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LETTER TO THE EDITOR

A thank you note for Julian Eaton-Rye, the wonderful staff at *Photosynthetica*, and all the scientists who participated in the 2018 special issue

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To express my heartfelt thanks, I briefly highlight, in this letter, research papers by all the scientists (*see* Appendix) who were invited by Julian Eaton-Rye (Eaton-Rye 2018) (Fig. 1) to commemorate my 85th birthday in *Photosynthetica*. Garab (2018) has wonderfully given special thanks to Eaton-Rye for the great job he did. I fully agree with him. In addition, we all thank Helena Synková, Ivana Štětinová, and Petra Spoustová of *Photosynthetica*. Here, I briefly mention all the 45 papers for the readers of this letter to revisit them, as they are all still pertinent.

Photosynthesis begins with light absorption, which is followed by excitation energy transfer, regulation of energy distribution between the two photosystems: Photosystem II (PSII) and PSI, primary photochemistry, electron transport, oxygen evolution in PSII, and NADP reduction in PSI. Then, there is the carbon fixation and regulation of the process. I was and I am happy that all these areas were covered in this special issue. [Győző Garab (Fig. 2), who read this letter, before its publication, wrote: "By giving a nearly comprehensive overview on the mechanisms of photosynthesis, reflecting the deep and broad-minded knowledge of the author, and because of the multi-sided approaches of the papers in the 2018 SI, it is an interesting reading to all who browse the pages of *Photosynthetica*".]

Fig. 1. *Left to right*: Govindjee and Julian Eaton-Rye, in Pushchino, Russia, in 2016. Source: Győző Garab.

Overviews

First, Larkum *et al.* (2018) presented a beautiful description of the history of the evolution of pigments (absorbing light from 350 to 1,050 nm) on our Earth since 3.5 billion years ago – starting with bacteriorhodopsin, and bacteriochlorophylls followed by chlorophylls – the latter in cyanobacteria, algae, and higher plants; in addition, we were left with several questions that still need to be resolved. Another very interesting historical paper was by Nickelsen (2018) on the life and work of the Nobel laureate Otto H. Warburg from Berlin, Germany; Nickelsen pointed out that Warburg was one of the very few scientists of Jewish ancestry who was allowed by the Nazis to keep working. We all know that Warburg was wrong in claiming that the minimum quantum requirement is 2.8–4 rather than 8–12, per molecule of oxygen evolved.

Photosystem II

Photosystem II (PSII) involves the evolution of oxygen and the reduction of plastoquinone to plastoquinol. Chen *et al.* (2018) reviewed the role of a specific Chl *a*-antenna

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Acknowledgements: I thank all the authors (*see* Appendix), who published in the special issue (SI) of *Photosynthetica* (volume 56) – from the bottom of my heart – for this special gift to me. My special thanks go to an anonymous graduate student who had earlier given me a draft of this "Letter". I am highly indebted to Győző Garab for reading this letter to the editor and for making valuable suggestions, and to Hartmut Lichtenthaler for a 2005 photograph of himself with me and Arthur Grossman [*see* Lichtenthaler *et al.* (2022) for an article on my single-authored papers].
Conflict of interest: The author declares no conflict of interest.

Fig. 2. *Left to right*: Reto J. Strasser, Rajni Govindjee, and Győző Garab, in 2010, when they were at the 15th International Photosynthesis Congress in Beijing, China; reproduced from Fig. 6 in Govindjee (2023b).

protein, labeled as IsiA, in cyanobacteria. They showed that out of 390 cyanobacterial strains, growing in many niches, only 125 had IsiA's homolog present; this suggested that its presence is a niche-specific requirement, and those that lack it must have evolved other mechanisms to deal with its deficiency – a rather interesting finding!

In this special issue, Acuña *et al.* (2018) elegantly demonstrated that the time for excitation energy transfer from the phycobilins to the PS II reaction center complex was within 20 picoseconds – a very fast process indeed. In addition, Borisov and Björn (2018) provided an estimate of the incident solar energy that is used for oxygen evolution as well as the time, about 3,000 years, needed for the generation of the present amount of molecular oxygen in the biosphere by oxygenic photosynthesis on both the land and in the oceans; further, these authors noted that the oceans produce 22% more oxygen than the land surface. On the other hand, Hartmann *et al.* (2018) showed that there is an increased stability of high-light-adapted PsbA3-PSIIs, and then extended earlier observations by showing that PsbA3-PSII has increased charge recombination between $P680^{+\bullet}$ and $Q_A^{-\bullet}$, and thus the overall electron flow is much less efficient than it is in the PsbA1-PSII, which is optimized for efficient electron transfer.

For Photosystem II, Ananyev *et al.* (2018) presented a paper that dealt with the multiple roles of bicarbonate in high-carbonate-requiring *Arthrospira maxima*. [I am reminded of reviews that David Vinyard and Dima Shevela have recently published on this topic: Shevela *et al.* (2023) and Vinyard and Govindjee (2024)]. Further, the following seven topics were covered: (i) Tikhonov *et al.* (2018) provided detailed information on the bound bicarbonate ions in PSII; (ii) Biswas and Eaton-Rye (2018) showed that PsbY is really needed to keep the PSII from being damaged in PsbM-lacking mutant of *Synechocystis* sp. PCC 68093; (iii) Khorobrykh *et al.* (2018) showed that after different treatment(s) of the water-oxidizing complex, PSII preparations show different results on the photooxidation and photoreduction of externally added cytochrome *c*; (iv) Kondo and Noguchi (2018) provided new information on conformational changes around the chloride ions in the water-oxidizing complex of PSII; (v) Kotakis *et al.* (2018) showed how specific solutes can be used to increase thermal stability of PSII; (vi) Mamedov *et al.* (2018) presented their results on the influence of the disaccharide trehalose on the oxidizing side of PSII; and (vii) Langley *et al.* (2018) provided details on a novel deep-red state (DRS) of PSII in the data on NPQ in algae, at longer wavelength than P680, in the red algae *Cyanidioschyzon merolae* – as was already known in spinach and cyanobacteria *Thermosynechococcus vulcanus*.

In addition, there were several more papers, in this special issue, dealing with Chl *a* fluorescence, a good part of which is from PSII – a topic very dear to me; *see e.g.*, some recent memories: Govindjee (2023a) and Govindjee (2024). Lamb *et al.* (2018) reviewed not only the published data on fluorescence emission spectra down to 77K but also provided information on practical aspects for the same. Reading these papers, I was reminded of the discoveries made by the late Fred Cho (*see* Govindjee *et al.* 2017). And I note that Prášil *et al.* (2018) published key detailed information, as well as a new model, on how the binding site for Q_B controls the maximal Chl *a* fluorescence yield; their model predicts that this yield is controlled by the capacity of the secondary electron acceptor (Q_B) to re-oxidize reduced Q_A. Furthermore, Yamada *et al.* (2018) showed that the PsbQ' protein, which is present nearby, affects the redox potential of the Q_A in PSII, and, thus, the PSII activity – this could be of interest to the function of bicarbonate on the electron acceptor side of PSII, a topic of great interest to me (*see e.g.*, Shevela *et al.* 2023).

In order for the system to function normally, PSIIs need to be regularly repaired as they are normally damaged in real life. For this, Shao *et al.* (2018) presented key information on how the FtsH protease is involved in this process.

Chlorophyll *a* fluorescence induction

Exploitation of Chl *a* fluorescence induction to understand the various steps in photosynthesis has been very dear to me, especially because I remembered the key and extensive contributions of dear George C. Papageorgiou (*see* the special issue on him in *Photosynthetica*, edited by Prášil *et al.* 2022). I gladly joined Alexandrina (Sandra) Stirbet, Dušan Lazár, and Johannes Kromdijk in this special issue, in coauthoring a perspective on how this tool has been used to quantify abiotic stress responses in photosynthetic systems (*see* Stirbet *et al.* 2018).

Photosynthetic systems protect themselves against excess light through nonphotochemical quenching (NPQ) of the excited state of Chl *a* – through heat dissipation (*see e.g.*, Papageorgiou and Govindjee 2014). In this special issue, there are two papers on this topic: Kaňa (2018) provided an excellent perspective on the then available spectrally resolved fluorescence induction data on NPQ of the excited state of Chl *a* in algae, and

Vredenberg (2018) provided quantitative information on the relation of NPQ to phosphorylation, especially through the state of the enzyme ATP synthase. Further, Zhu *et al.* (2018) showed that when there is insufficient photoprotection by the NPQ mechanism in the winter, the leaves of *Acmena acuminatissima* do compensate for it by using anthocyanins as a light attenuator.

In addition, Sipka *et al.* (2018) presented detailed information on bacteriochlorophyll (BChl) fluorescence induction in *Rhodobacter sphaeroides*, a purple non-sulfur bacterium; here, the observed BChl fluorescence induction curve was shown to reflect redox changes and electron carrier dynamics in the system.

Photosystem I

Photosystem (PS) I involves the reduction of $NADP^+$ to NADPH from the electrons received from PSII *via* the cytochrome b_6f complex. Strašková *et al.* (2018) presented data on an ingenious method of isolation of PSI, and Gao *et al.* (2018) published data on the effects of green light on a PSI supercomplex from the cyanobacteria *Synechocystis* sp. PCC 6803. Further, Li *et al.* (2018) provided novel information on the PSI from *Halomicronema hongdechloris*, a chlorophyll *f*-producing cyanobacterium, and Zakar *et al.* (2018) described the status of PSI from several cyanobacterial strains and mutants by using several noninvasive methods. On the other hand, Mondal and Bruce (2018) gave us in-depth information on the functioning of ferredoxin, a key intermediate that connects PSI to the overall cellular metabolism of plants, algae, and cyanobacteria.

Photosystem I can also lead to H_2 production – by using electrons from PSI – that can reduce protons – using the enzyme hydrogenase. Yodsang *et al.* (2018) gave us key information on this process in five different cyanobacteria, all from Thailand. Just as Gao *et al.* (2018) had studied the effect of green light, Gómez-Lojero *et al.* (2018) looked at the effect of far-red light on another cyanobacteria *Leptolyngbya* sp., and showed that it acclimated to this light. Further, Huang *et al.* (2018) showed that still another species, *Synechocystis* sp., acclimated to a similar type of light.

Metabolism and making plants better

Mathur *et al.* (2018) reviewed differences in photosynthetic efficiency in sun and shade plants. They pointed out that these plants develop different types of chloroplasts, which help them "*survive and perform photosynthesis under adverse conditions*". Further, they showed that these plants adopt different strategies under different environmental conditions.

On another topic, related to the biosynthesis of porphyrins and Chl biosynthesis, Khusnutdinova *et al.* (2018) presented detailed characterization and properties of that system. Further, dealing with photoprotection in plants, Kothari *et al.* (2018) showed community-wide consequences of variations in photoprotective physiology among several prairie plants. On the other hand, Kreslavski *et al.* (2018) provided key information on the effects of phytochrome A and B deficiency on the photosynthetic apparatus of *Arabidopsis thaliana*, when it was exposed to UV radiation; the latter was shown to decrease the PSII activity and change the chloroplast structure: a clear decrease in the quantum yield of photochemistry and an increase in heat loss was observed.

It is well-known that without proteins, there is no photosynthesis and there is no life! We know that the proteins are made of amino acids, and the latter are "dictated" by RNA, which, in turn, is dictated by DNA. For this, Lu (2018) published an article on RNA editing of plastid-encoded genes, where he pointed out that there are at least four types of proteins needed for the overall process: (a) penta-tri-co-peptide repeat proteins; (b) RNA editing interacting proteins/multiple organellar RNA editing factors; (c) organelle RNA recognition motif proteins; and (d) organelle zinc-finger proteins; and that they all work together! This is not all – three other types of proteins were found to be important for plastid RNA editing that may play a regulatory role. However, in *Physcomitrella patens*, a moss, Uchiyama *et al.* (2018) showed that ribonucleoprotein-like proteins are not involved in RNA stability and even in RNA editing!

On the other hand, Biswal and Pandey (2018) pointed out that during senescence of green leaves, cell wall hydrolases play an important role, and that "loss of photosynthesis" signals a metabolic reprogramming to sustain "sugar homeostasis". In addition, an important link between photosynthetic capacity and leaf organization was elegantly presented by Polutchko *et al.* (2018). Further, Shirke *et al.* (2018) described adaptation strategies of two leaf cohorts of *Prosopis juliflora* produced in the spring and in the monsoon seasons. And, Stewart *et al.* (2018) provided new information on the role of tocopherols in modulating leaf vein arrangement without impacting photosynthesis!

We cannot forget that too much light is not a good thing, although NPQ works, as mentioned earlier. However, when one has a deficiency of ascorbate, *e.g.*, in *Arabidopsis*, the plant is highly susceptible to high-light stress (*see* Zeng *et al.* 2018). Just like light, too much salt in the soil is not a good thing for plant life. For an overview of this area, *see* Wungrampha *et al.* (2018).

At the end, it is important to remind ourselves that attempts are being made – all over the world – to improve photosynthesis and, thus, plant productivity. For example, Nonomura *et al.* (2018) designed and constructed efficient plant growth regulators/chambers, whereas Ohnishi *et al.* (2018) showed data on improved photosynthesis in *Arabidopsis* when they had activated specific transcription factors. Yes, it is obvious that a lot more needs to be done and is being done to reach the goal of more photosynthesis for the benefit of us all. I note that the contributions of the authors, to this end, in this special issue are really remarkable. However, due to the rapid progress of photosynthesis research, in all cases of specific interest, besides re-reading the referenced papers, it is a good idea to find the present state-of-the-art as well as the open questions that are still before us.

Fig. 3. *Left to right*: Arthur Grossman, Hartmut K. Lichtenthaler, and Govindjee Govindjee, in 2005, standing in front of the historical plaque honoring Robert Emerson (1903–1959) and Eugene Rabinowitch (1898–1973), two pioneers of photosynthesis research. Place: Outside the Natural History Building of the University of Illinois, Urbana, where Emerson, Rabinowitch, and Govindjee did their research; this photo was taken during the "International Symposium on Chloroplast Engineering", held at the University of Illinois at Urbana-Champaign. Source: Hartmut K. Lichtenthaler.

I end my "Thank You" letter with a photograph of two friends Hartmut Lichtenthaler and Arthur Grossman (*see* Fig. 3).

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Appendix. List of authors followed by their paper number, in the 2018 special issue of *Photosynthetica* (volume 56) and their country; *those italicized have been in e-mail contact with Govindjee.*

A: Acuña, Alonsa M. (025) – The Netherlands; *Adams III*, *William W.* (037, 038) – USA; Akhtar, Parveen (024) – Hungary; *Allakhverdiev*, *Suleyman I.* (041) – Russia; *Ananyev*, *Gennady* (020) – USA; Arai, Yasuke (016) – Japan; *Aro*, *Eva–Marie* (033) – Finland;

B: Bandyopadhyay, Anindita (032) – USA; Barrera-Rojas, Jesús (034) – Mexico; Beiler, Anna M. (006) – USA; *Biswal*, *Basanti* (039) – India; Biswas, Sandeo (018) – New Zealand; Bitan, Karen (045) – USA; *Björn*, *Lars Olof* (003) – Sweden; *Borisov*, *Alex Yu.* (003) – Russia; *Bruce*, *Barry D.* (027) – USA; Brummel, Danny P. (040) –USA;

C: *Cardona*, *Tanai* (014) – UK; Cavender-Bares, Jeannine (045) – USA; *Chen*, *Min* (030) – Australia; Chen, Steven Hui-Yuan (032) – USA; Chiu, Yi-Fang (017) – Taiwan; *Chow*, *Wah Soon* (*Fred*) (044) – Australia; Chu, Hsiu-An (017) – Taiwan; Cohu, Christopher M. (037) –USA;

D: *Demmig-Adams*, *Barbara* (037, 038) – USA; *Dismukes*, *G. Charles* (020) – USA;

E: *Eaton-Rye*, *Julian J.* (001, 018) – New Zealand;

F: *Falkowski*, *Paul G.* (013) – USA; Flores, Marco (006) – USA;

G: Gamon, John A. (045) – Canada; Gao, Fudan (031) – Japan; *Garab*, *Győző* (024) – Hungary; Gates, Colin (020) – USA; Gombos, Zoltán (028) – Hungary; Gómez-Lojero, Carlos (034) –

Mexico; Govindjee, Govindjee (008) – USA; Gutierrez-Cirlos, Emma Berta (034) – Mexico;

H: Han, Guangye (026) – China; Hartmann, Volker (021) – Germany; Haschemeyer, Brian (040) – USA; Herman, Éva (028) – Hungary; Herrera-Salgado, Priscila (034) – Mexico; *Hohmann-Marriott*, *Martin F.* (009) – Norway; Huang, Jine-Yung (017) – Taiwan; Huang, Xuan Dong (044) – China; Hung, Nien-Tzu (017) – Taiwan;

I: Ichinose, Mizuho (005) – Japan; Incharoensakdi, Aran (033) – Thailand; Iwai, Masako (016) – Japan;

J: Jain, Lakshmi (035) – India; *Jajoo*, *Anjana* (035) – India; *Joshi*, *Rohit* (036) – India;

K: *Kaňa*, *Radek* (011) – Czech Republic; Khorobrykh, Andrew A. (023) – Russia; Khudyakova, Alexandra Yu. (041) – Russia; Khusnutdinova, Diana (006) – USA; Kis, Marianne (010, 028) – Hungary; *Klimov*, *Vyacheslav* (*Slava*) *V.* (019, 023) – Russia; Knoppová, Jana (029) – Czech Republic; Kobayashi, Koichi (043) – Japan; Kolber, Zbigniew S. (013) – USA; Komenda, Josef (029) – Czech Republic; Kondo, Junpei (015) – Japan; Kotakis, Christos (024) – Hungary; Kothari, Shan (045) – USA; Kovács, László (028) – Hungary; *Krausz*, *Elmars* (026) – Australia; Kreslavski, Vladimir D. (041) – Russia; *Kromdijk*, *Johannes* (*Wanne*) (008) – USA;

L: Laczkó-Dobos, Hajnalka (028) – Hungary; Lamb, Jake J. (009) – Norway; Lambrev, Petar H. (024) – Hungary; Langley, Julian (026) – Australia; *Larkum*, *Anthony* (*Tony*) *W.D.* (002) – Australia; Lauria, Allison (040) – USA; *Lazár*, *Dušan* (008) – Czech Republic; Leyya-Castillo, Lourdes Elizabeth (034) – Mexico; Li, Mei (042) – China; Li, Yaqiong (030) – Australia; Lin, Keng-Min (017) – Taiwan; Loveless, Lucas (040) – USA; Lu, Yan (004) – USA; Lyubimov, Valery Yu. (041) – Russia;

M: Ma, Weimin (031) – Japan; *Maenpaa*, *Pirkko* (033) – Finland; Makita, Akari (016) – Japan; *Mamedov*, *Mahir D.* (022) – Russia; *Maróti*, *Péter* (010) – Hungary; *Mathur*, *Sonal* (035) – India; McBride, Michael (Mike) S. (040) – USA; *Messinger*, *Johannes* (019) – Sweden; Mondal, Jyotirmoy (027) – USA; Montgomery, Rebecca A. (045) – USA; *Moore*, *Gary F.* (006) – USA; Morton, Jennifer (026) – Australia;

N: Nagao, Ryo (016) – Japan; *Nickelsen*, *Kärin* (007) – Germany; *Nixon*, *Peter J.* (014) – UK; Noguchi, Takumi (015) – Japan; *Nonomura*, *Arthur M.* (040) – USA; Nosikova, Ekaterina S. (022) – Russia; Nowaczyk, Marc M. (021) – Germany;

O: *Ogawa*, *Teruo* (031) – Japan; Ohnishi, Ai (043) – Japan; Ohta, Hisataka (016) – Japan;

P: *Pakrasi*, *Himadri B.* (032) – USA; Pandey, Jitendra Kumar (039) – India; *Pareek*, *Ashwani* (036) – India; Pathre, Uday Vasudev (046) – India; Pedersen, Andrew (040) – USA; Peng, Chang-Lian (044) – China; Polutchko, Stephani K. (038) – USA; *Prášil*, *Ondřej* (013) – Czech Republic; Purchase, Robin (026) – Australia;

R: Raksajit, Wuttinun (033) – Thailand; *Raven John A.* (002) – UK; Rios-Castro, Emmanuel (034) – Mexico; Ritchie, Raymond James (002) – Thailand; *Rögner*, *Matthias* (021) – Germany; Røkke, Gunvor (009) – Norway; Ruff, Adrian (021) – Germany;

S: *Sane*, *Prafullachandra Vishnu* (046) – India; Schuhmann, Wolfgang (021) – Germany; Semenov, Alexey Yu. (022) – Russia; Semenova, Galina A. (041) – Russia; Shao, Shengxi (014) – UK; *Shen*, *Jian-Ren* (026) – Japan; Shen, Lianglian (026) – China; *Shevela*, *Dimitriy* (*Dima*) (019) – Sweden; Shirke, Pramod Arvind (046) – India; Shirshikova, Galina N. (041) – Russia; Shmarev, Alexander N. (041) – Russia; *Singla-Pareek*, *Sneh Lata* (036) – India; Sipka, Gábor (010) – Hungary; Smart, James Leonard (010) – USA; Stewart, Jared J. (037, 038) – USA; *Stirbet*, *Alexandrina* (*Sandra*) (008) – USA; Strašková, Adéla (029) – Czech Republic; Sugita, Mamoru (005) – Japan;

T: Tian, Lirong (026) – China; Tikhonov, Konstatin G. (019) – Russia; Tomo, Tatsuya (016) – Japan;

U: Uchiyama, Hiromichi (005) – Japan;

V: Vajravel, Sindhujaa (028) – Hungary; van Alphen, Pascal (025) – The Netherlands; *van Grondelle*, *Rienk* (025) – The Netherlands; van Stokkum, Ivo H.M. (025) – The Netherlands; Vella, Natalie (030) – Australia; Verhoven, Amy S. (045) – USA; Vitukhnovskaya, Lia A. (022) – Russia; *Vredenberg*, *Willem* (*Wim*) *J.* (012) – The Netherlands;

W: Wada, Hazime (043) – Japan; Wang, Ran (045) – USA; *Wungrampha*, *Silas* (*Graham*) (036) – India;

Y: Yamada, Masato (016) – Japan; Yanykin, Dennis V. (023) – Russia; Yodsang, Panutda (033) – Thailand; Yu, Zhen-Chao (044) – China;

Z: Zakar, Tomas (028) – Hungary; Zaspa, Andrey A. (022) – Russia; Zeng, Ling-Da (042) – China; Zhang, Tai-Jie (044) – China; Zharmukhamedov, Sergey K. (041) – Russia; Zheng, Jin (044) – China; Zhu, Hui (044) – China; and Zsiros, Ottó (024) – Hungary.