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MINIREVIEW

On the evolution of the concept of two light reactions and two photosystems for oxygenic photosynthesis: A personal perspective

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Abstract

I present here a personal perspective of the evolution of the two-light reaction two-pigment scheme for the electron transport in oxygenic photosynthesis – as I have lived through it – first as a graduate student of Robert Emerson, from September 1956–January 1959, and then of Eugene Rabinowitch from February 1959–September 1960. I have provided here some of the key published work in my way and have also provided a few photographs. It is essential to remind ourselves upfront that different individuals may have different recollections of the same event (*see e.g.*, the Japanese movie 'Rashomon' https://en.wikipedia.org/wiki/Rashomon). Thus, I encourage others to write about their perspective. Further, I recognize, upfront, the support and encouragement I have received from Robert Blankenship for writing this perspective, and from Győző Garab for submission of this story to *Photosynthetica*. I begin my perspective with a dedication to Robert Emerson, whose pioneering work led to the concept of the two-light reaction two-pigment system in oxygenic photosynthesis.

Keywords: Bessel Kok; cytochromes; Emerson enhancement effect; Louis N.M. Duysens; P700; red drop in photosynthesis; Robert (Robin) Hill; Z-scheme.

Dedication to Robert Emerson

'History is the action and reaction of these two, nature and thought.' – Ralph Waldo Emerson

I dedicate this perspective to my mentor Robert (Bob) Emerson (1903–1959) at the University of Illinois at Urbana-Champaign (UIUC); *see* Fig. 1 for a 1957 portrait of Emerson. His discoveries, in the 1930s, of the existence of a 'photosynthetic unit' (large number of chlorophyll *a* molecules serving a photo-enzyme, now 'reaction center'), in the 1940s, of the minimum quantum requirement for oxygen evolution to be 8–12 (not 3–4), and in the 1950s, of the enhancement effect on photosynthesis of far-red light by supplementing with different short wavelengths of light (that we now call the Emerson enhancement) was the basis and key to the realization of the two-light reaction two-pigment system of all oxygenic photosynthesis, now known as the Z-scheme. (*See* Appendix 1 for information on what UIUC has done to recognize the contributions

Highlights

- The history of the Z-scheme of the photosynthetic electron transport
- The nature of the Emerson enhancement effect – not a respiration artifact
- Contributions of Rabinowitch, Hill, Kok, Duysens, and a few others

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Fig. 1. A 1957 portrait of Robert Emerson at his desk in the Natural History Building, 505 South Mathews Avenue, Urbana, Illinois. Photo by the author (Govindjee).

of Emerson by having a plaque, a named professorship, and a student award; Appendix 2 lists the names of all the student awardees.)

Introduction

I now present a brief story of the historical timeline for the evolution of the concept of two light reactions and two photosystems for oxygenic photosynthesis that began in the early 1940s and was firmly established by the mid-1960s, leading to the concept of the current Z-scheme that we know today. It is presented here, on the New Year of 2023, in memory of Robert (Bob) Emerson (*see* 'Dedication'; and Govindjee 2004, 2018, 2020; Govindjee and Govindjee 2021), as well as of other topmost scientists of our time – with whom I had personally interacted. They include James Franck (1882–1964; https://www.nobelprize.org/prizes/physics/1925/franck/biographical/); Eugene Rabinowitch (1898–1973; Govindjee 2004, Govindjee *et al*. 2019); Robert (Robin) Hill (1899–1991; Kamen 1992, Krasnovsky 1992, Walker 1992, Bendall 1994); William (Bill) Arnold (1904–2001; Choules and Govindjee 2014, Govindjee and Srivastava 2014); C. Stacy French (1907–1995; Govindjee and Fork 2006); Martin D. Kamen (1913–2002; Govindjee and Blankenship 2021); Bessel Kok (1918–1979; Govindjee and Renger 1993); Louis (Lou) N.M. Duysens (1921–2015; Govindjee and Pulles 2016); and Horst T. Witt (1922–2007; Renger 2008).

For our earlier review on the evolution of the Z-scheme of photosynthesis, *see* Govindjee *et al*. (2013, 2017).

Before any thought on the concept of two light reactions–two pigment systems, we had the concept of what was then called the 'Photosynthetic Unit', *i.e*., hundreds of chlorophyll *a* molecules serving to collect and funnel energy, obtained from light to a few 'photo-enzyme' molecules, later known as 'reaction centers'. It was based on the original research of Emerson and Arnold (1932a,b), but clearly enunciated by Gaffron and Wohl (1936).

The first theoretical two-light reaction scheme of oxygenic photosynthesis

During the 1940s, electron transport from water to X (now known as $NADP^+$-nicotinamide adenine dinucleotide phosphate) was suggested, on theoretical grounds, to involve two light reactions – one to take electrons from an intermediate ZH to Y, and the other from YH to X (Franck and Herzfeld 1941, Rabinowitch 1945); it was basically to accommodate the fact that the minimum quantum requirement for the evolution of one molecule of oxygen was 8–10. Only much later, Govindjee *et al.* (2013) stated that the photosystem that runs ZH to Y reaction must be considered to be run by what we now call Photosystem II (PSII), and the other for electron transfer from YH to X to be Photosystem I (PSI). The minimum number of 8–10 photons, over 3–4 photons, per oxygen, has stood the test of time, despite persistent challenges by Otto Warburg [*see* R. Govindjee *et al.* (1968), and discussion in Govindjee (1999), Nickelsen and Govindjee (2011) and in Hill and Govindjee (2014)].

Fig. 2 shows Robert Emerson, in the late 1940s, with Otto Warburg (1883–1970), and others, at the University of Illinois at Urbana-Champaign, while Warburg was invited by Emerson, hopefully, to solve the controversy on the minimum quantum requirement for oxygen evolution. We all know that Warburg claimed that a minimum of 3–4 quanta were needed for the evolution of one oxygen molecule, whereas Emerson's values were always 8–12 quanta for the same – and the latter was and is the correct value (*see e.g*., Nickelsen and Govindjee 2011).

The 'red drop' and the 'Emerson enhancement effect'

Emerson and Lewis (1943) discovered an intriguing phenomenon that the above-mentioned maximum quantum

Fig. 2. A late 1940s photograph of Otto Warburg holding the manometer that he and Emerson used to measure the maximum quantum yield of oxygen evolution to solve the differences in values the two had earlier published; Emerson is on the extreme right attentively looking, and Dean Burk is pointing his finger to it. Source: Nickelsen and Govindjee (2011).

yield (inverse of the minimum quantum requirement) decreased dramatically beyond ~685 nm in the green alga *Chlorella*; this was the famous 'red drop' that had puzzled Emerson for years (*see* Fig. 3, *left*); it also puzzled me, when I was a student of Botany at Allahabad University, in India, and led me to join Emerson's laboratory in 1956 (*see* Govindjee 2019; also *see* Block 2022). And this was what was tackled (and solved) by Emerson in the 1950s, presented first at a conference in 1956 (Emerson *et al.* 1956); then in 1957 (Emerson 1957); and finally at two conferences in 1958 (Emerson 1958, Emerson and Chalmers 1958). In addition, Emerson published two papers: Emerson *et al.* (1957) on the single-cell green alga *Chlorella*; and Brody and Emerson (1959) on the unicellular red alga *Porphyridium* on what Emerson had discovered – an enhancement of photosynthesis when two light beams, one in the 'red drop' region, and another in the shorter wavelength region were given together than when given separately. This became known as the 'Emerson enhancement effect' (*see* Fig. 3, *right*; cf. Emerson *et al.* 1957) and was explained to be due to the functioning of two light reactions sensitized by two different pigment systems. Emerson died in a plane crash on 4 February 1959, and did not get to see how his work was and is the experimental basis of the current 'two-pigment system and two-light reaction concept'. The action spectra of this Emerson enhancement effect, obtained by Emerson and Chalmers (1958), were published by E. Rabinowitch, after Emerson's death, in Emerson and Rabinowitch (1960). Emerson had concluded in all the above-mentioned research that one photoreaction (what we now call Light Reaction I in Photosystem I) is run by chlorophyll *a*, and the other (what we now call Light Reaction II in Photosystem II) is run by accessory pigments (chlorophyll *b* in the green algae; fucoxanthol in the diatoms; and a phycobilin in the red algae). This is where I stepped into the picture and made an important modification to the latter (*see* below).

My question to Emerson and its solution

Since the fall of 1956, I was a graduate student of Emerson in a program then called 'Physico-Chemical Biology' (later changed to 'Biophysics'). I had great difficulties with the concept of Emerson (*see e.g.*, Emerson and Chalmers 1958) that the accessory pigments would run any light reaction since Duysens (1952) had shown that light energy absorbed by accessory pigments was efficiently transferred, as excitation energy, to chlorophyll *a*. In the case of chlorophyll *b*, 100% of light is transferred to chlorophyll *a*. When I would walk back with Emerson, in 1957, going to my apartment (after classes), I would raise this concern.

I would say to him, 'Professor Emerson, your conclusion does not fit Duysens's experiments.'

His answer was, 'These are our results.'

He would often add, 'Duysens is a physicist, and I cannot be sure if his cells were really alive.'

Emerson died too soon to see my results on photosynthesis (Govindjee and Rabinowitch 1960a,b), and that of Rajni Govindjee (Govindjee *et al.* 1960a, R. Govindjee and Rabinowitch 1961) on the Hill reaction, since both showed the presence of Chl *a* 670 in addition to the accessory pigment (Chl *b*) implying that the second light reaction is run by Chl *a*. This solved the dilemma I had presented to Emerson during our walks (*see* above). We have always regretted that Emerson could not be a co-author of our papers, but all our work was published with Eugene Rabinowitch (*see* Fig. 4), PhD advisor of both Rajni and myself.

Interestingly, I read, just when writing this perspective, that Rabinowitch (1959) had also written his views on

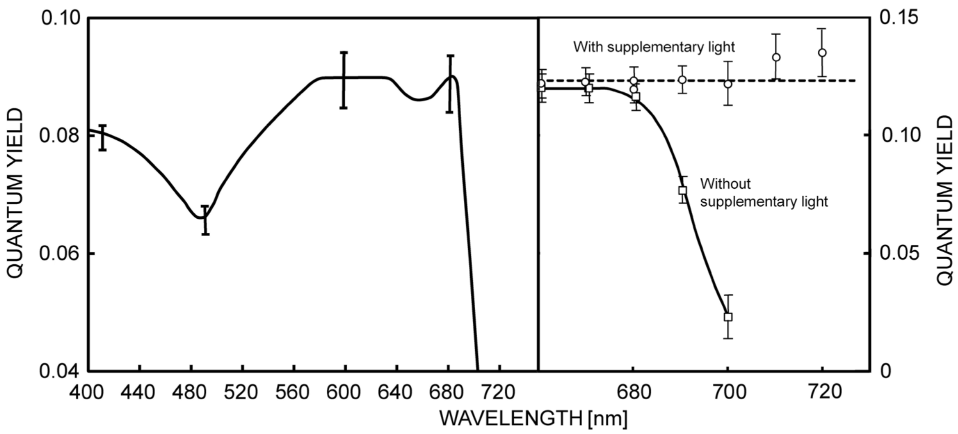

Fig. 3. Maximum quantum yield of oxygen evolution as a function of wavelength of light in the green alga *Chlorella pyrenoidosa*. *Left*: Data of Robert Emerson and Charleton Lewis (Emerson and Lewis 1943); the 'red drop' is the decline in the yield of photosynthesis beyond 685 nm; the 'dip' in the 500 nm region is due to absorption by some inactive carotenoids. *Right*: Data of Govindjee (1963) in the 'red drop' region, as well as the 'Emerson enhancement effect' in it, using supplementary light of shorter wavelengths – confirming the data of Emerson *et al*. (1957) – with corrections for the effects of light on respiration and the measured absorbance values. For another version of this figure, and of Figs. 5–8, *see* Govindjee's lecture: 'A journey for photosynthesis in Urbana with a focus on Robert Emerson, 25 April 2022', available at: https://www.life.illinois.edu/govindjee/talks.html.

Fig. 4. Eugene Rabinowitch in his office in 156 Natural History building, of the University of Illinois at Urbana-Champaign, on 505 Matthews Avenue, Urbana, Illinois, USA – Rajni Govindjee is behind him doing experiments; ~ mid-1960s. Source: Govindjee family archives.

the dilemma of how accessory pigments can run a photo-reaction, to which, he had added 'Thus, the problem remains open and calls for more experimentation with the skill and patience Emerson would have applied to it.' It is now apparent that this was done, in the 1960s, by those who were trained by Emerson (*see* below for further discussion). Fig. 5 shows the action spectra of the Emerson enhancement effect in photosynthesis (Govindjee and Rabinowitch 1960a,b), and Fig. 6 shows the action spectra of the Emerson enhancement effect in para-benzoquinone Hill reaction (R. Govindjee *et al.* 1960a, R. Govindjee 1961), both showing the presence of Chl *a* 670 in the system that has accessory pigments, *e.g.*, Chl *b*.

I received my PhD (Biophysics), in 1960, under Eugene Rabinowitch (Govindjee 1960) and Rajni, in 1961, in Botany (R. Govindjee 1961). I joined the Faculty of Botany (later renamed Plant Biology) at UIUC in 1961; at that time, I urged Emerson's technical assistant, Carl Cederstrand, a Physics graduate, to join my research group as a PhD student, but jointly with Eugene Rabinowitch, who served as his major advisor (*see* Cederstrand and Govindjee 2022). For our observations of different spectral forms of chlorophyll *a* in the two photosystems, *see* Cederstrand *et al*. (1966a,b) – in line with the action spectra of the Emerson enhancement effect (*see* Govindjee 1960).

Was Emerson enhancement effect in photosynthesis or respiration?

A crucial question had arisen in our minds as well as during conferences and sometimes in phone conversations: Is Emerson enhancement effect in photosynthesis or respiration? This was because we all had used manometry which cannot distinguish between the effects of light on oxygen uptake and oxygen evolution! Emerson was not there to respond to it. It was R. Govindjee *et al*. (1960a) and R. Govindjee and Rabinowitch (1961), as noted above, who showed that para-benzoquinone Hill reaction in *Chlorella* cells exhibits the Emerson enhancement effect. Since this was not a natural system, Rajni and I decided to go to Bessel Kok's laboratory, in Baltimore, Maryland, to work with George Hoch to check the enhancement effect in NADP reduction. George taught us everything there was to learn about this system. Soon, R. Govindjee *et al.* (1962, 1964) established the Emerson enhancement effect in NADP reduction in chloroplasts. In addition, Govindjee *et al*. (1963) established, through mass spectroscopy, that this effect was indeed in photosynthesis – although there were effects of light on respiration. Thus, by 1963,

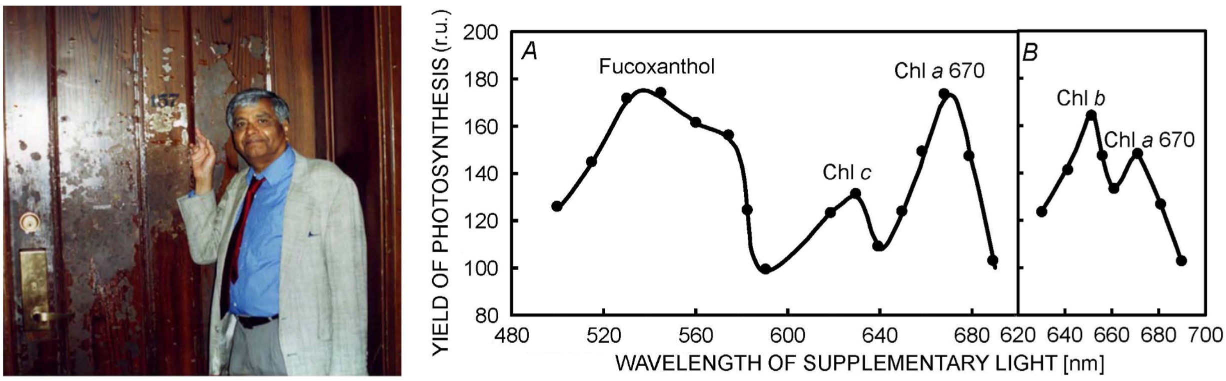

Fig. 5. *Right* (*A*): Action spectra of the Emerson enhancement effect in the diatom *Navicula*, when a second light beam of different wavelengths was given on top of far-red light – showing the presence of peaks for fucoxanthol, chlorophyll *c*, and chlorophyll (Chl) *a* 670. *Right* (*B*): The same as above but for the green alga *Chlorella* showing chlorophyll *b* and Chl *a* 670. Data of Govindjee (1960) and Govindjee and Rabinowitch (1960a). *Left*: A photograph of the author in front of the historical door of 157 Natural History Building (NHB) through which Emerson and all his students would go through each day to do their experiments.

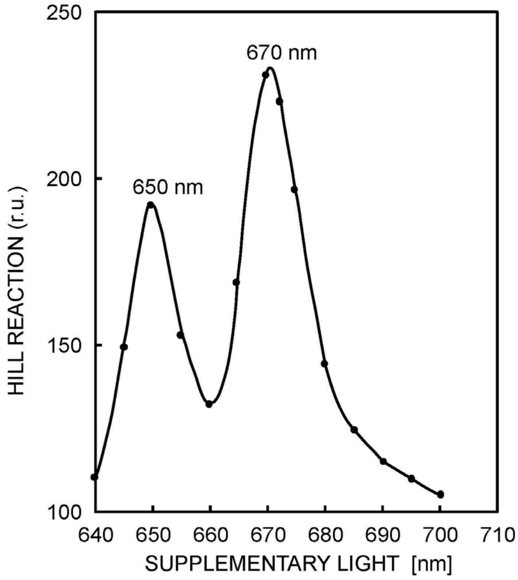

Fig. 6. *Right*: Action spectra of the Emerson enhancement effect in para-benzoquinone Hill reaction in *Chlorella* cells showing that the effect is not in respiration and that Chl *a* 670 is in the same system as Chl *b*. Redrawn from R. Govindjee (1961) and R. Govindjee *et al*. (1960a), with permission. *Left*: A 2001 photograph of Rajni Govindjee reflecting on the days she did these and other experiments discussed here; photo by G. Govindjee.

we had proven the Emerson enhancement effect to be in photosynthesis (*see* Govindjee 1963). In addition, working in C. Stacy French's laboratory at the Carnegie Institute of Science, Stanford, Govindjee and Govindjee (1965a,b) provided further confirmation of the Emerson enhancement effect through polarography and absorbance changes in the blue-green region.

For a research paper on Emerson enhancement in a diatom *Phaeodactylum*, *see* Mann and Myers (1968), and for an excellent review of the literature on the Emerson enhancement effect, *see* Myers (1971).

Two-light effect in chlorophyll *a* fluorescence

Already in 1960, I wanted to prove the existence of the two-light effect and two-pigment systems through chlorophyll *a* fluorescence, which originates mostly from what we now call Photosystem II: for a discussion of all aspects of Chl *a* fluorescence, *see* chapters in Papageorgiou and Govindjee (2004). Indeed, Govindjee *et al*. (1960b) discovered that far-red light (absorbed in the 'red drop' region) quenches chlorophyll *a* fluorescence excited by short-wavelength light. This antagonistic effect of light on fluorescence supported clearly the two-light reaction two-pigment scheme in photosynthesis. I could not pursue this phenomenon then since I had to return to India to fulfill my Fulbright Travel grant requirement. It was, however, wonderfully expanded by Warren Butler (Butler 1962) and by L.N.M. Duysens and H.E. Sweers (Duysens and Sweers 1963), the latter recognizing our 1960 paper prominently, and explaining the phenomenon with the 'Q' hypothesis: Photosystem II reducing Q (later called Q_A, which is a quencher of chlorophyll *a* fluorescence) and Photosystem I oxidizing the reduced Q, causing quenching of fluorescence – which is what was observed by us.

Support from around the world

I was then, and even now, impressed with the imaginative work of Bessel Kok (Kok 1959; *see* Fig. 7) where the antagonistic effect of two light beams of different wavelengths was observed: far-red light oxidizing P700, and orange-red light reducing it; for the discovery of P700, *see* Kok (1956, 1957). This work was also presented, soon thereafter, at another conference by Bessel Kok and George Hoch in 1960, held at John Hopkins University (Kok and Hoch 1961), where a two-light reaction scheme involving the reaction center P700 was presented.

It is essential to remind ourselves of a crucial experiment by Duysens *et al*. (1961), and Duysens and Amesz (1962) showing that 'light 1' oxidizes cytochrome *f* and 'light 2' (added on top of it) reduces the oxidized cytochrome *f* – this antagonistic effect of light 1 and light 2 is the key for the acceptance of the 'Z'-scheme of photosynthesis (*see* Fig. 8; also *see* Duysens 1989). [Note: the term 'light 1 (later I)' and 'light 2 (later II)' used by Duysens led to the use of the term(s) 'light reaction 1 (or I)' and 'light reaction 2 (or II)' as well as 'photosystem 1 (or I) and photosystem 2 (or II)'.] Furthermore, from the biological point of view, it was the experiment of Boardman and Anderson (1964), who physically separated the two photosystems, that was highly convincing to us all (also *see*: Cederstrand and Govindjee 1966, who had done the experiments already in 1964, but completed it only in 1966). Concerning the role of cytochromes, a detailed paper by Cramer and Butler (1967) documented

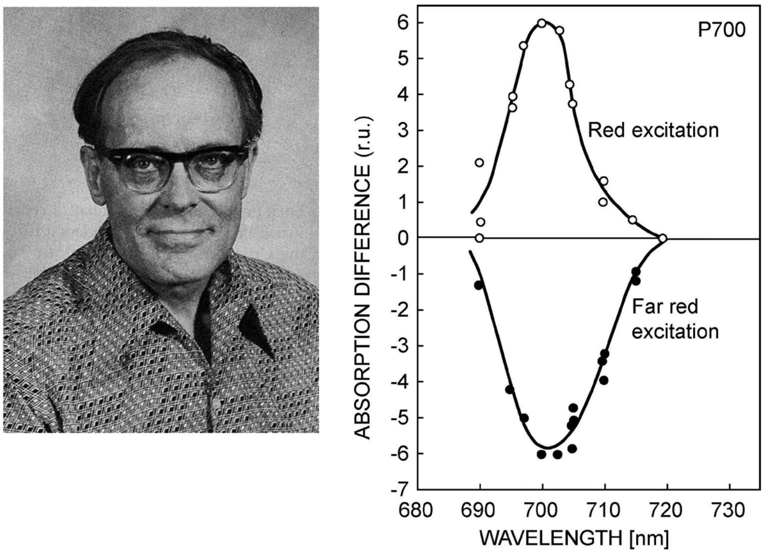

Fig. 7. *Right*: Data of Bessel Kok (Kok 1959) on absorption changes in the reaction center chlorophyll *a* P700 showing that far-red light [what we call 'light 1 (or I)' oxidizes P700 leading to decreased absorption, and orange-red light (what we call 'light 2 (or II)'] reduces P700. In my view, this antagonistic effect is historically the first of its kind showing the existence of a two-light reaction series scheme in photosynthesis. *Left*: A photograph of Bessel Kok (*see* Myers 1987).

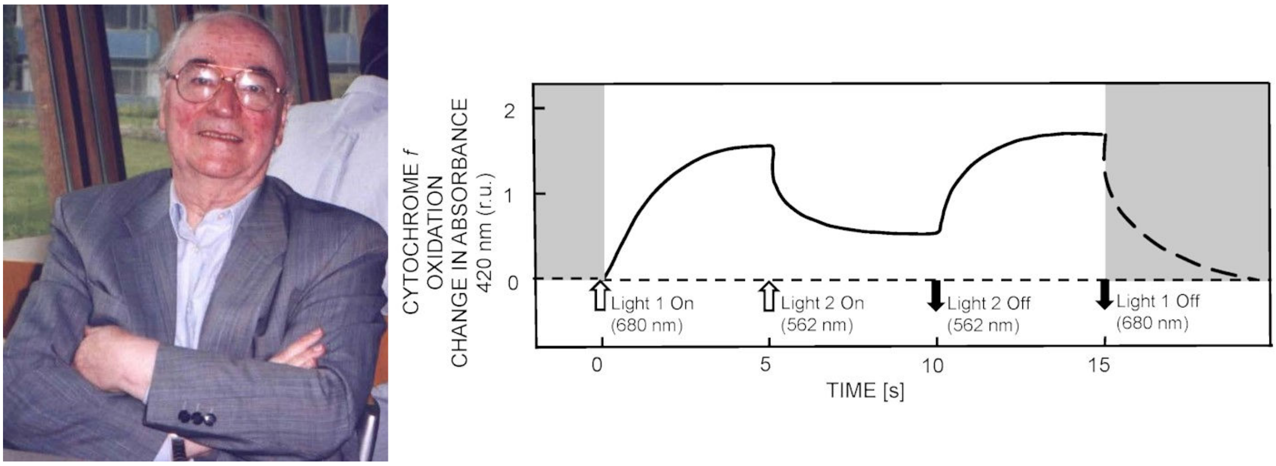

Fig. 8. *Right*: Data of Duysens *et al*. (1961) showing the antagonistic effect of 'light 1' (680 nm light) and 'light 2' (562 nm) on redox change in cytochrome *f* in the red alga *Porphyridium cruentum*. In my view, this is the real crucial historical experiment that has provided the key evidence for the series diagram (the Z-scheme) for the light reactions of photosynthesis. *Left*: A photograph of L.N.M. Duysens (*see* Govindjee and Pulles 2016).

the antagonistic effect of red and far-red light on the cytochrome *f* redox state and provided initial information on the cytochromes *b* in spinach chloroplasts. For the properties of algal and plant cytochromes, along with relevant physical and chemical background, *see* chapters 6 and 7 in Cramer and Knaff (1990).

A personal commentary on the 1960 paper of Robert (Robin) Hill and Fay Bendall

It was on 9 April 1960 that the Z-scheme of Hill and Bendall (1960) was published in the world-renowned journal *Nature*. It was a pleasant surprise (shock?) to us because already, we were drawing such a scheme on the small blackboard in the basement of the Natural History Building (NHB) at the University of Illinois at Urbana-Champaign (UIUC).

Fig. 9 shows a 1950s photograph of Robin Hill – when he was visiting Emerson's lab; this was before I had come to Urbana; I had learned from Eugene Rabinowitch (personal communication) that Emerson had invited many including Hill as well as Martin Kamen to show his newly done unpublished two-light effect (enhancement) experiments.

During 1957–1960, as graduate students in Emerson–Rabinowitch's 'Photosynthesis Project', we were following the 1945 scheme in Rabinowitch (1945), but with cytochrome *f* in it since Rabinowitch (1956) had already discussed this cytochrome as an intermediate (for 'Y' in the earlier scheme). In fact, he had based this idea on the observations of Duysens (1955) and Lundegårdh (1954); cf. Duysens (1989). It is obvious that the scheme of Hill and Bendall (1960) was well thought out although we were surprised that they did not mention the Emerson

Fig. 9. A 1950s photograph. From left to right: Robert (Robin) Hill; A. Stanley Holt; Robert Emerson; and Martin Kamen, in Emerson's Lab in Urbana, Illinois. Reproduced from Govindjee and Blankenship (2021).

enhancement effect – already the known basis for the 'two-light reaction–two-pigment system' concept.

Our usual discussion, at the University of Illinois, involved a reiteration of what Rabinowitch (1956; page 1862) had written, '*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 first acceptor.*'

Because of all that I just mentioned, our minds were already in a two-light reaction scheme, with a cytochrome in it, before the Hill and Bendall (1960) scheme was published! Further, just a few days before this scheme had appeared, a symposium on 'Light and Life' was held at the Johns Hopkins University – where many including James Franck, Eugene Rabinowitch (& Govindjee), Bessel Kok (& George Hoch), C. Stacy French, and Robert Hill (& Walter Bonner), Jan Thomas (& Govindjee), and Daniel Arnon gave talks related to the already published Emerson enhancement effect and the two light reaction concept. [I note that a separate perspective is needed on the work and ideas of Arnon – since he published many schemes – changing from one to another and back to the first one; for his latest view, *see* Arnon (1995).]

According to the reminiscence of George Hoch (on 31 December 2022, *via* e-mail and a telephone conversation), Robin Hill had neither made any comment on the 1960 Kok and Hoch presentation on the two-light effect on P700 nor mentioned the Hill and Bendall (1960) scheme at the 'Light and Life' meeting (*see* above); it seems to us that the scheme must have been added in the proceedings, published a year later [McElroy and Glass 1961]. Derek Bendall (Bendall 1994) has hinted that Robin Hill knew about the Emerson enhancement effect but did not consider citing it as his 1960 theoretical paper was focused and based on the redox potentials of cytochrome b_6 and cytochrome *f*. [We note that no evidence was found for cytochrome b_6 being in the scheme as proposed by Hill and Bendall (1960).]

Hill (1965) did recognize the Emerson enhancement effect, but to my surprise, he either forgot or missed citing any paper of Emerson (*see e.g.*, Emerson *et al.* 1957, Emerson and Rabinowitch 1960) or that of ours (Govindjee and Rabinowitch 1960a, R. Govindjee *et al.* 1960a). However, he did cite that of Myers and French (1960). In hindsight, I note that we (*i.e.*, Govindjee and Rabinowitch 1960a,b) did not cite Rabinowitch (1956) and Hill and Bendall (1960) since we were asked, by an anonymous reviewer, to focus on the experimental discovery – rather than on any theory for which we had no experiments. Still, I felt that it was unfair of Hill (1965) not to have cited young scientists as Rajni and I were then. However, all is now understandable after reading what D. Bendall (Bendall 1994) has said about Hill's lectures at Cambridge – where he would begin stating things clearly and then would lose the audience. In my opinion, Hill was a brilliant scientist who may have been absent-minded at times.

Since the above is my essay, I wanted to state a few things on this historical topic in the way I know it. Since there are two photosystems and two light reactions, there are also two 'reaction centers'. P700, the reaction center of Photosystem I, discovered by Bessel Kok, is noted above, but that of Photosystem II is P680 (*see* Döring *et al.* 1969). I will be amiss if I did not mention that I had speculated on the existence of P680 before its discovery (*see* Krey and Govindjee 1964, Rabinowitch and Govindjee 1965); further, we had proved that it was not a fluorescence artifact (Govindjee *et al*. 1970), as was suspected by some including the late Warren Butler. For a detailed review, of various Z-schemes, *see* Govindjee *et al.* (2017).

Concluding remarks

It is clear that the concept of two light reactions and two pigment systems was 'in the air', so to say, in the late 1950s, but there was no clear experimental observation for anyone to formulate it into a specific proposal. We note that Rabinowitch (1956), Kok (1959), and a few others, had made clear statements about it, the former mentioning cytochrome as an intermediate and the latter 'P700', but Hill and Bendall (1960) were the ones who presented the two-light reaction scheme, with a redox potential on the Y-axis (although plotted upside down from how we now always show it). This Z-scheme was clearly supported and extended by the work of many including, *e.g*., Duysens *et al*. (1961), Kok and Hoch (1961), and Witt *et al*. (1961a,b) with their versions of the Z-scheme. I agree with Robert Blankenship (personal communication, 2022) who wrote to me: '*In a way, it is a lesson to all of us that conceptual breakthroughs like this are very difficult to achieve, even when all the evidence is there in front of us*.'

I welcome others who were around the period 1940 to 1960 to participate in the discussion of the origin and the evolution of the Z-scheme of photosynthesis. I end this personal historical minireview with a photograph (*see* Fig. 10) of two of us (Rajni and myself) reflecting on the 'good old days' of 1956–1965, first with Emerson and then with Rabinowitch and several others, when the entire drama of the two-light reaction and two photosystems was being played live before us.

Fig. 10. A 2020 photograph of Rajni (*left*) and Govindjee (*right*) reflecting on the events leading to the current Z-scheme of oxygenic photosynthesis, the wonderful friends, and the comradery at the time of our PhD days and just a few years beyond. Source: Ashwani Pareek.

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Appendix 1. Recognition of Robert Emerson, by UIUC.

The UIUC has elegantly recognized Robert Emerson by establishing a professorship in his name at UIUC, by a plaque on its Urbana campus, and by 'The Robert Emerson Memorial Award' to graduate students at UIUC (*see* https://sib.illinois.edu/graduate/grants/Emerson).

The current Robert Emerson Professor is Donald (Don) R. Ort. He is a Professor of Plant Biology and Crop Sciences, where he leads 'groundbreaking research on uncovering the underlying causes for photosynthetic inefficiency' (https://lab.igb.illinois.edu/ort/). During 1999–2008, the Emerson professorship was held by Stephen (Steve) P. Long; among other top projects, Steve is engaged in understanding the mechanism of plant responses to atmospheric CO_2 rise and tropospheric ozone – with particular reference to photosynthesis and thus of plant productivity (https://lab.igb.illinois.edu/long/team/long/).

The plaque on behalf of the University of Illinois reads '*Understanding Photosynthesis: Illinois was home to two pioneers of photosynthesis research. Robert Emerson and Eugene Rabinowitch made fundamental discoveries that revealed the mechanisms for converting light to chemical energy in photosynthesis, Rabinowitch applied physical principles to understanding this process by forging a link between the biological and physical sciences, and they helped establish the discipline of biophysics*'. *See* a photograph of this plaque on my website at: https://www.life.illinois.edu/govindjee/.

Appendix 2. Alphabetical list of Robert Emerson Awardees: 1969–2022

Almon, Richard R. (1969; Physiology); Toth, Amy (2006; Ecology and Evolutionary Biology); Apte, Dipali (1989; Physiology & Biophysics); Aronica, Susan M. (1993; Physiology & Biophysics); Beckstead, Julie (2000; Plant Biology); Benner, Barbara L. (1983; Botany); Bernacchi, Carl J. (2002; Plant Biology); Blakely, Eleanor A. (1974; Physiology); Brighty, Elaine L. (1977; Biology); Chen, Ci-Di (1997; Molecular & Integrative Physiology); Chipman, Melisa (2016; Ecology and Evolutionary Biology); Clarke, H. David (1994; Plant Biology); Clegg, Benjamin (2011; Ecology and Evolutionary Biology); Curtis, Amanda (2021; Ecology, Evolution, and Conservation Biology); Dohleman, Frank (2009; Plant Biology); Edwards, Joseph (2022; Plant Biology); Feiler, Heidi S. (1992; Plant Biology); Franson, Susan E. (1980; Ecology, Ethology & Evolution); Gray, Sharon (2013; Plant Biology); Green, Ellen (1998; Entomology); Grogan, Dennis W. (1983,1984; Microbiology); Hagan, Ann Pelz (1973; Physiology); Hansen, Lonnie P. (1976; Ecology, Ethology & Evolution); Hines, Heather M. (2008; Entomology); Hunsicker, Mary E. (1971; Physiology); Jarvis, Michael R. (1981; Microbiology); Jarvis, Michael R. (1982; Microbiology); Jones, Beryl (2018; Ecology, Evolution, and Conservation Biology); Jursinic, Paul A. (1975; Biophysics); Kelly, Ryan (2014; Plant Biology); Koutalos, Joannis (1988; Physiology & Biophysics); Lee, Thomas D. (1979; Botany); Lowry II, Porter P. (1978; Botany); Maherali, Hafiz (1999; Plant Biology); Mallender, William D. (1996; Microbiology); Markowitz, Melvin M. (1972; Botany); McPheron, Bruce A. (1987; Entomology); Mezga, Duane M. (1969; Botany); Mills, Steven H. (1969; Physiology); Mitchell, Robert E. (2012; Entomology); Mohanty, Prasanna K. (1970; Botany); Moran, Rachel (2019; Animal Biology); Morgan, Patrick B. (2004; Plant Biology); Nabity, Paul (2010; Plant Biology); Naidu, Shawna (1995; Plant Biology); Paietta, John V. (1981; Genetics & Development); Pescitelli, Jr., Maurice J. (1977; Genetics & Development); Read, Linnea D. (1990; Physiology & Biophysics); Rodriguez, Josephine (2009; Entomology); Rowe, Kevin C. (2005; Animal Biology); Ruoff, Berthie M. (1985; Genetics & Development); Russo, Sabrina E. (2003; Animal Biology); Schulz, David J. (2001; Entomology); Smith, Christpher R.

(2007; Ecology and Evolutionary Biology); Spitze, Ken R. (1984, 1986; Ecology, Ethology & Evolution); Stein, Laura (2015; Animal Biology); Swofford, David L. (1984; Genetics & Development); Valero, Ingrid Carolina Romero (2020; Plant Biology); Vigneulle, Roy M. (1972; Physiology); Wittig, Victoria (2008; Plant Biology); Xu, Xiao-Ping (1991; Physiology & Biophysics); Zilinskas, Barbara A. (1974; Biology).