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NEWS REPORT

# Teaching the Z-Scheme of electron transport in photosynthesis: a perspective

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**Abstract** This paper deals with how Govindjee taught the Z-Scheme of electron transport in oxygenic photosynthesis at Ravenshaw University, Cuttack, Odisha, India, in 2014, in a unique and highly effective fashion—using students to act as molecules, representing the entire electron transport chain from water to nicotinamide adenine dinucleotide phosphate ($NADP^+$). It culminated in a show by B.Sc. students in the garden of the Department of Botany, Ravenshaw University. The first author (PKM) personally acted as Ferredoxin NADP Reductase (FNR) catalyzing the reduction of $NADP^+$ to NADPH, taking electrons from reduced ferredoxin at the end of Photosystem I. On the other hand, the Q-cycle was played by M.Sc. students, who acted as molecules running this ingenious cycle that produces extra protons. An interesting event was when a student, acting as a herbicide, who was dressed like a devil (fierce looking, in black clothes with a sword; "*Yamaraj*: The God of Death", as he called himself), stopped all reactions by throwing out $Q_B$, the second plastoquinone molecule of Photosystem II, and that too aggressively, taking its position instead. The second author was the major organizer of the Z-scheme show. We provide here a basic background on the process, a bit on Govindjee's teaching, and some selected pictures from the drama played in March, 2014 at Ravenshaw University. Here, we also recognize the teacher Govindjee for his ingenious and fun-filled teaching methods that touched the hearts and the souls of the students as well as the teachers of Ravenshaw University. He was rated as one of the most-admired teachers of plant biology at our university.

**Keywords** Electron transport · Govindjee · Photosynthesis · Q-cycle · Z-scheme drama

## Prologue

This manuscript was read by Robert Blankenship, Govindjee, Julian Eaton-Rye and Baishnab Charan Tripathy before its publication in Photosynthesis Research. Robert Blankenship wrote: "….the paper is interesting, especially the part about the dramatization of the Z scheme. Others may be inspired to try something similar. It obviously made a very strong impact on the students." (See comments in the Supplementary Material, and the quote below.)

> *Govindjee stands out as "perhaps the world's most recognized photosynthesis researcher," says Donald Ort, University of Illinois, Professor of Plant Physiology. "Driven by a single-minded fascination with the process of photosynthesis, Govindjee's research contributions have been paradoxically far-reaching and diverse." –News Report by Doug Peterson, LAS (Liberal Arts and Sciences), University of Illinois at Urbana-Champaign (UIUC), 2009*, published at the time Govindjee received the Lifetime Achievement Award of LAS, UIUC. Here, we present a glimpse of Govindjee's innovative method of teaching, in 2014, of the Z-Scheme of photosynthesis, at Ravenshaw University, Cuttack, India.

**Electronic supplementary material** The online version of this article (doi:10.1007/s11120-014-0034-4) contains supplementary material, which is available to authorized users.

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## Introduction

Photosynthesis is a highly complex process carried out by all oxygen-producing organisms: plants, algae and cyanobacteria (Rabinowitch and Govindjee 1969—available free on line at http://www.life.illinois.edu/govindjee/photosynBook.html; Shevela et al. 2013; Blankenship 2014). Of course, there is also anoxygenic photosynthesis, carried out by green and purple photosynthetic bacteria (see Blankenship et al. 1995). Our basic understanding of the complex life-sustaining process of photosynthesis is based on the discoveries and research of many scientists including (in alphabetical order; with their nicknames, if used): William (Bill) Arnold (the photosynthetic unit; delayed light from plants), Daniel (Dan) I. Arnon (photophosphorylation), Melvin (Mel) Calvin & Andrew (Andy) Benson (carbon fixation in C3 plants), Louis (Lou) N. M. Duysens (excitation energy transfer; two light reactions, and two-pigment systems), Robert (Bob) Emerson (photosynthetic unit; quantum yield; and two light reactions), Hans Gaffron (hydrogen evolution), M.D. (Hal) Hatch (carbon fixation in C4 plants), André Jagendorf & Wolfgang Junge (ATP synthesis), Pierre Joliot (oxygen evolution), Robert (Robin) Hill (Hill reaction; and Z-scheme), Martin Kamen & Samuel (Sam) Ruben (discovery of $^{14}C$), Bessel Kok (reaction center of PS I/P700; and oxygen evolution), Eugene Rabinowitch (photochemistry), Horst Witt (reaction center PS II/P680); and many others (see Rabinowitch 1945; Rabinowitch and Govindjee 1969; Benson 2002; Govindjee et al. 2005; Govindjee and Björn 2012; Blankenship 2014). In his lectures, Govindjee brought these scientists alive before the students by not only presenting their scientific discoveries, but also by mentioning stories and their personalities.

The Z-scheme of photosynthesis, which is based on the existence of two light reactions and two-pigment systems in the electron transport from water to $NADP^+$, has been known for a long time (see Govindjee and Björn 2012 for its evolution; a simple version of the Z-scheme is on Govindjee's web site: http://www.life.illinois.edu/govindjee/z-scheme.html) (Fig. 1); it can be downloaded free from http://www.life.illinois.edu/govindjee/2010_z-

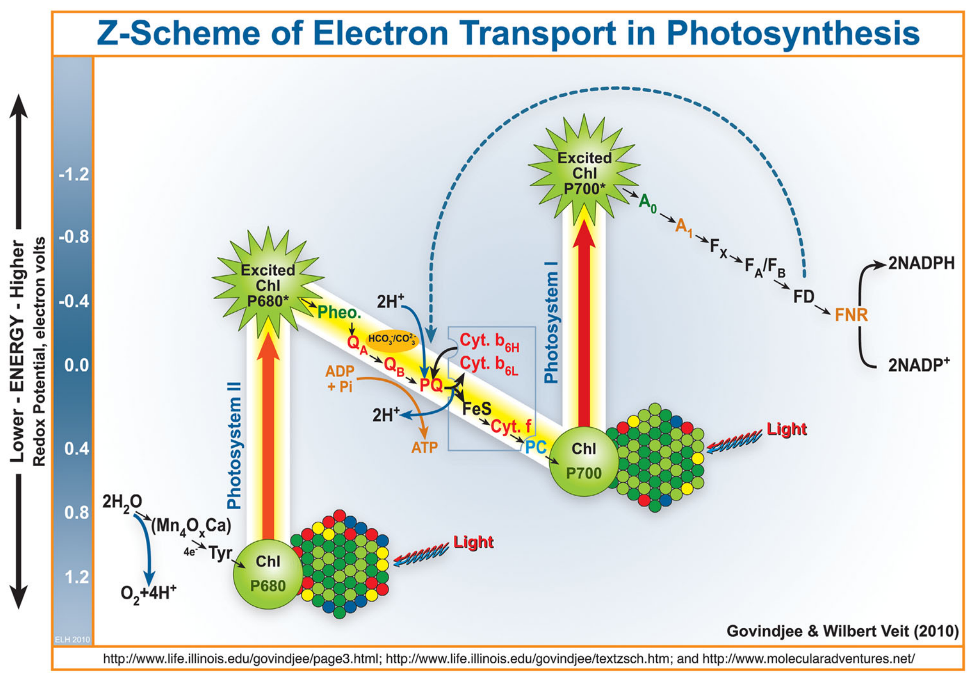


**Fig. 1** The Z-Scheme for electron transport from water-$NADP^+$. There are two Photosystems—I (PS I) and II (PS II)-connected in series, with a cytochrome $b_6f$ complex in between; a cyclic electron transport around PS I also occurs. In PS II, there is a manganese–oxygen–calcium cluster ($Mn_4O_xCa$); Tyr is the tyrosine-161 on the D1 protein; P680, primary electron donor of PS II; P680*, excited electronic state of P680; Pheo, pheophytin; $Q_A$, a tightly bound, one electron acceptor, plastoquinone; $Q_B$, a two-electron acceptor plastoquinone that binds and unbinds from PS II; PQ, a pool of mobile plastoquinone molecules; Cyt $b_6$, cytochrome $b_6$; FeS, an iron–sulfur protein known as Rieske FeS protein, Cyt *f*, cytochrome *f*; PC, plastocyanin; P700, primary electron donor of PS I; P700*, excited electronic state of P700; $A_0$, a special chlorophyll *a* molecule; $A_1$, vitamin $K_1$; $F_X$, $F_A/F_B$, iron–sulfur centers; Fd, ferredoxin; FNR, ferredoxin NADP reductase; $NADP^+$, nicotinamide adenine dinucleotide phosphate. The cyclic electron flow, that is usually a small fraction of noncyclic electron flow, begins at the iron sulfur centers. $HCO_3^-/CO_3^{2-}$ plays an essential role in protonation at the $Q_B$ site. The figure is reproduced from the scheme prepared and distributed by Govindjee and Veit (2010), with the permission of the authors (also see http://www.life.illinois.edu/govindjee/2010_z-scheme.pdf; a text on "Photosynthesis and the Z-scheme" by Govindjee and Rajni Govindjee at http://www.life.illinois.edu/govindjee/textzsch.htm; and see Fig. 4 at http://www.life.illinois.edu/govindjee/photoweb/subjects.html#oxygen

scheme.pdf. It is briefly described at: http://www.life.illinois.edu/govindjee/z-scheme.html. To put it in the perspective of photosynthesis and related web sites, see: "Photosynthesis Web Resources by Orr and Govindjee, at http://www.life.illinois.edu/govindjee/photoweb/.

The Z-scheme includes more than 20 intermediates; in addition, there is also a Q-cycle around the cytochrome $b_6f$ complex, which allows for additional proton transport across the membrane, and thus more ATP, as well as cyclic electron transport involving PS I and the cytochrome $b_6$-$f$ complex. (Govindjee showed us the webpage of A.R. Crofts: http://www.life.illinois.edu/crofts/ahab/home.html; and Crofts et al. 2008).

We provide here an educational *News Report* where B.Sc. and M.Sc. students at Ravenshaw University, learned this scheme in a unique and highly effective way taught to them by Govindjee, of the University of Illinois at Urbana-Champaign, during January–March, 2014. See Supplementary Material for further information on Govindjee; he has been called "*Mr. Photosynthesis*"; also, he is the de facto *Ambasador of Photosynthesis* around the world–propagating the knowledge on the basics, the history and the evolution of the process. Govindjee has earlier taught the Z-Scheme in a similar manner to his undergraduate students at the University of Illinois at Urbana-Champaign; then at the University of Indore (where the students had enacted a drama on a stage inside an auditorium, with music and dances); and in Finland at a workshop. However, this is the first time, this drama was performed, in full, in a garden, and we provide here the first report with pictures.

Students volunteered to become one of the ~20 intermediates and played in an outdoor drama demonstrating the entire scheme until one oxygen molecule was evolved, and 2 molecules of 2 $NADP^+$ (nicotinamide adenine dinucleotide phosphate) were reduced. The drama included the mechanism of how certain herbicides kill plants, and how the Q-cycle makes extra protons. We present here a brief background and illustrate this news report with some pictures (see Figs. 1, 2, 3, 4 in the main text, and Figs. S1, S2 in the Supplementary Material).


**Fig. 2** (**a**) Students performing the Q-cycle drama (*left to right*: Sripadma Debata, Soumyajit Mohapatra, Ankita Prusty, Bhaskar C. Sahoo, Anita Rani Sahoo, Debasmita Panda); (**b**) Govindjee (standing 9th from left) with actors of the Z-scheme and the Q-cycle; the authors are standing third (P.K. Mohapatra) and fourth (N. R. Singh) from *left* (*in the back row*); see text for the names of the actors of the Z-scheme

## Lectures: the background some highlights

Govindjee lectured to both B.Sc. and M.Sc. students of Botany of Ravenshaw University on all aspects of photosynthesis, and interestingly, at the same time in the same lecture hall during the first week of January–first week of March, 2014; for some aspects of his teaching philosophy, see Govindjee (2008). Here, we mention mainly the lectures that were related to the "Z-scheme" of photosynthesis. Some of the remarks made by the students are in the Supplementary Material. These show how great was his impact on students, and how much they enjoyed him and his lectures including the Z-scheme drama.

The Z-scheme lecture and drama was preceded by an introductory lecture on the "History of Photosynthesis", which began with the quote of Jules Verne: "*I believe that water will one day be used as a fuel, because the hydrogen and oxygen which constitute it, used separately or together, will furnish an inexhaustible source of heat and light. I therefore believe that, when coal (oil) deposits are oxidised, we will heat ourselves by means of water. Water is the fuel of the future*" (Verne 1875). Govindjee with his animated style of lecturing engrossed the audience with his slides and stories of the giants of photosynthesis and taught their contributions towards shaping the present day concept of photosynthesis.

Govindjee et al. (2005) have stated that "major advances in understanding photosynthesis (and biological systems in general) occurred when new knowledge and


**Fig. 3** (**a**) Students performing the Z-scheme drama in the lawn of the Department of Botany, Ravenshaw University, the *yellow line* shows the flow of electrons from water (left) to $NADP^+$; (**b**) Students listening to the description of the structure and function of Cyt $b_6f$ (by Bikash Rout, standing); (**c**) Actors, representing P700, jumping to signify excitation of P700 to P700* state, shouting I am in an "*excited state*"; (**d**) P. K. Mohapatra acting as FNR (see text); (**e**) Big balls (representing electrons) were transferred downhill energy-wise from P700* to $NADP^+$ (FNR has given one electron to $NADP^+$; another one, after another light reaction, is on its way from $A_0$; and (**f**) DCMU (Gupteswar Rath, in black clothes, with stretched hands) is announcing his victory that he has blocked the electron flow after physically throwing $Q_B$ from its binding site. The entire Z-scheme drama was played on March 5, 2014, as indicated by the dates in Fig. 3(**e**) and (**f**)

techniques from other sciences (physics, chemistry) were applied". It is because of this, Govindjee emphasized that an integrated approach must be used in teaching of biology, where chemistry and physics must play an essential role. Other important aspects that he covered were: evolution of photosynthetic pigments; transition to oxygenic photosynthesis; origin and evolution of antenna; the Frank–Condon principle of excitation and de-excitation of molecules, and FRET (Förster Resonance Excitation Energy Transfer).

The lectures of Govindjee on the evolution of the Z scheme began by citation to the contribution of his mentor Rabinowitch (1945) where he had discussed a theoretical scheme of two-light reactions based on the ideas of James Franck, and on the minimum quantum requirement (inverse of the maximum quantum yield) of 8–12 for the evolution of one oxygen molecule, measured by many including Robert Emerson, Govindjee's first professor. The question of whether this number is 3–4, as obtained by Otto Warburg, or

**Fig. 4** **a** Govindjee lecturing to High School Students showing a set of 10 baloons of 3 different sizes and colors, representing 2 molecules of water (4 electrons; 4 protons and 2 oxygen atoms) that are oxidized to a oxygen molecule; **b** Govindjee and Prakash Prasad on a motorbike going to the local market to purchase "tonic water" for fluorescence demonstration; **c** Govindjee demonstrating fluorescence from tonic water under UV light to students

8–12, as obtained by Emerson and later by Govindjee and Rajni Govindjee, was discussed in the class (see Hill and Govindjee 2014, for references). The lucid explanation by Govindjee on the history of the quantum yield controversy between Otto Warburg and his doctoral student Robert Emerson interested the students a lot since Warburg was a Nobel laureate and Emerson was his student (Nickelsen and Govindjee 2011; Hill and Govindjee 2014; also see Govindjee 1999a). The existence of two light reactions became established only during 1957–1961 (see below), and, thus, quantum yield controversy was no longer an issue!

## The red drop, the enhancement effect, and the two light reactions

While teaching the history of the discovery of two light reactions, Govindjee mentioned the experimental findings of Emerson and Lewis (1943) on the green alga *Chlorella* that led to the discovery of the curious *"Red Drop"* phenomenon. Quoting the observation of Emerson, Govindjee explained that the maximum quantum yield of oxygen evolution was not the same at all wavelength of light. Instead, oxygen evolution dipped at about 500 nm, due perhaps, to the presence of yellow pigments in the cell walls far away from chloroplasts, as well as by the low efficiency of excitation energy transfer from carotenoids to chlorophyll *a* (see Govindjee 1999b). Further the causes of a smaller decrease in the quantum yield at 660 nm and a more abrupt decline (*red drop*) above ~680 nm was also discussed. Govindjee mentioned how Emerson and Lewis were unsuccessful in explaining why the decline in the quantum yield action spectrum with the increase of wavelength of light was more than that of the absorption spectrum. Govindjee told the students that Rabinowitch (1956) was ahead of his time. He had made one of the most significant statements on the possibility of two-light reactions in oxygenic photosynthesis long before the two-light effect was experimentally discovered. Rabinowitch stated that "…*two quanta will be needed to transfer each of the four required H atoms (or electrons), first from water to the cytochrome, and then from the cytochrome to the final acceptor*".

After Emerson's death on February 4, 1959, Warburg seemed to think that the quantum yield controversy will be solved in his favor, and he started telling others that Emerson had not used young synchronous cultures of algae, and 10 % $CO_2$, and thus Emerson had the wrong minimum quantum requirement number (Hill and Govindjee 2014). However, Govindjee told us about the experiments of Govindjee et al. (1968) showing that the minimum quantum number for oxygen evolution was 8–12 even in young synchronous cultures of *Chlorella*, and in the presence of 10 % $CO_2$. This finally "nailed down" the results and conclusions of Emerson under the precise experimental conditions that Warburg said Emerson had not used. Further, Govindjee also told the students about the experiments of Warburg et al. (1969), where they had experimentally obtained a minimum value of 12 photons per oxygen evolved, but, by the so-called '*photolyte theory'*, calculated the number to be 3–4! The battle of minimum quantum requirement of oxygen went on for some time (also see Govindjee 1999a). After the acceptance of the two-light effect and the two pigment systems (see Govindjee and Björn 2012), clear explanation became available of all the key biophysical experiments: Robert Emerson's discovery of the Red Drop in the action spectrum of photosynthesis, as mentioned above (Emerson and Lewis 1943), Enhancement effect, i.e., the two-light effect in photosynthesis (Emerson et al.1957; Govindjee and Rabinowitch 1960), Kok's two light effect on the reaction center P700 (Kok 1959), and the most important experiment of Duysens et al. (1961) where the push–pull effects of two light reactions on cytochrome *f* was discovered—concepts that are not easily understandable from the text books for student use. It was easy to understand the experiments of Duysens et al. (1961) as Govindjee used students sitting on two sides of the class as PS I and PS II placing a student in the middle to be the cytochrome *f* molecule; he demonstrated the oxidation–reduction by using a "ball" as an electron. Who can miss such an explanation!

Govindjee explained to the students the evolution of Z scheme also through the contributions of biochemists including the most famous concepts of Hill and Bendall (1960). As an example, he quoted Losada et al. (1961), from Dan Arnon's research group, who provided one of the first biochemical measurements supporting the "Z-Scheme". The two-light reaction and two-pigment system scheme was soon supported by the physical separation of two photosystems, biochemical surgery of the entire scheme by the use of specific inhibitors, artificial donors and acceptors of partial reactions, and through the use of mutants that lacked specific intermediates in the electron transport chain (see Rabinowitch and Govindjee 1969; Govindjee and Björn 2012; Blankenship 2014 for references). By late 1960s, a basic version of the Z-scheme was in place with coordinated efforts of chemists, biochemists and geneticists.

The mechanism of electron flow involving "The Marcus Theory", which includes the concept of reorganizational energy, was also explained (see Marcus 1993; Govindjee 2000), and on the favorable distance between a donor and acceptor for successful and efficient electron transfer (which is inversely proportional to the distance, and decreases by an order of magnitude at every 1.4 Å distance) was also brought before the students (see Moser et al. 1992). Although this was a difficult concept, yet it was made personal and lively because he described his association with Rudolf Marcus, who had once attended all of Govindjee's semester-long lectures in photosynthesis, when he was still at the University of Illinois at Urbana-Champaign. (We note that Marcus received the Nobel Prize in Chemistry in 1992 for his contributions to the theory of electron transfer reactions in chemical systems).

## The teaching of two light reactions and two photosystems

As indicated above, Govindjee made special mention of the contribution of the work of Bessel Kok and soon thereafter of Louis N.M. Duysens on the discovery of two photosystems and two light reactions in photosynthesis. Kok (1959) showed a two-light effect in a cyanobacterium *Anacystis nidulans*, on the redox state of the reaction center chlorophyll "P700". He showed that a long wavelength light (far-red) oxidized "P700", and when a short wavelength light (orange-red) was added, the oxidized P700 became reduced. In this paper, Kok related these findings to the Emerson Enhancement Effect and two pigment system concept. Duysens (1989) has presented his own story about his discoveries. After the discovery of the Emerson Enhancement Effect, Duysens examined the action spectra for cytochrome oxidation and $NADP^+$ reduction in different wavelengths of light; it was the antagonistic effect of light 1 and 2 on the redox state of cytochrome *f* that clinched the field. Duysens (1989) wrote that at the time of the famous Hill and Bendall (1960) paper, "*I [had already] postulated the existence of two major photosystems 1 and 2. System 1 contained the weakly fluorescent chlorophyll a, formerly said to be inactive, and oxidized cytochrome, [whereas] system 2 contained the fluorescent chlorophyll a*[See *Appendix* 1 for Govindjee showing the power of chlorophyll fluorescence, in understanding photosynthesis, to students]. *An interaction between the two systems was shown by the different kinetics of cytochrome oxidation at different actinic wavelengths*". On the other hand, in March, 1960, Rabinowitch and Govindjee had stated "*…the primary photochemical process in photosynthesis might consist of two steps: whereas one type of chlorophyll a was able to bring about both, the other type was restricted to one of these steps"* (Rabinowitch and Govindjee 1961).

Govindjee explained to the students the capacity of chlorophyll *a* to absorb light and the kinetics of light absorption and the bottle neck reaction(s) of the entire process during the operation of the "Z-scheme" of photosynthesis. On an average, there are 300 chlorophyll *a* molecules in the antenna per reaction center, with ~20 ms, being the slowest step involving plasoquinone/plastoquinol molecules between PS II and PS I (see Ke 2001; Govindjee and Björn 2012). He mentioned that if one were to improve overall photosynthesis, one might want to examine how one can make this step faster! On the electron donor side of PS II, there are also slow steps (ms range) during the entire water oxidation process (see e.g., Shinkarev and Wraight 1993; Grabolle and Dau 2005). For further information on "Photosynthesis", see some web sites mentioned in Appendix 2. However, for a complete basic background, see chapters 7, 8 and 9 in Taiz and Zeiger (2010).

Govindjee presented to the class the excitement in now having atomic level structures of the two photosystems, particularly of the manganese-oxygen-calcium cluster [$Mn_4\ O_5Ca(H_2O)_4$] (see e.g., the 1.9 Å structure of PS II, by Umena et al. 2011). He succeded in motivating students to deliver lectures as well as to write reviews on various aspects of photosynthesis including the structure and function of PS II and of manganese-oxygen-calcium cluster; structure and function of ATP synthase; and on the function of bicarbonate in PS II.

## The unique bicarbonate in the Z-scheme

Most text books have, thus far, left out a key role of bicarbonate in the Z-scheme. The work of Govindjee and his students has clearly established that a major role of bicarbonate is at the plastoquinone level (see Shevela et al. 2012). Govindjee explained the discovery of bicarbonate effect on the Hill Reaction by Otto Warburg but focused, during his lecture, on the role of $CO_2/HCO_3^-$ at the plastoquinone level in the Z-scheme: on the regulation of electron and proton transport between PS II and the cytochrome $b_6f$ complex. Govindjee made it a point to give credit to the people who did the work to reach a logical conclusion on the process. In his lecture on the bicarbonate effect in PS II, he paid special tribute to his past graduate students: Alan Stemler, Thomas (Tom) Wdrzynski, Paul Jursinic, Rita Khanna, and Julian Eaton-Rye, who contributed to the deciphering of the role of bicarbonate effect in PS II in his Laboratory at the University of Illinois at Urbana–Champaign. Wydrzynski and Govindjee (1975) showed that without bicarbonate the PS II behaved the way as if DCMU was present, i.e., electron flow beyond the first plastoquinone $Q_A$, on the electron acceptor side was blocked, more or less completely. The hypothesis is that for this bicarbonate effect, bicarbonate, which is bound on the non-heme iron between $Q_A$, and $Q_B$ (Umena et al. 2011), plays an essential role in providing protons to stabilize the reduced form(s) of $Q_B$ (see Shevela et al. 2012). [For further information, we cite just a few papers of Govindjee's laboratory: see Govindjee et al. (1976), Khanna et al. (1977, 1980, 1981), Eaton-Rye and Govindjee (1988a, b), and Van Rensen et al. (1999).] He mentioned that there is also another role of bicarbonate on the water side of PS II as studied by the research groups of Alan Stemler, Vyacheslav Klimov, Charles Dismukes, Johannes Messinger, among others. He hinted at the idea that bicarbonate may be involved in picking up protons released by water, as being investigated in the laboratory of Messinger in Sweden (Koroidova et al. 2014). In addition to this idea, Govindjee had included the play on the Q cycle by the M.Sc. students, explaining theatrically the movement of protons and electrons in the cycle and beyond as well as of the role of bicarbonate in regulating the PS II—PS I electron flow (see the web site of A.R. Crofts, cited above, and Crofts et al. 2008). (Fig. 2).

## The play for teaching of Z-scheme

The concept of Govindjee to involve students for teaching the Z-scheme of photosynthesis was quite interesting and effective. The play was a dramatized explanation of the Z-scheme by the students representing the components of the water to $NADP^+$ electron transport chain (Fig. 3).

The characters of the Z-scheme drama were for: Water—Khirachand Nayak; LHC (Light harvesting complex) II—Subhadra Pattnayak; PS II—Nadia Anwar and Amrita Ray Priyadarshini (representing the reaction center dimer, P680); Pheophytin—Priti Sagarika; $Q_A$—Santoshini Kanaur; $Q_B$—Sharmilla Kerketta; Plastohydroquinone—Kedarnath Kamura; Cytochrome $b_6f$ complex—Bikash Raul; Plastocyanin—Ansuman Sahoo; PS I -Rasesh Das and Bishnu Priya Das (representing the reaction center P700); $A_0$ (Chlorophyll)—Debasish Tarai; $A_1$ (Vitamin K)-Sabita Hansdah; $FeS_x$ - Debashish Sahu; $FeS_{A/B}$ - Nilima Murmu; Ferredoxin—Anil Kumar Gamango; FNR - Pradipta Kumar Mohapatra (one of the authors); $NADP^+$—Smita Suman Mohapatra; LHC I—Alena Patnaik; $HCO_3^-$(bicarbonate)—Sasalipi Nayak; $H^+$ (protons)—Swadhinata Sahani and Debasmita Panda; and DCMU—Gupteshwar Rath. Two students, as a unit, performed the role of reaction center P680 symbolizing that it is a dimer. Similarly two students performed the role of protons ($H^+$s) signifying that during electron transport, two protons are needed by $Q_B^{2-}$ to protonate it to make $Q_BH_2$ (i.e., a plastoquinol); these protons come from the stroma side and are ultimately transported into the thylakoid lumen with the Q-cycle.

The play began with a background explanation of the concept of Z-scheme, the artists and the contribution of Govindjee in this field by Ankita Prusty, one of the M.Sc. students. Each actor not only explained the history of his/her discovery, location, and role in the Z-scheme, but also moved the way the change occurs during light absorption and electron movement in and across the thylakoid membrane with respect to his/her energy level and the conformational alteration. It was quite exciting for all to see the

P680 (Nadia Anwar and Amrita Ray Priyadarshini) leaping from one end to the other end of the field shouting "*we are excited*" to signify the movement of electron from a lower energy level at the reaction center to a higher energy level, leading to electron transfer to pheophytin *a*. Similarly the movement of protons across the thylakoid membrane during the reduction and oxidation of plastoquinone, the role of bicarbonate in these events and the aggressive role of DCMU, symbolizing its strong inhibitory effect on PS II were quite exciting. The play presented an outline of the Z-scheme integrating the knowledge of the students gained through the class room teaching and through active participation in the play.

During the stay of Govindjee at Ravenshaw University, the students introduced themselves (to Govindjee) outside and inside the class room by their names gained from the Z-scheme and not by their real names signifying their deep interest in the subject (Govindjee also liked to remember the students, especially undergraduates, by the names of the Z-scheme components they acted).

## Concluding remarks

Govindjee's lectures and drama were dedicated to Prasanna Mohanty (1934-2013), a former alumnus of Ravenshaw College and a former student of Govindjee (Prakash and Tiwari 2013; Tiwari et al. 2014). Govindjee's stay at Ravenshaw University not only encouraged the students to understand the complexity of photosynthesis but it also motivated the faculty. His innovative style of teaching showed how one can be so engrossed in a particular subject as a teacher. His enthusiasm about answering various questions on photosynthesis delighted the students. At the end of the photosynthesis course, M.Sc. students presented brief seminars on various topics of photosynthesis research; all the presentations were well done, and showed how deeply the students understood the intricacies of the topics; Govindjee appreciated these talks by M.Sc. students, as well as their active participation in the "Q-cycle"; he was, of course, just as we were, thrilled by the participation by B.Sc. students in performing the Z-Scheme drama.

During Govindjee's visit, an idea of another drama for the future arose: How plants protect themselves against excess light using the so-called xanthophyll cycle, releasing the excess energy as heat (the non-photochemical quenching of chlorophyll *a* fluorescence) (see Demmig-Adams et al. 2014)—something to think about!

A few students received prizes for their talk. Bhaskar Sahoo won the red tie of Robert Emerson for his outstanding seminar presentation on "the role of bicarbonate on PS II". We recommend the readers to read the *Supplementary Material* for wonderful comments by some of the students. They talked about his energy, dedication, informality, interactions, simplicity, and emphasis on constant questioning everything and everyone including yourself. One student talks about how Govindjee convinced the students to call him Govindjee, not "Sir" or "Professor"; another was inspired to plan a drama on the Calvin-Benson cycle. Further, one talked about the "G (for Govindjee) impact; and another told him that "You are my Google". Additional interesting photographs are included in the supplementary material (Figures S.1 and S.2).

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## Appendix 1

Demonstration of Chlorophyll *a* fluorescence

The exciting power of chlorophyll *a* fluorescence as a signature of photosynthesis was shown by Govindjee to all the higher secondary school level students in a special lecture he was invited to give at Ravenshaw University; this lecture was coupled with practical demonstration, which was attended by ~160 students, and many teachers, from different colleges of the state of Odisha. Without taking the help of any sophisticated equipment Govindjee demonstrated how the tiny (2–10 % of the absorbed light; see e.g., Trissl et al. 1993) chlorophyll *a* fluorescence can be seen through naked eye in a comparatively dark room. Using leaves, he showed that the red chlorophyll *a* fluorescence, in a leaf, was not visible at all; and that from extracted chlorophyll was barely visible in the lecture hall. When he excited the leaf with a UV lamp, however, it was brilliant red in extracted chlorophyll (see a photograph of chlorophyll fluorescence in Govindjee and Govindjee 1974). What was interesting for students was to see that as leaves were infused with DCMU, they could observe red fluorescence, from the surface of the leaves with their eyes. This was so because when electron flow was inhibited beyond $Q_A$, the first plastoquinone acceptor of PS II, chlorophyll *a* fluorescence was high since the reaction center of PS II was "closed", and photochemistry was not possible leading to lowered competition with fluorescence. He also explained how chlorophyll *a* fluorescence has proved to be an open window of photosynthesis research in general and light reactions in particular due to its intricate connection with a series of interactive and interdependent processes that take place during light-induced electron transport (see chapters in Govindjee et al. 1986; Papageorgiou and Govindjee 2004). While lecturing on fluorescence Govindjee did not forget to mention about the origin of the concept of fluorescence and showed the "celestial blue" light under UV light from tonic water. Like a young man he searched around the city of Cuttack, with a motorbike (driven by Prakash Prasad, in his class), to procure tonic water for his lecture-demonstration class, which shows his passion and commitment for the subject and deserves appreciation. (Fig. 4).

## Appendix 2

(A) Some useful web sites are:

(1) Photosynthesis Web resources by L.Orr and Govindjee is at: http://www.life.illinois.edu/govindjee/Electronic%20Publications/2006/2006_gov_krogmann.pdf
(2) The Photosynthetic Process by J. Whitmarsh and Govindjee is at: http://www.life.illinois.edu/govindjee/paper/gov.html
(3) Milestones in Photosynthesis Research by Govindjee is at: http://www.life.illinois.edu/govindjee/papers/milestones.html
(4) Photosynthesis and Time is at: http://www.life.illinois.edu/cgi-bin/gov/gov.cgi
(5) Introduction of Photosynthesis and its Applications by Wim Vermaas is at http://photoscience.la.asu.edu/photosyn/education/photointro.html
(6) TimeLine of Photosynthesis by Govindjee and D. Krogmann is at: http://www.life.illinois.edu/govindjee/Electronic%20Publications/2006/2006_gov_krogmann.pdf
(7) Govindjee's book collections are at: http://www.life.illinois.edu/govindjee/g/Books.html
(8) Publications of Govindjee from 1994-2014 can be found at (there are some educational reviews there) http://www.life.illinois.edu/govindjee/recent_papers.html

(B) Other web sites students may want to explore include:
http://www.hansatech instruments.com/forum/uploads/david_walker/down %20hill.pdf
http://en.wikipedia.org/wiki/Photosynthesis
http://en.wikipedia.org/wiki/Light-dependent_reactions
http://chemwiki.ucdavis.edu/Biological_Chemistry/Photosynthesis/Photosynthesis_overview/The_Light_Reactions
http://icewater.cms.udel.edu/mast634/lectures/12-photosynthesis.pdf

(C) You-Tube presentations can be searched through "Google"; two are mentioned below:

(1) An interview with Govindjee is at: https://www.youtube.com/watch?v=cOzuL0vxEi0
(2) An interview with Pierre Joliot is at: https://www.youtube.com/watch?v=Tz4uIveE2hI

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# Supplementary Material
# for
# “Teaching the Z-Scheme of Electron Transport in Photosynthesis: A Perspective”

**by** Pradipta Kumar Mohapatra and Nihar Ranjan Singh

(DOI # 10.1007/s11120-014-0034-4)

First, we present here some pictures from Govindjee’s visit (see Figs. S.1 and S.2); this is followed by information on Govindjee, and then we present comments from students. The rest of the students echoed similar sentiments. In the end, we have provided some concluding remarks and references for the supplementry material.

**Figure S.1** shows several photos with staff and students involved in the Z-scheme drama, and **Figure S.2** shows students receiving prizes/recognition for their performance in the Z-Scheme drama.

Figures are on pages 2 and 3; information on Govindjee is on pages 3 and 4, comments by 11 students are on pages 4-8 (others echoed similar views), and concluding remarks & references for the supplementary material are on pages 8 and 9.

## I. Photographs


**Fig. S1.** Govindjee **(a)** in front of the Department of Botany with Soumendra Kumar (S.K.) Naik, **(b)** in the department garden with students discussing electron transport in the Z-scheme (baloons, seen in the photo, were used as electrons), **(c)** in the class room with one of the authors, Pradipta Kumar Mohapatra (front row, left), **(d)** inaugurating the annual day of the department with traditional Indian ritual, lighting a candle, **(e)** receiving a momento from S.K. Naik (*left*) and the Vice Chancellor Baishnab Charan Tripathy (*right*), and **(f)** with the students and staff of the department receiving a huge greeting card as a token of appreciation from several students


**Fig. S2 (a)** Prakash Prasad (*left*) is receiving a prize, for being the best student of his M.Sc. class, from Govindjee, **(b)** Govindjee and Bhaskar Sahoo (with the Emerson's red tie) after his seminar presentation, **(c)** Govindjee with P680 (Amrita Ray Priyadarshini) after the Z-scheme drama

## II. Govindjee

Govindjee, called by many as **Mr. Photosynthesis**, is the de-facto **Ambassador of Photosynthesis** around the world–propagating the knowledge on the basics, the history and the evolution of the process (for futher information on him, see Eaton-Rye 2007a, 2007b, 2012, 2013; Clegg 2012; Papageorgiou 2012; Prasil 2014; http://en.wikipedia.org/wiki/Govindjee). Even after 15 years of retirement, he is tirelessly writing, researching and teaching photosynthesis (see his web page at: http://www.life.illinois.edu/govindjee). For his recent publications, see <http://www.life.illinois.edu/govindjee/recent_papers.html>. For detailed information on all aspects of photosynthesis, see his "**Advances of Photosynthesis and Respiration Including Bioenergy and Related Processes**" Series, now in its 40$^{th}$ volume (Demmig-Adams et al. 2014; http://www.springer.com/series/5599); the first volume was produced in 1994, 20 years ago.

The energy, the passion and the spirit of teaching photosynthesis is well reflected in Govindjee, and as a token of appreciation of his tireless contribution he was given the Communication Award of the International Society of Photosynthesis Research (see Blankenship 2007).

## III. Comments by students (arranged alphabetically)

***1. Nadia Anwar** (one of the chlorophyll molecules of P680), a B.Sc. student, on calling Govindjee …Govindjee*

"Govindjee: First of all, I feel great to be a student of Ravenshaw University because of which I had the privilege of meeting such a personality, as yourself, and share the same space with a person like you. I remember the very first lecture of yours where you had said that your name has a "Jee" at the end so that we all can address you as "Govindjee", and the bridge of "Sir" is not built. I really admire your gesture of being friends with the students. Words cannot convey my gratitude– still trying to write it down. The type of interactive classes, the presentations, the rock music, and the movies– everything has left a great impact on my mind. Thank you for your visit and stay at Ravenshw University. We are glad that even though your visit was for a short span of time, yet you provided us with your valuable thoughts and time. You enlightened us with your knowledge. The topic of "Photosynthesis" is crystal clear in my mind simply because of you. Whatever little bit I did not understand, I would try and clear it up by myself, or by mailing you my questions ... The most important thing I want to tell you is that I got inspired by your energy. You have been a superb guide. Thank you."

***2. Sripadma Debata** (involved in the fluorescence show and a participant in the Q-cycle), a M.Sc. student, about punctuality; simplicity; a way of honoring each and every person*

"Dear Govindjee: First of all, I am very much excited that I am writing few lines for you, but unhappy that this paper and pen are not enough to express my feelings. If I go on writing, it will become a book!

I am the luckiest student of the luckiest batch to whom you have taught and inspired with a lot of love, affection and care. From the beginning to the end [of your stay in Cuttack], I have learned a number of things from you. They are: qualities like *punctuality; simplicity; a way of honoring each and every person, whether he is a student or a teacher*. One thing is that I don't know how good my seminar presentation was, but after giving the presentation, I felt that it was an *enhancement in my confidence* level. Besides what was in our course (the subject matter), I have learned many more things from your lectures.

I enjoyed very much working as your assistant during the INSPIRE program for High School students. One request is: I want to keep interacting with you through e-mails. You have stayed with us, although for a short time, and gave us the most memorable moments of our lives. We need you to come again and spend more time with us.

We miss you a lot. Dear Govindjee, you are like the Sun, distributing a vast amount of knowledge to us, and enlightening us! Your obedient and loving student"

***3. Nilima Murmu,*** *(iron-sulfur center;$FeS_{A,B}$), a B.Sc. student, about patience and energy*

"Dear Govindjee: It was a great privilege that I attended your lectures. I have never seen such a person *with so much patience and energy.* The BBC movie, you showed, was excellent. I will never forget the Z-scheme in my life. It is because of your lectures, we know more about photosynthesis. I wish you could lecture at our University for one more year. Thank you, Sir for giving such a precious and valuable time to us."

We know that Govindjee has been called "Mr. Photosynthesis", but one student coined the word G-impact (see below).

***4. Subhadra Pattanayak*** *(LHC of PS II), a B.Sc. student, talked about the "G"impact, i.e., the "Govindjee Impact"*

"Sir, I really feel honored to have attended your lectures; I am very fortunate to have had this opportunity. The first day that included the BBC movie was really very interesting. Well, I cannot forget the "Rap" music... that fluorescence class and most importantly, the 'Z-scheme'! *Sir, the 'Z-scheme'left almost a "G-impact" (the Govindjee impact) on us; and I tell you, I will never forget it...* Thank you, Sir, for spending your valuable time with us and making us understand the topics which are not there in our books. Thank you!"

***5. Swapnarani Pradhan,*** *a M.Sc. student, who quoted Govindjee "Even Nobel laureates make mistakes; so never feel shy in asking questions"*

"Dear Govindjee: I am very lucky that I had chosen Botany (Plant Biology), with special paper in Biochemistry, as my subject for "honors" program at Ravenshaw University, and, thus, I was able to be your student.

You taught us that *Photosynthesis* is very important for the world, and you did that in a very interesting way. We learned many new things about the process. Not only your teaching style, but your great personal character, *caring and loving* nature, *punctuality* and your *encouraging words* will keep you in my heart. *I also learned from you to respect everyone.*

Your *friendly interaction with students and your dedication to teaching* has impressed me very much. I had chosen to give my seminar on "Structure and Function of Cytochrome $b_6f$ Complex", which was, at first, very complicated for me. But, when you taught me the "Q-cycle" just before my presentation, it became easier for me. *You always encouraged by saying "Even Nobel laureates make mistakes; so never feel shy in asking questions.* I took to heart all your lectures. Everything I will write about you will not do justice to you, as it will be "too little". I really miss you a lot."

**6. Prakash Prasad** *(who received the prize for being the best M.Sc. student) summarized his thoughts on Govindjee and the recent impact of his work* (see Fletcher 2014)

"Govindjee is a man of wisdom with enormous knowledge in the field of photosynthesis. We were very lucky to have spent quality time with him; we had a glimpse of his excellence, while he was at Cuttack, and we learnt about his pioneering contributions in photosynthesis research, such as, to name just a few: **(1)** the first picosecond measurements on both the photosystems (PS) I and II; **(2)** establishment of an unique role of bicarbonate in PS II; I note that this discovery has caught the eyes of Sydney Fletcher, a physical chemist, in UK, who has discussed the contribution of Govindjee to the development of ideas of bicarbonate-reversible catalysis in PS II, and has built a new theory on how bicarbonate functions as a "gate" in electron flow in this photosystem, and, thus, in photosynthesis –see: Fletcher 2014; and **(3)** the first comprehensive theory of thermoluminescence in algae and plants. Each time Govindjee discussed these topics with us, he relived those moments when he was actually working on them with his many coworkers. This "*flying back*" in time, and sharing, with us, the real time experiences, made the topics come alive and real than it was ever before. Govindjee has an uncanny knack of making topics really easy to understand. Photosynthesis for us was like any other chapter in our textbook, but Govindjee changed our perspective of looking at it. Govindjee, with his lively lectures, has compelled us to believe that *photosynthesis* is in no way a dead topic as we used to believe, and that there is tremendous scope of improvement and improvisation in this field and in our society with its help, like making rice a C4 plant which will increase its productivity and help the world in removing hunger among the poor in our world. Lastly, his demonstrations on chlorophyll *a* fluorescence, and that of *tonic water*, were mesmerizing. On the personal side, he was very friendly to all the students and understood the psychology and the individual problems of the students very quickly. His confident attitude, clarity in voice, and his punctuality has made him an ideal teacher to students around the world. "

**7. Ankita Prusty**, *(introducer of the Z-scheme drama to the group), a M.Sc. student*

"Dear Govindjee: My first introduction to you was highly academic, enthusiastic and determined towards learning and teaching. You made a profound impact as a medium for learning through your interaction and dedication to students. Your larger aim was to facilitate the students' ability to think critically, and reason soundly. In short, the goal of many of your classes was to learn '*to learn'*. To me your classes were by far the most interesting and the style promoted an open debate. You tirelessly insisted that each student must question every source of information, including yourself. Your classes especially those on the Z- scheme were highly informative which inspired us to perform a *live show on the Z – scheme*. We all together made preparations, which were supervised by you with full enthusiasm. I am highly obliged to you for your benevolent behavior and affection during the preparation period. In fact, the Z-scheme show was a medium which led us to feel more comfortable engaging in conversations with you. The play was done successfully and all the students participating in it were highly appreciated by the Vice Chancellor and all other faculty members. It has imprinted an impression of highly knowledgeable performance to life. We love you, we were helped by you, and we will remember you even if the 'forget-me-nots' have withered."

***8. Gupteshwar Rath, (****DCMU in the Z-Scheme drama), a M.Sc. student*

"Dear Govindjee, Namaste, *I am your "lovely" DCMU.* I have attended your first class where you discussed "Photosynthesis", and I became excited with the topic. It was the first time, I had attended such a great class. Sir, what a [fantastic] class it was!! And the BBC movie, where you were listed in their credit line, was not less than a Hollywood movie. Every time, I would see you anywhere, I would say to myself : How? How?

Thank you Sir for being with us. Your compliments on my acting as the Yamaraj (God of Death) in a social satire gave me a boost to my confidence. Thank you Sir for selecting me as DCMU for the Z-scheme drama. I enjoyed it thoroughly—in displacing $Q_B$ and in "killing the plant"! (see Fig. 3f in the main text) I need your blessings for my future. I will really miss you, Sir"

***9. Bhaskar C. Sahoo,*** *a M.Sc. student, who was inspired to plan a drama on the Calvin-Benson cycle*

"Dear Govindjee: It was a great privilege for me to be with you during your lectures that I have attended. At first, many things about "Photosynthesis" just bounced on my head, but after your talk and guidance given by Ankita Prusty, it all became easy to me.

I am curious about your fitness level at your age [you are $80^+$]; I wonder if I will have the same health as you have when I will be in my 80s. *If I will ever become a teacher in my future life, I will surely conduct a drama on the C-3 cycle (the Calvin-Benson cycle).* I want to thank you for coming to our University [in Cuttack, India], and in guiding us. I noticed during your lectures that you were enjoying and showing great interest in the topic more than we were.

I will be praying for you so that all the diseases are kept away from you, and that you will always be smiling. Please excuse me for any grammatical or spelling mistakes, Sir, since I am a little weak in English. Thanking you."

***10. Debashish Sahu, (****Iron- Sulfur Center;* $FeS_X$*), a B.Sc. student*

"Dear Govindjee: I really felt very proud to be a part of your class. *You are so active, and so energetic at this $80^+$ age*. *You are so student friendly*, and have many years of teaching experience. *You always want us to ask questions*; you want to clear all our doubts about "Photosynthesis". *It is because of you, I cannot "delete" the "Z-scheme" from my mind. You have an innovative style of teaching. Really, you are a very good person.* Thank you."

***11. An Unidentified Student** labelled Govindjee as "You are My Google"*

This student had become free in asking questions, as Govindjee had encouraged all to do, asked a question to which Govindjee responded by saying "why don't you ask "Google", and you will get an instant answer, to which the student replied "But, *you are my Google*."–indeed there was laughter!

## IV. Concluding remarks

**In conclusion**, we do want to mention that a huge (over 2 feet by 3 feet card) card was personally presented to him by eight students (listed by first names: Debasmita, Swadhinita, Amrita, Priti, Subhadra, Nadia, Bishnupriya and Sulagna) (see Fig. S1 f). The text on the card said that Govindjee was being simply *"the best"!!* They said that he was kind, free, and caring and a *passionate teacher*, but "*one of the guys*".

## V. References for the Supplementary Material


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