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Historical corner

Celebrating 20 years of historical papers in *Photosynthesis Research*★

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Abstract

This Editorial has four goals: (1) to inform the readers of *Photosynthesis Research* about the past of the 'Historical corner'; which began 20 years ago; (2) to encourage photosynthesis researchers and historians of science to contact me for publishing papers of historical interest; these include: (a) Obituaries and Tributes; (b) historical papers on current and past discoveries and controversies; (c) history of research in specific laboratories, or in specific countries, or at specific conferences; (d) Personal perspectives (not discussed any further); (3) to encourage researchers not to discard, but to save correspondence and data of their discoveries for the future historians by donating them to their Archives, when appropriate (not discussed any further); and (4) to reinforce to the readers that the concept of two-light reaction and two-pigment system was already there in 1959. I mention here three key papers presented at the IXth International Botanical Congress, held at Montreal Canada (in August, 1959) prior to the famous April 9, 1960 paper by Robert Hill and Fay Bendall on the 'Z-scheme' of photosynthesis, that was based on thermodynamic and energetic considerations.

Historical corner of *Photosynthesis Research* since 1986: then to now

My association with the Editorial Board of *Photosynthesis Research*, then published by Martinus Nijhoff/ Dr W. Junk Publishers, began with issue 4(1) in 1983. (For a history of the journal *Photosynthesis Research*, see Govindjee et al. (2002).[1]) The Historical corner of *Photosynthesis Research* began publishing dedications, historical papers, personal perspectives, tributes and obituaries only in 1986. In 2006, we celebrate its 20th anniversary. The very first dedication volume was to Louis N. M. Duysens (of Leiden, The Netherlands), edited by the late Jan Amesz, late Arnold Hoff and Hans van Gorkom (Current Topics in Photosynthesis. Photosynth Res **9**: 1–283, 1986); this was followed immediately by a dedication volume to Warren L. Butler (of La Jolla/San Diego, California), edited by Govindjee, James Barber, William Cramer, Jean Lavorel, René Marcelle and Barbara Zilinskas (Excitation Energy and Electron Transfer in Photosynthesis. Photosynth Res **10**: 147–518, 1986). The first published obituary was that of the great master of photosynthesis Cornelis B. van Niel (1897–1985) (of Pacific Grove, California), by R.E. Hungate (Photosynth Res **10**: 139–142, 1986). The first personal perspective was published 2 years later; it was by Roderick K. Clayton (of

★This *Historical corner* Editorial is dedicated to Bessel Kok (1918–1978).

Cornell University, Ithaca, New York) (Photosynth Res **19**: 205–224, 1988). It was not until a year later that a historical note, entitled 'Emil L. Smith: the discovery of a chlorophyll–protein complex during 1937–1941, was published by Govindjee (Photosynth Res **16**: 285–289, 1989).

We have come a long way since then. (For a list of historical papers and dedications, published during 1986–2002, see Govindjee and David Krogmann (Photosynth Res **73**: 11–20, 2002).) We specifically note that special volumes have been published dedicated to several pioneers: For example, Don DeVault (R. Blankenship, late J. Amesz, D. Holten and J. Jortner (eds) Tunneling Processes in Photosynthesis. Photosynth Res **22**: 1–122, 1989 and others); Robin Hill (P. Rich (ed) Robin Hill. Photosynth Res **34**: 319–477, 1991); Bessel Kok and Pierre Joliot (G. Renger and Govindjee (eds) How Plants and Cyanobacteria Make Oxygen: 25 Years of Period Four Oscillations. Photosynth Res **38**: 211–469, 1993); Daniel Arnon (A. Melis and B. Buchanan (eds) A Tribute to Daniel I. Arnon. Photosynth Res **46**: 1–377); and William Arnold (Govindjee, late J. Amesz and R.S. Knox (eds) Photosynthetic Unit: Antenna and Reaction Centers. Photosynth Res **48**: 1–319, 1996).

A major effort was launched in 2001 when we initiated a celebration of the millennium for the historical highlights of photosynthesis research. This depended on the close collaboration and guidance of Howard Gest, who is one of the few historians amongst us. We were soon joined by J. Thomas Beatty and John F. Allen (Govindjee and H. Gest, Photosynth Res **73**: 1–320, 2002; Govindjee, J. Thomas Beatty and H. Gest, Photosynth Res **76**: 1–476, 2003; Govindjee, J.T. Beatty, and John F. Allen, Photosynth Res **80**: 1–480). I am extremely delighted that a book 'Discoveries in Photosynthesis', based on these three volumes, will be released, in 2005, by Springer (as Volume 20 of Advances in Photosynthesis and Respiration Series, ISBN: 1-4020-3323-0).

Papers of historical interest published since volume 80 (2004) include obituaries or tributes[2] to: André Pirson (1910–2004); Jean-Marie Briantais (1936–2004); Gerald J. Small (1941–2004); Birgit Vennesland (1913–2001); Lawrence Bogorad (1921–2003); Theodor Engelmann (1843–1909); August Ried (1924–2004); Julio-López Gorgé (1935–2004); Gauri Singhal (1933–2004); and John Biggins (1936–2004). Obituaries that are in press at the moment are of Allan Brown (1917–2004); and Lee McIntosh (1949–2004) and Yoshihiko Fujita (1932–2005). R. G. Jensen (2004)[3] has written a perspective on the discovery of the activation of Rubisco controlling CO_2 assimilation in light and R.J.P. Williams (2005)[3] a historical paper about the discovery of the physico-chemical nature of ferredoxin. In addition, A. J. Keys has written his perspective on 'Re-assimilation of ammonia produced by photorespiration and the nitrogen economy of C_3 higher plants'; this article is currently in press. Further, a perspective 'Photosynthesis Research in Canada from 1945 to the early 1970s' (by Paul R. Gorham and Constance G. Nozzolillo) is also in press in *Photosynthesis Research*. Another perspective, 'Studies on chlorophyll biosynthesis and other things', by Paul A. Castelfranco, has been submitted for publication. Invitations for submission of six obituaries (tributes) and two perspectives have been made for editing in 2006.

Three presentations on the two-light effects (August, 1959, Montreal, Quebec, Canada): by Bessel Kok; Jack Myers; and Eugene Rabinowitch

There were three speakers who discussed two-light effects at the IXth (1959) International Botanical Congress in Montreal (see Appendix 1 for details and for the abstracts that were submitted ahead of the Congress): Bessel Kok; Jack Myers; and Eugene Rabinowitch. Long abstracts of Kok[4] and Myers[5] presentations (with one key figure in each paper) were published in the 'Recent Advances in Botany, volume II' book (1961). However, it was noted on the bottom of p. 1076, the last page of Myers' paper, that the 1959 presentation by Rabinowitch[6] was published in Plant Physiology, as R. Emerson and E. Rabinowitch, in 1960. I know that a paper by Kok[7] (1959) also contained data and discussion on the two-light effect. These presentations preceded the famous scheme of Hill and Fay Bendall (1960),[8] Emerson enhancement effect papers of Govindjee and Rabinowitch (1960),[9] Rajni Govindjee et al. (1960)[9] and of Myers and French (1960a, b),[10] as well as the crucial experiments of Duysens et al. (1961)[11] who did the clearest experiments proving the existence of two-light reactions and two pigment systems. Further, it was Duysens et al.[11] who named the light reactions as 1 and 2 and the pigment systems as 1 and 2. [For further references to others (not mentioned here) and discussion on this topic, see Govindjee and Krogmann (2004);[12] a special recognition is, however, made for the paper by Witt et al. (1961)[13].]

I note that Robert Emerson, not Rabinowitch, was initially invited to the Montreal Congress, but, tragically, Emerson was killed in a plane crash on February 4, 1959; thus, Rabinowitch gave the talk. The special condition of the Rabinowitch presentation is stated in the R. Emerson and E. Rabinowitch paper[6] (also see Appendix 1). This paper was received on November 2, 1959 for publication; and a note, by E. Rabinowitch, on the top of the paper reads:

> When Robert Emerson was killed in a plane accident on February 4, 1959, much of the experimental material accumulated in his two years work on the action spectrum of photosynthesis in the far-red region remained unpublished. He was to present these results to the Botanical Congress in Montreal in August, 1959. Instead the following paper was presented on the basis of Emerson's earlier talks and laboratory notes, and after consultation with his collaborators, R.V. Chalmers and C. Cederstrand. The theoretical discussion of the results is my own.

This IXth International Botanical Congress was held 2 years after the pioneering 1957 paper on the discovery, in photosynthesis, of the (Emerson) Enhancement effect by Robert Emerson et al.[14] and on the discovery of the chromatic transients by Lawrence R. Blinks.[15] (Blinks, had, however, suggested the effect to be due possibly to effects on respiration.) Myers related the Blinks and the Emerson effects, and Kok related the antagonistic effect of two-lights on P700 to the Emerson effect.

The 1959 Kok presentation[4] included the following statements (also see Appendix 1 for Kok's abstract submitted ahead of the Congress):

- It appeared that the bleaching of P700 was sensitized by chlorophyll *a*. However, the accelerated regeneration of P700 was largely sensitized by accessory pigments (such as chlorophyll *b* in green plants, phycocyanin in *Anacystis*). The activation spectra indicated a small contribution of chlorophyll *a* also in the latter process. [*I have not yet succeeded in finding this action spectra in print... Govindjee (G).*] This indicates that the accessory pigment acts in conjunction with part of chlorophyll *a* – probably by transferring absorbed quanta to it (G: Also see Duysens[16]) This type of antagonistic action between two beams absorbed by different pigments is illustrated in Figure 1 [in the Conference Proceedings].
- A more profound analysis of data as shown in Figure 1 [in the Conference Proceedings] leads to the inevitable conclusion that two antagonistic light reactions and at least one dark step determine the concentration of (the absorbing form of) P700.
- *[Kok recognized Emerson enhancement effect and what it meant – G]* He stated: A requirement of two quanta per electron transfer in photosynthesis seems well established by now, and there is abundant additional evidence – such as that derived from studies of color transients and of the so-called enhancement effect – that more than one photochemical act must play a role in photosynthesis.
- *If indeed P700 does play such a key role, the finding of two opposite effects of light, sensitized by different pigment entities, leads to the hypothesis of a cyclic process, driven one way by quanta received by chlorophyll a and back by quanta received by accessory pigment[s].* [G: Also see Kok (1959),[7] that was published earlier in May, 1959, where Kok showed (on pp. 190–192) for the first time the antagonistic effect of two lights on the redox state of P700; in this issue of Plant Physiology, authors included Duysens, Hill and others, but no one gave any hint of their findings on the two-light effect.]
- The last statement (in italics) did not explicitly state the idea of the two-light reactions leading to a non-cyclic flow of electrons from water to NADP, that came later in the hypothesis of Hill and Fay Bendall (1960)[8] and experimental and theoretical insight of Duysens et al. (1961)[11] as well as that of Horst Witt et al. (1961)[13] that followed soon thereafter.

The 1959 Myers presentation[5] included the following statements (also see Appendix 1):

- The almost identical action spectra (Figure 1 [in these Proceedings]) for the (Blinks) chromatic transients and for (Emerson) enhancement are taken as evidence for a specific contribution of chlorophyll *b* to both phenomena. [G: It soon became clear that chlorophyll *b* does not do any photochemistry itself.]
- From these considerations one cannot escape the conclusion that there must be two kinds of photo-events in photosynthesis, one of them specifically associated with chlorophyll *b* (or other accessory pigment) [G: Also see Myers and French (1960a, b)[10] where the idea that there was a dark step between the two photo-events was clearly observed.]

I note that Kok's presentation was ahead of Myers as regards the evolution of the two-light reaction concept; the major contribution of Myers was to show the equivalence of the action spectra of the Emerson Enhancement Effect and the Blinks Chromatic transients. Although the shoulder for chlorophyll *a* can be seen in the action spectra of the Enhancement Effect, its existence and meaning was not recognized by Myers:[5] it was left to Govindjee and Rabinowitch (1960)[9] to recognize it, particularly because they observed a clear-cut peak at 670 nm (for chlorophyll *a*) in the action spectrum of the Enhancement effect in a diatom *Navicula*. In addition, at the 'Light and Life' symposium, held during March 28–31, 1960, and published in 1961, C. Stacy French[17] independently recognized the role of chlorophyll *a* 670. L.N.M. Duysens has pointed out to me that this peak in the Emerson effect is, most likely, a peak in the difference spectrum between photosystems 2 and 1.

The 1959 Rabinowitch presentation (R. Emerson and E. Rabinowitch (1960)[6]):

Rabinowitch reviewed extensively the experimental results of Robert Emerson and his associates on the red drop in the quantum yield of photosynthesis, and on the action spectrum of the Emerson effect in several algae. The idea that chlorophyll *b* must function by transferring energy to chlorophyll *a* in that system was there since Duysens (1952),[16] but it became obvious for one of the two photosystems in the work of Kok,[4] Govindjee and Rabinowitch (1960);[9] Rajni Govindjee et al. (1960);[9] and French (1961).[17] [This idea was not stated by Rabinowitch in the 1959 abstract at the Congress (see Appendix 1).]

The effect of the time interval between the two beams of light on the Emerson Effect was recognized by Rabinowitch.[6] [Myers and French (1960a, b)[10] clearly established that the Enhancement took place even with a dark interval of 0.6 s, and, thus, a biochemical, rather than a photophysical, explanation should be favored.] (Emerson and) Rabinowitch (1960) wrote:

> The simplest one [explanation] is to postulate that two (or more) different photochemical processes are involved in photosynthesis, and are preferentially sensitized by the several pigments. For example, one could imagine that photosynthesis requires both photoreduction (of CO_2 or of a substrate derived from it) and photooxidation (of water or a substrate derived from it). One could derive essentially the same concept by saying that each hydrogen atom (or electron) must be photoactivated twice on its path from the ultimate donor, water, to the ultimate acceptor, carbon dioxide, and that each of these two steps is preferentially sensitized by one or the other pigments.

There may have been bits and pieces of ideas for a simple two-light reaction 'Z-scheme' in Rabinowitch's mind already since (1) E. Rabinowitch (1945)[18] had presented a 1941 'Z-scheme' of James Franck and Karl F. Herzfeld (1941) without the names of any intermediates, and without the 'energy drop' as in the Hill and Bendall (1960) scheme; and (2) Rabinowitch (1956)[19] wrote:

> The quantum requirement of the hydrogen transfer reaction as a whole would be (at least) 8, since two quanta will be needed to transfer each of the four required H atoms (or electrons), first from water to the cytochrome, and then from the cytochrome to the final acceptor.

Additional remarks

Just a few years after oxygen evolution and P700 were measured in two-light beams, measurements on a two-light effect on chlorophyll fluorescence were reported by Govindjee et al. (1960)[20] and Kautsky et al. (1960).[20] More importantly, Bessel Kok and George Hoch[21] expanded Kok's ideas of 1959, in March, 1960, and presented a two-photoact scheme, independent of the Hill and Fay Bendall (1960)[8] and Duysens et al. (1961)[11] schemes. Now, I understand a bit better why Jack Myers had such a high regard for Kok's contributions to the two-light reaction two-pigment system concept. He knew of the 1959 presentation of Kok at Montreal that many of us had missed since it was only a short abstract (see Appendix 1) and then only a 2-page abstract at the 1959 Congress. I am ashamed that I found it only on September 7, 2005, and read it for the first time! Surprisingly, I was alerted by a manuscript of D.C. Fork and C.S. French that I discovered in August, 2005, in the Archives of the Carnegie Institute of Washington, Washington, DC.

Kok's 1959 scheme, however, basically used one reaction center (P700): an accessory pigment system (containing some chlorophyll *a*) oxidized water and reduced oxidized P700, whereas the chlorophyll *a* system oxidized P700 and reduced an electron acceptor labeled as 'X'. A closer look shows a dark step between the two photoacts. The schemes of Hill and Fay Bendall (1960)[8] and of Duysens et al. (1961)[11] were more complete and thorough; although they have been extensively modified and continue to be challenged and modified, their basics have survived.

The idea of Blinks (1957)[15] that the two-light effect was in respiration was proven to be an error when Rajni Govindjee et al. (1960)[9] observed the Emerson effect in the 'Hill reaction' in quinone-treated *Chlorella*, where respiration is inhibited; this experiment further showed that the two-light effect is involved in electron flow from water to the Hill oxidant, not CO_2 fixation.

Kok's 1959 experiments and those of Duysens et al., in 1961, take a central stage rather than the '*ahead-of-time*' model in Rabinowitch (1945) and the prophecy[19] of 1956. However, the Hill and Fay Bendall scheme, although initially a hypothesis, holds a special position because it provided a clear energetic framework for linking the two-light reactions and the dark reactions, and showed how a dark electron transfer step, similar to that in mitochondria, might provide energy for ATP synthesis.

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I thank Robert Blankenship and now David Knaff for their support to what we have been doing for the last 20 years for the history of photosynthesis research and that of the researchers. I am also grateful to Derek Bendall and David Walker for their advice and criticism. The final touches were given generously by Julian Eaton-Rye and Kärin Nickelsen. I owe gratitude to Ellen Girmscheid and Jacco Flipsen (formerly of Kluwer, now Springer) for their continued help. My personal association with Bessel Kok dates back to the summer of 1962 when my wife Rajni and I spent 2 months in his laboratory in Baltimore, discovering, with George Hoch, Emerson enhancement effect in the NADP Hill reaction, and establishing, with Olga Owens and George Hoch, using mass spectroscopy, that the Emerson effect was on photosynthesis, not on respiration. My respect for Bessel and his work rose exponentially after this initial interaction. I enjoyed discussing science as well as people with him; he was always very frank in his criticism of 'poor research' and 'incompetent scientists'. He was a top-notch scientist (see his Biography by Jack Myers[22]); a dedication to his 1959 paper on the 'two-light' effect at Montreal means a lot to me. Cheers, Bessel!

Notes

1. Govindjee, Z. Šesták and W.R. Peters (2002) The early history of 'Photosynthetica', 'Photosynthesis Research', and their publishers. *Photosynthetica* **40**: 1–11.
2. H. Saenger (2004) Tribute: In memory of Professor Dr h.c. André **Pirson**, a pioneer in photosynthesis and a dedicated academic teacher. Photosynth Res **82**: 111–114; Y. de Kouchkovsky and Z.G. Cerovic (2005) Jean-Marie **Briantais** (1936–2004), a friend and a champion of interactive and integrative research. Photosynth Res **83**: 1–3; R. Jankowiak and M. Seibert (2005) Remembering Gerald J. **Small** (1941–2004), who tackled everything in life with an intrinsic and enviable passion. Photosynth Res **83**: 5–9; E.C. Conn, E.K. Pistorius and L.P. Solomonson (2005) Remembering Birgit **Vennesland** (1913–2001), a great biochemist. Photosynth Res **83**: 11–16; S. Rodermel, J.-F. Viret and E. Klebbers (2005) Lawrence **Bogorad** (1921–

2003), a pioneer in photosynthesis research: a tribute. Photosynth Res **83**: 17–24; G. Drews (2005) Contributions of Thoedor Wilhelm **Engelmann** on phototaxis, chemotaxis and photosynthesis. Photosynth Res **83**: 25–34; H. Strotmann and C.-J. Soeder (2005) August **Ried** (1924–2004), an outstanding researcher, an artist and a dear friend. Photosynth Res **83**: 279–281; M.S. Barragan (2005) A tribute to Julio **López-Gorgé** (1935–2004): The music in science. Photosynth Res **83**: 283–286, 2005; U.P. Andley, P.N.R. Velagaleti, A. Sen and B.C. Tripathy (2005) Gauri Shankar **Singhal** (1933–2004): A photochemist, a photobiologist, a great mentor and a generous friend. Photosynth Res **85**: 145–148; and D. Bruce and K. Sauer (2005). John **Biggins** (1936–2004): His ingenuity, tenacity and humor; no-nonsense science with a big heart. Photosynth Res **85**: 261–265.

3. R.G. Jensen (2004) Activation of Rubisco controls CO_2 assimilation in light: a perspective. Photosynth Res **82**: 187–193; and R.J.P. Williams (2005) The discovery of the nature of ferredoxin in photosynthesis: a recollection. Photosynth Res **85**: 247–250.
4. B. Kok (1961): Does photosynthesis require the interaction of two photochemical steps? In: Recent Advances in Botany, Volume II: From Lectures and Symposia presented to the IXth International Botanical Congress, Montreal, August, **1959**, pp. 1071–1072, University of Toronto Press, Toronto, Canada.
5. J. Myers (1961) Evidences for a specific participation of chlorophyll *b* in photosynthesis. In: Recent Advances in Botany, Volume II: From Lectures and Symposia presented to the IXth International Botanical Congress, Montreal, August, **1959**, pp. 1073–1076, University of Toronto Press, Toronto, Canada.
6. R. Emerson and E. Rabinowitch (1960) Red drop and role of auxiliary pigments in photosynthesis. Plant Physiol **35**: 477–485 (November 2, **1959,** published in July, 1960).
7. B. Kok (1959) Light-induced absorption changes in photosynthetic organisms. II. A split-beam difference spectrophotometer. Plant Physiol (Robert Emerson Memorial Issue) **34**: 184–192 (March 23, 1959; published May, 1959).
8. R. Hill and F. Bendall (1960) Function of the cytochrome components in chloroplasts: A working hypothesis. Nature **186**: 136–137. (April 9, 1960) [There were citations to Daniel Arnon (photophosphorylation), Louis N.M. Duysens (cytochromes); and to Al Frenkel (review).]
9. Govindjee and E. Rabinowitch (1960) Two forms of chlorophyll *a in vivo* with distinct photochemical functions. Science **132**: 355–356. (March 21, 1960; published August 5, 1960); R. Govindjee, J.B. Thomas and E. Rabinowitch (1960) Second Emerson effect in the Hill reaction of *Chlorella* cells with quinone as oxidant. Science **132**: 421–421 (June 7, 1960; published August 12, 1960).
10. J. Myers and C.S. French (1960a) Evidences from action spectra for a specific participation of chlorophyll *b* in photosynthesis. J Gen Physiol **43**: 723–736. (July 23, 1959; published in March, 1960); J. Myers and C.S. French (1960b) Relationships between time course, chromatic transient, and enhancement phenomena of photosynthesis. Plant Physiol **35**: 963–969.
11. L.N.M. Duysens, J. Amesz and B.M. Kamp (1961) Two photochemical systems in photosynthesis. Nature **190**: 510–511 (May 6, 1961). Duysens had recognized in this paper the work of Robert Emerson et al. (1957) and of Rajni Govindjee et al. (1960) stating that it is this work that showed that light reactions 1 and 2 operated in the Hill reaction.
12. Govindjee and Krogmann D (2004) Discoveries in oxygenic photosynthesis (1727–2003): a perspective. Photosynth Res **80**: 15–57 (Received May 7, 2003; accepted in revised form August 24, 2003).
13. H.T. Witt, A. Müller and B. Rumberg (1961) Experimental evidence for the mechanism of photosynthesis. Nature **191**: 194–195. (July 8, 1961; two-light effects suggested involvement of a cytochrome, and indirectly of a plastoquinone called 'X' as intermediate between the 'Chl *a*-670' and 'Chl *a*-680' systems of Govindjee et al. (1960); Witt and Rabinowitch had recognized the work of Robert Emerson and coworkers; Myers and French (1960a, b); and Rajni Govindjee et al. (1960), among others, as well as the paper of Hill and Bendall (1960).)
14. R. Emerson, R.V. Chalmers and C.N. Cederstrand (1957) Some factors influencing the long wave limit of photosynthesis. Proc Natl Acad Sci USA **43**: 133–143. (Communicated November 19, 1956; published in January, 1957) Also, see the following abstracts: (a) R. Emerson, R.V. Chalmers, C. Cederstrand and M. Brody (1956) Effect of temperature on the long-wave limit of photosynthesis. Science **123**: 673; (b) R. Emerson (1957) Dependence of the yield of photosynthesis in the long-wave red on wavelength and intensity of supplementary light. Science **125**: 746; R.Emerson (1958) Yield of photosynthesis from simultaneous illumination with pairs of wavelengths. Science **127**: 1059–1060. A presentation of Emerson, that I had heard at Bloomington, Indiana, was published as: R. Emerson and R.V. Chalmers (1958) Speculations concerning the function and phylogenetic significance of the accessory pigments of algae. Phycological Society of America News Bulletin **11**(35): 51–56.
15. L.R. Blinks (1957) Chromatic transients in photosynthesis of red algae. In: Gaffron H, Brown AH, French CS, Livingston R, Rabinowitch EI, Strehler BL and Tolbert NE (eds) Research in Photosynthesis, pp. 444–449, Interscience Publishers, New York. (Conference date: October 25–29, 1955) [Blinks explained the transients in two-light beams as possibly due to 'an altered respiratory rate during the first moments of light absorption by phycoerythrin'. Emerson commented 'We have been doing somewhat similar experiments with red and green algae, looking at the subsequent respiration after exposure to different wavelengths of light. In the case of red algae there is a strong promoter effect of green and blue-green light on the subsequent respiration, analogous to the depressing effect on photosynthesis described by Emerson and Lewis for *Chlorella* at about 480 mμ in the blue'. Thus, neither Blinks, nor Emerson, knew of the Enhancement effect in photosynthesis in 1955.]
16. L.N.M. Duysens (1952) Transfer of Excitation Energy in Photosynthesis. Doctoral Thesis, State University, Utrecht, The Netherlands.
17. C.S. French (1961) Light, pigments and photosynthesis. In: W.D. McElroy and B. Glass (Eds.) Light and Life, pp. 447–474. The Johns Hopkins Press, Baltimore, MD (Conference was held on March 31, 1960).

18. E. Rabinowitch (1945) Photosynthesis and Related Processes. Volume I (see scheme 7. V., page p. 162). Interscience Publishers, New York.
19. E. Rabinowitch (1956) Photosynthesis and Related Processes. Volume II, Part 2 (see p. 1862). Interscience Publishers, New York.
20. Govindjee, S. Ichimura, C. Cederstrand and E. Rabinowitch (1960) Effect of combining far-red light with shorter wave light on the excitation of fluorescence in *Chlorella*. Arch Biochem Biophys **89**: 322–323. (June 15, 1960; published August, 1960); H. Kautsky, W. Appel and H. Amann (1960) Chlorophyll Fluoreszenz und Kohlensaureassimilation. XIII. Mitteilung. Die Fluorescenzecurve und die Photochemie der Pflanze. Biochem. Z. 332: 277–292. (October 7, 1959; published January, 1960)
21. B. Kok and G.E. Hoch (1961) Spectral changes in photosynthesis. In: W.D. McElroy and B. Glass (Eds.) Light and Life, pp. 397–423. The Johns Hopkins Press, Baltimore, MD (Conference was held on March 31, 1960).
22. J. Myers (1987) Bessel Kok (November 7, 1918–April 27, 1979). Biographical Memoirs (The National Academy Press, Washington, DC) **57**: 124–149.

Appendix 1

The Time and the Place of the Three 1959 Talks

Four volumes of the proceedings (labeled as Volumes I (Program), II (Abstracts), 2A (Abstracts) and III (Plenary Sessions, Nomenclature) were distributed at the 'IXth International Botanical Congress, held in Montréal, Canada' during August 19–29, 1959. Page 145 of Volume I (printed by The Runge Press Limited, Ottawa, 1959) shows the program for the 1st session of the symposium on 'Photochemistry and Spectroscopy of Chlorophyll *in vivo* and *in vitro*'. This session was held on Monday, August 24, 1959, at the Sir Arthur Currie Gymnasium (West) at the McGill University; it was chaired by C.S. French and had 5 speakers (A.A. Krasnovsky at 9:00 AM; A.S. Holt at 9:45 AM; B. Kok at 10:30 AM; A. Pugh and R. Livingston at 11:00 AM; and H.J. Trurnit at 11:30 AM). The title of **Bessel Kok**'s talk is listed as 'Does photosynthesis require the interaction of two photochemical steps?' Page 149 of Volume I shows the program for the final (called 'concluded') session of the symposium on 'Photochemistry and Spectroscopy of Chlorophyll *in vivo* and *in vitro*'; it was held in the afternoon of August 24, 1959, and in the same lecture hall as the first session; it was also chaired by C.S. French and had 5 speakers (J.E. Myers at 2: 00 PM; E. Rabinowitch at 2:25 PM; J.H.C. Smith at 2:50 PM; W. Vishniac at 3:10 PM; and G. Tollin at 3:35 PM). The title of **Jack Myers**'s talk is listed as 'Evidences for a specific participation of chlorophyll *b* in photosynthesis', whereas that of **Eugene Rabinowitch** as 'Robert Emerson's investigations of the action spectra of photosynthesis (In memory of Robert Emerson)'.

The three 1959 abstracts

Volume II A of the proceedings of the 'IXth International Botanical Congress, held in Montréal, Canada', printed by the Mortimer Limited (1959), contains the abstracts submitted by the speakers before the Congress.

Page 18 (volume II A) has the following abstract by **Bessel Kok**:

Kok, Bessel. Research Institute for Advanced Studies, Baltimore, U.S.A. *Does photosynthesis require the interaction of two photochemical steps?* Based directly on recent different spectroscopic data and indirectly on various other observations, a hypothesis will be discussed **which conceives a cycle of two photochemical acts in photosynthesis** [bolded by G]. Indicative of these two steps are the formation and disappearance of an absorption band around 700 mμ. Both effects are photo-induced, but the activation spectra are different. In *Anacystis*, light absorbed by chlorophyll-*a* or transferred to it causes breakdown [G: equivalent to 'bleaching']; in the restoration of the 700 mμ pigment only light absorbed by phycocyanin is active [G: Kok may not have realized prior to the Congress the role of chlorophyll *a* in this system as he did in the publication cited in the main text above]. It looks as if breakdown is a direct photochemical process **whereas the restoration, though photo-induced, requires intermediate dark steps** [bolded by G]'.

Page 24 (Volume II A) has the following abstract by **Jack Myers**:

Myers, Jack. Carnegie Institution of Washington, Stanford and University of Texas, Austin, U.S.A. *Evidences for a specific participation of chlorophyll b in photosynthesis.* Rate of oxygen evolution in photosynthesis was measured as the current from a platinum electrode covered by a layer of *Chlorella* cells about 15 μ thick. The arrangement gave a reproducible measurable rate of photosynthesis proportional to light intensity at the low levels used and gave rapid response to changes in illumination. Three phenomena have been explored. (1) The Emerson effect was studied as enhancement of photosynthesis in long wavelength red light (700 mμ) when shorter wavelengths were added. (2) Large and reproducible transients in oxygen evolution were observed accompanying change in illumination between two wavelengths adjusted in intensity to support equal steady rates of photosynthesis. (3) Differences in the time kinetics of photosynthesis were found to be wavelength dependent. The three phenomena have identical action spectra which are interpreted as demonstrating a specific photochemical participation of chlorophyll *b* in photosynthesis.

Pages 29 and 30 (Volume II A) have the following abstract by **Eugene Rabinowitch**:

Rabinowitch, Eugene. University of Illinois, Urbana, U.S.A. *Robert Emerson's investigations of the action spectra of photosynthesis (in memory of Robert Emerson).* Robert Emerson's investigations of the photosynthesis action spectra of algae of different classes extended from 1941 to his tragic death in February, 1959, and were characterized from the beginning by clear understanding of the significance of these spectra. He measured maximum quantum yields, in truly monochromatic light, as a function of wavelength, rather than – as others did and still do – the rate of photosynthesis somewhere between the regions of light limitation and light saturation, in broad spectral regions isolated by color filters. Through this work, the contribution of different pigments to photosynthesis were first established reliably and precisely, in *Chlorophyceae* (Emerson and Lewis, 1941–1943) *Diatomeae* (Tanadad, 1951 [G: the name should be Tanada]), *Cyanophyceae* (Emerson and Lewis, 1942) and *Rhodophyceae* (Emerson and M. Brody, in press). In modern physics, the derivation of new qualitative understanding from precise quantitative measurement of phenomena is a common path of advance; in biology, this path is only rarely available, due to difficulties in precise measurement and the complexity of the phenomena. Emerson's studies of action spectra were of this rare kind. Among their most recent successes was the discovery, with M. Brody, of the dependence of the relative photosynthetic efficiency of phycobilins and of the chlorophyll in red algae on the pre-treatment of the organisms (which suggests a new aspect of the problem of mutual coupling and energy transfer between the molecules of these pigments in the chloroplasts); and the analysis (with R. Chalmers, C. Cederstrand and M. Brody) of the decline of the efficiency of chlorophyll *a* in spectral regions where it is the only absorbing pigment – above 680 mμ in green algae and above 650 mμ in red algae. These observations solved the puzzle of 'inactive chlorophyll *a*' in red algae, raised by less precise spectral studies of other investigators, and raised instead a more fundamental puzzle of the specific function of accessory pigments (chlorophyll *b* in green algae, phycobilins in red algae, etc.) in photosynthesis. Emerson's last months were dedicated to the attempts to approach this problem in his characteristic way – by further improvement of measurements, and wider variation and better control of the physiological state of the algae (such as composition of the pigment system, intensity of respiration, variations in nutrition) and of possibly relevant physical conditions (such as spatial distribution of the absorption of the far red light, absorbed only by chlorophyll *a*, and of light of shorter wavelengths, absorbed also – or mainly – by one of the accessory pigments). An attempt will be made in the paper to review as far as possible these unpublished experimental results, and to discuss their significance for our present concepts of the primary photochemical process in photosynthesis.

A partial list of photosynthesis-related scientists attending the Congress

In addition to the speakers mentioned in the first paragraph of this *Appendix*, the following, among others, were listed to have been members of this IXth International Congress: Mary Belle Allen (USA); Daniel Arnon (USA); Sam Aronoff (USA); Thomas T. Bannister (USA); Andrew A. Benson (USA); Norman Bishop (USA); Lawrence Bogorad (USA); Warren Butler (USA); George Cheniae (USA); V. B. Evstigneev (USSR); Giorgio Forti (Italy and USA); Albert Frey-Wyssling (Switzerland); Clint R. Fuller (USA); Hans Gaffron (USA); Martin Gibbs (USA); Norman Good (then in Canada); Paul Gorham (Canada); Per Halldal (Sweden); Francis T. Haxo (USA); David M. Krogmann (USA); Gleb Krotkov (Canada); Paul Latimer (USA); Ralph Lewin (USA); Berger Mayne (USA); Alex Moyese (France); Kurt Mühlethaler, (Switzerland); Anatoly Nichiporovich (USSR); André Pirson (Germany); Elver Steeman-Nielsen (Denmark); Mary Stiller (USA); Ralph C Stocking (Canada); Hiroshi Tamiya (Japan); Achim Trebst (Germany); Evert C. Wassink (The Netherlands); and Diter von Wettstein (Sweden).