

DESCENDENTS OF KANĀDA

LIFE SKETCHES OF SOME INDIAN SCIENTISTS

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ABOUT THE BOOK

India is celebrating 75 years of its Independence (Azadi Ka Amrit Mahotsav). The book '*Descendents of Kaṇāda*', is an attempt to celebrate the lives of scientists who paved the way for our intellectual and scientific growth. Many of them have been well-recognized for their contributions while some remained unsung. An important facet of their lives is that besides being extraordinary in their research, they have been excellent students and teachers. Our choice of scientists was simple; those who devoted their lives to promoting the culture of science, not just publishing scores of scientific articles in journals of repute. It has been a common observation that ineffective communication with society and a lack of interest in historical accounts among young scientists are major hurdles to the popularization of science in India, which is uncalled for, history allows us to put things in perspective. The book is a compilation of biosketches of some of those who worked with immense dedication and practiced science as *Dharma*.

Declaration

In case of any discrepancies or authenticity of the information given in the chapters, the author/s of the respective chapters shall be solely responsible. Editors and the University owe no such responsibility.



Govindjee Govindjee

(Born 24 October 1932)



GOVINDJEE GOVINDJEE: INDIA'S GIFT TO THE PHOTOSYNTHETIC COMMUNITY

Naveen Kumar Sharma

Govindjee and photosynthesis research are synonymous. In his long scientific career, he has made vital discoveries, written trendsetting publications, and been conferred numerous awards and honors. A researcher and educator *par excellence*, he has been an incredible and persuasive communicator on photosynthesis including its history for students, professional scientists, and the general public. He is one of the luminaries of photosynthesis, who learned from the great fathers, worked with masters, and trained many leading lights of the disciplines. A legend that we are immensely proud of.

Early Life and Education

Govindjee was born on October 24, 1932 to Mrs. Savitri Devi and Mr. Vishveshwar Prasad in Allahabad (now Prayagraj), India. His father was first a college teacher, who also served as the General Secretary of the U.P. (United Provinces) Teachers Association, and then as the representative of the Oxford University Press in Northern India. The couple had three sons and one daughter, namely – Krishnaji, Gopalji and Govindjee (sons), and Malati (daughter). Govindjee was the youngest of the siblings. Though by birth an “Asthana”, which represents a specific caste. The family never used last name, as his father was an ‘Arya Samajist’ and did not believe in the caste system. Therefore, he always has been known by only one name ‘Govindjee’, which remained his legal name, but in 2019, he changed it to “Govindjee Govindjee”. Because of citations and many other problems, intermittently, from 1956 to 2018, he has been known by many other names (see Eaton-Rye, 2007).

Like any ordinary student, Govindjee too was reluctant to learn. He started his formal schooling from the 4th class onwards. Govindjee completed his schooling (4th – 10th class) at Colonelganj High School (1943–1948), and Kayastha Pathshala (K.P.) Intermediate College (11 & 12th class) (1948–1950) at Allahabad, India. According to Govindjee, he studied all the subjects in High School, but Science! rather than Arts was his focus. Sadly,

his father passed away in 1943, and his older brother Krishnaji, who was a Professor of Physics, at Allahabad University, took care of him. He was his role model (Krishnaji passed away in August 1997). He remembered Govindjee as an inquisitive child, wanting to know the why and how of everything he saw. Also, Govindjee's passion for discussions was to the extent that he disliked those who avoided discussion. The early life of Govindjee had a significant impact of ongoing India's Independence, still, he vividly recalls all those moments. His sister Malati took it upon herself to boycott West-made clothes, she used to spin her own yarn, and always wore "khadi" fabric. Govindjee was touched deeply by the powerful speeches of Gandhiji and Nehruji whom he listened to at Purushottam Das Tandon Park (see Block 2022 for further details). In fact, his family never owned a house in Allahabad; they always lived in rented homes and therefore kept on moving from one neighbourhood to another until they settled at 14 B Bank Road (now Lala Ram Narain Road). This allowed Govindjee to see the whole city of Allahabad.

In 1950, he took admission at Allahabad University (1950–1954) and completed his Bachelor of Science (B.Sc.) with Chemistry, Botany, and Zoology, in the first division, and Master of Science (M.Sc.) in Botany, (in the first division, and first position) in 1952, and 1954, respectively. He specialized in Plant Physiology under Shri Ranjan (a former student of Felix Frost Blackman). In his college days, Govindjee was influenced and helped by many good teachers, notably, the late Jalpa Prasad (Chemistry) and M.L. Gaur (Biology) who ignited his interest in both Chemistry and Biology, and were used to loan their personal books to him. Govindjee fondly remembers that he was good at learning from books, but was always unsure of himself in practical's. He found sectioning plants easier than dissecting animals. Maybe, this was the reason why he took up Botany as a subject.

Since Govindjee had secured the first position and first class, and someone was needed to teach "Plant Physiology", After completing his M.Sc. in the autumn of 1954, he was hired as a Lecturer in Botany at Allahabad University and worked there from 1954 to 1956. While teaching plant physiology, he got interested in the research of Richard Willstätter, Hans Fischer, and Robert Emerson. He applied for admission to the University of Illinois at Urbana-Champaign (UIUC), Illinois, USA, under its Fellowship Program (UIUC Graduate Fellowship) and was accepted into its doctoral program in 1955. He also received the prestigious Fulbright Foundation

travel grant to go to the USA. In 1956, he reached UIUC to work for his Ph.D. in Physico-Chemical Biology (later changed to Biophysics) under Robert Emerson. However, after Emerson's untimely death in a plane crash in February 1959, he worked with Eugene Rabinowitch, and obtained his Ph.D. in Biophysics from UIUC (1960) on the topic '*Action Spectra of the Emerson Enhancement Effect in Algae.*' Meantime, on October 24, 1957, Govindjee married Rajni Varma in Urbana, Illinois. He had met Rajni in 1953 when both were M.Sc. students at Allahabad University. There, she was a year junior to him. At UIUC they were Ph.D. students of Robert Emerson.

From 1960 to 1961, Govindjee worked as a Postdoctoral Fellow at United States Public Health (USPH). And from 1961 to today, he has served the UIUC in various capacities: From 1961-1965 as an Assistant Professor of Botany (later renamed Plant Biology); from 1965 to 1969 an Associate Professor of Biophysics and Botany; from 1969 to 1999 a Professor of Biophysics and Plant Biology, and from 1998–1999, as a Professor of Plant Biology, Biochemistry and Biophysics. On August 1, 1999, he became Professor Emeritus of Plant Biology, Biochemistry and Biophysics, at UIUC.

Contribution to the Science^{20,21,22, 23, 32, 57, 69}

A. Pre-Photosynthesis days' work on the effect of virus infection on plant metabolism and use of paper chromatography (1955-56)

While working as a lecturer at Allahabad University, Govindjee became interested in the viruses, organisms responsible for yellowed and sickly plants growing in his uncle's garden. At that time, he was working in the laboratory of Shri Ranjan with his schoolmate Manmohan Laloraya, who was a Ph.D. student of Shri Ranjan (Fig. 1). They reported that the tobacco-mosaic virus and tobacco-leaf curl virus causes an increase in asparagine and several amino acids, especially aspartic acid, supporting the idea that virus infection may cause the formation of new proteins in the infected plants (*Croton sparsiflorus*). They for the first time used a 16-sector radial-cut circular filter paper horizontal chromatography (suggested by T. Rajarao) to separate free amino acids (Laloraya, and Govindjee, 1955; Laloraya et al. 1955, 1956).



Figure 1: Left to right: T. Rajarao, Rajni Varma, Manmohan Laloraya, and Govindjee, graduate students of Professor Shri Ranjan at the University of Allahabad, India, in 1955 (Source: Govindjee’s Archives).

B. Contribution to Photosynthesis Research (1960 - onwards)

Govindjee has made a seminal contribution to photosynthesis research, particularly on Photosystem II (PSII). This system oxidizes water to oxygen and reduces plastoquinone to plastoquinol. He has co-authored more than 400 research papers and reviews on many aspects of photosynthesis including PSII; the topics have ranged from the mechanism of excitation energy transfer, prompt and delayed fluorescence, thermoluminescence, primary charge separation, and the role of bicarbonate in PSII. Besides, Govindjee and colleagues worked on the primary photochemistry of both PSII and photosystem I (PSI) including those from cyanobacteria. He also pioneered and exploited the use of chlorophyll (Chl)*a* fluorescence measurements to study the phenomenon of photoprotection in plants and algae. Some of his notable contributions are mentioned below -

1. The two-light reaction and two-pigment system in oxygenic photosynthesis and minimum quantum requirement

The singular process of photosynthesis completes in two steps - the “light” and the “dark” reactions, the latter being carbon fixation. Govindjee was curious about the phenomenon of the “Red Drop” i.e., low photosynthesis yield when plants receive only far-red light. However, by the time he

reached UIUC, Robert Emerson had discovered the “Enhancement Effect” in photosynthesis. Wherein two beams of different wavelengths of light (short and long) given simultaneously resulted in a higher photosynthetic rate than the sum of the rates when both beams were given separately. This phenomenon became known as Emerson Enhancement Effect; it suggested the existence of two light reactions and two pigment systems in photosynthesis (Emerson et al. 1957) (Fig. 2). However, the very conclusion of Emerson that one system was run by chlorophyll *a* and another by chlorophyll *b* (or other accessory pigments) was wrong, as Govindjee has told us personally. He knew that Duysens (1952) had already shown that 100% of the energy absorbed by chlorophyll *b* was transferred to chlorophyll *a*. The second issue was, as Govindjee told us, that Emerson had used manometry, which could not establish with surety whether the effect was on photosynthesis or respiration. First, Govindjee established that both the photosystems are run by chlorophyll *a* (Govindjee and Rabinovitch 1960); in addition, he showed a two-light effect in chlorophyll *a* fluorescence (Govindjee et al. 1960a) where no respiration was involved. In addition, his wife Rajni Govindjee used para-benzoquinone (pbQ) to inactivate respiration and discovered Emerson Effect in pbQ Hill reaction (Govindjee R et al., 1960b). Further work on NADP (nicotinamide adenine dinucleotide phosphate) reduction in spinach thylakoids (Govindjee R et al. 1964) and the use of mass spectroscopy with oxygen -18 water isotopes clearly established the involvement of photosynthesis, not respiration (Govindjee et al. 1963; also see Bedell and Govindjee 1966; Govindjee and Björn 2012 for further details. See Govindjee (2023) for the above in his own words.

Emerson had already shown that during photosynthesis a minimum of 8-10 quanta of light is required to release one molecule of oxygen, which had been disputed by Emerson’s doctoral thesis advisor Otto Warburg, who had insisted the number is 3-4. Govindjee and Rajni Govindjee repeated the experiments under Warburg’s conditions (using young synchronous *Chlorella* culture provided with 10% CO₂, and blue catalytic light) and proved their former mentor Emerson to be right and the Nobel laureate Warburg to be wrong (Govindjee R et al. 1968; Govindjee 1999 for further information; see Nickelson and Govindjee 2011).

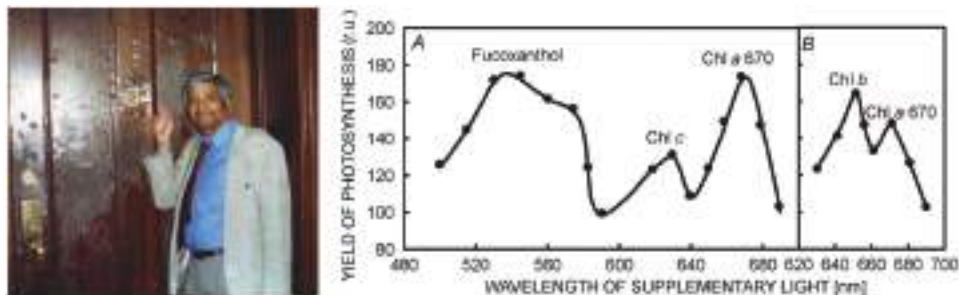


Figure 2: Govindjee in front of the historical door of 157 Natural History Building (NHB) through which Emerson and all his students would go through each day to do their experiments (left); the action spectra of the Emerson enhancement effect in the diatom *Navicula*, when a second light beam of different wavelengths was given on top of far-red light – showing the presence of peaks for fucoxanthol, chlorophyll *c*, and chlorophyll (Chl) *a* 670 (right A), and the same for the green alga *Chlorella* showing chlorophyll *b* and Chl *a* 670. (Right b) (after Govindjee 2023).

2. The discovery of new absorption and emission bands in photosynthetic organisms

In their pursuit to characterize the pigment systems, Govindjee, and his graduate students discovered many new absorption and emission bands - earlier, there was the discovery of P750 in the cyanobacterium *Anacystis nidulans* (now *Synechococcus elongates* strain PCCC 7942) (Govindjee et al. 1961), which is unfortunately not involved in photosynthesis. However, Govindjee's research group discovered a new fluorescence band at 696 nm (at 77K), labeled as F696; later found to be arising from the PSII core antenna protein CP47; further, his group discovered an emission band in the 693-700nm range when photosynthesis is saturated at high light, or inhibited by the DCMU (3-(3,4-dichlorophenyl)-1, 1-dimethylurea), which was a counterpart of the 77K F696 at room temperature (see Govindjee and Shevela 2011 for details and original references).

3. Thermoluminescence and delayed light emission in photosynthetic systems

William Arnold, a student of Emerson had discovered the phenomenon of delayed light emission (Strehler and Arnold 1951) as thermoluminescence (Arnold and Sherwood 1957). Arnold had proposed electron-hole

recombination theory to explain the process. However, Mar and Govindjee (1971) found that when pre-illuminated spinach chloroplasts, and cells of *Chlorella pyrenoidosa*, were given a quick temperature jump of about 15°C, they emitted light both in normal and in DCMU-treated samples (where electron transport to PS I is blocked). However, the thermoluminescence was absent when hydroxylamine which blocks electron transport on the electron donor side of PS II was added into these samples, due to a back reaction of PS II of photosynthesis. Later on, Govindjee and coworkers reported that the temperature-dependent equilibria between two or more electron carriers in PS II act as traps for electrons or holes. Thus, he modified the existing theory of thermoluminescence and explained the abnormally large activation energies and the abnormal frequency factors involved in the process (see e.g., Tataka et al. 1981; DeVault et al. 1983; DeVault and Govindjee 1990).

Earlier, Govindjee had proposed an alternative triplet-triplet fusion hypothesis for delayed light emission in photosynthetic systems (Stacy et al. 1971), which did not survive. On the other hand, Govindjee proved his idea of a back reaction of PS II in various ways – by using DCMU to block the electron transport on the electron acceptor side of PS II (Jursinic and Govindjee 1972); by diverting electrons from PS II to silicomolybdate from Q_A (Zilinskas and Govindjee 1975); and by blocking electron donation on the water side of PS II by Tris-washing the samples (Jursinic and Govindjee 1977a). Jursinic and Govindjee (1977b) measured the temperature dependence of delayed light in a few to hundreds of microseconds and discovered that the former was independent of temperature in the 0 to 35°C range, whereas the latter was not. The short-term component was I^2 dependent, whereas the latter remained linear with light intensity. Further, Govindjee discovered that there was a major difference in the microsecond and the millisecond delayed light, the former was insensitive to membrane potential, whereas the latter was sensitive to it in the presence of ΔpH (Jursinic et al. 1978). Thus, although most delayed light is due to a back reaction of PS II, detailed mechanisms are different for the fast and slower components was his conclusion.

4. Measurement of Photosystem II reactions including primary charge separation

Govindjee started studies on the mechanism of excitation energy transfer as a function of temperature down to liquid helium temperature (Cho and Govindjee 1970a, b), and on oxygen evolution (Mar and Govindjee 1972).

For the first time his group applied Nuclear Magnetic Resonance (NMR) to monitor the oxygen clock (Wydrzynski et al. 1976; Baianu et al. 1984). Govindjee studied the nature of the very first intermediates involved, and the efficiency and speed of the primary charge separation in PSII, and showed that the charge separation occurred from chlorophyll to a pheophytin molecule, within a few picoseconds (Wasielewski et al. 1989). Also, his works on PS I primary photochemistry (Fenton et al. 1979; Wasielewski et al. 1987) were pivotal, and subsequent refinements to these findings have led to a clearer and more detailed picture.

5. Chlorophyll *a* fluorescence and its relationship to photosynthesis

Govindjee was the first one to introduce measurements of the lifetime of chlorophyll *a* fluorescence to understand photoprotection in plants. Steve Brody at the University of Illinois was the first to measure the lifetime of chlorophyll *a* fluorescence in a photosynthetic system. However, Govindjee and Henri Merkelo used mode-locked lasers to make such measurements (Merkelo et al. 1969). Followed by the use of the phase method (with Enrico Gratton's group) to measure the lifetime of chlorophyll *a* fluorescence (Govindjee et al., 1990), which was the first of its kind in understanding photoprotection by plants, under excess light, in terms of changes in rate constants of deactivation of the excited states of chlorophyll. Since fluorescence intensity changes alone could not distinguish between changes in chlorophyll concentration and changes in rate constants of de-excitation of excited states. Gilmore et al. (1995) used a *dimmer switch* to explain it. As more and more light was given to a photosynthetic system, a proportion of chlorophyll *a* that had a ~ 2 ns lifetime of chlorophyll fluorescence was converted into a component that had a 0.4 ns lifetime! A relationship with carotenoids (zeaxanthin and antheraxanthin) was also established (Gilmore et al. 1998). Subsequently, in collaboration with the late Robert Clegg, and Oliver Holub Fluorescence Lifetime Imaging Microscopy (FLIM) was introduced, to observe differences in lifetimes of chlorophyll fluorescence in single cells with fluorescence intensity remaining the same.

6. The role of bicarbonate (hydrogen carbonate) in electron (and proton) transport in Photosystem II (PSII)

Govindjee is one of many scientists who has stated that Otto Warburg was wrong in his conclusion that during photosynthesis oxygen comes from

CO₂. However, his suggestion on the requirement of ‘bicarbonate’ in the Hill reaction inspired Govindjee and his graduate students to study this ‘bicarbonate effect’ on the relaxation of the ‘S-states’ of the oxygen-evolving complex (Stemler et al. 1974). They studied the effects of ‘bicarbonate’ on the electron and proton flow on the intermediates in Z-scheme of photosynthesis. Govindjee’s research group was the first to establish the effect of bicarbonate at the ‘two-electron gate’ of PS II (see Wydrzynski and Govindjee 1975; Govindjee et al. 1976; Eaton-Rye and Govindjee 1988a, b). They found that without bicarbonate, Cytb₆f complex would not receive any electrons from PS II. 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. The ‘bicarbonate’ effect on the electron acceptor side is essential at a site where several herbicides inhibit photosynthesis. Govindjee et al. (1991) showed that formate can be used to achieve a state deficient in bicarbonate that releases CO₂. The role of bicarbonate on the electron donor side clearly needs to be studied further. Govindjee is eager to learn about that aspect of the functioning.

C. Other contributions

Govindjee’s current scientific interests include improving photosynthesis through genetic engineering, and understanding how slow chlorophyll *a* fluorescence changes can be used to monitor regulation mechanisms in plants, algae, and cyanobacteria. In the later part of his career, he started working on the *History of Photosynthesis Research*; in addition, he is actively involved in photosynthesis education, and in remembering and recognizing other scientists in the field. In 1994, he started the book series ‘*Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes*’ which shows his interest in the subject. He has documented the progress of research in photosynthesis, through interviews, obituaries, tributes, personal perspectives, and news of scientists around the world. He is the founder of the ‘History & Biography’ section of the journal ‘Photosynthesis Research’. These publications, accompanied by photographs of key people and places, are unique contributions to the history of science, and photosynthesis, in particular. Apart from his research and educational activities, Govindjee encourages young students at conferences by giving them book awards. At UIUC, he and his wife have established the Govindjee and Rajni Govindjee Awards for Excellence in Biological Sciences.

He has authored/edited many books, including - “Photosynthesis” (John Wiley, 1969); with Rabinowitch; “Bioenergetics of Photosynthesis” (Academic Press, 1975); “Photosynthesis” (in 2 volumes, Academic Press, 1982, Russian translation, 1987); “Light Emission by Plants and Bacteria” (Academic Press, 1986); “Chlorophyll a Fluorescence: A Signature of Photosynthesis” (Kluwer/Springer, 2004); and “Discoveries in Photosynthesis” (Springer, 2006). He has edited special issues of journals dedicated to leading figures in the biophysics of photosynthesis: Eugene Rabinowitch (Biophysical Journal, 1972), Warren Butler (Photosynthesis Research, 1986), Bessel Kok (Photosynthesis Research, 1993), and William Arnold (Photosynthesis Research, 1996). He has always been an outstanding teacher, highly sought after by students. His collaborative spirit is unparalleled. As on July 4, 2022, he has worked with 580 researchers including 238 from The USA, 63 from India, 55 from China, 24 from Russia, 22 from Germany, 18 each from France and the Czech Republic, 17 from The Netherlands, 13 from Japan, 11 from Canada, 11 each from Hungary, Mexico and The UK, 8 from Australia, 6 from Finland, 5 each from Azerbaijan, Sweden, Israel, Switzerland, 4 from Greece and Iran, 3 from Poland and Slovak Republic, 2 each from Belgium, Estonia and Egypt, and 1 each from New Zealand, Norway, Bulgaria, and South Korea.

Awards and Honors

- He is Fellow of the American Association for the Advancement of Science (AAAS) (1976);
- Fellow and Life Member of the National Academy of Sciences (NASI), India (1979);
- President of the American Society for Photobiology (1981);
- Fulbright Senior Lecturer to India (1996–1997);
- Honorary President of the 2004 International Photosynthesis Congress (Montreal, Canada);
- The first recipient of the Lifetime Achievement award from the Rebeiz Foundation for Basic Research (2006);
- Communication Award of the International Society of Photosynthesis Research (2007);
- Alumni Achievement Award from the University of Illinois at Urbana-Champaign (2008);

- In 2013, in honor of his 80th birthday, a tribute to Govindjee's life's work in photosynthesis appeared in the journal *Photosynthesis Research* [116(2), 111–144, doi: 10.1007/s11120-013-9921-3];
- Dr. B.M. Johri Memorial award of the Society for Plant Research, India (2016);
- Pravasi (Foreign) Fellow of the National Academy of Agricultural Sciences (NAAS), India (2018);
- In 2018, in honor of his 85th birthday, a special issue of *Photosynthetica* [56(4), 1235–1236; doi: 10.1007/s11099-018-0826-4] was released;
- In 2019, the University of Illinois at Urbana-Champaign published an article on his research in photosynthesis and dedicated a museum to him “Govindjee's Photosynthesis Museum”;
- In 2020, Govindjee's innovative research and historical contributions (1999–2020) were highlighted, with messages from around the world (refer to Eaton-Rye et al. 2020; Stirbet et al. 2020);
- Lifetime Award of the ISPR (2022).
- Emeritus member of the American Society of Plant Biology (formerly Physiology).
- Member of the Biophysical Society of America;
- Member, Sigma Xi;
- Member of the International Society of Photosynthesis Research;

Personal Life

Govindjee is married to Rajni Varma nee Govindjee (Fig. 3). They have two children – a daughter, Anita, who is a software engineer for IBM, and she is married to Morten Christiansen, Professor of Psychology at Cornell University, Ithaca, NY; they have one daughter, Sunita. His son, Sanjay is a Distinguished Professor of Civil and Environmental Engineering and the Horace, Dorothy, and Katherine Johnson Endowed Professor at the University of California, Berkeley; and is married to Marilyn Hubbs, the couple have two sons: Arjun and Rajiv.

Rajni Govindjee played a major role in the life and early research of Govindjee. She is a leading authority in photosynthesis and photobiology. She completed her Ph.D. in Botany in 1961 under Eugene Rabinowitch at UIUC. Her works demonstrated that Emerson's two-light effect was due to

photosynthesis and that the minimum quantum requirement be 8-10., Post-1974, she worked in photobiology with retinal proteins. Thomas Ebrey described her as “*Brighter than the sun: Rajni Govindjee at 80 and her fifty years in photobiology*” (Ebrey 2015).



Figure 3: Govindjee in a bus with his wife Rajni (Source: Govindjee’s Archives).

Epilogue

Govindjee is a Professor Emeritus of Plant Biology, Biochemistry and Biophysics at UIUC, USA. He made path-setting contributions to the mechanism of Photosystem II. He demonstrated that the first step of conversion of light into chemical energy occurs in a picosecond time scale, and bicarbonate ions are uniquely required in steps other than in carbon fixation. He established the participation of Chla in both the light reactions I and II, and along with his wife Rajni, he showed the effect of the two-light reactions and two pigment systems in the reduction of NADP in chloroplasts, providing a fundamental background to the current Z- scheme of the “Light Reactions” of photosynthesis. He has also been an immensely effective and energetic advocate for photosynthesis research and has dedicated his entire life to educating students and researchers throughout the world. His advocacy and educational outreach have included numerous lectures around the world, delivered at various workshops, and conferences, in Universities and Colleges. He is a scientific gem, a gift from India to the global science communities. Though, he himself says “Scientists belong to the World, not just one country.” May God bless him with a long and healthy life.

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