



A sixty-year tryst with photosynthesis and related processes: an informal personal perspective

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Abstract

After briefly describing my early collaborative work at the University of Allahabad, that had laid the foundation of my research life, I present here some of our research on photosynthesis at the University of Illinois at Urbana-Champaign, randomly selected from light absorption to NADP⁺ reduction in plants, algae, and cyanobacteria. These include the fact that (i) both the light reactions I and II are powered by light absorbed by chlorophyll (Chl) *a* of different spectral forms; (ii) light emission (fluorescence, delayed fluorescence, and thermoluminescence) by plants, algae, and cyanobacteria provides detailed information on these reactions and beyond; (iii) primary photochemistry in both the photosystems I (PS I) and II (PS II) occurs within a few picoseconds; and (iv) most importantly, *bicarbonate* plays a unique role on the electron acceptor side of PS II, specifically at the two-electron gate of PS II. Currently, the ongoing research around the world is, and should be, directed towards making photosynthesis better able to deal with the global issues (such as increasing population, dwindling resources, and rising temperature) particularly through genetic modification. However, basic research is necessary to continue to provide us with an understanding of the molecular mechanism of the process and to guide us in reaching our goals of increasing food production and other chemicals we need for our lives.

Keywords Bicarbonate effect · Chlorophyll *a* fluorescence · Photosystem II · Primary photochemistry · State changes · Thermoluminescence

*“The firefly seems afire, the sky looks flat;
Yet sky and fly are neither this nor that”
Panchatantra (see Ryder 1925)*

Introduction

Before I begin saying anything about my work, I wish to let the readers know that what I have accomplished is because of interactions with many individuals especially my past

graduate students (see “[Appendix](#)”). I owe them my gratitude and thanks for working with me; what I am today is because of them. I have included here photographs of those that were available on my computer. In my perspective, I have included some stories, but it is important to recognize upfront that different individuals may have different recollections of the same event (see e.g., Schacter 2012; Eayrs and Lavie 2018; and a 1951 Japanese movie “Rashomon” <https://en.wikipedia.org/wiki/Rashomon>¹). My presentation here is only partly based on the talk I gave at the University of Hyderabad at the 8th International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability (see the 2nd item at: <http://www.life.illinois.edu/govindjee/world-historical.html>).

I dedicate this *Tryst* in research to my mentors: Shri Ranjan of Allahabad University, India (1899–1969), Robert Emerson (1903–1959), and Eugene I. Rabinowitch (1901–1973) of the University of Illinois at Champaign-Urbana, Illinois, USA.

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How did I get into the area of photosynthesis?

My tryst with ‘Photosynthesis Research’² began quite early in my life—it was when I was an undergraduate student at Allahabad University, and had organized a ‘mock symposium’ on ‘Photosynthesis’ in 1952.³ Although it is hard for me to remember precise details, I believe six of us students enacted the discovery of photosynthesis (see Fig. 1.1, p. 8, in Rabinowitch and Govindjee 1969). If my recollection is correct, I played the role of Jan Ingenhousz (1733–1799), who had shown that *photosynthesis takes place only in the presence of light*. I do recall that there was much laughter and applause from the audience. It was great fun.

My initial interest in photosynthesis research had its beginning in 1954 when Professor Shri Ranjan asked the students to write *term papers* and deliver *seminars* on topics of interest to them: I chose ‘*The role of Chlorophyll in Photosynthesis*.’ I discussed its chemistry and function, but what intrigued me most, at that time, was Why was there a ‘drop’ in the maximum quantum yield of photosynthesis beyond 680 nm (the ‘*Red Drop*’), when Chl *a* was still absorbing light! (Emerson and Lewis 1943).

It was this curious phenomenon of the “Red Drop” that inspired me to pursue my PhD with Robert Emerson (1903–1959), at the University of Illinois at Urbana-Champaign (UIUC). I arrived in Urbana in September 1956 through the support of a Fulbright travel grant and a UIUC Graduate Fellowship. It turned out that Emerson was already solving the mystery of this ‘*Red Drop*’; by 1957 he had discovered an *Enhancement Effect* in photosynthesis, which is as follows: the rate of oxygen evolution measured when far-red light was given together with another light of shorter wavelength was greater than the sum total of oxygen evolution measured when these lights were given separately (Emerson et al. 1957). This new observation suggested the existence of two light reactions and two pigment systems in photosynthesis!

I shall discuss this phenomenon, now known as the Emerson Enhancement Effect, after a brief interlude. But, first, how did I get interested in research? It was during the 1954–1956 period in Shri Ranjan’s lab in the Department

of Botany of the University of Allahabad, as I will describe below.

The first taste of real research, 1954–1956: the effect of plant viruses on the amino acids of the host plants

After finishing my MSc (Botany, with specialization in Plant Physiology) in 1954, I was immediately appointed as a *Lecturer* at the University of Allahabad to teach Plant Physiology. Although I did not sign up for a PhD at Allahabad as my mind was made up to go ultimately into photosynthesis research, I had full access to the laboratory of Shri Ranjan.

Manmohan Laloraya (my longtime class fellow) and I wanted to find out about the effects of virus infection (biotic) on plant metabolism, since we would see all those motley looking plants around us. In addition, I was to find about the effect of X-ray treatment (abiotic) on plant metabolism since Ranjan seemed interested in my working on the effects of cosmic rays on plants, but I had convinced him to let me look at the effects of X-rays first; both the topics were to be focused on their effects on the physiology and the proteins of plants, specifically on their amino acids.

My early research work on the effects of virus infection on the physiology and proteins was all collaborative. The story of the first chromatogram and Shri Ranjan’s excitement and support was crucial to our future research.⁴ During 1955, we published four papers on the effects of virus infection on the amino acids and amides of the host plants, and, discovered remarkable effects; only the first paper was a detailed one (Ranjan et al. 1955; it was on the effects of virus infection on *Croton sparsiflorus*, and was published in the Proceedings of the National Institute of Science, India), the other three were one-page Brief Communications: in Nature (on *Nicotiana tabacum* (tobacco); Laloraya and Govindjee

² Readers can get a glimpse of certain aspects of my research life by watching an Annual Reviews, Inc video of an interview by Donald R. Ort at: <https://www.youtube.com/watch?v=cOzuL0vxEi0> (Also, see the second item on <http://www.life.illinois.edu/govindjee/>; and <https://podtail.com/podcast/annual-reviews-conversations/a-conversation-with-govindjee/>.)

³ An informal account is on a web site: <https://www.linkedin.com/pulse/govindjee-living-legend-i-met-dr-ravi-sharma>; also see <https://www.linkedin.com/pulse/govindjee-rajni-confluence-photosynthesis-dr-ravi-sharma>.

⁴ Laloraya (1970) wrote the following (which matches exactly with my own memory of the occasion): “I vividly remember the morning Govindjee and I carried the first successful amino acid separation chromatogram to Dr. Shri Ranjan’s house at 8:30 in the morning. He was in his veranda in half-sleeve shirt resting in his big chair after his early morning garden activity. He looked towards us and shouted, ‘What brings you so early in the morning to my house! Is there a fire in the department!’ Quietly we moved towards him and opened the newspaper wrapping the chromatogram on a table kept in front of him. He looked at it and shouted ‘Oh it is beautiful’ and jumped out of the chair. He held us by our shoulders and virtually had a swing. He rushed inside with joy saying ‘Wait for 5 min. I shall get ready and be with you.’ He came out dressed up, took out his big Ford car, asked us to sit by his side and drove us to the department. He was excited and happy like a child, as we were, and he made us forget that he was our great Professor with whom no one could be so close as we were at that moment. He ordered everything that we needed for research work and we were granted access at any time to meet him in connection with our research work.”

1955), in *Current Science* (on *Acalypha indica*; Laloraya et al. 1955), and in *Naturwissenschaften* (on *Pisum sativum* (peas); Laloraya 1955). Rajni Varma coauthored the next paper on the effect of virus infection on the amino acids of *Carica papaya* (papaya; Laloraya et al. 1956). Two more papers followed this, before I left Allahabad to go to Urbana, Illinois, USA. They were on the effects of virus infection on *Abelmoschus esculentus* (okra; Govindjee et al. 1956), and on *Trichosanthes anguina* (snake gourd; Rajarao et al. 1956). I am pleased to note that our work has been recognized by many including Magyarosy et al. (1973), and in excellent early overviews, by e.g., Kiraly and Farkas (1959). Although our early work may now seem obsolete, yet the new results on virus infection on the increase and decrease in specific amino acids in several plants (see e.g., Fernandez-Calvino et al. 2014; Mauk et al. 2014) are consistent with our observations in the 1950s.

Although I never followed up on this research area in my life, this foray into research was nevertheless the ‘foundation’ of my future endeavors. Further, I valued then and value still the camaraderie and friendship that comes with team, work. *I learned independence to ask questions, to think, to plan, to execute, to submit papers, to proofread, and to enjoy the fruits of my involvement, which I continue to do.*

The second project on the effect of X-rays was miniscule as compared to the effects of virus infection; it will not be discussed here further except that I will refer to the two brief one-page reports on the effects of X-rays on *Cicer arietinum* (i) on oxygen uptake (Govindjee 1956) and (ii) on the content of free amino acids and amides (Govindjee 1957); the second one was submitted from Urbana, Illinois, after I had joined Emerson’s Lab.

The early research on photosynthesis: two light reactions and two photosystems are real

While at the University of Illinois at Urbana-Champaign, I have played with various aspects of oxygenic photosynthesis (see some of our overviews⁵). I have worked with cyanobacteria, algae, and several plants.

⁵ Among others, Govindjee (2000) and Shevela et al. (2013a) have reviewed oxygenic photosynthesis. A history of the Z-scheme, involving two light reactions, and two pigment systems was published by Govindjee et al. (2017). The Z-scheme can be downloaded from my web site <http://www.life.illinois.edu/govindjee/> (see 4th and 7th items from the top).

Chlorophyll *a* is in both the pigment systems: a short-wavelength form is in what we now call Photosystem II

The beginning

I arrived in Urbana, Illinois, in September 1956 and joined the *Photosynthesis Project* of the UIUC, administered by its Graduate College, as a Fulbright student, and a UIUC fellow. The goal was to earn a PhD in Physico-Chemical Biology, under Robert Emerson. (see footnote⁶ for a story of my name, and footnote⁷ for a story of my 24th birthday in Urbana).

As mentioned above, Emerson et al. (1957) had discovered the *Two-Light Effect* in photosynthesis, and soon thereafter Emerson gave a seminar to the Photosynthesis Group at UIUC in early 1957 about the role of ‘auxiliary’ pigments—his data suggested that one light reaction is run by Chl *a* and the other by Chl *b* (or other auxiliary pigments in other algae, e.g., fucoxanthin (fucoxanthol) in diatoms, and phycoerythrin in red algae). To my simple mind, this seemed impossible since I had already read the PhD thesis of Duysens (1952) wherein he had shown that there is 100% transfer of excitation energy from Chl *b* to Chl *a*. Thus, for Chl *b* (or other pigments) to function independently made

⁶ On my second day in Urbana, Illinois, I went to the administration building of UIUC to officially register and to receive advance payment on my UIUC fellowship since the Government of India had allowed me to carry only seven US dollars. The clerk asked me what my name was. I said “Govindjee, starting with the letter G.” He looked in his files, and said: “*Mr. Govindjee, I am sorry, but we don’t have any fellowship for you.*” I was shocked and showed him the letter of my UIUC fellowship award. He said, after a brief moment “Oh, Mr. G. Jee, OK, you do have an award.” I immediately responded, “Sir, please note that my name is ‘Govindjee,’ not ‘G. Jee’; it is one name, and please put the two words together.” He did and since then I have been ‘Govindjee.’ Why did I do that? Well, “G.Jee” sounds like “Jeeji” which means elder sister in Hindi, and I did not want to be ridiculed by my Indian friends, as I was in school in India! Now, one name has given me more trouble than the sound of “Jeeji” since I am now called ‘Fnu Govindjee’ (where Fnu stands for First Name Unknown); I do not like ‘Fnu’ at all. Thus, I am going back to the ‘Jeeji’ sound, but as ‘G.G.’ for ‘Govindjee Govindjee,’ with both first and last names the same, although I will continue to publish under one name only. (My US passport and other formal documents are now under two names.)

⁷ When I entered Emerson’s lab in the morning of October 24, 1956, I was quite surprised to see Emerson cutting vegetables (including onions) in preparation for cooking an omelet, with his assistant Ruth (Shorty) Chalmers, standing next to him. He said with a smile “*Happy birthday! This is for you, but I will show you how to cook an omelet since I am worried that you will not survive here unless you know how to cook, and I do want you to do experiments for your PhD.*” (I was quite lean and thin.) Yes, I did learn to cook omelets, and I am here writing this article.

no sense to me. I would walk home with Emerson on Mondays through Fridays after work as the room I was living in was several blocks before his home. During one such walk, I asked him to explain his conclusion in view of Duysens' results. His answer was "Govindjee, I am an experimentalist, and this is what I see; my conclusion must be true to my results." However, Emerson's explanation still did not make sense to me. Tragically, Emerson died in a plane crash on Feb 4, 1959. Unfortunately, neither Rajni nor I could finish our PhDs under Emerson (see Rabinowitch 1961; Govindjee 2001, 2004). However, to our benefit, Eugene Rabinowitch accepted both of us as his graduate students [see Bannister (1972) for the contributions of Rabinowitch]. Figure 1 shows a 1961 photograph of both Rajni and I, with Rabinowitch, after we had finished our PhDs, and a 1966 photograph of several scientists attending Brookhaven Symposia in Biology, #19 on Energy Conversion by the Photosynthetic Apparatus (BNL 989).

How could Emerson miss the chlorophyll *a* band in what we now call Photosystem II; in other words, how did I find it?

I discovered in mid-February 1959 that Emerson had used the far-red (long wave) light (in today's language, PSI light) from his home-built monochromator, and the short-wave light (in today's language, PS II light) from a second optical system, using a Hg–Cd lamp, which has one of its emission lines at 644 nm (just right for Chl *b*). In the spring of 1959, and with the help of a former assistant of Emerson, Carl Cederstrand, I changed the way the two light experiments were done by Emerson. I used the monochromator for different wavelengths of light (to get what one would call PS II light) and the second optical system (a tungsten lamp and a Schott glass, RG-9 filter) to provide the far-red light. By the end of 1959, I was able to resolve the dilemma between Duysens' data where all energy absorbed in Chl *b* is transferred to Chl *a*, and Emerson's where the Chl *a* band was not seen by him in the second system. I discovered the peak for the short-wavelength form of Chl *a*, Chl *a* 670. Emerson and Chalmers (1958) had missed it simply because they had not used light absorbed by Chl *a*. I published this result in *Science* (Govindjee and Rabinowitch 1960). (For an important contribution of Rajni Govindjee at about the same time, see "The two-light effect is in electron flow from water to NADP: arguments with Dan Arnon" section).

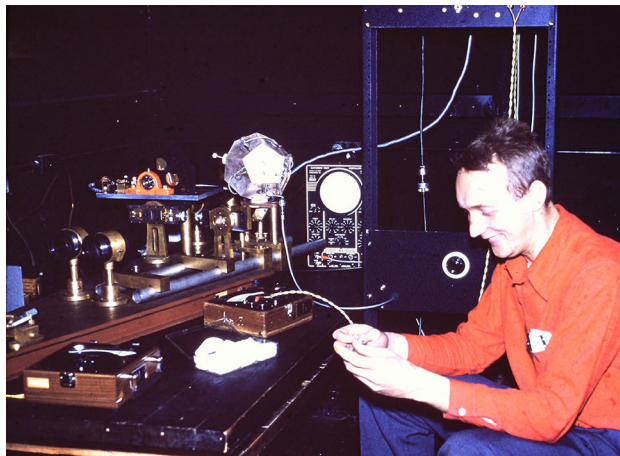
Two other papers in *Science* followed. In the first paper (Rabinowitch et al. 1960), we reported the discovery of a reversible inhibitory effect of extreme red light (750 nm) on oxygen evolution at far-red (700 nm); this work on several algal species was done jointly with Jan B. Thomas, who had been invited from the Netherlands to be a replacement for Emerson and to look after Emerson's students, namely, Rajni and myself. In the second paper (Govindjee et al. 1961), we



Fig. 1 Top: Left to right: Eugene Rabinowitch (reading a swedish newspaper); Rajni Govindjee and Govindjee at the 1st International Biophysics Conference in 1961, Stockholm, Sweden. Bottom: A 1966 photograph at a conference held at Brookhaven National Lab. Front row (left to right): Rod Clayton; Bob Pearlstein; Eugene Rabinowitch; Govindjee; David Fork; and Mordhay Avron; among others shown are: William Arnold (behind Govindjee, in the second row); Lou Duysens (behind Avron, in the second row); and Horst Witt (behind Duysens, in the 3rd row). Source: Archives of Govindjee's collection

reported the discovery of a new absorption band at 750 nm in *Anacystis nidulans*. It was an attempt to find if there were any undiscovered pigments in the 700–800 nm region; to my disappointment, this new pigment (P750) seemed to be not involved in any way in photosynthesis. However, it took us a few years to see Chl *a* 670 (and Chl *a* 680) directly in the absorption spectrum of cells; this was done with Carl Cederstrand (PhD, 1965) when he made state-of-the art direct absorption measurements on the green alga *Chlorella pyrenoidosa* and a few other algae, using a home-made integrating sphere (actually a dodecahedron): see Cederstrand et al. (1966). I show Carl Cederstrand working at his instrument, as well as the original housing of Emerson's second beam set-up that was mentioned above (Fig. 2). At about the same time, Govindjee and Yang (1966) provided an almost complete picture of the 77K fluorescence bands (F685; F696; and F720–F740), and discussed their origin; this was followed by the experiments of Das and Govindjee (1967) who showed that the long-wavelength Chl *a* was responsible for

Fig. 2 Left: Carl Cederstrand (PhD 1965; with Rabinowitch and Govindjee) at the special absorption spectrophotometer he had built that allowed us to see directly the absorption peaks of Chl *a* 670 and Chl *a* 680. Right: Emerson's original metal housing used to give the second beam of light in the Enhancement studies; Emerson had used a Hg–Cd lamp (1956–1958), but Govindjee used a tungsten lamp (1959–1962) with appropriate filters. Photo by Govindjee



F730, and Gasanov et al. (1979; cf. Gasanov and Govindjee 1974) who showed that a Chl *a* in CP47 was responsible for F696. We need to check these conclusions with extensive data now being collected from newer elegant experiments in labs around the World.

*Let us get back to the question of how did the “two-light effect paper” on Chl *a* 670 come about?* It was an easy task for me to answer the question I had asked while walking with Emerson in early 1957 and even in 1958: How did Emerson miss it? Or, how did I find it? As noted above, I had simply changed the set-up that provided the supplementary light. To reiterate: I used Emerson's monochromator to give different wavelengths of light in the visible region, and the second beam was no longer from the Hg–Cd lamp but was from a tungsten lamp with a Schott RG 9 filter to provide far-red light (essentially the same housing was used, as shown in Fig. 2). *It is ironic that the work that should have been done and published under Emerson was done only later; there was no way I could include Emerson as my coauthor.*

The two-light effect in chlorophyll *a* fluorescence: yes, it was there

Since chlorophyll *a* fluorescence and primary photochemistry are competing processes, I began to ask another basic question: If there is an *enhancement* in photosynthesis with two lights (one long wave; and another short wave), then shouldn't one have the opposite effect in Chl *a* fluorescence? [I was already fascinated by fluorescence (the beautiful red light from chlorophyll *a*), although Emerson had always discouraged me from measuring fluorescence.] I gave a seminar to the UIUC photosynthesis group and proposed to do this experiment just after the Govindjee and Rabinowitch (1960) paper was published. Indeed, our quickly done experiments on the discovery of the two-light effect on Chl fluorescence led to a *brief communication* (see Govindjee et al. 1960). Unfortunately, other projects took precedence, and I did not

pursue it then. I am, however, still thrilled that Duysens and Sweers (1963), who took this further and proposed that “Q” (a “bound” plastoquinone Q_A) is a quencher of Chl *a* fluorescence and had explained the two-light effect, wrote:

The first direct experimental suggestion of a different effect on fluorescence of two light beams of different colors was obtained by Govindjee et al. (1960). These authors concluded from experiments with *Chlorella* that the total fluorescence intensities in each beam, and also that the fluorescence yield at both wavelengths, was independent of intensity. No explanation was given of the phenomena. The first conclusion is consistent with our results.

The two-light effect is in electron flow from water to NADP: arguments with Dan Arnon

The two-light effect is not in respiration

There was another question lurking around all of us. Larry Blinks (1959), based on his two-light effect experiments using polarography, had raised the question as to whether the two-light effect may be an effect of light on respiration! Rajni Govindjee proved that the Emerson Enhancement Effect was indeed in photosynthesis (Hill reaction), and not in respiration, and she published it in *Science* (R. Govindjee et al. 1960); she also saw the Chl *a* band at 670 nm in the Emerson Effect, mentioned in “[How could Emerson miss the chlorophyll *a* band in what we now call Photosystem II; in other word, how did I find it?](#)” section. Rajni did her experiments by using *p*-benzoquinone as a Hill oxidant, which also ‘kills’ respiration. Since Blinks had used polarography, Rajni and I went to the lab of Stacy French, and discovered, using polarography, two different manifestations of Emerson Enhancement in whole cells of algae, using flashes of different wavelengths of light: one dealt with increased rate of

oxygen evolution, and the other led to longer-lasting oxygen evolution (Govindjee and Govindjee 1965).

The two-light effect is in NADP⁺ reduction

The above idea was further confirmed by the discovery of the two-light effect in NADP⁺ reduction, at the Research Institute for Advanced Studies (RIAS), in Baltimore, MD. This was done together with George Hoch (R. Govindjee et al. 1962, 1964; also see Govindjee and Bazzaz (1967) for conditions, where ferricyanide was shown to accept electrons from PS I, and had an Emerson Enhancement Effect) and by proving that the effect was on photosynthesis through mass spectroscopy (Govindjee et al. 1963). Although the Z-scheme, for NADP⁺ reduction (Govindjee et al. 2017), is now accepted by the entire photosynthesis community (see e.g., Blankenship 2014; Shevela et al. 2018), Daniel (Dan) Arnon did not accept it then. He could not observe the Emerson Enhancement effect in NADP reduction (McSwain and Arnon 1968). Instead, he suggested the existence of three light reactions, where NADP⁺ reduction is run by two different photosystems II (PS IIa and PS IIb), and PS I runs only cyclic electron flow (Knaff and Arnon 1969; Arnon 1971), an idea that has not been supported, as far as I know, by any other research group. What I remember vividly is Dan Arnon telling me before a very large audience at the 11th International Congress of Botany (held in 1969 in Seattle) that I must be doing something wrong although it was and is clear that he had it wrong.

The take home message is that there was a consistent picture explaining the enhancement work of all the major researchers including Jack Myers and Stacy French as well [see an authoritative review by Myers (1971)].

What is the minimum quantum requirement of oxygen evolution?: it is 10–12, not 4; yes, Warburg was wrong

I have been emotionally and personally involved with the question of the minimum quantum requirement from the time I had started doing experiments for my PhD thesis. The current Z-scheme of electron transport from water to NADP⁺ requires two light reactions, and since four electrons must be removed from two molecules of water to release one O₂ molecule, a minimum of eight photons must be required for it (see Fig. 3 for a Z-Scheme; Shevela et al. 2018). However, since cyclic electron transport occurs around PS I to get extra ATP, a minimum quantum requirement of 10–12 is needed for the release of one O₂ molecule. In the past, there had been a controversy between the 1931 Nobel laureate Otto Warburg and Robert Emerson (who earned his PhD in 1928 in Warburg's lab). For one molecule of O₂ evolved, Warburg obtained 3–4 quanta as the minimum requirement,

whereas Emerson measured 10–12 quanta per O₂. In all my experiments in the 1960s, I had always obtained 8–12 quanta per O₂ (Govindjee 1960; see Bedell and Govindjee 1966 for data on deuterated algae, and Ghosh et al. (1966) for spectral properties of these deuterated algae). Many years after Emerson's death, Otto Warburg [communication that came to me via Eugene Rabinowitch (also see Warburg et al. 1955; Warburg 1963)] told others that the reasons for the discrepancy in the minimum quantum requirement, per oxygen evolved, is that Emerson (and, by implication, his students) (i) did not use young synchronous cells; (ii) did not provide 10% CO₂ to the cells; and (iii) did not provide blue catalytic light. To satisfy ourselves, and the rest of the scientific community, Rajni and I made measurements under the conditions given by Warburg, but still obtained 8–12 quanta, instead of 3–4 quanta per O₂ (R. Govindjee et al. 1968). See Govindjee (1999), Nickelsen and Govindjee (2011), and Hill and Govindjee (2014) for a complete story.

Light absorption, excitation energy transfer, primary photochemistry, and light emission: these steps take place in the sub-picosecond to nanosecond time scale

I provide here a very brief glimpse of some selected highlights of our research and discoveries on the topic of this section, done with many wonderful students and scientists, that led to an understanding of the basics of oxygenic photosynthesis. See Govindjee and Govindjee (1974) for a background and summary of the primary events of the overall process. A very important question has been: Why the same Chl *a* molecule has different properties and functions? Björn et al. (2009) have discussed this issue; the answer lies in the fact that they have different microenvironments and they are bound differently to different amino acids. Further, I do know that there are many differences between various photosynthetic organisms, but this is true within a chloroplast and certainly within a leaf (see e.g., observations on “mesophyll” and “bundle sheath” chloroplasts by Maarib Bazzaz (PhD, 1972; Bazzaz and Govindjee 1973). Instead of describing our work in detail, I refer the readers to articles by others on my life and work (see Eaton-Rye 2018, for references). Following light absorption, which occurs in femtoseconds, our research has dealt with the events that follow it.

Excitation energy transfer

This process was studied by Fred Cho (PhD, 1969) in both the green algae and cyanobacteria, down to 4K (liquid helium temperature) (Cho and Govindjee 1970a, b; review by Mirkovic et al. 2017). Yes, there is clear temperature

Fig. 3 A Z-Scheme of photosynthesis. The top part is Photosystem II (water-plastoquinone oxidoreductase), with P680 as its reaction center Chl *a* complex. Bicarbonate is bound on the non-heme iron between Q_A and Q_B , the first and the second bound plastoquinone electron acceptors. The middle part is intersystem electron transport chain involving Cytochrome b_6/f complex; and the bottom part is Photosystem I (plastocyanin-NADP⁺ oxidoreductase), with P700 as its reaction center Chl *a* complex. For details including the names of all the intermediates, see Fig. 6 in Govindjee et al. (2017) (also see Shevela et al. 2018). Copyright: reproduced with permission from the authors of: Shevela et al. (2013a)

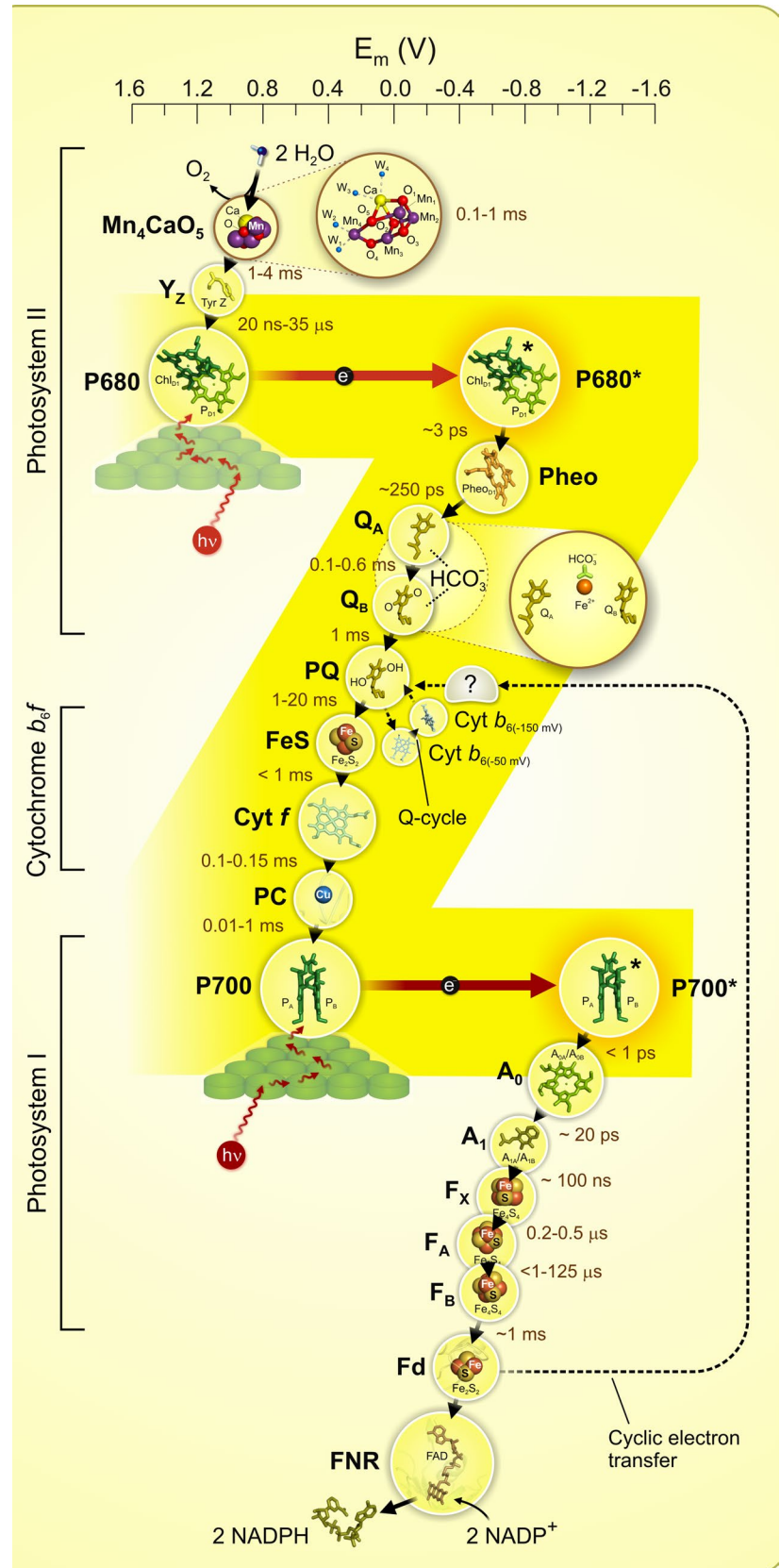




Fig. 4 Photographs of several past coauthors (dates unknown). Top left: Anne Krey; middle left: Louisa Yang (Ni). Top right: (left to right): Michael Seibert, Gary Wiederrecht, Mike Wasielewski,

Govindjee, and Mike Pellin. Bottom: George Papageorgiou (extreme right), Ondrej Prasil (4th from left), and Radek Kaňa (extreme right). Source: Govindjee's Archives

dependence, and Förster's resonance energy transfer theory is still valid. Ghosh and Govindjee (1966) had already shown that in cyanobacteria, there is a dynamic regulation of excitation energy transfer, even at room temperature, when we grew them under different wavelengths of light.

Primary photochemistry

In both PS I and PS II, the primary charge separation takes place within a few picoseconds (Fenton et al. 1979; Wasielewski et al. 1989a; Govindjee and Seibert 2010). To obtain information on our extensive early experimental results, as well as all the "ins" and "outs," I refer the readers to examine our papers, published with the research group of Mike Wasielewski, then at the Argonne National Lab: Wasielewski et al. (1987, 1989); Greenfield et al. (1996, 1997); Wiederrecht et al. (1994). However, for overviews of this area of research, see Govindjee and Wasielewski (1989)

and Mamedov et al. (2015). See Fig. 4 for Mike Wasielewski and a few others.

Thermoluminescence (TL)

TL occurs due to the reversal of PS II reactions involving different redox carriers giving different TL peaks at different temperatures (see DeVault et al. 1983; DeVault and Govindjee 1990, for theory; also see Rutherford et al. 1984; Brinkert et al. 2016). Here, I do not discuss our experimental contributions, but refer the readers to our extensive studies with Raj Sane, Vidyadhar Tatake, H. Koike, Y. Inoue, T.S. Desai, Dave Kramer, and Stuart Rose (Sane et al. 1977, 1984; Tatake et al. 1981; Govindjee et al. 1985b; Kramer et al. 1994; Rose et al. 2008).

Chl *a* fluorescence transient

When a dark-adapted photosynthetic organism is exposed to light, Chl *a* fluorescence changes in a characteristic manner

(Govindjee 1995, 2004). There are fast (milliseconds to seconds) as well as slow (minutes) changes. These changes are a unique and sensitive monitor, not only of PS II, but also of PS I reactions. This area of research was pioneered, in my lab, by George Papageorgiou (PhD, 1968) and John C. Munday Jr, (PhD, 1968). For the observation and understanding of the fast (within a second) changes, see Munday and Govindjee (1969a, b); cf. Stirbet and Govindjee (2011). For the slow changes (within a few minutes) related to photophosphorylation and to distribution and re-distribution of excitation energy (e.g., “state changes”) between the two photosystems, see Papageorgiou and Govindjee (1968a, b, 2011); cf. Kaňa et al. (2012); Kodru et al. (2015); Stirbet and Govindjee (2016); Mishra et al. (2018). Here again, I do not discuss our contributions, and details, but refer the readers to chapters in a book edited by Govindjee et al. (1986) and a review by Papageorgiou and Govindjee (2014), as well, as to papers (or reviews) by Reto Strasser, Kumud Mishra, and Sandra Stirbet: Strasser et al. (2000); Stirbet and Govindjee (2011, 2012); Mishra et al. (2016); Stirbet et al. (1998, 2014, 2018).

Chunhe Xu (PhD, 1992), who came from Shanghai, China, exploited Chl *a* fluorescence in many different ways, including the use of flow cytometry, to understand basic differences in the physiology of photoautotrophic cultures of soybean, of *Amaranthus*, cotton, and spinach (see Xu et al. 1988, 1989, 1990).

I now present my stories on the concept of P680 (the reaction center of PS II) followed by our first measurements of charge separation in PS II.

Suggestion of P680 being the Trap II (PS II reaction center)

Kok (1957) discovered P700, a reaction center of photosynthesis, which was shown later to be that of PS I. Anna Krey and Govindjee (1964) were the first to suggest that their results on the existence of a difference fluorescence band at 693 nm, when algae were exposed to high light indicate the existence of a “second trap,” the first one being P700. They wrote: “The 693 nm difference band in the fluorescence spectrum can be tentatively attributed to fluorescence from trap II... We believe that the 693 nm fluorescence band emanates from ‘photochemically frustrated’ trap II under these conditions.” I (Govindjee) suggested to Rabinowitch that we call this trap (the reaction center) “P680” in the Z-scheme. Thus, Rabinowitch and Govindjee (1965) wrote: “We believe, however, that a pigment we have tentatively named pigment [P] 680—from the anticipated position of its absorption band does serve as an energy trap in [Pigment]-System (II) Its existence is supported by the discovery of a new fluorescence emission band of chlorophyll at 693 millimicrons [nanometers], which is compatible with absorption

at 680 millimicrons [nanometers]. This band is emitted by certain algae when they are exposed to strong light of the wavelengths absorbed by [Pigment] System II.” The first refereed scientific paper to call trap II—P680—was that of Govindjee et al. (1970) when they convinced themselves that the absorption changes for *Chla_{II}*, discovered in Horst Witt’s Lab (Döring et al. 1969), were not due to a fluorescence artifact. However, it was only after Floyd et al. (1971) published 77K spectroscopic measurements that P680 became the established term for the primary electron donor for PS II.

The first measurements on charge separation in PS II

After we had published, from UIUC, the first measurement of charge separation in PS I (Fenton et al. 1979), I (Govindjee) began to look for ways to do the same for PS II, but our attempts to make stable PS II particles were unsuccessful at that time since they would degrade quickly. Then one day, I received a paper to review from Plant Physiology in 1988; it was from Michael (Mike) Seibert’s lab, and if my memory serves me right, it was later published as McTavish et al. (1989); they had succeeded in stabilizing their PS II preps. I took the decision to invite Mike Seibert to join us in Illinois, and thankfully, he did. After Wasielewski et al. (1989) published the time for charge separation in PS II, from the reaction center of PS II P680 to pheophytin, to be 3 picoseconds (ps), results from George Porter’s group (see e.g., Booth et al. 1991; Klug et al. 1995) gave a the value of 20 ps; I was told at conferences that we were wrong since we may have had some exciton annihilation; this was not so. However, it was considered plausible that the data from Porter’s group might have included excitation energy transfer times. In the long run, new intermediates prior to pheophytin have been discovered and the primary charge separation to those acceptors is even faster [see e.g., a review by Mamedov et al. (2015), and papers by Romero et al. (2010, 2012)]. I hasten to add that *George Porter and James Barber were always considerate, polite, and open-minded.*

Now, back to Chl *a* fluorescence.

Lifetime of Chl *a* fluorescence in vivo: it is the best way to measure its quantum yield

Lifetime of fluorescence is directly proportional to the quantum yield of fluorescence, whereas fluorescence intensity is proportional to the yield as well as the concentration of the chromophore. In Eugene Rabinowitch’s lab, Steve Brody in 1957 had pioneered the use of lifetime of fluorescence measurements in studying photosynthesis [see Brody (2002) for a review, and Hirsch et al. (2010) for a tribute to Brody]. At that time, it was my dream to use this tool.

Fig. 5 Photographs of several past coauthors. Top left (left to right): Daniel Wong; Govindjee and William Coleman (2018). Bottom left: Govindjee and Chunhe Xu (2013). Top right: Adam Gilmore visiting Scotland (2017). Bottom right: My son Sanjay Govindjee and Maarib Bazzaz (2018). Source: Govindjee's Archives



I became seriously interested in using this technique and collaborated with three different research teams at UIUC, each time to get better instrumentation to answer newer questions.

The first period lasted for 20 years: 1970s–1980s. I had approached Henri Merkelo of the Department of Electrical Engineering (at UIUC) to build us a new instrument. Together, we did so using a mode-locked system, and we published this endeavor in *Science* (Merkelo et al. 1969). Together with Ted Mar (PhD, 1971) we measured the lifetime of Chl *a* fluorescence in different algae (Mar et al. 1972), as well as during the Chl *a* fluorescence transient [the O (J I) P] phase (Strasser et al. 1995) to monitor whether excitation energy transfer involves a “separate package” or a “lake” model in algae (Briantais et al. 1972). (Jean Marie Briantais had joined my lab as a postdoctorate associate.) This new instrument also provided the means to decipher the mechanism by which cations regulate excitation energy transfer (Moya et al. 1977; Wong et al. 1981; Wong (PhD, 1979); Ismael Moya had come to our lab for a short period as a research scientist). In addition, Ogawa et al. (1982) studied the relation of cations with abscisic acid in guard cells of *Vicia faba*.

Figure 5 shows photographs of Daniel Wong (PhD, 1979), William (Bill) Coleman (PhD, 1987), Chunhe Xu (PhD, 1992), Maarib Bazzaz (PhD, 1972), and of Adam Gilmore, all mentioned in this perspective.

The second period was in the 1990s when I approached Enrico Gratton at the Laser Fluorescence Dynamics (LFD) Lab in the Physics Department at the UIUC. We studied changes in the lifetime of Chl *a* fluorescence as the PS II reaction centers were taken from the ‘open’ state to the ‘closed’ state (Govindjee et al. 1990); at the same time, Hyunsuk Shim (PhD, 1992) made highly active PS II particles (Shim et al. 1990) from *Chlamydomonas reinhardtii* that became very useful for many later experiments. Adam Gilmore joined my lab, as a postdoctoral associate, and worked day and night to understand how the ‘dimmer switch’ of plants functions, protecting it against excess light (Gilmore et al. 1995, 1996a, b, 1998, 2000). These experiments provided important mechanistic details since Adam had measured simultaneously both the lifetime of fluorescence (that gave direct information on quantum yield) and fluorescence intensity (that was affected also by changes in Chl concentrations).

During the last phase of my research life—after my retirement in 1999 (from UIUC) and after closing my lab in 2002, I walked over to the Physics Department and began collaboration with Robert (Bob) Clegg, using an instrument they had built to measure lifetime of fluorescence. It was a wonderful period filled with friendship and camaraderie. [See Noomnarm and Clegg (2009) for a basic background on lifetime of fluorescence and instrumentation used.] Making parallel fluorescence intensity and lifetime measurements, we began to ask questions concerning how the non-photochemical quenching (NPQ) of Chl *a* fluorescence functions during fluorescence transients in *C. reinhardtii* and in its various xanthophyll cycle mutants. For results and conclusions, see Govindjee and Seufferheld (2002); Holub et al. (2007); and Clegg et al. (2010); for an overview on NPQ, see Demmig-Adams et al. (2014).

The results of the above measurements were complex as if several processes function at the same time. Thus, we decided to dig deeper: new experiments were (and are still) needed. However, then, an important notable finding was made by Shizue Matsubara when she came to work with us asking an important question: Do avocado leaves protect themselves only through the xanthophyll cycle or do they also use the lutein oxide cycle? With Yi-Chen, a PhD student of Bob Clegg, we discovered that both cycles are involved in photoprotection (see Matsubara et al. 2011; for a timeline of various aspects of the problem, see: Papageorgiou and Govindjee 2014), and for a review on general application to plant physiology, see e.g., Kalaji et al. (2012).

Circadian rhythm in Chl *a* fluorescence: yes, it is real

I do not want to forget to mention one particular experimental study, which showed the existence of the circadian rhythm in Chl *a* fluorescence. I was approached by Beazy Sweeny (1914–1989; see Vanden Driesshe 1990), who had once delighted me by showing beautiful ‘bioluminescence,’ during a boat ride off the coast of Puerto Rico. Her enthusiasm for circadian rhythms was infectious. She was curious to examine the molecular basis of the circadian rhythm in photosynthesis in the dinoflagellate *Gonyaulax polyedra* in the late 1970s. I gladly encouraged her and Barbara Prezelin to come to my lab in Urbana. We worked day and night: Beazy and I worked during the day and Barbara Prezelin and one of my PhD students, Daniel Wong, in the night. We grew *G. polyedra* and, indeed, discovered a circadian rhythm in chlorophyll *a* fluorescence—it was great fun doing these experiments (see Sweeny et al. 1979; Govindjee et al. 1979).

I will never forget the wonderful experience working with Beazy on circadian rhythm. Since then, I have been telling students to do their experiments on photosynthesis

by taking samples at about the same time of the day to get reproducible results! (See Sweeny 1987 for her review.)

Role of ions in regulating photosynthesis

Divalent cation effects are complex

Regulation of photosynthetic light harvesting in thylakoids is one of the key factors affecting the efficiency of photosynthesis, except at high light when the enzymes of the carbon assimilation reactions regulate it. There are, as we all know, two photosystems in oxygenic photosynthesis (see Fig. 3), and the two need balanced excitation for optimum electron flow from water to NADP⁺. Following the findings of Peter Homann (1969) and Norio Murata (1969) that Mg²⁺ causes an increase in Chl *a* fluorescence, implying more light going to the higher fluorescent PS II, Prasanna Mohanty (PhD, 1972) and Barbara Zilinskas (PhD, 1975) added magnesium to isolated chloroplasts and saw that it increased Chl *a* fluorescence intensity; based on several other experiments, they came to the conclusion that the effect must involve structural changes in the thylakoid membrane (Mohanty et al. 1973). When Mg²⁺ is added to whole cells, there are additional “osmotic” effects, and instead of an increase in Chl *a* fluorescence, there is a decline (Mohanty et al. 1974). Another student, David VanderMeulen (PhD, 1977), who later worked on the ‘coupling factor’ (see “Deciding if we could do something new to understand how chloroplasts make ATP” section), investigated the effect of Mg²⁺ on the associated conformational changes using light scattering changes and by monitoring intensity changes in ANS (1-anilinonaphthalene-8-sulfonate), NPN (n-phenyl-1-naphthylamine), and Auramine O (tetramethyl diamino diphenyl ketoamine) that are sensitive to the microenvironment they are located in (VanderMeulen and Govindjee 1974a, b, 1976): changes in the “spill-over” of excitation energy from PS II to PS I explained only some of our results.

Opposite effects of monovalent and divalent cations

At about that time, Elizabeth (Liz) Gross (1940–2007), at Ohio State University, had discovered that monovalent ions (Na⁺) gave an effect opposite of that of Mg²⁺—thus, we collaborated with her. She came to Urbana and was our houseguest. Thomas (Tom) John Wydrzynski (PhD, 1977) provided a detailed picture of the cation effects [Wydrzynski et al. (1975a, b)]: Low concentrations of Na⁺ led to an increase in PS I/PS II fluorescence ratio (measured at room temperature as well as at 77K), which was reversed by Mg²⁺;

Fig. 6 Top: Past PhD students on the occasion of Govindjee's retirement function (in 1999), organized by John Whitmarsh. Top: Left to right: Rajni Govindjee; Julian Eaton-Rye; Alan Stemler; Govindjee; Rita Khanna; Barbara Zilinskas; Tom Wydrzynski and Paul Jursinic; Bob Gennis is between Barbara and Tom. Bottom: Left to right: Govindjee; Jobie Spencer (who was the engineer in the lab during the 1960s and 1970s); Julian Eaton-Rye; Barbara Zilinskas; Rajni Govindjee; Alan Stemler; Rita Khanna, and Jin Xiong. Source: Govindjee's Archives



no such effect was seen in PS II particles. In addition, a specific Mg^{2+} effect on PS II was observed (that still needs further experimentation): the ratio of F696/F685 increased; this suggested that energy transfer from LHCII to CP47, in PS II, must increase.

Figure 6 shows photographs of Julian Eaton-Rye (PhD, 1987), Alan Stemler (PhD, 1974), Tom Wydrzynski (PhD, 1977), Barbara Zilinskas (PhD, 1975), Rita Khanna (PhD, 1980), Paul Jursinic (PhD, 1977), Jiancheng Cao (PhD, 1992), and Jin Xiong (PhD, 1996), all mentioned in this perspective.

Regulation of excitation energy distribution between the two photosystems

Soon thereafter, Ralph Schooley (Schooley and Govindjee 1976) looked at the salt effects through circular dichroism (CD) suggesting conformational changes are involved. In my view, a distinction can be made between the 'separate package' model and the 'spill-over' model: if there is change in excitation energy transfer from PS II to PS I (spill-over),

without change in the concentration of the pigments in the photosystems, then the lifetime of fluorescence (that measures quantum yield of fluorescence) will change in concert with change in fluorescence intensity. Essentially, this is what Moya et al. (1977) found. Soon thereafter, the question of regulation of excitation energy transfer by cations was studied by Daniel Wong; he investigated the problem in detail, looking at microsecond fluorescence yield and delayed light emission (DLE) after single flashes (Wong et al. 1978), polarization of fluorescence (Wong and Govindjee 1979), and wavelength-resolved fluorescence lifetime changes measured at 77K (Wong et al. 1979). I note that it was Jursinic et al. (1978) who had already laid the foundation to understand the mechanism of DLE, used in some of these studies, which included the effects of membrane potential. Finally, Daniel compared the effects of cations (Mg^{2+} ; Na^+) with the effects of protons (H^+) (Wong et al. 1980). A highly detailed picture is now available on the role of cations in regulating photosynthesis (see a review by Kaňa and Govindjee 2016, dedicated to Jim Barber, a pioneer in that field).

Anions cause an opposite effect to that of cations

Lastly, I end this section by citing the research published by Jajoo et al. (1998), where she and her coauthors discovered that the effect of anions is opposite to that of cations. We are far from a clear biochemical and biophysical understanding of this phenomenon.

Attempts to probe the oxygen clock: a complex process

Modeling and reviews

I was fascinated with the discoveries of Joliot et al. (1969) and Kok et al. (1970) on the OEC (oxygen-evolving clock or cycle or center), that is, the period four oscillations in oxygen evolution. Mar and Govindjee (1972) proposed several early models ready for testing (for a review, see Joliot and Kok 1975). We summarized the status of molecular mechanism of the oxygen evolution in the mid to late 1980s [see reviews by Renger and Govindjee (1985), Govindjee et al. (1985a) and Govindjee and Coleman (1990, published in *Scientific American*)]. Furthermore, Kambara and Govindjee (1985) discussed several novel models, especially with Mn in two different environments, and Padhye et al. (1986) suggested that Mn may be bound to a specific histidine residue. Roffey et al. (1994) and Kramer et al. (1994) mutated a histidine in the OEC and showed its importance in the function of the enzyme. In addition, Naber et al. (1993) discovered unequal misses during the progression of Kok's S-states, Shinkarev and Govindjee (1993) provided an insight into the relationship of Chl *a* fluorescence with the natural quenchers *in vivo*, and Shinkarev et al. (1997) examined period oscillations in oxygen evolution via Chl *a* fluorescence changes, whereas Srivastava et al. (1999) looked at these oscillations during the greening process. These early observations need to be integrated, modified, or challenged as the case may be. Furthermore, we need to carefully check how much of all this is valid or useful today in view of the 1.9 angstrom structure of PS II (Umena et al. 2011). For comprehensive, but basic, overviews on the functioning of OEC, see Najafpour et al. (2012a, b) and Shevela et al. (2013a, b).

The oxygen-evolving complex (OEC)

Barbara Zilinskas (PhD, 1975) joined our lab in the early 1970s, as a graduate student (on a National Aeronautics and Space Administration (NASA) fellowship), and she wanted to probe the 'biochemical' side of the OEC. A basic question was: *Is the component involved in oxygen evolution a protein?* She initiated an immunological approach to answer

this question with the ultimate goal of having the means to identify the OEC. Interestingly, it was the first time ever that we had rabbits in our lab! However, after some initial observations (Braun (Zilinskas) and Govindjee 1972, 1974), we decided to move on to other interesting projects.

Barbara pursued other important questions, such as finding a biochemical way to monitor PS II reaction, from water to Q_A [see e.g., the use of silicomolybdate in the paper by Zilinskas and Govindjee (1975)] and a way to stabilize chloroplasts by using glutaraldehyde (Zilinskas and Govindjee 1976).

A wild goose chase

I was excited in 1980 in understanding how OEC works, as I read (at that time) a 'great' paper by Spector and Winget (1980; published in the February issue of the *Proceedings of the National Academy of Science, USA*), where a 'Mn-containing' OEC protein was claimed to have been isolated, characterized, and tested. (In hindsight, I should have had some concerns since it had only 2 Mn/protein, and the *in vivo* OEC needs 4 Mn to function.) The excitement led me to go to Doug Winget's lab and learn directly from the experts. When I was there, I followed the steps given by Mark Spector, but I did not get the 'OEC' protein band in the chromatogram at the time Mark predicted it will appear. Mark (and Doug) said "*Oh, this happens...it will come.*" Well, I went to the bathroom, and when I returned, the band was there; it was eluted and kept in the refrigerator. Anyhow, I then went back to my lab at UIUC and invited Mark and Doug to come to do experiments testing their OEC protein through flash-induced oxygen evolution, and chlorophyll fluorescence; we called the "OEC-depleted samples" to which the isolated protein was added "photosomes," and those without the added protein, "depleted photosomes." Everything seemed to work just fine. Tom Wydrzynski helped me in doing these experiments. Then, I wanted these experiments to be confirmed in another lab, so, I went to the Carnegie Institute of Washington (now Science) at Stanford and used David Fork's instrument and expertise, and the results of Urbana were confirmed. Everything was repeated over and over again. *However, in both cases the samples were provided by Mark and Doug, and we stated this fact in the paper* submitted to a newly started journal 'Photobiology and Photobiophysics,' edited by Hartmut Metzner (Govindjee et al. 1980). It was received on July 3, 1980 and accepted on July 8, 1980. The rest is history. No one else, including myself (in my own Lab or in RIKEN, Wako-Shi, Japan, with excellent biochemists there) could reproduce the preparation of the "OEC" protein of Spector and Winget (1980) [see an account by C. D. Dismukes in Allakhverdiev et al. (2018)]. Our guess is that Mark Spector may have sent us broken thylakoids or active PS II particles, but not the

“claimed” OECs. *All of the above shows how science moves to ultimately get to the truth.*

Looking for manganese in the 1970s and 1980s: application of NMR

Even before the above foray in biochemistry, our lab had taken a different direction to examine if we can take a look at changes in manganese indirectly via water proton relaxation rates. This direction was taken because Tom Wydrzynski (mentioned above) took a chemistry course given by Paul Schmidt, wherein he was inspired to use NMR in understanding photosynthesis—a novel idea indeed—to look at changes in manganese (albeit indirectly).

I approached Herb Gutowsky (1919–2000), one of the founders of NMR in chemistry, and he gladly agreed to collaborate with us; we were able to work with two research scientists in Gutowsky’s group, namely, Nick Zumbulyadis and Steve Marks. Wydrzynski et al. (1975) showed that NMR can indeed monitor changes in the redox state of manganese in thylakoid suspensions. Soon thereafter, Wydrzynski et al. (1976) showed period four oscillations in the longitudinal proton relaxation rates ($1/T_1$) that were out of synch with the flash pattern of oxygen release. Indeed, the above findings were truly exciting.

Then, Wydrzynski et al. (1978) and Khanna et al. (1981a, b, 1983) proceeded to provide a thorough background and detailed analysis of this phenomenon. In spite of the novelty of the method, and even with the thought that it is better to use transverse proton relaxation rates ($1/T_2$) that provide better and more pertinent results (see e.g., Bovet et al. 1993), this method had to be “happily” abandoned (so-to-say) because of the application and improvement of more direct methods, using Synchrotron radiation, first by the group of Mel Klein and Ken Sauer at the Lawrence Berkeley Lab (LBL) and at the University of California, Berkeley, and later in Japan (see e.g., Young et al. 2016; cf.; Umena et al. 2011). Yes, there are important differences between the detailed pictures by the two groups, but I am optimistic that they will be resolved soon in the near future. To get an overview of the evolution of the oxygen-evolving system, see Cardona et al. (2015) and for the status of Mn, see Najafpour et al. (2016).

In many laboratories around the world, attempts are being made to mimic the Mn cluster (as a whole, or in part) to learn precisely how water is oxidized to oxygen. I particularly refer to the efforts of Mohammad Najafpour, who had involved me in his studies. Najafpour et al. (2012a, b) used a Mn–O model with phenyl group; we called it a *Golden Fish*. Then, Najafpour et al. (2013a, b) used another Mn–O hybrid, which mimicked Mn cluster with Yz (tyrosine) in it, and then Najafpour et al. (2013) added gold and silver

on layered Mn. He and many other research groups, around the World, are indeed providing outstanding ways to mimic the OEC (see e.g., Najafpour et al. 2016). *I would say to all “Good Hunting!”*

Looking for chloride in the 1980s: chloride NMR

Christa Critchley joined our lab, as a postdoctoral research associate, in late 1981, and initiated research on the role of chloride in photosynthesis (Critchley et al. 1982), and this led to the first application of Cl-NMR to monitor chloride and its function, with the help of Ion Baianu (1947–2013), working in Gutowsky’s lab (Baianu et al. 1984, published in the Proceedings of the National Academy of Sciences, USA). Detailed observations on the role of chloride were then made by William Coleman (PhD, 1987): See Coleman et al. (1987a, b, 1988). For a discussion of these (and many other observations, made at that time), see reviews on the role of chloride in oxygen evolution by Coleman and Govindjee (1987) and by Govindjee and Homann (1989). Obviously, there is a need of a review of the older literature to put it all in the context of the current status of this field. Although much research has gone by, we still need to understand the precise roles of chloride as well as of calcium in the oxygen-evolving system.

Now, to a totally different topic—of ATP and ATP synthase—one that we touched only briefly, but had great fun.

Deciding if we could do something new to understand how chloroplasts make ATP

Measurements of ATP production in cells

The first thing we wanted to know was whether we can measure ATP *in vivo*, using the method available at that time, namely, the luciferin-luciferase assay perfected by Bernie Strehler (see e.g., Strehler and Totter 1952). Glenn Bedell, one of my graduate students (PhD, 1972), built the instrument to do just that, and used a very sensitive method of Lyman and DeVincenzo (1967). His findings were published in a detailed paper on the light-induced ATP produced by the cells of the green alga *Chlorella pyrenoidosa* and of the cyanobacterium *Anacystis nidulans* (Bedell and Govindjee 1973): *Chlorella* had more of “non-cyclic,” photophosphorylation, whereas *Anacystis* had more of “cyclic.” It was quite an achievement at that time from a biochemical viewpoint.

Searching for how ATP synthase functions

In view of our interest, at that time, in going into the mechanism of how ATP is synthesized, David VanderMeulen



Fig. 7 Top: Left to right: Wim Vermaas; Bill Rutherford; and Sandra Stirbet, all with Govindjee. Bottom: Bob Blankenship, with Govindjee. Source: Govindjee's Archives

(PhD, 1977) isolated and characterized the “coupling factor” from lettuce; he began a study of its binding to the fluorescent nucleotides (1,N6-ethenoadenosine diphosphate and triphosphate, *epsilon*-ADP and *epsilon*-ATP), using polarization of fluorescence (VanderMeulen and Govindjee 1975, 1977). Our data led to only one conclusion: “Any model for phosphorylation, which is contingent upon equivalent sites for ADP and ATP on the coupling factor (when not energized) is questionable!” When Hasan Younis came from Egypt to UIUC to work with John Boyer, I collaborated with them (see Younis et al. 1979) to look at the conformational changes in the “coupling factor,” when leaves were exposed to low water potential—all was done in order to find a clue to the mechanism of ATP synthesis. *This was it: nothing more and nothing less!* Everyone knows the extraordinary theory of “chemiosmosis” by Peter Mitchell, and the wonderful rotary model of Paul Boyer and John Walker, and the fantastic contribution of Arie Warschel. Just to get a glimpse of the current status of this field, see Mukherjee and Warschel (2017). At that time, we did not have the means or interest to pursue this area of research further—other labs were better at it, although I remain fascinated by our old observations. Yes, we did once look at a few mutants of *Arabidopsis thaliana* altered in the gamma subunit of ATP synthase, and we

did establish a relationship of this system with NPQ of the excited state of Chl *a* (Govindjee and Spilotro 2002). As an aside, I refer the readers to read about a possible role of cyclic phosphorylation in CO₂ fixation (Schürmann et al. 1971). At the time of writing this section, I am hopeful that someone will explain all our old results and, possibly, use them to their benefit.

On the unique and exciting role of bicarbonate in PS II: without it Cytb₆f will not receive any electrons from PS II

I had the greatest pleasure in helping decipher the unique and exciting role of ‘bicarbonate’ on the electron and proton flow in the Z-scheme of photosynthesis (see reviews by Govindjee and Van Rensen 1978; Vermaas et al. 1981a, b; Shevela et al. 2012; cf.; Govindjee et al. 2017). For a current understanding of the role of bicarbonate, I take the liberty of recognizing below those, in my lab, whose work has led to the ideas we have today. First of all, there are two effects of bicarbonate: one is on the electron acceptor side of PS II—bicarbonate is bound to the non-heme iron located between “Q_A” and “Q_B,” and the other is on the

electron donor side of PS II. Most of our work has been on the Q_B side although we know, for sure, that a second effect exists on the electron donor side of PS II (Stemler et al. 1974; Wydrzynski and Govindjee 1975; El-Shintanawy et al. 1990). However, I consider it essential that all of us read the latest papers from the research groups of A. William (Bill) Rutherford (Brinkert et al. 2016), of Charles (Chuck) D. Dismukes (Khorobrykh et al. 2013; Ananyev et al. 2018), and of Johannes Messinger and the late Slava Klimov (Koroidov et al. 2014; Tikhonov et al. 2018) that provide current information on the role of bicarbonate on the electron acceptor and electron donor sides of PS II. We still need a better understanding of the mechanisms involved.

Figure 7 shows photographs of Wim Vermaas; Bill Rutherford; and Sandra Stirbet, all mentioned in this perspective.

How did we get into studying the bicarbonate effect in Photosystem II?

I start with the story of how our lab began to work on the role of bicarbonate in PS II. For many years, I taught a course at the UIUC, called ‘*Bioenergetics of Photosynthesis*.’ In my lecture on the source of ‘oxygen’ in photosynthesis, I presented the O^{18}/O^{16} experiment of Ruben et al. (1941) showing that oxygen comes from water, not CO_2 . I did not stop there, and I mentioned, in a dramatic manner, the experiments of Otto Warburg (Warburg and Krippahl 1958) on the requirement of ‘*bicarbonate*’ in the Hill reaction, which had led him to state that oxygen in photosynthesis comes from CO_2 . (For an account on water oxidation, see Najafpour et al. 2012a, b; and for a historical commentary on oxygen coming from water, see; Joliot et al. 2016.) To my surprise, one of my own graduate students, Alan Stemler (PhD, 1974), who had been working on another project, told me that he wanted to work on this ‘bicarbonate effect’ for his doctoral thesis to find the truth behind it all. If I remember it right, I tried hard to discourage him from doing so as it made no sense to me. However, Alan’s thoughts prevailed, and our lab entered this field (see e.g., Stemler and Govindjee 1973; Stemler et al. 1974), and I continue to remain interested in understanding the mechanism of how bicarbonate functions in PS II. In short, I am thankful for Alan’s insistence in opening this area in our lab as we have learned so much about the role of bicarbonate in PS II in the years that followed. Of course, Warburg was wrong in his conclusion that oxygen comes from CO_2 (see Stemler and Radmer 1975).

Effects on the electron acceptor side of Photosystem II

It was Tom Wydrzynski (PhD, 1977) who was the first one to show, using Chl *a* fluorescence transient measurements, that bicarbonate functions on the electron acceptor side of PS II (Wydrzynski and Govindjee 1975). And, it was the experiment of Govindjee et al. (1976) that established the effect of bicarbonate on the ‘*two-electron gate*’ of PS II. Furthermore, Paul Jursinic (PhD, 1977) studied this effect through Delayed Light Emission (DLE; Jursinic et al. 1976), which was then followed by thermoluminescence measurements (Govindjee et al. 1984), as well as through ‘biochemical surgery’ of the entire system (Rita Khanna; PhD, 1980); all these experiments, taken together, led to the establishment of a major site of bicarbonate between PS II and the Cyt *b₆f* complex, more precisely after ‘ Q_A ’ and before the ‘PQ’ pool (see e.g., Khanna et al. 1977; Siggel et al. 1977). This ‘bicarbonate’ effect seemed to be essentially at a site where several herbicides inhibit photosynthesis, as shown by Rita Khanna; Wim Vermaas, Jiancheng Cao (PhD, 1992); and Jin Xiong (PhD, 1996). For a review, see Shevela et al. (2012), but for details, I refer the readers to the following publications: Khanna et al. (1981); Vermaas et al. (1982a, b); Govindjee et al. (1990, 1991b, 1992); Cao et al. (1992); Xiong et al. (1997, 1998). Rita and Wim were the first ones to show that the bicarbonate and herbicide binding sites were close enough. And, Jiancheng was the first one to demonstrate the existence of the bicarbonate effect in cyanobacteria (see Cao and Govindjee 1988), and to ‘make’ one of the first mutants near the binding site, whereas Jin was the first one to provide the model of PS II based on the available structure of anoxygenic bacteria.

In addition, the involvement of protonation was clearly shown by Khanna et al. (1980), while working with Wolfgang Junge in Berlin. Further, it was Danny Blubaugh (PhD, 1987) who showed that the active species was bicarbonate, not CO_2 (see Blubaugh and Govindjee 1986; cf.; Sarojini and Govindjee 1981). Danny wrote an authoritative summary on the role of bicarbonate in PS II (Blubaugh and Govindjee 1988). However, experiments by Julian Eaton-Rye (PhD, 1987) and Chunhe Xu (PhD, 1992) provided a real detailed understanding of the bicarbonate effect at the Q_B site (see Robinson et al. 1984; Eaton-Rye and; Govindjee 1988a, b; also see; Xu et al. 1991). Govindjee et al. (1991b) showed that formate, used to get bicarbonate-deficient state, indeed releases CO_2 !

Searching for the mechanism of how bicarbonate functions: a long-way to go?

Our entry into site-directed mutagenesis of the D1 and D2 proteins began with the work of Jincheng Cao (Cao et al.



Fig. 8 Top: Left to right: Min Chen (discoverer of Chl f), Govindjee [advertising Shevela et al. (2018) book], and Dima Shevela. Govindjee with Eva-Mari Aro (bottom left), with Gyozo Garab and Alison Telfer (bottom middle), and with Esa Tyystjarvi (bottom right)



Fig. 9 Top (left to right): K. Anwar, Govindjee; Brijesh Gupta, Neelam Soda, Ashwani Pareek, and Sneha Lata Singla-Pareek. Bottom: Govindjee, Deepika Kandoi, and Baishnab C. Tripathy (2017). Source: Govindjee's Archives

1991, 1992) and Jin Xiong (Hutchison et al. 1996; Xiong et al. 1997, 1998; also see; Mulo et al. 1997: coauthors included Esa Tyystjarvi and Eva-Mari Aro), but the detailed picture of how bicarbonate functions, at a precise molecular level, remains unknown and only future experiments and modeling will provide us the answer (see the model of Xiong et al. 1996, 1998, and that of; Shevela et al. 2012). There is hope both through genetic engineering and theoretical calculations (see e.g., Adam et al. 2018) that one day we may have the answer (see e.g., Saito et al. 2013)—and as I am an optimist, I think it will come sooner than later.

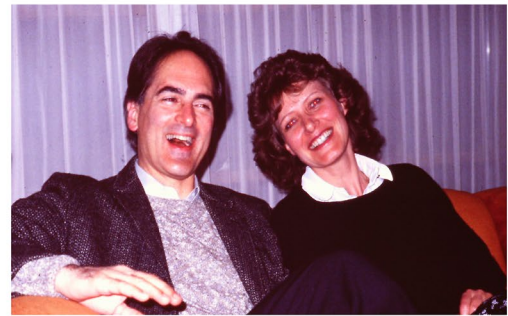
Figure 8 shows recent photographs of several scientists Govindjee met in Uppsala (Sweden).

Where do we go from here?

Almost all my past research publications are on my web site (recent publications are at http://www.life.illinois.edu/govindjee/recent_papers.html; and chronologically arranged papers are at <http://www.life.illinois.edu/govindjee/pubshron.html>). For background on the basics of photosynthesis, see Rabinowitch and Govindjee (1969); Eaton-Rye et al. (2012); Blankenship (2014); Shevela et al. (2018).

I often wonder as to what is still relevant and what is not: only the future will tell. The real future, for me, is in making photosynthesis better able to deal with the Global

Fig. 10 (Left top): Colin Wraight; (right top): John & Barbara Whitmarsh; (left bottom): Tony Crofts, Christine Yerkes, and Wim Vermaas; (right bottom): Don Ort, Govindjee, & Sarah Ort. Dates of photos are unknown. Govindjee's Archives



Issues (e.g., increasing human population, rising temperature, and increasing CO₂). Personally, I believe that these will form the foundation for us to take any rational approach to improve photosynthesis to benefit humanity. With climate change, there is an overriding issue of food security. Though photosynthesis has evolved for billions of years, it is far from being optimal from the perspective of modern agriculture. For example, plants are now operating in a denser canopy and under different CO₂ levels. For identifying targets to modify to gain increased efficiency, very often one uses a systems approach (Long et al. 2015; Xiao et al. 2017; also see; Hunter et al. 2018), with the current global issues, and the predicted future climate conditions becoming a major challenge and focus of future research. It is a huge field, and many outstanding labs are working in this area. I cite here, just as an example, a wonderful paper by Kromdijk et al. (2016) that deals with improving photosynthesis and even crop productivity by accelerating recovery from photoprotection. My own involvement in this area has been with two research groups at Jawaharlal Nehru University in New Delhi (see Fig. 9): (i) Baishnab C. Tripathy: Biswal et al. (2012) looked at the regulation of Chl *b* biosynthesis, and Kandoi et al. (2016) obtained improved *Arabidopsis* (C-3) plants when a gene for PEPC'ase from maize (a C-4 plant) was transferred to it; and (ii) Ashwani Pareek (& Sneha Singla-Pareek): Neelam Soda et al. (2018) obtained much better rice plants when a particular gene *OSIF* was up-regulated. Further, collaboration with Rajagopal Subramaniam at

University of Hyderabad has led to the use of slow Chl *a* fluorescence as a means to monitor state changes (Kodru et al. 2015) and that with Paradha-Saradhi (Shabnam et al. 2017) has the potential of 'mining' heavy metals. In addition, collaboration with the group of Ondrej Prasil (in the Czech Republic) continues on exploiting slow fluorescence changes in understanding regulation of photosynthesis (cited in "Light absorption, excitation energy transfer, primary photochemistry, and light emission: these steps take place in the sub-picosecond to nanosecond time scale" section). Clearly, these types of experiments hold promise for the future. On the other hand, we have many native and elite varieties of rice in this world, and a survey of all could help us find the specific component(s) present in high yielding rice, and then exploit it to our advantage. This is being exploited in the research group of Xin-Guang Zhu in Shanghai, China; see e.g., Hamdani et al. (2015, 2018).

My association with some of the best at UIUC

In addition to those mentioned already (Henri Merkelo; Enrico Gratton; John Boyer; Bob Clegg), there were special associations with the "photosynthesis gang," which included C. John Whitmarsh; William (Bill) Ogren; Colin A. Wraight (1945–2014); Anthony (Tony) R. Crofts; and Donald (Don) R. Ort, authorities and major discoverers themselves. (See Fig. 10 for a few photographs.) It was a pleasant time and fun for me to learn from them. Just to



Fig. 11 Top: At the University of Indore in 2008. Row 1 (left to right): Gyozo Garab; --; Basanti Biswal; Julian Eaton-Rye; Rajni Govindjee; Govindjee; Prasanna Mohanty; Raj Sane; S. Itoh; and Reto Strasser. Some others are Eva-Mari Aro (in row 2: to the left of Basanti); Mike Seibert (in row 2 to the left of Julian); Lou Sherman (in row 2 to the left of Rajni); Jim Barber (behind Govindjee); George Papageorgiou (behind Mohanty); K.N. Guruprasad (in row 2 to the

left of Itoh); Ralph Gasanov (right of Mike Seibert). Bottom left: Left to right: At the University of Huderabad in 2017. Left to right: Julian Eaton-Rye; Suleyman Allakhverdiev; A.S. Raghavendra; William (Bill) Cramer; and Govindjee. Bottom right: At the University of Uppsala, Sweden in 2018: (Sitting): Gary Moore (left); Rick Debus (right). (Standing; Left to right): Johannes Messinger, Stenbjorn Styring, and Govindjee

give a glimpse of our joint activity, I refer to a few publications. (i) With Polly Wang in John Whitmarsh's lab, we discovered short-term oxygen evolution in a Photosystem I-deficient mutant of a cyanobacterium (Wang et al. 2012), and with John, we wrote several reviews on the basics of photosynthesis for teaching (Govindjee and Whitmarsh 1982; Govindjee et al. 2010; Whitmarsh and Govindjee 1995, 1999); (ii) Together with Bill Ogren, I taught a comprehensive course on *Photosynthesis*, and together Bill and I along with Martin Spalding and Christa Critchley discovered that chlorophyll *a* fluorescence could be used to monitor interactions of light intensity and different [CO₂] in *Chlamydomonas reinhardtii* cells (Spalding et al. 1984). Then, Portis and Govindjee (2012) honored Ogren

for his many discoveries including those that defined the enzymatic steps of photorespiration. (iii) I have already mentioned above our collaboration with Colin Wraight on understanding the mechanism of Delayed Light Emission, and on the kinetics of oxygen evolution. In addition, Colin helped us greatly in determining that anoxygenic photosynthetic bacteria do not need bicarbonate to reduce quinones (Shopes et al. 1989; Wang et al. 1992). Colin's death was very sad for our University of Illinois community and a great loss to the global photosynthesis research community (see Govindjee et al. 2015, 2016; Maroti and Govindjee 2016). (iv) My collaboration with Tony Crofts (and his students) on where and how bicarbonate functions in oxygenic photosynthesis has already been included above (see "On the unique and exciting role of bicarbonate in PS II: Without it Cytb6f will not receive any electrons



Fig. 12 Top left: A group photograph at a conference showing Daniel Arnon (standing on the right, in suit & tie; with dark glasses); Marcia Brody (in red dress; Emerson's last PhD student) sitting next to her is Eugene Rabinowitch; and, in the front row on the right is: Tom Bannister (in red tie; 1958 PhD under Rabinowitch) and Tom Punnett (PhD under Emerson); readers will have fun recognizing many oth-

ers. Bottom left: Jim Barber with Les Dutton; bottom middle: Govindjee with Sabeeha Merchant (sitting on the left) and Eva-Mari Aro (sitting on the right). Top right: Rajni and Govindjee celebrating their life together (cf. with Fig. 1). Bottom right: Govindjee relaxing after 60 years of Tryst with Photosynthesis. Source: Govindjee's Archives

or protons from PS II" section). I would like to add that we, along with others, edited a book on oxygen evolution (Inoue et al. 1983). (v) My collaboration with Don Ort has been at various levels. He has saved me from making mistakes in my life, and even interviewed me once about my accomplishments (see footnote #3). Even now, I look upon him for advise on various matters. In addition, I mention that, together, we did write a wonderful chapter on photosynthesis (Ort and Govindjee 1987), which was translated into Russian. And, lastly, together with him, and a few others, Xin-Guang Zhu, then a student of Steve Long (an authority and another major discover in our field) explained Chl a fluorescence transients in leaves predicted from a thorough model of Photosystem II. This has led to a wonderful collaboration with Xin-Guang's group in Shanghai, China.

Epilogue

My tryst includes not only some "dents" made in the understanding of some aspects of Photosystem II, but also quite a lot of failures as well. This is what research life has been for me. For me the friendship and camaraderie is what has been most important. And, this included that with Martin Kamen (deKlerk et al. 1969), co-discoverer of C-14; I recommend the readers to read Kamen (1985). Yes, I do want to make sure that the readers recognize that my real joy has been with research, although I was not a highly skilled experimenter; my research has been particularly significant for the primary events in oxygenic photosynthesis, especially the use of Chlorophyll *a* fluorescence in understanding photosynthesis and on the unique role of bicarbonate in the electron and proton flow on the electron acceptor side of Photosystem II

(the water-plastoquinone oxidoreductase), as mentioned in earlier sections in this perspective.

I end my *tryst* by showing several group photographs (Fig. 11) and some special photographs (Fig. 12).

Whenever I finish reading any perspective, I am reminded of a quote of Frans de Waal (see p. 139 in Hoddeson and Daitch 2002): “In hindsight, the path taken may look straight running from ignorance to profound insight, but only because our memory for ‘dead-ends’ is so much worse than a rat in a maize.” I know I did not get to any profound insight yet, and, I do trust my memory, but I must still search to understand how bicarbonate functions in Photosystem II.

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Appendix

I list those who trusted me to be their advisor (mentor and friend) for their graduate research; they are (chronologically arranged, with the names of countries from where they had come): Carl N. Cederstrand (PhD, Biophysics, 1965; USA; co-advisor: Eugene Rabinowitch); Louisa Yang (Chen Chou Ni) (Master of Science (MS), Biology, 1965; USA); Anne Krey (MS, Biophysics, 1966; USA & Germany); George C. Papageorgiou (PhD, Biophysics, 1968; Greece); John C. Munday, Jr. (PhD, Biophysics, 1968; USA); Frederick Y.T. Cho # (PhD, Biophysics, 1969; USA); Ted Mar (PhD, Biophysics, 1971; Canada); Maarib D.L. Bakri (Bazzaz) (PhD, Biology, 1972; USA & Iraq); Prasanna K. Mohanty# (PhD, Biology, 1972; India); Glenn W. Bedell, II (PhD, Biology, 1972; USA); Alan J. Stemler (PhD, Biology, 1974, USA); Barbara A. (Braun) Zilinskas (PhD, Biology, 1975, USA); Ralph Schooley (MS, Biophysics, 1976; USA); Paul A. Jursinic (PhD, Biophysics, 1977, USA); David L. VanderMeulen

(PhD, Biophysics, 1977, USA); Thomas J. Wydrzynski# (PhD, Biology, 1977; USA); Daniel Wong (PhD, Biophysics, 1979; USA); James M. Fenton (Biophysics, 1980, USA); Willem F. J. (Wim) Vermaas (D, Sc., Agriculture, the Netherlands, 1984; USA & the Netherlands; advisor: Jack Van Rensen); Rita Khanna (PhD, Biology, 1980; India & USA); William J. Coleman (PhD, Biology, 1987; USA); Julian J. Eaton-Rye (PhD in Biology, 1987; UK & New Zealand); Danny J. Blubaugh (PhD, Biology, 1987, USA); Jiancheng Cao (PhD, Biology, 1992; China & USA); Chunhe Xu (PhD, Biophysics, 1992; China); Hyunsuk Shim (PhD, Biophysics, 1992; S. Korea & USA; co-advisor: Peter Debrunner); Jin Xiong (PhD, Biology, 1996; USA & China); Paul Spilotro (MS, Biology, 1999; USA); and Oliver Holub (PhD, Physics; advisor: Robert M. Clegg; Germany).

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