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HISTORY AND BIOGRAPHY

Honoring two stalwarts of photosynthesis research: Eva-Mari Aro and Govindjee

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Abstract
On behalf of the entire photosynthesis community, it is an honor, for us, to write about two very eminent scientists who were recently recognised with a Lifetime Achievement Award from the International Society of Photosynthesis Research (ISPR) on August 5, 2022; this prestigious Award was given during the closing ceremony of the 18th International Congress on Photosynthesis Research in Dunedin, New Zealand. The awardees were: Professor Eva-Mari Aro (Finland) and Professor Emeritus Govindjee Govindjee (USA). One of the authors, Anjana Jajoo, is especially delighted to be a part of this tribute to professors Aro and Govindjee as she was lucky enough to have worked with both of them.

Keywords Govindjee Govindjee · Eva-Mari Aro · Photosynthesis · ISPR awards

It is our pleasure to write about these two stalwarts of the photosynthesis community who were recently honored at ISPR 2022 (Fig. 1): Eva-Mari Aro and Govindjee.

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Eva-Mari Aro

Eva-Mari Aro (Fig. 2) is a very accomplished academician in photosynthesis community who has made a significant impact on photosynthesis research all over the globe. Eva-Mari Aro is a research director and professor (emeritus) of Molecular Plant Biology in the Department of Life Technologies at the University of Turku, Finland. Aro has been a professor in Plant Physiology and Molecular Biology (currently Molecular Plant Biology) at the University of Turku, since 1987. Her name is taken with great respect because of her unparalleled contribution to photosynthesis research.

Brief biography

Eva-Mari Aro (born in 1950) grew up in a family of seven children. Her father was a university lecturer and education activist whilst her mother was a housewife. Already at a very young age, Aro had to fight for gender equality, which dictated her work later on as a supervisor of younger generation students and researchers. Aro received her doctorate in 1982 and in 1987 she was appointed to a tenured position as an Associate Professor of Plant Physiology in the Department of Biology at the University of Turku. She became Full Professor of Plant Molecular Biology in the Department of Biochemistry in 1998.

Fig. 1 President of ISPR Prof. Wim Vermaas (on the right) showed photos of winners at the New Zealand Conference; Left to right: Govindjee, and Eva-Mari Aro. (Source: Julian Eaton- Rye)

Fig. 2 A 2022 photograph of Eva-Marie Aro (Source: Eva-Mari Aro)

Research

Aro's dissertation "*Molecular components of the thylakoid membranes and the chloroplast ultrastructure in some bryophytes*" was eco-physiologically oriented research on the thylakoid response to environmental cues. A similar research line was continued for nearly 10 more years with a focus on vascular plants collected from their natural habitats in the course of their growth season. Her international collaborations started in 1990 in the lab of Bertil Andersson at Stockholm University, Sweden, and a couple of years later in the lab of Jan Anderson in CSIRO, Canberra, Australia. These years opened up possibilities for in-depth biochemical research on mechanisms and regulation of the Photosystem II (PSII) photoinhibition-repair cycle. Since then, the research in Aro group has continued in numerous EU, Nordic, Finnish-Japanese and other bi-national research and training networks. The focus in the Aro team has been on evolutionary divergences in photosynthetic auxiliary proteins and electron transfer pathways, in thylakoid ultrastructure and in the regulation of photosynthesis by environmental and metabolic cues, by investigating several distinct groups of oxygenic photosynthetic organisms, including cyanobacteria, algae, mosses, lycophytes, conifers and angiosperms. Her impressive publication list contains more than 400 papers and she has an h-index of 97 (Google scholar). She has supervised over 50 PhD theses in Turku and in collaboration with researchers world-wide. The laboratory, which Prof. Aro leads at the University of Turku, Finland, has become one of the most esteemed centers of photosynthesis research. Aro's research on light reactions of photosynthesis in plants and cyanobacteria has contributed significantly to the basic understanding of the molecular composition of Photosystems I and II and the protection mechanisms of the photosynthetic machinery (Aro et al. 1993a, b, 2005; Tyystjärvi and Aro 1996; Rintamäki et al. 1997, 2000; Tiwari et al. 2016). Her research based on photosynthesis concepts (Najafpour et al. 2012a, b, 2015, 2016), specific thylakoid protein phosphorylations (Grebe et al. 2020; Gerotto et al. 2022), and auxiliary electron transfer pathways (Zhang et al. 2012; Suorsa et al. 2012; Allahverdiyeva et al. 2013; Fitzpatrick et al. 2022) has been extended for applied purposes on biohydrogen production in cyanobacteria and engineering of efficient metabolic pathways for

carbon-based biofuel and chemicals production (Kosourov et al. 2014; Tikkanen et al. 2014; Raleiras et al. 2016; Huokko et al. 2017; Thiel et al. 2019). One of her scientific goals for the Centre of Excellence was to merge photosynthesis research with modern plant and cyanobacteria molecular biology research, including systems biology at different omics levels, in order "to make a quantum leap in our understanding of how the autotrophic organisms cope with the environment and direct their growth and development under changing environmental cues" (Zhang et al. 2004, 2012; Herranen et al. 2004; Tikkanen et al. 2010, 2014; Muth-Pawlak et al. 2022).

Awards

Eva-Mari Aro was awarded an Academy professorship, the highest academic researcher position in Finland, three times 1998–2002, 2003–2008, and 2014–2018. She has also been awarded several esteemed national and international acknowledgements and awards, and has served many academies and scientific societies: vice president and board member of the Scandinavian Society of Plant Physiology; past president, president and board member of the International Society of Photosynthesis Research (ISPR) (2001–2010); board member of the European Plant Society Organization (2009–2014); president, vice president and board member of the Finnish Academy of Science and Letters (2009–2016); member of the Scientific Advisory Board at the Max Planck Institute of Molecular Plant Physiology, Potsdam, Germany (2011–2017); member of the external counseling body Hungarian Academy of Sciences Biological Research Centre, Szeged (2019–2021); vice president and member of the European Academies Science Advisory Council (EASAC) (2014–2020); Biosciences Steering Panel of EASAC (2010–2013); member of the International board of the Millennium Technology Prize (2009–2014); member of the search committee of the Körber European Science Awards (2006–2015).

The president of Finland awarded Aro the highest academic honorary title in Finland, "Academician" in 2017 and in 2019 the Commander First Class of the Order of the Lion of Finland in 2019.

In 2018 Aro was elected a foreign associate of the US National Academy of Sciences. She is an Honorary Doctor of the Chinese Academy of Sciences, the Faculty of Science and Technology at Umeå University, Sweden, and the faculty of agriculture and forestry at the University of Helsinki.

Distinguished personality comments

Berry Osmond: early encounters and lasting appreciation

The oldest of my long-since expired passports confirmed my first visit to Finland after the 4th International Congress on Photosynthesis at the University of Reading (1977) when Elina Vapaavouri (née Repo) introduced me to Eva-Mari Aro. With Hal Hatch in Canberra Elina had published a comprehensive evaluation of C4 photosynthesis in the enigmatic dicot *Gomphrena celosioides* (Rapo and Hatch 1976). She also frequented the 'C4 pathway', a well worn track between our labs and accompanied our peripatetic fieldwork on the invasive CAM plant (*Oputia stricta*). With their mentor Nina Valanne Eva-Mari and Elina later published on changes in photosynthetic capacity and activity of RuBPC-ase and glycolate oxidase in the protonemata of moss (Valanne et al 1978). The same passport records a second longer visit to Finland in late summer 1980 when, in a testament to their holistic approach to photosynthesis, I found myself in a rowboat caught in a rainstorm on Kuivajärvi with this trio. We had been using wine cask liners to collect water samples for $\delta_{13}C$ measurements of CO_2/HCO_3^- in Finnish lakes to explain the $\delta_{13}C$ values of submerged and emergent leaves of aquatic macrophytes (Osmond et al. 1981). Eva-Mari then was as adroit with the oars as she was throughout her subsequent career that led photosynthesis research in Finland to the front of the discipline internationally. We landed safely and I was treated to my first sauna.

By the 10th Photosynthesis Congress in Montpellier 1995 Eva-Mari had published > 50 contributions on most aspects of structure and function of the photosynthetic apparatus in diverse plants from different environments with about the same number of different students and colleagues. Her presentation at that meeting: "Do grana margins of thylakoid membranes form functional domain during repair cycle of PSII?" was to remain emblematic of her research underpinning photoinhibition and acclimation of photosynthesis. Years later, as president of the International Society of Photosynthesis Research (ISPR) Eva-Mari convened a meeting with several of the Society's officers at her lakeside hideaway prior an impending congress. On that occasion we were invited to select our own flagellation apparatus to test photosynthetic responses of leaves to high temperature and humidity stress in the sauna. Who can forget Eva-Mari's challenge as President of the Society to colleagues at the 14th Congress in Glasgow 2007? She emphasized that the discipline must address the need to improve photosynthetic productivity in specific plant groups in response to climate change, and seek to exploit biotechnological applications for green energy. She highlighted the need to understand the plethora of ways that photosynthesis, the most energetic of biological processes, copes with the unregulated solar flux in the natural environment in diverse autotrophic systems. Academician Professor Emerita Aro's empathetic and supportive leadership continues to change the way we think about photosynthetic processes. She has recieved numerous civil honours and her contributions to research were recognised by election to the National Academy of Sciences

(USA) but in recent correspondence she mentioned her particular appreciation of the Life Membership Award from ISPR. In my dotage I have come to identify with old leaves in the shade and so continue to look to Turku for insights into how they optimise use of sun flecks. Eva-Mari my colleagues and I salute you and look to your leadership for years to come.

Toshiharu Shikanai

It was 2002 in the Finnish-Japanese binational meeting held in Turku when I first met Professor Eva-Mari Aro. She was already a leading figure in our field and I was a little nervous. She was very friendly and all Japanese participants really enjoyed the meeting. This is because of the hospitality of the Finnish side and also the character of Eva-Mari. We are repeating the binational meeting every two years although it was on-line in 2021. My research interest is partly overlapped with that of Eva-Mari especially on cyclic electron transport. Although our opinion was not always same, she was always open for discussion and respected our results. One of my good memories with Eva-Mari is the binational meeting held in Ivalo. It is hard to forget the beautiful Lapland village. In an excursion, we visited an old gold mine. It was unexpected that we had to wear boots and dig the soil like an old miner. I was in the same group with Eva-Mari and dreamed of getting rich quickly instead of making a fascinating scientific discovery.

Anjana Jajoo

I shared her office during my visit to her lab for a few months. I found her to manage her time exceptionally well, finding time between meetings to discuss research with group members. I learned from her how to address fundamental questions while doing experiments and writing papers. I found her a very straightforward, strong academician as well as a very kind woman. I could also understand that because of her excellent qualities of time-management, hard work and scientific aptitude, she could manage such a big research group at the University of Turku. I have yet to see a more passionate person than her.

Győző Garab

For many years, I admired from a distance Eva-Mari Aro as one of the brightest stars of the molecular biology and biochemistry of photosynthesis research—at international congresses, including the Budapest Congress, where she was invited and presented 12 contributions, mainly on gene regulation and expression and environmental stresses (Sippola and Aro 1998). We also enjoyed her excellent organization for our meeting in Naantali, Finland, closing the ESF Programme, Biophysics of Photosynthesis (1993–2000). During her frequent visits to Szeged, Hungary—where she has decades-long collaboration with Imre Vass (Vass and Aro 2008) and acts as a member of the International Advisory Board of the Biological Research Centre—I enjoyed all the enlightening discussions with her about the complex, multilevel regulatory processes. I had the opportunity to visit her lab in 2019 upon the occasion of the PhD defence of her student Sanna Rantala. During this short visit, I better understood how she was able to build an immensely successful laboratory in Turku with outstanding professionalism combined with a friendly and joyful atmosphere. I am convinced that as professor emerita, she will provide all support to her beloved institute and will also continue serving our big family of Photosynthesis Researchers. I wish her further successes and much happiness in this great adventure of being a Scientist.

Cheryl Kerfeld

This synopsis readily attests to Eva-Mari's scientific achievements. However, it's important to consider the context. *She was* a *pioneer in bringing molecular techniques that were emerging in the 1980s to the study of photosynthetic organisms*. This required considerable acumen and ingenuity as these techniques were in their infancy and mainly being applied to bacteria and non-photosynthetic eukaryotes. It also exemplifies some of her distinguishing personal attributes her vision and resourcefulness as she found a way as a graduate student to study abroad at the epicenter of the emergence of molecular techniques as applied to photosynthesis. Eva-Mari was visionary in anticipating their importance for opening up the frontier of understanding photosynthetic processes in molecular detail, laying a lasting foundation for improvement of agricultural yield and the development of artificial photosynthesis one of the key solutions to powering life on earth in the twenty-first century. There is another, somewhat less obvious, but no less game-changing dimension to Eva-Mari's career the impact of her career, her example, on the research community. *She is a path breaking female scientist.* The example she sets, not only in Finland but internationally which I can attest to has inspired the careers of female scientists, such as myself, who look up to her lifetime of achievement and her grace and dignity and well-rounded life as a role model for how a woman can be a creative thought leader in science and one with global impact all accomplished during an era in which women also contended with a sometimes less enlightened, male dominated system.

Govindjee Govindjee

Although Govindjee has used one name only all his life, we would like the readers to know that since 2020, his legal name is Govindjee Govindjee (Fig. 3). *He has recently reached 90 years and is still very active in photosynthesis research.*

Contributions

Govindjee has made pioneering and extensive contributions in the field of Photosynthesis: right from hardcore research related to chlorophyll *a* fluorescence to very popular historical perspectives and immensely popular lectures for the students. Amongst students, he has a real talent to spark their interest in Photosynthesis. It is a particularly significant achievement in being able to nurture and inspire the next generation of young scientists in this field. Everyone who has studied photosynthesis knows Govindjee very well because of his Z scheme posters, books, articles, and personal interactions that always leave a lasting impression, and as a result, his contributions over the years have greatly helped to popularize the field. His extremely long list of publications speaks for itself and his contributions. (See: <https://www.life.illinois.edu/govindjee/g/Publications.html>).

Brief Biography

Govindjee was born on October 24, 1932, and grew up as the youngest of four siblings of Mrs. Savitri Devi and Mr. Vishveshwar Prasad in Allahabad, India. At the very young age of a primary school student, he was attracted to plants and nature because of the inspiration provided by his teacher Mehrotra Saheb. He studied at the University of Allahabad, receiving his BSc in 1952, and MSc in Botany in 1954. He was always at the top of his class! In 1956, he went to the USA and studied at the University of Illinois at Urbana-Champaign (UIUC) for a doctorate in Physico-Chemical Biology under Robert Emerson, the discoverer of the *Red Drop* phenomenon (Emerson and Lewis 1943) and the Enhancement effect (Emerson et al. 1957). In 1960, Govindjee finished his PhD thesis, in Biophysics, titled: "*Effect of combining two wavelengths of light on the photosynthesis of algae"*, under Eugene Rabinowitch, dedicating it to the memory of Robert Emerson. A key discovery was that different spectral forms of chlorophyll *a* were involved in the two photosystems. Then during 1964, he made the earliest speculation for the existence of the reaction center of Photosystem II (PSII), now known as 'P680'.

Govindjee taught at the UIUC from 1961 until his retirement in 1999 and, during this period, advised more than 25 graduate students and many post-doc researchers. He retired in 1999 but continued to work as earlier, following his passion for popularizing photosynthesis amongst students, by involving them as 'molecules', through lectures worldwide. Govindjee has collaborated, even after retirement, with hundreds of scientists from almost two dozen countries.

Fig. 3 Govindjee Govindjee (Source: The University of Illinois at Urbana-Champaign; photograph by Tina Della Penna in 2022)

Research

Govindjee and co-workers have studied the absorption of light, excitation energy transfer, primary photochemistry and electron transport in oxygenic photosynthesis. As an Emeritus Professor, Govindjee, in collaboration with his colleagues from other labs, has summed up this field in several excellent overviews (see e.g., Ostroumov et al. 2014). He is best known for the following: role of chlorophyll *a* in the antenna as well as the reaction center of PS II (see e.g., Krey and Govindjee 1964); the very first picosecond measurements on both PS I and PSII (see e.g., Fenton et al. 1979; Wasielewski et al. 1989; for an overview, see Mirkovic et al. 2017); on the theory of thermoluminescence (DeVault et al. 1983) in algae and plants; and on the unique role of bicarbonate on the electron and proton transport on the electron acceptor site of PSII, a topic which is very close to his heart (see e.g., Stemler and Govindjee 1973; Shevela et al. 2012).

Govindjee has always enjoyed working on "Chlorophyll (Chl) *a* Fluorescence", beginning with his 1960 discovery of the two-light effect through it (Govindjee et al. 1960); since then, he has always enjoyed working on the *'light that the plants are giving out'* during illumination. The well-known book '*Chlorophyll a Fluorescence: A Signature of Photosynthesis*' (George Papageorgiou and Govindjee (Eds.) 2004); and numerous papers and review articles on this topic are lighting the path of young researchers even now (Szalay et al. 1967; Govindjee 1982, 2014; Robinson et al. 1984; Garab et al. 1988; Orr and Govindjee 1998; Strasser et al.

2004; Kalaji et al. 2012; Stirbet and Govindjee 2012; Papageorgiou and Govindjee 2014; Kodru et al. 2015; Stirbet et al. 2019). His publication list contains around 600 papers and he has an h-index of 83 (Google scholar). In fact, his list of relevant publications is so exhaustive that it is not possible to mention them here, but readers can find (and even download) them from: <https://www.life.illinois.edu/govindjee/pubschron.html> and from: <https://www.life.illinois.edu/govindjee/recent_papers.html>.

Awards

In 1976, he became a fellow of the American Association for the Advancement of Science, and in 1979 of the National Academy of Sciences of India. His outstanding scientific achievements, in deciphering important aspects of photosynthesis, and promoting photosynthesis research, have been recognized by prestigious awards from all over the globe. In 2007, he received the Lifetime Achievement Award from the Rebeiz Foundation for Basic Research at the University of Illinois at Urbana-Champaign (UIUC), and the prestigious Communication Award of the International Society of Photosynthesis Research, at the 14th International Congress of Photosynthesis Research, held in Glasgow, UK. Further, he received the 2008 LAS (Liberal Arts and Sciences) alumni achievement award from the UIUC, followed by the Prof. B.M. Johri Memorial Award of the Society of Plant Research in 2016, and the Foreign Fellow Award of the National Academy of Agricultural Sciences in 2018, both in New Delhi, India. He was honored on his 75th birthday at an International Symposium in 2008 at Indore, India (Jajoo et al. 2009), and on his 85th birthday at the International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability in 2017 at Hyderabad, India (Allakhverdiev et al. 2019). Also see Govindjee (2019) and https://www.life.illinois.edu/govindjee/awardsandhonors.html.

Comments on Govindjee's personality

We include just a few comments below.

Elisabeth Gantt

(Member of the National Academy of Sciences, USA): Dear Govindjee, Congratulations on receiving the Lifetime Achievement Award. You richly deserve it; I cannot think of anyone else that has done as much in the area of photosynthesis, as you have. With best regards.

Anjana Jajoo

Govindjee turned 90 in Oct. 2022. Still, many youngsters cannot match the energy he exhibits. He is a lively and vivacious person whose presence can be easily felt in any gathering by his jovial and friendly voice. Researchers in the field know Govindjee because of his books, articles, personal and social interactions that always leave a remarkable impression on young minds. I share my memory of working with Govindjee during his visit to Indore in 1997. He would come into the lab, check for the experimental set-up precisely and sit there until the experiments were over. During the experiment, he would share his knowledge, wisdom, and jokes to motivate everyone around and be light-hearted. It was fun to work with him, but he would be very serious while discussing the results!! See Jajoo et al. (1998) for our results on anion-induced "state changes". I always wish I could have energy and enthusiasm for the work as much as him. He always inspired and motivated us to work harder. He was ever ready to discuss on research topics of doctoral students and sit with them for hours, guiding them to think deeper about the research.

Győző Garab

My most important 'meeting' with Govindjee was in 1982—when I took his book (Govindjee 1982; see Govindjee and Whitmnarsh 1982) in my hands and read the excellent chapters on virtually all that was photosynthesis research at that time. This was our '*Bible*' for many years; I still have this book on my shelf and look up things in it from time to time. A year later, it was great to meet him in person as a member of the US scientific delegation arriving in Szeged for the Hungarian – USA Binational Conference on Photosynthesis, organized by Ágnes Faludi-Dániel (1927–1985) and Martin Gibbs (1922–2006). During my fellowship at UIUC, in John Whitmarsh's lab in 1984–1985, I attended Govindjee's course on photosynthesis – and enjoyed his lectures very much; they always had a personal touch of a professor who not only presented the facts and explained mechanisms very clearly but also knew the history behind the discoveries. Later, upon occasional trips together or at white-table conversations, I had to realize that all these and his excellent series of historical papers and tributes to outstanding scientists of our era did not stem simply from systematic research back in the library (while he evidently looked up details and carefully selected the proper references), but through his intense personal involvement with others. However, he got it all by heart; that was and still is his life! All these are conferred to us deep from his heart and we are able to "*see*" the scientist behind the science.

I had the privilege to have two joint works with Govindjee, a research paper and a book edited together. The joint

article was on the topic of the bicarbonate effect (Garab et al. 1988)—the experiments were performed during his short visit to Szeged, where he had colleagues and friends (among others, László and Erzsébet Szalay, who had stayed in his lab in the 1960s (Szalay et al. 1967), and Sándor Demeter, with whom he had worked on thermoluminescence (Demeter and Govindjee 1989). When editing the book on the 'non-photochemical quenching of the excited state of chlorophyll *a*' (Demmig-Adams et al. 2014), we all profited from Govindjee's enormous experience in editing books; we found out that he pays attention to all minor details while seeing the big picture.

Govindjee passionately loves educating not only PhD and MS students, but even BS students. Many of us have heard how he taught them photosynthesis by involving them as molecules in the process. He pioneered the use of web in education and in photosynthesis research (Orr and Govindjee 1998)—decades before the epoch of open access publications. In conferences and schools, he is always surrounded by young scientists. This might be the secret that keeps him young and fully 'energized'.

Rajagopal Subramanyam

I started my research career through my supervisor, Prof. Prasanna Mohanty, at Jawaharlal Nehru University, New Delhi, India, and he happened to be Govindjee's graduate student. During my student days, Prasanna Mohanty told me much about Govindjee's contribution to photosynthesis research. I met him, for the first time, in 1998 during the XIth International Photosynthesis Congress in Budapest, Hungary. Later, I enjoyed scientific discussion with Govindjee at several international meetings. His suggestions always helped me to improve the quality of my research. Our students also had a chance to interact with him on several platforms. He visited the University of Hyderabad several times and we collaborated on research that led to our paper: "The slow S to M rise of chlorophyll a fluorescence reflects the transition from state 2 to state 1 in the green alga *Chlamydomonas reinhardtii*" (Kodru et al. 2015). In this work, we concluded that the slow PSMT fluorescence transient in *C. reinhardtii* is due to the superimposition of two phenomena: (1) qE, the energy-dependent non-photochemical quenching of the excited state of Chl a and (2) state transitions. We also held the 10th International Conference on Photosynthesis and Hydrogen Energy Research for Sustainability—2017, at the University of Hyderabad, where we honored Govindjee, and two other scientists: Agepati S. Raghavendra and William A. Cramer (Allakhverdiev et al. 2019). During his visit to the University of Hyderabad, Govindjee ignited the importance of photosynthesis research among many young students. This resulted in many of our students doing research in the photosynthesis field in several places across the globe. I have known Govindjee for a long time; I have observed that he is a passionate researcher, a guide, a fatherly person in nature, and a good human being.

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Data Availability Data will be made available, if required.

Declarations

Competing interests The authors declare no competing interests.

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