

Single-authored Work of Govindjee, Mister Photosynthesis[#]

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ABSTRACT

Govindjee is a prolific and influential writer in the arena of oxygenic photosynthesis. He is internationally revered as one of the most prominent plant scientists of the 21st century, who enhanced 'Emerson Enhancement'. He is widely regarded for extensive collaborations with hundreds of scientists from around the World and moreover, his solely authored publications are impressive in quality and quantity—a virtue not known to many—thus, we list them here. In 2022, he was recognised for his work with a Lifetime Achievement Award from the International Society of Photosynthesis Research <<https://mcb.web.illinois.edu/news/2022-09-12/govindjee-receives-lifetime-achievement-award-photosynthesis-research>>.

Keywords: Robert Emerson, Eugene Rabinowitch, Rajni Govindjee, Emerson-Govindjee enhancement effect, Advances in photosynthesis and respiration

INTRODUCTION

Much has been written on Govindjee (now Govindjee Govindjee) (Figure 1), also known as Mister Photosynthesis of the 21st Century (Block, 2022), for he is a pioneer of oxygenic photosynthesis as well as a charming, young-at-heart researcher in both basic and applied aspects of photosynthesis (see e.g. Block, 2022; Kumar *et al.*, 2021; Lichtenthaler, 2020; Stirbet *et al.*, 2022). In addition, Govindjee (2019a) has provided us with detailed descriptions of his research with excellent photographs of those who have worked with

him over the years. In addition, he is unique in his ways of recognising others who have helped him in his research life by giving them personal thanks (see Govindjee, 2019b)—something quite sincere and unique to his lifestyle. Since he is what one may call a 'people person', we have discovered that he has helped produce a list of all his 580 coauthors from 30 countries, out of which, the majority are from USA, India and China (see his web site <https://www.life.illinois.edu/govindjee/CoauthorsOfGovindjeeThru22.pdf>>). In view of this, we focus here on articles that he has published as the sole

[#]School of Integrative Biology Newsletter, the University of Illinois at Urbana-Champaign (Fall, 2012) Govindjee, Mister Photosynthesis, p. 9 (reproduced in Appendix 1).



Figure 1: Govindjee Govindjee 2015 at the Rebeiz Foundation for Advanced Studies, Champaign, Illinois [Photo by H.K. Lichtenthaler].

author. We have found many papers written by himself and we present them in this overview. With the exception of his PhD thesis (Govindjee, 1960), this does not include his most important research, but it shows his deep interest in educating others on his way of thinking. Govindjee's single-authored papers are described under the following headings: (1) Effect of X-rays on the biochemistry of plants; (2) Enhancing Emerson enhancement; (3) His outstanding service to the plant science research community through excellent editorial service and by announcement of resources for students and scholars; (4) Overviews of the field of photosynthesis for the benefit of graduate students and beginning researchers; and (5) Tributes to other scientists. We emphasise that we mention here only the papers he has written by himself alone. For the majority of his work, we refer the readers to Govindjee (2019a) and to his website.

FIRST RESEARCH PROJECT, ALLAHABAD UNIVERSITY: EFFECT OF X-RAYS ON PLANTS

Govindjee's major professor, Shri Ranjan (see Laloraya, 1970; <https://www.life.illinois.edu/govindjee/ranjan.html>),

had asked Govindjee to study the effect of cosmic rays on the growth of plants. Initially, Govindjee commented, 'I was disinterested in the project and really did nothing except to grow some *Cicer arietinum* plants'. However, Govindjee worked independently by taking a trip from his lab in the Department of Botany at Allahabad University, to the Kamla Nehru Hospital, where he found the instrumentation he needed to determine the effects of exposure to X-rays on the biochemistry of *Cicer* seedlings. He published two brief communications and in one, Govindjee (1956) exposed *Cicer* seedlings to 2000r X-rays (65 r per minute), obtained from an X-ray therapy model that was run at 250 kV and 10 m Amps. As a result, he showed that the seedlings grown from the 4th day on had a drastic reduction in their respiration (measured by manometry as oxygen uptake). From those first observations, he hypothesised that the reductions could have been due to the known effects of X-rays on the enzymes. Thus, Govindjee (1957) exposed *Cicer* seedlings to X-rays at a lower dose of 450 r (30 r per minute), obtained from a different X-ray therapy model. After publishing the aforementioned two brief articles, this subject was not pursued further—except for the joy he had doing these experiments.

ENHANCING EMERSON ENHANCEMENT

Govindjee began working with Robert Emerson in September 1956; however, Emerson tragically died in a plane crash on 4 February 1959. Thus, Govindjee moved on to complete his PhD thesis in September 1960, under the supervision of Eugene Rabinowitch (in Physico-Chemical Biology, which changed to Biophysics). Initially, quite a challenge, the move from 'Botany', his MSc subject at Allahabad, to Biophysics, required taking core courses in physics, chemistry and mathematics, which he did wonderfully well. It was a success! Clearly, Govindjee (1960) showed that there were two light reactions and two photosystems in oxygenic photosynthesis. Although Robert Emerson had suggested such in 1957, what was new was that Govindjee was the very first to establish that Chlorophyll *a* was the pigment in both the photosystems—one absorbing at a

shorter wavelength of light than the other (see Govindjee, 2022a)—the latter challenged Emerson’s hypothesis that one reaction was run by chlorophyll *a* and, the other, by accessory pigments. Indeed, Govindjee created a paradigm shift when he enhanced Emerson’s enhancement! If the truth is known, this fundamental process of photosynthesis should be referred to, hereafter, as the Emerson-Govindjee enhancement effect.



OUTSTANDING SERVICE

In 1960, Govindjee completed his doctoral thesis under the mentorship of Eugene Rabinowitch, as mentioned above; and by 1969 he was already a full professor at the University of Illinois at Urbana-Champaign. He had the highest regard for Rabinowitch, to whom he dedicated the July 1972 issue of the ‘Biophysical Journal’ that he edited (Govindjee, 1972). In addition, to commemorate his two esteemed scientific mentors, Robert Emerson and Eugene Rabinowitch, Govindjee and his wife Rajni have recently planted a tree in Meadow Brook Park in Urbana, Illinois, USA (see Figure 2).

Moreover, for teaching and research purposes, Govindjee (1975) edited a thorough book on the ‘Bioenergetics of Photosynthesis’ (see Vernon 1975). This did not satisfy

the educator—the teacher and above all, the researcher in Govindjee. Thus, he decided to cover the entire field of photosynthesis from the time light is absorbed to the time food is made. Govindjee (1982) edited a two-volume book on ‘Photosynthesis’, volume I, covering the energy conversion process in plants, algae and bacteria; and volume II, covering carbon metabolism and overall productivity (see Malkin, 1983 for a review).

It seems that Govindjee realised that some of the authors of ‘Photosynthesis Research’ and even in the books he was editing, were unaware of basic formatting rules. Therefore, he decided to guide them by publishing an editorial on a list of symbols, on the system of international units and the conversion factors (see Govindjee, 1987a). Following that, he even informed the readership about all the editors of ‘Photosynthesis Research’, something that had not been done before. Last, but not least, from his point of view, there was a need for an editorial: ‘Celebrating 20 years of ‘historical papers’ that he had published in ‘Photosynthesis Research’ (Govindjee, 2006a).

For the benefit of teachers and students, Govindjee has edited and coauthored books with many others (see <https://www.life.illinois.edu/govindjee/g/>

Figure 2: Early Glow Ohio Buckeye Tree (*Aesculus glabra* J. N. Select) Planted in Memory of Govindjee’s Mentors *Robert Emerson* (1903–1959) and *Eugene Rabinowitch* (1898–1973), in Meadow Brook Park in Urbana, Illinois, USA. The tree and plaque were donated by Rajni and Govindjee in 2022. The Govindjee family is highly thankful to Kayla Boparai (Planning and Operations Manager of Urbana Park District) for the implementation of the project.



Publications.html). Over the years, Govindjee has written on subjects that he felt would be a means of further serving students and teachers, which included reviews and announcements, including those for books in the series, he had pioneered ‘Advances in Photosynthesis and Respiration’. We list here some of these items.

Book Reviews

Addressing various aspects of photosynthesis except for the subject of ‘Biohydrogen production’ (Rögner, 2015), Govindjee (1998), Govindjee (2010c), Govindjee (2014) and Govindjee (2015) expounded on the good, as well as the missing parts of Wild and Ball (1997), Renger (2008) and Ruban (2012). In addition, Govindjee (2006d) reviewed a book on ‘Photosynthesis: Regulation under Varying Light Regimes’. It was quite useful for students to read these overviews.

Announcements

For the benefit of graduate students, postdoctoral scientists and beginning faculty, Govindjee initiated single-handedly, the most useful book series, mentioned above: *Advances in Photosynthesis and Respiration*, published first by Kluwer and then by Springer. He is its ‘Founding Editor’. It is being edited now by Thomas Sharkey and Julian Eaton-Rye (<https://www.springer.com/series/5599>/editors). Since Govindjee wanted to be sure that others learned about each book, he announced these books by describing their content and profiling the authors. Govindjee (2004c) provided not only a list of all available edited books in photosynthesis but all the photosynthesis conferences until then. For example, Govindjee (2005a) announced and described the content of Volume 19 of his Series on ‘Chlorophyll a Fluorescence: A Signature of Photosynthesis’. Govindjee (2005b) did the same for volumes 17 and 18 which focused on *Respiration*. The year 2006 was a very active year and although he had been retired for 6 years already, he completed ‘Discoveries of Photosynthesis’ (Govindjee, 2006c), Photosystem II (Govindjee, 2006e), *Photoprotection and Photoinhibition* (Govindjee, 2006f); *Structure and Function of Plastids* (Govindjee, 2006g); and

Photosystem I (Govindjee, 2006h), as well as *Chlorophylls and Bacteriochlorophylls*. In addition to announcing these books, Govindjee (2006b) encouraged a dialogue discussion between Steve Vik and Wolfgang Junge—one needs to really read it to appreciate it. And, finally, Govindjee (2007b) announced the tale of naming a bacterium and its associated controversy!

OVERVIEWS

As a talented science writer, Govindjee has communicated critical thinking insights either with research reviews on photosynthesis in his own research group or by an overview of broad areas of photosynthesis, many of which were written for ‘lay readers’ in encyclopedias or in scientific journals. Here, these publications are listed in chronological order.

Govindjee (1963a) summarised his original research, including the progress made in his PhD thesis and discoveries 3 years, thereafter. It includes new findings on the composition of the two photosystems in terms of different spectral forms of chlorophyll *a*, as well as new information on chlorophyll *a* fluorescence in the two photosystems. He tells us that he also ‘played’ with some fun things related to pigments in a green alga and a cyanobacterium (Govindjee, 1963b, 1963c), something he thinks was ‘good’ for him to keep interested in science! This was followed by a serious scientific article by Govindjee (1966b); in addition, for researchers in the field, Govindjee (1993) presented a minireview of the field.

Govindjee’s main love of research always has been the exploitation of chlorophyll fluorescence to measure various aspects of photosynthesis. For this, Govindjee gave an in-depth overview talk in Australia and published a thorough review of it (Govindjee, 1995). In addition, he did not forget the long-standing controversy between his own professor Robert Emerson, who had measured that the evolution of one oxygen molecule required a minimum of 8–12 photons of light) and Emerson’s professor, Otto Warburg, who incorrectly insisted that three to four photons are enough (see Govindjee, 1999a).

Finally, in 1999, just the year of his retirement from active teaching duties, Govindjee (1999b) wrote a thorough review of the role of carotenoids in photosynthesis. One wonders why? There is a story to it, as told by Govindjee: Emerson had assigned him the PhD thesis topic on the ‘Role of xanthophylls versus carotenes in photosynthesis of algae’. That involved growing the alga *Polyedriella helvetica*, under different intensities and colours of light. In pursuit of the answer, Govindjee became frustrated with this project since this alga grew all too slowly. So, he gave up that project, much as he had given up what his first professor, in India, had wanted him to do (see above). In his PhD thesis, he had shown that ‘fucoxanthol’, along with ‘chlorophyll c’, serves as an antenna in one of the two photosystems of *Navicula minima*, a diatom. As a consequence, Govindjee (1999b) wrote an excellent review on the role of carotenoids in photosynthesis.

Post Retirement: 2000s

We are told that 2000 was the beginning of his fun years. It began with Govindjee (2000) publishing the history of the major concepts in the light reactions of photosynthesis as evolved through its history, that is, the ‘milestones’. We recommend it to all graduate students in plant sciences because it discusses the key properties of the master pigment, chlorophyll, the concept of the ‘photosynthetic unit’ (the antenna and the reaction centres P680 and P700), the evolution of the Z-scheme of electron transport, photophosphorylation and what ‘Light Emission (s)’ from plants tell us about the basic reactions of photosynthesis. Govindjee (2002) followed it up with a wonderful editorial on the photoprotective role of a light-harvesting antenna complex of Photosystem II. From the perspective of teaching photosynthesis, we emphasise the importance of (1) a wonderful overview by Govindjee (2004a) on the basics and the history of the use of chlorophyll *a* fluorescence in understanding photosynthesis; and (2) his innovative ideas and ways of teaching photosynthesis (Govindjee, 2008a) which involved using students to represent the dynamic flow of molecules!

TRIBUTES TO OTHERS IN PHOTOSYNTHESIS RESEARCH

Recognising others, young and old, has been Govindjee’s major objective for a very long time. He told us that this gives him great satisfaction and he considers this activity to be the most important in his life. For example, Govindjee (2009b) recognised the young scientists at one of the Gordon Conferences on Photosynthesis.

Govindjee has recognised and honoured many colleagues. They include, in alphabetical order, Sam Aronoff (Govindjee, 2010b); James (Jim) Barber (Govindjee, 2021b); Andrew A. Benson (Govindjee, 2010a); Olle Bjorkman (Govindjee, 2001a); Warren Butler (Govindjee, 1986a); Robert (Bob) Emerson (Govindjee, 2001c, 2004c, 2018, 2021c); C. Stacy French (Govindjee, 1989); Andre Jagendorf (Govindjee, 2017); Eugene Rabinowitch (Govindjee, 2004c); T. Raja Rao (Govindjee *et al.*, 2022); Emil Smith (Govindjee, 1988); Achim Trebst (Govindjee, 2009c); Robert (Bob) Whatley (Govindjee, 2022b); Thomas (Tom) Wydrzynski (Govindjee, 2008b); and his own parents (Govindjee, 2007a)-whom he called Amma (for his mother) and Babuji (for his father).

Moreover, in a special issue of the journal *Photosynthetica* on Chlorophyll Fluorescence Imaging he wrote an honouring laudatory article on Hartmut K. Lichtenthaler, to whom this issue was dedicated (Govindjee, 2021a). In addition, Govindjee has recognised many young scientists and colleagues who have received awards. Furthermore, Govindjee (2009a) has provided a list of biography and history up to that time in ‘Photosynthesis Research’.

With this, we end our presentation of what Govindjee has published alone for all of us. We wish him a very happy 90th birthday with the expectation that he now will dig into his paperwork both in his office at the University and at his home and write the ‘hidden stories’ – not yet available to anyone, except perhaps, himself!

CONCLUDING REMARKS

We conclude from this description of Govindjee’s sole author works, that he is the true educator of our time,

selflessly giving knowledge to humanity through his reviews, overviews, editorials, lectures and books. For his research contributions, see Govindjee (2019a) and you may join us in concluding that Govindjee Govindjee and Rajni Govindjee (see Ebrey, 2015) have had a lifetime enhancement effect on the entire field of photosynthesis. We wish both of them many more happy years together (see Figure 3 for a photograph of this wonderful couple).



Figure 3: A 2022 Photo of Govindjee (Right) with His Wife Rajni in Urbana, Illinois.

Source: Govindjee's family

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APPENDIX 1



GOVINDJEE, MR. PHOTOSYNTHESIS

Photosynthesis is a complex, multi-step process that sustains all animal life on our planet. The discovery of its molecular mechanism was a landmark achievement in the field of integrative biology—and a milestone for the leading scientist Govindjee has studied for more than a half-century.

Govindjee, professor emeritus of biochemistry, bioinformatics, and plant biology, first became interested in photosynthesis as a student at the Indian Institute of Technology in India. While earning his master's degree there, he began a correspondence with photochemist and pioneer Robert Emerson. He soon moved to the United States to work under Emerson at the University of Illinois after earning his Ph.D. in physics under Eugene Rabinowitch in 1963. He joined the faculty in 1965 and has been a central figure in the scientific community.

Over the course of 50 years, Govindjee's research has uncovered many of the key aspects of photosynthesis, especially the initial events of the process, the so-called light reactions. In his studies, he discovered that the photosynthetic reaction center produces energy during photosynthesis, but also steps of electron transfer processes, providing insights into the steps of photosynthesis.

His work also made important contributions to the field of bioenergetics and thermodynamics research. He has developed a method of measuring the kinetic of bioenergetic reactions, which has been widely used to understand the relation of the kinetic thermodynamic and photosynthesis.

These discoveries led to a new paradigm in photosynthesis research—over 300 research publications, many in leading journals like *Nature*, *Science*, and *PNAS*. As founding editor of *Photosynthesis Research*, Govindjee has helped push the frontiers of research in this field.

His research has been widely cited and recognized. He was elected to the National Academy of Sciences in 2001. He has also received numerous awards, including the National Science Foundation Award for Integrative Biology (2001) and the 2007 recipient of the prestigious Garvan Medal of the International Society of Photochemists and Photobiologists.

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Source: School of Integrative Biology Newsletter, University of Illinois at Urbana-Champaign, Fall, 2012