

*Dedication*

## **In appreciation of Bessel Kok**

Govindjee<sup>1</sup> & G. Renger<sup>2</sup>

<sup>1</sup>*Department of Plant Biology, University of Illinois, 265 Morrill Hall, 505 S. Goodwin Avenue, Urbana, IL 61801-3707, USA;* <sup>2</sup>*Technische Universität Berlin, Max-Volmer-Institut für Biophysikalische und Physikalische Chemie, Strasse des 17. Juni 135, D-10623 Berlin, Germany*

Received and accepted 7 November 1993

*Key words:* Bessel Kok, Pierre Joliot, oxygen clock

### **Abstract**

This issue of *Photosynthesis Research* is dedicated to the memory of Bessel Kok, the discoverer of the photoactive reaction center pigment of Photosystem I, P700, and a pioneer in the field of biophysics of photosynthesis. We particularly salute his formulation of the '5-step S-state O<sub>2</sub> clock,' based on the elegant experiments of Pierre Joliot. Pierre observed a characteristic period four oscillation of the O<sub>2</sub> yield when dark-adapted photosynthetic samples were illuminated with a train of single turn-over flashes. We honor Pierre by inviting him to write his personal perspective in which he discusses the events that led to this seminal discovery.



Bessel Kok and Pierre Joliot. Gordon Conference, 'Regulatory Mechanism in Photosynthesis,' 13–17 August 1973. Photo by Achber Studio, Laconia, NH, used by permission.

At the time of writing this dedication, our thoughts go back in memory of a fascinating person and a pioneer of modern photosynthesis research: Bessel Kok. The occasion of his 75th birthday (November 7, 1993) is an appropriate opportunity to recall the eminent role of Bessel's work. Coincidentally, this is also the time to celebrate the 25th anniversary of discovery of the characteristic period four oscillation in oxygen evolution by Pierre Joliot and his coworkers. It was this experimental finding and Bessel's straightforward analysis that led to the famous '5-step S-state O<sub>2</sub> clock' (Kok et al. 1970), often referred to as the 'Kok-cycle' in the literature.

Both of us (G and GR) appreciate the tremendous impact of this discovery on the present-day research in the field of photosynthetic water oxidation. In addition, however, another very important point appears to us worth emphasizing. The discovery of the 'Kok cycle' illustrates how much can be achieved by a fruitful cooperation of open-minded scientists who are free of selfish competition (see also Cheniae 1993, Joliot 1993).

It was fortunate for the USA that Bessel Kok accepted, in 1958, a position at the Research Institute of Advanced Studies (RIAS) of the Martin Marietta Company in Baltimore, MD, USA. Already in Wageningen (The Netherlands) in E. C. Wassink's laboratory, shaped interestingly on the outside like a ship, Bessel had made extraordinary discoveries. He had solved with elegant experiments, performed during World War II, the controversy on the maximum quantum yield of oxygen evolution in photosynthesis (Kok 1948, Emerson 1958). Also, through elegant experimentation, he removed all doubts to the validity of the concept of photosynthetic unit (Kok and Businger 1956, 1957), developed by Hans Gaffron and K. Wohl (1936) on the basis of the classical experiments of Robert Emerson and William Arnold (1932a,b). More excitingly, he discovered the photoactive pigment of the reaction center of Photosystem I, that he called P700 (Kok 1956, 1957a,b). Duysens (1981) wrote: 'The long working hours and inexhaustible inventivity and drive necessary to get such an apparatus working successfully in a relatively short time, and to carry out and analyze a large number of experiments, were amply rewarded – Bessel discovered the far-red absorption changes associated with the reaction center P700 of system I.'

In Baltimore, Bessel discovered that P700 was

oxidized by far-red (red) light and reduced by orange light in cyanobacteria (called blue-green algae then), and he was the first one, in the special issue of *Plant Physiology* dedicated to Robert Emerson, to discuss the relationship of this novel observation (Kok 1959) with the Emerson enhancement effect (Emerson et al. 1957, Emerson and Chalmers 1958). Thus, Bessel was a pioneer before others came into the picture that led to the current concept of the two-light reaction – two pigment systems (see e.g. Duysens 1989). It was in the summer of 1962 that one of us (G) was fortunate to work and to make discoveries, in Bessel's laboratory, with George Hoch and Rajni Govindjee, on the Emerson enhancement effect in Chloroplast reactions. The memories of wonderful Bessel are still fresh; he was pleasant, but sharp; he was intuitive but logical; sometimes he was even insulting but friendly. His smile always gave him away: He acted like an older brother who would scold you, while loving you at the same time. G also remembers his first wonderful meeting at the Airlie house arranged by Bessel and Andre Jagendorf (1963). The most exciting event was the social organized mostly by Bessel and Hans Rurainski. Among other unforgettable jokes, Giorgio Forti was made the 'King of Chloroplast'; he sat on a throne and gave away prizes; some of the recipients had to kneel before the King! (The only one spared of this humor was the Nobel-prize winning physicist, James Franck.) Eugene Rabinowitch got a scroll that started, 'In the beginning there was light ...,' as he was the biblical prophet of photosynthesis. It was great fun and left an important impression on one of us (G).

To our sorrow, our beloved friend Bessel Kok left us on April 27, 1979. (For memorials to Bessel, see Duysens 1981, Jagendorf 1981, Cheniae and Myers 1982, Myers 1987, Cheniae 1993 and Joliot 1993). 1994 will be the 15th anniversary of Bessel's death. Myers (1987) has summarized a description of Bessel as: 'He appreciated a good hypothesis deeply and had the strength of character not to let an ugly fact stand in the way. He had a knack of discerning the "nuggets" (Bessel's own word) of a problem. He was extraordinarily open minded to any new concept or experiment, even if it was in contradiction to his own ideas. He could make you a better scientist just by asking questions. He had a basic belief that, if he could measure anything with a ten times greater sensitivity than had been achieved

before, he was bound to discover something new. He had learned to smile while criticizing. And, he was always searching, either for a simpler hypothesis or for a better joke.' Both of us share these thoughts about Bessel. One of us (G) laughed enough with Bessel at the 1970 Gatlinburg Conference on the 'Photosynthetic Unit' that the stomach still hurts from laughter, just by thinking about that time. (It was a Conference that honored giants like Hans Gaffron, Eugene Rabinowitch, Stacy French, Robin Hill, William Arnold and Larry Blinks.)

Pierre Joliot was at this conference, too. He had already discovered a year earlier (Joliot et al. 1969) the period four oscillations of oxygen yield as a function of flash number, in dark adapted samples illuminated with a series of saturating 'single turnover flashes'. That key paper was the basis of Kok's oxygen clock. For one of us, (GR), Pierre's discovery was also the catalyst for the completion of the Ph.D. thesis (1969) because it provided the framework for a consistent explanation of a number of observations by assuming that some chemicals are able to induce shorter lifetimes of intermediary redox states in the water oxidase. An exciting and unforgettable stay of only two weeks in Pierre's lab was sufficient to confirm this idea and characterize the phenomenon now called the ADRY (Acceleration of the Deactivation Reactions of the water splitting enzyme system Y) effect.

We both feel it appropriate to honor Pierre Joliot and to remember Bessel Kok through this special issue of *Photosynthesis Research*. Leading scientists in the field were invited to share our idea by submitting their contributions. Almost all of them were willing and able to accept our invitation. The result of all the efforts made is this special issue before you. It includes refereed minireviews and research papers that touch upon the various aspects of photosynthetic water cleavage. We thank all the authors in joining us in dedicating this issue to Bessel and in honoring Pierre.

## References

- Cheniae GM (1993) A recollection of the development of the Kok-Joliot model for photosynthetic oxygen evolution. *Photosynth Res* 38: 225–227
- Cheniae GM and Myers J (1982) Bessel Kok (1918–1979): A tribute. In: Govindjee (ed) *Photosynthesis, Vol I: Energy Conversion by Plants and Bacteria*, pp xxi–xxiii. Academic Press, New York
- Duysens LNM (1981) In memory of Bessel Kok. In: Akoyunoglou G (ed) *Proceedings of the Fifth International Congress on Photosynthesis, Vol I*, pp xix–xx, Balaban International Science Services, Philadelphia
- Duysens LNM (1989) The discovery of the two photosynthetic systems: A personal account. *Photosynth Res* 21: 69–79
- Emerson R (1958) The quantum yield of photosynthesis. *Ann Rev Plant Physiol* 9: 1–24
- Emerson R and Arnold W (1932a) A separation of the reactions in photosynthesis by means of intermittent light. *J Gen Physiol* 15: 391–420
- Emerson R and Arnold W (1932b) The photochemical reaction in photosynthesis. *J Gen Physiol* 16: 191–205
- Emerson R and Chalmers RV (1958) Speculations concerning the function and phylogenetic significance of the accessory pigments in algae. *Phycol Soc Amer News Bull* 11: 51–56
- Emerson R, Chalmers RV and Cederstrand CN (1957) Some factors influencing the long-wave limit of photosynthesis. *Proc Natl Acad Sci USA* 43: 133–143
- Gaffron H and Wohl K (1936) *Zur Theorie der Assimilation* (in German) *Naturwiss* 24: 81–90
- Jagendorf A (1981) In memory of Bessel Kok. In: Akoyunoglou G (ed) *Proceedings of the Fifth International Congress on Photosynthesis, Vol I*, pp xxi–xxiii. Balaban International Science Services, Philadelphia
- Joliot P (1993) Earlier researches on the mechanism of oxygen evolution: A personal account. *Photosynth Res* 38: 214–223
- Joliot P, Barbieri G and Chabaud R (1969) Un nouveau modèle des centres photochimiques du système II. *Photochem Photobiol* 10: 309–329
- Kok B (1948) A critical consideration of the quantum yield of *Chlorella* photosynthesis. *Enzymologia* 13: 1–56
- Kok B (1956) On the reversible absorption change at 705 nm in photosynthetic organisms. *Biochim Biophys Acta* 22: 394–401
- Kok B (1957a) Absorption changes induced by the photochemical reaction of photosynthesis. *Nature (London)* 179: 583–584
- Kok B (1957b) Light-induced absorption changes in photosynthetic organisms. *Acta Bot Neerlan.* 6: 16–36
- Kok B (1959) Light-induced absorption changes in photosynthetic organisms II. A split beam difference spectrophotometer. *Plant Physiol* 34: 184–192
- Kok B (chairman) and Jagendorf A (organizer) (1963) *Photosynthetic Mechanisms of Green Plants*. Publication #1145, National Academy of Sciences–National Research Council, Washington, DC, 766 pp
- Kok B and Businger JA (1956) Kinetics of photosynthesis and photoinhibition. *Nature (London)* 177: 135–136
- Kok B and Businger JA (1957) Kinetics of photosynthesis. In: Gaffron H, Brown AH, French CS, Livingston R, Rabinowitch EI, Strehler BL and Tolbert NE (eds.) *Research in Photosynthesis*, pp 354–357. Interscience, New York
- Kok B, Forbush B and McGloin M (1970) Cooperation of charges in photosynthetic oxygen evolution I. A linear four-step mechanism. *Photochem Photobiol* 11: 457–475
- Myers J (1987) Bessel Kok, Nov 7, 1918–April 27, 1979. *Biographical Memoirs, National Academy of Science USA*, 57: 125–148

