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Govindjee's Breakthrough Research Before His Retirement and Accomplishments During the Following 25 Years

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ABSTRACT

This is a tribute dedicated to Govindjee for his 92nd birthday. He is Professor Emeritus of Plant Biology, Biochemistry, and Biophysics at the University of Illinois in Urbana-Champaign (UIUC) since 1999. He is highly acclaimed as a pioneer and discoverer in photosynthesis research, having contributed to the concept of two pigment systems and two light reactions working in series in oxygenic photosynthesis (known as the Z-Scheme), and for his innovative research on the different processes involved in the light phase of photosynthesis. Moreover, Govindjee is much praised for his outstanding work as an editor, historian, and teacher of photosynthesis. Here, we celebrate his many achievements with an emphasis on his continuing scientific activity during twenty-five years of retirement. For this, we have analyzed all his publications between 1999 and 2024, grouped into six themes, as well as his work as an editor and a teacher.

Keywords: Bicarbonate in Photosystem II; Book series: Advances in Photosynthesis and Respiration, including Bioenergy and Related Processes; Chlorophyll absorption and emission; Govindjee Govindjee; History and Biography; Non-photochemical quenching of chlorophyll *a* fluorescence; Primary reactions in photosystems; Two light effects on photosynthesis, Hill reaction, and chlorophyll fluorescence; Z-Scheme

INTRODUCTION

Govindjee (born on October 24, 1932, in Allahabad, India) is Professor Emeritus of Plant Biology, Biochemistry, and Biophysics at the University of Illinois in Urbana-Champaign (UIUC) since 1999 and is well-known as an ambassador of photosynthesis in the world, often called “Mr. Photosynthesis” (see Figure 1; also see e.g., Allakhverdiev et al. 2019; Block 2022; Kumar et al. 2021; and https://en.wikipedia.org/wiki/Govindjee).

About his early life in India, we recommend two of his books: Govindjee (ed.) (2007), dedicated to his parents, and Govindjee and Srivastava (eds.) (2010), dedicated to his elder brother Krishnaji (1922–1997). We also highlight the major influence in Govindjee’s life of his brother Krishnaji (see Figure 1), who took care of the entire family after the premature death of their father when Govindjee was only 11 years old. Krishnaji became a well-recognized physicist, an expert in microwaves and wireless technology. We will not discuss Govindjee’s high school and college education below, as it has been recounted in depth in Eaton-Rye (2007a,b), Stirbet et al. (2020b, 2022), and Block (2022). After finishing his MSc in 1954 in Botany (Plant Biology) at the University of Allahabad, Govindjee specialized in Plant Physiology under the late Shri Ranjan (1889–1969), a former student of Frederick Frost Blackman (1866–1947) of Cambridge (UK), and then he was appointed Lecturer at the University of Allahabad (1954–1956), where he taught plant physiology and conducted very successful research on the amino acid metabolism of healthy and diseased leaves of different plants (e.g., *Croton sparsiflorus*, *Acalypha indica*, *Nicotiana tabacum*, *Abelmoschus esculentus*, *Trichosanthes anguina*) in collaboration with Manmohan Laloraya, Tadimeti Raja Rao, his professor Shri Ranjan, and Rajni Verma. He came to UIUC in 1956 to be a graduate student of Robert Emerson (1903–1959), the discoverer of three important effects in photosynthesis: the Photosynthetic Unit (Emerson and Arnold 1932), the Red Drop (Emerson and Lewis 1943), and the Emerson Enhancement (Emerson et al. 1957). However, due to Emerson’s unforeseen death in 1959, Govindjee became a student of Eugene Rabinowitch (1903-1973) and received his PhD in Biophysics in 1960 (see e.g., Govindjee 2004a). In his thesis, on the “Action spectra of the Emerson Enhancement Effect in algae,” he showed for the first time that a short wavelength absorbing form of chlorophyll *a* (Chl *a* 670) is in the

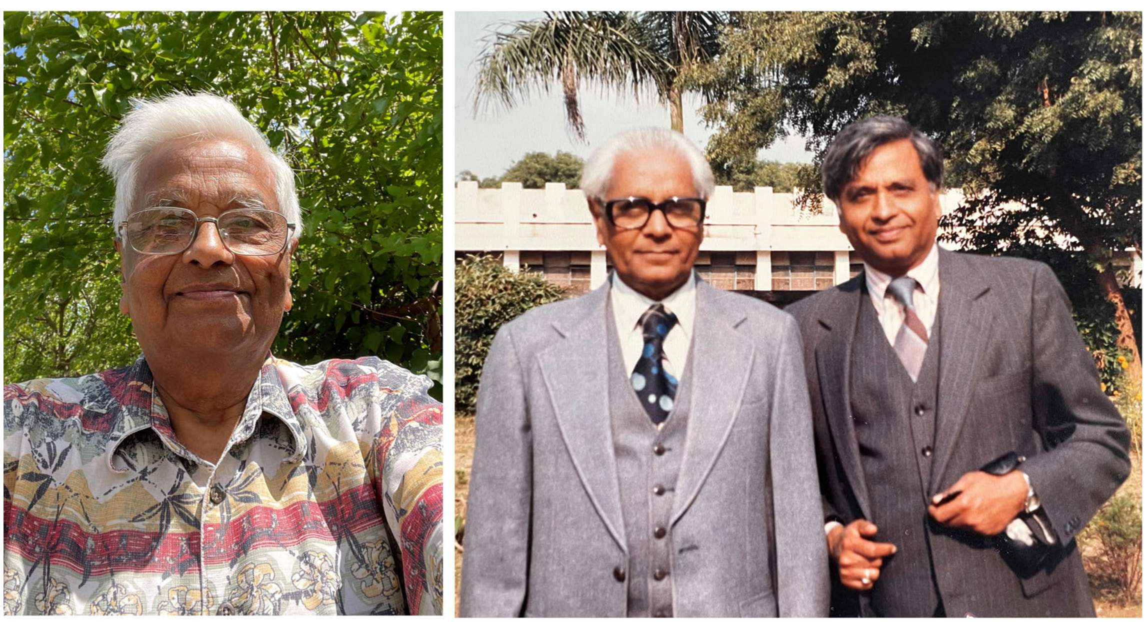

Figure 1: (Left) A 2024 photograph of Govindjee on a bright summer day in Urbana. **(Right)** A 1984 photograph of Govindjee (on the right) with his elder brother Krishnaji in Allahabad, India (see the text). *Source:* Archives of Govindjee’s family.

same system as Chl *b* in the green alga *Chlorella*, and fucoxanthin (carotenoid) in the diatom *Navicula minima* (see discussion below, and also Govindjee and Rabinowitch 1960).

Besides his research contributions to the understanding of the essential processes related to the light phase of photosynthesis (see e.g., Govindjee 2019a), for which he is regarded as one of the pioneers and an authority in the field, Govindjee is renowned for his outstanding work as an editor, for his prolific and invaluable activity as a historian of photosynthesis, and for his dedication and talent as a teacher of photosynthesis to students of all ages around the world (see e.g., Govindjee 2008; Prášil 2014; Mohapatra and Singh 2015; Jaiswal et al. 2017; and a series of papers informing us about all the “Photosynthesis” sites on the Web by Orr and Govindjee 1999, 2001, 2007, 2010, 2013).

About his role in modern photosynthesis research, we cite here what Nathan Nelson, from Tel Aviv, Israel, wrote in a paper dedicated to both Pierre Joliot and Govindjee (Nelson 2013), on the occasion of their 80th birthdays: “Pierre Joliot and Govindjee helped in building the foundation of modern photosynthetic research and in establishing a unique group of followers who can design and execute highly advanced experiments and interpret the results with the utmost scientific proficiency.”

Regarding his personal life, Govindjee has been married for more than 65 years to Rajni Verma (see Figure 2), and they have two children, Anita and Sanjay. Rajni, who studied Botany (Plant Biology) at Allahabad University, obtained her PhD in 1961, also with Rabinowitch as her supervisor (see Govindjee and Govindjee R. 2021); the topic of her thesis was “The two-light effect in Hill reaction” (Govindjee R. et al. 1960; Govindjee R. and Rabinowitch 1961; also see Govindjee R. et al., 1962, 1964). After that, she worked as a researcher at UIUC until her retirement, mostly on how *Halobacterium halobium* converts light energy into chemical energy, in which she obtained remarkable results (for her scientific contributions see Ebrey 2015; Balashov et al. 2023).

During his professional career, Govindjee received many honors for important scientific discoveries and significant contributions to oxygenic photosynthesis (see a list in Stirbet et al. 2022); we mention here that he is a Fellow of the American Association for the Advancement of Science of the USA, of the National Academy of Agricultural Science of India, and of the National Academy of Sciences of India. Moreover, he has also received many awards from scientific societies, and a very important one was in 2022, from the International Society of Photosynthesis Research (ISPR): the Lifetime Achievement Award, during the 18th International Congress of Photosynthesis Research in Dunedin, New

Figure 2: (Left) Govindjee and Rajni honored at Mohanlal Sukhadia University in Udaipur, India, during the National Symposium on Photosynthesis in their honor, on December 8, 2017; **(Right)** Govindjee and Rajni visiting China in 2003. *Source:* Archives of Govindjee’s family.

Zealand (see Nonomura and Kumar 2022; Jajoo et al. 2023; Bricker and Eaton-Rye 2023).

Major Research Breakthroughs Before Retirement

Below, we present a summary of the main breakthrough results obtained by Govindjee and collaborators in the study of photosynthesis until his retirement in 1999. Note that his contributions during this period were also presented in e.g., Eaton-Rye (2012, 2013, 2018, 2019), Lichtenthaler (2020), Kumar et al. (2021), Lichtenthaler et al. (2022), Stirbet et al. (2023), and Veena et al. (2023).

Two-light effect in photosynthesis – The Emerson Enhancement Effect

The pigment system II is not powered just by chlorophyll (Chl) *b* (or other auxiliary pigments), as implied by Emerson and Chalmers (1958), but by a Chl *a* that has a different absorption peak than the Chl *a* in the pigment system I (Govindjee and Rabinowitch 1960; also see Cederstrand et al. 1966; Govindjee and Yang 1966).

Two-light effect in Chl a fluorescence

The intensity of Chl *a* fluorescence emitted by *Chlorella*, when simultaneously illuminated with 670 nm and 700 nm light, was found to be less than the sum of the fluorescence intensities obtained with 670 nm (or 440 nm) and 700 nm beams separately (Govindjee et al. 1960). From these results, the authors concluded that the 700 nm light decreases the yield of fluorescence excited by 670 nm (or blue light), and Butler (1962) confirmed these results using higher plants. Moreover, this effect was not only recognized but explained by Duysens and Sweers (1963) in their theory on the photochemical quenching of Chl fluorescence by the bound plastoquinone of PSII, which they named ‘Q’ for quencher (now known as Q_A) (see also Govindjee 2024c).

Two-light effect in Hill reaction

The two-light effect (i.e., the Emerson Enhancement Effect) is also present in $NADP^+$ reduction (R. Govindjee et al. 1962, 1964; also see Govindjee and Bazzaz 1967), which proves that this effect is in photosynthesis, not in respiration.

The primary donor of PSII is a Chl a pigment with absorption at 680 nm, which Govindjee named P680.

Krey and Govindjee (1964) were the first to observe the existence of a new fluorescence band at 693 nm in algae illuminated with strong light, which indicated to Govindjee the existence of a “second trap” (the first one being P700); it was named P680 by Govindjee (Rabinowitch and Govindjee 1965).

Exploitation of all types of light emission by the oxygenic organisms

All types of light emission by plants, algae, and cyanobacteria, i.e., ***fluorescence*** (see e.g., Papageorgiou and Govindjee 1968a,b; Munday and Govindjee 1969; Wydrzynski and Govindjee 1975; Govindjee et al. 1976; Strasser and Govindjee 1991, 1992; Shinkarev and Govindjee 1993; Strasser et al. 1995; Stirbet et al. 1995, 1998), ***delayed fluorescence*** (see e.g., Jursinic et al. 1976, 1978; Wong et al. 1978), and ***thermoluminescence*** (Sane et al. 1977, 1984; Tatake et al. 1981; Govindjee et al. 1984; Kramer et al. 1994; for theory see DeVault et al. 1983; DeVault and Govindjee 1990) provides detailed information on photosystem (PS) II reactions and beyond. See Figure 3 for photographs of some of Govindjee’s collaborators mentioned here, as well as in the following sections.

Primary photoreaction rate in Photosystem I and Photosystem II

Primary photochemistry, both in Photosystem I (PSI) and Photosystem II (PSII), was shown to occur within a few picoseconds by Govindjee and coauthors (Fenton et al. 1979; Wasielewski et al. 1987; Wasielewski et al. 1989; Wasielewski et al. 1990; for reviews, see: Govindjee and Wasielewski 1989; Govindjee and Seibert 2010; and Mamedov et al. 2015).

Photosynthetic oxygen evolution process

Mar and Govindjee (1972) discussed several models of the oxygen evolution process in PSII, and Wydrzynski

Figure 3: Left to right: (**Top left**) (*First row*): Rajni and Govindjee in front of their home in Urbana with their visitors (in 1999); (*second row*) Alan Stemler, Julian Eaton-Rye, and Tom Wydrzynski (1947–2018); **(Top right)** Paul Jursinic, Tom Wydrzynski, Alan Stemler, and Rita Khanna at the retirement party of Govindjee (in 1999); **(Bottom left):** Govindjee, George Papageorgiou (1933–1920), and Julian Eaton-Rye in 2011 (in Spain); **(Bottom right)** C. Leisner & S. Gray (the 2012 Govindjee & Rajni Govindjee Awardees; see: <https://www.life.illinois.edu/govindjee/photooftheyear2012.html>), and Govindjee wearing Emerson's apron, showing the 1965 poster of the Z-Scheme designed by him, where P680 was suggested for the first time to be the primary electron donor of Photosystem II (photo by Joan Huber). *Source:* Archives of Govindjee's family.

et al. (1976, 1978) used, essentially for the first time, nuclear magnetic resonance (NMR) to measure the proton relaxation and charge accumulation during oxygen evolution, and, respectively, the NMR by the manganese in aqueous suspensions of chloroplasts; another new model of oxygen evolution was proposed later by Kambara and Govindjee (1985). Then, Shinkarev et al. (1997) studied the period four oscillations of oxygen evolution in PSII via Chl *a* fluorescence changes, and Srivastava et al. (1999) studied the period four oscillation of the initial Chl *a* fluorescence level, delayed light emission, and P700 in greening peas, all providing detailed information on the biophysical aspects of oxygenic photosynthesis.

The role of bicarbonate in Photosystem II

Govindjee and coworkers pioneered the research regarding the essential role of bicarbonate on the electron acceptor side of PSII, specifically at the two-electron gate (i.e., for the reduction of plastoquinone Q_B by plastoquinone Q_A^-); see e.g., Stemler and Govindjee (1973), Govindjee et al. (1976), Khanna et al. (1977), Siggel et al. (1977), Vermaas et al. (1982), Eaton-Rye and Govindjee (1988a,b), Govindjee et al. (1990, 1991a,b, 1992), Cao et al. (1992), Xiong et al. (1997, 1998), and a review by Shevela et al. (2012).

Figure 4: (Left) (from left to right): Robert J. Jones, Chancellor of the University of Illinois at Urbana-Champaign (UIUC); Jerry Nelson, Professor Emeritus, Plant Science & Technology, University of Missouri, Columbia, Missouri; Govindjee; and Rajni Govindjee (July 22, 2022); Source: UIUC Archives. **(Right)** Katy Denise Heath, Head and Professor, Plant Biology at UIUC, and Govindjee (on October 2, 2024); *Source:* Penny Broga, Senior Associate Director for Business Affairs, School of Integrative Biology, UIUC.

Nonphotochemical quenching of Chl a fluorescence

Govindjee and his coworkers also explained the mechanism of nonphotochemical quenching (NPQ) of Chl *a* fluorescence, involving the xanthophyll cycle, through the formation of a quenching complex with a short fluorescence lifetime (see e.g., Gilmore et al. 1995, 1996a,b, 1998).

Furthermore, Govindjee never stopped his remarkable research activity after his retirement in 1999, but he continues to work, remaining in contact with activities and the leaders at UIUC (see Figure 4), and publishing in collaboration with many scientists around the world (see a list of Govindjee's collaborators in Appendix 1; also see: <https://www.life.illinois.edu/govindjee/recent_papers.html>). He has a total of over 600 publications, more than 30,000 citations, and an h-index of at least 89. For tributes honoring Govindjee after retirement, see Stirbet et al. (2020b, 2022), and for messages received by Govindjee from colleagues and friends on his 90th birthday, see Naithani et al. (2022), Seibert et al. (2022), and Shitov (2022) (for further tributes and interviews in Govindjee's honor during the years see Appendix 2). Below we will show more exactly the outstanding scientific achievements of Govindjee over the last 25 years since he closed his laboratory.

RESEARCH PAPERS AND REVIEWS PUBLISHED BY GOVINDJEE AND HIS COAUTHORS AFTER HIS RETIREMENT, FROM 1999 THROUGH 2024

During his career at UIUC, Govindjee has studied the photosynthesis process with his graduate students as well as many other scientists, which included visiting professors and postdoc associates (see Figure 3), focusing on a series of research topics that we have presented in the Introduction (also see: Eaton-Rye 2012, 2013; Govindjee 2019a,b; Stirbet et al. 2023). However, after closing his laboratory in 2002, Govindjee has continued to work and publish with many scientists around the world, either by visiting them or through online collaboration. He is still very much interested in the photosynthetic processes that he studied earlier, but, as he recognized in his paper "Sixty-year tryst with photosynthesis and related processes" (Govindjee 2019a), he now considers it very important to focus on two main objectives: **(i)** to participate in the general effort to find ways to make photosynthesis better able to deal with relevant global issues (such as energy security, food security and climate change); and **(ii)** to invest a good part of his time in writing on the history of photosynthesis research.

Below, we present his contributions during the last 25 years on different photosynthesis research areas. For ease in seeing what he has really done, they are presented under the following subtitles: **(1)** *Research based on data obtained using Chl a fluorescence techniques*; **(2)** *Different approaches to improve the efficacy of photosynthesis and increase the crop yield under global climatic changes*; **(3)** *Photosystem II, the role of bicarbonate in PSII function, photosynthetic water splitting mechanism, and artificial photosynthesis*; **(4)** *The Z-scheme, light harvesting in photosynthetic antenna, and primary charge separation in the reaction centers*; **(5)** *Models of different processes involved in photosynthesis;* and **(6)** *Oxygenic and non-oxygenic photosynthesis in general, and diverse photosynthetic studies*. For his publications between 1994 2024, see: <https://www.life.illinois.edu/govindjee/recent_papers.html>; also see Stirbet et al. (2020b, 2022) and Lichtenthaler et al. (2022) for further information.

Research Based on Data Obtained Using Chl *a* Fluorescence Techniques

The use of Chl *a* fluorescence in the study of photosynthesis is one of Govindjee’s most loved areas of research (see an interview of Govindjee by Donald Ort, Professor of Plant Biology at UIUC, for Annual Reviews, at https://www.youtube.com/watch?v=cOzuL0vxEi0). He has taken advantage of the fact that new and versatile fluorimeters have become available since his retirement, as well as improved theoretical approaches to analyze the Chl *a* fluorescence data (see e.g., Strasser et al. 2004; Baker 2008; Lazár 2015). Govindjee continued to use especially the slow (~300 s) Chl *a* fluorescence induction curves, as well as the fast (less than 1 s) Chl *a* fluorescence rise (the OJIP curve), to characterize the photosynthetic activity of different plants, algae, and cyanobacteria (see the early pioneering work of Kautsky and Hirsch, 1931; as well as of Papageorgiou and Govindjee 1968a,b; and Munday and Govindjee 1969; cf. Govindjee 2019a). Moreover, in the 1990s, Govindjee began an important collaboration in this domain with Reto Jörg Strasser of the Bioenergetics laboratory at the University of Geneva, Switzerland, which led to several papers published before and after 1999; also see Govindjee et al. (2019), which is a tribute in honor of Reto Jörg Strasser at his 75th birthday. Further, in many papers, published by Govindjee after his retirement, the experimental OJIP fluorescence curves of different oxygenic organisms were analyzed using the so-called “JIP-test,” which was proposed initially by Strasser and Strasser (1995) and was further developed by Strasser and his collaborators (see e.g., Strasser et al. 2004). Below, we will present Govindjee’s publications on this topic arranged on different themes. However, we note that some of the papers in which Chl *a* fluorescence was used in parallel with other techniques, listed in other sections, will follow in those sections. Figure 5 shows photographs of Govindjee with some of his collaborators in this area.

Fast chlorophyll a fluorescence induction, the OJIP curve

Schansker et al. (2003) provided data on the 820-nm signal from PSI, paralleling the OJIP fluorescence rise from PSII in pea leaves; Stirbet and Govindjee (2011) wrote a review on the basics and applications of the OJIP fluorescence transient curves the so-called JIP test; Kalaji et al. (2011) studied the salt stress tolerance of two Syrian barley landraces by using the OJIP fluorescence transients and gas exchange measurements; Stirbet and Govindjee (2012) presented a perspective on the analysis of the thermal phase of the Chl *a* fluorescence transient, the J-I-P phase; Zivcak et al. (2014) used the OJIP fluorescence transients to calculate the PSII connectivity in sun- and shade-grown barley leaves and concluded that the lower PSII connectivity in shade-grown barley leaves is likely associated with protection against excessive light, as it helps to maintain a lower excitation pressure within the photosynthetic apparatus when exposed to high light conditions; Stamatakis et al. (2016) studied the effects of β-carotene, a chemical scavenger of singlet oxygen, on the millisecond rise of Chl *a* fluorescence of cyanobacteria *Synechococcus* sp. PCC 7942; Wungrampha et al. (2019)

Figure 5: (Top left) A photo of Govindjee and George Papageorgiou during their visit to Ondřej Prášil in Třeboň, The Czech Republic, in 2011, in relation to a study of state changes in cyanobacteria (see Kaňa et al. 2012): Ondrej Prášil is second on the left; next to him is George C. Papageorgiou (1933–2018), then Govindjee, and Willem (Wim) Vredenberg; **(Top Right)** Reto J. Strasser (University of Geneva, Switzerland) showing Xin-Guang Zhu (Chinese Academy of Sciences, Shanghai, China) the set-up for measuring Chl a fluorescence transients**. (Bottom)** Govindjee with the research group of Ashwani Pareek at Jawaharlal Nehru University, New Delhi, India, in 2018, with which he had a very successful collaboration and had visited during 2012 and then 2015–2019: (Right to left): Ashwani Pareek, Jayram Bagri, Rakesh Tiwari, Govindjee, Anjali Shailani, Harshita Pandey, Nishtha Rawqat, Chhaya Yadav, Deepti Singh, Silas Wungrampha, unidentified, Plaban Pratima, and Kamlesh Kant Nutan. *Source:* Archives of Govindjee's family and of Ashwani Pareek.

analyzed Chl *a* fluorescence and CO_2 gas exchange measurements of *Suaeda fruticosa* L. plants that survive under extreme xerohalophytic conditions as influenced by diurnal rhythm or continuous dark conditions; Jimenez-Francisco et al. (2019) wrote a comparative study of intact leaves and isolated cells from *Bouteloua gracilis* (blue grama grass) by using OJIP transient measurements; Khan et al. (2021) presented data on the natural variation of the OJIP transient in a global rice minicore panel; Padhi et al. (2021) compared the OJIP transients measured using Handy PEA and FluorPen fluorometers; and Badshah et al. (2024) studied the inhibition of CO_2 fixation as a potential target for the control of freshwater cyanobacterial harmful algal blooms.

State changes and Chl a fluorescence

Papageorgiou et al. (1999) presented data on light-induced and osmotically induced changes in Chl *a* fluorescence in two *Synechocystis* sp. PCC 6803 strains that differ in membrane lipid unsaturation; Papageorgiou and Govindjee (2011) wrote a perspective on the PSII fluorescence induction slow changes; Kaňa et al. (2012) showed evidence that the state 2 to state 1 transition in cyanobacteria is the origin of the slow S to M fluorescence rise in the Chl *a* fluorescence induction curve; Kodru et al. (2015) found that the slow S to M rise of Chl *a* fluorescence induction measured on *Chlamydomonas reinhardtii* cells, previously dark adapted in anoxic conditions, is due to a state 2 to state 1 transition; Bernát et al. (2018) presented new data on the origin of the slow M-T Chl *a* fluorescence decline in cyanobacteria; and Mishra et al. (2019) studied the modulation of photosynthetic induction by low temperature in non-acclimated and cold-acclimated *Arabidopsis thaliana*.

Nonphotochemical quenching (NPQ) of Chl a fluorescence

On NPQ, we mention the following contributions: Gilmore and Govindjee (1999) reviewed the energy dissipation in PSII of higher plants as a response to excess light; Gilmore et al. (2000) presented a global spectral-kinetic analysis of Chl *a* fluorescence (at room temperature) from light-harvesting antenna mutants in barley; Govindjee and Spilotro (2002) studied the NPQ of Chl *a* fluorescence and the intensity-dependent changes of the Chl *a* fluorescence transient in leaves of a mutant of *Arabidopsis thaliana*; Govindjee and Seufferheld (2002) analyzed the NPQ of Chl *a* fluorescence of two xanthophyll cycle mutants of *Chlamydomonas reinhardtii*; Nedbal et al. (2003) made Chl *a* fluorescence measurements showing that the non-linear modulation of photosynthetic activity in plants and cyanobacteria, exposed to a dynamic light environment, is due to negative feedback regulation; Holub et al. (2007) reported the use of fluorescence lifetime imaging microscopy to study the NPQ of Chl *a* fluorescence in *Chlamydomonas reinhardtii* mutants, and measured the effect of photosynthetic inhibitors on their slow (300 s) Chl *a* fluorescence induction curves; Matsubara et al. (2011) presented the contributions of lutein-epoxide and violaxanthin cycles to the fluorescence quenching in avocado leaves a study using PSII fluorescence lifetime imaging; Papageorgiou and Govindjee (2014) wrote a review on the NPQ of the excited state of Chl *a* in plants.

General information on the Chl a fluorescence and its measurement

Govindjee and Nedbal (2000) wrote a perspective on the use of imaging techniques based on Chl *a* fluorescence; Holub et al. (2000) presented a new technique to study photosynthesis using fluorescence lifetime imaging (FLI); Govindjee (2004b) wrote a review on the basics and history of Chl *a* fluorescence measurements; Kaňa et al. (2009) studied the spectral characteristics of the fluorescence induction in *Synechococcus* sp. PCC 7942; Kalaji et al. (2012) wrote a perspective (dedicated to David Walker) on in vivo measurements of light emission in plants; Kalaji et al. (2014) wrote a review on measurements of light emission in plants; Stirbet et al. (2019) contributed a review on Chl *a* fluorescence in cyanobacteria and its relation with photosynthesis; and Hu et al. (2020) presented a co-author and co-cited reference network analysis for Chl *a* fluorescence research from 1991 to 2018.

Different Approaches to Improve the Efficacy of Photosynthesis and Increase Crop Yield Under Global Climatic Changes

The high grain production attained during the Green Revolution in the late twentieth century is actually decreasing due to climate change, and the enhancement of photosynthesis is now considered to be an important target to increase crop yield (see e.g., Zhu et al. 2010; Ort et al. 2015); also see a paper by Ort et al. (2022), an editorial to a special issue of the journal Plant Physiology Reports that contains papers describing different aspects of plant adaptation to climate change; we note that it was dedicated to Govindjee on his 90th birthday for his highly significant scientific contribution in the domain of photosynthesis. Below, we present different approaches used by Govindjee and his collaborators to attain such goals (for a photograph of

Figure 6: Rajni Govindjee and Govindjee with the research group of Baishnab Tripathy at JNU, New Delhi, India (in 2018). Govindjee had participated with this group in a number of studies related to the increase of the efficacy of photosynthesis and biomass. Left to right: **(First row)** Rajni Govindjee, Govindjee, Baishnab Tripathy, Deepika Kandoi, Kamal Ruhil, and Barnali Padhi; **(Second Row)** Garima Chauhan, Kanchan Kumari, and Pratishtha Verma; **(Third Row)** Satpal Turan and Ranjan Sahoo. *Source*: Archives of Baishnab Tripathy.

Govindjee with some of his collaborators in this area of research, see Figure 6).

Producing genetically modified organisms with increased biomass or crop production

Yusuf et al. (2010) used Chl *a* fluorescence induction curves (the OJIP transients) and physiological measurements to show that the overexpression of the ã-tocopherol methyl transferase gene in transgenic *Brassica juncea* plants alleviates abiotic stress; Biswal et al. (2012) studied the light intensity-dependent modulation of Chl *b* biosynthesis and photosynthesis in tobacco (*Nicotiana tabacum*) when the chlorophyllide *a* oxygenase (CAO) from *Arabidopsis thaliana* was overexpressed; Zhou et al. (2015) investigated a *Chlamydomonas reinhardtii* mutant with improved biomass production under low light and mixotrophic conditions; Kandoi et al. (2016) found an increase in protein abundance and phosphoenolpyruvate carboxylase (PEPC) activity in *Arabidopsis thaliana* after the overexpression of PEPC from *Zea mays*, suggesting that the expression of C4 photosynthesis enzyme(s) in a C3 plant can improve its photosynthetic capacity and enhance its tolerance to salinity stress; Soda et al. (2018) determined that the overexpression of *Oryza sativa* intermediate filament (OsIF) in transgenic rice enhances tolerance to salinity and heat stress; Kandoi et al. (2022) showed that the overexpression of cytoplasmic C4 *Flaveria bidentis* carbonic anhydrase in C3 *Arabidopsis thaliana* increases amino acids, photosynthetic potential, and biomass; Negi et al. (2020) proposed a translational control system to obtain algae having light-regulated antenna size, which shows substantially higher photosynthetic rates and two-fold greater biomass productivity; Sayre et al. (2020) showed how light regulation of photosynthetic light harvesting can double the biomass yield in the green alga *Chlamydomonas reinhardtii*; and Biswal et al. (2024) found that a reduced expression of CAO decreases the metabolic flux for Chl synthesis and downregulates photosynthesis in tobacco plants.

Exploration of the natural variations of photosynthetic properties of different crops

Hamdani et al. (2015) determined the variations between the photosynthetic properties of elite and landrace Chinese rice cultivars through simultaneous measurements of PSI and PSII activities; Hamdani et al. (2019b) presented a genome-wide association study, which shows that the variation of glucosidase is linked to the natural variation of the maximum quantum yield of PSII photochemistry.

Examination of plant stress sensibilities

Mishra et al. (2016) published a perspective on high-throughput phenotyping in plant stress responses; Stirbet et al. (2018) reviewed the use of the Performance Index, calculated using Chl *a* fluorescence data from the OJIP transient curves, to quantify abiotic stress responses in plants; Pandiyan et al. (2022) assessed the impact of summer drought on vegetation growth, using space-based solar-induced Chl *a* fluorescence; and Anwar et al. (2024) studied the impact of individual, combined, and sequential stress on the photosynthesis machinery in rice.

Possible roles of plant lectins in increasing plant productivity

Nonomura et al. (2020) reviewed the modulation of glycoregulation in agriculture and presented a bypass of lectins that prevents free sugars from binding, making them available for increased productivity; Naithani et al. (2021) discussed plant lectins and their many roles.

Photosystem II, Role of Bicarbonate in PSII Function, Photosynthetic Water Splitting, and Artificial Photosynthesis

The structure and function of PSII, the role of bicarbonate in PSII, and the photosynthetic water-splitting process are important research areas in which Govindjee has made pioneering contributions during his career at UIUC (see the Introduction). Below are summarized the papers published by Govindjee and his collaborators on these topics after his retirement (for photographs of Govindjee with some of his collaborators in these areas, see Figure 7).

The Z-Scheme, Light Harvesting in Photosynthetic Antenna, and Photoreactions in Reaction Centers

Reviews on the structure and function of Photosystem II, and on the role of bicarbonate

Whitmarsh and Govindjee (2001a), Govindjee et al. (2010), Shevela et al. (2021), and Shevela et al. (2023) presented general reviews on PSII. Earlier, Van Rensen et al. (1999) had published a thorough review on the role of bicarbonate in PSII, and this was followed by a historical perspective on the unique role of bicarbonate in PSII by Shevela et al. (2012). Subsequently, Li et al. (2023) contributed a review on light-driven CO_2 assimilation by PSII and its relation to photosynthesis, and Vinyard and Govindjee (2024) added a review on bicarbonate as a key regulator of PSII activity and assembly, but not a substrate for O_2 evolution.

Oxygen-Evolving Complex in Photosystem II

Yu et al. (2001) showed that the tryptophan 241 at the C-terminus hydrophobic region of the manganese-stabilizing protein of the PSII complex influences its structure and function; Najafpour and Govindjee (2011) presented the structure and function of the Oxygen-Evolving Complex (OEC) in PSII as a model for artificial photosynthesis; Najafpour et al. (2012a) reviewed biological water oxidation as an appealing lesson from Nature for hydrogen production by water splitting for future energy needs; and Najafpour et al. (2013b) reviewed the steps of water oxidation and the Water-Oxidizing Complex (or OEC) in cyanobacteria.

Artificial photosynthesis: Structural models of the oxygen-evolving complex in Photosystem II

Najafpour et al. (2012b) proposed a manganese oxide, with phenol groups, as a promising structural model for the water-oxidizing complex in PSII; Najafpour et al. (2012c) presented a perspective on light energy

Figure 7: (Top left) Govindjee with Dima Shevela (*right*) announcing the publication of their book Shevela et al. (2019); on the left is Min Chen; **(Top right)** Govindjee and Jian-Ren Shen (Okayama University, Japan); **(Bottom left)** Govindjee in Russia, with Mahia Salmanion and Mahdi Najafpour (IASBS Department of Chemistry, Iran), in 2013; **(Bottom right)** Govindjee with Johannes Messinger at the First European Congress of Photosynthesis Research (in June 2018, Uppsala Sweden). *Source:* Archives of Govindjee's family.

conversion titled "Running on Sun"; then, Najafpour et al. (2013a) proposed a 2-(2-hydroxyphenyl)-1H-benzimidazole-manganese oxide hybrid as a structural model for the tyrosine 161/histidine 190-manganese cluster in PSII; and then, Hou et al. (2014, 2023) discussed the many current challenges in photosynthesis—from natural to artificial.

The Z-scheme

As noted in the Introduction, already at the beginning of his career, Govindjee had published pioneering studies on the concept of two pigment systems and two light reactions in oxygenic photosynthesis. Also, a few decades later, Govindjee and his collaborators were the first to measure the kinetics of primary photochemistry in both PSI and PSII (Fenton et al. 1979; Wasielewski et al. 1989; also see: Wasielewski et al. 1987, 1990; Greenfield et al. 1996, 1997). After retirement, he considered himself responsible for explaining to the new generation of researchers in photosynthesis how the idea of the two pigment systems and two photoreactions evolved in time and crystallized in the actual "Z-Scheme", in which the two systems work in series (see also Kutschera and Khanna 2023; Kumar and Nonomura 2023). Moreover, Govindjee has used newly designed posters to familiarize students, around the world, with the Z-scheme (see Figure 8; and reviews by Govindjee and Björn (2012) and Govindjee et al. (2017a) and has been distributing them free during photosynthesis conferences. Although after his retirement, Govindjee did not publish experimental studies on light harvesting and primary photoreactions, he has coauthored with others in these areas several important reviews and perspectives (see below):

Light harvesting in photosynthetic antenna, and photoreactions in reaction centers

Clegg et al. (2010) published a perspective: "From Förster Resonance Energy Transfer (FRET) to Coherent Resonance Energy Transfer (CRET) and back"; Kaňa and Govindjee (2016) reviewed the role of ions in the regulation of light harvesting; Mirkovic et al. (2017) reviewed "light absorption and energy transfer" in the antenna complexes of photosynthetic organisms; and Govindjee and Seibert (2010) summarized research on the picosecond spectroscopy of isolated reaction centers from both the photosystems of oxygenic photosynthesis, which was a review in honor of Michael R. Wasielewski, at his 60th birthday. Then, Ostroumov et al. (2014) published a review on the photophysics of photosynthetic pigment-protein complexes; and Mamedov et al. (2015) contributed a review on the primary electron transfer processes in photosynthetic reaction centers from oxygenic organisms.

Models of Different Processes Involved in Photosynthesis

Govindjee has shown his interest in modeling photosynthetic processes early in his career (for several early models of the oxygen evolution mechanism, see Mar and Govindjee 1972), and in the 1990s, he

Figure 8: *Left to right:* **(Top left)** Mahdi Najafpour, Govindjee, and Mahir Mamedov in Russia, 2019; **(Top right)** Rienk van Grondelle, Govindjee, Alfred Holzwarth, and Barbara Demmig Adams in Germany, 2008; (**Bottom left)** A visit to the UIUC office of Govindjee by Gonzalo Estavillo (holding a "Z-Scheme" poster) and Jose Barrero Sanchez (holding a "Rubisco" poster), both from CSIRO of Australia (photo by Karl Schliepf, Dec 7, 2023); (**Bottom right**) Govindjee (standing) with Sabeeha Merchant, Benjamin Engel, and Roberta Croce at the 2017 Gordon Research Conference on "Photosynthesis." *Source:* Archives of Govindjee's family.

coauthored, for the first time, papers presenting mathematical models simulating the OJIP fluorescence curves in plants (see Stirbet et al. 1995, 1998). After his retirement, he continued to publish in this field (for photographs of Govindjee with collaborators on this topic, see Figure 9). The list of papers on this topic follows.

Zhu et al. (2005) proposed a mathematical model for Chl *a* fluorescence induction kinetics in leaves, describing each discrete step of excitation energy and electron transfer associated with PSII; then, Stirbet et al. (2014) presented a review on modeling the Chl *a* fluorescence induction and its relation to different photosynthetic processes; Stirbet and Govindjee (2016) published an in silico study of the slow phase of Chl *a* fluorescence induction, showing that the transition from State 2 to State 1 is at the origin of the S-M fluorescence rise in *Chlamydomonas reinhardtii* cells that had been dark-adapted under anoxic conditions; this was followed by Fu et al. (2020) presenting a minimized mathematical model and a feedback control framework for regulating photosynthetic activities; Stirbet et al. (2020a) published a review on the history, the basics, and mathematical models of photosynthesis; then, Xia et al. (2023) used a machine learning algorithm (i.e., a least squares support vector machine model, LSSVM) to evaluate the Fv/Fm ratio from the fast Chl *a* fluorescence transient (OJIP curve), without dark adaptation; Ye et al. (2024) addressed the long-standing limitations of double

Figure 9: (Top left) *Left to right*: Govindjee, Galina Yu. Riznichenko, and Andrey B. Rubin from Lomonosov University in Moscow, Russia, 2013; (**Top right)** Xin-Guang Zhu (from Shanghai, China), Govindjee, and Min Chen, at the International Congress of Photosynthesis Research (ICPR) in Saint Louis, USA, 2013; (**Bottom left**) Alexandrina (Sandra) Stirbet, Rajni Govindjee, Govindjee, and Moonshiram Dooshaye, at the ICPR in Saint Louis, USA, 2013; (**Bottom right**) George Papageorgiou, Govindjee, and Dušan Lazár in The Czech Republic. *Source:* Archives of Govindjee's family.

exponential and non-rectangular hyperbolic models in quantifying the light response of electron transport rates in different photosynthetic organisms, under various conditions; and Stirbet et al. (2024) reviewed leaf to multiscale models of photosynthesis and their use in studies targeting crop improvement.

Reviews on Oxygenic and Non-Oxygenic Photosynthesis, and Diverse Photosynthetic Studies

Below we present the reviews published by Govindjee on oxygenic and anoxygenic photosynthesis, the evolution of photosynthesis and its environmental impact, as well as studies related to a multitude of other subjects, such as the greening of plants, the relationship between chloroplasts and mitochondria, spectral signatures of photosynthesis on Earth and extra-solar worlds, and more (for photographs of two of Govindjee's collaborators on this topic, Lars Olof Björn and Robert Blankenship, see Figure 10).

Whitmarsh and Govindjee (1999) reviewed the photosynthetic process; Renger et al. (1999) presented an introduction to photobiology, photosynthesis, and photomorphogenesis; Blankenship and Govindjee (2007) published a general review on photosynthesis; Govindjee et al. (2007a) reviewed bacterial photosynthesis; Björn et al. (2023) presented the photosynthesis process based on a broader and more inclusive definition. Björn and Govindjee (2009) summarized their views on the evolution of photosynthesis and chloroplasts; Govindjee and Shevela (2011) published a personal perspective on cyanobacterial photosynthesis based on their results obtained in studies using diverse measurement techniques; Shevela et al. (2013a) reviewed oxygenic photosynthesis in cyanobacteria; Shevela et al. (2013b) wrote a general review on oxygenic photosynthesis; Berkowitz et al. (2007) presented an overview of carbon dioxide fixation; Björn and Govindjee (2015) discussed the evolution of photosynthesis and its environmental impact; Govindjee (1999a) presented his perspective on the requirement of a minimum number of four versus eight quanta of light for the evolution of one molecule of oxygen in photosynthesis; further, Govindjee (1999b) published a historical perspective on the carotenoids in photosynthesis; Govindjee et al. (2007b) wrote a minireview on chlorophyll; and Lazár et al. (2022) a review on the light quality effects on oxygenic photosynthesis and more.

Chlorophyll in Photosynthesis and Astrobiology, and Studies on a Variety of Other Topics

Kiang et al. (2007a) published a review on the spectral signatures of photosynthesis for Earth organisms, and Kiang et al. (2007b) on the spectral signatures of

Figure 10: (**Left**) Lars Olof Björn, Professor Emeritus of Molecular Biosciences at Lund University (Sweden), an important collaborator of Govindjee; (**Right**) Robert Blankenship, Professor Emeritus of Arts and Sciences at Washington University in Saint Louis (USA), a good friend and an equally important collaborator of Govindjee – the two are known to interact with Govindjee on a regular basis; Blankenship is the current Editor of the Historical Corner of *Photosynthesis Research*. *Source*: Archives of Govindjee's family.

photosynthesis, coevolution with other stars, and the atmosphere on extra-solar worlds; further, Björn et al. (2009a) presented a viewpoint on why Chl *a* is the most widespread photosynthetic pigment on the surface of the Earth, and Björn et al. (2009b) presented their thoughts on the detectability of life on exoplanets. On a different note, Srivastava et al. (1999) summarized their studies on photosynthesis in greening peas by using different measuring techniques; Chow et al. (2000) examined the photosynthetic performance and capacity for photoprotection during the greening of intermittent-light-grown bean plants in continuous light; Yu et al. (2000) investigated how trichloroacetate affects the EPR signal II slow and signal I in the thylakoid membranes of *Chlamydomonas reinhardtii*; then, Ruiz et al. (2001) published their results on the polyphosphate bodies of *Chlamydomonas reinhardtii*, which possess a proton-pumping pyrophosphatase and are similar to acidocalcisomes; Rose et al. (2008) showed that the D1-arginine mutants (R257E, K, and Q) of *Chlamydomonas reinhardtii* have a lowered Q_B redox potential; Ernesto Garcia-Mendoza et al. (2011) provided information on photoprotection in the brown alga *Macrocystis pyrifera* and its evolutionary implications; Chen et al. (2012) observed that the reactive oxygen species from chloroplasts contribute to 3-acetyl-5-isopropyltetramic acid-induced leaf necrosis of *Arabidopsis thaliana*; Wang et al. (2012) reported their results on the net light-induced oxygen evolution in PSI deletion mutants of the cyanobacterium *Synechocystis* sp. PCC 6803 grown mixotrophically; Ocampo-Alvarez et al. (2013) described the antagonistic effect between violaxanthin and de-epoxidated pigments in nonphotochemical quenching induction in the qE deficient brown alga *Macrocystis pyrifera*; Shabnam et al. (2015) showed that the mitochondrial electron transport protects floating leaves of long leaf pondweed (*Potamogeton nodosus* Poir) against photoinhibition, in comparison with those in the submerged leaves; Shabnam et al. (2017) described the differential response of floating and submerged leaves of longleaf pondweed to silver ions; Hamdani et al. (2019a) described the changes in photosynthesis and photoprotection capacity in rice (*Oryza sativa*) grown under red, blue, or white light; Yilimulati et al. (2021) reported on the regulation of photosynthesis in bloom-forming cyanobacteria with the simplest β-diketone; Yuan et al. (2022) published on "an open Internet of Things (IoT)-based framework for feedback control of photosynthetic activities"; and Korres et al. (2023) evaluated secondary sexual dimorphism of the dioecious *Amaranthus palmeri* under abiotic stress.

Editorial Work, History and Biography, News Reports, and Book Reviews

Even before his retirement, Govindjee had decided to enlarge his activity as a historian of photosynthesis; in addition, he increased his contributions to the education of younger generations. In 1983 and 1984, he served as Executive Editor, and from 1985 to 1988 as the co-Editor-in-Chief of the journal *Photosynthesis Research*, which was established in 1980, with René Marcelle as Editor-in-Chief (see Govindjee et al. 2002). After that, Govindjee accepted to be the Editor of the Historical Corner of *Photosynthesis Research*; he not only wrote numerous history-related papers, but he encouraged many others to do the same.

After leaving the Historical Corner, he continued to publish numerous papers on History and Biography there, but also in several other journals (e.g., *Photosynthetica* and *The Journal of Plant Science Research*). Furthermore, in 1994, Govindjee had initiated the publication of a new book series, now known as *Advances in Photosynthesis and Respiration, including Bioenergy and Related Processes* (AIPH), where he had been the Series Editor of 43 volumes until 2017 (together with Thomas D. Sharkey from 2012; see https://www.springer.com/series/5599). In addition, he had co-edited volume 19 on *Chlorophyll a fluorescence* (Papageorgiou and Govindjee 2004a), 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).

During his retirement, Govindjee also co-edited a book on *Abiotic stress adaptation in plants* (Pareek et al. eds. 2009) and co-authored two other important books: one about the *Controversy on the maximum quantum yield of photosynthesis* (Nickelsen and Govindjee 2011) between the Nobel laureate Otto Warburg and his student Robert Emerson, and another a wonderful summary of photosynthesis, *Photosynthesis: Solar energy for life* (Shevela et al. 2019).

Besides the above contributions after his retirement, Govindjee has authored (or co-authored) several editorials, announcements of new books or photosynthesis conferences, and news reports on conferences that he had attended (for news reports from the conferences on "Photosynthesis and Hydrogen Energy Research for Sustainability," see e.g., Stirbet et al. 2020b). A list of papers on History and Biography published by Govindjee after his retirement is available in Stirbet et al. (2022). Thus, we present here only a list of his 2023 and 2024 historical papers, as well as a list of tributes honoring others.

Recent historical papers

(1) Govindjee et al. (2023): an overview of the remarkable life and outstanding research on oxygenic photosynthesis of ***David (Dave) Charles Fork (1929–2020),*** especially related to light absorption, excitation energy distribution, and redistribution among the two photosystems, electron transfer, and their relation to dynamic membrane changes as affected by variations in environmental conditions, especially in temperature; **(2)** Foyer et al. (2023): a tribute to ***Charles Percival Whittingham (1922–2011),*** who was a pioneer in photosynthesis excelling in research on the light reactions, glycolate production, and photorespiration; **(3)** Govindjee and Frenkel (2023): a tribute to ***Albert W. Frenkel (1919–2015),*** a pioneer in photosynthesis research, who is known for the discovery of photophosphorylation and NAD reduction in anoxygenic photosynthetic bacteria; **(4)** Breidenbach et al. (2023): a tribute to ***Paul A. Castelfranco (1921–2021),*** a top chemist of chlorophyll biosynthesis, who also made major contributions on fatty acid oxidation, acetate metabolism, and cellular organization; **(5)** Guru et al. (2023): a tribute to ***Dinesh Chandra Uprety (1945–2023),*** a remarkable plant scientist of India, who devoted most of his life to how best to tune the crop plants so that they can serve the growing human population in this world**; (6)** Govindjee et al. (2023): a tribute to ***Manmohan Manohar Laloraya (1932–2023***), a distinguished plant physiologist and life-long friend of Govindjee; **(7)** Pandey et al. (2023): a tribute to ***Someshwar Nath Bhargava (1937–1983),*** an outstanding plant pathologist and mycologist from Allahabad University, Prayagraj; **(8)** Govindjee (2023a): on the evolution of the concept of two light reactions and two photosystems for oxygenic photosynthesis; **(9)** Govindjee (2023b): a paper written in honor of ***Győző Garab,*** for his 75th birthday, an ingenious scientist and a great friend; **(10)** Govindjee (2024a): a tribute to ***George Edward Hoch (1931–2023),*** one of the top leaders in deciphering the primary steps of oxygenic photosynthesis; **(11)** Govindjee (2024b): a paper presenting the scientific contributions of ***Christa Critchley***, a distinguished researcher in basic and applied photosynthesis research, who used in her studies two important biophysical tools, Nuclear Magnetic Resonance and Chl *a* fluorescence, as well as other biochemical and plant physiological methods; **(12)** Govindjee et al. (2024a): a historical paper presenting the translations in English of two papers on chlorophyll, Pelletier and Caventou (1817, 1888), and a brief timeline concerning key events in chlorophyll chemistry, particularly in relation to the understanding of photosynthesis; **(13)** Govindjee et al. (2024b): a tribute in honor of ***Hartmut Karl Lichtenthaler*** on his 90th birthday, for his groundbreaking and creative contributions to plant science, being well-known as a highly innovative pioneer of photosynthesis research, plant physiology, isoprenoid biochemistry, and stress physiology of plants; **(14)** Govindjee et al. (2024c): a tribute to ***Jan Amesz (1934–2001***), a great gentleman, a major discoverer, and an internationally renowned biophysicist of both oxygenic and anoxygenic photosynthesis; and **(15)** Govindjee (2024c): on the Two Light Effect in Chl fluorescence.

A list of tributes published by Govindjee honoring several UIUC alumni

(1) Seymour Steven Brody (1927–2010) (see Hirsch et al. 2010) [PhD: 1956: UIUC] Brody did his PhD under Eugene Rabinowitch; **(2) Thomas Roosevelt Punnett, Jr. (1926–2008)** (see Hagar et al. 2011) [PhD: 1954, UIUC]. Punnett did his PhD under Robert Emerson; **(3) Prasanna K. Mohanty (1934–2013)** (see Tiwari et al. 2014) [PhD: 1972, UIUC]. Mohanty did his PhD under Govindjee; **(4) Frederick Yi-Tung Cho (1939–2011)** (see Govindjee et al. 2017b) [PhD: 1969, UIUC]. Cho did his PhD under Govindjee; **(5) Paul Henry Latimer (1925–2011)** (see Latimer et al. 2017) [PhD: 1956, UIUC]. Latimer did his PhD under Eugene Rabinowitch; **(6) Thomas Wydrzynski (1947–2018)** (see Govindjee et al. 2018) [PhD: 1977, UIUC]. Wydrzynski did his PhD under Govindjee; **(7) Thomas Turpin Bannister (1930–2018)** (see Laws et al. 2018) [MS: 1953; PhD: 1959, UIUC]; Bannister did his MS under Robert Emerson but his PhD under Eugene Rabinowitch; **(8) Maarib (Darwish Lutfi Bakri) Bazzaz (1940–2020)** (see Govindjee et al. 2020) [BS: 1961; MS: 1963; PhD: 1972; UIUC]. Bazzaz did her PhD under Govindjee; **(9) Carl Nelson Cederstrand (1927–2022)** (see Cederstrand and Govindjee 2022) [BS: 1956; PhD: 1965; UIUC]. Cederstrand did his PhD jointly under Govindjee and Eugene Rabinowitch.

CONCLUDING REMARKS

Govindjee's scientific activity after his retirement (from 1999 to the present date in 2024) has included 227 articles in scientific journals or as chapters in books, out of which 115 are research papers (61 original research and 54 reviews or perspectives), and 112 are in the area of History and Biography (the majority being tributes in honor of scientists working on photosynthesis). Further, the list of Govindjee's research papers published during his retirement shows that he has been working on a variety of topics, but his preference has been: **(i)** in exploiting Chl *a* fluorescence techniques to understand photosynthesis (34 papers); **(ii)** on the use of different approaches to improve the efficacy of photosynthesis and to increase the crop yield under global climatic changes (18 papers), and **(iii)** on the general structure and function of Photosystem II, with emphasis on the role of bicarbonate in PSII function and on the photosynthetic or artificial water-splitting mechanism (15 papers). Regarding the books during his retirement, Govindjee has coedited Volume 19 (Papageorgiou and Govindjee 2004a), 20 (Govindjee et al. 2005), 29 (Laisk et al. 2009), and 40 (Demmig-Adams et al. 2014) from the AIPH book series. In addition, as noted earlier, he has co-authored two important books: Nickelsen and Govindjee (2011) and Shevela et al. (2019); and co-edited another: Pareek et al. (eds.) (2009). Besides the above papers and books, Govindjee has also published 19 news reports (the last one in 2019), 10 editorials, 4 book reviews, and 7 book announcements. The above educational activity of Govindjee is appreciated by everybody in the field, and he was honored with a Communication Award of the ISPR, which he received at the 14th International Congress of Photosynthesis Research held in 2007 in Glasgow, UK. From the above, it is clear that during the 1999–2024 period, Govindjee had a very fruitful scientific period, but different from that between 1954–1999. Reto Strasser said in his message to Govindjee in 2018, during the National Symposium of Photosynthesis at the Mohanlal Sukhadia University (Udaipur, India), on the occasion of his 85th birthday: "*Govindjee is a great writer, and he always was. A lot would get lost if he had not written several books about the history of Photosynthesis*."

Since Govindjee has published many news reports until 2020 (i.e., at the start of the "Covid period," one can easily conclude that he remained for a long time very active socially, participating in person at the most important photosynthesis conferences, such as "The International Congress of Photosynthesis," "Photosynthesis and Hydrogen Energy Research for Sustainability," and "The Gordon Research Conference" (see Figure 11).

Being curious to learn about new developments in photosynthesis research, Govindjee also participated in the "International Symposium on Chloroplast Engineering"

Figure 11: What is Govindjee doing between scientific sessions at different conferences. (**Top Left**) Govindjee meets his scientific friends; here, he is with his friend Nathan Nelson (Tel Aviv University, Israel) and Hila Toporik (a former student of Nelson) at a Gordon Research Conference (GRC) in 2017; (**Top Right**) (*First row*) Govindjee, wearing Emerson's lab apron, offering books from the AIPH series to four young researchers for their presentations at the GRC 2014; in the second row are (*left to right*): P. Les Dutton, Fabrice Rappaport (1967–2016), and David Kramer; (**Bottom left**) Govindjee (in the middle) holding Z-Scheme posters (that he presented to young researchers at the GRC 2011); (**Bottom right**) Govindjee (on left), dancing after the banquet at the International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability in Baku, Azerbaijan, in 2011. *Source:* Archives of Govindjee's family.

held in Urbana, Illinois, in May 2005, which was organized by Constantin (Tino) Rebeiz (1936–2019). This gave him the chance to meet his international friends, such as Hartmut Lichtenthaler and Diter von Wettstein (1929–2017) (see Figure 12, Top). On this occasion, he demonstrated that he is not only a reliable friend but also a generous host. Thus, after this symposium, he invited Hartmut Lichtenthaler and Arthur Grossman to a special afternoon tea hour at his home in Urbana (see Figure 12, Bottom).

In fact, Govindjee has always been interested in being in touch with researchers working in photosynthesis laboratories around the world, to hear all the new ideas and developments, and to be open to eventual possible collaboration. Indeed, he understood early on that photosynthesis research is a multidisciplinary endeavor, appreciating the importance of teamwork, and many of the discoveries made in his laboratory were in part due to his ability to bring together the "right" people. An illustration of how Govindjee's meetings with scientists at conferences can lead to fruitful collaborations is his encounter with Alexandr Shitov and Leyla Abasova (see Figure 13), both from Russia, after a banquet at the International Conference "Photosynthesis Research for

Figure 12: (Top): Govindjee meets his scientific friends, Diter von Wettstein (*middle*) and Hartmut Lichtenthaler (*right*), at the International Symposium on Chloroplast Engineering held in Urbana-Champaign, Illinois, in May 2005; (**Bottom left**): Hartmut Lichtenthaler (*left*) with Govindjee and his wife Rajni in front of their house in Urbana in May 2005, where Hartmut was invited to a tea hour; (**Bottom right**): Hartmut Lichtenthaler (*left*) and Arthur Grossman (*right*) during the afternoon tea hour in the home of Govindjee (*middle*), in May 2005. *Source:* Hartmut K. Lichtenthaler.

Sustainability," held during July 24–30, 2011, in Baku, Azerbaijan. [For a full description of this conference and many historical photographs, see Allakhverdiev et al. (2011).] We note that Govindjee, in his usual self, used the time after the banquet as an opportunity to informally network with scientists from around the world. An amazing outcome – that surfaced ~10 years later led to a collaborative research project with Alex Shitov on the discovery of a very high carbonic anhydrase activity on the electron donor side of PSII, which has unique implications for the role of bicarbonate in this system (paper in preparation). For a recent review on the role of bicarbonate in PSII, which was dedicated to Govindjee on his 90th birthday, see Shitov (2022).

In addition to all of the above, Govindjee loves to meet and discuss with students and young scientists at conferences, at UIUC, and at other universities to encourage them and eventually help them in their research whenever possible. One such occasion happened recently last summer when Govindjee was at UIUC one day (read this short story in Appendix 3). Moreover, many young researchers have received from him, at conferences, signed Z-scheme posters or books (volumes from the AIPH series) (see Figure 11). Finally, we, the authors of this Tribute, and his worldwide friends have already wished Happy Birthday to Govindjee for his 92nd anniversary (on October 24, 2024) and have raised a toast in his honor for all the amazing things he has done and hopefully will do in the years to come. [For several personal messages sent to Govindjee on this occasion, see Appendix 3.]

Figure 13: A 2011 photograph from a conference in Baku, Azerbaijan. (*Left to right*): Leyla Abasova, Govindjee, and Alexandr Shitov. *Source:* A. Shitov.

APPENDIX 1

Govindjee's Coauthors — A Truly International List

The following is a list of all the coauthors (close to 580; from 1955 through 2024) of Govindjee, as finalized in late 2024, and arranged in alphabetical order by countries. From these, the USA is at the top (262), followed by India (66), China (53), Russia (24), Germany (22), France and the Netherlands (18 each), the Czech Republic (17), Japan (13), Canada and the United Kingdom (11 each), Mexico (9), Australia (8), Finland and Israel (6 each), Azerbaijan, Greece, Hungary, Poland, Sweden, and Switzerland (5 each), Iran (4), Belgium, Egypt, Estonia, and the Slovak Republic (2 each), and Bulgaria, Korea, New Zealand, and Norway (1 each). [Those who were research associates in Govindjee's Lab at the time of their research, are Underlined, Govindjee's graduate students are written in *Italic* and the collaborators that are now deceased are written in **Bold**.]

Australia

Bottomley, Warwick W.; Chow, Wah S. (Fred); Conlan, Brendon; Critchley, Christa; Downton, W. John S.; Funk, Christiane; **Hope, Alexander (Alex) Beaumont (1928-2008); Porra, Robert (Bob) John (1931-2019)**

Azerbaijan

Abilov, Ziya Kagranan; Gasanov, Ralphreed (Ralph) Ahad; Gazanchyan, Rafael Mikhaylovich; Huseynova, Irada M.; Kurbanova, Inna Musa

Belgium

Marcelle, Dominique; **Marcelle, René (1931-2011**)

Bulgaria

Goltsev, Vasilej

Canada

Beatty, J. Thomas (Tom); Cullen, John J.; Gorham, Hariet H.; Khan, Yaser R.; *Mar, Ted*; Mirkovic, Tihana; Nozzolillo, Constance G.; Ostroumov, Evgeny E.; Roy, Guy; Turpin, David Howard; Weger, Harold G.

China

An, Ting; Chen, Shiguo; Chu, Chengcai; Dai, Zongming; Essemine, Jemaa; Fu, Lijiang; Guo, Ya (David); Hamdani, Saber; Hao, Xing-Yu; Hou, Cai Xia; Jia, Yunlu; Jiang, Jiangjun; Jin, Jiyuan; Kang, Hua-Jing; Khan, Naveed; Khan, Waqasuddin; Li, Kuen Bao; Li, Ming; Li, Rong; Lin, Nianyun; Liu, Xinyu; Lyu, Ming Ju Amy; Mi, Hualing; Pan, Bingcai; Pandiyan, Sanjeevi; Perveen, Shahnaz; Qiang, Sheng; Qu, Mingnan; Ruan, Kang-Cheng; Shen, Yun-Kang; Song, Hong-Yu; Tang, Hao; Wang, Fu-Biao; Wang, Hongru; Wang, Kai; Wang, Xiaomeng; Wang, Xin; Wang, Xu-Tong; Wu, Bing; Xia, Qian; Xin, Chang Peng; Xu, C (full name not yet found); *Xu, Chun-He*; Yang, Chunlong; Yang, Xiao-Long; Ye, Ji-Yu; Ye, Zi-Piao; Yilimulati, Mihebai; Yin, Chunyan; Yu, Hao; Yu, Xin Jian; Zhou, Xin-Guang; Zhu, Yan

The Czech Republic

Adamec, František; Bøezina, Vitìzslav; Kaňa, Radek; Klem, Karel; Komárek, Ondřej; Kotabová, Eva; Kubásek, Jiři; Lazár, Dušan; Mishra, Anamika (she is from India); Mishra, Kumud Bandhu (he is from India); Nedbal, Ladislav (Lada); Prášil, Ondøej; Šedivá, Barbora; **Šesták, Zdeněk (1932–2008);** Štys, Dalibor; Urban, Otmar; Vacek, Karel

Egypt

El-Shintinawy, Fatima; Younis, Hasan M.

Estonia

Laisk, Agu; **Oja, Vello (1943-2020)**

Finland

Aro, Eva-Mari; Keränen, Mika; Maenpää, Pirkko; Mulo, Paola; Tyystjärvi, Esa; Tyystjärvi, Taina T.

France

Astier, Chantal; Babin, Marcel; **Briantais, Jean-Marie (1936-2004);** de Klerk, Henk; de Kouchkovsky, Yaroslav; **Douce, Roland (1939-2018); Ducruet, Jean-Marc (dates unavailable);** Etienne, Anne-Lise; Freyssinet, Georges; Joliot, Pierre; Kirilovsky, Diana; **Lavorel, Jean (1928-2021**); Mathis, Paul; Miranda, Teresa; Moya, Ismael; Peteri, Brigitta; **Rappaport, Fabrice (1967–2016)**; Vernotte, Claudie

Germany

Caliandro, Rosanna; Dau, Holgar; Döring, Günter; Finkele, Ulrich; Heiss, Gregor J.; Heyer, Arnd G; Holub, Oliver (Olli); Irrgang, Klaus-Dieter; Junge, Wolfgang; Lauterwasse, Christoph; Lichtenthaler, Hartmut K.; Matsubara, Shizue; Nickelsen, Kärin; Oesterhelt, Dieter; Pfister, Klaus; **Renger, Gernot (1937-2013)**; Scheer, Hugo; Siggel, Ulrich (Uli); Stilz, Hans Ulrich; Tanner, Widmar; Wagner, Richard; Zinth, Wolfgang

Greece

Alygizaki-Zorba, Aikaterini; Korres, Nicholas E.; ***Papageorgiou, George C. (1933-2020);*** Stamatakis, Kostas; Tsimilli-Michael, Merope

Hungary

Bernát, Gábor; Garab, *Győző*; **Szalay, Laszlo (1920-1997);** Török, Miklós; Vass, Imre

India

Anwar, Khalid; Bahugna, Rajeev N.; Biswal, Ajaya K.; Bharti, Sudhakar; Bose, Salil; Chauhan, Garima; Das, Anath Bandhu; Das, Mrinmoyee; Desai, Tanaji S.; Devadasu, Elsinraju; Elchuri, Sailaja V.; **Ghosh, Ashish K. (dates unavailable)**; Gunasekaran, Ganesan; Gupta, Brijesh K.; Jajoo, Anjana; Joshi, Rohit; Kandoi, Deepika; Kaur, Harbans Kehri; Kodru, Sireesa; Komath, Sneh S.; Kumar, Deepak; **Laloraya, Manmohan Manohar (1932-2023**); Leelavathi, Sadhu; Malavath, Tirupathi; Meenatchi, Navaneethan; ***Mohanty, Prasanna K. (1934-2013)***; Mohanty, Sasmita; Misra, Amarendra N.; Murti, Gummadi Sri Ramachandra; Narsimhan, Sushila; Nellaepalli, Sreedhar; Padhi, Barnali; Padhye, Subhash; Pandey, Shiv S.; Pardha-Saradhi, P (Pedisetty); Pareek, Ashwani; Prasad, Sheo Mohan; Prasanna, Santhanam; **Rajarao, Tadimeti (1930-2022)**; Rajwanshi, Ravi; **Ranjan, Shri (1899-1969)**; Rathore, Ray Singh; Reddy, D. Venkata Raghava; Reddy, Vanga S.; Ruhil, Kamal; Sane, Prafullachandra Vishnu (Raj); Sarin, Neera Bhalla; Sasidharan, Rashmi; Shabnam, Nisha (Korea/India); Sharan, Ashutosh; Sharma, Anuradha; Sharmila, Peddisetty; **Singhal, Gauri Shankar (1933-2004)**; Singla-Pareek, Sneh Lata; Soda, Neelam; Soni, Vineet; Sopory, Sudhir K.; Sree, K. Sowjanya; Srivastava, Shyam Lal; Subramanyam, Rajagopal; **Tatake, Vidyadhar Govind (Pandit) (1926-2004)**; Tiwari, Swati; Tripathy, Baishnab Charan; Tyagi, Akhilesh K.; Wungrampha, S. (Graham); Yusuf, Mohd. Aslam

Iran

Haghighi, Behzad; Moghaddam, Atefeh Nemati; Najafpour, Mohammad Mahdi; Tabrizi, Mahmoud Amouzadeh

Israel

Canaani, Ora; Hirschberg, Joseph (Yossi); **Malkin, Shmuel (1934 2017)**; Ohad, Nir; Siderer, Yona; Shimony, Carmela

Japan

Ichimura, Shoji; Inoue, Yorinao; Kambara, Takeshi; Koike, Hiroyuki; **Mimuro, Mamoru (1949-2011**); Minagawa, Jun; Murata, Norio; Ogawa, Teruo; Satoh, Kazuhiko; Satoh, Kimiyuki; Shen, Jian-Ren; Tokutsu, Ryutaro; Tomo, Tatsuya

Korea

Kim, Hyunsook

Mexico

Aguado-Santacruz, Gerardo Armando; Campos, Huitziméngri; Conde-Martínez, Florentino Victor; García-Mendoza, Ernesto; Jimenez-Francisco, Beatrice; Ocampo-Alvarez, Héctor; Padilla-Chacón, Daniel; Segura, Antigona; Trejo, Carlos

The Netherlands

Alia, Alia; Amesz, Bas; **Amesz, Jan (1934-2001)**; de Vos, Oscar J.; **Duysens, Louis (Lou) Nico Marie (1921-2015); Goedheer, Joop H. C. (dates unavailable)**; **Hoff, Arnold (1939-2002)**; Naber, J. Dirk; Peters, Wil R.; Pulles, Martinus Petrus Johannes (Tinus); Romijn, Johannes C.; Schansker, Gert; Snel, Jan F. H.; **Thomas, Jan Bartholomeus (B.) (1907-1991)**; van Gorkom, Hans J.; van Grondelle, Rienk; van Rensen, Jack J.S.; Vredenberg, Willem (Wim) J.

New Zealand

Eaton-Rye, Julian J.

Norway

Eichacker, Lutz A.

Poland

Bosa, Karolina; Kalaji Hazem M. "Koœcielniak, Janusz; Robakowski, Piotr; Zuk-Gołaszewska", Krystyna

Russia

Allakhverdiev, Suleyman I.; Biel, Karl Y.; Borisova-Mubarakshina, Maria M.; Kaminskaya, Olga P.; Kotova, Elena A.; Kozlovsky, Vladimir S.; Krasnovsky, Jr. Alexander (Sasha) A.; **Karapetyan, Navik V. (1936–2015)**; Mamedov, Mahir D.; Nadtochenko, Victor A.; Pishchalinikov, Roman Y.; Popov, Vladimir O.; Razjivin, Andrei P.; Riznichenko, Galina Yu; Rodionova, Margarita V.; Rubin, Alexander B.; Semenov, Alexey Yu; Shkuropatov, Anatoliy Ya.; **Shuvalov, Vladimir (Vlad) Anatolievich (1943-2022)**; Tsygankov, Anatoly A.; Vasilieva, Lyudmila G.; Yakovlev, Andrei G.; Yurina, Nadezhda P.; Zharmukhamedov, Sergey K.

The Slovak Republic

Brestič, Marián; Živčák, Marek

Sweden

Björn, Lars-Olof; Dravins, Dainis; Messinger, Johannes; Samuelsson, Göran; Shevela, Dmitry (Dima)

Switzerland

Eggenberg, Peter; Rochaix, Jean-David; Schwarz, Beatrice; Strasser, Bruno; Strasser, Reto Jörg

United Kingdom

Allen, John F.; Baker, Neil R.; **Barber, James (Jim) (1940-2020)**; Brereton, Richard G.; Foyer, Christine H.; Keys, A. J.; Kromdijk, Johannes; Parry, M. A. J.; Rutherford, A. William (Bill); Suggett, David J.; Telfer, Alison

The United States of America

Ananyev, Gennady M.; Anna, Jessica M.; Anton, John A.; Armond, Paul A.; Armstrong, William (Bill) H.; **Arnold, William (Bill) Archibald (1904-2001)**; Auger, Julie; **Babcock, Gerald (Gerry) T. (1946-2000); Baianu, Ion C. (1947-2013)**; Balashov, Sergei; Bannister, Horatio; **Bannister, Thomas Turpin (1930-2018)**; Barry, Howard; Amanda N.Bassham, Helen; Bassham, Susan; Bauer, Carl; **Bazzaz, Maarib Darwish Lutfi Bakri (1940-2020)**; Bedell, Glenn Wesley II; Benning, Christoph; Berg, Howard R.; Berkowitz, Gerald A.; Bernacchi, Carl J.; Berry, Joseph A.; Bhaya, Devaki; **Black, Clanton C. (1931-2011)**; Blair, L. Curt; Blankenship, Robert (Bob) E.; Blubaugh, Danny J.; Bohnert, Hans J.; Bose, Sarojini G. (earlier: G. Sarojini); Boyer, John S.; Brand, Jerry J.; Breidenbach, R. W.; **Briggs, Winslow R. (1928-2019)**; Briskin, Donald (Don) P.; Britt, R. David (Dave); Bryant, Donald (Don) A.; Buchanan, Bob B.; Burnap, Robert (Rob); *Cao, Jiancheng (Jin)*; Carlson, Susan; Castelfranco, Ann M.; Castelfranco, John; ***Cederstrand, Carl Nelson (1927-2022)*** ; Cederstrand, Laura; Cellarius, Richard; Chen, Yi-Chun; ***Cho, Frederick (Fred) Yi-Tung (1939-2011)***; Choules, Lucinda; **Clegg, Robert M. (1945–2012)**; Cohen, Martin; *Coleman, William (Bill) Joseph*; Cooley, Jason; Cooney, Robert; Cramer, William (Bill) A.; Crespi, Henry L.; Crisp, David; Crofts, Antony (Tony) R.; Daniell, Henry;

Debrunner, Peter G.; deSturler, Eric; **DeVault, Don Charles (1915-1990)**; Diner, Bruce; Dismukes, Charles (Chuck); Docampo, Roberto; Downie, Stephen (Steve) R.; Dutcher, Susan; Ebrey, Thomas G.; Edwards, Gerald (Gerry) E.; Fenton, James (Jim); FitzSimons, Toby; Fleischman, Darrel; **Fork, David (Dave) C. (1929-2020)**; Frenkel, Susan; Friedland, Natalia; Fromme, Petra; **Gest, Howard (1922-2012)**; Gilmore, Adam M.; Gisriel, Christopher; Gohlke, Christoph; Goldstein, Cindy S.; Govindjee (Varma), Rajni; Grantz, David; Gratton, Enrico; Greenbaum, Elias; Greenfield, Scot R.; **Gross, Elizabeth (Liz) Louise (1941-2007)**; Grossman, Arthur (Art) R.; **Gutowsky, Herbert (Herb) Sander (1919-2000)**; Hagar, William; Halls, Steven C.; Hammond, Jack H.; Hartman, S. R.; Hazlett, Theodore L.; Hendrickson, David N.; Herbert, Steven (Steve) K.; Hill, Jane F.; Hirsch, Rhoda Eleson; Hoch, George; Holtz, Barry; Homann, Peter; Hou, Harvey J. M.; Hutchison, Ronald (Ron) S.; Imasheva, Ella; Jacobsen-Mispagel, Karen; Johnson, Douglas G.; Jordan, Douglas (Doug); *Jursinic, Paul Andrew*; **Kamen, Martin D. (1913–2002)**; Kaufmann, Kenneth (Ken); Kerfeld, Cheryl A.; Kern, Jan F.; *Khanna, Rita*; Kiang, Nancy Y.; **Knaff, David (1941-2016)**; Knox, Robert (Bob) S.; Kolling, Derrick R. J.; Kolossov, Vladimir; Kono, Masahiro; Kramer, David (Dave) M.; *Krey, Anne*; **Krogmann, David W. (1931-2016)**; Kumar, Anil; Kumar, Dhirendra; Latimer, Margaret Gwyn; Lauterbur, M. Elise; Laws, Edward (Ed); Li, Hong; Liang, Jie; Liu, Suyi; Lindsey, Jonathan; Loach, Paul A.; Long, Stephen (Steve) P.; Lorimer, George; Malkin, Richard (Dick); Malnoë, Alizée; Marchesini, Norma; Markley, John L.; Marks, Steve B.; Mattoo, Autar; Mauzerall, Denise; Mauzerall, Michele; Mayne, Leland; McCain, Douglas C.; Meadows, Victoria S.; Melis, Anastasios (Tasso); Merkelo, Henri; Misra, Saurav; Moore, Gary; Mullet, John E.; *Munday, John Clingman Jr.*; Murty, Neti R.; Musick, Jason; Naithani, Sushma; Nakatani, Herbert (Herb) Y.; Negi, Sangeeta; Nonomura, Arthur M.; Norsworthy, Jason K.; O'Neil, Michael P.; Ogren, William (Bill) L.; Oosterhuis, Derrick M.; Orr, Larry; Ort, Donald (Don) R.; Owens, Olga v. H.; Padden, Sean; Pakrasi, Himadri; Paolillo, Dominick; Park, David S.; Parson, William (Bill) W.; Patil, Saya C.; Pattanayak, Gopal K.; Pellin, Michael (Mike) J.; Perrine, Zoee; Portis, Archie R. Jr.; Preston, Christopher; **Prezelin, Barbara Berntsen (1948-2021)**; Prince, Roger C.; Punnett, Hope; Punnett, Laura; **Rabinowitch, Evgenii (Eugene) I. (Isaakovich) (1898-1973)**; Rajan, Srinivasan; Ramundo, Silvia; **Rebeiz, Constantin (Tino) Rebeiz (1936-2019)**; Rebeiz, Mark; Redding, Kevin; Rich, Marvin; Roberts, Trenton L.; Robinson, Howie D.; Roffey, Robin A.; Rogers, Suzanne Marguerite Dethier; Rose, Stuart; Royer, Catherine (Cathy); Ruiz, Felix A.; Rupassara, S. Indumati (Indu) S.; Saphon, Sathom; Saroussi, Shai; Savikhin, Sergei; Sawhney, Brij; Sayre, Richard (Dick) T.; Schideman, Lance C.; Schmidt, Paul G.; Scholes, Gregory D.; *Schooley, Ralph*; Seibert, Michael (Mike); Selig, Ted C.; Sener, Melih; Seufferheld, Manfredo J.; Sharkey, Thomas (Tom) D.; Sherman, Louis (Lou) A.; *Shim, Hyunsuk*; Shinkarev, Vladimir (Vlad) P.; Shopes, Robert (Bob) J.; Siefert, Janet; Singh, Abhay; Smith, Kevin M.; Smith, William (Bill) R. Jr.; Somerville, Christopher (Chris) Roland; Spalding, Martin (Marty) H.; Spector, Marc; **Spencer, Jobie C. (1931-2015)**; *Spilotro, Paul J.*; Srivastava, Alaka; Srivastava, Nupur; Stacy, William (Bill) T.; **Steinback, Katherine (Kit) E. (1956-1996)**; *Stemler, Alan (Al) James*; Stirbet, Alexandrina (Sandra); Subramaniam, Shankar; Summons, Roger E.; Svensson, Bengt D.; **Sweeney, Eleanor Beatrice Marcy (Beazy) (1914-1989)**; Swenberg, Charles E.; Tan, JingLu; Taoka, Shinichi; Thorhaug, Anitra; **Thornber, James Philip (Phil) (1934-1996)**; Tinetti, Giovanna; Toon, Stephen; Tyagi, Vijai; Vacquier, Victor; Van de Ven, Martin; *VanderMeulen, David (Dave) Lee*; *Vermaas, Willem (Wim) Frederik Johan*; Vinyard, David J.; Wang, Qing Jun (Polly); Warden, Joseph (Joe); Wasielewski, Micheal (Mike) R.; Weidemann, Alan; Whitmarsh, C. John; Widholm, Jack M.; Wiederrecht, Gary P.; Winget, G. Douglas (Doug); *Wong, Daniel (Danny)*; **Wraight, Colin Allen (1945-2014)**; ***Wydrzynski, Thomas (Tom) John (1947-2018)***; *Xiong, Jin; Yang [Ni], Louisa*; Yerkes, Christine (Chris) T.; Yoo, Hyungshim; Zhou, Yan; *Zilinskas, Barbara Ann*; Zumbulyadis, Nicholas (Nick)

APPENDIX 2

A List of Some of the Articles/Interviews Related to Govindjee - Who Turned 92 on October 24, 2024

(see also Wikipedia: https://en.wikipedia.org/wiki/Govindjee)

Block JE (2022) Life of Govindjee, known as Mister Photosynthesis. Journal of Plant Science Research 38(1):1–22.

Eaton-Rye JJ (2007a) Celebrating Govindjee's 50 years in photosynthesis research and his 75th birthday. Photosynthesis Research 93:1–15. https://doi.org/10.1007/s11120-007-9217-6

Eaton-Rye JJ (2007b) Snapshots of the Govindjee lab from the late 1960s to the late 1990s and beyond. Photosynthesis Research 94:153–178. https://doi.org/10.1007/s11120-007-9275-9

Eaton-Rye JJ (2013) Govindjee at 80: more than 50 years of free energy for photosynthesis. Photosynthesis Research 116:111–144. https://doi.org/10.1007/s11120-013-9921-3

Eaton-Rye JJ (2018a) Govindjee – a lifetime in photosynthesis. Photosynthesis Research 122:121–158.

Eaton-Rye JJ (2018b) Foreword to a special issue, celebrating Govindjee's 85th birthday. Photosynthetica 56:1–10.

Jajoo A, Guruprasad KN, Bharti S, Mohanty P (2009) International conference "Photosynthesis in the Global Perspective" held in honor of Govindjee, November 27–29, 2008, Indore, India. Photosynthesis Research 100:49–55. https://doi.org/10.1007/s11120-009-9409-3

Kumar A, Nonomura A (2023) Govindjee, who revealed the secrets of photosynthesis and inspired five generations of explorers. LS - An International Journal of Life Sciences 12:141–150. DOI: 10.5958/2319-1198.2023.00014.3 (Translation from Hindi to English of an interview article by M. Jain, published in "Science India," in June 2019, on pp 14–24.)

Kumar V (2020) Wings to a Child's Dream: A Tribute to Govindjee. Invincible Publishers, Gurgaon, India; 46 pages; ISBN: 978-93-89600-66-7

Kutschera U, Khanna R (2023) Why teaching evolution and photosynthesis is imperative for an understanding of the living world. IJISET - International Journal of Innovative Science, Engineering & Technology 10:1–4.

Lichtenthaler H, Kumar A, Mohan PS, Nonomura A (2022) Single-authored work of Govindjee, Mister Photosynthesis. International Journal of Life Sciences 11(3):176–184. https://doi.org/10.5958/2319-1198.2022.00016.1

Mohapatra PK, Swain BB, Mishra S (2023) Govindjee: One of the major architects for the conceptual evolution of the Z-scheme of photosynthesis. IJLS - An International Journal of Life Sciences 12:21–43. https://doi.org/10.5958/2319-1198.2023.00003.

Naithani S, Stirbet A, Shevela D, Pareek A, Björn LO, Eaton-Rye JJ, Nonomura A (2022) Govindjee's 90th birthday - Congratulations from friends and colleagues. Current Plant Biology 32:100263. https://doi.org/10.1016/j.cpb.2022.100263

Nonomura A and Kumar A (2022) Celebrating the 2022 Lifetime Achievement Award of the International Society of Photosynthesis Research to Govindjee, who hails from Allahabad. International Journal of Life Sciences 11:153–155. https://doi.org/10.5958/2319-1198.2022.00014.8

Ort DR (2011) An interview with Govindjee. Annual Reviews Inc. Conversations; 11 pages; <www.annualreviews.org>; <https://www.youtube.com/watch?v=cOzuL0vxEi0>

Ort DR, Chinnusamy V, Pareek A (2022) Photosynthesis: diving deep into the process in the era of climate change. Plant Physiology Reports 27:539–542. https://doi.org/10.1007/s40502-022-00703-7

Prasil O (2014) Govindjee, an institution, at his 80th (really 81st) birthday in Trebon in October 2013: a pictorial essay. Photosynthesis Research 122:113–119. https://doi.org/10.1007/s11120-014-9972-0

Rajya Sabha (Upper House of India) TV Eureka: A presentation and an interview with Govindjee <https://www.youtube.com/watch?v=OBKusHc-jMzw>

Seibert M, Mattoo A, Kumar A (2022) A Special Toast to Govindjee on Celebrating his 90th Birthday on October 24, 2022. International Journal of Life Sciences 11:156–175. https://doi.org/10.5958/2319-1198.2022.00015.X

Sen A (2019) Govindjee, a pioneer in photosynthesis <https://mcb.illinois.edu/news/article/512/>

Sharma NK (2023) Govindjee (born 24 October 1932): India's Gift to the Photosynthetic Community. In: "Descendants of Kanada: Life Sketches of Some Indian Scientists" (S. P. M. Tripathi, N. K. Sharma, V. Paramanik, and V. P. Singh, eds.), published on India's Independence Day (August 15), Indira Gandhi National Tribal University & Scientific Publishers, Jodhpur & New Delhi, pp. 199–218; ISBN: 978-81-962465-1-8 (H/B).

Sharma R (2016) Govindjee and Rajni Govindjee – Confluence of photosynthesis and photobiology. <https://www.linkedin.com/pulse/govindjee-rajni-confluence-photosynthesis-dr-ravi-sharma>

Stirbet A, Naithani S, Shevela D, Björn LO, Eaton-Rye JJ, Nonomura A (2023) On the Reactions in Oxygenic Photosynthesis as Related to the Z-scheme: Contributions by Govindjee. LS - An International Journal of Life Sciences 12(3):151–185. https://doi.org/10.5958/2319-1198.2023.00015.5

Stirbet A, Shevela D, Pareek A, Naithani S, Björn LO, Eaton-Rye JJ, Nonomura A (2022) Govindjee's 90th birthday: a life dedicated to photosynthesis. Plant Physiology Reports 27:543–557. https://doi.org/10.1007/s40502-022-00690-9

Swain BB, Mishra S, Mohapatra PK (2023) Fifty Years of Research on the "Bicarbonate Effect" in Photosystem II: A Mini-Review. LS - An International Journal of Life Sciences 12:115–140. https://doi.org/10.5958/2319-1198.2023.00013.1.

UIUC News article, 2009: An absorbing interest (of) Govindjee: <https://las.illinois.edu/news/2009-10-01/absorbing-interest>

Veena M, Sameena PP, Sarath NG, Noble L, Raj Aswathi KP, Amritha MS, Johnson R, Joel JM, Anjitha KS, Hou HJM, Puthur JT (2023) Revelations on Photosystem II, thermoluminescence, and artificial photosynthesis: A retrospective of Govindjee from fundamentals to applications. Physiology and Molecular Biology of Plants 29:1225–1238. https://doi.org/10.1007/s12298-023-01373-x

Yates D (2019) Govindjee's photosynthesis museum. <https://news.illinois.edu/view/6367/801235>

APPENDIX 3

Messages to Govindjee for his 92nd Birthday

1. President Tim Killeen (donorrelations@uif.uillinois.edu)

Date: October 1, 2024 at 11:01:57/ AM CDT

To: gov@life.illinois.edu

Subject: Happy Birthday, Govindjee! Reply-To: President Tim Killeen <inbox.uif.uillinois.edu@parse.gratavid.com>

Dear Govindjee,

Your birthday is just around the corner, and I wanted to be the first to celebrate! As a President's Council member, you enable numerous areas across our three campuses to foster and grow, allow students to prosper in their fields, and create a new generation of leaders and innovators. I am grateful for your dedication. Happy birthday! Warm regards, Tim Killeen

2. Mauro Martínez (maurom2@illinois.edu)

When I decided to do my Bachelor's degree under Dr. Gastón Quero in Uruguay, he told me, "You may start reading an article (https://doi.org/10.1093/aob/mcz171) by Govindjee (Stirbet et al. 2020a)." As everything was new for me, I asked, "Who is Govindjee?" To that, he responded, "His research is like the 'Bible of

Photosynthesis'; you need to understand the Z-scheme to comprehend our work, and that paper explains the basis very well." After that, Govindjee's work was a constant in the equation of my progress towards my Bachelor's degree. On August 30, 2024, when I had just walked out of the National Soybean Research Center building on the University of Illinois at Urbana-Champaign (UIUC) campus, where I am now a graduate student under Dr. Eliana Monteverde in the Department of Crop Sciences, I saw someone who looked like Professor Govindjee (based on a photo I had seen before). Thus, I waved my hand and politely but excitedly asked, "Are you Govindjee?" He responded, "Yes, I am." I then told him, "I was looking forward to meeting you, and thus, it is so nice that I ran into you today." I gave him my name. It was indeed a coincidence and a great pleasure for me. I then took the photo of the two of us on my phone and sent it to him by e-mail (see Figure 14) with a note: "I'm attaching the photo I took yesterday and thanking you again for the encounter and your good spirit." Govindjee also appreciated this wonderful,

Figure 14: A photograph of Govindjee and Mauro Martínez in Urbana in September 2024. *Source:* M. Martínez

unexpected, and pleasant encounter and thanked me for this photo. He also wished me the best for my research at UIUC.

My heartfelt best wishes to Govindjee on his upcoming 92nd birthday on October 24, 2024!

3. Ashwani Kumar (ashwanikumar214@gmail.com)

My visit to Govindjee's lab and the stay at his home in Urbana are my most memorable experiences with him. He discussed with me the role of CO2 in the Z-scheme and showed me his library. He also visited my son's house in Arlington, Chicago, USA. My father, Professor S. D. Tewari, did his MSc in Botany in 1946 at Allahabad University, where Govindjee also completed his studies. I had the chance to meet Govindjee for the first time in the 1980s in Rhode Island at a photosynthesis conference where I went with my teacher, the late Professor Dr. K. H. Neumann. I also met Govindjee again some years ago in India at the International Conference in Hyderabad. He is a great innovator in science and a great human being who treats everyone with love and affection, which is why he is called Mr. Photosynthesis. His students are all over the world. I must mention that his wife, Dr. Rajni Govindjee (Rajni Ji to me), also cares for all and especially receives the guests of Govindjee very well. I wish him a long life and that I am still expecting to publish some articles written by him and about him.

4. Alexandrina Stirbet (sstirbet@gmail.com)

I met Govindjee in the 1990s in the laboratory of Reto Strasser in Jussi-Lullier, near Geneva (Switzerland). At that time, we published together a mathematical model of the OJIP fluorescence transient (see Stirbet et al. 1998). However, I moved to the USA in 2000, and we restarted our collaboration much later, in 2011. We first wrote a review on the JIP-test and its use in the study of photosynthesis (Stirbet and Govindjee 2011), which is a theoretical approach for the analysis of the OJIP transients that was proposed by Reto Strasser and popularized by him all over the world (see e.g., Strasser et al., 2004; and a tribute to Strasser at his 75th birthday by Govindjee et al. 2019). Since then, over the years, we have co-authored over 20 papers together, the majority related to modeling in photosynthesis and diverse Chl fluorescence studies or reviews. From my experience during our work together, Govindjee is indeed a great scientist, mentor, and friend who knows how to enhance in his partners and students the passion for the study of photosynthesis and the aspiration for perfection in scientific work, which makes him truly special and an inspiration for all. On the occasion of his 92nd birthday, I wish him many more years full of satisfaction and good health!

5. Dušan Lazár (dusan.lazar@upol.cz)

I did not perform any experiments with Govindjee, but my first experience with him dates back to the final stages of my PhD studies when I submitted a review paper to Biochimica et Biophysica Acta on chlorophyll fluorescence induction (published in 1999). Govindjee was then one of the reviewers of the manuscript, and he had declared his identity. After that, Govindjee was also a reviewer for some other papers that I coauthored. Only around 2017, I started cooperating with Govindjee, Sandra Stirbet, and other coauthors on several reviews, mostly on chlorophyll fluorescence and theoretical approaches to studying photosynthesis. From my experience with him, I know Govindjee as a bright, accurate, and enthusiastic scientist, who also supports alternative views on a problem. For the next years, I wish him a lot of good health and joy from doing research on photosynthesis and writing papers on history and biography!

6. Ya (David) Guo (guoy@jiangnan.edu.cn)

I am very lucky to know Professor Govindjee and get his help in my research. In my opinion, Professor Govindjee has always been so efficient in work, including replying to emails. He has made outstanding contributions to the research of photosynthesis and the education of young scholars, setting a lofty example for us. In 2018, I invited him to attend an academic conference in Hefei, China. During that period, he caught a severe cold and his throat was hoarse. I suggested he go to his room to have a rest, but he replied that he should respect his table card and insisted on staying until the meeting was over. We have collaborated with Professor Govindjee on a lot of studies. In the process of guiding our research and writing, he has never missed any details, including references. We even used special software to manage references automatically, which, however, inevitably led to some small errors. Govindjee was very firm in his position. He told us that references must be completely correct; otherwise, the wrong information will be spread and expanded in the academic community. Govindjee is a legend, and I often mention him in my lectures to the students (see Figure 15 for a photograph of the two of us). I wish Professor Govindjee a happy birthday and good health!

Figure 15: Ya (David) Guo and Govindjee visiting Lingshan Mountain, Wuxi City, Jiangsu Province, China (photo taken in November 2018). *Source:* David Guo.

7. Julian Eaton-Rye (julian.eaton-rye@otago.ac.nz)

Dear Gov,

Best wishes for your 92nd birthday. We met in August 1981 when I arrived in the lab to start my PhD. You went out of your way to help me find an apartment and I remember many talks in your office as you explained the basics of the light reactions to me. Your ability to explain photosynthesis to beginners and to help so many with their writing skills, alongside your connections, collaborations, and friendships with so many scientists at all stages in their careers, is remarkable. Your energy in your retirement is inspirational. May every day continue to bring you energy from the sun for your ongoing photosynthesis contributions that are appreciated by so many.

--- Julian

DECLARATIONS

Conflict of interest. The authors declare no conflict of interest.

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