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HISTORY & BIOGRAPHY

George Edward Hoch (1931–2023): a great photosynthesis scholar, a real family man, and a wonderful friend to many

G. GOVINDJEE

Department of Plant Biology, Department of Biochemistry, and Center of Biophysics and Quantitative Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801, USA

Abstract

We present here a tribute to George E. Hoch, one of the top leaders in deciphering the primary steps of oxygenic photosynthesis. After providing his academic background, we discuss his selected research on the photoreactions of photosynthesis. We end this tribute with reminiscences by Robert S. Knox, Jerome Kaye, and Doris Teichler-Zallen.

Keywords: Bessel Kok; Louis N.M. Duysens; RIAS (Research Institute of Advancement of Sciences), Baltimore, Maryland; University of Wisconsin at Madison.

Introduction

George Edward Hoch, born in 1931, passed away in 2023. Fig. 1 shows a photograph of George taken by his wife Sally Free on 2 February 2019. He was a distinguished scholar and a great human being. For personal information on George, we refer the readers to his obituary at https://obituaries.nationalcremation.com/obituaries/north-fort-myers-fl/george-hoch-11392711.

Academic background and research

George's keen interest in science was through his undergraduate and graduate studies. In 1953, he obtained his BS (in Biology) from South Dakota State College (now University). Soon thereafter, he joined, as a graduate student, the Department of Chemistry at the University of

Fig. 1. A 2019 photograph of George E. Hoch. Source: Sally Free.

Highlights

- G. E. Hoch was one of the pioneers of the two-light reaction scheme of oxygenic photosynthesis
- He exploited mass spectroscopy to distinguish between the effects of light on respiration and on photosynthesis
- He interacted well with Bessel Kok, the discoverer of P700

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e-mail: gov@illiniois.edu

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Conflict of interest: The author declares no conflict of interest.

Wisconsin, Madison. His studies were interrupted when he was called into active duty. He was stationed in England and served as a first lieutenant in the Army Chemical Corp (1953–1955). Following this assignment, he returned to the University of Wisconsin to continue his research and studies. In 1958, he received his PhD in Biochemistry, focusing his work, under the mentorship of Robert (Bob) H. Burris (1914–2010) on the nitrogenase and the hydrogenase, enzymes involved in nitrogen fixation (*see* Hoch 1958, and Appendix 1); for his discovery of hydrogen evolution using soybean root nodules, *see* Hoch *et al.* (1957).

After his PhD, George focused on the basics of photosynthesis and spent the next six years at RIAS (Research Institute for Advanced Studies, in Baltimore, MD), working with Bessel Kok, the discoverer of the reaction center of Photosystem I (PSI), P700. His discoveries related to the two-light reaction two-pigment system concept are included in an extremely thorough, detailed, and a most critical review (Hoch and Kok 1961) I have ever read in my life, and in a 1960 presentation at a conference on 'Light and Life' (Kok and Hoch 1961). In addition, George was involved, at that time, in showing that P700 can be observed not only by absorbance changes but by ESR (electron spin resonance): *see* Beinert *et al.* (1962). For a historical overview of research in this area, which includes the discovery of Robert Emerson (1903–1959) on the two-light effect in photosynthesis, *see* Govindjee (2023).

My association with George and his research

Rajni (my life partner) and I have known George Hoch, both as a wonderful person and as a great scientist, since the summer of 1962 at the RIAS. When we arrived in Baltimore, none of the major hotels would rent us a room. Seeing this discrimination against us, George immediately took charge and within a day found us a nice apartment to rent so that we could begin our research. We have remained highly thankful to George for this. I vividly remember his large friendly family, where we were often invited for dinner; we had a great time together. What is important for the 'history of photosynthesis research' is the problem we went to solve in Kok's research group. The 1957 discovery of the 'enhancement effect' by Robert Emerson, suggesting that oxygenic photosynthesis is run by two-light reactions and two pigment systems, was being challenged by many. The problem was that Emerson had used manometry that could not distinguish between changes in photosynthesis (oxygen evolution) from that in respiration (oxygen uptake). Rajni had already shown that the Emerson enhancement effect existed in the 'light reactions' of photosynthesis since she had observed it in the para-benzoquinone Hill reaction (R. Govindjee *et al.* 1960). However, it was necessary to show it by mass spectroscopy in whole cells, and in NADP reduction in chloroplasts. George was busy perfecting the technique of mass spectroscopy for this purpose in order to differentiate between the changes in oxygen exchange due to respiration and photosynthesis (*see e.g.*, Hoch and Kok 1963). It was for these reasons that we sought collaboration with George Hoch. R. Govindjee *et al.* (1962, 1964) published the crucial positive existence of the 'two light reactions and two pigment systems' in NADP reduction, and Govindjee *et al*. (1963) showed, by mass spectroscopy, that this effect was in photosynthesis of whole cells. Both were done in friendly collaboration with George. Hoch *et al*. (1963a,b) had just then been providing details of their research separating oxygen exchange due to photosynthesis from that in respiration, and all the nuances associated with them, involving not only the effects of different intensities of light, but of physiological changes, and even those caused by the addition of inhibitors, on oxygen production as well as on oxygen uptake. Thus, I would say that our joint research was a timely event! Thus, no one could question the existence of the two-light and two-pigment system concept. At the International congress held in Gif-sur-Yvette, France, Kok and Hoch (1963) summarized all their joint discoveries on this topic, whereas Rabinowitch (1963) summarized all the discoveries, at the University of Illinois at Urbana-Champaign, on the same topic. It is essential to mention that the Z-scheme of photosynthesis (Hill and Bendall 1960), the key experiment of Duysens *et al.* (1961) on the antagonistic effect of light 1 and 2 on cytochrome *f*, and that of Kok and Gott (1960; also *see*: Kok 1959) on the two light effects on P700 were already known by 1963! For history, it is important to mention that George Hoch had been heavily involved in discussing all of the above thoughts and ideas on 28–31 March 1960 at Johns Hopkins University, at the symposium on 'Light and Life', about the time the Hill and Bendall (1960) scheme was published (*see* Govindjee *et al.* 2017, for a history of the Z-scheme). As happens in science, many ideas come together for the same concept, and George Hoch definitely had an important part in it.

Following the above and more at RIAS, George continued his research as a professor in biochemistry at the University of Pennsylvania, University of Rochester, University of California San Diego, and Stanford University. He retired as Professor Emeritus from the University of Rochester in 1992. Here, George had a great comradery with Thomas (Tom) Bannister and after Tom's passing away, we both participated in writing a tribute to Tom (Laws *et al.* 2018). Fig. 2 is a photograph of George with Tom: *see* Teichler-Zallen *et al*. (1972) for their earlier joint research on cyclic electron flow in wild type and mutants of the green alga *Chlamydomonas reinhardtii.*

What has been important for us is that George remained a wonderful friend over the years through phone calls until almost the end – two of us remembering many personal and scientific stories of Bessel Kok, Robin Hill, Eugene Rabinowitch, Lou Duysens, and many more. And, for all this, we thank George for his collaborative and friendly spirit. We all miss George.

We end this tribute to George Edward Hoch with reminiscences by Robert (Bob) Knox (which includes two photographs from his archives, Figs. 3 and 4), by Jerome Kaye, and by Doris Teichler-Zallen.

Fig. 2. A 2014 photograph of George Hoch (*left*) with Thomas Bannister, discussing science, when George visited the University of Rochester. Source: archives of George Hoch family (also *see* Laws *et al*. 2018).

Reminiscence by Robert Knox
(e-mail: rknox@ur.rochester.edu)

"George Hoch was my first coauthor in the field of photosynthesis. Our review chapter (Hoch and Knox 1968) was a patch of two mini-reviews that hardly related to each other (molecular energy transfer, mine, and fluorescence kinetics, his), but we owned each other's work, and thus began my appreciation of a science distant from physics."

"George welcomed my experimentalist students into his laboratory and helped them with the instrumentation. In retrospect, he should have been included as a coauthor of their papers, but I was still following the policy of many physicists: encouraging solo authorship of students. Let this reminiscence set the record straight. My students and I owed George a great deal."

Reminiscences by Jerome Kaye
(e-mail: skayej@rochester.rr.com)

"George Hoch was a colleague and a close friend to me and my wife Susan. He had the ability to make people feel important, and that was certainly true for us. This ability was carried over to the students who took his courses. They thought that they were being taught by a distinctly unusual professor who really cared about their learning."

"On a personal level, George helped me through a difficult period when my first wife died, something which I will never forget. When Susan and I married, I decided to take a sabbatical in France to explore a field new to me, molecular biology. George rented our house and made it easy for us to extend our stay in France an extra year.

Fig. 3. A 1968 photograph of George Hoch (*right*) with Robert Knox, at Dartmouth (Hanover, New Hampshire) during the 5th International Congress on Photobiology. Source: archives of the Knox family.

Fig. 4. A 1985 photograph of George Hoch (*left front*) and Louis (Lou) N. M. Duysens (*right front*). Behind George (*in the back row*) is Bob Knox with his wife Myrta (standing); next to her sitting (and partly hidden) is Lou's wife Willy Duysens. On the right (*in the back row*) is the physicist Gérard Albert Mourou, cowinner of – with his student Donna Strickland and Arthur Ashkin – the 2018 Physics Nobel Prize for the invention of a method to make high power and short duration laser pulses. The person sitting between Duysens and Mourou is unidentified. Source: archives of the Knox family.

George always loved sailing and when he retired, he sailed the inland waterway to Florida. Along the way he met Sally, a fellow sailor, and they remained together for the rest of his life in Florida. We visited them several times there. George always wondered why we didn't move to Florida, away from the frigid north."

"George had a wonderful family, and he was devoted to them, always telling us about their accomplishments. We miss George and are grateful for the times we spent with him."

Reminiscences by Doris Teichler-Zallen
(e-mail: dtzallen@vt.edu)

"I first met George Hoch in 1965 at the Hotel Cadillac – an old and fading hotel in downtown Rochester, N.Y. My physicist husband and I were staying there while apartment hunting. He was hired by the Xerox Research Laboratories, but I was still finishing my dissertation under the mentorship of Paul Levine at Harvard (for Levine, *see* Rochaix 2022), studying the role of manganese in photosynthesis in the unicellular green alga *Chlamydomonas reinhardtii* (*see* Teichler-Zallen 1969)."

"I recall being really nervous while sitting in that gloomy lobby. I was, of course, quite familiar with Hoch's work conducted with Bessel Kok which had helped underpin the two-light reaction two-photosystem model of oxygenic photosynthesis and wished to work in areas opened up by this fundamental insight. But, given the sad reality of those days, I was even more concerned about whether he would even accept a woman as a post-doc into the laboratory he was just starting up at the University of Rochester. I needn't have worried. He was keenly interested in my dissertation research, discussed new areas we could pursue, and invited me to join him."

"George had a very impressive ability to design and build equipment. This enabled us to report results on such things as the cyclic electron flow in Photosystem I in algae in which Photosystem II had been inhibited (Teichler-Zallen and Hoch 1967; also *see* Teichler-Zallen *et al*. 1972). Also impressive was the large number of cups of coffee he would consume throughout each day. This beverage was randomly concocted in an Erlenmeyer flask by anyone who arrived first in the lab that morning. It was generally regarded as undrinkable by the rest of us."

"When my research interests shifted into the then-expanding realm of human and medical genetics, George was disappointed but, nevertheless, became a strong supporter. He would always keep an eye out for ways to help me negotiate my entrance into this very different field – suggesting possible contacts and writing letters of support whenever needed. I will always be grateful for that post-doc experience and for George's many kindnesses even after it ended. We all miss him."

Appendix 1. George Hoch's PhD thesis, in Biochemistry, was defended by him on 3 June 1958; his committee members were Robert (Bob) H. Burris (1910–2010), Robert A. Alberty (1921–2014), and Karl Paul G. Link (1901–1978). George's thesis, that dealt with nitrogenases and hydrogenases, was in two parts. Part I (26 pages) dealt with the use of cell-free preparations (in sucrose) of *Closteridium pasteurianum* and *Azotobacter vuenlandii* – where he studied the effects of partial pressures of H_2 on N_2 fixation. On the other hand, Part II (22 pages) dealt with the relationship of hydrogenase activity to nitrogen fixation; here, George used freshly excised soybean root nodules – and showed it – to evolve H_2 when placed under oxygen (Hoch *et al.* 1957). Further, George showed that these nodules could also convert NO to N_2. It is time to exploit these early observations by George to our benefit!

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