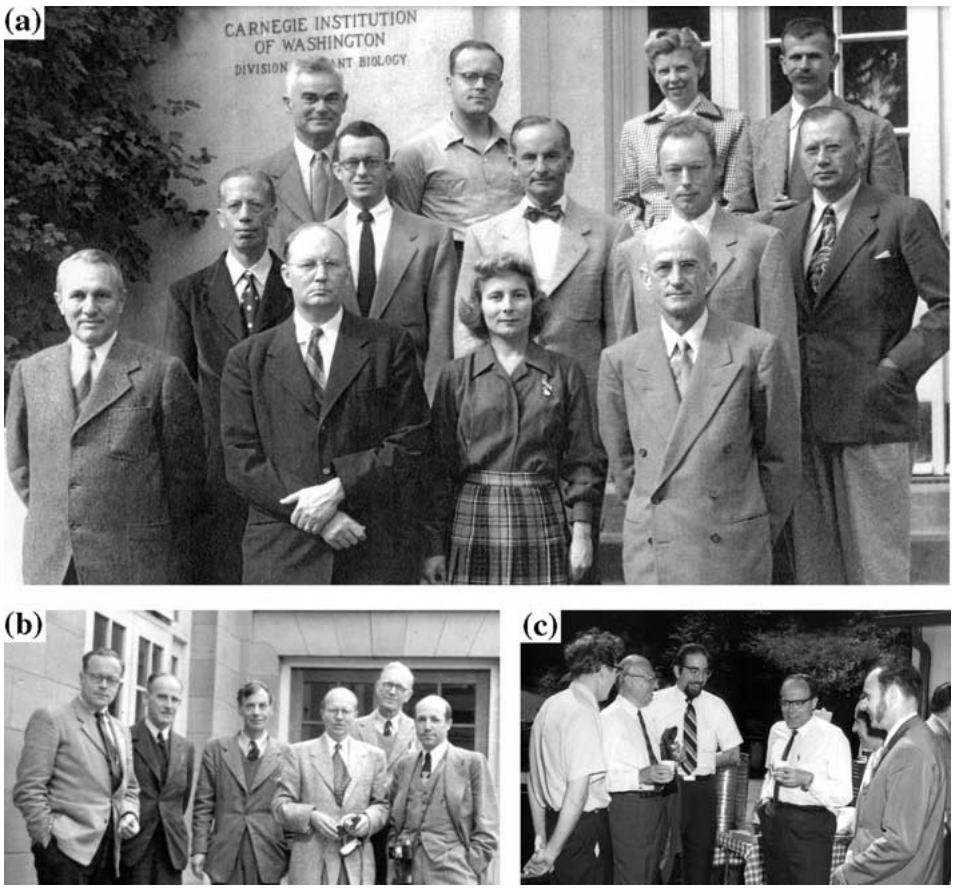

Figure 9. (a) A photograph of Bessel Kok, with others, taken at the Division of Plant Biology, Carnegie Institute of Washington (CIW), Stanford, California (date, somewhere between 1954–1959), showing Kok (back row, second from left); James H.C. Smith (middle row, third from left; wearing a bow tie), Hans Spoehr (front row, first from left), C. Stacy French (front row, second from left), and V.M.K. Young (Victoria Lynch) (front row, third from left), among others. Photo is a courtesy of CIW. (b) *Left to right*: Bessel Kok, Meirion Thomas, Robin Hill, Hans Gaffron, unidentified, and Melvin Calvin. (c) A 1963 photograph of Hans Gaffron (second from left), and Bessel Kok (fourth from left), among others.

1956: Horecker, Weissbach, and Hurwitz purify a 'carboxylation enzyme'

Horecker et al. (1956) purified 'carboxylation enzyme' (their term) with high specific activity (equivalent to contemporary rates) and they performed an extensive characterization of its properties, but they did not recognize it to be the fraction I protein described by Wildman. Jacoby et al. (1956) showed formation of 3-phophoglyceric acid by carbon dioxide fixation with spinach leaf enzymes. Further, Weissbach et al. (1956) showed the enzymatic formation of phosphoglyceric acid from ribulose bisphosphate and carbon dioxide.

1956: Walker and CO_2 fixation in CAM

David Walker established that the malic acid synthesis in CAM is the result of CO_2 fixation by phosphoenolpyruvate (PEP) carboxylase and the reduction of oxaloacetate by NAD malic dehydrogenase. Several photographs of Walker appear in Walker (2003).

1956: Commoner and the electron spin resonance of Photosystem II

Barry Commoner et al. (1956) detected an electron spin resonance signal associated with what we now call Photosystem II.

1957–1965: Fraction I protein of Wildman was shown to have carboxylase activity

Mayadoun (1957) described carboxydismutase activity in a fraction that was prepared just as fraction I protein was prepared. Dorner et al. (1957) recognized carboxylase activity in their fraction I protein

preparation. Van Noort and Wildman (1964) used specific antibodies to establish the enzymatic activity of fraction I protein.

Benson (2002, see pp. 46 and 47) recalls a story of his own involvement in 1954 on this topic.

Mayaudon et al. (1957) described experiments with *Tetragonia expansa* leaves; a footnote states that the work was completed in January 1955. Benson (2002) gives credit to Calvin for inventing the term 'carboxydismutase.'

Trown (1965) showed convincingly the equivalence of fraction I protein and carboxydismutase (Rubisco). For a discussion of the history of Rubisco, see Wildman (1998).

1957: Arnold and the discovery of thermoluminescence in plants

William Arnold and Helen Sherwood reported thermoluminescence in plants [see Vass (2003) for a historical review on thermoluminescence].

1957: Discovery of the so-called 'Shibata' shift

Shibata (1957; also see Thorne 1971) discovered that, during the greening of etiolated plants, a long-wavelength form of chlorophyllide blue shifts to produce a shorter wavelength form of chlorophyllide. It was suggested that this shift represents the release of free chlorophyllide from pigment aggregates to enzyme complexes; and this then leads to subsequent formation of chlorophyll *a* by esterification (see, e.g., Sironval et al. 1965; Belyaeva 2003).

1957–1958: Robert Emerson and the discovery of the enhancement effect in photosynthesis

The most dramatic discovery during 1956–1958 was that of the enhancement effect which occurred in oxygen evolution when two beams of light, with different wavelengths, were given simultaneously. The yield of oxygen was then greater than the sum of the yields with each beam alone. Emerson et al. (1957) discovered an enhancement effect of shorter wavelength of light on photosynthesis by far-red light (in the 'red drop' region) in the green alga *Chlorella pyrenoidosa*. (See a photograph of Robert Emerson, with Cederstrand and Chalmers, in Figure 8c.) In 1958, a similar enhancement effect was observed in red algae, diatoms and a cyanobacterium (see Emerson and Chalmers 1958; Emerson and Rabinowitch 1960). These experiments led to the concept of two pigment systems and two light reactions, and the enhancement effect became known as the Emerson enhancement effect (see Govindjee 2000).

1957–1959: Lawrence Blinks and transient changes in oxygen

During 1957–1959, Lawrence Blinks (1900–1989) observed transient changes in oxygen exchange when one wavelength of light is replaced by another (Blinks 1957; see Myers and French 1960). His preferred explanation of these effects was in terms of changes in respiration, but they are also explained by two light reactions (see '1960: Hill, Bendall and the 'Z' scheme'), and later became important experimental evidence in favor of the hypothesis of two photosystems. (See a photograph of Blinks in Figure 3b.)

1958: Warburg, Krippahl and the discovery of the bicarbonate effect in the Hill reaction

Otto Warburg and Günter Krippahl discovered that bicarbonate or CO_2 was necessary for the Hill reaction. Warburg used it to support his photolyte hypothesis and rejected the concept that oxygen originated in water.

Govindjee and coworkers, during 1972–1998, established the role of bicarbonate in Photosystem II [see J.J.S. van Rensen (2002) and Stemler (2002), respectively, for the current understanding of this phenomenon: both on the electron acceptor and donor sides of PS II, and for several photographs]. Although photosynthetic bacteria and plants have what is called a two-electron gate (see Vermeglio 2002), the bicarbonate effect is found only in oxygenic photosynthesis.

1958: Allen, Whatley and Arnon and 'non-cyclic' and 'cyclic' photophosphorylation

Allen et al. (1958) demonstrated that photophosphorylation was coupled stoichiometrically to linear electron transport, and realized that this 'non-cyclic photophosphorylation' was distinct from the 'cyclic photophosphorylation' they had previously demonstrated (see '1954: Arnon, Allen, Whatley and the discovery of photophosphorylation'). A third pathway, 'pseudocyclic photophosphorylation,' resembles the cyclic pathway because ATP synthesis is driven by light, and no net oxidation–reduction is observed. However, 'pseudocyclic' photophosphorylation is in fact a type of non-cyclic, one in which oxygen functions as the terminal electron acceptor, or Hill oxidant

(see Heber 2002). [See Allen (2003) for the discoveries and the links of cyclic, pseudocyclic, and non-cyclic phosphorylation.]

1959: Kok: antagonistic effect of red and orange lights on P700

Kok (1959) observed, in a cyanobacterium, that P700 was oxidized by red light, but further addition of orange light reduced the oxidized P700. This paper is of great historical importance since it was the first independent observation relating to the Emerson enhancement effect (see also '1957–1959: Blinks', above); both phenomena are explained by the hypothesis of two photosystems (see '1960: Hill, Bendall and the 'Z' scheme', below).

1959: Krogmann, Avron, Jagendorf and Good: coupling of ATP synthesis with electron transport

Dave Krogmann (see Figure 7d), Mordhay Avron and André Jagendorf presented evidence for the coupling of ATP synthesis to electron transport in illuminated chloroplasts (Krogmann et al. 1959; see also 1954: Arnon, Allen and Whatley). Ammonium ions were an excellent 'uncoupler.' Rupture by osmotic shock of the chloroplast membranes also uncoupled phosphorylation from electron transport. Good (1960) showed uncoupling of phosphorylation by various organic amines. These results established a strong similarity between the mechanisms of oxidative phosphorylation in mitochondria and photophosphorylation in chloroplasts. [For a history of photophosphorylation, see Jagendorf (2002).]

Work of Good and Sei Izawa (see, e.g., Good and Izawa 1972) on pH buffers that would not cause uncoupling led to the development of a series of so-called '*Good's Buffers*' that are today almost universally used in biological research (Ferguson et al. 1980). (Photographs of Good and Izawa are shown in Figures 10b and c, respectively.)

1957–1959: Lynch, French, Crane, Bishop and plastoquinone

Lynch and French (1957) found that a non-polar lipid in chloroplasts was required for Hill reaction activity. This led to the discovery of plastoquinone. Crane (1959) reported the presence of two Coenzyme Q type molecules in alfalfa, one of which would later be identified as plastoquinone. In the same year, Bishop (1959) identified the non-polar lipid of Lynch and French as a naturally occurring quinone reactive in the light driven electron transport process of isolated chloroplasts, that is, plastoquinone. [Figure 7e shows a photograph of Crane; Bishop's photograph appears in Homann (2003).]

1960: Hill, Bendall and the 'Z' scheme

Around 1959–1960, the idea of two light reactions was clearly 'in the air' (Bendall 1994). An important paper was published, on 9 April 1960, by Robin Hill and Fay Bendall, describing a 'Z'-scheme for the two light reactions of photosynthesis. This theoretical scheme was based on two thermodynamic arguments: (1) the two cytochromes (*b* and *f*), as intermediates, must be located energetically between water and CO_2 since their redox potentials are intermediate between those of water/O_2 and CO_2/{CH_2O}; and (2) energy for ATP synthesis could be provided from the downhill transfer of electrons from one cytochrome to the other. Although the position of cytochrome *b* turned out to be in error, the scheme has stood the test of time: one light reaction, Photosystem II, oxidizes water and reduces cytochrome *f*, and the other, Photosystem I, oxidizes reduced cytochrome *f* and reduces $NADP^+$.

The idea of two photosystems, in a general way, had already been stated by Rabinowitch [1956, p. 1862, lines 15–19; see front cover of Part 2 of the history issues, edited by Govindjee et al. (2003a)]. Further, Hill (1965) himself acknowledged that the concept of two light reactions and two pigment systems was already known to him, before 1960, from the work of Robert Emerson. The Hill and Bendall Z-scheme was a detailed, explicit, and testable formulation of the idea that there might be two separate light reactions: it made clear their relation to each other as a connection in series, and identified them with the two pigment systems (see '1960–1962: Rabinowitch and Govindjee' below). The Z-scheme also accounts for the observed minimum quantum requirement of oxygen evolution of eight, because each of the four electrons from water requires two quanta, one at each photosystem. The Z-scheme was therefore decisive in resolving the 'quantum yield' controversy (see '1941–1943: Emerson, Lewis, the minimum quantum requirement and the red drop in photosynthesis'). The Emerson enhancement effect (see '1957–1958: Robert Emerson and the discovery of the enhancement effect in photosynthesis') is likewise explained if the two pigment systems have different absorption spectra. The long-wave limit of system II produces the 'red drop,' and, at wavelengths beyond the red drop, a supplementary beam of smaller

wavelength is required in order for system II to supply electrons to system I. The discovery of the Z-scheme is beautifully described by Walker (2002b). Figure 8f shows a photograph of Hill with Achim Trebst.

It is important to mention a key presentation of Bessel Kok and George Hoch at a symposium on 'Light and Life' held at the Johns Hopkins University and organized by William D. McElroy on 28–31 March 1960; the work they presented was published in 1961 (Kok and Hoch 1961). Here they had posed the question: is photosynthesis driven by two light reactions? With experimental data on changes in the redox state of P700 and on the action spectra of partial reactions, the answer to the question was clearly 'yes.' They provided a two light reaction scheme, but with one reaction center. Hill and Bonner (1961), in the proceedings of the same conference, cited the Hill and Bendall (1960) hypothesis (see above); Rabinowitch and Govindjee (1961) speculated that the primary photochemical process in photosynthesis might consist of two steps; excited Chl *a* 690 may be able to bring about one of these steps, while excited Chl *a* 670 may be able to sensitize both of them (also see French 1961).

1960–1962: Govindjee and Rabinowitch: chlorophyll a *is in two pigment systems; discovery of two-light effect in chlorophyll* a *fluorescence*

Robert Emerson had earlier surmised (see Emerson and Chalmers 1958) that one light reaction was sensitized directly by chlorophyll *a* and another directly by one of the accessory pigments (Chl *b* in green algae; phycoerythrin in red algae; phycocyanin in cyanobacteria; and fucoxanthin in diatoms and brown algae). This, however, contradicted the Duysens (1952) experiment where light energy absorbed by accessory pigments was transferred to Chl *a*. In the case of Chl *b*, the transfer was 100%. Thus, Emerson's hypothesis was untenable. In 1960, Govindjee and Eugene Rabinowitch (1901–1973) suggested that two spectroscopically different forms of chlorophyll *a* had different photochemical functions; in one case, the energy absorbed by Chl *b* or fucoxanthol must have been transferred to one form of Chl *a* (corresponding to an action spectrum peak at 670 nm, in the Emerson enhancement effect), and used from there. A similar concept was presented, independently, by French (1961). [A photograph of French appears in Myers (2002); and of Rabinowitch in Govindjee et al. (2003a, b); Figure 8d shows a recent photograph of Govindjee at the door to Emerson's laboratory.]

Kautsky et al. (1960) suggested, based on the kinetics of fluorescence transients, that photosynthesis may involve two light reactions, but there was no hint of two pigment systems in this suggestion.

Independently, Govindjee et al. (1960) observed quenching of blue-light excited Chl fluorescence by far-red light. As with enhancement ('1957: Emerson') and antagonistic effects on P700 ('1959: Kok') the phenomenon is now explained by two light reactions each with a separate pigment system: the variable fluorescence arises from Photosystem II, and the far-red light is absorbed by Photosystem I.

In 1962, Warren Butler (1925–1986) (Figure 10a) presented quantitative and more convincing data on this phenomenon (Butler 1962). (For a tribute to Butler, see Govindjee et al. 1986.)

1960: Katoh and the discovery of plastocyanin

Katoh (1960) showed the existence of the copper protein plastocyanin in plants. This lead to the identification of plastocyanin as the electron carrier between cytochrome *f* and P700 [see Katoh (2003) for details and photographs]. Among others, W. Haehnel et al. (1980) studied electron transfer from plastocyanin to P700).

1961–1962: Rajni Govindjee and coworkers discover Emerson effect in the Hill reaction

In 1961, the discovery of the two-light effect (Emerson enhancement) in the Hill reaction in intact algal cells, by Rajni Govindjee, Eugene Rabinowitch and Jan B. Thomas, clearly established that the effect was in the 'light reactions of photosynthesis,' not in respiration as Larry Blinks had suggested in 1957. (See Appendix E for Thomas.) The discovery of the Emerson enhancement effect in $NADP^+$ reduction by Govindjee et al. (1962) left no doubt that the two light reaction two pigment system scheme must exist in chloroplast reactions. Figure 8e shows a photograph of Rajni Govindjee with Iris Martin, and Govindjee who had worked with George Hoch in the summer of 1962.

1961: Duysens and Amesz: antagonistic effect of light 1 and 2 on the redox-state of cytochrome f*; evidence for the series scheme*

The classical paper of Duysens et al. (1961) provided the crucial evidence for the two light reaction two-pigment system, working in series. In the red alga *Porphyridium cruentum*, red light absorbed by chlorophyll *a* oxidized cytochrome *f*. When green light,

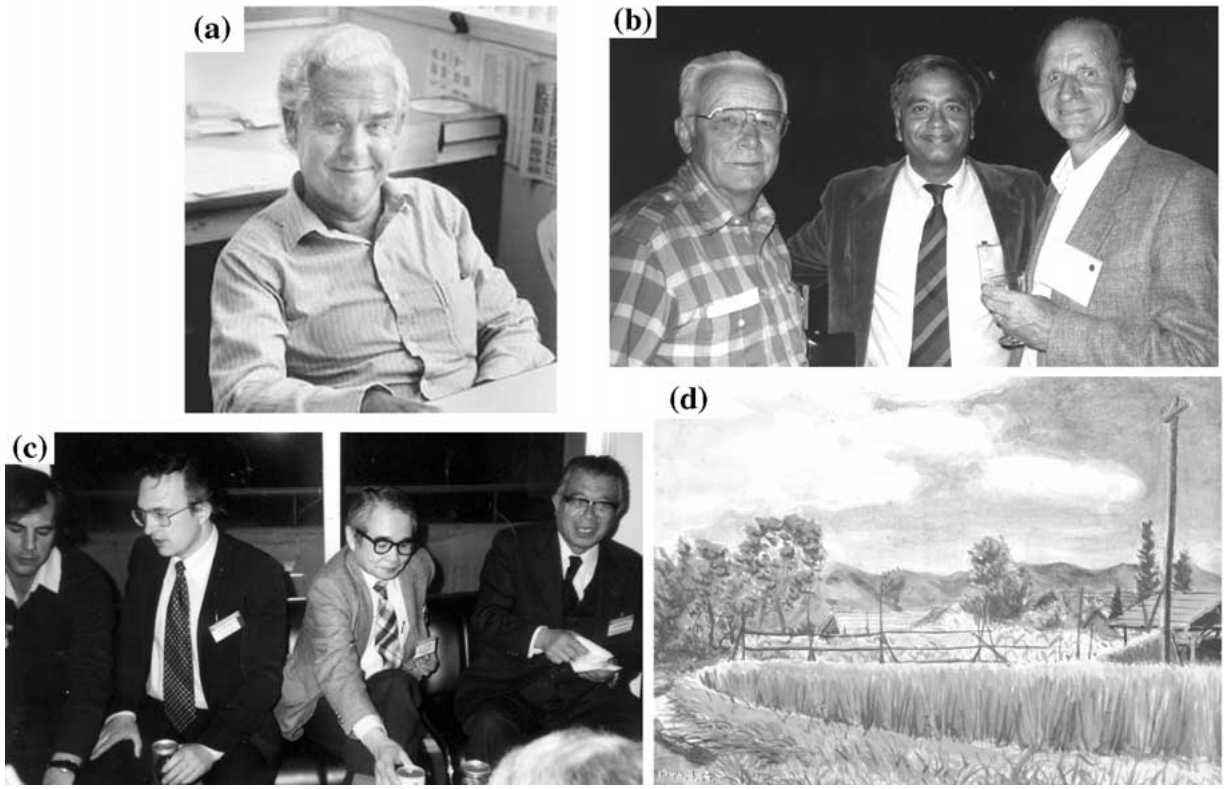

Figure 10. (a) Warren Butler. (b) Norman Good (*left*), Govindjee (*center*), and Achim Trebst (*right*). (c) Seikichi Izawa (third from left), with Gernot Renger and Tony Crofts (*on his right*), and the late Hirose Huzisige (*on his left*). (d) 'A rural Japanese scene, 1946' by Seikichi Izawa, courtesy of the Izawa family. For a color version of this figure, see color section in the front of the issue.

absorbed by phycoerythrin, was superimposed, the oxidized cytochrome *f* became reduced. Duysens et al. called the red light 'light 1,' and the chlorophyll *a*-containing system 'system 1.' The other light, they called 'light 2,' was absorbed by 'system 2.' Although Kok (1959) did not have the notion of two separate reaction centers, he had shown that red light oxidized P700 and orange light reduced oxidized P700, as noted earlier. [See Duysens (1989); a photograph of Duysens appears in Govindjee et al. (2003b); of Amesz in Amesz and Neerken (2002); and of Kok in Figures 9a–c).]

An obituary and a photograph of Jan Amesz (1934–2001) by the late Arnold Hoff and T.J. Aartsma (2002) appear in *Photosynthesis Research.*

1961: Witt and coworkers: flashing light experiments provide evidence for kinetics and intermediates of the steps in the 'Z' scheme

The concept of the above scheme received quantitative support and highly significant extension from the kinetic work of Witt et al. (1961a, b); further, the role of 'X-320,' a quinone, (later known as Q_A), was established. [A photograph of Witt appears in Witt (this issue).]

1961: Losada, Whatley and Arnon and the two-light reaction scheme

Losada et al. (1961; see Tagawa et al. 1963) also published a two light reaction scheme for NADP reduction. However, this was later abandoned by Dan Arnon and co-workers in favor of one light reaction for NADP reduction.

1961: Peter Mitchell's chemiosmotic hypothesis

The year of 1961 was a landmark for photosynthesis research and bioenergetics in general. Peter Mitchell (1920–1992) enunciated the chemiosmotic theory, in which a proton motive force couples electron transfer to ATP synthesis in both oxidative and photosynthetic phosphorylation. In thylakoid membranes, the protonmotive force was proposed to be generated

by transmembrane charge separation in the primary photoprocesses, complemented by hydrogen transport in the opposite direction by plastoquinonol. Experimental evidence for generation of an electric field across photosynthetic membranes was soon provided by the extensive investigations of field effect absorbance changes in chloroplast thylakoids by Horst Witt and colleagues (Witt 1971; also see Witt, this issue), and of the 515 nm 'carotenoid bandshift' of photosynthetic bacteria (Vredenberg et al. 1965; also see Crofts, this issue). (Note that L.N.M. Duysens, cited under '1954: Duysens and the observation of 515 nm absorbance change' was the first to observe this change in *Chlorella*; also see '1966: Jagendorf and Uribe discover acid-base phosphorylation'). Peter Mitchell received the Nobel Prize in Chemistry in 1978 for this contribution (see Mitchell 1961a, b, 1976; photographs of Mitchell appear in Jagendorf 2002; and Crofts, this issue; also see Govindjee et al., this issue).

1962: Shen and Shen: a photophosphorylation 'intermediate'?

Shen and Shen (1962) showed the existence of intermediate steps of photophosphorylation. See Shen (1994) and Jagendorf (2002) for discussion.

1963: Duysens and the 'Q' hypothesis

Louis Nicole Marie Duysens and H.E. Sweers used modulated fluorescence techniques, obtained new data, and provided full rationale to the earlier experiments of Govindjee et al. (1961) and of Butler (1962): Photosystem II reduces a quencher of chlorophyll *a* fluorescence (Q), whereas Photosystem I light oxidizes the reduced Q to oxidized Q leading to quenching of Chl fluorescence. This quencher is now called Q_A.

1963: Avron discovers the coupling factor of photophosphorylation

Avron (1963) discovered the chloroplast coupling factor, CF_1, for photophosphorylation, later known as 'ATP synthase.'

1964: Boardman, Anderson and others: physical and chemical separation of the pigment systems

The physical separation of the two Photosystems by Boardman and Anderson (1964), followed by experiments of Leo Vernon, J.S.C. Wessels; Jean-Marie Briantais and others, left no doubt about the physical reality of the two systems (see Anderson 2002; Ogawa 2003; Vernon 2003). A photograph of Boardman and Anderson appears in Anderson (2002), Vernon in Vernon (2003) and Ogawa in Ogawa (2003).

Further, biochemical experiments were done in which the partial reactions of the two light reactions were revealed in the laboratories of George Hoch, Norman Good (1917–1992), Seikichi Izawa (1926–1997), and Achim Trebst. (See Figure 10b for a photograph of Good and Trebst, and Figure 10c for a photograph of Izawa.) *Chlamydomonas* mutants that lacked one or the other intermediates, used by Paul Levine, at Harvard, provided further evidence for the 'Z'-scheme (for various aspects of this topic, see Anderson 2002; Ogawa 2003; Vernon et al. 1971; Vernon 2003).

Figure 10d shows an example of the artistic talent of Sei Izawa (a painting entitled 'A farmer's field'). For his research contributions, see Berg (1998).

D. 1965–1985: from Don DeVault and Britton Chance to Hartmut Michel and Johann Deisenhofer

1965: DeVault and the discovery of electron tunneling

Don DeVault and Britton Chance discovered electron tunneling in biology (see DeVault and Chance 1966; DeVault 1984; DeVault 1989; Parson 1989). A photograph of De Vault appears in Figure 11a.

1965: Woodward receives the Nobel Prize for total synthesis of chlorophyll

Robert Burns Woodward received the Nobel Prize for the total synthesis of chlorophyll and other natural products. [His photograph appears in Porra (2002) and in Govindjee et al. (this issue).]

1965–1966: Kortschak, Hatch and Slack and the C-4 pathway

During the period of 1965–1966, Hugo Kortschak, Hal Hatch, C.R. Slack, and others, discovered the C-4 pathway (Kortschak et al. 1965; Hatch and Slack 1966) in photosynthesis (also see the early work by Karpilov 1960). For a historical account and photographs, see Hatch (2002).

Figure 11. (a) Don DeVault (*center*) with Andrej Rubin (*right*) and Mike Seibert (*left*). (b) Institut de Physico Chimique Biologie Building at 13 Rue Pierre et Marie Curie, Paris V (France); it is in this building that one of us (G) had met R. Wurmser, and where Pierre and Anne Joliot, R. Delosme and many other scientists work. Photo by Govindjee. (c) Wolfgang Junge in front of Emerson's door at Urbana, Illinois. Photo taken in 2002 by Govindjee. (d) Norio Murata (*extreme right*), with Prasanna Mohanty (*sitting on the floor; extreme left*), George Papageorgiou, Rajni Govindjee, and Govindjee in Norio Murata's home in Okazaki, Japan. Photo taken by Mrs Murata in 1996.

1966: Jagendorf and Uribe discover acid-base phosphorylation

André Jagendorf and Ernest Uribe (1966) showed that in an acid–base experiment, ATP was synthesized: this was a key experiment supporting Mitchell's chemiosmotic theory for ATP synthesis. To be precise, they discovered that a pH gradient (established by pretreating chloroplasts with dicarboxylic organic acids) in the dark produced ATP in chloroplasts. Jagendorf and Geoffrey Hind showed that a similar pH gradient was produced on illumination (see Jagendorf 1998, 2002).

Also in 1966, Dick McCarty and Ephraim Racker found that chloroplast CF_1 is similar in structure and properties to the F_1 coupling factor of mitochondria (see Jagendorf 2002). A photograph of Racker appears in Nelson and Ben-Shem (2002), and that of Jagendorf in Govindjee et al. (2003b).

1966: Gantt and the phycobilisome

Elisabeth Gantt and S. Conti (1966) described the phycobiliprotein containing particles, which would become known as phycobilisomes, that are the antenna(e) complexes of PS II in cyanobacteria and

some algae [See Tandeau de Marsac (2003) for a photograph of Gantt and others.] The organization and the arrangement of pigments, in phycobilisomes, were shown by Gantt et al. (1976). Rita Khanna et al. (1983) showed the association of the phycobilisome with Photosystem II.

See Glazer (1989) and Ong and Glazer (1991) for the directionality of excitation energy transfer in photosynthetic antenna (also see Mimuro 2002).

1967: CO_2-dependent O_2 evolution by intact isolated chloroplasts

Walker and Hill (1967) made the first oxygen electrode measurements of CO_2-dependent O_2 evolution by isolated intact chloroplasts. 'Fully functional chloroplasts' capable of sustaining photosynthetic carboxylation at rates equal to the parent tissue were isolated by Dick Jensen, David Walker and others, and Dennis Greenwood demonstrated that these retained intact double envelopes. [For citations of the early work of Daniel I. Arnon et al., R. Jensen and J. Bassham, and others, see Walker (2003), and the 1954 listing in this paper.]

1968: Ed Tolbert and the peroxisome

N. Ed Tolbert (1918–1998) discovered leaf peroxisomes. For his contributions and his photograph, see Goyal (2000).

1969–1970: Pierre Joliot and the period 4 oscillations; Bessel Kok and the S-state cycle of oxygen evolution

Joliot et al. (1969) discovered period 4 oscillations in oxygen evolution of algae after exposure to a sequence of short (single turnover) saturating flashes of light. Kok et al. (1970) proposed a linear, four-step scheme (the S-state hypothesis) for Photosystem II oxygen evolution (see Renger and Govindjee 1993 for a tribute to this discovery; Joliot 2003; Renger 2003). [For photographs of Kok, see Figures 9a–c and Myers (2002), and for a photograph of Joliot, see Joliot and Joliot (2003).] Figure 11b shows a photograph of the Institut de Biologie Physico-Chimique in Paris (France) where Pierre and Anne Joliot work.

1968–1970: Junge and Witt: membrane potential leads to ATP synthesis

Wolfgang Junge and Horst Witt (in Berlin) discovered that the membrane potential contributes to ATP synthesis, as predicted by Mitchell's chemiosmotic theory. In bacterial chromatophores, Baz Jackson and Tony Crofts (in Bristol, UK) discovered that photosynthetic bacterial membranes did the same; see Gest and Blankenship, this issue. (For a photograph of Witt, see Witt, this issue, and see Figure 11c for a photograph of Junge; a photograph of Crofts appears in Crofts, this issue.)

1969: Döring, Witt and others: P680, the reaction center of Photosystem II

Gunter Döring and others in Witt's laboratory (1969) discovered the second reaction center chlorophyll P680. It was Floyd, Chance and DeVault (1971) who established the key function of P680 at low temperature. [See Seibert and Wasielewski (2003) for the first picosecond measurements; Witt (this issue) for structure.]

1969: Murata, Bonaventura and Myers: discovery of the 'state changes'

Norio Murata observed 'state transitions' in excitation energy utilization in the red alga *Porphorydium cruentum,* and Cecilia Bonaventura and Jack Myers detected these phenomena in the green alga *Chlorella pyrenoidosa* (see Myers 2002). [A photograph of Myers is shown in Figure 6c and in Myers (2002); of Murata in Figure 11d.] John Allen et al. (1981) were the first to relate 'state changes' to the redox level of plastoquinone (see Allen 2002).

1969: Heldt and coworkers and the transporters

Hans W. Heldt and coworkers reported on the first in a series of chloroplast envelope membrane transporters; they showed them to be responsible for the movement of photosynthetic intermediates between the chloroplast stroma and the cytosol (see Heldt 2002; Walker 2003). [Heldt's photograph appears in Heldt (2002).]

1971: Achim Trebst and coworkers and energy coupling sites; Park, Sane and a model for distribution of photosystems

Böhme et al. (1971) discovered an antagonist of plastoquinone that led to clear evidence of energy coupling sites between the two photoreactions. Trebst (1975) summarized this work; his photographs are shown in Figures 8f and 10b.

Rod Park and Raj Sane (1971) proposed a model in which Photosystem I (PS I) was located on stroma lamellae, grana margins and end membranes, whereas both PS II and PS I were present in the appressed grana regions.

1971: Edwards, Black and the locations of key C4 enzymes

Edwards and Black (1971) developed procedures to isolate mesophyll and bundle sheath cells from C4 plants and established the locations of key C4 enzymes. [A photograph of Edwards appears in Heldt (2002), of Black in Black and Osmond (2003).]

1971–1974: Ke, Hiyama, Malkin, Bearden, Evans and Cammack discover the identity of 'X', the primary electron acceptor of Photosystem I

Hiyama and Ke (1971a, b) discovered P430, the 'X' of Photosystem I, and Malkin and Bearden (1971) used electron paramagnetic resonance spectroscopy to demonstrate a photoreduction of chloroplast bound ferredoxin. Evans et al. (1974) provided detailed evidence for the resolution of X from other bound Fe-S centers, A and B. This work would evolve into the definition of the three iron-sulfur centers on the acceptor side of Photosystem 1. [Photographs of Ke and Hiyama appear in Ke (2002).]

1971: Dissection of the components of photosystems by biochemists, particularly Vernon, Ogawa and Nelson

On the biochemical side, Leo Vernon, E.R. Shaw, T. Ogawa and D. Raveed began, in 1971, the dissection of Photosystem I and Photosystem II by detergent solubilization and gel electrophoresis (see Ogawa 2003; Vernon 2003; de Kouchkovsky 2002). On the other hand, Ephraim Racker, Gunter Hauska, Steven Lien, Richard Berzborn and Nathan Nelson achieved a resolution and reconstitution of the five subunits of the CF_1 coupling factor for photophosphorylation (see Jagendorf 2002). Nelson and Neumann (1972) isolated the cytochrome b_6/f complex from chloroplasts (see G. Hauska, this issue; W. Cramer, this issue; D.S. Bendall, this issue). [A photograph of Vernon appears in Vernon (2003), of Ogawa in Ogawa (2003), of Hauska, Racker and Nelson in Nelson and Ben-Shem (2002).]

1971–1972: Bowes and Ogren discover the oxygenase activity of Rubisco

Ogren and Bowes (1971) demonstrated that oxygen is a competitive inhibitor of isolated ribulose di (bis) phosphate carboxylase and showed how the activity of this single enzyme accounts for the rates of photosynthesis and photorespiration measured with soybean leaves. Then, they discovered (with Richard Hageman) that the enzyme also catalyzes the oxygenation of RuBP to produce phosphoglycolate, thereby identifying the oxygenase activity as the long sought, first step in photorespiration. [See Bowes et al. (1971); Ogren (2003) for photographs of Ogren and Bowes.]

In 1979, David Eisenberg proposed the acronym 'Rubisco' at a seminar honoring Sam Wildman, who had discovered the enzyme as fraction 1 protein in 1947. RuBP carboxylation activity, key to the photosynthetic carbon reduction cycle, was reported on and studied by several groups (Melvin Calvin, B. Horecker and others) in the early 1950s and was suspected and later proved to be fraction I protein [see Wildman 2002; Benson 2002; Bassham 2003; see an earlier listing under '1957'.]

1973–1974: Ellis and chloroplast protein synthesis

R. John Ellis showed that isolated chloroplasts synthesized proteins, including the large subunit of Rubisco (Blair and Ellis 1973), and 'peak D' (Eaglesham and Ellis 1974), later identified as the D1 protein (see Ellis, this issue).

1973–1974: Bouges-Bocquet; Velthuys and Amesz discover the two-electron gate of Photosystem II

A two electron gate, on the acceptor side of Photosystem II, was discovered independently by Bernadette Bouges-Bocquet (in Paris; published in 1973), and by Bruno Velthuys and Jan Amesz (in Leiden; published in 1974); such an electron gate was discovered later in bacteria, independently by Colin Wraight and André Vermeglio (see Vermeglio 2002). (Figures 12a and b show photographs of Bouges-Bocquet and of Velthuys, respectively.)

1975: Mitchell proposes the 'Q-cycle'

Peter Mitchell suggested a recycling of electrons between two cytochromes *b* and two quinone-binding

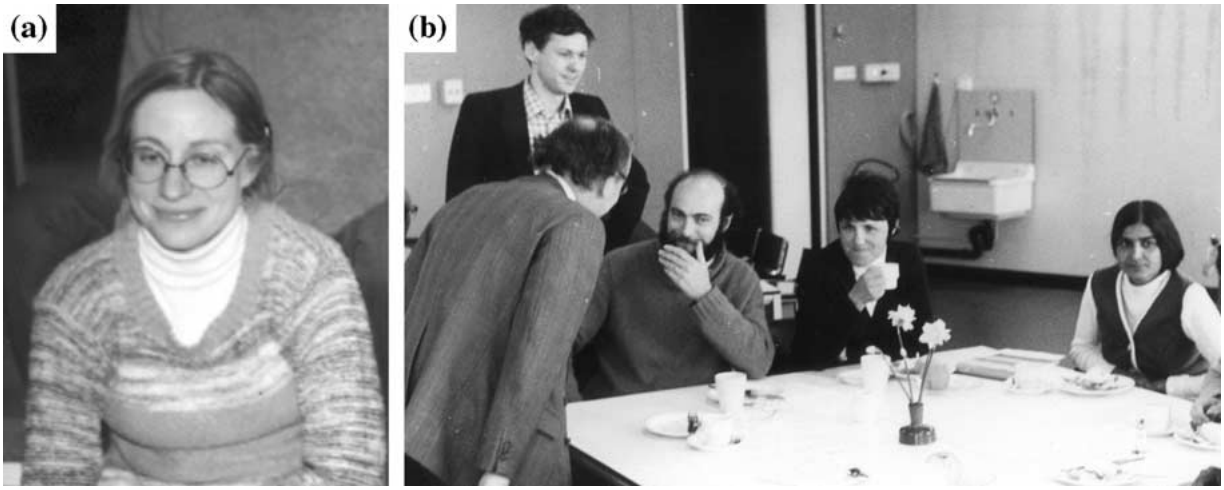

Figure 12. (a) Bernadette Bouges-Bocquet. Photo by Govindjee, taken in the 1980s, at 1101 McHenry Street, Urbana, Illinois. (b) Bruno Velthuys (*standing*) with L.N.M. Duysens (*in the process of sitting down*). Guy Paillotin (*hand on his beard*), Anne-Lise Eienne (*with cup in hand*) and Rajni Govindjee. Photo taken by Govindjee in the Netherlands, around 1976.

sites (the Q-cycle) to explain the stoichiometry of protons to electrons in cytochrome *b*-c_1 and cytochrome b_6-*f* complexes. [See Tony Crofts (this issue) on the history of the 'Q-cycle'.]

Velthuys (1979) provided evidence for a Q cycle in electron flow through plastoquinone, in plants, to the cytochrome b_6/*f* complex, as proposed by Mitchell (1975).

1975: Bengis, Nelson and the isolation of the Photosystem I reaction center

C. Bengis and Nathan Nelson published a detailed analysis of the proteins in Photosystem I reaction center (see Bengis and Nelson 1975, and discussion in Nelson and Ben-Shem 2002).

1975: Thornber and chlorophyll–protein complexes

Phil Thornber (1975) used non-denaturing gel electrophoresis (green gels) to show that chlorophyll is bound to apoproteins in pigment–protein complexes within thylakoid membranes, equivalent to the holochromes postulated by Smith in 1956 (also see Ogawa 2003).

1975: Cohen, Padan and Shilo: electron flow from sulfide to CO_2

Cohen et al. (1975) described a path of electron flow from sulfide through Photosystem I for CO_2 fixation in a cyanobacterium *Oscillatoria limnetica* (see a review by Padan 1979). *Oscillatoria* is phototrophic but facultatively oxygenic – its anoxygenic pathway resembles that of the green anoxygenic bacterium *Chlorobium*.

1975–1978: Wydrzynski and coworkers: first application of NMR and EPR to identify intermediate states in oxygen evolution

Tom Wydrzynski, Nick Zumbulyadis, Paul Schmidt, Steve Marks, Govindjee and Herb Gutowsky were the first to use NMR to monitor Mn in photosynthetic membranes (see Wydrzynski et al. 1975, 1976; see Wydrzynski, this issue, for a historical account).

Wyrdzynski and Ken Sauer used EPR spectroscopy to observe periodic changes in the manganese of PS II and correlated them with the periodic changes in O_2 evolution. [Photographs of Wydrzynski and of Gutowski appear in Wydrzynski (this issue).]

1976–1978: Isolation of inside-out, PS II enriched vesicles and the lateral and transverse heterogeneity of thylakoids

During 1976–1978, Hans-Erik Åkerlund, Per-Åke Albertsson and Bertil Andersson applied aqueous polymer phase partitioning for the isolation of inside-out, Photosystem II vesicles, which were used for the study of the transverse localization of thylakoid components and isolation of polypeptides localized on the lumen side of Photosystem II (Åkerlund et al. 1976; Andersson et al. 1977). This work led to the presentation of a model for the thylakoid membrane in which

Photosystem (PS) II was almost exclusively localized in the appressed region of the grana while PS I was confined to the regions facing the stroma (Andersson 1978).

The general acceptance of such a model was achieved when Andersson and Anderson (1980) published their model in which PS I was excluded from stacked granal membranes. Independently, Jim Barber (see a review by Barber 1982) proposed a physical mechanism for the existence of PS II in the stacked grana membranes and PS I in the stroma lamellae and the grana end membranes (also see Barber, this issue).

1977: Wolosiuk and Buchanan: regulatory role of thioredoxin

Wolosiuk and Buchanan (1977) established the regulatory role of thioredoxin in the light-dark regulation of photosynthetic CO_2 fixation. [See Buchanan et al. (2002) for photographs of Buchanan and Wolosiuk; also see Figure 8b.]

1977: Klimov and coworkers: pheophytin in Photosystem II

Vyacheslav (friends call him Slava) Klimov, Alexander Klevanik, Vladimir (friends call him Vlad) Shuvalov and Alexander Krasnovsky provided unambiguous evidence that pheophytin is the primary electron acceptor in Photosystem II reaction centers (Klimov et al. 1977). For details, see Klimov (2003).

1977: Bennett discovers chloroplast phosphoproteins, including light-harvesting complex II

John Bennett (1977) discovered phosphorylation of light-harvesting complex (LHC) II. [For its effect on energy transfer, see Bennett et al. (1980), and for a description of its history, see Allen (2002).]

Twenty-six years later, Depège et al. (2003) discovered, using a genetic approach, one of the protein kinases responsible for LHC II phosphorylation and state transitions.

1978: Colman and others solve the crystal structure of plastocyanin

Peter Colman, Hans Freeman, J.M. Guss, M. Murata, V.A. Noriss, J.A.M. Ramshaw and M.P. Verikatappa solved the crystal structure of plastocyanin [Colman et al. (1978); see Katoh (2003) for a discussion of plastocyanin].

1978: Bahr and Jensen and the light activation state of Rubisco; Keys and coworkers and the massive flow of ammonia through the photorespiratory cycle

J.T. Bahr and Richard J. Jensen (1978) showed that the activation state of Rubisco in chloroplasts was not the same as total extractable activity, but was a function of light intensity and the CO_2 concentration. Later work in Richard Jensen's laboratory extended this important observation to intact leaves. Further, A.J. Keys, I.F. Bird, M.J. Cornelius, P.J. Lea, R.M. Wallsgrove and B.J. Miflin (1978) revealed the previously unrecognized massive flow of ammonia through the photorespiratory cycle.

1978–1982: Bogorad and his associates provide the first sequence of a D1 protein

Lawrence Bogorad, and coworkers, sequenced the D1 gene of Photosystem II (see Zurawski et al. 1982; Bogorad 2003). [Photographs of Bogorad and coworkers appear in Bogorad (2003).]

1979–1983: Somerville, Ogren and Arabidopsis mutants

Chris Sommerville and William Ogren isolated the first nuclear gene mutants in higher plants with defects in photosynthetic carbon metabolism and thereby drew attention to *Arabidopsis thaliana* as a powerful model plant system. [See Ogren (2003) for photographs.]

1980: Dismukes and Siderer discover Mn changes by multiline EPR

Chuck Dismukes and Yona Siderer (1980) published the first electron paramagnetic resonance (EPR) signal providing evidence for manganese participation in Kok's S-states.

1980: McIntosh, Bedbrook and coworkers and the sequence of the large and the small subunits of Rubisco

Lee McIntosh et al. (1980) deduced the amino acid sequence of the large subunit of Rubisco from the

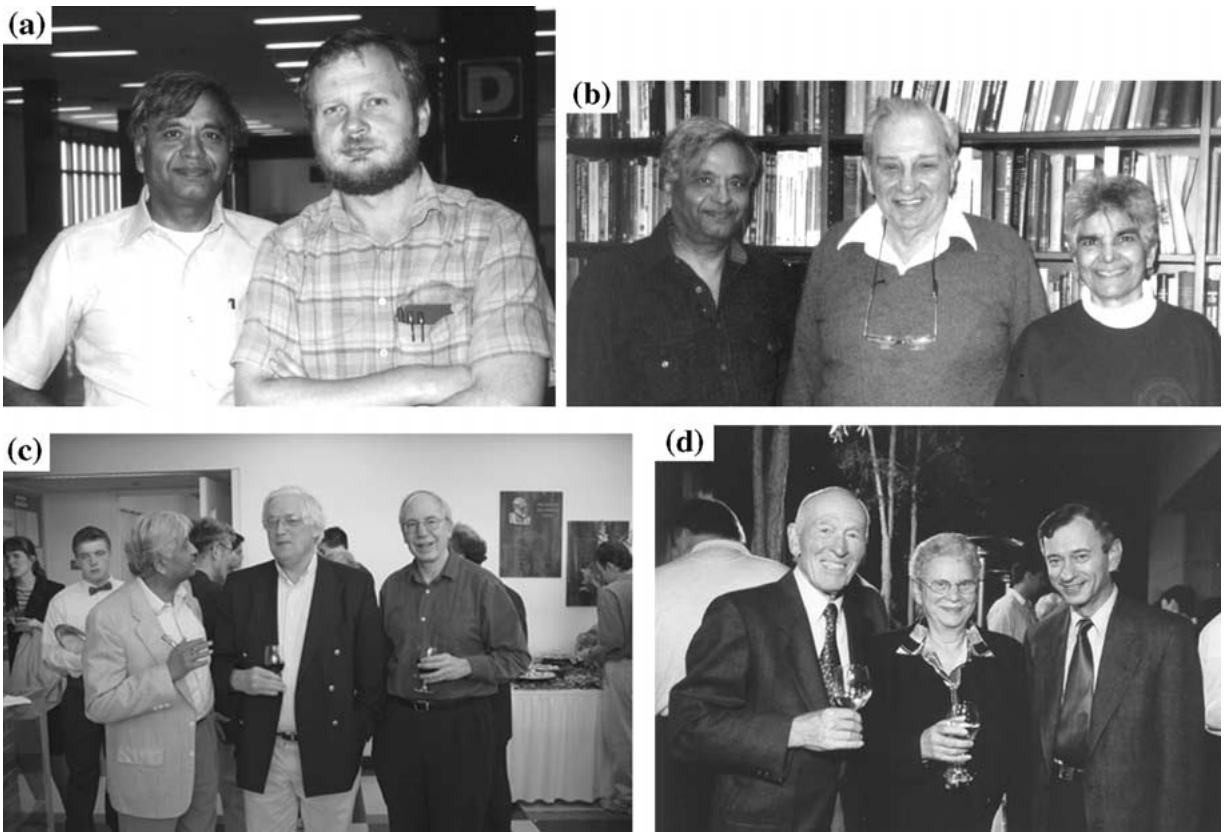

Figure 13. (a) Hartmut Michel (*right*) with Govindjee (*left*). Photo: circa 1990. (b) Rudolph Marcus (*center*) with Rajni Govindjee (*right*) and Govindjee (*left*) in Marcus's office at Cal Tech, Pasadena, California. Photo: circa 1995. (c) John Walker (*center*) with Robert Gennis (*right*) and Govindjee (*left*) at a reception given by the Department of Biochemistry, University of Illinois at Urbana, Illinois. Photo taken in 2002 by Ashtamurthy S. Pawate. (d) (*left to right*) Paul Boyer, Elizabeth Neufeld (Chair and Professor, Department of Biological Chemistry, University of California at Los Angeles, UCLA) and Emil Reisler (then Chair and current Professor UCLA Department of Chemistry and Biochemistry) at a reception following special ceremony dedicating the new name of the MBI Building on the UCLA campus to Paul D. Boyer Hall on Monday, November 15, 1999, at Paul D. Boyer Hall patio. Photo courtesy of Sabeeha Merchant.

nucleotide sequence of its gene, and Bedbrook et al. (1980) sequenced the small subunit of Rubisco.

Martin (1979) had obtained the amino acid sequence of the small subunit of Rubisco by classical means (Edman degradation). [For the history of advances through molecular biology, see Bogorad (2003).]

1981: Allen, Bennett, Steinback and Arntzen implicate the redox state of plastoquinone in protein phosphorylation and 'state changes'

John Allen, John Bennett, Kit Steinback and Charles Arntzen demonstrated that the redox state of plastoquinone controlled phosphorylation of Photosystem II antenna proteins as well as excitation energy distribution between Photosystem I and Photosystem II (see Allen 2002). [Photographs of Allen, Bennett, Steinback and Arntzen appear in Allen (2002).]

1981: Wraight and Velthuys discover the mechanism of action of some herbicides

Colin Wraight, and independently, Bruno Velthuys discovered that several herbicides (e.g., diuron and atrazine) inhibit electron flow by displacing the Q_B of Photosystem II. [A photograph of Wraight appears in Vermeglio (2002); see Figure 12b for a photograph of Velthuys.]

1981: Tsukihara and coworkers solve the crystal structure of ferredoxin from Spirulina

Tsukihara et al. (1981) solved the crystal structure of ferredoxin from *Spirulina platensis*.

1981: Berthold, Babcock and Yocum and oxygen-evolving Photosystem II preparations

Berthold et al. (1981) isolated active oxygen-evolving Photosystem II preparations that have been used in many spectroscopic studies during the last two decades [also see de Kouchkovsky (2002) and Vernon (2003) for other preparations].

1982: Shestakov discovers transformation in Synechocystis

Gregoriova and Shestakov (1982) found that *Synechocystis* sp. 6803 can be transformed by exogenous DNA and created a path for the genetic manipulation of oxygenic photosynthesis. [See Shestakov (2002) for details and for his photograph.]

1983: DeVault, Govindjee and Arnold provide a theory for thermoluminescence

Don DeVault, Govindjee and William Arnold provided the first comprehensive theory for thermoluminescence in plants. [See Figure 11a for a photograph of DeVault; and Imre Vass (2003) for a history of thermoluminescence.]

1984: Deisenhofer, Michel, Huber and coworkers solve the crystal structure of the purple bacterial reaction center and propose its homology with Photosystem II

In 1984, J. Deisenhofer, O. Epp, K. Miki, R. Huber and Hartmut Michel, of Martinsried in Germany, solved the first crystal structure of a membrane protein complex. The complex was the photosynthetic reaction center from chromatophores of *Rhodopseudomonas viridis* (see Deisenhofer et al. 1984; Deisenhofer and Michel 1989). Deisenhofer, Michel and Huber were awarded the Nobel Prize for Chemistry in 1988 (also see Feher 1998; James Allen, this issue). (See Figure 13a for a photograph of Michel.) For a complete list of Nobel laureates related to photosynthesis, see Govindjee and Krogmann (2002); and for photographs of Nobel laureates, related to photosynthesis, see Govindjee et al. (this issue).

1984–2003: Mel Klein, Vittal Yachandra, Ken Sauer and coworkers: manganese by EXAFS

Mel Klein, Ken Sauer, Vittal Yachandra and coworkers made direct measurement of redox changes in manganese by EXAFS during steps leading to oxygen evolution (see, e.g., J.A. Kirby et al. 1981; D.B. Goodin et al. 1984; Yachandra et al. 1996).

E. 1985–2003: from Lawrence Bogorad to William Cramer and Jean-Luc Popot and their coworkers

1985: Bogorad and coworkers sequence Photosystem I genes

Lawrence (Laurie) Bogorad and coworkers sequenced Photosystem I reaction center genes (see Fish et al. 1985; Bogorad 2003).

1985: Salvucci, Portis and Ogren discover Rubisco activase

Michael Salvucci, Archie Portis and William Ogren discovered the enzyme that facilitates the activation and maintenance of Rubisco [see Portis and Salvucci (2002) for details and photographs].

1986: Sugiura and others: the complete sequence of chloroplast genomes

In 1986, M. Sugiura and coworkers announced the complete sequence of the tobacco chloroplast genome (Shinozaki et al. 1986; see Sugiura 2003 for details and photographs).

Ohyama et al. (1986) completed the nucleotide sequence of the chloroplast genome of *Marchantia*.

Hiratsuka et al. (1989) provided the complete sequence of the rice chloroplast genome.

1986: Merchant and Bogorad and metal-regulated synthesis of plastocyanin

Sabeeha Merchant and Laurie Bogorad (1986) discover the role of copper in regulating expression of plastocyanin and cytochrome *c*-552 in the green alga *Chlamydomonas reinhardtii.*

1986: Brändén, Lorimer and the structure of Rubisco

Schneider et al. (1986) obtained the three-dimensional structure of *Rhodospirillum rubrum* Rubisco, composed of a dimer of large subunits. This was soon followed by a structure for tobacco Rubisco (David Eisenberg and coworkers; see Chapman

et al. 1987, 1988), composed of eight large and eight small subunits. The structure of the spinach Rubisco was solved two years later by Andersson et al. (1989). It contained important differences from the model from Eisenberg's laboratory, and gave better assignments of structural features for all plant-type Rubiscos.

1986: Nanba and Kimiyuki Satoh isolate the reaction center of Photosystem II

O. Nanba and Kimiyuki Satoh isolated and purified a complex containing D1, D2 and cytochrome b_{559} and showed that it had the properties of the reaction center of Photosystem II, overturning models in which D1 and D2 were peripheral to the reaction center itself. [See Satoh (2003) for details and photographs.]

1987: Cheniae and photoactivation of the oxygen evolving complex

N. Tamura and George Cheniae (1987) discovered photoactivation of manganese rebinding to Photosystem II in chloroplasts depleted of both manganese and the extrinsic proteins. [See Frasch and Sayre (2002) for a photograph of Cheniae.]

1988: Biggins and Mathis establish that vitamin K is an acceptor of Photosystem I

John Biggins and Paul Mathis (1988) established the participation of phylloquinone (vitamin K) in Photosystem I by solvent extraction and reconstitution (see Ke 2001).

1988: Debus, Barry, Babcock and Lee McIntosh identify Y_z with tyrosine-161 of the D1 protein

Rick Debus, Bridgette Barry, Jerry Babcock and Lee McIntosh provided the first molecular biological evidence that Y_z on the donor side of Photosystem II is tyrosine-161 on the D1 protein. [Photographs of Babcock appear in Renger (2003).]

1988–1989: Boynton, Gilham, Rochaix, Kindle, Maliga and coworkers: nuclear and chloroplast transformation

Boynton et al. (1988) obtained chloroplast transformation in *Chlamydomonas* with high velocity microprojectiles. In 1989, nuclear transformations, in *Chlamydomonas*, were achieved by the groups of Jean-David Rochaix and Karin L. Kindle (see Debuchy et al. 1989; Kindle et al. 1989; Rochaix 2002). These techniques strengthened the position of *Chlamydomonas* as the 'green yeast' for studies of eukaryotic chloroplast-based photosynthesis (see review by Rochaix 1995). In 1992, Pal Maliga provided data on chloroplast transformation in tobacco (see Staub and Maliga 1992). Xiong and Sayre, this issue, discuss the progress obtained by the use of site-directed mutagenesis in *Chlamydomonas*.

1989: Wasielewski, Seibert, Govindjee and coworkers: the first picosecond measurements on Photosystem II reaction centers

Wasielewski et al. (1989) published the first picosecond measurements of the primary photochemistry of Photosystem II. [See Seibert and Wasilewski (2003) for details and photographs.]

1990: Golbeck and coworkers dissociate and restore the Fe–S centers of Photosystem I

Kevin C. Parrett, Tetemke Mehari and John H. Golbeck devised treatments that dissociate and restore the FeS centers of both isolated proteins and chloroplast which recover their light-induced electron transport activity (see Parrett et al. 1990).

1992: Marcus receives the Nobel Prize for his theory of electron transfer reactions

Rudolph Marcus received the Nobel Prize in chemistry for his theory for the varying rates of electron transfer reactions including those in photosynthesis. The theory was based mainly on his work during 1956–1965 [See Marcus (1996); see Figure 13b for his photograph with one of the authors (G) who knew him when he was at the University of Illinois at Urbana, Illinois.]

1992–2001: Fromme, Jordan, Krauß, Klukas, Witt and Saenger describe the structure of Photosystem I

During 1992–2001, Petra Fromme, Patrick Jordan, Norbert Krauß, Horst Witt, Olaf Klukas, and Wolfgang Saenger resolved the X-ray crystallographic structure of Photosystem I of a thermophilic cyanobacterium [see Jordan et al. (2001) for a 3D structure at 2.5 Å resolution; Fromme and Mathis (this issue);

H.T. Witt (this issue) for details]. It is interesting to recall that it was I. Witt et al. (1987) who had first crystallized Photosystem I from a cyanobacterium.

1994: Kühlbrandt and coworkers provide atomic level structure of LHCII

Werner Kühlbrandt and coworkers provided electron crystallographic structure of the light harvesting complex II of plants (see Kühlbrandt 1984; Kühlbrandt and Wang 1991; Kühlbrandt et al. 1994). [For a higher resolution X-ray structure of this complex, see Liu et al. (2004).]

1994: Cramer and coworkers and the structure of part of cytochrome f

S.E. Martinez, D. Huang, A. Szczepaniak, W.A. Cramer and J.L. Smith (1994) solved the crystal structure of the membrane-extrinsic, lumen side domain of cytochrome *f*. [See Martinez et al. (1994) and Cramer (this issue) for details and photographs.]

1994–1997: Boyer, Walker and Skou receive the Nobel Prize in 1997 for the structure and function of ATPases

Paul Boyer and John E. Walker received the Nobel Prize in chemistry, in 1997, for the elucidation of the structure of F_1 mitochondrial ATPase and the mechanism of ATP synthesis. [See Boyer (2002) and Walker (1994); Figure 13c for a photograph of Walker, and Figure 13d for a photograph of Boyer.] Jens C. Skou shared this 1997 prize for his work on ion-transporting enzyme, Na^+, K^+-ATPase.

1995: Bruns and Karplus solve the structure of ferredoxin-NADP oxidoreductase

Christopher Bruns and P. Andrew Karplus (1995) solved the crystal structure of ferredoxin NADP oxidoreductase.

1996: Sugiura and coworkers complete the genome sequence of a cyanobacterium

Kaneko et al. (1996) published the sequence of the genome of the cyanobacterium *Synechocystis* sp. strain PCC 6803. [See Sugiura (2003) for details and photographs.]

1996–1997: Cramer and coworkers: the structure of Rieske iron–sulfur protein

Zhang et al. (1996) characterized and crystalized the lumen side domain of the chloroplast Rieske iron–sulfur protein. Carrell et al. (1997) solved the crystal structure of the lumen side domain of the Rieske iron–sulfur protein.

1999: Pfannschmidt, Nilsson and Allen demonstrate photosynthetic control of chloroplast gene expression

Photosynthetic electron transport, through plastoquinone redox state, governs transcription of chloroplast genes for reaction center apoproteins, both of Photosystem I and Photosystem II, suggesting redox regulation as a function of chloroplast genomes (Pfannschmidt et al. 1999).

2000: the Arabidopsis *genome*

An international consortium publishes the first almost complete genome sequence of a plant, the cruci-

Figure 14. Cytochrome b_6/f structure research groups. (*Top*) The Paris (France) group: *From left to right*: Jean-Luc Popot, Francesca Zito, Yves Pierre, Daniel Picot, David Stroebel, Cécile Breyton and Claudine Lebreton. (*Bottom*) The Purdue (Indiana, USA) group: *From left to right*: Janet L. Smith, Huamin Zhang, Genji Kurisu and William A. Cramer.

fer *Arabidopsis thaliana* (The Arabidopsis Genome Initiative 2000).

2001: Zouni, Fromme, Witt, Sänger and coworkers solve the structure of Photosystem II reaction center

Zouni et al. (2001) solved the X-ray crystallographic structure of Photosystem II reaction center of a thermophilic cyanobacteria at 3.8 Å resolution. [See J. Barber (this issue); H.T.Witt (this issue) for details and photographs.]

Kamiya and Shen (2003) and, more importantly, Ferreira et al. (2004) have now provided further details, particularly on the amino acid ligands to the manganese cluster of the oxygen-evolving complex.

2003: William Cramer and Jean-Luc Popot and their coworkers independently describe the structure of cytochrome b_6*f*

The latest structure is that of cytochrome b_6f, recently (2003) solved by two research groups, one, from *Mastigocladu*s (in alphabetical order: William Cramer, Genji Kurisu, Janet L. Smith and Huamin Zhang, headed by Cramer, at Purdue University, Indiana, USA), and the other, from *Chlamydomonas reinhardtii* (in alphabetical order: Daniel Picot, Jean-Luc Popot and David Stroebel, headed by Popot at Centre National Researche Scientifique (CNRS) Lab, Paris, France). See Figure 14, Kurisu et al. (2003); Stroebel et al. (2003), and Cramer (this issue).

'Hypotheses are nets. He who casts will catch.'
– Novalis (1772–1801)

Concluding remarks

This incomplete listing of historical discoveries spans a period of ∼275 years and begins with the recognition of light, carbon dioxide and oxygen as participants in the growth of plants. The time line ends with the atomic level structures of the reaction centers and intermediate electron carriers of oxygenic photosynthesis. Appendix F provides a list of the proceedings of all the international congresses on photosynthesis since they also provide a time line of the discoveries. Figure 15a shows a photograph of Andy Benson dancing with Christa Critchley, a host and co-organizer, at the 12th International Photosynthesis Congress held in Brisbane, Australia. The tools of the 20th-century science included subcellular fractionation, optical spectroscopy, enzymology and radioactive tracers. The growth in knowledge,

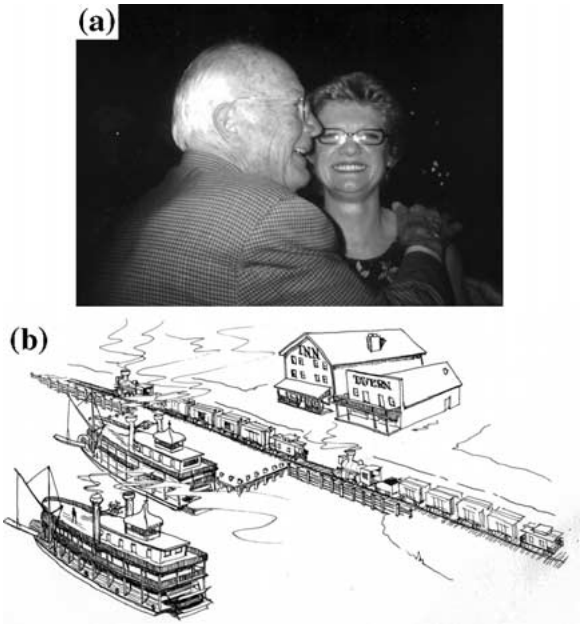

Figure 15. (a) Andrew Benson and Christa Critchley dancing at Brisbane, Australia, in 2001, celebrating the progress of photosynthesis research from Stephen Hales (1727) to Horst Witt (2001). (b) An unpublished (ca. 1950) ink drawing by Eugene Rabinowitch explaining to students the bottleneck reactions of photosynthesis. Electron (or hydrogen atom) transfer as a faster reaction analogous to soldiers being brought by fast trains to the sea shore; and the loading of the soldiers on the slow ships, being the bottleneck event. We imagine that it hints at the slower reactions of the Calvin–Benson–Bassham cycle, and the faster reactions of the production of ATP and reduced NADP.

in money spent, and in the number of investigators has been enormous. The experience of Eugene Rabinowitch, who attempted to summarize all of the research done in photosynthesis, provides a measure of this expansion. Dr Rabinowitch published a book in 1945 entitled 'Photosynthesis, Volume I' of ∼599 pages. In 1951, he published Volume II, Part 1 of ∼609 pages (see Rabinowitch 1951). In 1956, he published Volume II, Part 2 of ∼880 pages (total pages, 2088). In the years that followed, the growth of research results continued and challenged the capacity of any individual to analyze and integrate the new findings in the scholarly fashion that was Dr Rabinowitch's standard. The editors have appropriately dedicated Part 2 of the historical issues to him (see Govindjee et al. 2003b). Figure 15b shows a copy of an ink drawing by Rabinowitch showing the transport of soldiers by trains, and then by ship to Europe during World War II, a faster reaction followed by a bottleneck reaction, in analogy to electron transport in photosynthesis. After 1965, a new level of understanding came into sight. The borders of

spectroscopy would expand to include electron spin resonance (ESR), nuclear magnetic resonance (NMR) and Fourier transform infra-red (FTIR) spectroscopy. The growing availability of crystal structures of proteins and of functional aggregates of proteins contributed greatly to an understanding of the mechanisms of energy capture and stabilization. The highly powerful tools of molecular biology are revealing details of both mechanism of action and the ontogeny of those mechanisms. The atomic level structures are just a beginning for a molecular description of the mechanism of photosynthesis in terms of physics and chemistry. This challenge promises to provide understanding that may enable us to meet the needs facing our World to provide food and energy, giving freedom from hunger and from the dwindling resources of petroleum and oil.

Acknowledgments

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Our sincere apologies to many whose work could not be included here. Readers are requested to send corrections for future revisions to Govindjee (gov@uiuc.edu).

Appendix A. On experiments of Timiriazeff (by A.A. Krasnovsky Jr)

'Timeline A.' '1874–1877: Timiriazeff and red light'

Action spectra of photosynthesis were measured using the set-ups which Timiriazeff had assembled himself. They were based on recording of CO_2 consumption or starch accumulation by plant leaves (Timiriazeff 1874, 1875, 1877). Figure 2 illustrates the results of CO_2 measurement. In this experiment, Timiriazeff used a method of gas analysis proposed by R.W. Bunsen and modified by J.B. Boussingault for work with plant leaves. Timiriazeff found a way to measure very small gas volumes; therefore, his set-ups were smaller and much more sensitive than that of Boussingault. The first and simplest set-up was described by Timiriazeff (1868): there was a small glass tube that contained a leaf, CO_2, water, a small mercury manometer and a special pipette, which allowed titration of the gas mixture using a solution of KOH. Illumination caused consumption of CO_2. The change of the CO_2 volume was measured using the mercury manometer after reaction of the gas mixture with KOH. The action spectrum shown in Figure 2 was measured using more sophisticated devices, based on the same principle.

The lower picture is a series of the absorption spectra of chlorophyll solutions with different optical densities obtained using a spectrophotometer constructed by Timiriazeff. Light provided by the sun or artificial light sources passed through a spectroscope, which consisted of an entrance slit, lens and a prism, and through a cell containing chlorophyll solution. A sheet of paper was placed behind the spectroscope. He drew the spectrum, which he saw, using chlorophyll solutions of different thickness. The major absorption maximum was in the red. With the increase of the optical density of the solutions, green and yellow bands became more and more pronounced in the absorption spectra. Note that at that time nobody knew whether these additional bands belonged to chlorophyll or degradation products. In modern terms, this figure shows the spectra of the fractional absorbance of the chlorophyll solutions. In addition to this experiment, Timiriazeff assembled a microspectroscope, which was a combination of a microscope and a spectroscope. This allowed him to compare the absorption spectra of isolated chlorophyll and 'chlorophyll graines' of plant and algae. This experiment had shown that the absorption spectra were similar within the precision of his measurements (Timiriazeff 1874, 1875, 1877).

Appendix B. A note on E.D. MacAlister from Jack Myers

'Timeline B.' '1940: McAlister, Myers, photosynthesis and chlorophyll fluorescence'

E-mail to Govindjee from Jack Myers, dated 17 October 2002, regarding his 1940 work with MacAlister

Subject: Re: MacAlister
Date: Thursday, 17 October 2002 16:07

Gov: I worked with MacAlister as a National Research Council (NRC) postdoc. I had chosen to go to the Smithsonian Institution in Washington, DC, to work with Mac because I was then interested in the induction period of photosynthesis and thought that the revving up process ought to reveal some insight into what processes were involved. I worked with him from l939 to 1941. He was a very practical optician. The signal from the gas-analysis IR (infra-red) spectrometer was read out from a low resistance vacuum thermocouple for which there was then no reliable electronic amplifier. We built our own using his design for two galvanometers. The primary galvanometer moved a rectangular light spot across a photocell reading out on a second galvanometer which moved its spot across a

slit in front of photographic paper on a moving drum. Naturally, there was a problem in adjusting mirrors for the galvanometer light beams. One mirror was positioned on a wad of chewing gum and (to my amazement) held steady in place for 2 years. Frederick Bracket had left the Division of Radiation and Organisms for National Institute of Health (NIH) and the Division was well down from its earlier hayday but still had a wonderful machine shop and a glass blower, L.B. Clark, who made the marvelous tiny single junction thermocouples. It was with him that we designed and he built the first model of our continuous culture apparatus for algae that held a growing culture in steady state. (Journal of General Physiology, Myers and Clark, about 1942.)
Regards, Jack

Appendix C. Charlton M. Lewis (1905–1996) (by Govindjee)

'Timeline B.' '1941–1943: Emerson, Lewis, the minimum quantum requirement and the red drop in photosynthesis'

After a prolonged illness, Charlton M. (Tony) Lewis died peacefully in his sleep in his home in Altadena, California, on 12 March 1996. Lewis was not only a co-discoverer with Robert Emerson of the famous 'Red Drop' in Photosynthesis (Emerson and Lewis 1943), but it was also he who, with Emerson, showed convincingly that the minimum quantum requirement for oxygen evolution in photosynthesis was 10–12 per oxygen molecule (Emerson and Lewis 1941, 1943), not 4 or less, as Otto Warburg and his colleagues had measured. Further, it was Emerson and Lewis (1942, 1943) who compared quantitatively data on the fractional absorption, *in vivo*, of the various photosynthetic pigments (including carotenoids) with the measured maximum quantum yield of oxygen evolution, as a function of wavelength of light, in cyanobacteria and green algae, reaching the conclusion that the efficiency of excitation energy transfer from cyanobacterial carotenoids to chlorophyll *a* was very small as compared to that in green algae. (It is highly likely that this low efficiency is only apparent since some carotenoids are present in the cell membranes, and act as screens.)

Born on 13 August 1905, in New Haven, Connecticut, Lewis graduated from Taft School (1924) and Yale University (1928), and received his PhD in Physics at California Institute of Technology in 1933 working on the Raman Effect with Professor William Houston. A postdoctoral fellowship at Princeton was interrupted by a 2-year bout with tuberculosis, but during 1937 and 1938, he was invited to the Carnegie Institute of Washington at Stanford, on the initiative of Robert Emerson. During 1939–1941, the two not only built a one-of-a-kind large monochromator and a system to measure precisely the rate of oxygen evolution in weak monochromatic light, but wrote a classical paper that started the famous Emerson–Warburg controversy. [Although both Emerson and Lewis served as 'Research Associates' at the Carnegie Institute at Stanford, Emerson was on the faculty of the Department of Biology at Cal Tech after 1930, with the title of Assistant Professor of Biophysics.] After working with Emerson, Lewis joined the Laboratory of Lawrence Blinks in Marine Biology for a brief period. During World War II, he did research with Ted Dunham in optics and radar at the Mount Wilson Observatory in Pasadena, designing bomb-sights for the Air Force. When the war was over, he entered patent work in partnership with Trimble Barkelew, which he continued until his retirement. The families of Lewis and Emerson have been close friends ever since Bob and Tony worked together on the Stanford campus. Lewis was an outstanding photographer. His black and white photographs of natural scenery as well as the portraits he took of friends and their families are excellent. He had several shows, the most recent one was at the Altadena library. During my visit to Pasadena in January, 1996, I found Tony Lewis to be a very gentle person who held his friend and co-worker Robert Emerson in very high esteem. Lewis is survived by his wife Catherine Woodward Lewis, whom he married in 1929, a son M. Charlton III of Brooklyn, New York, a daughter Meredith Stout of Berkeley, CA, five grand children, and two great grand children. A second daughter Joan died in 1985. Govindjee is thankful to M. Charlton III, and Catherine Lewis for their generous help in preparing this text.

Appendix D. Historical notes on E.C. Wassink (by Wim Vredenberg)

'Timeline B.' '1952: French, Young, Duysens and the energy transfer from accessory pigments to chlorophyll a*'*

E.C. Wassink had pioneered studies on 'chlorophyll fluorescence and photosynthesis' during 1935–1946, in the Physics Biological Spectroscopy Group of the State University at Utrecht (headed by A.J. Kluyver (of Delft) and L.S. Ornstein (Utrecht)). Biophysical research in photosynthesis in the Netherlands received a considerable boost from his work. Some of his papers were published in *Enzymologia* (see, e.g. Wassink and Kersten 1945). It was at Utrecht that LNM Duysens did his classical PhD work on excitation energy transfer in 1952. This was followed by the thesis of J.H.C. Goedheer on orientation of pigment molecules in photosynthesis. Later Jan B. Thomas was a Professor in Utrecht.

Wassink had obtained his PhD in 1934, under F.C. Went, Biology, State University at Utrecht: 'Limiting Factors in Respiration of Phycomyces.' [The thesis was clearly not on photosynthesis; this was like the life of Robert Emerson who did his PhD on 'respiration' in the laboratory of Otto Warburg.] Wassink died at age 76 when he was Emeritus Professor of Plant Physiology at the Agricultural University in Wageningen, on Generaal Foulkesweg 72. (The building was shaped like a ship; an idea of Wassink, we are told. It was in this building that Bessel Kok discovered 'P700.') Wassink was Professor there from 1947 till 1974, a 27-year period.

Wassink was a personality who could justly be called a scholar, for he also had a broad range of knowledge and interests outside the area of botany. He was a well-known collector of rocks, tiles and books and of quite everyday utensils having botanical decorative patterns. His strong willpower and his 'passionate' drive gave himself and the laboratory a leading position within the wider scientific community. Light was always a central theme in his work: Light as the source of energy and of information for all forms of life on earth, in particular in plants. For him this light has now been extinguished after a productive life as an esteemed and memorable photobiologist. (Vredenberg 1982)

Appendix E. Tidbits on the PhD thesis of Jan B. Thomas (by Gijs van Ginkel)

'Timeline C.' '1961: Rajni Govindjee and coworkers discover Emerson effect in the Hill reaction.' See also Appendix F

After the death of Robert Emerson on 4 February 1959, the University of Illinois at Urbana had invited Jan B. Thomas from the Netherlands to look after the students of Emerson: Govindjee and Rajni Govindjee. Thomas was a co-advisor of Rajni Govindjee, and had participated in the discovery of the Emerson enhancement in the Hill reaction. It is of historical interest to note that the PhD thesis of Jan B. Thomas was titled: 'Electric Control of Polarity in Plants'; The thesis was defended on Monday, 20 March 1939, at 4 o'clock in the afternoon in Utrecht, The Netherlands. Thomas' PhD supervisor was Professor V.J. Koningsberger, Head of the Laboratory of Botany, which was part of the Faculty of Biology of the State University in Utrecht. The PhD ceremony ended at 4.45 P.M. and at approximately 5.00 P.M. everybody went to the reception in the historic main building of the university. In his thesis, Jan Thomas wrote about his PhD advisor: 'The years I have spent with you as your assistant will always be with me as a pleasant memory. Apart from your scientific guidance I have appreciated your sympathy. I also highly appreciate the hospitality from Mrs Koningsberger.' See van Ginkel and Goedheer (1991) for an obituary of Thomas.

Appendix F. A list of international photosynthesis congresses

Covering 'Timeline C, D, and E' (Govindjee et al. 2002)

In the early 1960s, Jan B. Thomas (see Appendix E) of the State University of Utrecht, the Netherlands, pushed for the idea of congresses in photosynthesis to be held every 3 years in western Europe. The Americans had their Gatlinburg conferences. Thus, his initiative led to two congresses, one in France (1962), and another in the Netherlands (1965). The late Helmut Metzner was the first one to have expanded this idea into a real international congress in Germany (1968). We present below a list of publications from all the international congresses held thus far. Junk/Nijhoff/Kluwer have published proceedings of the second, and the sixth to the 11th congress. The year of the congress is above each listing, but the year of publication follows the name of the editor or organizer.

1962

Wurmser MR (President) (1963): La Photosynthèse. Colloques Internationaux du Centre National de la Recherche Scientifique (CNRS). No. 119, Gif-sur-Yvette and Saclay, France, July 23–27, 1962, 645 pages. CNRS, Paris

1965

Thomas JB and Goedheer JHC (ed) (1966): Currents in Photosynthesis. Proceedings of the second western-Europe conference on photosynthesis, Woudschoten, The Netherlands, September 1965, 486 pp. Ad Donker Publisher, Rotterdam

1968

Metzner H (ed) (1969): Progress in Photosynthesis Research, 3 volumes, 1807 pp, plus index. Proceedings of the First International Congress on Photosynthesis Research. Freudenstadt, Germany, June 4–8, 1968. Publication sponsored by International Union of Biological Sciences. H. Laupp Junior, Tübingen

1971

Forti G, Avron M and Melandri A (eds) (1972): Photosynthesis: Two Centuries after its Discovery by Joseph Priestley, 3 volumes, 2745 pp, plus index. Proceedings of the Second International Congress on Photosynthesis Research, Stresa, Italy, June 24–29, 1971. Junk, The Hague

1974

Avron M (ed) (1975): Proceedings of the Third International Congress on Photosynthesis, 3 volumes, 2194 pp, plus index. Proceedings of the Third International Congress on Photosynthesis Research, Rehovot, Israel, 1974. Elsevier, Amsterdam

1977

Hall DO, Coombs J and Goodwin TW (ed) (1978): Photosynthesis 77, 1 volume, 821 pp, plus index. (This is the only proceedings that did not include all the papers; only the symposia papers.) Proceedings of the Fourth International Congress on Photosynthesis Research, Reading, UK, September 4–9, 1977. The Biochemical Society, London

1980

Akoyunoglou G (ed) (1981): Photosynthesis, 6 volumes, 4553 pp, plus index. Proceedings of the Fifth International Congress on Photosynthesis Research, Halkidiki, Greece, September 7–13, 1980. Balaban International Science Services, Philadelphia

1983

Sybesma C (ed) (1984): Advances in Photosynthesis Research, 4 volumes, 3439 pp, including index. Proceedings of the Sixth International Congress on Photosynthesis, Brussels, Belgium, August 1–6, 1983. Martinus Nijhoff/ Junk, The Hague

1986

Biggins J (ed) (1987): Progress in Photosynthesis Research, 4 volumes, 3286 pp, including index. Proceedings of the Seventh International Congress on Photosynthesis, Providence, Rhode Island, USA, August 10–15, 1986. Martinus Nijhoff, Dordrecht

1989

Baltscheffsky M (ed) (1990): Current Research in Photosynthesis, 4 volumes, 3731 pp, plus index. Proceedings of the Eighth International Congress on Photosynthesis, Stockholm, Sweden, August 6–11, 1989. Kluwer Academic Publishers, Dordrecht

1992

Murata N (ed) (1992): Research in Photosynthesis, 4 volumes, 3308 pp, plus index. Proceedings of the Ninth International Congress on Photosynthesis. Nagoya, Japan, August 30–September 4, 1992. Kluwer Academic Publishers, Dordrecht

1995

Mathis P (ed) (1995): Photosynthesis: From Light to Biosphere, 5 volumes, 4932 pp, plus index. Proceedings of the 10th International Photosynthesis Congress, Montpellier, France, August 20–25, 1995. Kluwer Academic Publishers, Dordrecht

1998

Garab G (ed) (1998): Photosynthesis: Mechanisms and Effects, 5 volumes, 4397 pp, including index. Proceedings of the 11th International Conference on Photosynthesis, Budapest, Hungary, August 17–22, 1998. Kluwer Academic Publishers, Dordrecht

2001

Osmond B and Critchley C (organizers) (2001): 12th International Congress on Photosynthesis was held in Brisbane, Australia, from August 18–23, 2001. Its proceedings are available on CD entitled 'PS2001 Proceedings' (ISBN: 0 643 06711 6). CSIRO Publishing, 150 Oxford Street (PO Box 1139), Collingwood, Vic. 3066, Australia (e-mail: publishing.sales@csiro.au; web site: www.publish.csiro.au)

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Åkerlund HE, Andersson B and Albertsson PÅ (1976) Isolation of Photosystem II enriched membrane vesicles from spinach thylakoids by phase partition. Biochim Biophys Acta 449: 525–535

Albertsson P-A (2003) The contribution of photosynthetic pigments to the development of biochemical separation methods: 1900–1980. Photosynth Res 76: 217–225

Allen JF (2002) Plastoquinone redox control of chloroplast thylakoid protein phosphorylation and distribution of excitation energy between photosystems: discovery, background, implications. Photosynth Res 73: 139–148

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Anderson JM (2002) Changing concepts about the distribution of Photosystems 1 and 2 between grana-appressed and stroma-exposed thylakoid membranes. Photosynth Res 73: 157–164

Andersson B (1978) Separation of spinach chloroplast lamellae fragments by phase partition including the isolation of inside-out thylakoids, Doctoral thesis, Lund University, Sweden

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Arnon DI, Whatley FR and Allen MB (1954b) Photosynthesis by isolated chloroplasts. II. Photosynthetic phosphorylation, the conversion of light energy into phosphate bond energy. J Am Chem Soc 76: 6324–6329

Avron M (1963) A coupling factor in photophosphorylation. Biochim Biophys Acta 77: 699–702

Avron (Abramsky) M and Jagendorf AT (1956) A TPNH diaphorase from chloroplasts. Arch Biochem Biophys 65: 475–490

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Barber J (2004) Engine of life and big bang of evolution: a personal perspective. Photosynth Res 80: 137–155 (this issue)

Bassham JA (2003) Mapping the carbon reduction cycle: a personal retrospective. Photosynth Res 76: 35–52

Bedbrook JR, Smith SM and Ellis RJ (1980) Molecular cloning and sequencing of cDNA encoding the precursor to the small subunit of chloroplast ribulose-1,5-bisphosphate carboxylase. Nature 287: 692–697

Belyaeva OB (2003) Studies of chlorophyll biosynthesis in Russia. Photosynth Res 76: 405–411

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Bendall DS (2004) The unfinished story of cytochrome *f*. Photosynth Res 80: 265–276 (this issue)

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