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INTRODUCTION

Biology and biotechnological applications of microalgae and photosynthetic prokaryotes: part 2

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This issue of the *New Zealand Journal of Botany* is the second of a two-part Special Issue arising from the 3rd New Zealand Symposium on the Biology and Biotechnological Applications of Microalgae and Photosynthetic Prokaryotes. The first meeting took place in 2012 and was hosted by the Department of Biochemistry at Otago University (Eaton-Rye et al. 2014) and this was followed by the second meeting in 2015 held at the Cawthron Institute in Nelson in 2015 (Packer et al. 2017). The third meeting returned to the University of Otago and was held in February 2018 (Eaton-Rye et al. 2019).

The keynote speaker at the third symposium was Professor Susan Golden who contributed an article telling the story of the discovery and naming of *Synechococcus elongatus* which has served as an important cyanobacterial model organism for over 50 years (Golden 2019). Part 1 of this Special Issue also included an article on the expression of the *nifHDK* gene cluster in *Anabaena* sp. PCC 7120 heterocysts that encodes structural proteins of the molybdenum-containing nitrogenase enzyme (Kumar et al. 2019). This was followed by a review on microcystins in New Zealand (Puddick et al. 2019); these compounds are a common class of cyanobacterial toxins and the review documents their impact on New Zealand's native aquatic organisms. Part 1 then continued with a research article on the use of cationic polyacrylamide in harvesting algae from wastewater treatment high-rate algal ponds (Craggs et al. 2014; Park et al. 2019) and concluded with a system employing the cyanobacterium *Synechocystis* sp. PCC 6803 for studying the role of the PsbA (or D1) reaction centre subunit of Photosystem II – the light-driven water oxidase of oxygenic photosynthesis (Morris et al. 2014; Forsman et al. 2019).

The second part of this Special Issue collects together six further contributions covering a broad range of biological and biotechnological systems. The first article by Sutherland and Ralph (2020) sets out the progress and advantages of wastewater treatment high-rate algal pond technology in New Zealand. The potential for this technology to provide effective wastewater treatment in smaller and rural communities is discussed highlighting its ability to establish a circular bio-economy for wastewater cleaning, nutrient recovery and microalgal biomass production for reuse as fertiliser, feed or biofuel. In

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the next article, Handley et al. (2020) describe a system utilising cyanobacterial inteins from *Synechocystis* sp. PCC 6803 and *Nostoc punctiforme* PCC 73102 to create cyclic forms of bioactive peptides that offer the potential of generating bioactive peptides with improved stability for therapeutic applications. This is followed by a report from Güttler and colleagues describing the use of linear sweep voltammetry to assess the mode of electron donation from benthic cyanobacteria to an external electrode. This study found no evidence for the presence of redox mediators acting as electron shuttles and suggests electron transport from the benthic cyanobacteria examined may occur via direct electron transfer (Güttler et al. 2020).

The work by Khaing et al. (2020) describes an experimental system, employing *Synechocystis* sp. PCC 6803, to introduce mutations into two Photosystem II reaction centre proteins. These are the PsbD (or D2) reaction centre subunit and the PsbC (or CP43) chlorophyll-binding core antenna protein. Both of these proteins are encoded in a single operon. To demonstrate the system, mutations have been introduced to probe a putative interaction between the CP43 protein and the PsbT 5-kDa membrane-spanning subunit that is found at the monomer–monomer interface of the mature dimeric Photosystem II complex (Umena et al. 2011). The role of PsbT is further explored in the study by Forsman et al. (2020) where a *Synechocystis* sp. PCC 6803 strain (ΔPsbT) with its *psbT* gene inactivated has been characterised. The authors had previously found that the removal of PsbT resulted in an increased susceptibility to high light (Fagerlund et al. 2020). In the study included in this Special Issue the authors explore the influence of bicarbonate on mitigating the susceptibility of the ΔPsbT strain toward high-light-induced damage. A role for bicarbonate in electron transfer through Photosystem II has been recognised for many years (McConnell et al. 2012; Shevela et al. 2012).

Professor Govindejee is recognised as a leading expert on the use of chlorophyll fluorescence to study photosynthesis and for his pioneering studies on the role of bicarbonate in electron transport in Photosystem II. This Special Issue concludes with an article celebrating the extensive research achievements and other contributions of Professor Govindjee during his 20-year period as an Emeritus Professor of Biochemistry, Biophysics and Plant Biology at the University of Illinois at Urbana-Champaign in the USA (Stirbet et al. 2020). Professor Govindjee has made extensive contributions to photosynthesis research over a career spanning more than 60 years (Eaton-Rye 2013). Throughout his career Govindjee has worked with algae, beginning with his PhD thesis in 1960 focussing on the requirement for two pigment systems in the photosynthetic electron transport chain (Govindjee 1960) and continuing up to the present with a contribution investigating how regulating light-harvesting antenna size in green algae can substantially enhance photosynthetic efficiency and biomass yield (Negi et al. 2020). Similarly, Professor Govindjee has regularly used cyanobacteria for photosynthesis research (Govindjee and Shevela 2011).

Many who have worked with Govindjee during the past 20 years sent in their reminisces. The timing of this Special Issue also coincided with Govindjee's 88th birthday, and as word spread, many more colleagues and friends from across his illustrious career added to these tributes. We have gathered these into an Appendix to this Introduction. Together they show Govindjee's gift for working with beginners as well as established scientists with equal patience, appreciation and enthusiasm. We hear from five Nobel Laureates as well as recent postgraduate students. For example, Sir John Walker

notes Govindjee's 'deep engagement with science' and special ability to be 'an inspiration to younger colleagues'; we hear too from Dr Kamal Ruhil, who recounts how as a PhD student at Jawaharlal Nehru University in New Delhi, Govindjee sat with her for hours 'with immense patience' explaining how to write science and interpret chlorophyll fluorescence data. Many friends and colleagues of Professor Govindjee affectionately know him as 'Gov'. Professor Robert Blankenship from Washington University in St Louis, USA, who has known Govindjee for many years writes: 'the energy and enthusiasm that Gov has maintained for so long is a standard that no one else can ever meet' (see Figure 1).

We thank all the contributors to this Special Issue for their excellent submissions and all those who participated in the symposium. In addition, we would like to express our thanks to Associate Professor Chris Lusk, the senior editor of the *New Zealand Journal of Botany* and Fei He at the Royal Society Publications Office, as well as the staff at Taylor & Francis, for their professional an efficient assistance in bringing this Special Issue to completion.

21 November 2020

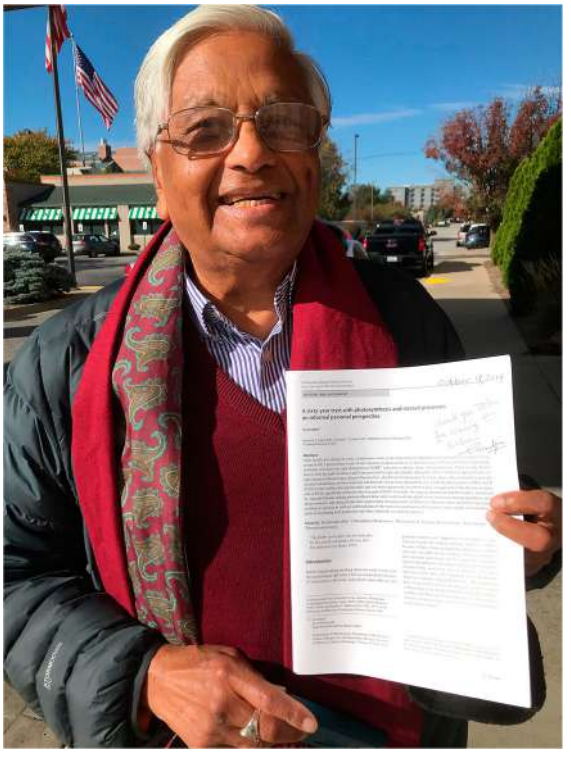

Figure 1. A 2019 portrait of Govindjee, holding his own paper on his 60-year tryst in research. Photo by John F. Allen.

Appendix

Tributes from friends and colleagues around the world celebrating Govindjee's 20-years of scientific contributions since retirement and his 88th *beiju* birthday.

Robert Alfano
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A festschrift to honour Govindjee's retirement and beyond

It is a great honour to recall my encounter with Govindjee for the 20-year anniversary of his retirement. He is well-known as a luminary for his understanding of the basic mechanism of light capture and excitation energy transfer in photosynthetic systems. My story about Govindjee centres around meetings I had with him during 'the early days' and parallels my personal quest to better understand the inner workings of primary events in plants following light absorption, which began in 1975 and continues still today in 2020. Oh, how those 45 years have passed by so fast – like a twinkle of an eye.

I started in the field of photosynthesis after a friend of Govindjee, Michael (Mike) Seibert, a biologist from the neighbouring building at GTE (General Telephone and Electronics, now Verizon) labs complex in Bayside Queens, NY, knocked on my lab door to see what was going on inside 'the room with those red flashing lights', as he put it. At GTE, many scientists had to pass by my lab on the way to the cafeteria. Naturally, most wondered what was going on with these red flashers on most of the day and into the night. Mike passed my lab on his journey to the cafeteria daily. One day, he came in and said he had heard I had a powerful short pulsed laser that could generate all colours (now known as the Supercontinuum). He was interested in using it to excite his sample – a 'green slime' in a flask. I immediately said 'No way! We heard you biologists are working on some weird material stuff.' He indignantly shouted: 'It's safe' and proceeded to drink it. It turned out to be a harmless suspension prepared from spinach leaves.

Stanley (Stan) Shapiro and I with Mike Seibert started to work on photosynthesis in 1971 at GTE labs and published our first paper (Seibert et al. 1973) on the primary kinetics of photosynthesis. A year later, the GTE labs were closed, and moved to Boston. Shortly after that time I moved to the Department of Physics at CCNY (City University of New York) to begin my academic career efforts in ultrafast laser research. Mike and I continued to study the primary events and mechanisms of photosynthesis, focusing on time-resolved fluorescence from spinach – *Popeye food*! This work utilised picosecond (ps) 532 nm green pulses, which were so intense that they caused exciton effects, which altered the primary events. Details on exciton effects at high intensity in millijoule range can be found in articles in my book on Ultrafast Laser Spectroscopy in Biology (Alfano 1982).

In late 1974, I came across one of Govindjee's classic overviews on 'Primary Events in Photosynthesis' (Govindjee and Govindjee 1974). This paper clearly explained and taught me the basics of primary events of photosynthesis, which I still use today. I was

so struck by his work that I contacted him in 1975 to seek advice on an underlying primary model of photosystem (PS) 1 and PS 2 from our picosecond time-resolved research. Since then, he has visited us many times at CCNY to discuss underlying photo-physics and quantum effects. Even Graham Fleming (from UC Berkeley) visited me together with Govindjee. To this day, I owe a great deal to Govindjee. I still remember his *funnel model* of the primary energy transfer of excited chlorophyll *a* (Chl *a*) to the reaction centre (RC) where thereafter the Z scheme takes over; one begins with about 300 or so Chl *a* antenna molecules located in PS units. Now this funnel model is being implemented to help explain new ultrafast optical research and to demonstrate the existence of quantum effects in photosynthesis (and furthermore, how quantum effects may be operational even in our brains!). The PS 2 reaction centre (RC) P680 and the PS 1 RC P700 are located at the heart of the *Z* scheme, and finally after many reactions, light converts $CO_2 + H_2O$ into O_2 and carbohydrate (sugar). For Govindjee's views on the evolution of the *Z*-Scheme, see Govindjee, Shevela et al. (2017), and on the primary photochemistry of photosynthesis, see Mirkovic et al. (2017). Even today, I seek Govindjee's advice on the funnel model to explain our latest work on photosynthesis, which highlights ps relaxation of the light emitted from chlorophylls in green plants, and the processes on the way to the RC. This new information shows whether quantum effects exist within the confinements of PS units. Recently, the size of PS 1 and PS 2 has been determined to be on a nanometre scale, where 300 or so molecules are packed in about a 10 nm region. Therefore, PS 1 and PS 2 in thylakoid membranes may be like quantum dot(s) (QD), where Chl *a* is coupled and emits fluorescence in an exponential decay manner. Most recently, together with Laura Sordillo, we have re-examined time-resolved emission from PS 2 (~690 nm) and PS 1 (~730 nm), from a spinach leaf, with better signal-to-noise (S/N) ratio and time resolution, using a 1 ps streak camera. From the observed single exponential decays in primary dynamics, we have concluded that a quantum effect is operational, using Dexter, but not Förster mechanism; this is so since all the 300 or so antenna Chl *a* molecules are packed within a 10 nm QD. Using intense short 100 fs pulses at a wavelength of 675 nm, which are weaker by about 1/1000 times than the 1974 work pumped by 532 nm, the emission time was longer at the higher pump intensity. The reason for the lifetime to be longer at high intensity and of shorter time at lower intensity can be explained by Govindjee's funnel model, i.e. a full funnel takes longer to empty than a less full funnel to the RC. The fluorescence continues until the excitations reach the RC.

Professor Emeritus Govindjee has made countless and key contributions with over 400 publications in the area of photosynthesis (see his highly informative web page: http://www.life.illinois.edu/govindjee/). Besides his scientific contributions, he is an historian of photosynthesis research. There is an informal private museum he has at the University of Illinois at Urbana-Champaign (UIUC) to help students and scientists learn about photosynthesis (https://news.illinois.edu/view/6367/801235). He continues to teach us that photosynthesis is the most important process used by plants and other organisms to convert light energy into chemical energy that can later be released to fuel the organisms' activities. This chemical energy is stored in carbohydrate molecules, such as sugars, which are synthesised from carbon dioxide and water and oxygen is given off. Let's all remember this as Govindjee emanates that photosynthesis is responsible for producing and

maintaining the oxygen content of the Earth's atmosphere and supplies most of the necessary energy and food for life on Earth.

Govindjee has been and continues to be at the heart of scientific research. Even in his retirement, he continues to give advice to help scientists, especially the younger ones around the world, to make key discoveries on the complex and baffling primary processes which occur in plants.

The overall process of photosynthesis takes place in four steps (the first three are within thylakoid membranes): (**1**) Energy transfer in antenna chlorophyll within femtoseconds to picoseconds; (**2**) Transfer of electrons in photochemical reactions within picoseconds to nanoseconds; (**3**) Electron transport and ATP synthesis within microseconds to milliseconds; and (**4**) Carbon fixation and export of stable products within milliseconds to a few seconds. We note that the above basic description was taken in part from Wikipedia, where Govindjee had helped to explain the process (for further details, see the classic 1969 book on 'Photosynthesis' by Govindjee, co-authored with Eugene Rabinowitch; available free at: http://www.life.illinois.edu/govindjee/; and a new short summarising book by Shevela et al. 2019).

Let me quote from what Diana Yates (https://news.illinois.edu/view/6367/801235) wrote: 'In the early days, some researchers debated the existence of two reaction centres in plants driving the two light reactions. At a scientific conference in the late 1960s, a researcher from another institution scribbled on Govindjee's poster that what is now universally accepted as a second reaction centre in the photosynthetic pathway was nothing more than an Illinois Fantasy'. Clearly, it was in 1964 that Govindjee had hinted (Krey and Govindjee 1964) in a Proceedings of National Science Academy USA paper the existence of 'Trap II' (also, see the Scientific American paper by Rabinowitch and Govindjee (1965), for the very inclusion of 'P680', long before its discovery).

Well this critical view has now passed – now the problem ahead, even after the pioneering work of Graham Fleming and Robert Blankenship on the existence of quantum effects in Bio media, is whether 'Coherence and Quantumness' (meaning the coherence in quantum mechanics) is not a sufficient condition – it appears that some of the critics of this notion do not know or have the information that the primary photosynthesis action occurs on the nanometre size of the PS units. From nm size, one needs to conclude from Quantum Mechanics in the PS unit of nanometre size, that quantum dots are quantised among excited 300 or so Chl *a* molecules and packed into the size of a QD – so quantum does exist! Most recently, we, Sordillo and I, have been working on time-resolved fluorescence with faster response and better S/N to show QD PS primary events exhibiting quantum behaviour.

Did Govindjee really retire in the August of 1999 and did he really stop running a lab since then, almost 20 years ago? Or is he now one of the luminaries of our time continuing on spreading the gospel of his knowledge and opinions on photosynthesis in the worldwide laboratory?

We urge Govindjee to continue as before, and help us, even after his 88th birthday on 24 October 2020!

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The name 'Govindjee' (Gov to me) has long been a key word in any account of research on photosynthesis. I first came across it in 1971, when 'Photosynthesis' by Rabinowitch and Govindjee (Wiley 1969) was a set book for an undergraduate course given by M. C. W. ('Mike') Evans at King's College London. That book was an inspiration. At King's, in the Plant Sciences Department headed by F. R. ('Bob') Whatley, photosynthesis was viewed from a biochemical perspective as electron transport and coupled ATP synthesis – 'photophosphorylation' – in isolated chloroplasts, and driven, in some slightly mysterious way, by light energy. Eugene Rabinowitch and Govindjee complemented this approach by explaining the importance of the quantum yield, the action spectra, the Emerson enhancement effect, and the biophysical discoveries of Robert (Bob) Emerson and William (Bill) Arnold.

I first met Govindjee in Urbana, Illinois, in January 1980, when I found myself working in the lab next to his – the lab of C. J. ('Charlie') Arntzen. Gov was a character; a charming and benevolent neighbour. I soon discovered that my project in Urbana in some way connected the biochemical ideas of 'Daniel (Dan) Arnon and Bob Whatley', with the biophysical, views of photosynthesis of 'Emerson and Arnold'; and, thus, there was this connection!

For me Gov has continued, to the present day, to be a photosynthesis '***éminence grise*'.** He knew everyone, understood what they had done, and took an almost paternal interest in the entire field. As we see in this celebration, his knowledge is encyclopaedic, and his activities wide-ranging.

I took it as a singular honour when Gov invited me to contribute to Part One of the 'History Issues' of the journal *Photosynthesis Research* (Allen 2002). It was even more of a compliment to be promoted to be a co-editor, with Howard Gest, Thomas (Tom) Beatty, and the inimitable Govindjee himself (Govindjee et al. 2005).

It is astonishing that one man can continue, long into retirement, to publish at such a pace as Gov. His energy and enthusiasm are undimmed. I can vouch for this conclusion on the basis of a whirlwind visit back to Urbana in October 2019, where Gov generously organised my seminar in the Carl R. Woese Institute for Genomic Biology, having conjured up an extremely well-informed audience at short notice. On my departure, Gov very kindly made sure I got the right shuttle bus to Chicago, even asking someone in the bus queue to make sure that I knew where and when to get off at O'Hare. Kindness itself. (See Govindjee's photograph in Figure 1).

I thank you, Gov, for all these things over so many years. Keep going, please. You are irreplaceable, and an international treasure**.**

Charles J. Arntzen
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On the occasion of Govindjee's 88th birthday, let me add to the chorus of congratulations to him. I've known Gov since I joined the University of Illinois at Urbana-Champaign (UIUC) faculty in the Department of Botany in 1970 and have followed his illustrious career since that time. He is really amazing – even in retirement he continues to

inspire his former students and colleagues through scientific reviews and historical reports.

When I joined the UIUC, I was assigned a laboratory adjacent to that of Govindjee. His lab was a treasure house of equipment for photosynthetic analysis, and even included some of those used by Robert Emerson back in the days when the university was first becoming known as a '*Mecca for Photosynthesis Research*'. I had the pleasure of getting to know many of Gov's students, and to join in our interdepartmental seminars – which tended to pit the 'light reaction guys' against the 'dark reactioners' (led by William (Bill) Ogren in the Department of Agronomy at UIUC). Our friendly seminar debates often focused on what was the most important rate limitation in photosynthetic productivity. Gov, of course, was on the side of light harvesting efficiency and Bill, of course, championed the role of RuBisCO since he was actively showing its pivotal role in photorespiration. It was a marvellous time to be a part of this highly active community as many new faculty members were added to encompass photosynthesis from nanosecond spectroscopy to ecological studies of crops. Throughout this time, Gov was always a *Grand Old Man* of the photosynthesis gatherings (even when he was still a young scientist!). Parties at his home, with Rajni sharing the hosting, were always fun with lots of inspiring science thrown in. And parties that Gov invariably organised over dinner at international meetings were equally memorable. He is a naturally gregarious and delightful individual.

Govindjee's earliest work on the Emerson Enhancement Effect and his quantum yield studies using the green alga *Chlorella* in the 1960s positioned him to become one of the central champions of the emerging Z-scheme for photosynthesis. By supporting the idea of two light reactions, he was pitted against more senior researchers, such as Daniel (Dan) Arnon at Berkeley, who argued for a simpler concept. Over the next decade the accumulating data overwhelmingly supported Gov and the other scientists who continued to define the components of the photosynthetic electron transport system involving Photosystems I and II (very nicely described in a historical review by Govindjee et al. 2017). Further, Gov's students/postdocs made many other discoveries relating to forms of chlorophylls in photosynthetic membranes, the role of bicarbonate in regulating electron transport, and others too numerous to elaborate here (see his earlier publications at: http://www.life.illinois.edu/govindjee/pubschron.html; and recent ones at http://www.life.illinois.edu/govindjee/recent_papers.html). I congratulate him and salute him as a friend and colleague of many years. I hope to keep tracking his contributions and write another congratulatory note on his 100th birthday!

Glenn W. Bedell

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Govindjee is an outstanding teacher and scientist. I enjoyed working, under his mentorship, in his lab, during the late 1960s and early 1970s at UIUC, and getting to know him and his wife, Rajni, both academically as well as socially. Furthermore, I have greatly appreciated his unique efforts to review and condense the research efforts of researchers and faculty around the world, who have contributed to understanding the basic mechanisms of photosynthesis.

I especially appreciated his efforts to recognise and acknowledge the research of others who contributed to his research either directly or indirectly. He provided me with knowledge and understanding of plant physiology, together with the opportunity to learn both electronics and the fundamentals of machine-shop technologies that have enriched my professional life.

One of my earliest research efforts, under his leadership, was the precise measurements of the maximum quantum yield of oxygen evolution and the existence of two light reactions in green algae grown in heavy water (D_2O) instead of normal water (H_2O); this work was published in *Science*. It supported Robert Emerson's conclusions instead of those by Nobel laureate Otto Warburg (see Bedell and Govindjee 1966). However, for my PhD thesis, I worked in an area that was not in the mainline of Govindjee's lab at all: '*Photophosphorylation in Intact Algae*,' as measured by the luciferin-luciferase method. For this, with the full support and encouragement of Govindjee, we built the entire system from scratch (see Bedell 1972; Bedell and Govindjee 1973). To me, this experience reflected the open-minded attitude of Govindjee. However, he was very tough and demanding, and spent hours in correcting, condensing, and editing my usual long texts.

Recently, Govindjee has been extremely helpful in encouraging me to publish my 30 years of work on my discovery and development of plants, that when dead, are capable of rapidly (24–48 h) converting some 50^+ metallic ionic elements into 100% pure metal crystals (as large as 60 microns, in some cases).

In short, I learned a lot from being his graduate student – and I have used these tools in my academic as well as in my current entrepreneur life. I am delighted to celebrate his highly productive 20-year retired life, and to congratulate him on his 88th birthday on 24 October 2020!

Robert E. Blankenship
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Govindjee 'retired' a little over 20 years ago. There was a retirement symposium at UIUC on 14 October 1999, to which I was an invited speaker. At that time, no one imagined that his would be the most active and productive retirement ever in the field of photosynthesis. He has continued a remarkable schedule of travelling, lecturing and mentoring, the latter especially for younger scientists.

Now that I am retired myself, I look to Gov's example as a model for my own retirement. However, the energy and enthusiasm that Gov has maintained for so long is a standard that no one else can ever meet.

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I was in Govindjee's lab as a post-doc in the late 1960s. It was a wonderfully friendly and productive place, and Govindjee excelled as a teacher, being both knowledgeable and enthusiastic, yet able to challenge our research work**.** To be honest, my contributions were limited to being an assistant to others for I lacked the skills and knowledge to

make original contributions to the programme. However, Govindjee never treated me as second-class; he was always so encouraging, kind, cheerful and upbeat. While I respect Govindjee for all the superb contributions he has made in the field of photosynthesis, I respect him even more for his qualities as a caring human being.

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Congratulations to Govindjee (Gov to me) on the occasion of his 88th birthday and his 20 years of retirement from the University of Illinois at Urbana-Champaign (UIUC)!!! Thinking back to my graduate days at Illinois during 1968–1971, I so fondly remember my formal connections with Gov and his laboratory in the Botany Department, first in a *Plant Physiology* course and, subsequently, in the *Photosynthesis* course offered by him and William (Bill) Ogren in 1969. This latter advanced course, both rigorous and stimulating in its content, was truly instrumental in my pursuing 35^{+} years in photosynthesis research after I left UIUC with my MS and PhD degrees! Beyond the more formal aspects of this lecture/lab course, I became very fond of several of my fellow classmates who later became highly established plant scientists, including Alan J. Stemler (now Emeritus at UC-Davis), the late Prasanna K. Mohanty (1934–2013), the late Thomas (Tom) Guilfoyle (1947–2017) and, tragically, the late Maarib D.L. Bakri Bazzaz (1940–2020). I am also greatly indebted to Govindjee for serving as my 'proxy' doctoral advisor in the department when my original mentor, Dominick (Dom) Paolillo, relocated to Cornell University, and I migrated to Bill Ogren's USDA-ARS laboratory to finish my PhD research on greening in a virescent mutant of maize, a C_4 plant (see Chollet and Ogren 1972; Chollet and Paolillo 1972). Yes, there was a direct connection with Gov because of a subsequent mutant study of Maarib's and his with Dom Paolillo (see Bazzaz et al. 1974). For all of the above and much more, I thank you immensely Govindjee! All my personal very best to Gov – Ray.

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I joined the Govindjee lab at the University of Illinois at Urbana-Champaign after graduating from the University of Pennsylvania in 1979. I was seeking a challenging thesis project, and so I chose to work on the oxygen-evolving complex of Photosystem II (PS II), ultimately receiving my PhD in 1987. Working in Govindjee's lab was a great experience because he provided a meaningful context for everything he taught and discussed, so that ideas and technologies were never just floating in a vacuum but were instead part of the intellectual continuum of photosynthesis research. Govindjee also encouraged people to work together and to seek out fellow scientists who might provide useful insights and advice. I always felt that I had significant freedom and responsibility in defining my thesis work, something that not all graduate students are allowed to benefit from, and it helped me to become an independent thinker. I believe I still follow that same scientific path today, and that is a tribute to his positive influence. Our detailed work on chloride

activation and the oxygen-evolving complex has been summarised in several reviews (Coleman and Govindjee 1987; Coleman 1990; Govindjee and Coleman 1990).

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Thanks and Best Wishes on the occasion of his LXXXVIII birthday to Govindjee for his conceptual, experimental, pedagogical and entrepreneurial contributions to the understanding and teaching of the basic and applied concepts of photosynthesis.

Mrinmoyee Das
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I know Dr Govindjee since 1965 when I joined the Department of Botany and the Program in Biophysics at the University of Illinois at Urbana- Champaign (UIUC) as a post-doctoral research associate with Professor Eugene Rabinowitch. Govindjee's laboratory was just next door. I describe here some memories about Govindjee, the person, he is! The following is mainly a personal recollection.

I reached the Champaign airport in October, 1965, all the way from India, and it was a cold late night; further, there was a heavy shower and storm. Professor Rabinowitch was in Europe, and Govindjee came to pick me up from the airport and drove me all the way to his house in Urbana, where I was warmly greeted by his wonderful wife Rajni Govindjee. It was the first time I had left my family and I was feeling helpless. It is Govindjee who spent the entire next day to help me complete my University formalities. I stayed in their house until I could rent an apartment of my own with the help of Govindjee. It was not only that he helped me this way, but he helped equally all the newcomers to the laboratory: whether his own or that of the others. All what I just wrote speaks highly of his friendly and caring nature.

I had a PhD in Physical Chemistry and had little idea about research in Photosynthesis. Without hesitation, Govindjee helped me search the literature about Photosynthesis, and even taught me how to handle the instruments installed by him and his research students. As a result, I learned a lot about this field of work before Professor Rabinowitch returned to the Lab. I will also never forget about his cooperative spirit in research (see e.g. Das and Govindjee 1967; Rabinowitch et al. 1967; Das and Govindjee 1975 – the last one completed long after I had left UIUC).

Govindjee had his own research group of very bright graduate students coming from different parts of the world, and different background. He treated them like his friends and always encouraged them whole-heartedly in their work. His research group was like one big family. All his students and postdocs had great respect for Govindjee, their real teacher. Every week they would meet in Govindjee's home to discuss their current research and plans for future experiments; fortunately, for me, I could also join. Govindjee's wife Rajni was also in the same field and she used to treat us with wonderful snacks after the discussion. Govindjee has been a very hard-working person, and always full of energy during his entire life. I pray that in his future retired life (he has already completed 20 years!), he will be equally energetic and will live a long healthy and a peaceful life with his lovely family.

Denise Devotta
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I have fond memories of Professor Govindjee excitedly sharing the latest breakthroughs in photosynthesis research with me whenever we bumped into each other in the hallway of Morrill Hall at UIUC. Having known one of the giants in photosynthesis research at UIUC continues to make me proud to be an alumnus of this great University. Congratulations to Govindjee on his 88th birthday and his 20 years of highly active retirement! May he continue to inspire people of all ages for many more years to come!

Sailaja Elchuri
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One fine morning on 24 November 2014 I received an email from my post-doctoral research mentor Dr Ting Huang (Stanford University) that Govindjee, Professor Emeritus, Biochemistry, Biophysics and Plant Biology of the University of Illinois at Urbana-Champaign, was looking for me as he was writing a tribute on my graduate advisor Prof V. S. Ramadas, popularly known as VSR, a renowned photosynthesis researcher from India. I must have read the email several times, just to believe that the iconic researcher of Photosynthesis, Govindjee, has really asked for me to help him with the tribute. I felt privileged that he had chosen me to help him write, rather than other illustrious students of my professor who had contributed significantly to the field of education and photosynthesis research in India. Immediately, I sent him an email about my willingness to write and, in the process, introduced myself. I remembered my University library hosting an entire shelf of books written, and, or edited by Govindjee – several assignments had been given to us by our teachers that required reading of Govindjee's reviews to answer the questions. During my 5 years of research under VSR, there were numerous occasions when he would remember Govindjee fondly and tell us about their association, in the 1950s, at the University of Allahabad. VSR and I would discuss numerous research papers of Govindjee. When I received the direct email on 27 December 2014, I was awe struck that I received a personal communication from Govindjee – and I treasured his correspondence with me. We finished our tribute to VSR together for the Historical Corner of *Photosynthesis Research* (Elchuri and Govindjee 2016). Thus, started our association for the past 5 years. I am delighted that he regularly keeps contact with me. It amazes me how tirelessly he conducts research at the age of 87 in addition to bringing to light the lives and research contributions of researchers in the field of Photosynthesis. The biographical accounts he has written provide inspiration to the younger generation who want to pursue their carrier in research. He has certainly ignited the spark of research fire in me and several other students and colleagues I know. I wish him many fruitful years of research ahead along side his towering presence in the field of photosynthesis.

Graham R. Fleming
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Govindjee's insatiable desire to keep learning about the infinite complexity of photosynthesis is both inspiring and infectious. He is special since he has connected across generations and across continents. He has my very best wishes to continue to inspire and to teach us all for a long time to come. – Graham

Ralphreed A. Gasanov
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Dear Govindjee: 88 is not 100 or even 90 and not 85 at all! So just go ahead and I follow you, 'One for all – and all for one' like the Three Musketeers by Alexandre Dumas. The prototype of which you once saw in our photo after the 10th International Photosynthesis Congress in Montpellier, France in August 1995 which was signed by you 'THREE Musketeers'.

I am sure that we will have a face-to-face meeting in the near future at some next symposium. Long creative years to you! – Yours, Ralph

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It is with sincere respect and with good memories that I briefly recount my time and experiences with Prof Govindjee. One of the things that I learned early on from Govindjee is that to solve problems in biology, we must interact with physicists. Thus, one of my earliest projects in Govindjee's Lab was in learning Mössbauer and ESR spectroscopy. However, exploitation of chlorophyll (Chl) *a* fluorescence to solve basic problems in photosynthesis was the '*living thing*' in Govindjee's Lab; this is what I decided to do for 2.5 years, which included close interaction with other physicists, who were biophysically oriented (Peter Debrunner; Theodore Hazlett; and Vladimir Shinkarev) – all encouraged and enthusiastically supported by Govindjee. We utilised frequency-domain Chl *a* fluorescence lifetime distribution measurements and global analysis methods that were pioneered earlier by Govindjee (Govindjee et al. 1990, 1993). We published four detailed papers (Gilmore et al. 1995, 1996a, 1996b, 1998), summarised in an overview by Gilmore and Govindjee (1999). They provided key information on the basic mechanism of how plants protect themselves against light through the use of the xanthophyll cycle and non-radiative dissipation; further, these experiments provided new information on how the light-harvesting antenna size affects this process. Our work has been recognised and heavily cited (see Hu et al. 2020). The publications resulting from this experience with Govindjee have played a key role in forming the basis of the rest of my academic, then later industrial, career. My association with Govindjee did not end here: when I went to the Australian National University (ANU), I met a 'star' student of Govindjee, the late Thomas (Tom) J. Wydrzynski (see e.g. Govindjee et al. 2018). Further, my research at ANU was in an area that Govindjee loved: designing a state-

of-the-art frequency domain lifetime instrument and developing global analysis methods that allowed me to understand how evergreen eucalypts adapt to winter conditions through reversible changes in their Photosystem II (PS II) apparatus associated with the xanthophyll cycle pigment composition, which included a new Chl *a* fluorescence band at 77 K, which we termed the 'cold-hard-band' (see e.g. Gilmore et al. 2003). I felt sure that Govindjee would appreciate this new fluorescence band in nature since he had already discovered several during his career (see Govindjee 2019).

It was my pleasure to host, while I was at ANU, Govindjee, as well as my PhD advisor Harry Yamamoto and my first postdoctoral advisor Olle Björkman. It was during 1999 when I attended Björkman's retirement symposium in Napa California that I met my future wife, Xiaoping Li, and her mentor Kris Niyogi. Soon thereafter, Xiaoping brought PsbS protein mutant plants to ANU. There, we asked if the PsbS mutants could be studied and interpreted in the framework of our aforementioned Chl *a* fluorescence lifetime distribution work, done earlier with Govindjee. We were in fact able to correlate the effects of PsbS on non-radiative dissipation with photoprotective capacity in higher plants and algae. It is with great pleasure I mention that our wedding, in 2003, was attended by a number of our mutual friends and colleagues, including Govindjee and his wife Rajni. In late 2003 I joined HORIBA Jobin–Yvon Inc. as a fluorescence applications scientist and was glad to have a strong recommendation from Govindjee. I was and still am able to capitalise on my experiences in time-resolved fluorescence learned during my research with Govindjee. During my tenure at HORIBA, I have had many a rewarding correspondence with Govindjee, especially during the Holiday season. *I never cease to be amazed at his energetic and still highly academic approach to retired life.* I have spent many hours enjoying his historical perspective articles on the topic of photosynthesis. It is my sincere hope that he continues these pursuits for another 20 years. In closing Xiaoping and I both wish Govindjee, his family and colleagues all the best for the future and thank him for his generosity and support over the years!

Ya (David) Guo
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Govindjee is especially interested in the study of photosynthesis using chlorophyll fluorescence and has made this research field a very special one. I am really lucky to know him, and to also communicate with several of his recent research collaborators, such as Alexandrina (Sandra) Stirbet (in the USA), Dusan Lazar (in the Czech Republic) and Xin-Guang Zhu (in China).

My first interaction with Govindjee dates back to 1 February 2007 when I was a second-year PhD student at the University of Missouri, USA. I sent him an email at 9:51 pm with five questions on chlorophyll fluorescence, and, surprisingly, by 11:33 pm, I received his detailed answers to all my questions! I would like to mention that both my BS and MS degrees were in mechanical engineering; thus, chlorophyll fluorescence and photosynthesis were brand new to me. I was deeply impressed by Govindjee's dedication to this research field and his willingness to help others, but his promptness in replying my email puzzled me, until I met him in person after we had communicated via emails for more than 10 years!

In November 2018, I invited Govindjee to attend an international conference on modelling, held in Hefei city, China, as a keynote speaker. He was 86 years old at that time but was very energetic. His speech at the conference was very interesting and convincing, and everybody wanted to really get to know him personally. During that time, Hefei was very cold with snow, and Govindjee caught a very bad 'cold' with fever, and had even lost his voice; thus, I took him to a hospital. On the next day, I tried to persuade him to stay in his hotel room to rest, but he insisted to go to the conference, because '*a seat had been reserved for him with his name on it*'. His participation made the conference really special, and he won the respect of many scientists from all over the world.

After this conference, Govindjee visited my lab at the college of IoT (Internet of Things), at the Jiangnan University. We talked about our research for many hours every day he was there with us. Further, he delivered to the students a lively presentation, which lasted for more than two and half hours, even though I had scheduled it for just one hour! He talked, with great enthusiasm, standing on the podium, without a break, even for a single moment. I invited Govindjee to visit several tourist attractions, but he agreed to visit only one: 'Ling Shan Grand Buddha'. We climbed 216 stairs before reaching the 88-meter-tall Grand Buddha. My wife (Juan Liu) and I really wanted to help him, but he politely declined our offer. His perseverance and momentum were amazing. Both my wife and I doubt that we could do this when we will be in our eighties**.** I appreciate very much all the help he has given us in writing our papers, and I wish him good health. We are really very proud of our joint papers on modelling (Fu et al. 2020; Stirbet et al. 2020) as well as on network analysis of published work on chlorophyll fluorescence (Hu et al. 2020). I do hope that the actual situation with Covid-19 will be gone soon, and all the eager worldwide photosynthesis scientists can meet Govindjee again to discuss their research and witness his charisma!

Saber Hamdani
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I am very happy and grateful to have been invited to participate in this tribute in Govindjee's honour. This is an opportunity for me to offer to Govindjee my gratitude and respect. I have known him since 2013, when Prof Xinguang Zhu had invited him to our lab in Shanghai, China. I remember that when he left, after spending 7 days with us, I wrote the following sentence to express my gratitude and respect for him: '*China has the Great Wall, but Photosynthesis has the Great Govindjee*'. This sentence was highly appreciated by Govindjee, as well as what I published with him on problems related to finding the best varieties of rice and best light conditions to get the best yield (see e.g. Hamdani et al. 2015; Hamdani, Khan, et al. 2019; Hamdani, Wang, et al. 2019).

Hans Henrich Hock
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I am delighted to celebrate the 88th birthday of my friend Govindjee as well as his 20-years of 'retired' life through the following **ślokas** (Sanskrit verses). His name *Govinda*

गा न विन्दति गोविन्दो गोनां सस्यं यथा रोहेत् ।
स एव तस्य विद्यार्थः सूर्यप्रकाशश्लेषणम् ।।

Govindjee does not search for cows - How the fodder of cows might grow
that is his research goal - photosynthesis through the splendor of the sun.

यद्वित्तं विदितं च यद् सर्वमेतत्प्रकाश्यते ।
विद्यार्थिनां च गोनां च हितार्थे गोपशासिना ।।

What has been found out, what is known, all that is published
for the benefit of both scholars and cows by the Lord of the Gopas (cowherds)

वसुधैव कुतुम्बकं गोविन्दस्य विवित्सया ।
गोसस्यरोहणज्ञानम् अर्बाना तस्य गोकुलम् ।।

The whole earth is a family because of Govindjee's desire to search
(on) the knowledge of how cows' fodder grows. Urbana is his Gokula or home.

Figure 2. Sanskrit 'shlokas' (and their translation) for Govindjee by Hans Hock; see text.

ultimately derives from ***go-pa-indra*** 'the Indra (chief) of cow-protectors or cow herds'. He has explored the process of 'Photosynthesis' which gives all of us, including the sacred cows, food and oxygen to live with, and he is also their protector in the ślokas in Figure 2. Yes, the cow's fodder grows through photosynthesis!

Oliver Holub
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Showing the white feather: It has been a great pleasure that I had the opportunity to apply real-time fluorescence lifetime imaging to the field of photosynthesis research, which never would have taken place, if there would not have been Govindjee. Experiments with such complex objects as plants require a lot of precautions. It requires somebody who has the overview of photosynthesis research. And hardly anyone has the awesome lifelong knowledge as Govindjee has in the field of photosynthesis. I have wonderful memories of my time in Urbana-Champaign at the Laboratory for Fluorescence Dynamics. One 'Photosynthesis Retreat' with Govindjee at the Robert Allerton Park in Monticello in 2001 is still on my mind. The location created a wonderful atmosphere for discussing our work and to learn a lot about the ongoing

photosynthesis research. Together with Govindjee we published some of the very first and detailed measurements on fluorescence lifetime imaging in the field of photosynthesis (Holub et al. 2000, 2007). I have already written down some of the memories regarding Govindjee (see Eaton-Rye 2007). There I had remarked on the many interesting items, which could be seen in Govindjee's laboratory. Several parts of old classical instruments were donated by Govindjee to the late Robert (Bob) Clegg (1945–2012; https://physics.illinois.edu/people/memorials/bob-clegg), my thesis advisor, for the building of his laboratory. One day I was walking in Govindjee's lab and saw *a box of long white feathers*. I think they were goose feathers and I really could not guess their intended use. Govindjee told me that they were used to clean optics in the old times. At every visit one learned something new from Govindjee. I was delighted to learn that he is exhibiting some of his treasures now in 'Govindjee's photosynthesis museum' (see https://news.illinois.edu/view/6367/801235) and of course the feathers are on display there. My heartiest congratulations to him on his 20-years of retired life and his 88th birthday.

Sagarika Jaiswal
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It is inspiring to me that Govindjee has contributed so much to academia for this long and so well! He has always encouraged all the students to push their limits for learning beyond the confines of the books and the classrooms. I have admired his amicable nature and infectious energy both while teaching and during informal chats about science over coffee. Govindjee has always been approachable and it is incredible that he could hold discussions about any topic under the sun (pun intended). I am, and so are most of my batchmates and friends, glad that we had the opportunity to learn from him (see how elegantly, and with dedication, he teaches the Z-Scheme of photosynthesis both 'indoors' (Jaiswal et al. 2017) and 'outdoors' (Mohapatra and Singh 2015)). We all hope that he would continue to inspire many more wide-eyed students, preparing to embark on the journey of scientific enquiry to solve the problem of 'food' and 'energy' for all by really improving photosynthesis and plant productivity. We thank him once again for all his wisdom and kindness.

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Some reminiscences on Govindjee: As an undergraduate, I studied engineering physics at the University of Illinois at Urbana-Champaign (UIUC) and included courses in radiation biology and biochemistry. I began graduate school at Johns Hopkins (Baltimore, MD), studying biophysics. I was not happy in Baltimore but read an article about photosynthesis by Govindjee in Scientific American (Rabinowitch and Govindjee 1965). On a trip home in Joliet, Illinois, I went to visit his laboratory at the UIUC. Govindjee was very welcoming and showed me his laboratory and I remember the large algal growth room and the world-famous Robert Emerson's manometers. Govindjee encouraged me to apply to graduate school and the UIUC's biophysics programme. All was successful and I returned to UIUC and entered Govindjee's laboratory. I remember not knowing

much biology but Govindjee assured me that physicists were important for understanding the 'physical' side of photosynthesis. He always made students feel they could contribute if they worked hard. I took my master's degree in 1971 and then went off to work for the US Navy. I was drafted during the Viet Nam war and volunteered for the submarine service. In 1974, I wrote Govindjee about my ending Navy service. He responded immediately and strongly suggested that I return for my doctorate work. By now, I had read another overview by him, also in Scientific American (Govindjee and Govindjee 1974). Again, Govindjee was a pivotal influence in my life as a scientist. He helped me obtain an assistantship and fellowship support (an Emerson Fellowship) and made room for me in a very busy laboratory. I completed my PhD in 1977, publishing papers on the topic of charge stabilisation in Photosystem II (PS II), which included measurements on thermoluminescence, but mostly on delayed light emission (Jursinic and Govindjee 1972, 1977). Two major conclusions dealt with as to where bicarbonate functions (Jursinic et al. 1976; in collaboration with Joe Warden) and how membrane potential affects these PS II processes (Jursinic et al. 1978, in collaboration with the late Colin Wraight (1945–2016); see Govindjee et al. 2016). Govindjee welcomed me into his laboratory twice, made me a much better writer (a lot of red ink on my drafts of papers), and gave me an opportunity to contribute to photosynthesis as a physicist. Yes. I do remember that he often did not understand my jokes and asked me to raise my left hand when I was joking! I am forever grateful for the guidance and encouragement I received from Govindjee, now legally Govindjee Govindjee (not a joke!).

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It has been more than 10 years since I have known Govindjee. I am lucky to have a close association with him and he has always been a source of motivation and inspiration to me. As a student, I always look up to him. I have been fortunate enough to reach out to him whenever I get stuck in my thoughts or when I am looking for a different perspective. With his unprecedented insight in all aspects of photosynthesis, I consider Govindjee to be synonymous with photosynthesis.

I still remember the insightful discussion my advisor Professor Baishnab C. Tripathy, and I used to have with Govindjee – continuing even during lunch and tea breaks. Even today, when Govindjee is in his late 80's, his energy and quest of knowledge is unique. Govindjee has strong work ethics and at same time he is humble and easy to approach. I have always found reaching out to him to be a cinch!

I am also lucky to have met Rajni, Govindjee's soulmate, an equally intelligent and insightful person. I still remember her – while having a discussion with Govindjee on one of our topics – Rajni Ji pitched in and suggested us the ways to do the experiment, something which she must have done 50 years back!

In terms of research collaboration, I am happy to have co-authored a paper with him on overexpressing phosphoenolpyruvate carboxylase (PEPC), a C4 enzyme, from *Zea mays*, into a C3 plant, *Arabidopsis thaliana* (Kandoi et al. 2016). I must say that the journey to finalise this paper was really fun and insightful. I am very happy that I have a mentor like Govindjee. I am lucky to continue staying in touch with him as the

experience and the knowledge shared by him is just priceless! Even today, we are working with him – on a daily basis – on another paper related to the benefits we will have in transferring PEPC, from *Flaveria bidentis*, into *Arabidopsis thaliana* (D. Kandoi, K. Ruhil, G. Govindjee and B.C. Tripathy, manuscript in preparation). Of course, the idea is to transfer this technology to rice. I wish Govindjee the best in his great desire to remain a perpetual student of photosynthesis and help us all in solving problems ahead of us!

Naveed Khan
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I just finished my PhD under the supervision of Prof Xinguang Zhu. I want to share my thoughts on Prof Govindjee at the celebration of 20 years of his retired life! We all know that he has really contributed a lot in the field of Photosynthesis. His kind, gentle and admiring nature encourages many young scientists to work in this field, and he has really helped me with his deep knowledge and experience. I have benefitted much from his professional advice; he has always been very encouraging to me. I feel really lucky to have had the opportunity to work with him, and to understand the work in my very first paper and that too on an important crop of rice (see Khan et al. 2020) in this field; this work was completed with his guidance and his advice. May God, the Almighty, keep his shadow on us forever and grant him a long life.

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Govindjee has had a distinguished career in the field of photosynthesis. His reputation is truly legendary, and he is regarded as one of the pioneers in the field. The field has and will continue to benefit from his deep and encyclopaedic knowledge. I feel very fortunate to have had the opportunity to work under his guidance. I am also ever so grateful to him, Rajni and the Govindjee family for providing me a home away from home when I first came to Urbana in 1974; I cherish the warmth and friendship that he has continued to extend over the years. Being part of Govindjee's research group was not only a great learning experience but I was also able to develop bonds with others who were part of the 'Photosynthesis Family' at the University of Illinois at Urbana-Champaign (see e.g. our research papers: Khanna et al. 1977, 1981, 1983; Freyssinet et al. 1980), and with others around the world (see e.g. Siggel et al. 1977; Gasanov et al. 1979; Khanna et al. 1980). Reflecting his unstinting commitment to advancing the scientific understanding of photosynthesis and to those who have worked in the field, he has stayed actively engaged in the field since his retirement 20 years ago. Govindjee has continued to make scientific contributions through collaboration with colleagues all across the world and has generously sought to highlight the contributions of others by taking the lead in inviting others to join in writing memorials for his colleagues, and his own former graduate students (see e.g. Govindjee, Munday, et al. 2017; Govindjee et al. 2019; Govindjee, Nonomura, et al. 2020; Govindjee, Zilinskas, et al. 2020).

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Govindjee was a key figure in bringing me, then a budding NASA astrobiologist, into the field of photosynthesis. I came from the field of 'ecosystem science' and 'remote sensing' and was struck by the vegetation red edge – a reflectance feature of plant leaves – as a potential 'biosignature' for detecting life from space. However, I was not educated in the rich body of work around photosynthetic light harvesting and came to Govindjee for help. He provided me with a solid disciplinary context for understanding the precise literature history of photosynthesis. In two seminal 2007 papers on 'Spectral Signatures of Photosynthesis' in 'Astrobiology' (Kiang, Segura et al. 2007; Kiang, Siefert et al. 2007), together with Govindjee, and other interdisciplinary co-authors, we wrote a critical review on the light harvesting pigments on our Earth as well as their likely spectral adaptations on the planets orbiting stars different from the Sun. The international news took inspiration, with one headlining, 'Plants on other planets will not be blue!' This work was also highlighted in Nature (Raven 2007), and resulted in a Scientific American cover article (Kiang 2008), and continues to be featured in numerous television science documentaries. This work is also a key reference in current efforts to design space telescopes for detecting life on the planets in other solar systems. Govindjee and I remain in contact, and I congratulate him on his completing 20 years of wonderful Emeritus Life.

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As a fellow retiree, I have greatly enjoyed corresponding with Gov over these years, including before our retirements. May Gov continue for another 20.

Johannes Kromdijk
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When Govindjee retired in 1999, I was just finishing my first lab experience at my Alma mater in Wageningen (The Netherlands). Whereas I had been exposed to some basic textbooks about photosynthesis, I was blissfully unaware of the incredible progress in the mechanistic understanding of the process made during the second half of the twentieth century. By the time I first met Govindjee (I think during the C4-CAM satellite meeting at the University of Illinois at Urbana-Champaign in the summer of 2013), I thought I had already developed a better historical sense of the research field that I had decided to focus my career on. How wrong I was! Govindjee was shocked at my lack of knowledge of key historical figures: 'What, you are Dutch and don't know Lou Duysens? Let me tell you … '; (see Govindjee and Pulles 2016) but was very happy to

school me. We made a habit out of meeting for coffee on a regular basis, where Govindjee would inspire me with his infectious enthusiasm, both for my work, and anything else photosynthetically related. Our coffee meetings would usually spark lots of anecdotal memories, often involving one of Govindjee's famous mentors or work done in his lab which had a link to the projects I was working on at the time. Like all good science story tellers, Govindjee was able to relay the role of *serendipity* in major breakthroughs, which was very reassuring for an ambitious postdoc. After chatting with Govindjee, I usually experienced a heightened feeling of excitement about my own work (even, or perhaps especially, when some of my experiments were not getting anywhere). We even wrote a 'fun' review together on what just a one-second chlorophyll measurement can tell us about abiotic stress in plants (Stirbet et al. 2018). When I moved back to Europe to start my own research group in 2018, Govindjee was incredibly supportive. His intentions to come visit Cambridge (UK) have been hard to realize, thus far, for obvious reasons, but I am hopeful we might still make it happen sometime in the future. They sure do have very nice coffee here! I wish Govindjee the very best at his 20th (actually 21st) retirement anniversary and his 88th birthday!

Tony Larkum [a]
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I am not certain when I first came across the work of Govindjee[a] (we call him Gov), but it was probably in 1961, when I was working for Prof Henrik Lundegårdh (1888–1969) in his private laboratory in Penninby, outside Nortällje in Sweden. I was fresh out of an undergraduate course at Imperial College, London, and the work of Lundegårdh had inspired me to try to come to grips with photosynthetic electron transport, especially the role of cytochromes, which was Lundegårdh's speciality.

I remember being fascinated by Gov's work with Robert Emerson, and then with Eugene Rabinowitch, at a time when the Nobel laureate Otto Warburg was preaching that evolution of one oxygen involved using a minimum of 4 photons, whereas the American school including Gov showed clearly that this number was 8–10 even under Warburg's conditions (for a full story, see Nickelsen and Govindjee 2011).

That was a wondrous time for Gov, me and everybody in the field of bioenergetics. The consensus, although controversial, was that there were two photosystems. Emerson was flying to go to Harvard University, in Cambridge, MA, when his American Airlines jet crashed in the East River, near La Guardia airport, New York. In hindsight, and, in my personal opinion, this providing a unique opportunity for Robert (Robin) Hill to seize the high ground and propose something like the 'Z' scheme, in 1960, that we all use today. Gov was in there already proposing some of the details (Govindjee 1960; see Govindjee et al. 2017).

For me, and many others, much more exciting at the time were the proposals of Peter Mitchell on how ATP was generated in the inner membranes of mitochondria and chloroplasts. I was an early convert; but I remember when I arrived at the Johnson Foundation with Britton Chance and Les Dutton in 1967 there was still much scepticism about. However, Gov was a firm believer and has never looked back.

That was fifty years ago! And Gov has not rested on his laurels ever since. I know that he has worked in many fields since that time but where I single his work out for being right up there in the front rank of photosynthesis workers, it is on the role of bicarbonate in Photosystem II. Gov staked his claim here with several of his early students (Alan Stemler, Tom Wydrzynski, and Rita Khanna) and again and again later (particularly with Julian Eaton-Rye; see Shevela et al. 2012). But serious notice was taken of this effect when Hartmut Michel and Johannes Deisenhofer, in 1988, proposed its binding on non-heme iron in Photosystem II, supported strongly by Jim Barber and So Iwata, in 2004, and conclusively established by the high resolution structure, in 2011, by Jian-Ren Shen and his coworkers.

It was indeed a pleasure for me to have edited volume 14 (Larkum et al. 2004) and then volume 45 (Larkum et al. 2020), both on Algae, in Govindjee's Series 'Advances in Photosynthesis and Respiration'. I had a great time interacting with Gov. Now. I would say to him: What a wonderful career! Thank you Gov for your fundamental contributions. But also thank you for your inspiring leadership to the young people, all around the world, in the field. And not the least for a wonderful friendship!

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[a]Govindjee, who had one name only, now uses two names: Govindjee Govindjee; for his curiosity, I want it known that my formal name is A.W.D. Larkum, where 'A' stands for Anthony, 'W' stands for William, and 'D' stands for Derek.

Anthony J. Leggett
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I have known Govindjee for quite some time and I am delighted to congratulate him on his long research career in the area of Photosynthesis and on his upcoming 88th birthday. I will say: Keep it up Beiju!

Hartmut Karl Lichtenthaler
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Govindjee and I met first in August 1963 at the annual meeting of ASPP (American Society of Plant Physiology, now Biology) in Amherst, Massachusetts, where we presented our new research findings. We both continued in photosynthesis research, saw each other again and again at many conferences of our worldwide photosynthetic community, and soon became friends. Over the past 50 years, we interacted and cooperated on many topics in particular on chlorophyll fluorescence, the major technique applied in our research. It was and is a great pleasure meeting and discussing with him.

With his communicative ways, his worldwide scientific cooperation, and his great research achievements, he has been one of the leading experts on chlorophyll

fluorescence with high international recognition. In addition, he is a passionate editor, always engaged in making public new scientific results of the present, and of the past, to the students, and the colleagues of our worldwide science community (Papageorgiou and Govindjee 2004; Govindjee et al. 1986, 2005). Like me, he has remained active after his retirement. Interested in historical matters, he authored the text for the memorial plaque at the University of Illinois at Urbana-Champaign, honouring Robert Emerson and Eugene Rabinowitch, two pioneers and his own mentors. He has written many historical papers and Tributes to colleagues who have passed away, but he and I have composed together those for Andy Benson (Lichtenthaler et al. 2015a, 2015b), and Melvin Calvin (Govindjee et al. 2020). In 2020, Govindjee celebrated his 88th birthday on October 24. Congratulations to him! I wish him many happy returns and further activities as an outstanding science communicator and as a passionate author of future historical perspectives in photosynthesis.

Stephen P. Long
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The first book that I ever read on photosynthesis as an undergraduate at Reading in England, and one that first stimulated my interest in the subject was 'Photosynthesis' by Rabinowitch and Govindjee (1969). Later I was captivated by the image of chlorophyll fluorescence in his Scientific American article with Rajni (Govindjee and Govindjee 1974). As my own career moved into photosynthesis research, I read more and more of his prolific works, and came to see Gov as one of the 'Gods' of photosynthesis research. It was beyond my wildest dreams that one day I would join him at this faraway place called Illinois, and actually be able to collaborate with him in research. Our joint paper with Xinguang Zhu, now cited almost 200 times, was a breakthrough in providing the quantitative means to evaluate and reconcile competing hypotheses on what underlies the OJIP chlorophyll fluorescence rise kinetics and the causes of variation (Zhu et al. 2005). It completed the circle from first reading about chlorophyll fluorescence as an undergraduate in Gov's papers and books.

Mahir Mamedov
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I have always had a dream that I will one day publish an article with Govindjee. While in Russia at a Conference in 2015, he suggested to me and to my colleagues to write, with him, a minireview on the topic of 'Primary electron transfer processes in photosynthetic reaction centres from oxygenic organisms', and that we dedicate it to a pioneer Vladimir A. Shuvalov. During the writing of this article, we constantly exchanged messages regarding the text, figures, and references, mostly by e-mail. In preparing the final version of the manuscript, I received from him more than 40 messages sent by mobile phone, and that too within 24 h; this was when he was at the airports or walking on the streets. I realized how critical Govindjee is in every detail. It seemed to me that he never slept or slept very

little. Finally, we published our excellent minireview in Photosynthesis Research (Mamedov et al. 2015). Note that his messages are still useful to me!

I would like to add that Govindjee's outstanding great abilities always delight me. I always enjoy talking with him not only about photosynthesis, but also about life, history, the future and so on. I love him so much!

Rudolph A. Marcus
Nobel Laureate in Chemistry, 1992; California Institute of Technology, Pasadena, CA, USA; e-mail: ram@caltech.edu

It was just 3 years ago, I sent Govindjee congratulations on his 85th birthday celebration in India. I am pleased to learn about a special (88th) birthday celebration, and his 20-year retirement, now in 2020. I still remember fondly his lectures on photosynthesis (at the University of Illinois at Urbana-Champaign (UIUC) when I was a member of the Chemistry faculty there), which included the Kok cycle and the many other aspects of photosynthesis. I benefited much from these lectures when, at the time, I was writing articles on the early electron transfer steps in the bacterial photosynthetic reaction centre.

At age 97, his age of 88, perhaps paradoxically, seems a little young. I am sure that in mind and spirit he is indeed as he was in the days when we were both at the UIUC. Congratulations to Govindjee: – 'just keep it up!'

Autar K. Mattoo
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Happy 88th Birthday to a giant of a scientist – the evergreen and dedicated Photosynthesis Scholar of all time. My heartfelt congratulations to Prof Govindjee (who prefers that I call him Govindjee) on his 88th birthday and wish him good health and continued involvement in the publishing world. I had heard about him and his work while working at the single digit name of Krishna (Govind) of Indian mythology. It was a pleasure and honour to meet him in his home, in Urbana, and at the University of Illinois at Urbana-Champaign (UIUC) several decades ago. I am personally enthralled with his tremendous devotion to science, photobiology, and photosynthesis in particular. It was the year of his retirement, when I had the pleasure to write a chapter (Booij et al. 1999) on photoregulation, and photoprotection of Photosystem II, a topic of great interest to Govindjee. I am blessed being a friend of this giant of photobiology/biophysics and a happy and loving human being, who has a bewitching smile and youthful outlook. I wonder how many of us can coauthor as many papers as he has after his retirement from UIUC! (See:http://www.life.illinois.edu/govindjee/recent_papers.html.) May he continue to be as productive as he has been so far, remain an inspiration for us all, and be in good health with his ever-smiling personality. Let all the higher powers bless you dear Govindjee; I am sure you had all the fun you deserved on your 88th birthday. As they say, Mazel Tov (Hebrew), Mubarak (Hindustani), Poshte (Kashmiri), Happy Birthday (English)! Finally, Namaste (Sanskrit) & Warm regards, Autar

Hartmut Michel
Nobel laureate in Chemistry, 1988; Max Planck Institute of Biophysics, Frankfurt am Main, Germany; e-mail: hartmut.michel@biophys.mpg.de

It is a pleasure to know that Govindjee's 88th birthday and his 20 years of retired life is being celebrated in 2020. After we had the high-resolution atomic level structure of the reaction centre of anoxygenic photosynthetic bacteria (Deisenhofer et al. 1984, 1985), we wondered as to where the bicarbonate that Govindjee's group had discovered (see e.g. Govindjee et al. 1976) to be essential near Q_A and Q_B in Photosystem II (PS II), fits in the picture. We proposed that it replaces a specific glutamyl residue in the reaction centre of bacteria (Michel and Deisenhofer 1988). Yes, indeed anoxygenic photosynthetic bacteria do not have the bicarbonate effect (see Govindjee's work with Colin Wraight: Shopes et al. 1989; Wang et al. 1992). It is about that time that Govindjee and the University of Illinois at Urbana-Champaign (UIUC) invited me to lecture there, and I remember having great conversations with Govindjee and his students that led them to consolidate and summarise their ideas concerning 'PS II and bicarbonate' (Xiong, Subramanium et al. 1996, 1998). Finally, the PS II structure from Jian-Ren Shen's group in Japan provided the proof and the details of this bicarbonate binding on the acceptor side of PS II (Umena et al. 2011). Now, the entire 'bicarbonate' story for the acceptor side of PS II, which seems to be 'loved' by Govindjee (as he tells me even now) has been nicely reviewed by Govindjee and others (Shevela et al. 2012). I wish him (now Govindjee Govindjee) happy 88th birthday on 24 October 2020. May he keep educating the young on the history and the excitement of photosynthesis research!

Jun Minagawa
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Govindjee (we call him Gov) and I shared a good time at the University of Illinois at Urbana- Champaign (UIUC), when I was a postdoc in the lab of Tony Crofts, and also after I became a staff researcher in the lab of Yorinao Inoue at Rikagaku Kenkyūjo, RIKEN (Japan). At UIUC, we did several experiments together, using the green alga *Chlamydomonas reinhardtii*: **(i)** Together with Jin Xiong, Govindjee's PhD student, we showed the crucial importance of arginine-257 on D1 in the 'bicarbonate' effect (Gov's favourite; see Shevela et al. 2012) on the electron acceptor side of Photosystem II (PS II), using newly constructed mutants and measurements on thermoluminescence (see Xiong, Minagawa et al. 1998; it was just when Gov was a year away from retirement); and **(ii)** Together with Manfredo Seufferheld, a postdoc of Govindjee, we extended this work, with additional D1-R257 mutants, long after Gov's retirement, which provided a new insight not only on the 'bicarbonate' effect, but into the theory of how thermoluminescence comes about (Rose et al. 2008). Our interaction was very recently renewed when Gov collaborated with Richard (Dick) Sayre's group; here, also using *C. reinhardtii*, Negi et al. (2020) showed that by manipulating the 'antenna' system, we can increase the biomass of this alga by two-fold!

At one point, Govindjee had visited RIKEN, and here, together, we did experiments on thermoluminescence, a phenomenon of great interest to Gov. Although I have no

recollection of the details of the results we got (perhaps, we never published them), I clearly remember the many stories Gov told me in the darkroom that were about the photosynthesis researchers in good old days – who I only knew through the literature. He knew all of them in person. The most impressive phrase I remember is 'Who found it really first is not important, the more important thing is that two groups found it independently.' Guess what? Govindjee taught me an important truth.

Kumud Bandhu Mishra
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I met Govindjee during my PhD days, in 2003, when he was visiting the University of Allahabad (which is also his alma mater); he inspired me to choose research in *Photosynthesis* as a career. We further met several times after, for example, in 2004 at the International Photosynthesis Congress, Montreal, Canada, where he was honoured by being appointed as its Honorary President. Govindjee has been my teacher of photosynthesis and a source of inspiration throughout my research career. A turning point came when we met in Nové Hrady, Czech Republic, where I was working in the laboratory of Ladislav Nedbal. We had our first discussion then on the processes behind the 'slow' (minute range) S-M-T fluorescence phase when I showed him our data where we had observed its strong modulation at low temperatures in several *Arabidopsis thaliana* natural accessions (see Mishra et al. 2011). Govindjee noticed that this was the first observation showing a very strong modulation in S-M-T fluorescence phase in *Arabidopsis thaliana* at low temperature, and he inspired me and my wife Anamika Mishra, to look for the cause of its strong modulation that led us to plan and complete a very complex experiment, together with him (Mishra et al. 2019). Govindjee had also inspired us a few years earlier to write a minireview on 'Plant phenotyping: A perspective' (Mishra et al. 2016), specifically, to promote the Indian Journal of Plant Physiology (now Plant Physiology Reports). Anamika and I always have a great time whenever he visits us in the Czech Republic. Both of us are extremely delighted to celebrate the completion of 20 years of his retired, but highly active life (see http://www.life.illinois.edu/govindjee/recent_papers.html).

John C. Munday Jr
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I remember particularly Dr Govindjee's wonderful spirit, both personally and in the pursuit of an ethical and responsible scientific research programme. Dr Govindjee has been a marvellous example to his students. Choosing a major professor is a major decision for a grad student. On reflection about the options in the Photosynthesis Laboratory at the University of Illinois, I concluded that Govindjee would be a wise mentor, a steady hand of guidance, and an encourager. He had already proven his skill at research and his deep knowledge of the field of photosynthesis.

Govindjee proved to be an exceptionally wise mentor. He was full of patience, manifested fully a teaching spirit, and with painstaking care instilled a sense of excellence and quality in research (see Munday and Govindjee 1969a, 1969b). He demonstrated in his

own research what he strove to teach. He was ever-present in the laboratory. Always with a cheerful smile, and obviously enjoying research, he made the laboratory a place where students, research associates, and visiting faculty wanted to be.

He organised seminars in the lab and at his home. His wife Rajni had the gift of hospitality and we enjoyed her refreshments. (She also made significant contributions of her own in photosynthesis research and cared for their young family.) Along the way his comments and critique about my research were the stimulus for pushing forward, solving problems, and thinking creatively. I distinctly remember various points he made about how to do quality research. And in my final PhD exam, he defended this student against a visitor's mistaken claims about unpublished research from abroad, pointing out the core principle that what counts in science is peer-reviewed publication. In this and other ways, his great skill in building up all his graduate students facilitated our professional fruitfulness and gave us confidence for the future.

Looking back over his distinguished career, and the large number of students he guided, we can see the consistency in his research productivity and his mentoring skill. Even in retirement he has worked to continue his contributions, and to remain in contact with all his students from over the years. The ongoing freshness of his spirit is inspiring. He is a most remarkable man.

Govindjee (now, Govindjee Govindjee), I salute you, and I have great joy in honouring you and the richness of your life.

Satish K. Nair
Head, Department of Biochemistry, and Director Biophysics & Quantitative Biology, University of Illinois at Urbana-Champaign (UIUC); e-mail: snair@illinois.edu

I am delighted that a collection of personal messages, and a discussion of Govindjee's academic activities during his 20-year retired life, has been assembled to highlight his contributions to the fields of plant biology and biophysics. This is indeed appropriate as at the UIUC, Gov (as he is known colloquially) has played a major role in both the departments, over the years, and has helped to shape their outlook over his decades of active research. I wish him a very happy 88th birthday and look forward to discussing what he has been doing when he is back on the UIUC campus!

Mohammad Mahdi Najafpour
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The first time I read about the role of a manganese (Mn) in biological water oxidation, it was in a book from Professor Govindjeès series (Advances in Photosynthesis and Respiration; see Ort and Yocum 1996). After that, water oxidation and artificial photosynthesis were not the same for me anymore, and I was looking upon them from a fundamentally different and much broader perspective.

Govindjee and I carried out a number of research projects on water oxidation and artificial photosynthesis together (see e.g. Najafpour and Govindjee 2011; Najafpour, Tabrizi, et al. 2012, 2013), and, at the same time, critically evaluated the chemistry of

water oxidation and its future directions (see e.g. Najafpour, Moghaddam, et al. 2012, 2013; Hou et al. 2014).

Words cannot capture my feelings of appreciation towards Govindjee. He is a wonderful, unassuming, and a charming person, who has taught and continues to teach me many things with the utmost kindness and consideration. Govindjee supervises the research projects of many young scientists, around the world, directly and indirectly. I admire him for his compassion, enthusiasm, vigour, and knowledge of photosynthesis and, above all, its history. *For me, Govindjee is the symbol of photosynthesis*. Happy 88th birthday to the great Govindjee on 24 October 2020; I wish him good health and a long and prosperous life.

Sushila Narsimhan
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Although my association with Govindjee, and his wonderful wife Rajni, is only a year old, it evolved very soon into a very special and significant one, since it involved writing jointly a personal and scientific tribute to my brother, Satish Chandra Maheshwari, a distinguished plant biologist of his time (see Pareek, Soni, et al. 2020). When Govindjee recently visited Jawaharlal Nehru University (JNU), New Delhi, we spent some quality time together, and it gave me an insight into his intellectual calibre, his super-friendly personality, and eventually fostered an in-depth and lasting bonding between us.

During my interactions with Govindjee, I found him to be a very committed, disciplined and an erudite scholar. The manner in which he initiated the writing of the tribute to my brother, and interacted intensely with the other co-authors, reflects his professionalism and passion towards disseminating knowledge for posterity about the contributions of top scientists, no matter where they are from.

Affable, soft spoken with gentle manners, he (and Rajni) smilingly endured the unexpected confinement, during Covid-19, in a small room (#14) at JNU's Aravali Guest House, surviving on simple meals and meagre facilities. Unruffled by the discomforts and age-related health issues, he kept himself totally and passionately occupied towards the accomplishments of his desired goals. This speaks volumes of his power of resilience!

It was indeed a privilege to have met and interacted with both Govindjee and Rajni. I found both of them extremely modest, warm and affectionate. I look forward to continuing our association and friendship well into the future.

Ladislav Nedbal
Research Centre Juelich GmbH, Juelich, Germany; email l.nedbal@fz-juelich.de

I would like to acknowledge Gov's contribution to generations of young scientists who have been in touch with him over many, many decades. He had a decisive influence also on my early years in science. I met him first in 1988 at the 14th International Congress of Biochemistry in Prague. As a humble graduate student, I approached him with my first, proudly assembled manuscript on photoinhibition of PS II and the D1 protein. Gov not only talked with me, but also read the manuscript and turned its dominant

colour to red by hundreds of corrections. My original text was hardly visible, covered by Gov's typical handwriting. Lessons learned: Writing is not easy and the reader is the king. Less than a year later, the manuscript was accepted, Gov visited our lab in Třeboň, the social system in our country changed to democracy and, with his recommendation I could start my first postdoc with such great scientists as John Whitmarsh, Donald (Don) Ort, (the late) Colin Wraight, Antony (Tony) Crofts, and Govindjee himself, and many others in Urbana. I learned from him the art and science of editing (see Govindjee and Nedbal 2000; Laisk et al. 2009), but more importantly, we had fun doing experiments (Nedbal et al. 2003). I am blessed now by handing over Govindjee's legacy to my students.

Teruo Ogawa
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I first met Govindjee (Gov to his friends) in 1983 when an international symposium 'Photosynthetic Water Oxidation and Photosystem II Photochemistry' was held at RIKEN (Wako Shi, Japan). In 1977, Yasuo Fukuda, former Prime Minister of Japan had already proposed a US-Japan collaborative project when he had visited President James (Jimmy) E. Carter. A project on 'Solar Energy Conversion by Means of Photosynthesis' proposed by Professor Kazuo Shibata (1917–1983) at RIKEN was accepted and the Solar Energy Research Group headed by Dr Yorinao Inoue (at RIKEN) was organised. The above symposium was held as an activity of the US-Japan project and Gov was one of the key invited US participants. Then an agreement was reached between RIKEN and the University of Illinois at Urbana-Champaign (UIUC) to exchange scientists. Based on this agreement I visited UIUC several times. When I visited Prof John S. Boyer in 1981 to study the process of stomatal opening, I spent a lot of time with Gov in his lab to measure chlorophyll *a* fluorescence (Gov's favourite) from guard cells. These results were published with Gov in Plant Physiology (Ogawa et al. 1982). Then, I visited Professor William (Bill) Ogren in 1983 to study the CO_2-concentrating mechanism in cyanobacteria. At this time Gov helped me a lot to measure the action spectra for inorganic carbon transport. Then Gov visited RIKEN, also on a US-Japan fellowship, and made key experiments on his favourite 'thermoluminescence' from plants with H. Koike and two visitors, Bill Rutherford and Herb Nakatani (see e.g. Govindjee et al. 1984, 1985; Rutherford et al. 1984). During these visits, together, we enjoyed great Japanese dinners. I wholeheartedly thank Gov for his help during my stay at UIUC and for over 35 years of constant friendship. Knowing him, I am sure he will continue his research and writing with great vigour and fervour!

William L. Ogren
Formerly in the Department of Agronomy, University of Illinois at Urbana-Champaign;
e-mail: wlogren@gmail.com

I first met Professor Govindjee in May 1965, when I interviewed for a research position with the United States Department of Agriculture (USDA), located in the Department of Agronomy at UIUC. Gov (as his friends called him) was very kind and welcoming during

Figure 3. A cropped version of a photograph of the 1969 class on 'Photosynthesis' (Govindjee and William Ogren, instructors) at the UIUC. 1st row (Left to right): Glenn Bedell; unidentified; Christine Grant (Newell); **Govindjee**; and William Hough (missing here). 2nd row (Left to right): Alan J. Stemler; Ray Chollet; Melvin Markowitz; and the late Tom Guilfoyle. 3rd row (Left to right): Thomas Threewitt; Gary Wells; Harold Coble; the late Prasanna Mohanty; George Bowes; and William Ogren. Source Portis and Govindjee (2012).

the interview process and showed me around the Botany Department, including a memorable tour of the relics of the prominent Robert Emerson/Otto Warburg photosynthesis quantum yield collaboration which occurred in Urbana several years previously (see Nickelsen and Govindjee 2011; also see <https://news.illinois.edu/view/6367/801235>). After I was offered and accepted the position and arrived on the campus in October 1965, Gov invited me to participate in the weekly photosynthesis seminars. This was quite a slog for some years, as my background in chemistry was not up to the high-powered biophysics being done in the laboratories of Gov, Eugene Rabinowitch, and Chris Sybesma, and discussed weekly by their gifted students and postdocs. However, the seminar did make me part of the campus photosynthesis community. As I developed a research programme that emphasised gas exchange and carbon fixation, Gov and I decided that together we could create a comprehensive course that would benefit all students interested in photosynthesis, and we did so (see a photograph in Figure 3). We taught it only once, as I found I spent too much time working on lectures and not enough time doing what I was hired to do, research. In the years that followed, Gov and I continued to share time, thoughts, and, occasionally, students and postdocs (see e.g. Spalding et al. 1984). We are also both recipients of the 'Lifetime Achievement Award by the Rebeiz Foundation for Basic Research', he being the first in 2007 (see Rebeiz et al. 2007), and I being the recipient in 2012 (Portis and Govindjee 2012). Govindjee's cheerful, ebullient nature has never dimmed, and it has been a delight to be a long-standing friend and colleague. My heartiest congratulations to Gov for his 20-year post retirement celebration, and for his 88th birthday on 24 October 2020!

George C. Papageorgiou[b]
National Centre of Scientific Research, Demokritos, Athens, Greece

I have known Govindjee for more than 60 years now. I met him at the University of Illinois at Urbana-Champaign (UIUC) where after obtaining my BS degree in Chemistry from the University of Thessaloniki, Greece, I was very fortunate to be accepted as a graduate student in the PhD Program in Biophysics in the late 1950s.

One of the first courses I took was *Biophysics of Photosynthesis*. The course was taught by Professor Eugene Rabinowitch and then Assistant Professor Govindjee in a large amphitheatre that was packed with students. In his first lecture, Govindjee stated that all that is important in photosynthesis we owe to the discoveries by the late Professor Robert Emerson and to Professor Rabinowitch, both of the UIUC. The statement was obviously an exaggeration, nevertheless it impressed me in such a way that I decided to visit the Photosynthesis Lab in order to explore the possibility of doing my PhD thesis research there. Govindjee made that happen for me. I became his graduate student and the first one to obtain a PhD with him (see e.g. Papageorgiou and Govindjee 1968a, 1968b). This was the very first attempt to relate the slow (seconds to minute) chlorophyll (Chl) *a* fluorescence changes to regulatory aspects of photosynthesis, including even the naming of the changes as SMT. From that point, we started a collaboration that led to the co-authorship of numerous papers (see e.g. Papageorgiou and Govindjee 2011; Kana et al. 2012), and reviews on the biophysical aspects of photosynthesis (see e.g. Papageorgiou and Govindjee 2014), co-hosting of many international conferences, and an edited book on the basics and applications of Chl *a* fluorescence (Papageorgiou and Govindjee 2004, reprinted in 2010).

What I will always remember about Govindjee was his excellent sense of humour with which he flavoured his lectures and some of his articles. I will never forget the story of how UIUC had problems understanding and registering correctly his name!

I owe Govindjee my deep gratitude for working with me and for what I accomplished with his selfless support. But most of all, I feel very lucky to have met such a wonderful lifetime friend: a friendship that has endured time and distance (Figure 4).

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[b]Sadly, we note the passing of George Papageorgiou (9 May 1933–22 November 2020) during the final preparation of this article.

Sheo Mohan Prasad
Ranjan Physiology and Biochemistry Laboratory, Department of Botany, University of Allahabad, India; e-mail: profsmprasad@gmail.com

Professor Govindjee's life after 20 years of retirement is still an inspiration. He was born on 24 October 1932 in Allahabad (now, Prayagraj). Since 2000, he has been Professor Emeritus of Biochemistry, Biophysics and Plant Biology at the University of Illinois at Urbana-Champaign (UIUC), where he had taught for almost 40 years. His name is synonymous with 'Photosynthesis'. He has been known only by his given name since his family by tradition did not use their surname 'Asthana'. His zeal for science and

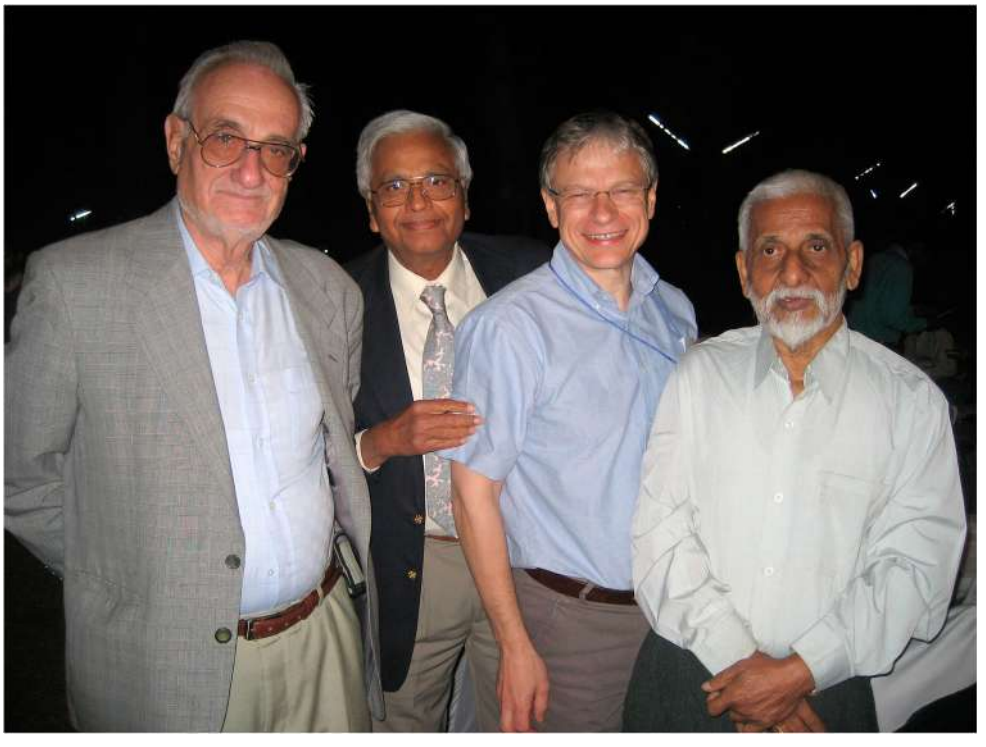

Figure 4. A 2008 photo of Govindjee with three of his past students. (Left to right): the late **George C. Papageorgiou** (Greece), Govindjee (USA), Julian Eaton-Rye (New Zealand) and the late Prasanna Mohanty (India). Source Jajoo et al. (2009).

knowledge can be imagined by the fact that he has continued to be active in the field of research via teaching and publishing even after 20 years of his retired life. He obtained his BSc (Chemistry, Botany and Zoology) from the University of Allahabad, in 1952. Then, in 1954, he stood first amongst all in his MSc (Botany) class; his special paper, dealing with the work of Robert Emerson, was presented in the Advanced Plant Physiology course under Prof Shri Ranjan (a former graduate student of Frederick Frost Blackmann). Once, while reminiscing his early days in the Department of Botany, he said that they were the 'three musketeers' together (Manmohan Laloraya, Krishna Sahai Bilgrami, and Govindjee). Indeed, this Department was the place where Govindjee developed interest in photosynthesis and from here his journey towards photosynthesis research began. He has been very passionate towards plants, science and was a hard-working student since his student days in Allahabad. There, he did collaborative research on the amino acid metabolism of virus-infected plants and published many papers including one in *Nature* (Laloraya and Govindjee 1955). In 1956, he went to UIUC, and in 1957, he was joined by Rajni Verma, also an alumnus of University of Allahabad; she was also a topper in her MSc in 1955; Rajni and Govindjee were married in Urbana on 24 October 1957. Govindjee had begun his PhD work with the world-famous Robert Emerson (who had just discovered the Emerson Enhancement Effect). However, due to Emerson's untimely death in a plane crash, Govindjee completed his PhD in Biophysics under Eugene Rabinowitch in 1960. His PhD work showed, among many things, that the

two light reactions are run by two different spectral forms of chlorophyll *a*, published in *Science* (Govindjee and Rabinowitch 1960).

The Department of Botany, University of Allahabad, has been the birthplace and work place of great scientists and I take great pride in declaring that Govindjee is one of them. Being an alumnus of this Department, he has brought laurels to it through his genius, systematic and dedicated work in the field of photosynthesis and has made unique and outstanding contributions to basic reactions in photosynthesis research. And I, being in-charge of the great Ranjan Plant Physiology and Biochemistry Laboratory, am blessed to carry forward the legacy of this laboratory. I have had the opportunity to have a close association with Govindjee each time he visited Allahabad. He is a renowned academician, scientist, researcher and last but not the least, a human being par excellence. He has been a teacher and a mentor in the true sense of the word inspiring every individual who comes to know him. His personality traits include unabridged simplicity, strict disciplinarian, and a stickler for punctuality. His scientific temperament, commitment and vision have crossed all borders.

Govindjee's pioneering discoveries are the outcome of his thoroughness, imagination and diligence. His trend setting and his novel research has proved the correctness of Emerson's result of the minimum requirement of 8–10 photons for the evolution of one O_2 molecule during photosynthesis (see Nickelsen and Govindjee 2011). He, together with several of his PhD students, discovered the unique involvement of bicarbonate ions in the reduction of plastoquinone on the electron acceptor side of Photosystem II (PS II); see the review by Shevela et al. (2012). Further, he has been deeply involved in basic research in several other steps of the Z-Scheme, and, more importantly, in its evolution to its current picture (see e.g. Govindjee et al. 2017). His expertise in chlorophyll *a* fluorescence spectroscopy continues to guide the research world even today when he just had his 88th birthday. His dedication towards science is unique as indeed even after 20 years of his retirement he has contributed over 100 articles related to research in photosynthesis. His contributions and pioneering research work include many important discoveries such as construction and characterisation of PS II D1 mutants, related to the functioning of bicarbonate (see e.g. Rose et al. 2008; Shevela et al. 2012), the correct minimum number of photons involved in oxygen evolution (Govindjee et al. 1968), characterisation of *Chlamydomonas* mutant strains with improved biomass production (see e.g. Zhou et al. 2015; Negi et al. 2020), and the exploitation of chlorophyll *a* fluorescence to 'measure' abiotic stress responses (see e.g. Wungrampha et al. 2019). In addition to writing tributes to many scientists, he has published tributes to his own teachers Robert Emerson and Eugene Rabinowitch (Govindjee 2004), as well as to his wonderful parents and his eldest brother Professor Krishnaji, who was responsible for taking care of him when he was young (Govindjee 2007; Govindjee and Srivastava 2010). His contributions have been acknowledged with many awards such as the first lifetime achievement award given by the Rebeiz Foundation for basic research (see the Reminiscence by Mark Rebeiz). The list is endless. *Thus, he truly deserves the title of 'Mr Photosynthesis'.*

Govindjee has remained closely connected to his alma mater: the University of Allahabad; since 1994, he has regularly visited the 'Ranjan Plant Physiology and Biochemistry Laboratory'. Great teachers make great students which is truly revealed through the life of Govindjee; he ascribes his success to his three great mentors: Shri Ranjan; Robert

Emerson; and Eugene Rabinowitch. His regular visits to our Department and to the National Academy of Sciences (NASI), Allahabad (he is a Fellow of this Academy) have been enriching and inspiring for research scholars, post-graduate, under-graduate and even high school students. His simple, straightforward, cheerful and ever welcoming nature invites children and students to mix and interact with him very easily. Students here at the Department of Botany, University of Allahabad, have been at the receiving end of his benevolent nature. He has initiated a cash prize for the student who stands first in MSc (Previous) and in MSc (Final) in our Department. He generously donates books, journals, computer systems for the departmental library for the benefit of our students. Govindjee is truly devoted to serving science and humanity. Distances do not matter for him; he is always within reach and readily available for everyone. He strongly believes in the dictum that one should be able to express oneself especially in the scientific world so that science can be easily available to all. I wish to specifically mention that he insists that each and every scientist must read and follow the rules of the small book '*Elements of Style*' by William Strunk and E.B. White. On behalf of all the members of the Department of Botany, of the University of Allahabad, I thank him for all that he has done for the students here.

I wish to emphasise that even today, Govindjee is engrossed in completing his commitment of research projects, is still passionate to conduct more research, and has the passion to effectively encourage others. It is my privilege to hold him really very high since he has educated (and continues to educate) thousands (and thousands) of students about photosynthesis throughout the world – directly, or through his books, Scientific American articles, and through Educational Posters (see his web site: http://www.life.illinois.edu/govindjee/). I am inspired always by his truthfulness, simplicity and hard work, and, thus, I do my own research, as best as I can, since this is the only way to pay tribute to Govindjee. See Figure 5A for a photograph of Govindjee's visit to his first Alma Mater: Ranjan Plant Physiology and Biochemistry Laboratory, Botany Department, Allahabad University.

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I initially met Govindjee in 2007, well after his retirement, when he was the first recipient of the Lifetime Achievement Award from the Constantin A. and Carole C. Rebeiz foundation for basic research (RFBR); see Rebeiz et al. (2007). My father, Constantin A. Rebeiz founded this organisation right after his own retirement to promote progress in basic research advances in chloroplast chemistry, biochemistry and molecular biology (Rebeiz 2014). The board of the foundation selected Govindjee in recognition of his scientific advances and original research in understanding photosynthesis, for his continuous efforts in disseminating knowledge on the history of photosynthesis, and for his legacy of organising knowledge in this field as the founding editor of the *Advances in Photosynthesis and Respiration* (AIPR) series. After receiving this award, Govindjee was invited to join the board of the RFBR, where he was an instrumental and dedicated member during its final eight years of operation. At annual award ceremonies, he would deliver lively, show-stopping presentations on both the scientific achievements and

Figure 5.
A, Govindjee (wearing a red tie) at an informal discussion session in Ranjan Plant Physiology and Biochemistry Laboratory during his visit to Allahabad University in 2009. Sheo Mohan Prasad is sitting on the extreme left; others are PhD students. Photograph from Sheo Mohan Prasad. **B**, Govindjee in New Mexico, USA, on 15 May 2007. Photograph by Rajni Govindjee.

personal anecdotes of the awardees. Further, Govindjee invited 8 international scientists to assemble and summarise all that was known until 2010 on the chloroplast: its basics as well as its applications (see Rebeiz, Benning et al. 2010). When my father passed away last year, we worked together on a tribute which appeared in Photosynthesis Research (Govindjee, Briskin et al. 2020a), where Govindjee had been the founding editor of the History and Biography section. It was such a pleasure and honour to work closely with him on this article as a lasting memory of my father and his work. Govindjee's tireless energy and commitment to the photosynthesis community is obvious to anyone who has the briefest of contact!

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I have everything good to say about Govindjee and I am sorry I have not been able to be around at all; however, we do have an important paper together (Rose et al. 2008). Congratulations on 20 years of retired life. My greatest fear is that this may be the beginning of my retired life but Govindjee has demonstrated a level of activity and productivity which anyone would be envious of in retirement.

Catherine A. Royer
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It is a great pleasure to wish the Happiest of Birthdays to Govindjee! I have known him now for over 30 years. We even published a paper together (my only foray into photosynthesis; Govindjee et al. 1993) 27 years ago. He is a giant in that most complicated

of fields. He stands with an impressive pantheon of outstanding biophysicists at the University of Illinois at Urbana-Champaign. An early member of that great tradition, his contributions to the field are enormous. This amazing cohort of Illini biophysicists inspired several of us who were students of these great scientists to serve the Biophysical Society in many ways, ultimately as President. We are Dorothy Beckett, Suzanne Scarlata, David Piston, and most recently myself. We owe our vision of Biophysics to the great scientists at Illinois, prominent among them, Govindjee. So again, Happy Birthday, all the best! And thank you for sharing your vision and enthusiasm with all of us.

Kamal Ruhil
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I did my PhD under Professor of Baishnab C. Tripathy, who was a student of the late Professor Prasanna Mohanty (see: Tiwari et al. 2014), who, in turn, was a student of Govindjee. My first introduction of Govindjee was, as done by my seniors and peers, that Govind Ji (as was his original name in India) and Photosynthesis are synonyms. I met him, for the first time, in 2010, looking forward to gain some knowledge about photosynthesis. He taught me not only the basics of photosynthesis, but the basics of editing. We sat together for hours and he was fine tuning, with immense patience, pointing out, and explaining, all the mistakes which I was making; his goal was to help me achieve perfection! This was followed by discussions on how best to collect, and interpret, chlorophyll *a* fluorescence data, and that too with different instruments. However, as the time passed, I realized that the tag of Mr Photosynthesis is such a small thing for a person who stands beyond books and papers. He is not just synonymous to photosynthesis, but a complete encyclopaedia, walking on two legs. In fact, the title 'Govindjee: Life after retirement' does not suit his immense personality as a *Strict Mentor, Friendly Teacher*, *Visionary Guide*, and of course an *Encyclopaedia* containing plethora of knowledge, not only about photosynthesis but all aspects of life. I do vividly and fondly remember acting as one of the protons in forming NADPH when Govindjee taught us, in a highly exciting and unique manner, the Z-scheme of photosynthesis, and each of us acted as one of the components in the electron flow from water to $NADP^+$ (see Jaiswal et al. 2017). Sanguine personalities such as Govindjee never retire! They just change the way things work to fit their ways. Who else, but our beloved Rajni Ji (Govindjee's dear wife) can understand this: I am sure, she will never agree to the term retire for Govindjee, as she has been giving active support and encouragement not only to him but to students like me. We love both Rajni and Govindjee, not only for the knowledge they have imparted us over the years, but the right way they have shown to each and every student that has come in contact with them; they are just like our caring and supporting parents. I am and will always be indebted to Govindjee for his unconditional support and in helping me overcome all stress. I do not know how to express my gratitude towards him in words but, from the bottom of my heart, I will always be praying for his long and healthy life. I wish both Rajni and Govindjee years of togetherness and caring life ahead.

Richard Sayre
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Here we are celebrating the 88th birthday of Govindjee. Clearly, there are few scientists who are so active at this stage in their lives. Govindjee has possibly done more than anyone of his generation to promote photosynthesis research. He is truly the international ambassador of photosynthesis. He promotes dissemination of knowledge through his collection of articles on the history of photosynthesis, through his extensive travels to scientific conferences and invited symposia, and through meetings with students. Govindjee has also championed the career development of each new generation of scientists just as he has challenged his more senior collaborators to respect the works of those who contributed to the advancement of photosynthesis in the past. His encyclopaedic knowledge of photosynthesis is world renowned and has been a resource many have come to rely upon. It has been an honour and privilege to be a research collaborator in the 1990s in learning about the role of specific amino acids in Photosystem II reactions (Kramer et al. 1994; Roffey et al. 1994; Hutchison et al. 1996; Xiong et al. 1997), now on improving photosynthesis in green algae (see Negi et al. 2020; Sayre et al. 2020). Over the years, we have been friends, and continuous communicators. I wish him continued good health and prosperity. Cheers!

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When walking through a forest, you see the global growth, but every once in a while, you come to an exceptionally large and prominent tree. In the photosynthesis research forest, Govindjee is such a tree. When I entered the field coming from chemistry, he was one of the dominant researchers. By producing excellent work and drawing other researchers to Urbana, Illinois, he made it a unique place where work on primary processes met applications in agriculture. Besides his numerous original publications, Govindjee contributed to the field by establishing 'Advances in Photosynthesis and Respiration' and acting as series editor for the first 43 volumes of this series, which has currently reached no. 45. I am grateful for the excellent help he gave us for our chlorophyll book (volume 25 in this series, Grimm et al. 2006). And now, 13 years after my retirement, he still is pivotal to the field. As recently as just a few days ago, we interacted wonderfully with each other in a Tribute to Tino Rebeiz (Govindjee, Briskin, et al. 2020a). I wish all the best to you, Govindjee: keep going strong, enjoy science and life together with your wife Rajni and stay well in the times of Covid-19.

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Memories of five decades of friendship and scientific collaboration with Govindjee

I begin this tribute by mentioning that my very first collaboration with Govindjee was in Illinois – not in Urbana, but in the greater Chicago area – it was in the lab of Michael

(Mike) Wasielewski first at the Argonne National laboratory and then at the Northwestern University. Here, we made, in 1989, the first direct measurements – in the picosecond (ps) time domain – of the primary charge separation rate in isolated Photosystem II (PS II) reaction centre preparations (RCPs), both at room temperature and at 15 K (Wasielewski, Johnson, Govindjee, et al. 1989; Wasielewski, Johnson, Seibert, et al. 1989); a good part of this work required us to work all-night, and Govindjee even took naps on the long lab tables! We then went on to make a number of refinements and additions to the original measurements over the next 10 years. Accurate measurements were difficult at the time due to the extreme light-, oxygen-, and temperature-sensitivity of the PS II chlorophyll-protein complexes, but we did not 'give-up'. For summary of this work, see Seibert and Wasielewski (2005) and Govindjee and Seibert (2010). In addition, in 1990, Govindjee and I collaborated, in work done at the University of Illinois at Urbana-Champaign, UIUC, on fluorescence lifetime distributions in isolated PS II RCPs (Govindjee et al. 1990).

We have been good friends since the 1970s, when we both helped establish the American Society for Photobiology (APS) as Charter Members in Sarasota, Florida, under the leadership of its founder and first President, Kendric C. Smith from Stanford University. And, Govindjee was its elected President in 1981; it was at this time that we first got to know each other well. While I never had the pleasure of being Govindjee's grad student or post doc, I did have the honour of hosting one of his former top students (Thomas (Tom) Wydrzynski-1947–2018) for 6 months on his sabbatical in my lab. Over the years, Govindjee has been very supportive in helping guide my career in many ways. I've been a guest in Govindjee's home (thanks to Rajni), while actually establishing a collaboration with another professor at UIUC and had the pleasure of speaking at a Photosynthesis Conference in Indore, India (2008), honouring Govindjee and his many professional contributions (Jajoo et al. 2009).

I especially remember several times at Gordon Conferences and Photosynthesis Congresses in beautiful outdoor surroundings listening to him reminisce about his experiences with some of the giants of the early days of photosynthesis, including Robert Emerson (Govindjee's first PhD advisor before his death in a plane crash on the way to Harvard), Eugene Rabinowitch (who was Govindjee's advisor after the tragedy; see Govindjee et al. 2020), Otto Warburg (Nickelsen and Govindjee 2011), Louis (Lou) N. M. Duysens (Govindjee and Pulles 2016), and Jack Meyers. Perhaps as much as Govindjee's many contributions to the scientific understanding of photosynthesis, though, he will certainly be remembered for his fastidious documentation of the history of photosynthesis (see e.g. Govindjee et al. 2005). His personal observations, prodigious memory for detail, and amazing comprehension of the scientific literature has always impressed me as everyone who knows him. I feel very proud to have had the privilege of knowing Govindjee and wish him and Rajni the very best in life on the occasion of his 88th birthday. I genuinely believe that he will show up on our long agreed upon dinner appointment on his 100th birthday (assuming that I live that long)!

Manfredo Seufferheld

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I had the privilege to be Govindjee's last post doc, which was a big honour for me. Although I am not working on photosynthesis now, I often visit him for guidance. For me, the most

remarkable characteristic of Govindjee is his love: Love is patient, and Govindjee's patience was an important factor in my success in his laboratory. I did my PhD in the area of *stress physiology* and photosynthesis was a new challenge for me. Govindjee always had time to discuss a paper or a concept that was difficult to understand. I still remember how much enthusiasm, dedication and especially patience he devoted to me. I treasure all the diagrams, figures, and notes that he wrote in my lab book, which are a testimony of his love for what he always did; science and creating mentor-disciple relationships that I believe he had himself experienced with his beloved mentors Eugene Rabinowitch and Robert Emerson. Govindjee taught with passion, creativity, simplicity, and endless patience. He climbed stairs, threw tennis balls as flying 'electrons', took pictures, walked up and down the classroom … all to be sure that everyone got 'the important message'. Only the greatest teachers can make such a profound impact on students as he did. Only the greatest teachers can simplify a very complex and difficult subject matter in a way that everyone feels that it is 'as easy as a pie'. Love is kind, and Govindjee's kindness is the virtue that resolved any misunderstanding and allowed me to feel connected with him. Love is not arrogant or rude and with Govindjee – no matter what the situation was, or who the person with whom he interacted – his humility stood out as a reflection of his great wisdom and humanity. Yes, love and his passion for knowledge is what makes Govindjee the great person and the scientist that he is. I really cherish the research I did with him (see e.g. Holub et al. 2000, 2007; Govindjee and Seufferheld 2002; Rose et al. 2008); for this, Govindjee guided me in learning to use the state-of-the art tools in the biophysics and physics labs of Prof Antony R. Crofts and the late Prof Robert Clegg, respectively. Thank you very much Govindjee for being such a great mentor and for all the great things you are still doing for science and its promotion.

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My personal story about knowing Professor Govindjee (who prefers that I call him Govindjee) follows. I learned about him, in 2017, from my professor Jos T. Puthur (of the University of Calicut, Kerala), while he was discussing the then upcoming 8th International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability, which was organised in honour of William A. Cramer, Govindjee and Agepati S. Raghavendra, in Hyderabad, India. Dr Puthur (see Allakhverdiev et al. 2019) shared with me his 1998 reminiscence of Govindjee, by proudly showing me his photo with Govindjee, taken at the 11th International Congress on Photosynthesis Research, in Budapest, Hungary. Till then, Govindjee was just one amongst the many legends in Plant Physiology for my peers and me. But Dr Puthur's gripping talk about Govindjee, and his discoveries, soon inspired me (and other students) to really want to know him. It was one of the reasons that most of us students participated in the 2017 conference, mentioned above … In Hyderabad, we were really lucky that our accommodation was near the guest house where Govindjee and his wife Rajni were staying. The first time we saw him in person was on the morning we all were going to the conference site. This moment was thrilling, but we had preconceived ideas about him based on his appearance and age; we assumed that he would be quite serious in nature. But we were soon proven

wrong as we reached the conference hall to witness his carefree and pleasant interaction with not just the invited speakers, but also with the audience. After the grand inaugural session, he was seen signing the *Z*-scheme posters and interacting with the conference participants in an extremely casual manner. It was then that we made our move to meet him. Each of us received a *Z*-scheme poster signed by him; it was a dream come true! We also had baby Faiha Fathima, a two-year-old with us, and Govindjee was more than glad to entertain her as well! Our first interaction with Govindjee and Rajni was indeed a memorable one, and, thus, we made sure to cherish it by taking photos (see Figure 2E in Stirbet et al. 2020).

In early 2020, Prof Puthur invited Govindjee to the University of Calicut for, what we call, a *Frontier Lecture*. I was then working as an Assistant Professor, at Sir Syed College, Kannur, and we were extremely happy to host a grand event where Govindjee would be our *Guest of Honour*. Unfortunately, this programme was postponed, and soon after that India was under lockdown due to Covid-19. Happily, and in a bold move of Sir Syed College, an online webinar series was planned: Govindjee was at the Jawaharlal Nehru University (JNU) guest house, New Delhi, and he agreed enthusiastically to participate in the webinar. Since he had not delivered a webinar lecture ever before, he had lot of apprehensions, but he ultimately became comfortable with it. (It was a pleasure to see Rajni helping Govindjee while he was on the Zoom.) His inaugural address including the following keynote lecture on '*The Past, Present and the Future of Photosynthesis*' was excellent, and was received with great enthusiasm by the audience (about 300 from around the world), from various disciplines of Plant Functional Biology. But what was the best and the happiest aspect of this entire webinar was that throughout all the sessions, Govindjee eagerly listened, and interacted with each and every speaker, almost like an enthusiastic schoolboy! It is indeed my great pleasure to wish him well at his 88th birthday on 24 October 2020.

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It is my great pleasure to honour Dr Govindjee at his 88th birthday and his 20-year retirement celebration. Govindjee (from Biophysics) and Peter Debrunner (from Physics) were my co-advisors for my PhD thesis at the University of Illinois at Urbana-Champaign (UIUC) during 1986–1992. First of all, in Govindjee's lab, we worked out the best (most highly active) oxygen-evolving Photosystem II (PS II) preparation at that time (Shim et al. 1990), which was used soon thereafter by many. During my PhD research, I took the water oxidation complex (WOC) apart and then put the components back together, and, using EPR, plasma emission, and chlorophyll (Chl) *a* fluorescence measurement, we concluded that**: (i)** all the 4 Mn are essential for water oxidation; **(ii)** all three 17, 23, and 33 kDa polypeptides are needed for full activity; and **(iii)** removal of 33 kDa polypeptide does not affect Mn binding, and more (Shim 1992). My training at UIUC was broad and support from both Govindjee and Debrunner was great, so that I took a postdoctoral fellowship in the Magnetic Resonance (MR) Spectroscopy Lab at Johns Hopkins, followed by another post-doctoral fellowship in Molecular Oncology. Then, I started an independent academic position at Emory in 2002, and I have had a productive career in drug discovery and medical imaging. I

emphasise that all this was possible because of my PhD training at UIUC, under Debrunner and Govindjee. I also remember Govindjee as an excellent editor (see e.g. Govindjee et al. 1986), an expert in primary photochemistry (having tackled the very first reactions (femtoseconds to picoseconds) in PS II and PS I; see e.g. Fenton et al. 1979; Wasielewski et al. 1987; Wasielewski, Johnson, Govindjee et al. 1989; Wasielewski, Johnson, Seibert et al. 1989)), and an invaluable historian of photosynthesis (see, e.g. his recent Tributes to his own PhD advisor Eugene Rabinowitch (Govindjee et al. 2019), and to the Nobel laureate Melvin Calvin (Govindjee, Nonomura, et al. 2020)). From my perspective, Govindjee has been very supportive, generous, and friendly. I was very fortunate that he took me as a student in his research group, despite my serious language barrier at that time.

I congratulate him on his 20 years of healthy and highly productive Emeritus life, and his 88th birthday. I wish him many more healthy birthdays and that he continues to be a passionate historian of photosynthesis and of the people in it.

Sudhir Sopory
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Govindjee is indeed a well-recognised authority in the field of photosynthesis. It has been my honour and privilege to have known him for over 3 decades; also, I had an opportunity to partner with him in editing two books (Singhal et al. 1999; Pareek et al. 2010). What has impressed me most about Govindjee is his in-depth understanding of the subject, his personal knowledge about the scientists, who have contributed to the field of photosynthesis, as well his 'art' of preparing and delivering his talks. His lectures are penetrating and make an immediate impression on the listener. And above all, I have been impressed by his excellent editorial skills, something I got to learn from him during our joint effort to publish the two books, mentioned above. He is persistent and passionate about whatever work he undertakes, a quality that each one of us must learn from him. He respects time and hence works – to me, it seems like *around the clock* – to meet the deadlines. I used to be surprised to get his mails in response to our queries, even when it would be past midnight in the USA.

Despite the scientific excellence and status that he has achieved, and the respect he has earned amongst his peers and colleagues, he is a very modest person, and is always ready to learn and teach. We love and respect Govindjee from the core of our hearts and wish him good health and happiness and many more years of productive life.

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Professor Govindjee: A friend of every photosynthetic organism

For many years, I had known Prof Govindjee mainly from the textbooks, like many other researchers do. However, I feel fortunate to have interacted with him for the past two years on several occasions. Throughout, I have admired his leadership skills and his persistent ability to encourage young researchers around the world. In several online

conferences, in 2020, during this pandemic season, Govindjee's active participation has indeed created a vibrant atmosphere for all of us. Overall, his outstanding scientific activities during his 20 years of retired life seem to me to come as if they are from a person half his age. Further, I am especially delighted to celebrate his 88th birthday.

Alaka Srivastava
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It is my pleasure to comment on my association with Govindjee. In December 1992 when I joined Professor Reto Strasser's lab in Geneva Switzerland, I was extremely happy to know that I would have the opportunity to work directly with Professor Govindjee on our chlorophyll *a* fluorescence project, the so-called OJIP-test. After a long wait, Govindjee arrived in the summer of 1993. Without wasting a minute, our passionate discussion on photosynthesis started. We would work together in the lab and afterward discuss intensely the results and the related literature. This collaboration continued effectively and successfully for a decade. In few words, I can say Govindjee is **(i)** a very enthusiastic person, and has an immense passion for his work; **(ii**) always open to embrace new ideas; **(iii)** a great communicator and a great thinker; **(iv)** amazingly patient with scientific writing/editing/presentation; **(v)** very supportive, helpful and friendly; **(vi)** always trusting young scientists, and never hesitates to support and help them to shape their future. Our collaboration was highly successful, and we published several research papers on using chlorophyll *a* fluorescence to probe the physiology of algae and plants (see e.g. Srivastava et al. 1995a, 1995b, 1999; Schansker et al. 2003). Personally, even now, he always pushes me to do better!

Thank you Govindjee for being a wonderful colleague and mentor and never letting me settle for anything less than I deserve. I am very fortunate to know you and Rajni for so long and hope you both have many more years of good health. I congratulate you for having completed 20 years of the so-called 'retired' life – when you continue to work as before, and even more.

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I have known Prof Govindjee since 1994, right after I had joined my PhD studies at the Sri Venkateswara University, India. However, I met him and his wife Rajni for the first time, in 1998, at the XIth International Congress on Photosynthesis, Budapest, Hungary; I was there with my mentor Prof Prasanna Mohanty. Afterwards I met him several times at different conferences around the world. We always had good scientific discussions whenever we met. He has been always very kind to me and it is always pleasant meeting him. I consider Govindjee (who prefers to be called by his first name) as my 'scientific grandfather' since my PhD supervisor Prof Prasanna Mohanty had been my scientific 'father' (for a Tribute to Mohanty, see Tiwari et al. 2014). Therefore, the roots of my research contributions to the field of photosynthesis had originated in Govindjee.

After I joined the faculty of the University of Hyderabad, I had a chance to invite him a couple of times to the Department of Plant Sciences, and he taught 'Photosynthesis' to our students. Whenever, he has visited us, our students have interacted intensely with him and all of them love him much. During one of these visits, together with him, we conducted experiments on slow chlorophyll (Chl) *a* fluorescence transient to characterise the '*state transitions*' in the green alga *Chlamydomonas reinhardtii*. We are the first ones to show that the slow P-S-M-T fluorescence transient in *C. reinhardtii* is due to the superimposition of two phenomena: qE dependent non photochemical quenching (NPQ) of the excited state of Chl, and the state 2 to state 1 transition. This work was published, jointly with my graduate students, and Sandra Stirbet, in Govindjee's favourite journal *Photosynthesis Research* (Kodru et al. 2015). We really enjoyed working with him. Later in 2017, we honoured him, along with William Cramer (Purdue University. West Lafayette, Indiana, USA), and Agepati S. Raghavendra (University of Hyderabad, India) at the 8th International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability-2017 (Allakhverdiev et al. 2019). We really had a great scientific discussion with him during the conference time. It has always been interesting to learn from him the real basics, discoveries and, above all, the history of photosynthesis research. I am really glad to celebrate 20 years of his so-called 'retired', but, highly active life of his 'passion in photosynthesis'!

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I met Professor Govindjee (who prefers that I call him Govindjee), through my student Betzaida Jiménez Francisco, who went to work with him, at Urbana, Illinois, in the fall of 2016. After three months with him, and Carl Bernacchi, Betzaida returned to Mexico. Then, Govindjee and I wrote up the results, with Sandra Stirbet helping us in its analysis (see Jimenez-Francisco et al. 2019**).** Govindjee's enthusiasm, and in-depth attention to the language, during this time of interaction, was indeed wonderful. In November 2019, the Mexican Network of Plant Physiologists organised a symposium on Plant Physiology at Mérida, Yucatán, México, for which we invited Govindjee to give its keynote opening address. To our great pleasure, he accepted our invitation, and gave a fantastic lecture on 'Photosynthesis: Past, Present, and Future'. What is remarkable is that although the entire conference was in Spanish, Govindjee attended all the lectures, fully participating in them, and even asking questions to the speakers! His energy and enthusiasm, and that of his wife Rajni, was surprising throughout the symposium. After the symposium, he indeed enjoyed the archaeological history and the special food of Mérida, Yucatán. All the organisers of the Conference, including myself, are very grateful for his participation in our conference, and, above all, his great enthusiasm for the 'future of photosynthesis'. Figure 5E in Stirbet, Björn et al. (2020) shows a group photograph of some of us standing under a *Ceiba pentandra* tree. I wish him the best in all his current and future endeavours.

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In 1971, I obtained my PhD under the supervision of Prof Dr Evert C. Wassink. My PhD thesis research addressed the mode of action of Photosystem II (PS II)-inhibiting herbicides, such as DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea) and atrazine. In 1977, I had the opportunity for a sabbatical leave of one year. I chose to work with Govindjee at the University of Illinois in Urbana-Champaign (UIUC). The reason for that choice was that Govindjee's group was involved in very interesting research on the bicarbonate effect in the Hill reaction. The site of the bicarbonate effect was very much related to the site of action of 'my' herbicides.

This sabbatical was a turning-point in my career. I had a great year in the stimulating laboratory of Govindjee. I vividly remember the Late Thomas (Tom) J. Wydrzynski, Daniel (Dan) Wong and Rita Khanna working on their PhD theses (see reminiscences of Khanna and Wong). Later, I returned twice to UIUC and Govindjee also visited my laboratory in Wageningen University & Research (WUR). Among the numerous papers, published by Govindjee, there are eight that we have jointly published over a period of about 20 years, almost all related to the unique role of bicarbonate on the electron acceptor side of PS II, the main 'love' of Govindjee since 1975 (see e.g. Govindjee and van Rensen 1978; Shevela et al. 2012).

I retired in 2006 but kept working until 2012. In that year, I published together with Julian Eaton-Rye and Iain McConnell, Chapter 20, which is on bicarbonate; and it is in Volume 34 of the Series 'Advances in Photosynthesis and Respiration', of which Govindjee is the Founding series editor (see McConnell et al. 2012). And now, Govindjee: the time has come, 20 years after your retirement, to enjoy, other activities as well, as I have that experience since 2012. I can tell you that it is wonderful having hobbies and taking daily walks in open air. I wish you all the best and I am sure you had a wonderful 88th birthday on 24 October 2020, together with Rajni, your dear wife.

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[c]Govindjee has asked me as to what J.J.S. stands for in my formal full name; please tell him that it is for *Jacobus Johannes Servatius*, named after my grandfather, god father and the first Bishop of The Netherlands, respectively.

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As a former graduate student from the 1970s, I am pleased to share this brief recollection – in appreciation and tribute – on the occasion of recognising Prof Govindjee, although I had initiated my graduate studies in Biophysics at the University of Illinois at Urbana-Champaign (UIUC) under the guidance of the Late Prof Christiaan Sybesma (1928–2018; see Vredenberg and Govindjee 2020). However, since Prof Sybesma had decided to accept a faculty position in Belgium, I opted to join Govindjee's research group; it

indeed was my good fortune to be in his lively group. Here, I received a solid and thorough training experience in the ways and means to perform sound experimentation, and in writing up publications, and I appreciate that even now. One titbit I never forgot was the advantage to use when proofreading a manuscript – go through it more than once, but put on 'different lenses' (clerical, content) each time you read through to better identify needed revisions. The very first experience I received was to write a mini-review on a topic different from that of my PhD thesis (VanderMeulen and Govindjee 1973). This was followed by a novel exploitation of fluorescence probes in understanding the regulation of thylakoid membrane energisation (VanderMeulen and Govindjee 1974a, 1974b, 1976) but, more significantly on the functioning of ATP by its binding to isolated coupling factor protein (VanderMeulen and Govindjee 1975, 1977), the latter being the major part of my 1977 PhD thesis in Biophysics (with Govindjee; Gregorio Weber (1916–1997); Thomas Ebrey, and Charles Arntzen, as my committee members).Yes, the emphasis was on fluorescence spectroscopy and protein chemistry!

Beyond the technical, strategic and analytical values gained from Govindjee's guidance, as mentioned above, I recall with fondness hearing the personal and historical stories about the lab and the key photosynthesis projects. Moreover, it was a special blessing to experience the warm sense of comradery he fostered among the student team, which was given a special boost from the regular meetings held at his home; these somehow managed to be not only effective but cordial, friendly and fun. In short, thank you Govindjee for your invaluable part in making one slice of my own history a treasured one! I congratulate you on completing 20 years of a highly productive academic and social life and my very best wishes for your 88th birthday.

Willem (Wim) Frederik Johan Vermaas
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I was a visiting grad student with Govindjee (Gov) about 40 years ago and view him to be one of my key mentors. He not only taught me photosynthesis and research approaches, but also how to drive a car and to adapt to life in the USA. When I was with him, I had a very productive academic life; he not only encouraged me to publish research papers on the unique role of bicarbonate in Photosystem II, his 'baby' so to say (see Vermaas and Govindjee 1982a; Vermaas et al. 1982), but also supported me in writing reviews and overviews on Photosystem II that reached a wide audience – in record time (see Vermaas and Govindjee 1981a, 1981b, 1982b). This collaboration did not end there; he came to Arizona to learn molecular biology tools from us, this time – staying late at night! (see e.g. Cao et al. 1991). Fast forward to when Govindjee 'retired': His idea of retirement was to do just as much and be just as active in photosynthesis and education as before, but now be unfettered from responsibilities toward the university and granting agencies. A great example!

And his and Rajni's sincere, welcoming warmness and hospitality did not change one bit over the years. For example, a decade ago our son Josh was starting grad studies in biophysics at the University of Illinois at Urbana-Champaign (UIUC), and at the last minute the move-in into his apartment had to be delayed by a week. Gov and Rajni did not think twice about having him stay with them for the week and storing his

stuff in the garage! And while my progeny was living in Urbana, I visited sometimes and stayed with Gov and Rajni, the same place as where I started in the US back in 1980.

Gov's involvement, mentorship and interest over the years are really inspiring and greatly appreciated by many!

Sir John Walker
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I am astonished to learn that Govindjee is about to reach the age of 88. His vitality and continued deep engagement with science, and especially with photosynthesis, is an inspiration to younger colleagues (such as myself).

I wish him a very happy *Beiju*, with the traditional banquet of sticky rice (cooked with adzuki beans) and sea bream!

Arieh Warshel
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Dear Professor Govindjee

I would like to congratulate you for your 88th birthday, and for your very great contributions to Science in general and to photosynthesis in particular.

With Very Best Wishes

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Dear Gov

We've been friends for 50 years, during which time you've published a ton of papers, given thousands of lectures, mentored a brigade of students and postdocs, and, amazingly, you are still charging ahead. I remember teaching with you, writing reviews with you, and, with particular vividness, travelling with you. You greeted every step and every challenge with enthusiasm, a marvellous smile, and humour. Your humour was sometimes innocent, sometimes ironic, and often mischievous, but always in good spirit. Not unlike your lectures, in which you were somehow able to make your students laugh while they were learning. They all experienced your commitment – it was clear that you cared for them as you shared your excitement for research and learning. And so, after 50 years I wish you well and remain your dear friend.

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[d]*We note that John Whitmarsh was a professor and administrator at the University of Illinois at Urbana-Champaign and a senior advisor at the National Institutes of Health, USA*. [Joint publications with John Whitmarsh during Govindjee's *retirement* include several teaching overviews (see Whitmarsh and Govindjee 1995, 1999, 2001; Govindjee et al. 2010) and an experimental paper on oxygen evolution in a mutant lacking Photosystem I (Wang et al. 2012)]

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I had the great privilege to have been trained by Govindjee to do research while in the Biophysics programme starting in 1972 at the University of Illinois at Urbana-Champaign (UIUC). Although my PhD research was focused on photosynthesis, the training I received and the skills I developed were readily transferable to other fields. Shortly after completing my PhD, my career took me on a four-decade journey away from photosynthesis into *in vitro* diagnostics – from being a bench scientist to leading large teams doing product development projects.

Govindjee provided a nurturing environment for a novice like me to grow and to develop into an independent scientist. Through his emphasis, I learned the importance of scientific rigour, efficiency in conducting experiments, developing understanding from the first principles, free exchange of ideas, collaboration with other researchers, and crediting others for their contributions (usually encountered while preparing citations in manuscripts). To this day, I have vivid memories of his regular individual discussions and weekly group meetings on research projects, and seminars in photosynthesis in a safe and friendly atmosphere. My PhD thesis dealt with '*Regulation of Excitation Energy in Photosynthesis*' and involved measuring lifetime of fluorescence, polarisation of fluorescence, delayed fluorescence and rates of electron transport. Govindjee's infectious enthusiasm of photosynthesis also attracted many leading researchers from around the world to visit, lecture, and do research in his laboratory. This included Jean-Marie Briantais (1936–2004) from France, Jack van Rensen from The Netherlands, Karel Vacek from the Czech Republic, and Shmuel Malkin (1934–2017) from Israel. Further, I was fortunate to work with leading circadian clock experts Beatrice (Beazy) Sweeney (1914–1989) and Barbara Prezelin (now at the University of California at Santa Barbara); this was great fun as we worked all night. From these interactions, I learned new viewpoints, styles, and approaches to research. We were very productive and obtained novel insights in the area of regulation of excitation energy distribution. For brevity, I list here only 5 out of 12 of our papers (see e.g. Wong et al. 1978, 1979, 1980; Govindjee et al. 1979; Wong and Govindjee 1979). Closer to home, Govindjee and Rajni often invited our little lab family of students (Alan Stemler, Barbara Zilinskas, David VanderMeulen, Paul Jursinic, the late Thomas (Tom) Wydrzynski (1947–2018), Rita Khanna, Ralph Schooley, and James (Jim) Fenton) to their home for evening laboratory meetings and social gatherings where we got to experience their humility, friendliness, generosity, and especially Rajni's wonderful culinary creations.

Govindjee must be proud to hear that many of the supporting skills and attitudes he practiced and imparted on his students have grown in importance over time. For example, in this internet age, in my industry, which depends heavily on research and development for growth, we increasingly turn to open exchange of new ideas, diversity, and collaboration to drive innovation. I am particularly grateful to Govindjee for having planted the seeds of these skills and attitudes. As he continues to be active in retirement, I will say, 'Keep up the great work, Govindjee!'

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I am very honoured that I had the chance to work with Professor Govindjee (who prefers that I call him Govindjee, without the title) and to have been mentored by him during my PhD study at the University of Illinois at Urbana-Champaign. He is a caring, diligent and an energetic professor. I started to work with him in my second year of PhD when doing research that involved photosynthesis. I did not know much about this area at that time, but Govindjee was extremely patient in guiding me into the intricate details of the world of photosynthesis and walking me through the very earliest experiments with the green alga *Chlamydomonas reinhardtii*. Even today, almost 10 years after that work, I still remember clearly the very first basic lecture he gave me about electron transfer in photosynthesis in his office in 669 Morrill Hall (505 South Goodwin Avenue, Urbana, Illinois). I am still very impressed how diligent and energetic he was and is even today. In our research project, he was extremely responsive with emails. He even replied to my emails that I sent at midnight, and his reply was in such details that it immediately cleared for me the next path to take for the experiment. I was very surprised that such an achieved and retired professor would still work this hard and care very much about his students. Without his help, I would not have completed the research work that laid a solid foundation for my PhD thesis. I still cherish the paper I published with him and other co-authors (Zhou et al. 2015); it was one of the earliest papers showing increased biomass in algae. I am pleased to note that Govindjee has continued his interest in this important topic of increasing biomass production in green algae (see Negi et al. 2020). I wish him a long productive life and continued interaction with beginning students around the world. *He has been rightly called Mister Photosynthesis* (Figure 5B).

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