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REVIEW ARTICLE

Celebrating the contributions of Govindjee after his retirement: 1999–2020

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ABSTRACT

Govindjee, Professor Emeritus of Biochemistry, Biophysics and Plant Biology at the University of Illinois at Urbana-Champaign since 1999, is renowned for his pioneering work in the light reactions of photosynthesis and important accomplishments as educator, editor, historian and advocate of photosynthesis. In his honour, we review his contributions over the last twenty years, which were often achieved in collaboration with scientists working in laboratories around the world. We start with a short presentation about Govindjee's career and continue with a section highlighting his passion and dedication to teach the younger generations of students and researchers about photosynthesis. His research work is grouped under different areas, including primary photochemistry; the relationship of chlorophyll *a* fluorescence to photosynthesis; short time-scale regulation processes of photosynthesis; studies toward improving photosynthesis and biomass yields; and, mathematical modelling of photosynthesis and artificial photosynthesis. He is best known for the discovery of the key role of bicarbonate on the electron acceptor side of Photosystem II. We also present his active involvement in the recognition of scientists at conferences and beyond, as well as of those who are no longer with us. He is committed to keeping alive the pioneers and discoverers in the field of photosynthesis in the collective memory of those in the field.

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I hunt for the golden stag.
You may smile, my friends, but I
pursue the vision that eludes me.
I run across hills and dales, I wander
through nameless lands, because I am
hunting for the golden stag …

Rabindranath Tagore (1861–1941). The Gardener LXIX: 'I hunt for the golden stag', available at https://www.inspirationalstories.com/poems/the-gardener-lxix-i-hunt-for-the-golden-stag-rabindranath-tagore-poems/

Introduction

Govindjee is a distinguished and charismatic figure in the photosynthesis community (see Figure 1). He is admired for scientific achievements in deciphering important aspects of the light reactions of photosynthesis, and outstanding promotion of this field of research. For his important contributions in photosynthesis research and education, he has received many honours and awards over the years. In 2007, he received the Lifetime Achievement Award from the Rebeiz Foundation for Basic Research at the University of Illinois at Urbana-Champaign (UIUC), and the prestigious Communication Award of the International Society of Photosynthesis Research, at the 14th International Congress of

Figure 1. A, A photograph of Govindjee and a huge leaf doing photosynthesis, on the Andaman Islands, 2016. **B**, Govindjee with Rajni Govindjee, at a party in Chicago, Illinois, in the 1990s. **C**, Govindjee drinking tea in Shanghai, China, 2003. Source: Archives of Rajni Govindjee.

Photosynthesis Research, held in Glasgow, UK. Further, Govindjee received the 2008 LAS (Liberal Arts and Sciences) alumni achievement award from UIUC, followed by the Prof. B.M. Johri Memorial Award of the Society of Plant Research in 2016, and the Foreign Fellow Award of the National Academy of Agricultural Sciences in 2018, both in New Delhi, India. In addition, two special issues of Photosynthesis Research, in 2007 and 2013, and a special issue of Photosynthetica in 2018, were published to pay tribute to Govindjee and his contributions. Moreover, he was honoured on his 75th birthday at an International Symposium in 2008 at Indore, India (Jajoo et al. 2009), and his 85th birthday at the International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability in 2017 at Hyderabad, India (Allakhverdiev et al. 2019).

Govindjee was born in India, on October 24, 1932, at Allahabad, Uttar Pradesh, to Savitri Devi and Vishveshwar Prasad. He studied at the University of Allahabad, receiving his BSc in Chemistry, Botany and Zoology in 1952, and MSc in Botany (Plant Physiology) in 1954. In 1956, he went to the USA and studied at UIUC for a doctorate in Physico-Chemical Biology under Robert Emerson (1903–1959), the discoverer of the *Red Drop* phenomenon (Emerson and Lewis 1943), and the *Enhancement* effect (Emerson et al. 1957), which led to the concept of two light reactions and two pigment systems in photosynthesis. In 1957, Govindjee married Rajni Varma, whom he knew from Allahabad, and who had just arrived at UIUC as a graduate student with Robert Emerson. After the premature death of their professor in 1959, they resumed working with Eugene Rabinowitch (1901–1973), well-known for several important discoveries in physical chemistry (e.g. Franck-Rabinowitch cage effect, published with the 1926 physics Nobel laureate James Franck; Franck and Rabinowitch 1934), and his three-volume description of photosynthesis published sequentially in 1945, 1951, and 1956 (see Govindjee 2004a). In 1960, Govindjee finished his PhD thesis titled: *Effect of combining two wavelengths of light on the photosynthesis of algae*, which he dedicated to the memory of Robert Emerson. In the Acknowledgement, he also thanked Eugene Rabinowitch 'for his guidance, stimulating discussions, encouragement and constructive criticism throughout the course of investigations', and confessed that his enthusiasm for new results 'was the best source of encouragement that he ever received from anyone'.

Afterwards, Govindjee taught at UIUC from 1961 until his retirement in 1999, and during this period advised more than 25 graduate students and many post-doc researchers working in his laboratory. In addition, as Professor Emeritus of Biochemistry, Biophysics and Plant Biology at the University of Illinois, he has continuously presented lectures on photosynthesis at universities in his beloved country, India. This boosts photosynthesis-research activities in India and sends the message to decision makers, both there and elsewhere, that global problems can be successfully tackled by education in every corner of our planet. Moreover, Govindjee has been intensely involved in research activity in association with other researchers (for his publications between 1999 and 2020, see his website http://www.life.illinois.edu/govindjee/recent_papers.html). During the past 20 years Govindjee (Govindjee Govindjee since 2019) has also published many papers relating to the history of photosynthesis (for an earlier edited book, see Govindjee et al. 2005) and has regularly written conference reports that highlight contributions from young researchers entering the field. Indeed, to follow his passion for understanding photosynthesis (his 'golden stag'; see quote by Rabindranath Tagore), Govindjee has collaborated, even after retirement, with hundreds of scientists from almost two dozen countries (see Appendix and Govindjee 2019b).

Over the years the research contributions of Govindjee have been highly significant in the area of light absorption, excitation energy transfer, primary photochemistry and electron transport, especially as related to Photosystem II (PS II; the water-plastoquinone oxido-reductase of photosynthesis), and on the regulation of excitation energy distribution between the two photosystems of the electron transport chain. In particular, Govindjee is best known for his novel, ingenious, and thorough use of chlorophyll (Chl) *a* fluorescence as a powerful, quick and highly sensitive tool for monitoring various steps and processes in photosynthesis - from the time of light absorption (femtoseconds) until carbohydrate formation (seconds to minutes). He is clearly recognised for the discovery that bicarbonate plays a critical role in plastoquinone reduction on the so-called Q_B side of PS II. Without it no photosynthesis is possible! In addition, Govindjee and his outstanding collaborators were the first to measure the time of primary charge separation on a picosecond time scale and provide the theory for the mechanism of thermoluminescence in photosynthetic systems. We refer the readers to wonderful tributes to Govindjee and his work by Eaton-Rye (2007a, 2007b, 2012, 2013, 2018, 2019), Jajoo et al. (2009), Clegg (2012), Papageorgiou (2012), Prášil (2014), and Sharma (2018). In addition, we would recommend Govindjee (2019a) for a summary of his journey and work in his own words. Also, Kumar (2020) wrote an inspirational book on Govindjee, titled: *Wings to a child's dreams*, describing how much he learned from him.

What is remarkable is that while being one of the top scientists in photosynthesis, Govindjee has been an extraordinarily popular and highly effective speaker and teacher, as well as an excellent editor. Probably the greatest hit ever among the books on photosynthesis was his 1982 book (Govindjee1982), which for generations of young researchers has been 'the Bible'. This book, with excellent eye-opening and highly motivating introductions by Govindjee, John Whitmarsh and Colin A. Wraight, and chapters written by the most prominent scientists of the time, was both comprehensive – ranging from biophysics to physiology, and from bacteria to plants - and highlighted the most interesting problems in the early eighties. (For additional edited books on the concepts of photobiology, as they relate to photosynthesis, see Govindjee et al. 1986; Singhal et al. 1999.)

Govindjee worked for the journalPhotosynthesis Research starting in 1983, as Associate Editor, and continued as co-Editor-in-Chief with René Marcelle until 1988 (vol. 15(3); see Govindjee et al. 2002), during which time he increased its quality immensely. He continued to serve the journal until recently as Editor of the Historical Corner. Moreover, Govindjee also founded the well-known series Advances in Photosynthesis and Respiration, including Bioenergy and Related Processes, on which he worked from 1994 to 2017, overseeing the publication of 44 volumes. One of us (G. Garab) had the opportunity to experience his tireless workstyle first hand, while editing a book together (Demmig-Adams et al. 2014), noting that Govindjee paid attention to the smallest detail without losing the broader view, never compromising on clarity and grammar, and having authors explain findings and underlying mechanisms, no matter how complicated. He is demanding, requiring timely responses to questions and requests. In this book, and in the completion of many projects across the years, collaborators felt his personal touch, something special and something more than just the writing on the page.

In this Tribute, we present Govindjee's contributions during the last 20 years under the following headings: (**1**) Teaching and educating the younger generation; (**2**) Excitation energy transfer, primary photochemistry, and the role of bicarbonate in oxygenic photosynthesis; (**3**) Relation of Chl *a* fluorescence to photosynthesis; (**4**) Regulation of photosynthetic processes: state changes, non-photochemical quenching, and more; (**5**) Attempts to augment photosynthesis and biomass; (**6**) Modelling of photosynthesis and artificial photosynthesis; (**7**) Recognition of scientists at conferences and more; and (**8**) Tributes to those no longer with us.

Teaching and educating the younger generation

In addition to his prodigious research and publishing achievements, Govindjee excels in his whole-hearted dedication to teaching younger generations of students and researchers about photosynthesis. Some of his collaborators who helped him in this endeavour are shown in Figure 2 and Supplemental Figures 1–3. Govindjee has outlined his thoughts about teaching photosynthesis (Govindjee 2008b) and dwells on stimulating interest in the following: the history of science; use of analogies, such as students acting as molecules (Jaiswal et al. 2017); use of the internet (the importance of which he emphasised in his symposium talk at the XIth International Congress on Photosynthesis, held in Budapest, in 1998; see also Orr and Govindjee 2013); and of reviews published in journals, books and encyclopedias. He teaches the Z-scheme through educational articles (Govindjee and Björn 2012; Mohapatra and Singh 2015; Govindjee, Shevela, et al. 2017) and posters (Figures 3 and 4). He discusses the historical controversy over the minimum quantum requirement for oxygen evolution (Nickelsen and Govindjee 2011; Hill and Govindjee 2014), natural and artificial water oxidation (Najafpour and Govindjee 2011; Najafpour, Barber, et al. 2012; Najafpour, Tabrizi, et al. 2012; Najafpour, Moghaddam, et al. 2013), and oxygenic photosynthesis in general (Shevela, Björn, et al. 2013; Shevela, Pishchalinikov, et al. 2013). Other important contributions are his reviews/viewpoints on the evolution of photosynthesis (Björn and Govindjee 2007, 2009; Björn, Papageorgiou, Blankenship, et al. 2009; Björn and Govindjee 2015), spectral signatures of photosynthesis on Earth (Kiang, Segura et al. 2007; Kiang, Siefert et al. 2007) and their possible presence and detectability on exoplanets (Björn, Papageorgiou, Dravins, et al. 2009).

Govindjee has been personally involved in all these methods of disseminating knowledge about photosynthesis to students of all ages and there is no other address more useful for those who want to learn about photosynthesis than http://www.life.illinois.edu/govindjee/photoweb/. This is the key to as much knowledge as can be gained, while, in addition, teachers may find useful lesson plans, tips for educational experiments, and videos.

Govindjee has provided invaluable contributions to the history of photosynthesis research, not only through his own papers (e.g. Govindjee and Krogmann 2004; Joliot et al. 2016), but by inviting many others to write about research carried out by themselves, their colleagues, or those who left us long ago. The 2002 lists in Govindjee and Krogmann (2002) are valuable resources for historians looking for personal perspectives, commented quotations, historical papers, Nobel prizes, and Charles F. Kettering awards. He has followed these up with many more biographies and tributes (see e.g. Govindjee

Figure 2. Photographs of Govindjee at scientific conferences in Sweden, the USA, Russia and India. **A**, Govindjee with Johannes Messinger in Uppsala, Sweden, at the first European Congress on Photosynthesis, 2018. **B**, Govindjee (in the centre); others include Divya Kaur (extreme left), Robert Blankenship (extreme right) and Junko Yano (holding her badge), at the Gordon Research Conference, 2019. **C**, Govindjee with Mahdi Najafpour (extreme right) and Mahya Salmanion at the International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability, 2019, held in Saint Petersburg, Russia. **D**, Govindjee with Dmitry Shevela (extreme left), and Lutz Eichacker in Uppsala, Sweden, at the first European Congress on Photosynthesis, 2018. **E**, Left to right: Rajni Govindjee; T.T. Dhanya Thomas; P. Faseela (with a child in her lap); P. Pravisya; and A.M. Shackira; and Govindjee Govindjee, at the 8th International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability, University of Hyderabad, 2017. Note that the Z-Scheme poster, designed by D. Shevela, L.O. Bjorn and Govindjee, and printed by Brandt iHammer (courtesy of Arthur Nonomura), is being displayed. Source: Archives of Rajni Govindjee, except for Figure 2E, which was provided by Shreya and A.M. Shackira.

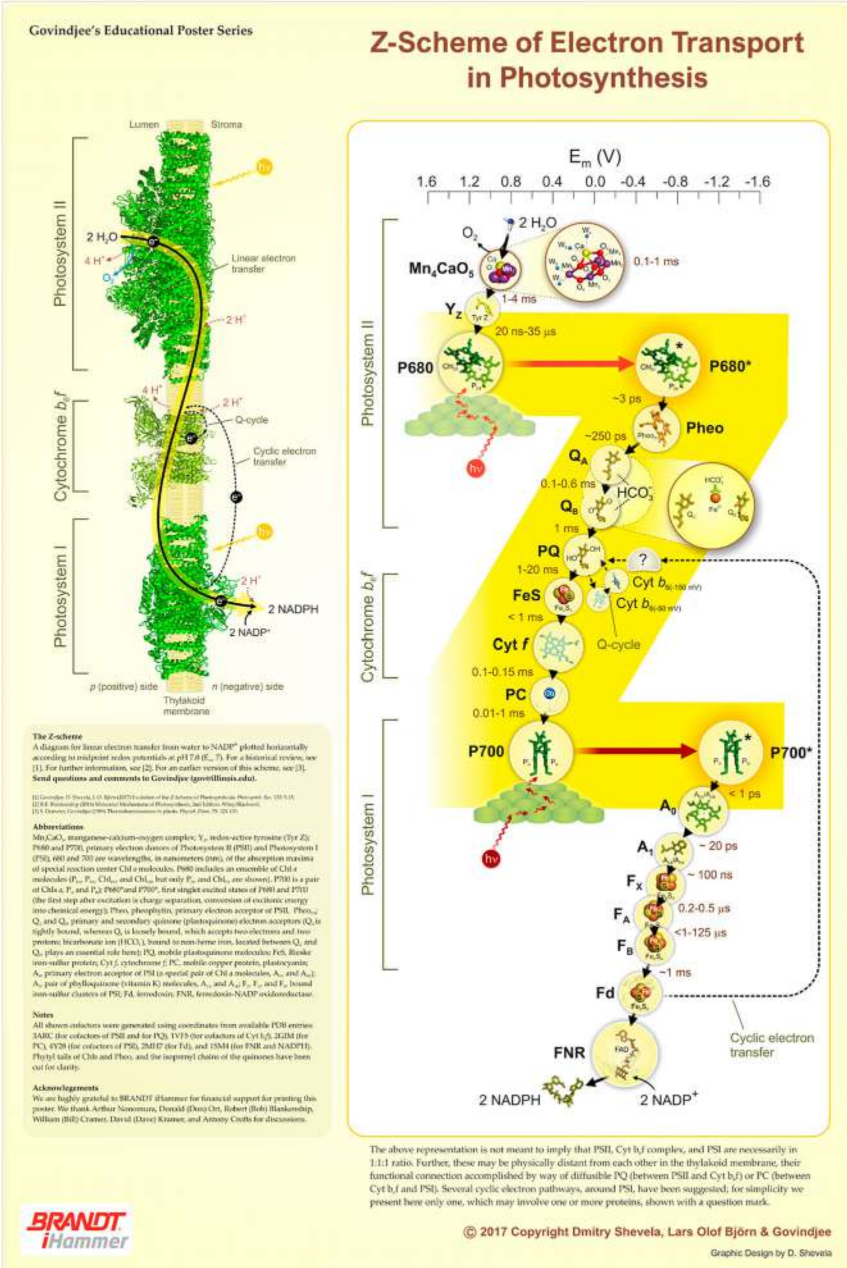

Figure 3. The Z-scheme poster of photosynthetic electron transport designed by Dmitry Shevela, Lars Olof Björn and Govindjee. The major abbreviations are: Mn_4CaO_5, manganese-calcium-oxygen complex; Y_Z, redox-active tyrosine; P680 and P700, primary electron donors of Photosystem II (PS II) and Photosystem I (PS I); P680* and P700*, first singlet excited states of P680 and P700; Pheo, pheophytin, primary electron acceptor of PS II; Q_A and Q_B, primary and secondary plastoquinone electron acceptors; HCO_3^-, the bicarbonate ion bound to the non-heme iron of PS II responsible for the *bicarbonate effect* established by the Govindjee laboratory; PQ, mobile plastoquinone molecules; FeS, Rieske iron-sulfur protein; Cyt *f*, cytochrome *f*; PC, mobile copper protein, plastocyanin; A_O, primary electron acceptor of PS I; A_1, phylloquinone (vitamin K); F_X, F_A and F_B, bound iron-sulfur clusters of PS I; Fd, ferredoxin; FNR, ferredoxin-NADP oxidoreductase. *Additional details can be viewed by magnifying the online version of the figure. Also, see Govindjee (2019a) and* Govindjee, Shevela, et al. (2017).

Figure 4. A collage of the educational posters on different aspects of photosynthesis that have been produced under the supervision of Govindjee. Further details, and instructions on how to download specific posters, are provided in the text. Also see: http://www.life.illinois.edu/govindjee/

and Pulles 2016; Allakhverdiev et al. 2018; Conlan et al. 2019; Govindjee and Messinger 2019), as well as recognitions of many emerging and established scientists and his many collaborators (see e.g. Govindjee 2009b, 2019b; Allakhverdiev et al. 2013, 2016; Govindjee, Srivastava, et al. 2019; Govindjee, Briskin, et al. 2020).

As for encyclopedias, during his retirement Govindjee has contributed to the tenth edition of The Encyclopedia of Science and Technology, McGraw Hill, with entries on chlorophyll (Govindjee, Porra, et al. 2007), bacterial photosynthesis (Govindjee, Blankenship, et al. 2007), carbon dioxide fixation (Berkowitz et al. 2007), and photosynthesis in general (Blankenship and Govindjee 2007). He also contributed with an article about PS II in Wiley's Encyclopedia of Life Sciences in 2001 and 2010 (Govindjee et al. 2010). His focus on the essential is demonstrated in a book chapter that provides an overview of all aspects of photosynthesis (Govindjee 2000).

As a young scientist, Govindjee had cooperated with Eugene Rabinowitch in the writing of a small textbook about photosynthesis (Rabinowitch and Govindjee 1969), which is freely available online (http://www.life.illinois.edu/govindjee/photosynBook.html). Half a century later, Govindjee remains active in writing overviews and books (see e.g. Shevela et al. 2019).

In his memoirs (Govindjee 2019a), Govindjee describes how he became fascinated at an early age by the fluorescence of photosynthetic organisms and its variations. Research on Chl *a* fluorescence is covered in a related section below. Here we reference an introduction to a special journal issue (Govindjee and Nedbal 2000), and two books (Papageorgiou and Govindjee 2004; Demmig-Adams et al. 2014), which provide an overview of this very complicated and fascinating subject.

During the 20 years since his retirement, Govindjee has been active in reviewing various aspects of photosynthesis – from regulation of photosynthetic light harvesting by different ions (Kaňa and Govindjee 2016) to plant phenotyping (Mishra et al. 2016). In one of his reviews, a description of his personal scientific adventure with the extremely successful oxygenic photosynthesizers living on Earth (cyanobacteria) is combined with factual information about adventures of many other past and current researchers in the field (Govindjee and Shevela 2011). Moreover, Govindjee was one of the editors of the books about abiotic stress adaptation in plants (Pareek et al. 2010) and mathematical modelling for understanding photosynthesis processes from molecular to ecosystem levels (Laisk et al. 2009), and he has contributed to two editions of a book on general photobiology (Björn and Govindjee 2007, 2015).

Govindjee was one of the editors of special educational issues in the journal Photosynthesis Research, which addressed the basics and application of biophysical methods (Messinger et al. 2009a, 2009b). As noted above, he has also been involved in the production of several educational posters (Figures 3 and 4). Printed posters have been distributed freely at most international plant science and photosynthesis conferences and meetings, and they are available online. Electronic versions of the Agrisera Educational Poster Collection, which consists of posters on Oxygenic Photosynthesis (2016), Vertical Z-Scheme (2018) (Figure 3), Photosynthesis and Respiration (2019) and Rubisco (2020), may be accessed at https://www.agrisera.com/en/info/educational-posters.html. Govindjee's Educational Poster Series (freely distributed as hard copies by Brandt iHammer, Powell, OH, USA), including the Horizontal Z-Scheme with Protein Complexes (2017) and A Plant Growth Regulator for Photosynthesis (2020), are available at http://www.life.illinois.edu/govindjee/. The original Z-Scheme Poster produced in 2010 is available on Govindjee's webpage (http://www.life.illinois.edu/govindjee/2010_z-scheme.pdf).

Excitation energy transfer, primary photochemistry, and the role of bicarbonate in oxygenic photosynthesis

Since the 1970s Govindjee and coworkers have been studying absorption of light, excitation energy transfer, primary photochemistry and electron transport. As an Emeritus Professor, Govindjee, in collaboration with his colleagues from other labs, has summed up this field in a number of excellent overviews.

In 2010, Govindjee and coworkers described the historical development of the concepts of the photosynthetic unit and energy transfer (Clegg et al. 2010). Interestingly, they pointed out that the Förster theory (Förster 1946) was preceded by an abstract by Robert Oppenheimer ('the father of the atomic bomb') (Oppenheimer 1941) stating that efficient energy transfer cannot take place by absorption of fluorescence, but rather by resonance transfer, and that a Chl *a* molecule located in the centre of a cavity of diameter '*d*' receives energy from a surrounding excited pigment distribution of density '*n*' with a rate proportional to nd^{-3}, which is in agreement with the Förster theory.Because of his leading role in the construction of the first nuclear bombs, Oppenheimer could not return to the topic until after the Second World War (Arnold and Oppenheimer 1950).

A pedagogical outline of the physical basis of photophysical processes involved in photosynthesis has been published by Govindjee and his co-workers in a book chapter in 2014 (Ostroumov et al. 2014). The authors also state that the primary photosynthetic processes must be very fast, since the excitation energy transfer must be faster than the rate at which the excited-state of Chl decays *via* fluorescence or nonradiative decay, in order for the excitation energy to reach the reaction centre, rather than be lost. In a review with Gregory Scholes and his group (Mirkovic et al. 2017) Govindjee discusses the photophysical principles by which excitation energy is absorbed by photopigments and describes mechanisms of electronic excitation energy transfer in general, as well as optical properties of various light-harvesting antenna complexes. Both are at the level of individual pigment chromophores and of collective pigment-pigment/pigment–protein interactions (for a photograph of Govindjee with Rienk van Grondelle, see Supplemental Figure 1A). Along with other aspects of light absorption and energy transfer, this highly-cited article provides an overview of the excitation energy pathways in the light-harvesting antennas of different photosynthetic organisms. Furthermore, together with Mamedov and others in Moscow (Mamedov et al. 2015), Govindjee included a discussion of the controversial subject of the formation of primary and secondary ion–radical pairs within PS II and PS I in oxygenic organisms.

Another field in photosynthesis research that Govindjee could not leave after his retirement was the *bicarbonate effect* in PS II. Govindjee and his co-workers had been heavily involved in this topic since the 1970s (Stemler and Govindjee 1973; Stemler et al. 1974; Govindjee and Van Rensen 1978, 1993; Eaton-Rye and Govindjee 1984, 1988a, 1988b; Blubaugh and Govindjee 1986; Govindjee et al. 1997; Xiong et al. 1998). In a 1988 visit to Szeged (Hungary), Govindjee undertook thermoluminescence experiments on leaves, which provided firm evidence that CO_2 (HCO_3^-) *in vivo* facilitates the flow of electrons from Q_A^- (the first plastoquinone acceptor of PS II) to Q_B (the second plastoquinione acceptor of PS II) and thereafter the electrons continue to flow to PS I (Garab et al. 1988). Govindjee was unable to perform experimental work himself after his retirement, but he has actively motivated many research groups to continue investigations on the role of bicarbonate in PS II. His constant reminder '**do not forget about bicarbonate**' was heard by many and active research on this topic has continued in other labs around the world (Van Rensen and Klimov 2005; Shevela et al. 2007; Ulas et al. 2008; Rose et al. 2008; Shevela, Noring, et al. 2013; Koroidov et al. 2014; Brinkert et al. 2016; Ananyev et al. 2018; Banerjee et al. 2019; Forsman et al. 2019, 2020; Forsman and Eaton-Rye 2020). On the other hand, Govindjee continued his own contributions to the bicarbonate field with historical reviews, which contain his current thoughts about the key regulatory role of bicarbonate in oxygenic photosynthesis and in the evolutionary development of O_2-evolving PS II (Govindjee and Shevela 2011; Shevela et al. 2012). Interestingly, Govindjee saw to it that the HCO_3^- ion on the electron-acceptor side on PS II became a firm part of all the latest Z-Scheme versions (e.g. Figure 3). This HCO_3^- has been shown to facilitate the protonation of the reduced Q_B, and to accelerate the electron transfer from Q_A to Q_B (see discussion in Shevela et al. 2012). In this sense, Brinkert et al. (2016) found that the light-induced formation of Q_A^- leads to a significant weakening of HCO_3^- binding, thus resulting in a higher chance to lose HCO_3^-, especially if the ambient concentration of HCO_3^- is low (Brinkert et al. 2016). This finding confirmed the earlier results suggesting that the absence of bicarbonate might down-regulate the electron transfer between Q_A and Q_B and the Q_BH_2 exchange with the plastoquinone pool (Shevela et al. 2012). On the electron-donor side of PS II, easily exchangeable HCO_3^- ions may stimulate water-oxidizing activity by helping to shuttle protons produced during water-splitting into the lumen (Villarejo et al. 2002; Shutova et al. 2008; Koroidov et al. 2014; Banerjee et al. 2019; Shevela et al. 2020) Research on the role of Govindjee's favourite ion, HCO_3^-, continues … *This makes him very happy indeed.*

The relationship of chlorophyll *a* fluorescence to photosynthesis

Govindjee confessed that the most exciting thing in his career was 'to play with the light that the plants are giving out' during illumination, meaning Chl *a* fluorescence (see Annual Reviews, Inc. Conversations: An Interview of Govindjee by Don Ort: https://www.youtube.com/watch?v=cOzuL0vxEi0), which he poetically described as 'red and beautiful' in his often cited review on this subject: Govindjee (1995). After retirement, he continues to follow this line of research, publishing numerous studies using various Chl *a* fluorescence techniques and methods of analysis, as well as reviews and book chapters. We present some of these here, and several others in the following three sections.

We start by mentioning the well-known book *Chlorophyll a Fluorescence: A Signature of Photosynthesis* (edited by Papageorgiou and Govindjee 2004); we note that George C. Papageorgiou[1] (of Greece) was not only Govindjee's first PhD student in 1968, but was also a close friend, and an expert in Chl *a* fluorescence (see e.g. Papageorgiou et al. 2007; Stirbet et al. 2019). This book starts with an introductory chapter by Govindjee entitled *Chlorophyll a fluorescence: A bit of basics and history* (Govindjee 2004b), and continues with chapters written by top specialists on many applications of Chl *a* fluorescence techniques, and methods of analysis in the study of various photosynthetic processes, such as: primary reactions in photosynthesis (including excitation energy migration and charge separation), thermoluminescence, water oxidation, photosynthetic electron transport, non-photochemical quenching (NPQ) of Chl *a* fluorescence, carbon assimilation, photosynthetic performance, and different types of stress affecting photosynthetic organisms.

Two outstanding reviews co-authored by Govindjee (Kalaji et al. 2012, 2014), which present prompt and delayed fluorescence measurements on plants, show his interest in various types of fluorescence techniques and phenomena. Indeed, Govindjee has worked with not-so common, but useful fluorescence methods in photosynthesis research, such as fluorescence lifetime measurements. As emphasised in Papageorgiou and Govindjee (2014), in a chapter about NPQ processes, the fluorescence lifetime data published by Adam M. Gilmore in collaboration with Govindjee (see e.g. Gilmore et al. 1995, 1996, 1998, 2000; Gilmore and Govindjee 1999) have been shown to be essential for the understanding of regulatory mechanisms in photosynthesis. These studies, related to the xanthophyll cycle-dependent quenching of PS II Chl *a* fluorescence in plants, revealed and characterised the formation of a quenching complex in PS II antenna with rather short fluorescence lifetime. After several years, Govindjee resumed fluorescence lifetime measurements in collaboration with Robert M. Clegg, at UIUC, and published papers on a new fluorescence technique for photosynthesis research called Fluorescence Lifetime Imaging Microscopy (FLIM) (Holub et al. 2000, 2007). With this technique, Holub et al. (2007) obtained fluorescence lifetime-resolved images during the first few minutes of Chl *a* fluorescence induction in wild type and NPQ mutants of *Chlamydomonas reinhardtii*. These experiments showed that the zeaxanthin-accumulating mutant *npq2* has lower fluorescence intensities and lifetimes during the slow fluorescence transient than both the wild type and the violaxanthin-accumulating mutant *npq1*, which demonstrates the photoprotective role played by zeaxanthin in this green alga. In another study (Matsubara et al. 2011), the FLIM technique was used to study the energy dependent component of NPQ (qE) in avocado, a species which uses the Lx-L xanthophyll cycle (where L is for lutein, and Lx for lutein epoxide) in addition to the VAZ cycle (where, V is for violaxanthin, A for antheraxanthin, and Z is for zeaxanthin); for information on different xanthophyll cycles, see Papageorgiou and Govindjee (2014). Furthermore, Matsubara et al. (2011) studied real-time changes of relative concentrations of quenched and unquenched Chl *a* molecules in leaves of avocado plants during illumination and the following dark adaptation period, and found two major pools of PS II fluorescence lifetimes: 1.5 and 0.5 ns (unquenched and quenched components). Unfortunately, this line of research was interrupted by the premature death of Govindjee's collaborator and friend Robert M. Clegg (1945–2012; https://physics.illinois.edu/people/memorials/bob-clegg).

Long before his retirement, Govindjee had started a fruitful partnership with Reto J. Strasser (of Switzerland) on Chl *a* fluorescence induction in plants, algae and cyanobacteria (Strasser and Govindjee 1991, 1992; Strasser et al. 1995). They used a shutterless fluorometer system that allowed measurements with high precision of the initial (minimum) fluorescence F_O, and of an early inflection point of the transient curve at ~2 ms illumination, which they called 'J'. The entire Chl *a* fluorescence induction curve, measured up to a few minutes, was labelled O-J-I-P-S-M-T, where: O is for origin (F_O); J and I are for the fluorescence inflections at 2 and 30 ms, respectively (F_J and F_I); P is for the peak (F_P, which is maximum fluorescence, Fm in saturating light); S stands for a semi-steady-state level; M is for a later maximum; and T is for the terminal steady state (for a history of this nomenclature, see Govindjee 1995). We, however, note that historically, Govindjee has been involved, from the very beginning, in the current nomenclature of the O-J-I-P-S-M-T transient (see Papageorgiou and Govindjee 1968a, 1968b; Munday and Govindjee 1969a, 1969b; Strasser and Govindjee 1991, 1992).

The collaboration with Reto J. Strasser continued after Govindjee's retirement: see Schansker et al. (2003), Yusuf et al. (2010), Chen et al. (2012), and Shabnam et al. (2015, 2017). Schansker et al. (2003) measured the O-J-I-P transient curves on different plants (i.e. pea, *Pisum sativum*; Camellia, *Camellia japonica*; and sugar beet, *Beta vulgaris*) simultaneously with the 820-nm transmission signal, with which they obtained complementary information on P700 (the primary electron donor of PS I), and plastocyanin (PC; which reduces $P700^+$). These data showed that PC is in a reduced state after darkness, and its contribution to the 820-nm signal is species-dependent, with a 50% contribution in pea and Camellia, and 40% in sugar beet. Furthermore, Yusuf et al. (2010) worked on Chl *a* fluorescence in transgenic *Brassica juncea* plants overexpressing a *γ*-tocopherol methyl transferase (*γ*-TMT) gene from *Arabidopsis thaliana,* and concluded that the transgenic plant had a better tolerance to different types of induced stress (i.e. salt, heavy metal, and osmotic). This effect was suggested to be due to increased total tocopherol levels. Furthermore, Chen et al. (2012) studied the effects of a new photosynthetic inhibitor (tenuazonic acid, TeA) on crofton weed (*Eupatorium adenophorum*), by using photoaffinity labelling with a radioactive technique, and measured the O-J-I-P transients on the plant. The results confirmed that TeA interrupts electron transport beyond Q_A by binding at the Q_B-binding site. However, experiments with [^{14}C]-atrazine showed that the region on which TeA binds on PS II is different from that of atrazine (a widely used herbicide), in spite of their common action. Furthermore, Shabnam et al. (2015) studied differences in photoinhibition between floating and submerged leaves of long-leaf pondweed (*Potamogeton nodosus*). Chloroplasts from floating leaves had higher PS I activity, a higher rate of photosynthetic electron transport, and a higher maximum efficiency of PS II photochemistry, as indicated by the ratio between the variable fluorescence (Fv) to the maximum fluorescence (Fm), and showed less photoinhibitory damage induced by high light. Moreover, the cells of floating leaves had a higher mitochondria/chloroplast ratio, and an alternative oxidase in their mitochondria, which was missing in the submerged leaves. From these experimental data, Shabnam et al. (2015) concluded that the protection of the photosynthetic apparatus against photoinhibition was better in the floating leaves, due to a beneficial interaction between mitochondria and chloroplasts.

For the analysis of the O-J-I-P transient, Strasser and Strasser (1995) had proposed an original method, known as the JIP-test, in which several selected fluorescence values are used to calculate parameters, characterising mainly PS II activity, which was further developed by Tsimilli-Michael and Strasser (2008). Later, for educational purposes, Govindjee decided to review this method in collaboration with one of us (A. Stirbet) (Stirbet and Govindjee 2011), with whom he had earlier worked in Reto Strasser's laboratory on a mathematical simulation of the O-J-I-P curves (Stirbet et al. 1998). They also discussed hypotheses and approximations used to define the JIP parameters, and reviewed several possible applications related to the energetic connectivity of PS IIs, and PS II heterogeneity. Govindjee initiated and co-authored a review (Stirbet et al. 2018) on the relevance of the Performance Index (an important JIP parameter) in stress studies, based on the results of experiments, where Chl *a* fluorescence induction was used to analyze different types of abiotic stress.

Other reviews on Chl *a* fluorescence, published by Govindjee after 1999, include those by (1) Stirbet and Govindjee (2012), about the controversy on the origin of the variable PS II fluorescence and the J-I-P phase of the fluorescence transient; (2) Stirbet et al. (2014), on Chl *a* fluorescence induction modelling and its relation to photosynthesis; (3) Stirbet et al. (2019), which is on the relation of Chl *a* fluorescence to photosynthesis in cyanobacteria; (4) Stirbet et al. (2020), on basics, history and modelling of photosynthesis, with a special emphasis on models of Chl *a* fluorescence induction; and (5) Hu et al. (2020), where Govindjee and coauthors present a co-author and co-cited reference network analysis for Chl *a* fluorescence research from 1991 to 2018. In addition, Stirbet et al. (2019) provides an up-to-date review on the organisation and function of the photosynthetic apparatus in cyanobacteria, as well as for discussions on several types of Chl *a* fluorescence measurements.

With all the international work done on Chl *a* fluorescence in the past half a century, Govindjee is nothing less than a Living Encyclopedia on this topic: knowing, as he does, the literature, as well as the major results and physical mechanisms (and the stories and arguments behind them). Moreover, Govindjee continues to keep an eager eye on new developments and alternative explanations. There is a clear and elegant explanation for the origin of the fast rise of Chl *a* fluorescence that occurs in all oxygenic photosynthetic organisms. According to this explanation, in order to reach Fm, it is necessary and sufficient to reduce Q_A in all the active PS II centres. This model has proved to be immensely successful and is widely used in numerous labs around the globe as it works well for different organisms and under a large variety of environmental and experimental conditions. Nevertheless, there are experimental data which may be at best difficult and at worst *impossible*, to reconcile with this widely accepted model. Thus, alternative models and explanations have popped up from time to time in the literature, since the 1960s and 1970s (see Schansker et al. (2011) and references therein). Govindjee, having had a firm standpoint, has assessed them critically (e.g. Stirbet and Govindjee 2012). A more recent paper, containing experimental data, published by Magyar et al. (2018) and reported at conferences by one of us (G. Garab) and coworkers, strongly urges refinements in the mainstream model. It appears that we do not fully understand what is going on in PS II during and after the primary photochemical events, and what fluorescence transients really mean in terms of, e.g. local electric field effects and dielectric relaxations in the protein matrix. Govindjee is closely following these developments and ideas and his deep understanding and exceptional experience will most certainly contribute to the elucidation of this problem and the better understanding of the underlying physical mechanisms. A new refined model is expected to accommodate all experimental observations and with the help of Govindjee (we have his promise) and collaborating partners, we hope to show how to retain the virtues of fluorescence transient measurements for everyday laboratory and field practice.

Regulation of photosynthetic processes: state changes, non-photochemical quenching, and more

Under environmental fluctuations, photosynthesis is regulated by feedback processes that reduce imbalance between the rate of excitation energy trapping by the two photosystems and the rate of carbon assimilation. Furthermore, there are short-term photoprotective responses in the thylakoid membrane, which include state transitions (assuring balanced excitation of PS II and PS I; see a review by Papageorgiou and Govindjee 2011), and NPQ of the electronically excited state of Chl *a* in plants and algae, or of phycobilins in cyanobacteria (see reviews by Papageorgiou and Govindjee 2014; Stirbet et al. 2019). Since Chl *a* fluorescence (mostly from PS II) changes during these processes, various parameters of these changes, obtained through different techniques, are used to understand them.

In collaboration with many research groups, Govindjee has published a large number of papers related to these processes in different photosynthetic organisms (see photographs of Govindjee with colleagues and some of his collaborators in this field in Supplemental Figure

1B–E). On state transitions in cyanobacteria, Govindjee worked with the research group of Ondřej Prášil (in Třeboň, The Czech Republic). Kaňa et al. (2009) measured Chl *a* fluorescence induction curves under both orange (622 nm) and blue (464 nm) light, as well as fluorescence spectra at specific times of actinic light illumination. Their results showed that the maximum M of the slow P-S-M-T fluorescence transient, measured with 622 nm excitation light, appeared ~30 s later than for illumination with 464 nm light. These data were discussed from the viewpoint of regulation of excitation energy distribution in the antenna of cyanobacteria during photosynthetic induction. In addition, Kaňa et al. (2012) showed that a transition from state 2 (low fluorescence; larger PS I antenna) to state 1 (high fluorescence; larger PS II antenna) is responsible for the S-M rise phase of the Chl *a* fluorescence transient, in several cyanobacteria. The same conclusion was obtained for *C. reinhardtii*, in a study by Govindjee, in collaboration with the research group of Rajagopal Subramaniam in Hyderabad, India (Kodru et al. 2015). In both cyanobacteria and *C. reinhardtii*, the S to M fluorescence increase was absent or reduced in mutants that had no state transitions. However, the origin of the fluorescence decrease from M to T has remained unclear, as shown in cyanobacteria by Bernát et al. (2017). On the other hand, Govindjee, working with the research group of Kumud Mishra (see Mishra et al. 2019) on non-acclimated and cold-acclimated leaves of the cold-sensitive *A. thaliana*, showed changes in the slow P-S-M-T phase of the fluorescence transient, as well as in fluorescence emission spectra (from 650 nm to 780 nm) at selected temperatures, during the controlled cooling of the plants from 22°C to −1.5°C. These results were discussed in terms of biochemical and photochemical effects induced by low temperature on the modulation of Chl *a* fluorescence induction, and point to the importance of cold acclimation in the regulation of photosynthetic processes at low temperatures.

Regarding NPQ of the electronically excited state of Chl *a*, besides the papers based on life-time fluorescence measurements discussed above, Govindjee has also co-authored various other important NPQ studies. For example, Govindjee and Spilotro (2002) examined the NPQ in a ΔpH mutant of *A. thaliana*. They measured Chl *a* fluorescence induction and showed the importance of the relationship between the ΔpH gradient, NPQ, and the P to S fluorescence decay. Govindjee and Seufferheld (2002) studied two xanthophyll-cycle mutants of *C. reinhardtii*: *npq1*, which accumulates violaxanthin; and *npq2*, which accumulates zeaxanthin. They measured the growth curves, Chl *a* fluorescence transients, and several PS II reactions. Based on these data, NPQ of the electronically excited state of Chl *a* in *C. reinhardtii* was considered to be different than in higher plants. Several years later, Peers et al. (2009) obtained *npq4,* another mutant of *C. reinhardtii* that is deficient in qE and lacks the Light-Harvesting Complex Stress-Related (LHCSR) protein, which shows that LHCSR is mainly responsible for triggering the qE in this organism. This is in contrast to plants, where the PS II protein subunit S (PsbS) plays this role (Li et al. 2000). In two other papers co-authored by Govindjee, Chl *a* fluorescence induction was used to examine NPQ in the kelp, *Macrocystis pyrifera* (Garcia-Mendoza et al. 2011; Ocampo-Alvarez et al. 2013). These data showed differences between the NPQ in this alga compared with other organisms. Thus, the NPQ mechanism can be quite flexible in different types of algae.

Several different collaborative studies by Govindjee on some other aspects of regulation of photosynthesis were published, among them, experiments by Nedbal et al. (2003) on the cyanobacterium *Synechocystis* sp. PCC 6803, and on tobacco (*Nicotiana* *tabacum*) leaves that were exposed to harmonically modulated light (i.e. with the intensity I ≈ const. + sin (ωt)). These experiments showed non-linear modulation of the photosynthetic activity, which was induced by a negative feedback regulation of the photosynthetic system. In cyanobacteria, Chl *a* fluorescence data suggested a mechanism involving the modulation of the energetic coupling between PS II and the phycobilisome (without changes in PS I excitation), while in tobacco, the photosynthetic electron transport was shown to be limited by the modulation of reactions in the Calvin-Benson cycle. Furthermore, Stamatakis et al. (2016) showed the photoprotective role of *β*-carotene (*β*-Car) in *Synechococcus* sp. PCC 7942, when the effect of exogenously added *β*-Car was measured on the initial O-J rise of the O-J-I-P transient. Under high-light intensity, the fluorescence difference, $\Delta F_{\pm} = F_{+\beta\text{-Car}} - F_{-\beta\text{-Car}}$, was positive, but close to zero in O_2-depleted cells. These results showed the importance of *β*-Car in photoprotecting PS II and confirmed its function as a $^1O_2^*$ scavenger. On the other hand, Zivcak et al. (2014) studied the photosynthetic responses to high light of sun- and shade-grown barley (*Hordeum vulgare*) leaves; here, analysis of the O-J-I-P transients revealed, in shade-grown barley, a decreased number of electron carriers, limiting electron transport between PS II and PS I, as well as a lower connectivity between PS IIs. Zivcak et al. (2014) suggested that the lower PS II connectivity in shade leaves may play a photoprotective role. In another study, Biswal et al. (2012) analyzed the overexpression of the *A. thaliana* full-length *AtCAO* (the gene encoding chlorophyllide *a* oxygenase, responsible for Chl *b* synthesis) in low-light grown and high-light grown tobacco. These data show that this overexpression results in increased Chl *b* synthesis, and that light harvesting and photosynthetic electron transport are improved, especially in the high-light grown plants.

Attempts to augment photosynthesis and biomass

Intense efforts are now being made to improve the efficiency of photosynthesis and to obtain more biomass (see e.g. Ort et al. 2015). Govindjee showed his special interest in this area of research by co-editing a book dedicated to abiotic stress in plants (Pareek et al. 2010), as well as publishing a review on the advances in plant phenomics and phenotyping of plants (Mishra et al. 2016). Govindjee has also been active in collaborating with several research groups from the USA, China, India, Mexico and Poland on this important topic (Kalaji et al. 2011; Zhou et al. 2015; Kandoi et al. 2016; Soda et al. 2018; Wungrampha, Joshi, Rathore, et al. 2019; Jimenez-Francisco et al. 2020). In addition, Govindjee has been working with the research group of Richard Sayre (Negi et al. 2020; also see Sayre et al. 2020), and with two of us: X.-G. Zhu (see e.g. Hamdani et al. 2015; Hamdani, Khan, et al. 2019; Hamdani, Wang, et al. 2019) and A. Pareek (see e.g. Soda et al. 2018; Wungrampha, Joshi, Rathore, et al. 2019). Figure 5 and Supplemental Figure 4 shows a few selected photographs of Govindjee with some of those with whom he has worked with in this area.

Kalaji et al. (2011) examined the salt tolerance of two Syrian barley varieties by measuring the O-J-I-P transients and gas exchange parameters. These results showed that the early effect of salinity on photosynthesis in barley plants was due to stomatal conductance limitation, rather than to low PS II activity, emphasising the necessity of including gas exchange measurements with Chl *a* fluorescence studies.

Working with a graduate student Yan Zhou at UIUC (see Zhou et al. 2015), Govindjee, Manfredo Seufferheld and others characterised a spontaneous mutant strain (IM) of *C. reinhardtii*, which was grown under low light and mixotrophic conditions. They showed that this mutant has an improved biomass production (5%–27% higher dry cell weight) compared to its progenitor (a knock-out mutant with defects in phototaxis) and the wild type. The IM mutant had higher rates of respiration as well as net oxygen evolution, a lower S-M rise phase of the Chl *a* fluorescence induction curve, and a faster rise and recovery of NPQ than several other strains.

With Deepika Kandoi, a graduate student of Baishnab Tripathy, in New Delhi, India (see Kandoi et al. 2016), he and others worked to improve *Zea mays*, a C_4 plant, in which phosphoenolpyruvate carboxylase (PEPC) catalyzes primary CO_2 fixation. They showed that, as compared with the controls, plants, with overexpressed PEPC, had 14%–18% higher CO_2 assimilation, 10%–18% higher starch content, and 6.5%–16% higher dry weight. They found that this increase in performance was associated with a higher Chl concentration, higher electron transport rates, lower NPQ, and a higher performance index.

With Betza Jimenez-Francisco, a graduate student of Carlos Trejo, from Mexico (see Jimenez-Francisco et al. 2020), Govindjee and others established, for the first time, a photoautotrophic cell culture of blue grama grass *Bouteloua gracilis*, which is one of the most drought and grazing tolerant plant species in the short-grass community. Jimenez-Francisco and her coworkers measured and analysed O-J-I-P fluorescence transients, obtained from isolated cells as compared with those from the intact leaves. One of the goals of this study was to test the effect of different sucrose concentrations on PS II activity in isolated cells. Jimenez-Francisco et al. (2020) found PS II activity to decrease with increasing sucrose concentrations, even when the Chl content of isolated cells was higher under these conditions. In contrast, the photoautotrophic cells had an optimal PS II activity, close to that found in leaves.

With Neelam Soda and Silas (Graham) Wungrampha, graduate students of one of us (A. Pareek) at JNU, New Delhi, India, Govindjee and others published two papers on rice (see Soda et al. 2018; Wungrampha, Joshi, Rathore, et al. 2019). This was possible because Govindjee had been invited to JNU during the 2017–2019 winter semesters. Pareek's group works mainly on plant responses to abiotic stress, such as salinity, drought and high temperature, which adversely affect the yield of crops and pose a major threat to agriculture worldwide (see e.g. Pareek et al. 2010; Wungrampha et al. 2018; Pareek et al. 2020). Ashwani Pareek's group has shown that the seedlings of Pokkali rice (used by farmers of the coastal areas in India) are much more tolerant to salt stress than those of IR64 rice, and that several salt stress related Quantitative Trait Loci (QTL) contribute to its high salt tolerance. Among these, Saltol QTL was responsible for almost 60% of the phenotype for salinity tolerance in Pokkali seedlings (Nutan et al. 2020). One important gene identified in Pokkali, i.e. *OsIFL* encoding cytoskeleton intermediate filament 1, was shown to interact with another gene, encoding metallothionein, when contributing to salinity tolerance (Soda et al. 2016). Then, Soda et al. (2018) in collaboration with Govindjee, found that *OsIFL* overexpressing rice plants showed enhanced tolerance to salinity compared with wild-type plants, while its knock-down mutant plants were more sensitive. Furthermore, compared to wild-type plants, *OsIFL* overexpressing rice showed higher PS I and PS II activity under salinity stress, and 2–

Figure 5. Photographs of Govindjee visiting China, Sweden, India and México. **A**, Left to right: Xin-Guang Zhu, Yungang Shen, Govindjee and Hualing Mi, Shanghai, China, 2019. **B**, Govindjee with Saber Hamdani, in Xin-Guang Zhu's Laboratory in Shanghai, China, 2019. **C**, Govindjee with Johannes Kromdijk, at the first European Congress on Photosynthesis, in Uppsala, Sweden, 2018. **D**, Left to right: Ashwani Pareek, Rajni Govindjee, Sneh Lata Singla-Pareek and Govindjee, in front of a market in Delhi, India, 2019. **E**, Left to right: Diana Daniela Ayala-Hernández, Xochitl Ortiz-Carbajal, Martha Elena Mora-Herrera, Diana Rocio Ruiz-Saenz, Govindjee, Rajni Govindjee, Humberto Antonio López-Delgado, Carlos Trejo and Alfonso Larqué-Saavedra; this photo was taken outside the restaurant 'Hacienda de Xcanatun', under the shade of a *Ceiba pentandra* tree, after a symposium on Plant Physiology at Mérida, Yucatán, México, 2019. Source: Figure 5A,B are from XinGuang Zhu, Figure 5C is from Govindjee, Figure 5D is from Ashwani Pareek; and Figure 5E is from Carlos Trejo.

4-fold higher accumulation of the osmolytes proline and trehalose. In another study on abiotic stress, Wungrampha, Joshi, Singla-Pareek, et al. (2019) and Wungrampha, Joshi, Rathore, et al. (2019) worked on the xero-halophyte *Suaeda fruticosa*, which is adapted to desert conditions, with extreme salt, high light, and drought. The goal in Wungrampha, Joshi, Rathore, et al. (2019) was to understand the adaptive advantages of this plant, by studying its photosynthetic activity by measuring the CO_2 gas exchange and Chl *a* fluorescence induction every three hours for three days, in its natural environment. The results showed that photosynthesis in this plant is influenced by diurnal rhythm or continuous dark conditions, and that the maximum quantum yield of PS II photochemistry (Fv/Fm) increases during the night.

Improving photosynthetic efficiency is expected to lead to increased biomass production (Zhu et al. 2010), and several engineering options towards this goal are being explored with major success in increasing the speed of recovery from the photoprotective state (Kromdijk et al. 2016) and engineering photorespiratory bypasses (South et al. 2019). A recent study in this area was published by Negi et al. (2020), where a mutant of *C. reinhardtii* dynamically adjusts the size of its light harvesting antenna as a function of the growth light intensity. This mutant shows significantly higher photosynthetic rates, and two to three-fold greater biomass productivity than the parental wild-type strains. Furthermore, the ability to induce state transitions and NPQ of the excited state of Chl *a* is well preserved in this mutant.

Due to restrictions on growing genetically modified crops in many countries, another approach, which has recently gained much attention, is to explore the natural variations of photosynthetic properties for which extensive phenotyping of photosynthetic properties in global mini-core diversity panels has been conducted (see: Hamdani et al. 2015; Qu et al. 2016; Qu et al. 2017). Substantial variations in the maximum quantum yield of PS II (inferred from the ratio of variable to maximum Chl *a* fluorescence, Fv/Fm) were observed, and a gene (for β-glucosidase 5) was identified to be associated with the variation of Fv/Fm by genome wide association studies followed by genetic functional testing (Hamdani, Wang, et al. 2019). We note that the promoter region of the β-glucosidase 5 gene shows four single-nucleotide polymorphisms, which are linked to the variations in Fv/Fm, potentially through the gibberellin pathway (Hamdani et al. 2015). The same approach is now being used to mine candidate genes controlling different phases of the Chl *a* fluorescence induction curve (Khan et al. 2020).

Interpretation of the results of extensive phenotyping of the natural variation in the Chl *a* fluorescence induction curve has suggested the use of new parameters that might provide deeper understanding of the physiology of the plants (see e.g. Hamdani et al. 2015). In particular, when the O-J-I-P fluorescence induction curves between the high-yielding elite cultivars and low-yielding landraces were compared, Hamdani et al. (2015) found that the elite cultivars had a higher IP phase compared to that in the landraces. It was suggested that this IP phase was linked to a transient electron jam on the PS I acceptor side, due to the time (> 1 s) necessary for ferredoxin-NADP reductase (FNR) to reactivate under light conditions. There is substantial variation in the time needed for FNR deactivation in darkness (Schansker et al. 2008), which can result in different $NADPH/NADP^+$ ratios, and hence, the observed IP increase may be related to this. More detailed experiments are needed to investigate this idea.

Besides mining natural variations of photosynthetic properties in rice, the research group of one of us (X.-G. Zhu) has evaluated, in collaboration with Govindjee, the long-term impact of different light quality on photosynthetic efficiency and photoprotective properties in rice (Hamdani, Khan, et al. 2019). For this purpose, three LED-based light regimes were used: red (648–672 nm), blue (438–460 nm), and 'warm' white light (529–624 nm), with an incident photon flux density of around 300 μmol photons m^{-2} s^{-1}. Hamdani, Khan et al. (2019) found that, compared to white light, the use of blue light induced a significant decrease in the maximum quantum yield of PS II (as inferred from Fv/Fm), an increase in NPQ, and a lower quantum yield (Y(II)) of PS II under illumination. In contrast, when red light was used, there was a decrease in Y(II), an increase in NPQ, but no change in Fv/Fm. It was further shown that growing plants under monochromatic red or blue light decreases the transcript abundance of both catalase and ascorbate peroxidase, reflecting a reduced anti-oxidant capacity of leaves, which might have contributed to the decreased Fv/Fm and increased NPQ. Govindjee has remained an enthusiastic collaborator (e.g. Hamdani et al. 2015; Hamdani, Khan, et al. 2019; Khan et al. 2020). In another example, Govindjee has collaborated on a minireview on the role of lectins in the carbon reactions of photosynthesis (Nonomura et al. 2020).

Modelling of photosynthesis and artificial photosynthesis

Govindjee has had fruitful collaborations with a number of modellers with whom several mathematical models of photosynthetic processes were used for the simulation and interpretation of Chl *a* fluorescence induction curves in plants and algae (Stirbet et al. 1998; Zhu et al. 2005; Stirbet and Govindjee 2016; Fu et al. 2020). In addition, he has co-authored two critical reviews on this subject (Stirbet et al. 2014, 2020).

In Zhu et al. (2005), the O-J-I-P transient was simulated based on an original reaction scheme of PS II redox reactions. The authors also explored the role of particular model parameters on the shape of simulated curves. The O-J-I-P transient was simulated by Fu et al. (2020) as well, but this model also included the subsequent decreasing P to S phase. For this, the authors used a complete, but very simplified model of photosynthesis (i.e. from the formation of excited state of Chl under illumination, to the synthesis of glucose). Additionally, Govindjee and his co-authors showed how the system analysis methods, such as extended Kalman filtering, and consideration of a PID (proportion, integral, and derivative) negative feedback regulator, can be used to study and extract information on the function of the photosynthetic apparatus and its regulation. Furthermore, Stirbet and Govindjee (2016) used a model of photosynthesis (including state transitions) with which they studied the slow P-S-M-T Chl *a* fluorescence transient by using *in silico* experiments. Here, Stirbet and Govindjee were able to simulate the S-to-M fluorescence rise, as was observed experimentally in *C. reinhardtii* cells, initially maintained under anaerobic conditions for a few minutes (e.g. Kodru et al. 2015), and confirmed that the S-to-M rise is related to a state 2 to state 1 transition (see above). However, the following M-to-T Chl *a* fluorescence decrease was not simulated in this study, and this part of the Chl *a* fluorescence transient needs further research.

Additionally, as mentioned earlier, Govindjee has co-authored reviews devoted to mathematical modelling, such as in Stirbet et al. (2014) and Stirbet et al. (2020), in which results obtained in many papers on modelling photosynthesis and Chl *a* fluorescence induction in plants and algae were compared and fully discussed. Moreover, efforts on modelling Chl *a* fluorescence in cyanobacteria have been discussed in a chapter by Stirbet et al. (2019).

Two articles have been co-authored by Govindjee on **artificial photosynthesis**, a research area related to his long-time interest in the PS II water-splitting process, on which he has published several reviews since 1999 (see e.g. Najafpour and Govindjee 2011; Najafpour, Barber, et al. 2012; Najafpour, Moghaddam, et al. 2012, 2013). Hydrogen production by water splitting is an important goal in artificial photosynthesis. Towards this goal, Najafpour, Tabrizi, et al. (2012, 2013) studied aggregated manganese oxide mono-sheets as possible systems that may be used to simulate the function of the Mn_4CaO_5 cluster of PS II. We also note that, besides these articles, Govindjee has co-edited a special issue in Frontiers in Plant Science devoted to this subject (see Hou et al. 2014).

Recognition of scientists at conferences and more

Govindjee has kept close contact with photosynthesis researchers, either by visiting their laboratories, or by meeting them regularly at important scientific conferences, such as the International Congress on Photosynthesis, Gordon Research Conference on Photosynthesis, and the International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability. Besides the benefit of always being well-informed, Govindjee has used these opportunities to communicate his perspective on photosynthesis to large audiences and recognise the contributions of other researchers through conference reports (see e.g. Govindjee, Rutherford, et al. 2007; Govindjee et al. 2011, 2016; Gisriel et al. 2018; Kaur et al. 2019), or by writing tributes dedicated to selected leaders in the field, such as Achim Trebst (Govindjee 2009a); Michael R. Wasielewski (Govindjee and Seibert 2010); William L. Ogren (Portis and Govindjee 2012); and, Jean-David Rochaix (Govindjee and Redding 2017). Supplemental Figure 2 shows photographs of Govindjee with some of the participants at these conferences.

What we all appreciate most is Govindjee's enthusiasm for recognising and honouring the young through awards of books, and his dedication to education, which he does with great fun and unmatched zeal. We all know that there are still many questions concerning the photochemical reactions and the photosynthetic apparatus that need to be understood and answered. In order to give the opportunity to scientists from all over the world to meet and discuss their findings in the field of photosynthesis, there is, of course, the most prestigious now quadrennial International Congress of Photosynthesis Research, organised by the International Society of Photosynthesis Research (ISPR).

At the Brisbane congress on Photosynthesis (12th Congress of ISPR) in 2001, arising from discussions between one of us (Suleyman I. Allakhverdiev) and Robert Carpentier (chairperson of 13th Congress of ISPR in Montreal, in 2004), Győző Garab (co-author of this article and chairperson of the 11th Congress of ISPR in Budapest, 1998), the late Prasanna Mohanty (1934–2013; Tiwari et al. 2014), and the late Slava Klimov (1945–2017; Allakhverdiev et al. 2018), the conclusion was reached that we need another, smaller and more focused conference. For this purpose, a new International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability was established and from that time, up to now, one of us (S.I. Allakhverdiev) has been the main organiser and main coordinator of these meetings. James Barber (1940–2020), Govindjee, and others have been key organisers of all these meetings. Since the very first conference, Govindjee has taken an active leadership role in almost all the conferences, and we are highly thankful to him.

The first conference took place in Trois-Rivières, Quebec, Canada in 2004, with Robert Carpentier as its chairman. This meeting *Photosynthesis and the Post-genomic Era: from Biophysics to Molecular Biology, a Path in the Research of Photosystem II* was held in honour of Norio Murata, a top authority in photosynthesis. One of the goals of this conference (see Carpentier and Allakhverdiev 2005) was to review the research achievements on PS II, a topic very dear to Govindjee (see Wydrzynski and Satoh 2005, volume 22 in Govindjee's wonderful series Advances in Photosynthesis and Respiration).

This 2004 meeting was highly successful, and this series of meetings became very popular in the photosynthesis community. The next conference *Photosynthesis in the Post-genomic Era: Structure and Function of Photosystems* was held in Pushchino, Russia, in 2006. Here, we honoured James (Jim) Barber, now sadly deceased (https://www.imperial.ac.uk/news/194710/professor-james-barber-1940-2020/), who made outstanding contributions to the understanding of PS II (Allakhverdiev et al. 2007; Allakhverdiev 2008).

The tradition of this meeting was continued when the *Photosynthesis Research for Sustainability* conference was held in Baku, Azerbaijan, in 2011. Here, we focused on the important aspects of photosynthesis, as related to global challenges. For the first time, the conference included hydrogen energy and artificial photosynthesis. Those attending were very appreciative of Govindjee's contributions to this meeting, which included his giving awards to selected students and emerging scientists (Allakhverdiev et al. 2011; see Govindjee's photographs, e.g. Figures 4 and 7 in that paper).

The next conference *Photosynthesis and Hydrogen Energy Research for Sustainability* was held in 2013, again in Baku, and, this time, it was in honour of Jalal A. Aliyev, who had made a significant contribution to the study of photosynthetic productivity of agricultural plants, especially wheat. Furthermore, this conference was special since the Nobel laureate John E. Walker (UK) was a keynote speaker delivering a lecture on ATP synthesis**.** A photograph of Govindjee with Sir John Walker can be seen in Figure 5 in Allakhverdiev et al. (2013). At this conference Govindjee continued his role of recognising and motivating young investigators (see Figure 8 in the 2013 paper).

Our photosynthesis research conference was then held, almost annually, honouring other top scientists in photosynthesis, such as Vladimir Shuvalov in 2014 (Pushchino, Russia; see Allakhverdiev et al. 2014), and George C. Papageorgiou[1] in 2015 (at the Orthodox Academy of Crete, Greece). As usual, in the 2015 meeting, Govindjee was a very responsive and attentive person, completely surrendering to his beloved business of science, education, and cultivation of young talented scientists (see Allakhverdiev et al. 2016). Next, Nathan Nelson and Turhan Nejat Veziroglu were honoured in 2016 (Pushchino; see Tsygankov et al. 2017), when one of the distinguished keynote speakers was the Nobel laureate Ada Yonath (Israel). Then, as mentioned earlier, Govindjee was honoured, together with William Cramer, and Agepati S. Raghavendra in 2017 (Hyderabad, India; see Allakhverdiev et al. 2019). In 2018, the conference was held again in Baku, but this time, it was a memorial to Jalal Aliyev, who passed away in 2016 (see Huseynova et al. 2016). At the most recent conference, held in 2019, in Saint Petersburg, Russia, the group honoured four top international scientists for their contributions: Tingyun Kuang, Anthony Larkum, Cesare Marchetti, and Kimiyuki Satoh (see Borisova-Mubarakshina et al. 2019, 2020). Here, Govindjee not only gave an outstanding perspective on his research – which he does wonderfully well, but then, after introducing Cesare Marchetti (see Supplemental Figure 2C), he even gave a talk on Cesare's research! And yes, he continued being his usual self, in giving awards and distributing posters.

It is noteworthy that Govindjee's contributions to the above conferences has also included his guidance in assembling and co-authoring the conference reports for eight of our conferences, along with his skilful editing up to the last moment before the reports went online (Allakhverdiev et al. 2007, 2011, 2013, 2014, 2016, 2019; Allakhverdiev 2008; Huseynova et al. 2016; Tsygankov et al. 2017; Borisova-Mubarakshina et al. 2019, 2020).

Tributes to those no longer with us

> Each of us has come to think with deep gratitude of those who have lighted the flame within us.
>
> Albert Schweitzer (1875–1965)

The world has undergone three major industrial revolutions. In the first one, during the late eighteenth century, mechanised production was powered by water and steam. For the second revolution, in the early twentieth century, electrical power was harnessed for mass production. Then the third industrial revolution subsequently adapted automation and manufacturing, which eventually became digitalised. A fourth biologically empowered revolution is being ushered in today, with molecular genetics and regulation of photosynthesis providing sustainable food, fuels, pharmaceuticals and fibre. In order to arrive at an advanced state of this revolution, we must remember those who paved the path before us.

As a historian of photosynthesis, Govindjee has recognised many great researchers of the past, among whom are included his mentors Robert Emerson and Eugene Rabinowitch (Govindjee 2004a, 2018, 2019a, 2020; Govindjee, Papageorgiou, et al. 2019; Govindjee and R Govindjee 2020), and some of his students (now deceased): Thomas J. Wydrzynski (1947-2018; see Govindjee 2008a; Govindjee et al. 2018; Conlan et al. 2019); Frederick Yi-Tung Cho (1939–2011; see Govindjee, Munday, et al. 2017); Prasanna Mohanty (1934-2013; see Tiwari et al. 2014; Naithani and Govindjee 2018); and, Maarib Bazzaz (1940–2020; see Govindjee, Zilinskas, et al. 2020).

There is nothing as evocative as a good story and, in the field of photosynthesis, the tales behind our scientific friends and colleagues have been the editorial domain of Govindjee, our legendary scientific writer who has distilled their thoughts and celebrated their fine characters and their extensive life work. More than 40 tributes to our predecessors in the field of photosynthesis by Govindjee and co-authors are available at (http://www.life.illinois.edu/govindjee/recent_papers.html). In addition to those mentioned above, these include: Govindjee and Fork (2006) for Charles Stacy French (1907–1995); Choules and Govindjee (2014) and Govindjee and Srivastava (2014) for

William A. Arnold (1904-2001); Govindjee et al. (2015) for Colin A. Wraight (1945-2014); Govindjee and Pulles (2016) for Louis N.M. Duysens; Govindjee (2017) for André Tridon Jagendorf (1926-2017); Herbert et al. (2018) for Shmuel Malkin (1934–2017); Govindjee, Briskin et al. (2020) for Constantin A. Rebeiz (1936–2019); and Vredenberg and Govindjee (2020) for Christiaan Sybesma (1928–2018). As standalone chapters, they are a good read. When taken together as a whole, they teach us the thought processes and virtues of the marvellous personalities, and the wonderful humanity behind our great discoverers in photosynthesis.

The majority of biographies by Govindjee were written in collaboration with those who were intimately acquainted with the deceased scientists' investigations and private lives. Often the memoirs included contributions by family members, graduate students, and colleagues who had lived and breathed photosynthesis side-by-side for decades. Indeed, there is no recipe for producing sweet memories of a scientist, and, yet, having watched Govindjee working on several biographies, some guidelines may be presented for the future. As a case in point, we would like to present Andrew (Andy) Benson, on whom Govindjee and others have authored several articles (Lichtenthaler et al. 2015a, 2015b; Nonomura et al. 2016, 2017). It was after celebrating Andy's 93rd birthday (Govindjee 2010) that Mario Aguilera (Scripps Communications Office, University of California San Diego scrippsnews@ucsd.edu), asked one of us (A. Nonomura) to initiate a work-up on Andy's biography. This was a wakeup call to be prepared. Andy's wife of 45 years, Dee Benson, was the natural contributor of family photographs and memorabilia. Thus, when Andy passed away four years later, jointly with Govindjee, several colleagues prepared a chronology of scientific contributions, a bibliography of over 300 publications, photographs, and a summary of academic highlights. It was soon, thereafter, that an excellent Biographical Memoir of the National Academy of Sciences USA (Buchanan et al. 2016) drew heavily upon this material for Andrew Alm Benson (1917–2015).

Govindjee has spent over half a century in education, but his years of experience account for only a fraction of his talent. In fact, it is his breadth of competence across the field of biology and physics and his inherent ability to understand how to approach an audience that makes him special. Concepts may be lost, particularly, in photosynthesis, when they are not expressed within your audience's grasp; however, when working with Govindjee, with whom education is at the forefront, clarity rings true. It makes all the difference in the world to write biographies for the next generation of scientists, but first, we must come to the self-realisation that we must address undergraduates! Govindjee comprehends, innovates, and teaches at all levels.

One of the enduring features of Govindjee's remembrances is his personal touch, in which he shows the human side of our scientists (see Fuller's memoir of Calvin in Govindjee, Nonomura, et al. 2020). In addition to considering the subject's career in science, Govindjee invites family and scientists to consider the intangibles by contributing views of love, shared joys, foibles, hobbies, sports, celebrations, awards, and rewarding experiences. What led the scholar to dedicate a lifetime of work to the field? Had historical events, such as, a war, affected the course of research and World peace? We need not look far, for example, the answers may be found in his tribute to his mentor Eugene I. Rabinowitch (Govindjee, Papageorgiou, et al. 2019).

As an editor extraordinaire, Govindjee has remembered those who had come before us by engaging multiple co-authors to contribute memories in common. Truly, this is a comforting experience. On the other hand, emotions may overwhelm our ability to recognise repeated phrases, rendering excisions nearly impossible because we may not allow ourselves to do so. Thus, we must be cognisant of human nature. Be that as it may, once all of the contributions are assembled, it is the duty of all the authors to work together to remove duplications. Not only does this portion of the review process streamline the article, it also results in a satisfied and appreciative reader.

At times, there is a revelation, the moment of discovery. For example, there is Melvin Calvin's 'Aha!' moment, when he was caught in a traffic jam (Govindjee, Nonomura, et al. 2020). For others, we gain insight into the clarity of thought and expression that is the keystone of first order science, for example, from remembrances of James A. Bassham (Bassham et al. 2016). And in the final 'C' article of the Nobel series, Govindjee and colleagues let Andy's autoradiograms speak with absolute certainty of discovery after discovery across the kingdoms of life (Nonomura et al. 2017).

Tributes from collaborators around the world

During the preparation of this tribute a number of scientific friends and colleagues who have worked with Govindjee during his *retirement* years submitted personnel recollections and tributes of their own. As word spread, and the additional fact that Govindjee will celebrate his 88th birthday on October 24, 2020, became more widely known, many more scientific friends and colleagues from throughout his career sent in their reminiscences, congratulations and heart-felt thanks for the many contributions Govindjee has made to photosynthesis, and to them, over such an illustrious career. These tributes from scientists at all stages of their career, including Nobel Laureates and graduate students, have been collected together and included in a special section in the Introduction to this Special Issue of the New Zealand Journal of Botany (Eaton-Rye et al. 2020).

Note

1. Govindjee was very proud to remind us that George C. Papageorgiou was his very first PhD student, with a highly original 1968 thesis: Fluorescence Induction in *Chlorella pyrenoidosa* and *Anacystis nidulans* and its Relation to Photophosphorylation, which is available at: http://www.life.illinois.edu/govindjee/theses.html. Sadly, George Papageorgiou passed away on November 22, 2020.

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Appendix

Names of more than 300 co-authors of Govindjee from around the world (from ~ 25 countries) during his retired life (1999–2020) are presented below. These names are arranged alphabetically, first by country, and then by last names, within each country**. Note**: All given (first) names are provided except when unavailable. Several authors are from more than one country, but their affiliation is listed arbitrarily from one country only. *(If there are any errors, please send an e-mail to one of the authors of this paper.*)

Australia: Wah S. (Fred) **C**how; Brendon Conlan; Alexander (Alex) B. **H**ope; Robert (Bob) J. **P**orra

Azerbaijan: Irada M. **H**useynova

Bulgaria: Vasilij **G**oltsev

Canada: Jessica M. **A**nna; J. Thomas (Tom) **B**eatty; Harriet H. **G**orham; Yaser R. **K**han; Constance G. **N**ozzolillo; Evgeny E. **O**stroumov

China: Shiguo **C**hen; Chengcai Chu; Zongming **D**ai; Lijiang **F**u; Ya (David) **G**uo; Saber **H**amdani; Kai Hu; Jiangjun Jiang; Naveed **K**han; Ming **L**i; Rong Li; Xinyu Liu; Shahnaz **P**erveen; Sheng **Q**iang; Mingnan Qu; Kang-Cheng **R**uan; Yun-Kang **S**hen; Hongru **W**ang; Qiang **X**ia; Chang-Peng Xin; Chun-He Xu; Chunlong **Y**ang; Ji-Yu Ye; Xin Jian Yu; Yong Yul; Guang-Yong **Z**heng; Yan Zhou; Xiaocen Zhu; Xin-Guang Zhu

Czech Republic: František **A**damec; Marcel **B**abin; Gábor Bernát; Vitězslav Březina; John J. **C**ullen; Radek **K**aňa; Karel Klem; Ondřej Komárek; Eva Kotabová; Jiři Kubásek; Dušan **L**azár; Annamika **M**ishra; Kumud Bandhu Mishra; Ladislav (Lada) **N**edbal; Ondřej **P**rášil; Barbora Šedivá; Zdeněk Šesták; Gábor Steinbach; Dalibor Štýs; David J. Suggett; Otmar **U**rban

Estonia: Agu **L**aisk; Vello **O**ja

France: Roland **D**ouce; Pierre **J**oliot; Fabrice **R**appaport

Germany: Lutz A. **E**ichacker; Arnd G. **H**eyer; Oliver Holub; Klaus-Dieter **I**rrgang; Hartmut K. **L**ichtenthaler; Shizue **M**atsubara; Kärin **N**ickelsen; Gernot **R**enger; Hugo **S**cheer; Widmar **T**anner

Greece: Aikaterni Alygizaki-Zorba; Kostas Stamatakis; George C. Papageorgiou; MeropeTsimilli-Michael

Hungary: Peter Maroti

India: Khalid **A**nwar; Ajaya K. **B**iswal; Anath Bandhu **D**as; Elsinraju Devadasu; SailajaV. **E**lchuri; Brijesh K. **G**upta; Anjana **J**ajoo; Rohit Joshi; Deepika **K**andoi; Jitendra (Jiten) P. Khurana; Sireesha Kodru; Sneha Sudha Komath; Deepak Kumar; Sadhu **L**eelavathi; Tirupathi **M**alavath; Amarendra N. Misra; Sasmita Mohanty; Sushila **N**arsimhan; Sreedhar Nellaepalli; Shiv S. **P**andey; P. Pardha-Saradhi; Ashwani Pareek; Gopal K. Pattanayak; Ravi **R**ajwanshi; Ray S. Rathore; Vanga S. Reddy; Prafullachandra Vishnu (Raj) **S**ane; Neera Bhalla Sarin; Nisha Shabnam; Ashutosh Sharan; Anuradha Sharma; P. Sharmila; Gauri Shankar Singhal; Sneh Lata Singla-Pareek; Neelam Soda; Vineet Soni; Sudhir K. Sopory; K. Sowjanya Sree; Shyam Lal Srivastava; Rajagopal Subramanyam; Swati **T**iwari; Baishnab Charan Tripathy; Akhilesh K. Tyagi; Silas (Graham) **W**ungrampha; Mohd. Aslam **Y**usuf

Iran: Behzad **H**aghighi; Atefeh Nemati **M**oghaddam; Mohammad Mahdi **N**ajafpour; Mahmoud Amouzadeh **T**abrizi

Japan: Shigeru S. **I**toh; Mamuro **M**imuro; Jun Minagawa; Norio Murata; Jian-Ren **S**hen; Ryutaro Tokutsu; Tatsuya Tomo
Korea (South): Hyunook **K**im
Mexico: Gerardo Armando H. Aguado-Santacruz; H. **C**ampos; Victor F. Conde-Martinez; Ernesto **G**arcia-Mendoza; Betzaida **J**imenez-Francisco, Hector **O**campo-Alvarez; Daniel **P**adilla-Chacon; Carlos Lopez **T**rejo
Netherlands: Alia **A**lia (Matysik); Wil R. **P**eters; M.P.J. (Tinus) Pulles; Gert Schansker; Rienk **v**an Grondelle; Jack J.S. van Rensen; Willem (Wim) J. Vredenberg
New Zealand: Julian J. **E**aton-Rye
Pakistan: Waqasuddin **K**han
Poland: Karolina **B**osa; Hazem M. **K**alaji; Janusz Košcielniak; Krystyna **Z**uk-Golaszewska
Russia: Suleyman I. **A**llakhverdiev; Maria M. **B**orisova-Mubarakshina; Navik V. **K**arapetyan; Elena A. Kotova; Vladimir S. Kozlovsky; Alexander (Alex) A. Krasnovsky, Jr; Mahir **M**amedov; Victor **N**adtochenko; Roman Y. **P**ishchalinikov; Vladimir O. Popov; Andre P. **R**azjivin; Galina Yu. Riznichenko; Margarita V. Rodionova; Alexander B. Rubin; Alexey **S**emenov; Vladimir (Vlad) A. Shuvalov; Anatoly A. **T**syganko*v*; Nadezhda P. **Y**urina; Sergey K. **Z**harmukhamedov
Slovakia: Marian **B**restic; Marek **Z**ivcak
Sweden: Lars Olof **B**jörn; Dainis **D**ravins; Alizee **M**alnoe; Johannes Messinger, Göran **S**amuelsson; Dmitry (Dima) Shevela
S**witzerland:** Reto Jörg Strasser
United Kingdom (UK): John F. **A**llen; Neil R. Baker; James (Jim) Barber; Christine H. **F**oyer; A. William (Bill) Rutherford; Alison **T**elfer
United States of America (USA): Gennady M. Ananyev; Horatio **B**annister; Thomas (Tom) Turpin Bannister; Amanda N. Barry; Helen Bassham; Susan Bassham; Christoph Benning; Howard R. Berg; Gerald A. Berkowitz; Carl J. Bernacchi; Devaki Bhaya; Karl Y. Biel; Clanton (Clint) C. Black; Robert E. Blankenship; Hans J. Bohnert; Jerry J. Brand; Winslow R. Briggs; Donald (Don) P. Briskin; R. David (Dave) Britt; Bob B. Buchanan; Robert (Bob) Burnap; Rosanna **C**alindro; Yi-Chun Chen; Lucinda Choules; Robert (Bob) M. Clegg; Martin Cohen; Jason Cooley; Robert Cooney; William (Bill) A. Cramer; David Crisp; Antony (Tony) R. Crofts; Henri **D**aniell; Charles (Chuck) Dismukes; Roberto Docampo; Susan Dutcher; Gerald (Gerry) E. **E**dwards; Darrell **F**leischman; David (Dave) C. **F**ork; Susan Frenkel; Natalia Friedland; Petra Fromme; Howard **G**est; Adam Gilmore; Christopher (Chris) Gisriel; Christoph Gohlke; Rajni Govindjee; Arthur (Art) R. Grossman; William **H**agar; Gregor J. Heiss; Steven (Steve) K. Herbert; Jane F. Hill; Rhoda Eleson Hirsch; George Hoch; Barry Holtz; Harvey J.M. Hou; Karen **J**acobsen-Mispagel; Divya **K**aur; Cheryl A. Kerfeld; Jan F. Kern; Rita Khanna; Nancy Y. Kiang; David Knaff; Robert (Bob) S. Knox; Derrick R.J. Kolling; Vladimir Kolossov; David (Dave) Krogmann; Johannes Kromdijk; Anil Kumar; Margaret Gwyn **L**atimer; Edward (Ed) Laws; Hong Li; Stephen (Steve) P. Long; George Lorimer; Norma **M**archesini; Leland Mayne; Victoria S. Meadows; Tihana Mirkovic; Gary Moore; John C. Munday Jr; Jason Musick; Sushma **N**aithani; Sangeeta Negi; Arthur M. Nonomura; Larry **O**rr; Sean **P**adden; David S. Park; Zoee Perrine; Archie R. Jr. Portis; Roger C. Prince; Hope Punnett; Laura Punnett; Silvia **R**amundo; Mark Rebeiz; Kevin Redding; Marvin Rich; Stuart Rose; Felix A. Ruiz; Indumati (Indu) S. Rupassara; Shai **S**aroussi; Sergei Savikhin; Richard (Dick) Sayre; Lance C. Schideman; Gregory (Greg) D. Scholes; Antigona Segura; Michael (Mike) Seibert; Melih Sener; Manfredo J. Seufferel eld; Thomas (Tom) D. Sharkey; Louis A. Sherman; Robert (Bob) Shopes; Janet Siefert; Abhay Singh; Paul Spilotro; Alaka Srivastava; Nupur Srivastava; Alexandrina (Sandra) Stirbet; Roger E. Summons; Bengt Svensson; Jinglu **T**an; Giovanna Tinetti; Vijai Tyagi; Victor **V**acquier; Jun (Polly) **W**ang; Alan Weidemann; C. John Whitmarsh; Christine (Chris) T. Yerkes; Chunyan Yin; Hyungshim Yoo; Barbara Zilinskas

Supplementary Material

Celebrating the contributions of Govindjee after his retirement: 1999-2020

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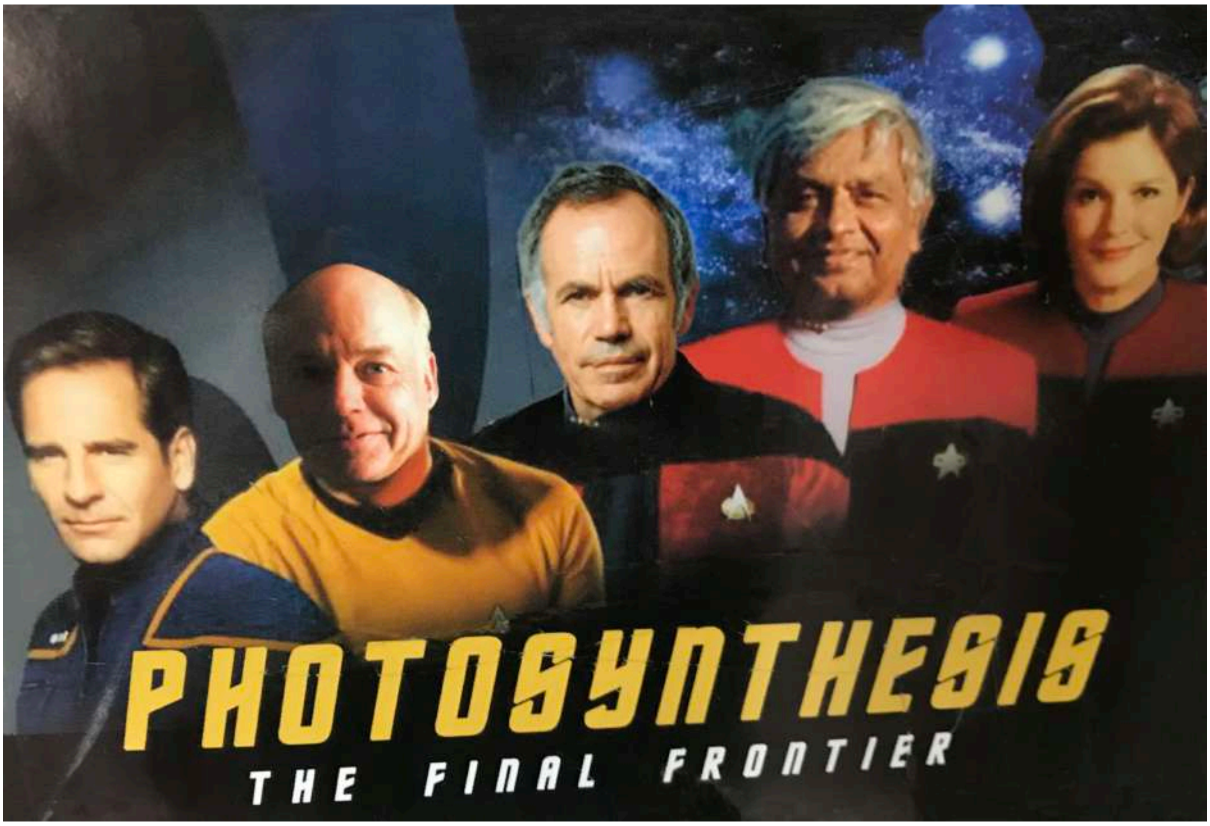
Supplemental Figure 1. See legend on the following page.

Supplemental Figure 1. Photographs of Govindjee at scientific conferences in the USA, Russia, Greece and India. **A**, Govindjee with Rienk van Grondelle at the Gordon Research Conference, 2019. **B**, Left to right: Rajagopal Subramanyam, Thriupathi Malavath, Govindjee, Nathan Nelson, Julian J. Eaton-Rye, and Tina C. Summerfield at the International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability, 2019, Saint Petersburg, Russia. **C**, Left to right: Győző Garab, an unidentified participant, Rajagopal Subramanyam, Govindjee, Rajni Govindjee, and Kostas Stamatakis, at the International Conference on Photosynthesis Research for Sustainability, 2015, Crete, Greece. **D,** Left to right: Marek Zivcak, Govindjee, and several students at the International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability, 2019, Saint Petersburg, Russia. **E,** A group photograph of Baishnab C. Tripathy, his research group, and their families, during the 2019 visit of Govindjee to Jawaharlal Nehru University (JNU), New Delhi. Left to right: Mehar Fatima, holding her daughter Zainab; Deepika Kandoi; Abhishek Gupta (Deepika's husband with their son Aryan); Satpal Turan; Anita Turan (their son Mayank is with Satpal; their daughter Avantika is with Anita); Rajni Govindjee; Padma Tripathy; Baishnab C. Tripathy; Govindjee; Kanchan Kumari; Garima Chauhan; V. Chandra Kaladhar (Garima's husband); and Ranjan Sahoo. Place: Near "Mezbaan", a favourite restaurant; host: Deepika Kandoi. Source: Archives of Rajni Govindjee, except for Figure 1E, which was provided by Barnali Padhi.

Supplemental Figure 2. Photographs of Govindjee with scientists attending conferences in the USA, India and Russia. **A**, Govindjee with Petra Fromme and Dorothe Eisele (in red dress, with two graduate students) at the Gordon Research Conference, 2019. **B**, Left to right: Govindjee, Barry Bruce and Suleyman Allakhverdiev, at Golcunda Fort area, Hyderabad, India, 2017. **C**, Left to right: Giovanna, Govindjee, and Cesare Augusto Mario Marchetti in Saint Petersburg, Russia, 2019. **D**, Kevin Redding, Roberta Croce, Govindjee, and Nicoletta Liquori, at the Gordon Research Conference, 2019. Source: Archives of Rajni Govindjee.



Supplemental Figure 3. An artist's rendering to focus on Photosynthesis for the Future. Left to right are: Jonathan Archer, played by Scott Bakula, from Star Trek Enterprise; Donald R. Ort; Stephen P. Long; Govindjee Govindjee; Captain Janeway, played by Kate Mulgrew, Star Trek Voyager. Image made by Hayley Ahlers (Department of Plant Pathology, Kansas State University, Manhattan, KS, USA)