Plant Physiol. Rep. (October–December 2022) 27(4):543–557
https://doi.org/10.1007/s40502-022-00690-9

ORIGINAL ARTICLE

Govindjee's 90th birthday: a life dedicated to photosynthesis

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Received: 29 July 2022 / Accepted: 23 September 2022 / Published online: 14 October 2022

Abstract We celebrate Govindjee, Professor Emeritus of Plant Biology, Biochemistry, and Biophysics, University of Illinois at Urbana-Champaign, on the occasion of his 90th birthday. He is renowned for his pioneering work in the discovery of the two-light reactions and two photosystems, PSI and PSII, leading to the Z-scheme of the electron transport chain; and for breakthrough advances in oxygenic photosynthesis. Govindjee's publications have been cited over 26,000 times. He is an elected Fellow of the American Association of the Advancement of Science, USA; National Academy of Agriculture Science, India; and National Academy of Sciences, India; and beyond that, he has received many awards from scientific societies, most recently, the ISPR Lifetime Achievement Award, August 2022. As even today, Govindjee continues to actively contribute to the field, we highlight the major events in his colorful personal and rigorous scientific life with emphasis on the work done after his retirement, and as well, his prodigious accomplishments as teacher, editor, and science historian.

Keywords Govindjee · History of science · Light reactions of photosynthesis · Oxygenic photosynthesis · Z-scheme

सूर्यभानुप्रभावेण वर्धन्त ओषधीर्यथा।
दशोनशतवर्षीयो गोविन्दाख्य: स वेत्ति तद्।।
अवन्दत स चैवान्यान् तद्विषये निरूपकान्।
जन्मदिनोत्सवे वै तं सर्वत: पूजयामहै।।

'How the plants grow because of the power of the sun's rays,
(He who is) ninety years old, named Govind(jee) knows that.
He has praised other investigators in the field of this topic;

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s40502-022-00690-9.

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On this birthday event, let us wholeheartedly praise him.'
Two ślokas for Govindjee by Hans Henrich Hock (professor emeritus, University of Illinois), 2022

Introduction

World-renowned for his outstanding scientific accomplishments, Govindjee (see Fig. 1) is an ambassador of photosynthesis, often called, "Mr. Photosynthesis" (see e.g., Allakhverdiev et al., 2019; Block, 2022; Kumar et al., 2021). It is remarkable that, while being one of the foremost specialists in photosynthesis, he is an extraordinarily popular and highly effective speaker, teacher, and outstanding editor. Indeed, in addition to his prodigious research and numerous scientific publications, Govindjee is globally regarded for his dedication to the education of our younger generations; and this includes placing high value to pedagogy and keeping up with the most advanced digital technologies, such as audio-visual internet tools for communicating scientific principles. In his career, Govindjee advised and mentored many young students and researchers in his own laboratory as well as those not directly working with him.

Govindjee is a prolific science writer and has edited highly influential books on photosynthesis. He worked as Associate Editor, and co-Editor-in-Chief (with René Marcelle) between 1983–1988 for the prestigious journal, *Photosynthesis Research,* and until recently, he served as the Editor of its Historical Corner, where he published numerous papers and encouraged others to do the same. His most valued achievements, however, are in the massive *Advances in Photosynthesis and Respiration* (AIPH) series of books. Govindjee, the founding editor, guided this series from 1994 to 2017, overseeing the publication of 43 of 47 volumes published to date, and co-edited Volume 19 on *Chlorophyll a fluorescence* (Papageorgiou & Govindjee, 2004a, 2004b), Volume 20 on *Discoveries in photosynthesis* (Govindjee et al., 2005), Volume 29 on *Photosynthesis* in silico (Laisk et al., 2009), and Volume 40 on *Non-Photochemical Quenching (NPQ) in oxygenic photosynthesis* (Demmig-Adams et al., 2014). Robert E. Blankenship, of Washington University, Saint Louis, Missouri, USA, commented:

When I look at the AIPH books on my shelf, I am struck with how effectively they collectively summarize the field. I am continually impressed with how Govindjee has added new books to the series that make sense and really provide the level of detail that is needed (see http://www.life.uiuc.edu/govindjee/newbook/Quotation.html and Eaton-Rye, 2012).

In 2006, Govindjee with his wife, Rajni, established the Robert Emerson Award as well as the Govindjee and Rajni Govindjee Award for Excellence in Biological Sciences at the University of Illinois at Urbana-Champaign (UIUC), to support graduate students in the School of Integrative Biology and the School of Molecular and Cell Biology conducting research in Plant Biology (see Fig. 2). In addition, to

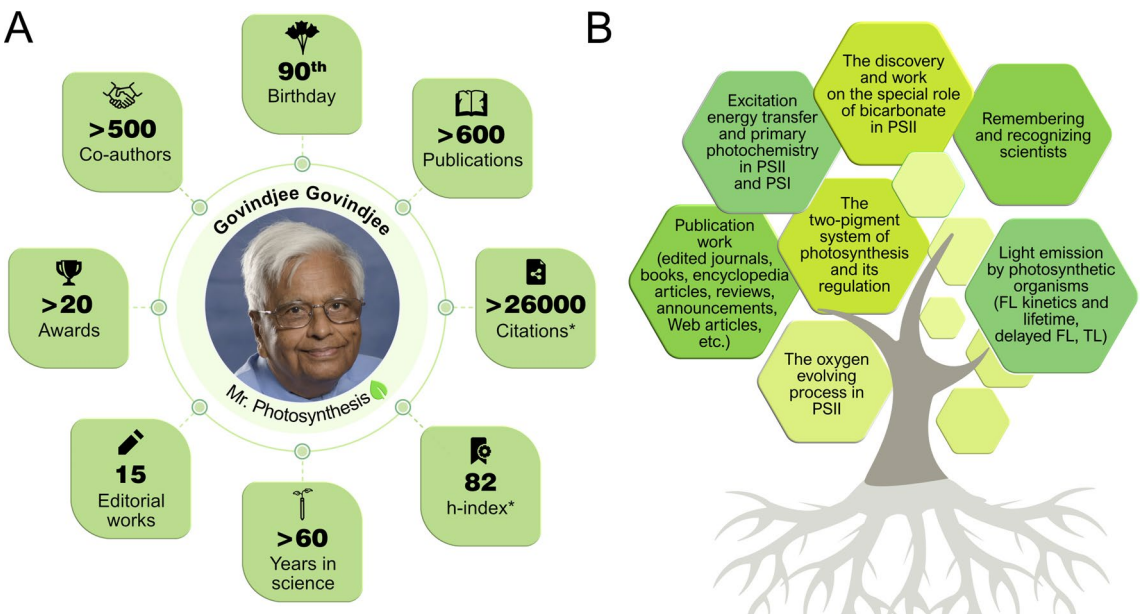

Fig. 1 Govindjee's achievements, by the numbers (**A**) and his main areas of interest in photosynthesis research (**B**). Numbers provided for citations and h-index, marked by *, are based on Google Scholar (May 2022). In reality, these quantities are much higher because his name often had been deleted from data bases and search engines since he went by one name only until 2018. *FL* fluorescence; *PSI* photosystem I; *PSII* photosystem II; *TL* thermoluminescence

Fig. 2 Left to right: Rajni Govindjee, Rodney Burton (who received the 2014 Govindjee and Rajni Govindjee Award for Excellence in Biological Sciences), and Govindjee. Rodney is wearing a red tie—the kind that Robert Emerson wore in the laboratory—as well as his apron, and holds a gift from the Govindjees, a book from the AIPH series. Govindjee has the metal housing for the second light source used by Emerson in 1957 to observe the enhancement effect. This led to the concept of two light reactions and two pigment systems that the Govindjees used in 1960. In the background, the 1965 Z-scheme of Govindjee (see Govindjee et al., 2017a), where he predicted the existence of the reaction center "P680" in Photosystem II ahead of its recognition by Horst Witt's laboratory (Döring et al., 1968). Photo taken by Jeff Goldberg, August 1, 2014

honor their professor, Govindjee and Rajni recently established a Eugene Rabinowitch lecture series at UIUC (https://sib.illinois.edu/news/272). Moreover, in many conferences, Govindjee has joyously given books from his AIPH series to student awardees and young researchers for their contributions in photosynthesis, and he distributes autographed posters comprising the Agrisera Educational Poster Collection (https://www.agrisera.com/en/info/educational-posters.html) and Govindjee's Educational Poster Series. For his commitment to educate and encourage students and young researchers to study photosynthesis, Govindjee was presented with the 2007 Communication Award of the International Society of Photosynthesis Research at the 14th International Congress of Photosynthesis Research, Glasgow, UK.

This tribute honors Govindjee on his 90th birthday. We summarize his scholarly journey in collaboration with those from his own laboratory and colleagues from around the world that led to a greater fundamental understanding of the process of photosynthesis. In addition, we summarize his contributions as educator, reviewer, editor, and science historian to three generations. The following descriptions of Govindjee's research work, his various collaborations, and personal life are based on personal conversations of the authors with Govindjee as well as notes & documents provided by Govindjee. For a complete list of Govindjee's past graduate students see Table S1 (Supplementary Materials).

Early life, education, and research at the University of Allahabad, India

Govindjee has used one name only almost all his life, changing it to Govindjee Govindjee in late 2018, to conform to the rules of international travel. Born on October 24, 1932, Allahabad, Uttar Pradesh, India, to Savitri Devi and Vishveshwar Prasad Asthana, the youngest of four siblings (Krishnaji, Gopalji, Malati Sahay, and Govindjee). Notably, the family surname Asthana (a Hindu caste) was dropped by the family by endorsing egalitarianism of Arya Samaj movement. His father was a college teacher, who served as the General Secretary of the United Provinces Teachers Association, but later worked as the sales representative of the Oxford University Press in Northern India. After his father's passing in 1943, his older brother Krishnaji (1922–1997) supported the family. Krishnaji's influence as a role model was determinant in Govindjee's life (see also Block, 2022; Govindjee & Srivastava, 2010). In fact, Krishnaji received his MSc in Physics at the University of Allahabad and later he was appointed as a lecturer in the same department. Krishnaji's work in microwaves and wireless technology was recognized by congratulations in audience with the first Prime Minister of India, Pandit Jawaharlal Nehru.

Govindjee studied at the Colonelganj High School (1943–1948), and then at the Kayastha Pathshala Intermediate College (1948–1950), where his teachers Jalpa Prasad and M.L. Gaur inspired him to study Chemistry and Biology. After that, Govindjee obtained a BS in Chemistry, Botany and Zoology (1950–1952) and MSc in Botany (1952–1954; 'First Class & First Position') from the University of Allahabad. For his MSc, he specialized in Plant Physiology under the late Shri Ranjan (1889–1969), a former student of Frederick Frost Blackman (1866–1947) of Cambridge (UK), and Govindjee's interest in experimental studies on plants began.

Govindjee was appointed Lecturer at the University of Allahabad (1954–1956), where he taught plant physiology and conducted research collaborating with Manmohan Laloraya, Tadimeti Raja Rao, his professor Shri Ranjan, and Rajni Verma. During this period, they analyzed the amino acid and sugar composition of healthy and diseased leaves. Later, he evoked the excitement of all in the Department, after their first amino acid chromatogram was obtained (see e.g., Govindjee, 2019a). In addition, Govindjee studied the effects of X-rays on the physiology and amino acid composition of leaves.

Photosynthesis research at UIUC

Govindjee's desire to acquire a deeper knowledge on photosynthesis began in 1953, when Shri Ranjan asked his

students to present topics of interest to them at seminars, and he decided to talk about "*The Role of Chlorophyll in Photosynthesis*". While consulting papers on this subject, he was especially impressed, and at the same time bewildered, by the "Red Drop Effect", discovered by Robert Emerson (1903–1959). This is an abrupt decrease in the maximum quantum yield of photosynthesis measured at wavelengths longer than 680 nm, when chlorophyll (Chl) *a* is still absorbing light (Emerson & Lewis, 1943). In 1955, Govindjee wrote to Emerson (Department of Botany, UIUC) about his interest in working with him as a doctoral student. He received an encouraging reply—Emerson asked him to apply for the Graduate Fellowship Program of UIUC, and a Fulbright Travel grant. In 1956, Govindjee arrived in the USA to begin doctoral studies in Physico-Chemical Biology which was later changed to Biophysics. In 1957, Rajni Verma was also accepted by Emerson as a graduate student in botany, and not long after her arrival, the two were married on October 24, Govindjee's 25th birthday.

At UIUC, Govindjee and Rajni first attended courses relevant to research in photosynthesis. At that time, Emerson was investigating what we now call, the "Emerson Enhancement Effect", in which the oxygen evolution measured with far-red light (720 nm) together with a supplementary light of a shorter wavelength absorbed primarily by accessory pigments was found to be higher than the sum of oxygen evolution measured when these two different light beams were given separately (for a study on the unicellular green alga, *Chlorella,* see Emerson et al., 1957). This discovery was crucial for the introduction of the important concept of two-light reactions and two photosystems working in series in oxygenic photosynthesis (see Govindjee, 1963), culminating with the Z-scheme (Hill & Bendall, 1960). However, on the basis of these action spectra measurements, Emerson had concluded that one of the light reactions is sensitized by Chl *a*, and the other by accessory pigments (e.g., Chl *b* in *Chlorella*), with the "Red Drop" occurring in the wavelength range where Chl *a* is the prime absorber of light (in relation to this, see a commentary by Govindjee, 2022). Sadly, in 1959, Emerson died in a plane crash, and, thus, his collaborator, Eugene Rabinowitch, became the advisor to both Govindjee and Rajni. Rabinowitch (1901–1973) was known for his 3-volume book on photosynthesis (published in 1945, 1951, 1956) and for investigations in physical chemistry (see Govindjee, 2004a, 2004b; Govindjee, 2019a; Govindjee & Govindjee, 2021).

Govindjee's life-long research focus is on the bioenergetics of photosynthesis. In 1960, Govindjee received his PhD in biophysics, UIUC, with a thesis on the "Action spectra of the Emerson enhancement effect in algae", in which he showed for the first time that a short wavelength absorbing form of chlorophyll *a* (Chl *a* 670) is in the same system as Chl *b* in the green alga *Chlorella*, and fucoxanthol (carotenoid) in the diatom *Navicula minima* (also, discussed in Govindjee & Rabinowitch, 1960). This was in contradiction to Emerson's initial conclusion and is an important contribution to the concept of two-light reactions and two photosystems (PSI and PSII) in oxygenic photosynthesis. He remained at UIUC, being appointed assistant professor, botany (1961–1965); associate professor (1966–1969); professor, plant biology and biophysics (1969–1999); and professor emeritus, plant biology, biochemistry and biophysics (2000). Over the years, he established, in collaboration with his graduate students and other researchers, multifaceted

Fig. 3 Govindjee showed his "Photosynthesis Museum" to Diana Yates during an interview on July 9, 2019. He had archived historically important pieces in his office at UIUC (669 Morrill Hall, 505 S. Goodwin Avenue, Urbana, Illinois). (**A**) Here, we can see some old instruments used by Robert Emerson. In the foreground, we see two of his published books on photosynthesis; (**B**) Govindjee reflects on a portrait of Emerson; (**C**) Govindjee, pointing out the primary donor of Photosystem II as 'P680' in his 1965 Z-scheme (see Rabinowitch & Govindjee, 1965); and (**D**) Govindjee at work in his office. Photos by Frederick H. Zwicky

research programs to probe the steps associated with the light reactions of photosynthesis, by using innovative techniques like chlorophyll *a* fluorescence, thermoluminescence, delayed fluorescence, and nuclear magnetic resonance. Much of the research conducted by Govindjee and his collaborators, spanning more than six decades, led to important discoveries regarding the function of various components involved in light absorbtion, primary photochemistry, and photosynthetic electron flow from water to NADP. Several of his breakthroughs cover light harvesting (see.g., Cedestrand et al., 1966; Cho et al., 1966), primary charge separation in PSI and PSII (Fenton et al., 1979; Wasielewski et al., 1989), the relation between chlorophyll fluorescence induction and photosynthesis (for experimental work see e.g., Munday & Govindjee, 1969; Govindjee & Papageorgiou, 1971), modeling (e.g., Zhu et al., 2005; Stirbet et al., 2020b), the role of bicarbonate on the two-electron gate of PSII (Shevela et al., 2012; Stemler & Govindjee, 1973), photosynthetic water oxidation (Govindjee et al., 1983; Wydrzynski et al., 1976), and nonphotochemical quenching of chlorophyll *a* fluorescence (Gilmore et al., 1995). Since 1978, Govindjee has been recognized for excellence in science by rank of Fellow of the National Academy of Science, India (NASI). Moreover, Govindjee is an elected Fellow of the American Association of the Advancement of Science, USA, and a Fellow of the National Academy of Agriculture Science, India. These are distinguished lifetime appointments that reflect the pride that these two scientifically advanced nations share in recognition of Govindjee's magnificent achievements.

Govindjee has coauthored more than 600 publications (see Fig. 1). His totality of work can be found on Govindjee's web site: https://www.life.illinois.edu/govindjee/pubschron.html for his publications from 1955 to 1993; and https://www.life.illinois.edu/govindjee/recent_papers.html from 1994 to present. Figure 3 shows a photograph of Govindjee displaying instruments and other tools used by Robert Emerson, Rajni Govindjee and himself during the 1950s-1960s; presented as "Govindjee's Photosynthesis Museum" in 2019 by the Illinois News Bureau at UIUC (for other photos, see Yates (2022), a prologue by Nonomura (2022), and https://news.illinois.edu/view/6367/801235).

Govindjee and Rajni Govindjee both have worked together on various aspects of photosynthesis research for about two decades. However, Rajni's active involvement in photosynthesis research ended in 1974, as she started very successful investigations on retinal proteins for over 25 years. On occasion, Rajni continued to publish with Govindjee on photosynthesis related papers (see two photos of Govindjee and Rajni in Fig. 4). For a paper recognizing Rajni's groundbreaking work in this area in which her main collaborator, Thomas Ebrey, characterized her as "*brighter than the sun*", see Ebrey (2015).

Govindjee's emeritus work: a rendezvous with photosynthesis and collaborators around the globe

Govindjee retired honorably as professor emeritus in 2000. Yet, even after he closed his laboratory in 2002, this was only the end of one chapter and the beginning

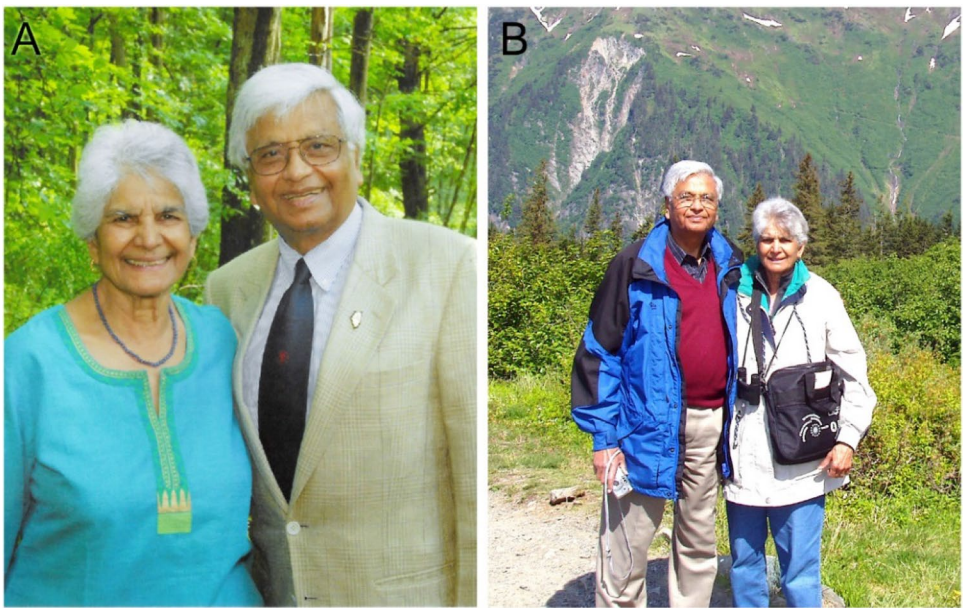

Fig. 4 Photos of Govindjee and Rajni taken around 2010, chosen because "photosynthesis" was going on marvelously around them: (**A**) In Ithaca (NY), while visiting their daughter, Anita; and (**B**) In California (where their son, Sanjay, works), perhaps recollecting their adventures in the 1960s, in solving some of the fundamental processes related to the "Light Reactions" in photosynthesis. Photos from Govindjee's family archive

of a new one, as Govindjee began his rendezvous with photosynthesis and friends around the world (for activities after retirement, see Stirbet et al., 2020a). He continued his research and scholarly collaborations with scientists around the world and visited many important laboratories involved in photosynthesis research in Australia, Azerbaijan, Belgium, Bulgaria, Canada, China, The Czech Republic, Estonia, France, Germany, Greece, Hungary,

Table 1 Laboratories and scientists visited by Govindjee during his academic career and as emeritus professor

Year (s)	Events	Location	Affiliation	Names of scientists, Govindjee interacted with
1962	Visiting Scientist	Baltimore, Maryland, USA	Research Institute of Advanced Studies, Martin Marietta Labs	Bessel Kok; George Hoch
1963	Visiting Scientist	Stanford, California, USA	Carnegie Institute of Washington, Department of Plant Biology	C. Stacey French
1968–1969	Subbatical #1	Gif-sur-Yvette, France	Laboratoire de Photosynthèse, CNRS	Jean Lavorel and Martin D. Kamen
		Berlin, Germany	Max Volmer Insttitute, TU Berlin	Horst T. Witt; Gunter Döring
1976–1977	Sabbatical #2	Leiden, The Netherlands	Leiden University, Biophysics Lab	Louis N. M. Duysens; Hans Van Gorkom; and Arnold Hoff
		Trombay, Bombay, India	Bhabha Atomic Research Centre (BARC)	P.V. (Raj) Sane and V.G. Tatake
		Berlin, Germany	Max Volmer Insttitute, Tech. Univ., Berlin	Gernot Renger and Uli Siggel
1979	Visiting Scientist	Stanford, CA USA	Carnegie Institute of Washington	David C. Fork
1983	Sabbatical #3	Wako-Shi, Japan	The Institute of Physical and Chemical Research (RIKEN)	Yorinao Inoue, Herb Nakatani and William (Bill) Rutherford
1989	Sabbatical #4	Szeged, Hungary	Biological Research Center	Sandor Demeter & Győző Garab
		Argonne, IL USA	Argonne National Laboratory	Michael (Mike) Wasielewski
		Tempe, AZ USA	Arizona State University	Wim F. J. Vermaas
1996–1997	Sabbatical #5	Turku, Finland	University of Turku	Eva-Mari Aro & Esa Tyystjärvi
		Shanghai, China	Chinese Academy of Science	Y.K. Shen & Xin-Guang Zhu
		Geneva, Switzerland	Bioenergetics Lab, University of Geneva, Experimental Station in Lullier	Reto J. Strasser
		Wageningen, The Netherlands	Laboratory of Plant Physiology, Agricultural University	Jack Van Rensen
		Okazaki, Japan	National Institute of Basic Biology	Norio Murata
2000	Visiting Professor of Biology	St. Louis, MO USA	Washington University	Himadri Pakrasi; Danny Kohl; and Robert Blankenship
2002, and later	Visiting Professor	Nové Hrady, Czech Republic	University of South Bohemia	Lada Nedbal
2003–2008	Visiting Professor of Life Sciences	New Delhi, India	Jawaharlal Nehru University	Prasanna Mohanty
2009; 2011	Visiting Research Scientist	Třeboň, Czech Republic	Institute of Microbiology, Department of Phototrophic Microorganisms	Ondřej Prášil; Radek Kana
2012; 2015–2019	Visiting Professor of Life Sciences	New Delhi, India	Jawaharlal Nehru University, School of Life Sciences	Baishnab Tripathy; Ashwani Pareek
2014	Visiting Professor of Botany	Cuttack, Odisha, India	Ravenshaw University,	Pradipta Mohapatra

Fig. 5 Govindjee attending conferences and visiting photosynthesis laboratories: (**A**): In Saint Petersburg, Russia, during the International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability (2019); Left to right: Rajagopal Subramanyam, Tirupathi Malavath, Govindjee, Nathan Nelson, Julian J. Eaton-Rye, and Tina C. Summerfield; (**B**): At the Gordon Conference (2017); Left to right: Divya Matta (Kaur), Michi Suga, Govindjee, Junko Yano, and Robert Blankenship; (**C**) At the School of Life Sciences, Jawaharlal Nehru University, New Delhi, India (2018); Left to right, conferee, Ashwani Pareek, and Govindjee; and (**D**) Govindjee and Rajni visiting University of California, Berkeley, USA (2017); Left to right: Krishna K. Niyogi, Govindjee, Bob B. Buchanan, Anastasios Melis, Rajni, and Roberto Bassi. Photos from Govindjee's archive

India, Iran, Israel, Japan, Mexico, The Netherlands, New Zealand, Poland, Russia, Slovakia, Sweden, Switzerland, UK, and USA (Table 1).

Below, we present just a few photos of Govindjee with other scientists, taken at conferences or in laboratories (see Fig. 5).

Notably, Govindjee wrote tributes to many photosynthesis researchers. Here, we present Govindjee's contributions after his retirement in the following categories: Reviewer and Editor; Science Historian; and Research collaborations on the regulation of photosystems and photosynthesis, and efforts to improve photosynthesis and plant productivity in agriculture.

A reviewer and editor

One of the goals of Govindjee after his retirement, in his own words, was that:

> "I wanted to be of service to graduate students and early career researchers in photosynthesis, to provide them basic information on it, through reviews, and to encourage them to find ways to improve plant productivity for the benefit of all of us".

Govindjee summarized basic available knowledge on *Bacterial Photosynthesis*, *Chlorophyll*, and *Carbon fixation* in a series of reviews including Govindjee et al. (2007a), Govindjee et al. (2007b), Berkowitz et al. (2007), and Blankenship and Govindjee (2007, 2007a, 2007bovindjee (2007). Notably, Govindjee published the aforementioned four co-edited AIPH series of books, and co-authored two books after his retirement: (1) a small, but thorough and penetrating historical book (Nickelsen & Govindjee, 2011), dealing with the controversy on the minimum quanta requirement for oxygen evolution between the Nobel laureate Otto Warburg (3–4) and Robert Emerson (8–12)—in favor of Emerson; and (2) Dmitry Shevela, Lars-Olof Björn and Govindjee (Shevela et al., 2019) published a book on all the key processes in photosynthesis for beginners. Also, Govindjee recorded the milestones of probing photosynthesis (Govindjee, 2000; Stirbet et al., 2020b) and provided one place to

which photosynthesis research on the internet may be linked (see Orr & Govindjee, 2013).

In addition, following a love for '*exploiting measurements on Chl a fluorescence for the understanding of photosynthesis, as well as its regulation*', Govindjee coauthored several reviews (Govindjee, 2004a; Papageorgiou & Govindjee, 2011; Stirbet & Govindjee, 2011, 2012; Stirbet et al., 2014, 2018, 2019). Furthermore, Papageorgiou and Govindjee (2014) wrote a highly useful and detailed review on the origin, the history, and the use of non-photochemical quenching of Chl *a* fluorescence in understanding how plants protect themselves against excess light. A notable publication on the use of Chl *a* fluorescence for phenotyping plants is by Mishra et al. (2016). Also, Mirkovic et al. (2017) provided an in-depth review of the steps of the primary events of photosynthesis, including light absorption and excitation energy transfer in photosynthetic light harvesting antenna. This review on the basics of photosynthesis was followed by that of Hu et al. (2020) presenting a co-author and co-cited reference network analysis for Chl fluorescence research from 1991 to 2018. Further, Lazar et al. (2022), honoring one of Govindjee's first graduate students, the late George C. Papageorgiou, reviewed how the color and intensity of light affects the pigment composition of the antenna, Chl *a* fluorescence, electron transport, and the overall growth of plants and algae.

Always, Govindjee has been fascinated with PSII—because it is the one that gives us "oxygen" and a key role for bicarbonate. Further, there may be a tie into the unification of light with carbon reactions implicated by that bicarbonate function in PSII (Govindjee, 1991; Xiong et al., 1997; Van Rensen et al., 1999; Shevela et al., 2012). Together with key PSII experts, he coauthored reviews on natural (PSII) and artificial photosynthetic water-splitting systems (Blankenship & Govindjee, 2007, 2007a, 2007bovindjee, 2007; Govindjee et al., 2010; Mirkovic et al., 2017; Najafpour & Govindjee, 2011; Najafpour et al., 2012; Shevela et al., 2013a, 2013b, 2021; Whitmarsh & Govindjee, 2002).

A major area of interest is Govindjee's perspective on the evolution of photosynthesis on our Earth and beyond! For thorough and critical discussions on evolution, see Björn and Govindjee (2007, 2009, 2015), and for why nature evolved chlorophyll, see Björn et al. (2009b). For a most interesting look at how plants may look in outer space, see Kiang et al., (2007a, 2007b) and Björn et al. (2009a). Additionally, Naithani et al. (2021) reviewed plant lectins, the reader of the sugar code, and their role in plant growth and development.

Science historian

A great passion of Govindjee has been the history of photosynthesis research, for example, Govindjee et al. (2002) traced the origin and evolution of the two major journals in photosynthesis: *Photosynthetica* and *Photosynthesis Research*. Then, Govindjee and Krogmann () provided, for posterity, an in-depth presentation of all the discoveries in photosynthesis—including its 'knitty-grittys'. This was followed by Govindjee and Shevela (2011) summarizing all their adventures in photosynthesis using the simplest oxygenic photosynthesizers, the cyanobacteria, and Govindjee and Björn (2012) and Govindjee et al. (2017a) presented before the world, their thoughts on the evolution of the current Z-scheme of photosynthesis. Govindjee's interest in writing on the discoveries and pioneers of the past began with, e.g., Govindjee (1989) about C. Stacy French (see also Govindjee and Fork (2006). In view of women's neglected role in science, Joliot et al. (2016) brought information by De Fourcroy, in 1787, for women—a book written about oxygen coming from water, long before any scientist accepted this concept.

Govindjee wrote several tributes in recognition of others, most of the time, with many coauthors. Lists of tributes and historical articles authored by Govindjee prior to retirement were published previously (see Govindjee & Krogmann, 2002; Govindjee, 2009a). A complete list of tributes and historical articles by Govindjee is available at https://www.life.illinois.edu/govindjee/recent_papers.html). In Table 2, we list tributes and articles coauthored by Govindjee after 2000; his past graduate students in *italics*.

In addition, Govindjee wrote tributes in honor of those who are no longer with us. These activities included tributes to his own parents (Govindjee, 2007, 2007a, 2007b), to his eldest brother, Krishnaji (Govindjee & Srivastava, 2010), and as well, to several friends who were not directly involved with photosynthesis research, but were from his home country, India: Satish C. Maheshwari (1933–2019), a plant biologist (Pareek et al., 2020); Ramesh C. Sinha (1934–2020), a plant virologist (Govindjee & Reddy, 2021); Ravindar Kaur Sawhney (1931–2020), a plant biologist (Govindjee et al., 2021); and Lalit M. Srivastava (1931–2012), a plant anatomist (Govindjee & Naithani, 2021).

Govindjee continues to honor others and encourage young researchers by highlighting their work and reporting on conferences. Govindjee (2004c) provided a list of conferences on photosynthesis. Furthermore, Govindjee has been active in writing reports on Gordon Research Conferences (GRCs)

on photosynthesis research with focus on recognizing young scientists; these include GRCs held during 2008–2019. Govindjee and Yoo (2007) summarized conferences of the International Society of Photosynthesis Research (ISPR). Further, Govindjee coauthored detailed reports on the International Conferences on Sustainability held in different countries (see e.g., Govindjee, 2009b; Allakhverdiev et al., 2014; Borisova-Mubarakshina et al., 2020). It is important to mention that one of Govindjee's favorite conferences was "Chlorophyll *a* fluorescence in aquatic sciences" that was held in the Czech Republic (see Prášil et al., 2008). Lastly, Govindjee wrote on his own 60 + year tryst in photosynthesis research (Govindjee, 2019a) and thanked all his mentors, coauthors and graduate students (Govindjee, 2019b).

Improving photosynthesis for the future

The research collaborations of Govindjee encompass projects focused on the primary events of photosynthesis, phosphorylation, the carbon reactions, and plant productivity (see Mamedov et al., 2015; Kaňa & Govindjee, 2016). Currently, Govindjee is collaborating with one of us, AP,

Table 2 List of tributes and historical articles coauthored by Govindjee after retirement

Year of publication	Names of scientists honored in the tribute articles
2001	Olle Bjorkman (1933–2021), Christopher Field, Alexander Glazer Krishna Niyogi (Melvin Calvin Award), Petra Fromme and Norbert Krauss (Robin Hill Award)
2004	Robert Emerson (1903–1959), see Govindjee (2001, 2004b, 2018, 2021) Eugene Rabinowitch (1898–1973), see Govindjee (2004b), Govindjee et al. (2019b) and Govindjee and Govindjee (2021)
2006	C. Stacy French (1907–1995)
2007	Paul Gorham (1918–2006)
2008	Martin Gibbs (1922–2006)
2010	Michael Wasielewski (see Govindjee & Seibert, 2010); Samuel Aronoff (1915–2010); Steve Brody (1927–2010), see Hirsch et al. (2010)
2011	Tom Punnett (1926–2008);
2012	William Ogren's Rebeiz Award Berger Mayne (1920–2011)
2014	William Arnold (1904–2001); Alexander A. Krasnovsky (1913–1993); *Prasanna Mohanty* (1934–2013), see Tiwari et al. (2014) and Naithani and Govindjee (2018)
2015	Albert Frenkel (1919–2015), *in 2015*; Colin Wraight (1945–2014), see Govindjee et al., (2015, 2016)
2016	Jalal A. Aliyev (1928–2016); James A. Bassham (1922–2012); Jeanette S. Brown (1925–2014); L. N. M. Duysens (1921–2015); René Marcelle (1931–2011); *George C. Papageorgiou* (1933–2020), see Prášil et al. (2022), but also Allakhverdiev et al. (2016); V.S. RamaDas (1933–2010); A special recognition of Hartmut Lichtenthaler (another article in 2021)
2017	About an International award to Jean David Rochaix; Nathan Nelson; T. Nejat Veziroglu Andrew A. Benson (1917–2015), see Nonomura et al., (2016, 2017); *Fred Cho* (1939–2011), see Govindjee et al. (2017b); André Jagendorf (1926–2017); N.V. Karapetyan (1936–2015); David Krogmann (1931–2016); Paul Latimer (1925–2011), see M.G. Latimer et al. (2017);
2018	Thomas T. Bannister (1930–2018), see Laws et al. (2018); Otto Kandler (1920–2017); Slava Klimov (1945–2017); Shmuel Malkin (1934–2017); *Tom Wydrzynski* (1947–2018), see Govindjee et al. (2018), and Conlan et al. (2019)
2019	T. Y. Kuang; Anthony Larkum; C. Marchetti; Kimiyuki Satoh; Reto J. Strasser Klaus Apel (1942–2017); Christoph Beck (1941–2017), Fred Crane (1925–2016); George Feher (1924–2017); Ulrich (Uli) Heber (1930–2016); Shigetoh Miyachi (1930–2016); Achim Trebst (1929–2017); William (Bill) Vidaver (1921–2017); and Diter Von Wettstein (1929–2017) see Govindjee and Messinger (2019)
2020	Melvin Calvin (1911–1997), see Govindjee et al. (2020b); *Maarib Bazzaz* (1940–2020) see Govindjee et al. (2020c); Alex Borisov (1930–2019)
2021	Jim Barber (1940–2020), *in 2021*; Martin Kamen (1913–2002); Tino Rebeiz (1936–2019), see Govindjee et al. (2020a); Chris Sybesma (1928–2018), see Vredenberg and Govindjee (2020)
2022	*Carl Nelson Cederstrand* (1927–2022), see Cederstrand and Govindjee (2022); Bacon Ke (1920–2022), see Govindjee et al. (2022c); Robert Togasaki (1932–2019); Bob Whatley (1924–2020); David Charles Fork (1929–2020); Paul C. Lauterbur (1929–2007), see Lauterbur and Govindjee (2022)—Nobel laureate for MRI

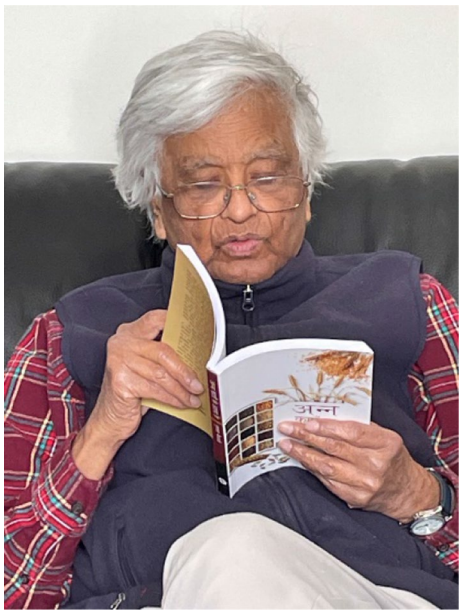

Fig. 6 Govindjee reading a book in Hindi by Sushma Naithani—the English translation is: "Where do our food grains come from?" The photo was taken in 2021 by Rajni Govindjee

and Baishnab Tripathy (India) on projects dealing with improving photosynthesis and plant productivity in several higher plants. For example, recent genetic experiments in Baishnab Tripathy's laboratory showed that overexpression of cytoplasmic C_4 carbonic anhydrase in a C_3 plant shows some potential for improving biomass (Kandoi et al., 2022). In another publication of AP's group, Soda et al. (2018) discovered that OsIF, a rice intermediate filament, stabilizes photosynthesis and consistent yields in rice under salt and heat stress, an important observation aimed at increasing food supplies in the future.

Likewise, in collaboration with Xin-Guan Zhu's laboratory (China), measurement of the rise of Chl *a* fluorescence (the OJIP transient) was applied to all the available rice varieties in China to study correlation of photosynthesis with the crop yield (Hamdani et al. (2015); Khan et al. (2020)). In addition, Hamdani et al. (2019) discovered the importance of the enzyme, glucosidase, in obtaining a higher quantum yield of photosynthesis—the mechanism of which is still unclear. Govindjee also is collaborating with David Guo (China) on Sun Induced Fluorescence to monitor the effect of drought on photosynthesis (Pandiyan et al., 2021), on development of models for enhancing crop productivity (see Fu et al., 2020), and on an open Internet of Things-based feedback control of photosynthetic activity (Yuan et al., 2022). Moreover, a very practical aspect of controlling bloom-forming cyanobacteria with a β-diketone—allowing other useful aquatic organisms to grow for our benefit—has been intiated by the group of Shujuan Zhang (China) (see Yilimulati et al., 2021).

Finally, Govindjee, with three of us, SN (USA), AN (USA) and DS (Sweden)—among other international collaborators, including S. S. Komath (India)—probed mechanisms behind the modulation of the carbon reactions of photosynthesis that is proven technology being utilized in agriculture to enhance quality and yields in food crops (for details see Nonomura et al., 2020; Naithani et al., 2021).

At the end of this tribute, which focused on Govindjee's long and passionate work on oxygenic photosynthesis, we show a recent photograph where he is reading a book in Hindi, written by one of us, SN, about the origins of crop plants, (see Fig. 6). He continues to look forward to future research for the benefit of humanity.

Awards and honors received after retirement

Govindjee is member to several scientific societies: Sigma Xi, American Society of Plant Biology, Biophysical Society of America, American Society of Photobiology, and the International Society for Photosynthesis Research. For outstanding scientific achievements and determination to promote photosynthesis research in younger generations, Govindjee has received prestigious awards and numerous honors. See Table 3 for awards received after retirement.

Concluding remarks

To Govindjee and Rajni, their children, Anita and Sanjay, and grandchildren, we wish good health and happiness in all their pursuits. We thank both Govindjee and Rajni for their pioneering work in the fields of photosynthesis and history of science. Thus, we end with Christoph Benning's introduction to Govindjee's Anton Lang lecture, "A Journey for Photosynthesis in Urbana, with a focus on Robert Emerson", since it wonderfully encapsulates the path of his life:

Table 3 Awards and honors received by Govindjee after retirement

Year	Award, Events, and publications in Honor of Govindjee
2004	Research Award from the Department of Biotechnology, Government of India
2006	The first Lifetime Achievement Award from the Rebeiz Foundation for Basic Research at the University of Illinois at Urbana-Champaign (UIUC)
2007	The Communication Award of the International Society of Photosynthesis Research, at the 14th International Congress of Photosynthesis Research, held in Glasgow, UK A special issue (in two parts) of Photosynthesis Research was published for Govindjee's 50 years in photosynthesis research, and at his 75th birthday
2008	The Liberal Arts and Sciences Alumni Achievement Award from UIUC (see http://www.las.uiuc.edu/alumni/magazine/articles/2009/govindjee) An International Symposium was held at Indore (India), on Govindjee's 75th birthday
2011	An interview with Govindjee for Annual Reviews of Plant Biology (American Society for Plant Biology) "*Dr. Donald Ort in conversation with Dr. Govindjee*" – see https://www.youtube.com/watch?v=cOzuL0vxEi0
2012	The volume 34 of the Advances in Photosynthesis and Respiration series (editors: Julian J. Eaton-Rye, Baishnab C. Tripathy, and Thomas D. Sharkey) was dedicated to Govindjee
2013	Photosynthesis Research (volumes 116 and 117) were dedicated to Govindjee for his 80th birthday Eaton-Rye (2013) dedicated a special article to Govindjee in the volume 116
2014	Prášil (2014) dedicated a special article to Govindjee in *Photosynthesis Research*
2016	The Prof. B. M. Johri Memorial Award of the Society of Plant Research (New Delhi, India)
2017	International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability, Hyderabad (India), celebrated Govindjee's 85th birthday In his honor, an article by Allakhverdiev et al. (2019) A National Symposium on Photosynthesis was held at Mohan Lal Sukhadia University, Udaipur, India, organized by Vineet Soni in honor of Govindjee
2018	A Special Issue of *Photosynthetica* – volume 56, was published to pay tribute to Govindjee at his 85th birthday, with Julian Eaton-Rye (2018) as Guest Editor The Foreign (Pravasi) Fellow Award of the *National Academy of Agricultural Sciences* was presented to Govindjee in New Delhi, India
2019	Ananya Sen, from the Illinois News Bureau at UIUC, wrote an article: "Govindjee, a pioneer in Photosynthesis" (see https://mcb.illinois.edu/news/2019-02-19/govindjee-pioneer-photosnythesis) Diana Yates, from the Illinois News Bureau at UIUC, wrote an article: "Govindjee's Photosynthesis Museum" (see https://news.illinois.edu/view/6367/801235), followed by Yates (2022) and Nonomura (2022)
2020	A tribute by Stirbet et al. (2020a) celebrating Govindjee's 20-years of retired life and 88th birthday A multitude of greetings and reminiscences were expressed on this occasion by friends and collaborators as presented by Eaton-Rye (2020) Wan Meher published an interview with Govindjee (see Meher, 2020): "In Conversation: Prof. Govindjee, a pioneer in photosynthesis research" A young student from India, Virendra Kumar, wrote a book, 'Wings to a child's dreams', describing how he was inspired by Govindjee (V. Kumar, 2020)
2021	An Award for Outstanding Achievements and Remarkable Contributions in the field of Education was presented to Govindjee by the *KTK Foundation* in New Delhi, India Two tributes, dedicated to Govindjee by Kumar et al. (2021) and Block (2022) were published
2022	Recipient of the prestigious Lifetime Achievement Award of the International Society of Photosynthesis Research, conferred during the 18th International Congress of Photosynthesis Research, Dunedin, New Zealand; https://mcb.illinois.edu/news/2022-09-12/govindjee-receives-lifetime-achievement-award-photosynthesis-research

Acknowledgements We thank Richa Okhandiar-MacDougall for reading and improving the manuscript.

Funding None.

Declarations

Conflict of interest The authors declare no conflict of interest.

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