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REVIEW

Outstanding women scientists that have broadened the knowledge on biological photoreceptors-III

Silvia E. Braslavsky[1]

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Abstract

This article is a continuation of the articles in *Photochemical and Photobiological Sciences*, https://doi.org/10.1007/s43630-023-00487-1 and https://doi.org/10.1007/s43630-024-00551-4, in which short biographies were made of women scientists born before 1958 (with the exception of the deceased Ulrike Alexiev in Part II), that have broadened the knowledge about biological photoreceptors. I now present four remarcable women who have worked mainly, but not only, in photosynthesis.

1 Introduction

This part III is a continuation of the articles in *Photochemical and Photobiological Sciences* [1, 2], in which short biographies were made of women scientists born before 1958 (with the exception of Ulrike Alexiev) who have broaden the knowledge about biological photoreceptors.

When writing Part I of this series, I was aware of my ignorance, or perhaps I should say, of not having paid enough attention to the fact that many of the papers on photoreceptors I read, cited, and admired for the precision and intelligent design of the experiments as well as for the clarity of the argumentation and conclusions, were authored or co-authored by women. In fact, often by women who had not been honored enough. Therefore, I deeply acknowledge G. Govindjee, who made me aware of the articles he co-authored about three remarkable women who had contributed to our knowledge in the area of photoreceptors: Rajni Govindjee, Maarib Bazzaz and Christa Critchley, and were not included in the previous two papers. A brief biographical sketch of each of them is now presented, mostly extracted from the papers co-authored by G. Govindjee (see below). Upon reading those papers I learned about the life of the three scientists and also about plant physiology and photobiology in general. I also add a biographical sketch of Barbara Zilinskas, a co-author of one of the biographies mentioned above.

Rajni (Varma) Govindjee [3]. Born as Rajni Varma in 1934 in India, she got her MSc in Botany in 1955 from the University of Allahabad. In 1957 she obtained a fellowship to work with Robert Emerson at University of Illinois at Urbana-Champaign (UIUC), where she started working on light reactions in photosynthesis. In October 1957 she married G. Govindjee and changed her name to Rajni Govindjee. Both G. and Rajni Govindjee joined Eugene Rabinowitch's group after the sudden death of Emerson in 1959. Rajni's work, as well as G. Govindjee's, contributed to the discovery of the two linked photosystems (now known as Photosystems I and II, PSI and PSII), particularly by showing that both contain chlorophyll *a* [4, 5].

In 1964, Rajni Govindjee *et al*., reported that, for the Hill reaction using NADP as electron acceptor, as well as for complete photosynthesis, common or similar mechanisms exist with two photochemical reactions showing different absorption maxima [6] (Fig. 1).

For a detailed history of the two linked photosystems and two light reactions in oxygenic photosynthesis see [7].

After some additional work on photosynthesis, Rajni Govindjee carried out ground braking research on retinal proteins in Tom Ebrey's lab. Among other things, the quantum yield for the photoconversion of bacteriorhodopsin was accurately determined in collaboration with S. Balashov [8], with whom she continued collaborating over many years [3]. Important questions about the functioning of the proton pump bacteriorhodopsin were addressed during the work of Rajni Govindjee in Ebrey's lab, also through extensive collaborations, *e.g.,* with Rosalie Crouch [9] on

✉ Silvia E. Braslavsky
silvia.braslavsky@cec.mpg.de

[1] Max Planck Institute for Chemical Energy Conversion, Stiftstrasse 34-36, 45410 Mülheim an der Ruhr, Germany

Fig. 1 Rajni Govindjee [3]

Fig. 2 Maarib Bazzaz [13]

Fig. 3 G. Govindjee, Christa Critchley and David Knaff [19]

bacteriorhodpsin apoprotein linked to retinal analogues and with Koji Nakanishi [10] as well as with Dieter Oesterheld, as described by T. Ebrey in the article dedicated to Rajni Govindjee on the occasion of her 80th birthday [11]. Until the year 2000 Rajni Govindjee continued publishing work on retinal proteins and also some work on photosynthetic organisms. She has kept collaborating in articles about her mentors and colleagues, *e.g.*, about Eugene Rabinowitch [12].

Balashov *et al.* [3] point out: "Further, the Department of Plant Biology of the University of Illinois administers an *Annual Govindjee and Rajni Govindjee Award for Excellence in Biological Sciences*—that is fitting to her (Rajni) interest in educating the young and the beginners (https://sib.illinois.edu/graduate/grants/Govindjee; and https://www.life.illinois.edu/govindjee/photooftheyear2022.html).

Maarib Bazzaz [13]. Maarib Darwish Lutfi Bakri (Bazzaz) was born on November 27, 1940 in Baghdad, Iraq. In 1958 she joined the University of Illinois at Urbana-Champaign (UIUC), after completion of her first year of undergraduate studies at the College of Sciences, University of Baghdad. In the same year she married Fakhri Bazzaz. After completing her Master degree in Botany in 1963, the couple returned to Iraq where she taught Plant Biology courses. In 1966 she returned to UIUC and joined a PhD program in Plant Physiology. She carried out her PhD work under the guidance of G. Govindjee. G. Govindjee et al., describe with great admiration and in great detail the work she performed in G. Govindjee's lab. In one of the paragraphs the authors say: "her observations were key to the later discovery of a "new" naturally-occurring Chl *a*, …..which she independently discovered in 1981 in G. Govindjee's laboratory [13–15] (Fig. 2)."

She worked from 1981 to 1983 at the Department of Chemistry in the University of Cambridge in the laboratory of Richard Brereton where she used very modern tools to isolate, and state-of-the-art spectroscopic tools to identify the chemical structure of the new chlorophylls, such as modern mas spectrometry and NMR techniques. Both 4-vinyl-4-desethyl-Chl *a*, commonly called divinyl Chl *a* [16, 17] and 4-vinyl-4-desethyl-Chl *b*, commonly called divinyl Chl *b* [18], were isolated and identified.

Maarib Bazzaz died from COVID in 2020. The very warm words used by the authors remembering Maarib [13] and by other colleagues and friends whose letters of condolences were reproduced in that paper, reveal that she was a very joyfull, knowledgeable, engaged person with science, teaching, family and friends. Maarib Bazzaz was, as the authors say, a wonderful citizen of the world, speaking several languages, knowing many cultures, and magnificently adapted to the scientific, social, and cultural life in the United States.

Christa Critchley [19]. Christa Critchley got her Diploma at the Albertus Magnus University of Cologne and her PhD in 1976 at the Heinrich Heine University of Düsseldorf (both in Germany) (Fig. 3).

She went as a post-doctoral fellow to the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in

Fig. 4 Barbara Zilinskas and G. Govindjee, October 1999, Govindjee retirement party [28]

Sydney, Australia, and in 1977 she started her own research group at the Australian National University in Canberra. Her work included the effect of high radiation fluences in plants, *i.e.,* photoinhibition of photosynthesis [20] and the use of fluorescence for the estimation of photoinhibitory damage to plants [21]. In 1981 she went to the University of Illinois at Urbana-Champaign (UIUC) as a Research Associate and performed work on the role of chloride ions in photosynthesis, specialy in salt-tolerant plants (*e.g.,* in mangroves) [22]. From 1988 to 2002 she held several academic positions at the University of Queensland in Brisbane, Australia, and became Head of the Department of Botany in 2001. Her group produced important data regarding the effect of salt stress in plants [23] and developed novel fluorescence techniques [24] to analyse plant rarity and stress responses [25]. These approaches were part of her general interest in plant ecology and conservation of the environment. Christa Critchley was president or secretary of several Australian scientific societies and organized the 12th International Congress on Photosynthesis Research in Brisbane in 2001 [19].

Barbara A. Zilinskas Born in 1947 in Massachussets, obtained her Master (1970) and PhD (1975) at the UIUC, University of Illinois, Urbana, in the group of G. Govindjee. She worked on Photosystem II and chlorophyll *a* fluorescence. As a Smithsonian post-doctoral fellow she worked with Elisabeth Gantt on the relatively recently discovered phycobilisomes [26, 27].

Barbara Zilinskas started as Assistant Professor at Rutgers University (New Jersey) in 1975 and became Full Professor in the same School in 1987 (Fig. 4).

Zilinskas was interested in the algal chromoproteins and established collaborations to perform very early studies on the energy transfer in the phycobilisomes, and between the phycocyanobilins isolated from the phycobilisomes, using time-resolved fluorescence and picosecond absorption spectroscopies [29–31]. She was also interested in the analysis of the proteins linking the phycobilisomes to the reaction centre, such as reported in, *e.g.*, [32, 33].

In 1990 Zilinskas started working on drought stress [34–36], ozone effect on plants, the action of superoxide dismutase and other ecological relevant questions. She has also been interested in turfgrass improvement through genetic modification.

Barbara Zilinskas was the Director of the new undergraduate program on Biotechnology at Rutgers University since 1991 and has been very engaged in restructuring teaching activities at the School of Environmental and Biological Sciences, particularly the Plant Biology graduate program. Barbara Zilinskas is now Professor Emerita at Rutgers University.

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Declarations

Conflict of interest The authors declare no competing interests.

References

1. Braslavsky, S. (2023). Outstanding women scientists that have broadened the knowledge on biological photoreceptors. *Photochemical & Photobiological Sciences, 22*, 2799–2815. https://doi.org/10.1007/s43630-023-00487-1
2. Braslavsky, S. (2024). Outstanding women scientists that have broadened the knowledge on biological photoreceptors Part II. *Photochemical and Photobiological Sciences, 23*, 757–761. https://doi.org/10.1007/s43630-024-00551-4

3. Balashov, S., Imasheva, E., Misra, S., Kono, M., Liu, S., Liang, J., Govindjee, G., & Ebrey, T. G. (2023). Contributions of Rajni Govindjee in the life sciences: Celebrating her 88th birthday. *LS-International Journal of Life Sciences, 12*, 1–14.
4. Govindjee, G., & Rabinowitch, E. (1960). Two forms of chlorophyll a in vivo with distinct photochemical functions. *Science, 132*, 355. https://doi.org/10.1126/science.132.3423.355
5. Govindjee, R., Thomas, J. B., & Rabinowitch, E. (1960). Second emerson effect in the hill reaction of *Chlorella* cells with quinone as oxidant. *Science, 132*, 421. https://doi.org/10.1126/science.132.3424.421
6. Govindjee, R., & Hoch, G. (1964). Emerson enhancement effect in chloroplast reactions. *Plant Physiology, 39*, 10–14. https://doi.org/10.1104/pp.39.1.10
7. Govindjee, G., Shevela, D., & Björn, L. O. (2017). Evolution of the Z-scheme of photosynthesis: A perspective. *Photosynthesis Research, 133*, 5–15. https://doi.org/10.1007/s11120-016-0333-z
8. Govindjee, R., Balashov, S. P., & Ebrey, T. (1990). Quantum efficiency of the photochemical cycle of bacteriorhodopsin. *Biophysical Journal, 58*, 597–608. https://doi.org/10.1016/S0006-3495(90)82403-6
9. Tokunaga, F., Govindjee, R., Ebrey, T., & Crouch, R. (1967). Synthetic pigments analogs of purple membrane protein. *Biophysical Journal, 19*, 191–198. https://doi.org/10.1016/S0006-3495(77)85580-X
10. Ebrey, T., Govindjee, R., Honig, B., Pollock, E., Chan, W., Crouch, R., Yudd, A., & Nakanishi, K. (1975). The properties of several sterically modified retinal analogues and their photosensitive pigments. *Biochemistry, 14*, 3933–3941. https://doi.org/10.1021/Bi00689A002
11. Ebrey, T. (2015). Brighter than the sun: Rajni Govindjee at 80 and her fifty years in photobiology. *Photosynthesis Research, 124*, 1–5. https://doi.org/10.1007/s11120-015-0106-0
12. Govindjee, G., Papageorgiou, G. C., & Govindjee, R. (2019). Eugene I. rabinowitch: A prophet of photosynthesis and of peace in the world. *Photosynthesis Research, 141*, 143–150. https://doi.org/10.1007/s11120-019-00641-w
13. Govindjee, G., Zilinskas, B. A., Brereton, R. G., Khanna, R., & Govindjee, R. (2020). A tribute to Maarib (Darwish Lutfi Bakri) Bazzaz (1940–2020): the one who proved the existence of '"new"' chlorophylls in plants. *Plant Physiology Reports, 25*, 377–385. https://doi.org/10.1007/s40502-020-00534-4
14. Bazzaz, M. B. (1981). New chlorophyll a and b chromophores isolated from a mutant of *Zea mays* L. *Naturwissenschaften, 68*, 94–95. (Chemicals and CAS Registry Numbers: chlorophyll, 1406–65-1, 15611–43-5).
15. Bazzaz, M. B. (1981). New chlorophyll chromophores isolated from a chlorophyll-deficient mutant of maize. *Photobiochemistry and Photobiophysics, 2*, 192–207. https://doi.org/10.1016/S0165-8646(24)00244-7
16. Bazzaz, M. B., & Brereton, R. G. (1982). 4-Vinyl-4-desethyl chlorophyll a: A new naturally occurring chlorophyll. *FEBS Letters, 138*, 104–108. https://doi.org/10.1016/0014-5793(82)80405-5
17. Bazzaz, M. B., Bradley, C. V., & Brereton, R. G. (1982). 4-vinyl-4-desethyl chlorophyll a: Characterization of a new naturally occurring chlorophyll using fast atom bombardment, field desorption and '"in beam"' electron impact mass spectroscopy. *Tetrahedron Letters, 23*, 1211–1214. https://doi.org/10.1016/S0040-4039(00)87062-8
18. Brereton, R. G., Bazzaz, M. B., Santikarn, S., & Williams, D. H. (1983). Positive and negative-ion fast atom bombardment mass-spectrometric studies on chlorophylls—Structure of 4-vinyl-4-desethyl chlorophyll-b. *Tetrahedron Letters, 24*, 5775–5778. https://doi.org/10.1016/S0040-4039(00)94198-4
19. Govindjee, G. (2024). Contributions by Christa Critchley to photosynthesis research and to plant ecophysiology. *Photosynthetica, 62*, 40–43. https://doi.org/10.32615/ps.2024.011
20. Powles, S. B., & Critchley, C. (1980). Effect of light intensity during growth on photoinhibition of intact attached bean leaflets. *Plant Physiology, 65*, 1181–1187. https://doi.org/10.1104/pp.65.6.1181
21. Critchley, C. (1981). Studies on the mechanism of photoinhibition in higher plants. 1. Effect of high light intensity on chloroplast activities in cucumber adapted to low light. *Plant Physiology, 67*, 1161–1165. https://doi.org/10.1104/pp.67.6.1161
22. Critchley, C. (1982). Stimulation of photosynthetic electron transport in a salt-tolerant plant by high chloride concentrations. *Nature, 298*, 483–485. https://doi.org/10.1038/298483a0
23. Seemann, J. R., & Critchley, C. (1985). Effects of salt stress on the growth, ion content, stomatal behaviour and photosynthetic capacity of a salt-sensitive species *Phaseolus vulgaris* L. *Planta, 164*, 151–162. https://doi.org/10.1007/BF00396077
24. White, A. J., & Critchley, C. (1999). Rapid light curves: A new fluorescence method to assess the state of the photosynthetic apparatus. *Photosynthesis Research, 59*, 63–72. https://doi.org/10.1023/A:1006188004189
25. Thach, L. B., Shapcott, A., Schmidt, S., & Critchley, C. (2007). The OJIP fast fluorescence rise characterizes *Graptophyllum* species and their stress responses. *Photosynthesis Research, 94*, 423–436.
26. Gantt, E., Lipschultz, C. A., & Zilinskas, B. (1976). Further evidence for a phycobilisome model from selective dissociation, fluorescence emission, immunoprecipitation, and electron microscropy. *Biochimica Et Biophysica Acta, 430*, 375–388. https://doi.org/10.1016/0005-2728(76)90093-1
27. Zilinskas, B. A., Zimmerman, B. K., & Gantt, E. (1978). Allophycocyanin forms isolated from *Nostoc* sp. phycobilisomes. *Photochemistry and Photobiology, 27*, 587–595. https://doi.org/10.1111/j.1751-1097.1978.tb07650.x
28. Govindjee G. (1999). Retirement party, 1999. Photos in: https://www.life.illinois.edu/govindjee/partypictures/slideshowRetirementParty.htm
29. Pellegrino, F., Wong, D., Alfano, R. R., & Zilinskas, B. A. (1981). Fluorescence relaxation kinetics and quantum yield from the phycobilisomes of the blue- green alga *Nostoc* sp. measured as a function of single picosecond pulse intensity. *Photochemistry And Photobiology, 34*, 691–696. https://doi.org/10.1111/j.1751-1097.1981.tb09065.x
30. Doukas, A. G., Stefancic, V., Buchert, J., Alfano, R. R., & Zilinskas, B. A. (1981). Exciton annihilation in the isolated phycobiliproteins from the blue-gree-alga *Nostoc* sp using picosecond absorption spectroscopy. *Photochemistry and Photobiology, 34*, 505–510. https://doi.org/10.1111/j.1751-1097.1981.tb09032.x
31. Dagen, A. J., Alfano, R. R., Zilinskas, B. A., & Swenberg, C. E. (1986). Analysis of fluorescence kinetics and energy transfer in isolated α subunits of phycoerythrin from Nostoc sp. *Photochemistry and Photobiology, 43*, 71–79. https://doi.org/10.1111/j.1751-1097.1986.tb05593.x
32. Rusckowski, M., & Zilinskas, B. A. (1982). Allophycocyanin I and the 95 kD polypeptide: The bridge between phycobilisomes and membranes. *Plant Physiology, 70*, 1055–1059. https://doi.org/10.1104/pp.70.4.1055
33. Zilinskas, B. A., & Howell, D. A. (1986). Comparative immunology of the phycobilisome linker polypeptides. In J. Biggins (Ed.), *Progress in Photosynthesis Research II* (pp. 161–164). Martinus Nijhoff Publ.
34. Mittler, R., & Zilinskas, B. A. (1994). Regulation of pea cytosolic ascorbate peroxidase and other antioxidant enzymes during the progression of drought stress and following recovery from drought.

Plant Journal, 5, 394–405. https://doi.org/10.1111/j.1365-313X.1994.00397.x

35. Gueta-Dahan, Y., Yaniv, Z., Zilinskas, B. A., & Ben-Hayyim, G. (1997). Salt and oxidative stress: similar and specific responses in citrus. *Planta, 203*, 460–469. https://doi.org/10.1007/s004250050215

36. Bick, J. A., Setterdahl, A. T., Knaff, D. B., Chen, Y., Pitcher, L. H., Zilinskas, B. A., & Leustek, T. (2001). Regulation of plant-type 5'-adenylylsulfate reductase by oxidative stress. *Biochemistry, 40*, 9040–9048. https://doi.org/10.1021/bi010518v