Photosynthesis Research **80:** 427–437, 2004.

Letter to the editor

Passage of a young Indian physical chemist through the world of photosynthesis research at Urbana, Illinois, in the 1960s: a personal essay

Ashish K. Ghosh
4C/19, S.N. Bose Road, Durgapur, 713 205, West Bengal, India

Received 15 August 2003; accepted in revised form 2 October 2003

Key words: Anacystis nidulans, chlorophyll, dye association, Govindjee, Charles F. Kettering, P. Mukerjee, John Olson, photochemistry, photosynthesis, phycobilins, Eugene Rabinowitch, Urbana

Abstract

In September 1963, I came to the famous Photosynthesis Laboratory of Eugene Rabinowitch (1901–1973) at the University of Illinois at Urbana, Illinois, after submitting my doctoral thesis, under Professor Pasupati Mukerjee, in physical chemistry, then at the Indian Association for the Cultivation of Science, Calcutta, India. I present here my personal impressions, my research and interactions at the then International Center of Photosynthesis at Urbana, Illinois. A brief mention is made of research of others at this center, my collaboration with Govindjee (Urbana) and with John Olson (at Brookhaven National Laboratory).

Abbreviations: Chl – chlorophyll; PS I – Photosystem I; PS II – Photosystem II; RC – reaction center

> ‘How much further will you take me?
> Tell me at which port will drop anchor
> this golden boat you are steering?
> Whenever I ask you, lady from some foreign land,
> sweet-smiling, you only smile,
> I fail to understand what you have in mind.
> What does your move suggest?
> You point your finger in silence
> to the overflowing water, endless,
> to the sun at one end of the sky
> going down in the west.
> What is it we shall find there?
> Why are we travelling, in which quest?’
> – Journey to an Unknown Destination by Rabindranath Tagore (from Sonar Tari, 1894,
> available from Nabarun Halder at: http://www.geocities.com/n-halder/pages/tagore/poem006.htm)

From Calcutta, India, to Urbana, Illinois

September, 1963. I was not yet 25 years of age; the world was young, and I had just arrived at the Photosynthesis Laboratory of the University of Illinois at Urbana, Illinois, as a Charles F. Kettering[1] International Fellow in Photosynthesis to work under the famous Professor Eugene Rabinowitch[2] (1901–1973). Could anything be better than this for a fresh Indian research worker who had just submitted a thesis to Calcutta University for the DPhil degree. I thought: anything is possible in this world, but the chances may be small.

I knew Rabinowitch's work even in my student days (e.g., the Franck–Rabinowitch cage effect, Franck and Rabinowitch 1934). Later, during my research I became familiar with some of his other work [see Bannister (1972) for Rabinowitch's

Figure 1. A part of the campus of the University of Illinois at Urbana-Champaign in the 1960s. *Left*: University of Illinois Student (Illini) Union; *right* (*from left to right*): Harker Hall, Natural History Building, Burrill Hall, and Noyes Laboratory, as seen from the main quadrangle. Photograph provided by the author (AG).

contributions]. I did my DPhil thesis on the problem of dye self-association. Rabinowitch was a pioneer in this field (Rabinowitch and Epstein 1941). He was well known for his work on the reversible bleaching (oxidation) of chlorophyll (Rabinowitch and Weiss 1936, 1937; Porret and Rabinowitch 1937), the photo-galvanic effect and photochromism (Rabinowitch 1940a, b). Now I was to work with him!

I had only one published paper at that time (Mukerjee and Ghosh 1963); the bulk of my research work was destined to be published almost seven years later (Ghosh and Mukerjee 1970a, b; Mukerjee and Ghosh 1970a, b). So, even though technically I was a post-doc, for all practical purposes I was more like a graduate student especially since my knowledge of photosynthesis was nil. No, that is not quite correct. I knew that plants make our food by this method, photosynthesis. That was good; I was a bit bored with the dyes, and welcomed the change.

The first few weeks went in a blur. I had to solve problems of existence: a place to stay, what food to eat, and, of course, social company. Figure 1 shows a photograph of the campus near the building I was to work in (The Natural History Building). I survived. In those golden days, expatriate Indians looked after each other. A good friend, Mr Matiur Rahman, who was doing his PhD in Washington, DC, sent me US$ 100 (handed to me at Idlewild Airport, John F. Kennedy Airport now), and Dr Govinda Basu provided accommodation. On October 1, 1963, I moved to a rented apartment in Urbana, Illinois, after receiving my first salary, with a fellow tenant (Mr Asit Das, a graduate student of the late Professor C. Ladd Prosser at the University of Illinois).

Photosynthesis laboratory at Urbana

Only then did it become possible for me to take a close look at my surroundings. Of course, during the month of September (1963), I had come to realize that the entire photosynthesis laboratory was a closely knit unit, extremely friendly and helpful to a newcomer. Now, I made a more careful study. Professor Rabinowitch was a benign, soft-spoken, absent-minded scientist. Then there was Professor Govindjee, 30 years old, with a dynamic personality. Dr N.R. Murty (a post-doc of Rabinowitch) was taciturn, so also were two other people, Jobie D. Spencer (assistant to Govindjee) and Mr Ervie Ditzler (the machinist). Then, there was Carl Cederstrand, a redheaded giant of a man, outgoing and an MG (automobile) enthusiast, who later obtained his PhD in 1965, jointly under Eugene Rabinowitch and Govindjee. Daniel (Danny) Rubinstein, an excitable chap, but highly intelligent, obtained his PhD in 1964 under Rabinowitch.

Dr Murty was busy measuring chlorophyll (Chl) *a* fluorescence lifetime (Murty and Rabinowitch 1965).

He observed a break in the decay curve of Chl *a* fluorescence, indicating the presence of more than one fluorescing species (however, see Singhal and Rabinowitch 1969). (For earlier discoveries on lifetime of fluorescence in this laboratory, see Brody 2002.) Cederstrand was mainly building instruments, but he decided to work for a PhD under Rabinowitch; however, he was basically guided by Govindjee; he demonstrated the existence of different spectral forms of Chl *a in vivo*, using a new integrating sphere (actually a dodecahedron with a photosensor on each of its 12 sides (Cederstrand et al. 1966a) and presented one of the earliest fluorescence spectra of the two pigment systems (Cederstrand and Govindjee 1966). Danny became a very good friend. He was working with the difference absorption spectrophotometer, studying the intermediates that are first formed upon shining light on the green alga *Chlorella.* 'L.N.M. Duysens built this instrument and worked here,' he told me. He showed that a 1957 claim by an earlier student of Rabinowitch in the laboratory for the discovery of 'P680' was a fluorescence artifact (Rubinstein and Rabinowitch 1963).

Working with dyes

Professor Rabinowitch had plans for me. He had been working on the solar energy project since his M.I.T. days and was still interested in it. Now he wanted me to continue the work of another post-doc of his, K.G. Mathai (Mathai and Rabinowitch 1962a, b), where they thought they had stored solar energy by separating oxidants and reductants in two immiscible phases. I am afraid I could not summon up enough enthusiasm for this project. One must remember this was in 1963; there was no energy-crisis, gasoline was sold for US$ 0.22 per gallon, cigarette-smoking was not a crime, we had not heard about AIDS, women's lib, green house gas, global warming, etc. Atomic energy was thought to be the energy source for the future: fission now, fusion later. The major concern was the possibility of nuclear war. In such a situation I did not feel that solar energy had much relevance. Besides, the basic science part had already been done – the only thing left was to make it viable. I had no interest in that type of work.

Moreover, I could not repeat Mathai's work! I asked myself: did he actually do these experiments or just make them up? As far as the photogalvanic effect in a Fe^{2+}/thionine aqueous system was concerned, it was all right (Rabinowitch 1940a, b). Now, they apparently had extracted leuco-thionine in ether, thus storing light energy as chemical energy! My task was to make a viable electrochemical cell, so as to extract the stored energy as electricity. But, I could not get any leuco-thionine extracted in ether! I was in a completely new country, new environment, new laboratory, among new people. I was not interested in getting into any controversy. So, I simply dabbled with that work and spent most of my time studying photosynthesis.

I got the basics of photosynthesis from a small book by Hill and Whittingham (1955). I learned CO_2 fixation from a book written by Bassham and Calvin (1957). From Daniel Arnon's article in 'Light and Life' (Arnon 1961), I gathered knowledge about photo-phosphorylation and related processes. But, for most of my studies, the treatise on 'Photosynthesis and Related Processes' written by Rabinowitch (1945, 1951, 1956) was indispensible.

Meanwhile, Rabinowitch was getting somewhat impatient, as he felt that I was not doing any research work. I had to do something about it, so I turned to my old field of study, 'dye association.' Rabinowitch (1940a, b) and Rabinowitch and Epstein (1941) had used absorption spectrophotometry and fluorimetry to study the self-association of thionine and methylene blue. I thought I could perhaps improve upon their work. And sure enough, I did, but I did not publish it for almost a decade (Ghosh 1974a–c, 1975). As far as absorption spectrophotometry was concerned, I devised new methods for extrapolation to obtain the extinction coefficients of the monomer, ε_{m}, and the aggregate, ε_{a}, and the dimerization and trimerization constants; the values obtained were quite in line with the values obtained by the 'iso-extraction' method (Ghosh 1970; Ghosh and Mukerjee 1970a, b; Mukerjee and Ghosh 1970a, b). This was a vast improvement upon the methods till then being used by workers in this field, the spectrophotometric method being the most popular of all the methods used for the study of dye self-association.

For the fluorimetry I had Govindjee's help. He had a very good spectrofluorimeter, which gave both the emission and the excitation spectra. It was so sensitive that I could excite methylene blue at 500 nm, and get very good data even at a concentration of 2 μM. Thus, many problems encountered by old workers, such as reabsorption of fluorescence and calculation of how much light has been absorbed by the *fluorescing* species, etc. were obviated. The monomer concentration, *b*, could be directly obtained from the relationship:

$$\frac{b}{B} = \frac{\phi}{\phi_0}$$

where, ϕ is the fluorescence of the dye at concentration B and ϕ_0 is the extrapolated value of ϕ to zero dye concentration.

The interesting point here was the fact that even though the dimerization constant was more or less of the same order as obtained by iso-extraction and by absorption spectrophotometry, the trimerization constant was 10 times the value obtained by other methods. This could only mean that self-quenching of dyes, even at high dilutions, was more than what could be assigned to the fraction of non-fluorescing aggregated dye molecules. There is dynamic or collisional quenching also. This was a point of debate among older workers. I was happy to clear it up.

Now, the main reason the previous workers considered that the 'apparent' quenching is all but due to aggregate formation was that at such high dilution, the collisional encounter between the two dye molecules would be rare. How, then, would fluorescence be quenched? But, experiments did show that such quenching actually occurs; therefore, we must visualize 'excitation energy transfer' by Förster's (1948) mechanism here. Still, however, such energy transfer cannot lead to fluorescence quenching; only excitation transfer from one dye molecule to another could. Thus we had to invoke the dye-dimer (or aggregate) as the 'excitation trap' or the 'quencher.' When the excitation, traveling from one dye molecule to another, reaches a dimer, it is quenched!

Brody and Brody (1961) in Rabinowitch's laboratory had studied what they considered to be a dimer of Chl *a* molecule *in vivo*, which they considered to be the reaction center (RC) of photosynthesis. This was, of course, long before the true P700, RC of Photosystem I (PS I), was known to be a dimer (see Jordan et al. 2001 for X-ray structures). That idea appealed to me, chiefly because I was familiar with the properties of the methylene blue dimer. So, now I started to think about this problem as it may relate to *in vivo* photosynthesis.

Working with cyanobacteria

The system I chose first was a cyanobacterium (then called a blue-green alga) *Anacystis nidulans* (now called *Synecococcus* sp. Pasteur Culture Collection (PCC) 6311) – first of all because it was available (Govindjee was doing lot of work with it at the time; see Govindjee 1963, 1965; also see Papageorgiou and Govindjee 1967, 1968a, b; Cho and Govindjee 1970a), but more so because it had no Chl *b* (as opposed to the green alga *Chlorella*, also available at that time in the photosynthesis laboratory). With *Anacystis*, the picture was clear: the blue pigment phycocyanin absorbs far away from Chl *a*; the problem of the overlap of the spectra was not a concern. Duysens (1952) had shown that light energy absorbed by phycocyanin is transferred to Chl *a* that then fluoresces; it could act only as an accessory pigment, and the photochemical reactions must be done by Chl *a*. (For visualization of energy transfer from phycobilins to Chl *a*, see Mimuro 2002.)

The first point to consider in the 1960s was the two RCs – for Photosystem I (PS I) and PS II, respectively. How can it be that both RCs contain Chl *a*, but one has a suggested absorption band at 680 nm, with the other at 700 nm? Kok (1956) had discovered P700, whereas P680 was only speculated to exist (Rabinowitch and Govindjee 1965; actually, it was discovered soon thereafter by Döring et al. (1969); also see Govindjee et al. 1970). Evidently, there was no problem for the RC of PS II: Spectroscopic evidence clearly indicates it to be a Chl *a* molecule. But what about the RC of PS I? How can it have its absorption maximum shifted to 700 nm? It is here that Brody's ideas made sense. It must be a Chl dimer! Of course, both the RCs would be attached to necessary 'enzymes,' but that was not my problem. The biochemists must and did solve those problems (see Nelson and Ben-Shem 2002; and Satoh 2003). Further, the X-ray structures proved the arrangements (see Witt for PS II and Fromme and Mathis for PS I, this issue). Ironically, high resolution X-ray diffraction proved the RC chromophore of PS II also to be a Chl *a* dimer, although the individual molecules of Chl are farther than in P700 (Zouni et al. 2001).

The second point we considered, for *A. nidulans*, was equally interesting: why is it that when phycocyanin absorbs light, we see Chl fluorescence, but there is very little Chl fluorescence when the light is actually absorbed by Chl *a*? This problem had been dealt with by Duysens (1952); he had postulated the existence of two types of Chl *a* – one-weakly or non-fluorescent (absorbing at longer wavelengths), and the other strongly fluorescent (that was sensitized by absorption in phycocyanin). This could have one and only one explanation. We assumed that PS II consisted mainly of phycocyanins and a small number of fluorescing Chl *a* molecules. But we suspected that the Chl *a* molecules in PS I were in an aggregated state and the vibrational deactivation (heat) of excitation was at least an order of magnitude faster compared to the fluorescence life-time, otherwise, these Chl *a* molecules in PS I would fluoresce. But then, we ran into another problem. How is it that although the excitation is lost as heat, chemical reactions do occur efficiently at the RC of PS I? This again, could have one and only one solution. The reaction rate at the PS I RC must be much faster ($\sim$1 ps range) than thermal degradation. Today, we could rationalize all the observations that were known to us regarding this matter (see Ke 2001; Blankenship 2002; Seibert and Wasielewski 2003). This, then, brought us to a third point: are the photosystems in 'separate packages'? Today, we know that Photosystems I and II are in different protein complexes [see Blankenship (2002) for a current picture]. The idea that the photosystems would be static did not appeal to me. I discussed all these points with Govindjee and made plans to grow *A. nidulans* in lights of various colors and intensities, so as to alter the phycocyanin or Chl *a* ratios. The experiments were mostly done by Govindjee; I just assisted him, simply to learn the various experimental techniques. The results were quite good (Ghosh and Govindjee 1966). [See Tandeau de Marsac (2003) for a discussion of the literature on phycobilisomes.] It seemed that one could change the amount of phycocyanin and Chl *a* in the pigment systems as revealed by their absorption and fluorescence spectra [see Figures 1 and 2 in Ghosh and Govindjee (1966); also see Ghosh et al. (1966) for experiments on green alga *Chlorella* grown in heavy water].

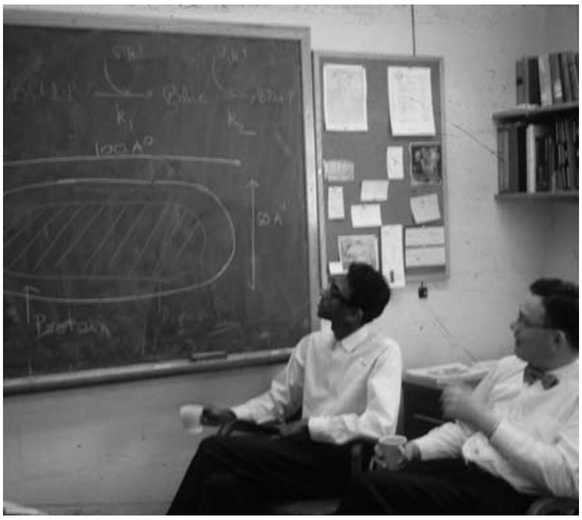

Figure 2. The author (AG) (left) and John Olson sitting in the Brookhaven National Laboratory, listening to Helen Hines (not shown). Photo taken in 1966. Photograph provided by the author (AG).

Back to chemical systems

So, I had to try a different approach. Why not test the hypothesis in model systems? Why not combine absorption spectrophotometry with fluorescence to see if a dimer can actually quench the fluorescence of monomers? I used for my experiments methylene blue dissolved in sodium lauryl sulfate solution (published after, again, a long incubation; Ghosh 1974b). The effect of varying concentrations of sodium lauryl sulfate showed that an aggregate of the dye was formed, under the influence of its anion, much below its critical micelle concentration. An interesting point here was that I obtained virtually the same results as obtained in the fluorescence studies of the dye itself (Ghosh 1974a). I could compute the amount of dimer in our system simply from the spectrophotometric data. Fluorescence, however, declined far more sharply. 'Where the fluorescence is 3% of the maximum yield, the absorbance data indicated only 35% aggregation' (Ghosh 1974b). I calculated that 6–8 dye molecules are enclosed in one dye-detergent micelle. If only one dye-dimer is present in any particular micelle, the entire fluorescence of that group is quenched. So, here I had a *primitive* model for PS I, the dimer of the pigment as the trap.

Next, I went one step further to attempt a model for PS II. In our framework, PS II consisted mostly of phycocyanins, with only a few Chl *a* molecules acting as energy acceptors. I asked what would happen if I enclosed two different dyes in dye-detergent micelles: thionine and methylene blue along with sodium lauryl sulfate. The results have been published (Ghosh 1973). Yes, I could observe transfer of excitation energy from thionine to methylene blue and could calculate the number of thionine molecules in a micelle. The number was 6–8, and the entire thionine fluorescence was quenched by one molecule of methylene blue and the energy was emitted as methylene blue fluorescence. Here I had my model, although again primitive, for PS II.

In all this work, I used the spectrofluorometer of Govindjee. In point of fact, the 2 years I spent in Urbana (1963–1965), I had the closest collaboration with him. Of the little that I learned about photosynthesis research (pretty little, I must admit), 75% was from Govindjee and 25% from all the other people, including Professor Rabinowitch.

Research of others at Urbana, Illinois

Rabinowitch's research was focused on (1) characterization of dyes (including Chl), photochemical storage, and transfer of energy in model systems (Ainsworth and Rabinowitch 1960; Ichimura and Rabinowitch 1960; Murty and Rabinowitch 1964; Frąckowiak and Rabinowitch 1966; Singhal and Rabinowitch 1967; Singhal et al. 1968a, b; Singhal and Rabinowitch 1970; Singhal et al. 1970; Srinivasan and Rabinowitch 1970); (2) lifetime of Chl *a* fluorescence (Tomita and Rabinowitch 1962; Murty and Rabinowitch 1965; Singhal and Rabinowitch 1969); and (3) spectral characterization of algal and chloroplast suspensions (Cederstrand et al. 1966b; Das et al. 1967; Szalay et al. 1967). Appendix 1 lists Rabinowitch's coworkers.

Govindjee's research, on the other hand, was focused on (1) two-light effects in Chl *a* fluorescence (Govindjee et al. 1960), in chloroplast reactions (R. Govindjee et al. 1964, 1968; Govindjee and Bazzaz 1967) and in algae (Govindjee and Rabinowitch 1960; Govindjee and Govindjee 1965; Bedell and Govindjee 1966; also see R. Govindjee et al. 1960); (2) new emission bands and temperature dependence of fluorescence, in photosynthetic organisms, down to 4 K (Krey and Govindjee 1964, 1966; Cho et al. 1966; Govindjee and Yang 1966; Das and Govindjee 1967; Cho and Govindjee 1970a–c); and (3) understanding of fluorescence induction (the Kautsky effect) in algae (Papageorgiou and Govindjee 1967, 1968a, b; Merkelo et al. 1969; Munday and Govindjee 1969a, b). Appendix 2 lists Govindjee's coworkers.

The discoveries of the famous Robert Emerson, who had passed away four years before I came to Urbana, were discussed by Rabinowitch (1959).

Move to Brookhaven National Laboratory (BNL): with John Olson

Professor Rabinowitch was enthusiastic about the work I was doing and wanted me to stay. But my time was up. I had an exchange visitor visa, with a time limit of three years. I felt it would be better for me to spend the final year in a different laboratory and moved to the Brookhaven National Laboratories (BNL) in 1965. There, I worked with Professor John Olson on a pigment–protein complex, the results of which have been published (Ghosh and Olson 1968; Ghosh et al. 1968). [See Olson, this issue, for a historical minireview on the Fenna–Matthews–Olson (FMO) protein.] Figure 2 shows a photograph of John Olson and the author (AG) discussing results of their joint research.

The high point of my stay in BNL was the Photosynthesis Symposium, held in 1966, organized by the photobiology group of the Biology Department

Figure 3. A photo taken in 1966 at the Brookhaven Symposium on Photosynthesis. *From left to right*: Ashish Ghosh, Laszlo Szalay and Mrinmoyee Das. Photograph provided by Mrinmoyee Das.

Figure 4. Another photo taken at the Brookhaven Symposium on Photosynthesis in 1966. *From left to right*: Patrick Williams, Laszlo Szalay, Elizabeth Tombacz and Mrinmoyee Das. Photograph provided by Mrinmoyee Das.

Figure 5. A 1967 group photograph of part of the Govindjee and Rabinowitch laboratories. Those working with Govindjee are italicized. *From left to right*: Gauri Singhal, *George Papageorgiou*, *Prasanna Mohanty*, Patrick Williams, N.R. Murty, Govindjee, Elizabeth Tombacz (Szalay), Laszlo Szalay, *Glenn Bedell*, and *Fred Cho*. Photograph provided by Mrinmoyee Das.

Figure 6. A 1967 group photograph at the residence of Govindjee (1101 McHenry Street, Urbana, Illinois). Govindjee's coworkers are italicized. In the foreground on the left is Paula Cho (wife of *Fred Cho*), Marion Bedell (wife of *Glenn Bedell*) is sitting near the table, Judy Munday (wife of *John C. Munday*) is sitting on the floor on the right. Sitting on chairs (*from left to right*): Eugene Rabinowitch, Mrinmoyee Das (with a gift box in her hand), Anya Rabinowitch (wife of Eugene Rabinowitch), *Ted Mar* (sitting on floor), Mrs Meenakshi Kumar (wife of Dr *Ashok Kumar*), *Paul Jursinic* (sitting on floor). *George Papageorgiou* (wearing a tie) is sitting on a chair (on the right). Standing in the door way (far in the back) includes *Patrick Breen* (the tallest person in the back), and *Alan Stemler* is on the right of Breen. Photograph provided by Mrinmoyee Das.

of BNL. We had the privilege of meeting all the stalwarts of photosynthesis research – William Arnold, Britton Chance, Louis N.M. Duysens, André Jagendorf, Bessel Kok, Horst T. Witt, and of course, Rabinowitch and Govindjee from Urbana. [The group photograph of speakers at this symposium appears on p. 123 in Pearlstein (2002).]

I was glad to meet my old friends. They were post-doctoral associates of Rabinowitch: Mrinmoyee Das, whom I knew from my college days in Calcutta and Gauri Shankar Singhal, who worked along with me in Jadavpur University while I was doing research there. Both joined Rabinowitch's lab after I had left Urbana.

Figure 3 is a photograph of the author (AG), Laszlo Szalay (visiting scientist from Hungary) and M. Das. Figure 4 is a photograph of Patrick Williams (post-doctoral associate of Rabinowitch from the UK), Laszlo Szalay, Elizabeth Tombacz (Mrs Szalay) and Mrinmoyee Das. Both photos were taken at the 1966 Brookhaven National Symposium. Figures 5 and 6 (which are, unfortunately, out-of-focus) are photographs of two separate gatherings of some of the members of the research groups of Govindjee and Rabinowitch at Urbana, Illinois, in the 1960s. Figure 7 shows Eugene Rabinowitch, Mrinmoyee Das and Ted Mar (a student of Govindjee) at the Champaign–Urbana airport when Das was leaving Urbana.

I also met Dr Pierre Joliot (actually, he was the only one who came to see our laboratory in BNL) during the symposium. I kept asking him, 'Are you really the grandson of Madame Curie?' He was amused. What I was thinking was: 'Why is he in photosynthesis? He should be in atomic or nuclear physics.'

Anyway, those were really very enjoyable days.

Figure 7. Urbana-Champaign Airport: *from left to right*: Eugene Rabinowitch, Mrinmoyee Das and Ted Mar.

Acknowledgments

I thank all the members of the photosynthesis labs of both Urbana and BNL. They were all responsible for my development as an individual and as a scientist. I am most grateful to Mrinmoyee Das for providing me Figures 3–7 from her collection. I am grateful to George Papageorgiou, who was one of the reviewers of this paper, for helpful suggestions; another reviewer provided several references that were not available to me. This paper was edited by J. Thomas Beatty.

Notes

1. See Vernon (2003) for a history of research at the Kettering Laboratory in Yellow Springs, Ohio.
2. Eugene Rabinowitch is known for several activities including the following: co-founder of 'Atomic Scientists of Chicago'; Editor and editorial writer of the *Bulletin of Atomic Scientists*; Editorial Board of *Biophysical Journal*; member and continuing committee of Pugwash-COSWA conferences; member of the Center of Advanced Study at the University of Illinois. He received several awards including: 'Outstanding Citizen of Foreign Birth' from the Immigrant League of Chicago; Honorary doctorate of Human Letter (Brandeis University); Honorary doctorate of Science (Dartmouth College); UNESCO's Kalinga Prize; Honorary doctorate of Science (Columbia College, Chicago); and the Kettering Award for Excellence in Photosynthesis Research.

Appendix 1: A list of coworkers of Eugene Rabinowitch (1960–1970)

A partial alphabetical list of postdoctoral associates and visiting scientists in Rabinowitch's laboratory included (those who worked also with Govindjee are italicized): Stanley Ainsworth (UK), *Mrinmoyee Das* (India), Danuta Frąckowiak (Poland), *Ashish Ghosh*, *Rajni Govindjee* (India), Janos Hevesi (Hungary), *Shoji Ichimura* (Japan), Jean Lavorel (France), K.G. Mathai (India), Neti Radhakrishnan Murty (India), Vitaly A. Sineshchekov (Soviet Union), *Gauri Shankar Singhal* (India), V. Srinivasan (India), *Laszlo Szalay* (India), Elizabeth Tombacz (Hungary), Giti Tomita (Japan), and Patrick Williams (UK). Danny Rubinstein and *Carl Cederstrand* were doctoral students.

Appendix 2: A list of coworkers of Govindjee (1960–1970)

Professor Govindjee's graduate students (in alphabetical order) were: Maarib Bazzaz, Glenn Bedell, Frederick Cho, Anne Krey, Ted

Mar, Prasanna Mohanty, John C. Munday, Jr, George Papageorgiou, and Louisa Yang (Ni). In addition, three research scientists (Drs Mrinmoyee Das, Rajni Govindjee and Gauri S. Singhal) worked with him. Postdoctoral associates of Govindjee included Patrick Breen and Ashok Kumar.

References

Ainsworth S and Rabinowitch E (1960) Electron transfer and absorption spectra of complexes. Science 131: 303

Arnon DI (1961) Cell-free photosynthesis and the energy conversion process. In: McElroy WD and Glass B (eds) Light and Life, pp 489–569. The Johns Hopkins Press, Baltimore, Maryland

Bannister TT (1972) The careers and contributions of Eugene Rabinowitch. Biophys J 12: 707–718

Bassham JA and Calvin M (1957) The Path of Carbon in Photosynthesis. Prentice Hall, Engelwood Cliffs, New Jersey

Bedell G and Govindjee (1966) Quantum yield of oxygen evolution and the Emerson enhancement effect in deuterated *Chlorella*. Science 152: 1383–1385

Blankenship RE (2002) Molecular Mechanisms of Photosynthesis. Blackwell Science, Oxford, UK

Brody SS (2002) Fluorescence lifetime, yield, energy transfer and spectrum in photosynthesis, 1950–1960. Photosynth Res 73: 127–132

Brody SS and Brody M (1961) Spectral characteristics of aggregated chlorophyll and its possible role in photosynthesis. Nature 19: 547–549

Cederstrand C and Govindjee (1966) Some properties of spinach chloroplast fractions obtained by digitonin solubilization. Biochim Biophys Acta 120: 177–180

Cederstrand C, Rabinowitch E and Govindjee (1966a) Analysis of the red absorption band of Chl *a in vivo*. Biochim Biophys Acta 126: 1–12

Cederstrand C, Rabinowitch E and Govindjee (1966b) Absorption and fluorescence spectra of spinach chloroplast fractions obtained by solvent extraction. Biochim Biophys Acta 120: 247–258

Cho F and Govindjee (1970a) Low-temperature (4–77 K) spectroscopy of *Anacystis:* temperature dependence of energy transfer efficiency. Biochim Biophys Acta 216: 151–161

Cho F and Govindjee (1970b) Fluorescence spectra of Chlorella in the 295–77 K range. Biochim Biophys Acta 205: 371–378

Cho F and Govindjee (1970c) Low-temperature (4–77 K) spectroscopy of Chlorella: temperature dependence of energy transfer efficiency. Biochim Biophys Acta 216: 139–150

Cho F, Spencer J and Govindjee (1966) Emission spectra of *Chlorella* at very low temperatures ($-269\,°\mathrm{C}$ to $-196\,°\mathrm{C}$). Biochim Biophys Acta 126: 174–176

Das M and Govindjee (1967) A long-wave absorbing form of chlorophyll *a* responsible for the red drop in fluorescence at 298 K and the F723 band at 77 K. Biochim Biophys Acta 143: 570–576

Das M, Rabinowitch E, Szalay L and Papageorgiou G (1967) The 'sieve effect' in Chlorella suspensions. J Phys Chem 71: 3543–3549

Döring G, Renger G, Vater J and Witt HT (1969) Properties of photoactive chlorophyll *a*II in photosynthesis. Z Naturforsch 24b: 1139–1143

Duysens LNM (1952) Transfer of excitation energy in photosynthesis. Thesis. State University at Utrecht, The Netherlands

Förster Th (1948) Intermolecular energy migration and fluorescence. Ann Physik 2: 55–75 (English translation by R.S. Knox, Department of Physics and Astronomy, University of Rochester, Rochester, New York 14627)

Franck J and Rabinowitch E (1934) Some remarks about free radicals and the photochemistry of solutions. Trans Faraday Soc 30: 120–130

Frąckowiak D and Rabinowitch E (1966) The methylene blue-ferrous iron reaction in a two phase system. J Phys Chem 70: 3012–3017

Fromme P and Mathis P (2004) Unraveling the Photosystem I reaction center: a history, or the sum of many efforts. Photosynth Res 80: 109–124 (this issue)

Ghosh AK (1970) Study of the self-association of methylene blue from protonation equilibriums. J Am Chem Soc 92: 6415

Ghosh AK (1973) Energy transfer in dye-detergent micelles: a model for the separate package photosynthetic unit. Ind J Chem 11: 1014–1016

Ghosh AK (1974a) Self association constant of methylene blue from the concentration dependence of the fluorescence efficiency. Curr Sci 43: 655–656

Ghosh AK (1974b) Quenching of fluorescence of methylene blue by the dye dimer. Ind J Chem 12: 313–314

Ghosh AK (1974c) Extinction coefficient of methylene blue monomer. Ind J Chem 12: 897

Ghosh AK (1975) A new variation of Rabinowitch and Epstein's method of studying self-association of the dyes: dimerisation and trimerisation constants of methylene blue. Z Physik Chem (Frankfurt) 94: 161

Ghosh AK and Govindjee (1966) Transfer of the excitation energy in *Anacystis nidulans* grown to obtain different pigment ratios. Biophys J 6: 611–619

Ghosh AK and Mukerjee P (1970a) Multiple association equilibria in the self-association of methylene blue and other dyes. J Am Chem Soc 92: 6408–6412

Ghosh AK and Mukerjee P (1970b) Ionic strength effects on the activity coefficient of methylene blue and its self-association. J Am Chem Soc 92: 6413–6415

Ghosh AK and Olson JM (1968) Effects of denaturants on the absorption spectrum of the bacteriochlorophyll-protein from the photosynthetic bacterium *Chloropseudomonas ethylium*. Biochim Biophys Acta 162: 135–148

Ghosh A, Govindjee, Crespi HL and Katz JJ (1966) Fluorescence studies on deuterated *Chlorella vulgaris*. Biochim Biophys Acta 120: 19–22

Ghosh AK, Broker TR and Olson JM (1968) A kinetic study of bacteriochlorophyll pheophytinization of the protein complex from a green photosynthetic organism. Biochim Biophys Acta 162: 402–413

Govindjee (1963) Emerson enhancement effect and two light reactions in photosynthesis: dedicated to the memory of Late Professor Robert Emerson. In: Kok B and Jagendorf AT (eds) Photosynthetic Mechanisms of Green Plants Publication 1145, pp 318–334. Natl Acad Sci Natl Res Council Washington, DC

Govindjee (1965) Fluorescence studies on algae, chloroplasts and chloroplast fragments. In: Thomas JB and Goedheer JC (eds) Currents in Photosynthesis, pp 93–103. Ad Donker Publisher, Rotterdam, The Netherlands

Govindjee and Bazzaz M (1967) On the Emerson enhancement effect in the ferricyanide Hill reaction in chloroplast fragments. Photochem Photobiol 6: 885–894

Govindjee and Govindjee R (1965) Two different manifestations of enhancement in the photosynthesis of *Porphyridium cruentum* in flashing monochromatic light. Photochem Photobiol 4: 401–415

Govindjee and Rabinowitch E (1960) Two forms of Chl *a in vivo* with distinct photochemical functions. Science 132: 355–356

Govindjee and Yang L (1966) Structure of the red fluorescence band in chloroplasts. J Gen Physiol 49: 763–780

Govindjee, Ichimura S, Cederstrand C and Rabinowitch E (1960) Effect of combining far-red light with shorter wave light on the excitation of fluorescence in Chlorella. Arch Biochem Biophys 89: 322–323

Govindjee, Döring G and Govindjee R (1970) The active chlorophyll *a* II in suspensions of lyophilized and tris-washed chloroplasts. Biochim Biophys Acta 205: 303–306

Govindjee R, Thomas JB and Rabinowitch E (1960) Second Emerson effect in the Hill reaction of Chlorella cells with quinone as oxidant. Science 132: 421

Govindjee R, Govindjee and Hoch G (1964) Emerson enhancement effect in chloroplast reactions. Plant Physiol 39: 10–14

Govindjee R, Rabinowitch E and Govindjee (1968) Maximum quantum yield and action spectra of photosynthesis and fluorescence in *Chlorella*. Biochim Biophys Acta 162: 530–544

Hill R and Whittingham CP (1955) Photosynthesis. Wiley, London

Ichimura S and Rabinowitch E (1960) Chlorophyll-sensitized photoreduction in the thionine ferrous system. Science 131: 1314

Jordan P, Fromme P, Witt HT, Klukas O, Sänger W and Krauss N (2001) Three-dimensional structure of cyanobacterial Photosystem I at 2.5 Angstrom resolution. Nature 411: 909–917

Ke B (2001) Photosynthesis: Photobiochemistry and Photobiophysics. Kluwer Academic Publishers, Dordrecht, The Netherlands

Kok B (1956) On the reversible absorption change at 705 nm in photosynthetic organisms. Biochim Biophys Acta 22: 399–401

Krey A and Govindjee (1964) Fluorescence changes in *Porphyridium* exposed to green light of different intensity: a new emission band at 693 m and its significance to photosynthesis. Proc Natl Acad Sci USA 52: 1568–1572

Krey A and Govindjee (1966) Fluorescence studies on a red alga *Porphyridium cruentum*. Biochim Biophys Acta 120: 1–18

Mathai KG and Rabinowitch E (1962a) Studies of the thionine ferrous iron reaction in a heterogeneous system. J Phys Chem 66: 663–664

Mathai KG and Rabinowitch E (1962b) The chlorophyll-sensitized photoreduction of thionine by ascorbic acid. J Phys Chem 66: 954–955

Merkelo H, Hartman SR, Mar T, Singhal GS and Govindjee (1969) Mode locked lasers: measurements of very fast radiative decay in fluorescent systems. Science 164: 301–302

Mimuro M (2002) Visualization of excitation energy transfer processes in plants and algae. Photosynth Res 73: 133–138

Mukerjee P and Ghosh AK (1963) The effect of urea in methylene blue, its self association, and interaction with polyelectrolytes in aqueous solution. J Phys Chem 67: 193–195

Mukerjee P and Ghosh AK (1970a) The 'isoextraction' method and the study of the self-association of methylene blue in aqueous solutions. J Am Chem Soc 92: 6403–6424

Mukerjee P and Ghosh AK (1970b) Thermodynamic aspects of self-association and hydrophobic bonding of methylene blue. Model system for stacking interactions. J Am Chem Soc 92: 6419–6424

Munday Jr JC and Govindjee (1969a) Light-induced changes in the fluorescence yield of chlorophyll *a in vivo* III. The dip and the peak in the fluorescence transient of *Chlorella pyrenoidosa*. Biophys J 9: 1–21

Munday Jr JC and Govindjee (1969b) Light-induced changes in the fluorescence yield of chlorophyll *a in vivo* IV. The effect of preillumination on the fluorescence transient of *Chlorella pyrenoidosa*. Biophys J 9: 22–35

Murty NR and Rabinowitch E (1964) Intermolecular quenching of higher excited states. J Chem Phys 41: 602–603

Murty NR and Rabinowitch E (1965) Fluorescence decay studies of chlorophyll *a in vivo*. Biophys J 5: 655–661

Nelson N and Ben-Shem A (2002) Photosystem I reaction center: past and future. Photosynth Res 73: 193–206

Papageorgiou G and Govindjee (1967) Changes in intensity and spectral distribution of fluorescence. Effect of light pretreatment on normal and DCMU-poisoned *Anacystis nidulans*. Biophys J 7: 375–390

Papageorgiou G and Govindjee (1968a) Light-induced changes in the fluorescence yield of chlorophyll *a in vivo*. I. *Anacystis nidulans*. Biophys J 8: 1299–1315

Papageorgiou G and Govindjee (1968b). Light-induced changes in the fluorescence yield of chlorophyll *a in vivo*. II. *Chlorella pyrenoidosa*. Biophys J 8: 1316–1328

Pearlstein RM (2002) Photosynthetic exciton theory in the 1960s. Photosynth Res 73: 119–126

Porret D and Rabinowitch E (1937) Reversible bleaching of chlorophyll. Nature 140: 321

Rabinowitch E (1940a) The photogalvanic effect. I. The photochemical properties of the thionine–iron system. J Chem Phys 8: 551–559

Rabinowitch E (1940b) The photogalvanic effect. II. The photogalvanic properties of the thionine–iron system. J Chem Phys 8: 560–566

Rabinowitch E (1945) Photosynthesis and Related Processes, Volume I. Interscience Publishers, New York

Rabinowitch E (1951) Photosynthesis and Related Processes, Volume II (Part 1). Interscience Publishers, New York

Rabinowitch E (1956) Photosynthesis and Related Processes, Volume II (Part 2). Interscience Publishers, New York

Rabinowitch E (1959) Robert Emerson, obituary. Plant Physiol 34: 179–184

Rabinowitch E and Epstein LF (1941) Polymerization of dyestuffs in solution; thionine and methylene blue. J Am Chem Soc 63: 69–78

Rabinowitch E and Govindjee (1965) The role of chlorophyll in photosynthesis. Sci Am 213: 74–83

Rabinowitch E and Weiss J (1936) Reversible oxidation and reduction of chlorophyll. Nature 138: 1098–1099

Rabinowitch E and Weiss J (1937) Reversible oxidation of chlorophyll. Proc R Soc London Ser A 162: 251–267

Rubinstein D and Rabinowitch E (1963) Fluorescence and absorption changes in Chlorella exposed to strong light: the red band. Science 142: 681–682

Satoh K (2003) The identification of the Photosystem II reaction center: a personal story. Photosynth Res 76: 233–240

Seibert M and Wasielewski M (2003) The isolated Photosystem II reaction center: first attempts to directly measure the kinetics of primary charge separation. Photosynth Res 76: 263–268

Singhal GS and Rabinowitch E (1967) Changes in the absorption spectrum of methylene blue with pH. J Phys Chem 71: 3347–3349

Singhal GS and Rabinowitch E (1969) Measurement of the fluorescence lifetime of chlorophyll *a in vivo*. Biophys J 9: 586–591

Singhal GS and Rabinowitch E (1970) Photochemical reduction of thionine and other thiazine dyes by Co(II) EDTA complex in a heterogeneous system. J Chem Phys 53: 4109–4110

Singhal GS, Hevesi J and Rabinowitch E (1968a) Excitation–energy migration between chlorophyll and *b*-carotene. J Chem Phys 49: 5206–5208

Singhal GS, Williams WP and Rabinowitch E (1968b) Fluorescence and absorption studies on chlorophyll *a in vitro* at 77 K. J Phys Chem 72: 3941–3951

Singhal GS, Rabinowitch E, Hevesi J and Srinivasan V (1970) Migration of excitation energy from thionine to methylene blue in micelles. Photochem Photobiol 11: 531–545

Srinivasan V and Rabinowitch E (1970) Photochemical reduction of thionine by cobalt (II) EDTA complex in water–ether emulsion. J Chem Phys 52: 1165–1168

Szalay L, Rabinowitch E, Murty N and Govindjee (1967) Relationship between the absorption and emission spectra and the 'red drop' in the action spectra of fluorescence *in vivo*. Biophys J 7: 137–149

Tandeau de Marsac N (2003) Phycobiliproteins and phycobilisomes: early observations. Photosynth Res 76: 197–205

Tomita G and Rabinowitch E (1962) Excitation energy transfer between pigments in photosynthetic cells. Biophys J 2: 483–499

Vernon LP (2003) Photosynthesis and the Charles F. Kettering research laboratory. Photosynth Res 76: 379–388

Zouni A, Witt HT, Kern J, Fromme P, Krauss N, Saenger W and Orth P (2001) Crystal structure of Photosystem II from *Synechococcus elongatus* at 3.8 Angstrom resolution. Nature 409: 739–743