

HISTORY & BIOGRAPHY

Dr. Autar Krishen Mattoo (1943–2024): an outstanding plant biologist with a focus on photosynthesis

A.K. HANDA^{*,†}, M. EDELMAN^{**}, W.W. ADAMS III^{***}, and G. GOVINDJEE^{#,†}

Department of Horticulture and Biology & Landscape Architecture, Purdue University, West Lafayette, Indiana 47906, USA^{}*

*Department of Plant and Environmental Sciences, Weizmann Institute of Science, Rehovot 76100, Israel^{**}*

*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309-0334, USA^{***}*

Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801, USA[#]

Abstract

We provide here the academic life of Dr. Autar Krishen Mattoo (1943–2024), including his role as a research leader at the United States Department of Agriculture and his outstanding contributions in photosynthesis, plant physiology and molecular biology with a focus to enhance nutrients. His work included ways to regulate Photosystem II (PSII) reaction center proteins, as well as to exploit, for our benefit, the role of polyamines in the plant world. Further, he provided the basis for beneficial aspects of sustainable agriculture systems and for selecting genes/proteins that provide better growth, higher disease resistance, and tolerance from abiotic stress. Autar K. Mattoo was a true international scholar and leader. We include below an overview of his selected research, his wonderful association with others, as well as a few reminiscences.

Keywords: abiotic stress; crop productivity; D1 protein; polyamines; regulation of photosynthesis.

Prologue

Autar Mattoo was recently elegantly recognized in “Duckweed Forum” [48th issue of the Duckweed Forum (DF26), 2024] with wonderful reminiscences and several photographs, which included (i) “Homage to a passionate duckweed researcher – Autar Krishen Mattoo (19 December 1943–29 December 2024)” by Marvin Edelman (of the Weizmann Institute of Science, Rehovot, Israel); (ii) “Autar Mattoo – A friend and a true well-wisher” by Sudhir Sopory (of the International Centre of Genetic Engineering and Biology, New Delhi,

India); (iii) “Autar Mattoo: An encouraging mentor” by K. Sowjanya Sree (of Banaras Hindu University, Varanasi, India); and (iv) “Autar Mattoo as a friend” by Klaus Appenroth (of the Friedrich Schiller University of Jena, Germany).

Here, we echo the wonderful words expressed earlier but add our own. The main text was drafted by A.K. Handa; most of the photographs and their legends were provided by M. Edelman, whereas Charles Arntzen and Adi Avni provided us with one photograph each. Figures 1–10 show Autar Mattoo with several scientists he interacted with. We end this Tribute with Reminiscences

Highlights

- Dr. Autar Krishen Mattoo identified and characterized the 32kDa D1, a key Photosystem II protein
- Made several crops much more productive for the benefit of us all
- Provided leadership in agriculture around the world, bringing science to the public

Received 7 April 2025

Accepted 11 April 2025

Published online 24 April 2025

[†]Corresponding authors

e-mail: ahanda@purdue.edu
gov@illinois.edu

Acknowledgements: We are highly grateful to Dr. Adi Avni (George S. White Chair in Life Sciences, Tel Aviv University, Israel) for Fig. 3 and its legend and to Dr. Charles (Charlie) J. Arntzen (Founding Director of Biodesign Institute, and Emeritus Regent Professor at the Arizona State University, Tempe, Arizona) for Fig. 5 and its legend.

Conflict of interest: The authors declare that they have no conflict of interest.

by William W. Adams III and Barbara Demmig-Adams, Ravinder Goyal, and G. Govindjee, followed by messages from Enzo Agostinelli, Susan Gilmour, and Otto Phanstiel IV.

Introduction

We are extremely saddened to learn that our dearest friend, Dr. Autar Krishen Mattoo, passed away on 29 December 2024. He was born in Kashmir, India, on 19 December 1943, but had to move to Bangalore due to the partitioning of India. He leaves an outstanding legacy of research in plant physiology. Autar Mattoo was a world-renowned plant biologist who made significant advances in diverse research areas, but particularly toward sustainable crop production to feed our ever-increasing population (see e.g., Roberts and Mattoo 2018).

Autar Mattoo's noteworthy achievements include several novel concepts in our understanding of the photosystem II (PSII) reaction center through characterization of the regulation of the 32-kDa protein (known now as D1) of the PSII reaction center complex (Mattoo *et al.* 1989). He also made significant contributions in establishing the role of polyamines in regulating ethylene production and fruit ripening (Handa *et al.* 2018). As a biotechnologist, Autar developed several genotypes of tomato to increase the content of health beneficial antioxidants and metabolites – the fruit of which also had an improved shelf life (Wang *et al.* 2017).

Autar had a distinguished post-PhD research period of 55 years with over 41 years' service at The Henry A. Wallace Beltsville Agricultural Research Center (ARC), United States Department of Agriculture (USDA), in Beltsville, MD, USA. Before returning to bench research in 2004, he served as a Research Leader for 16 years: nine years heading the Plant Molecular Biology Laboratory and seven years heading the Vegetable Laboratory at USDA-ARS. In 2021, Dr. Mattoo was recognized with the Presidential Rank Award for exceptional performance over an extended period by Joe Biden, then President of the United States of America.

Autar Mattoo had obtained his undergraduate (BSc) degree in 1963, studying chemistry, botany, zoology, and geology at the Jammu & Kashmir University, followed by a master's degree (MSc) in Biochemistry (1965), and then a PhD in Microbiology (1969) from the Maharaja Sayajirao University of Baroda, Gujarat – all in India. He was then, during 1975–1976, a postdoctoral fellow in the Department of Biochemistry at the University of Adelaide, and a visiting scientist (1976) at the University of New South Wales, Sydney, both in Australia. During 1976–1977, he worked at the Postharvest Physiology Lab of USDA-ARS, Beltsville, MD, USA. Before immigrating to the USA in November 1980, he was a DAAD (Deutscher Akademischer Austauschdienst) Scholar (German Academic Exchange) at the Weizmann Institute of Science, Rehovot, Israel (1979–1980). In 2018, Dr. Mattoo was elected to be a Fellow of the AAAS (American Association for the Advancement of Science).

Autar Mattoo was a prolific researcher in plant physiology and molecular biology with focus on both

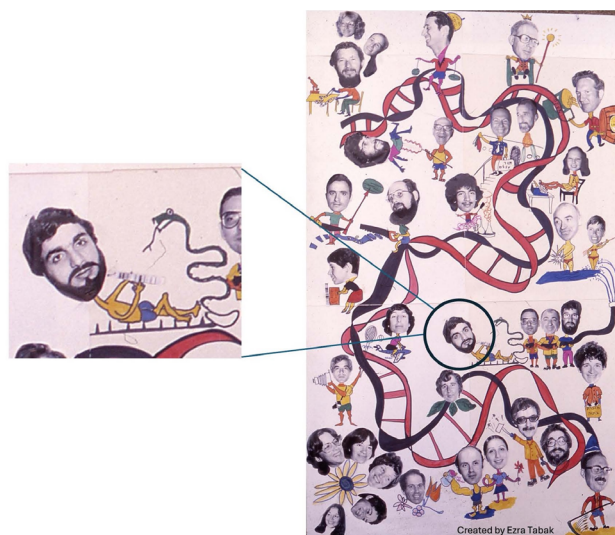


Fig. 1. Autar Mattoo, right in the center of things. A 1979 presentation at the Department of Plant Genetics, Weizmann Institute of Science, Rehovot, Israel. Source: Marvin Edelman.



Fig. 2. A 1983 photograph of Autar Mattoo (on the left) with Marvin Edelman before the door of his laboratory. Note that the protein they were studying was called “32 kDa protein” like the number on Mattoo's lab door, at the USDA Beltsville, Maryland, USA. Source: Marvin Edelman.

the basic and the applied areas, which included research on the value-added plants, sustainable agricultural systems, and molecular biotechnology for enhancing human health nutrients in fruits, unraveling the regulatory steps and life history of the PSII reaction center proteins, and on the role of polyamines in the plant world. His accomplishments are documented in over 400 publications (over 200 peer-reviewed papers, about 50 symposium proceedings, ~30 book chapters, and 7 edited books) and one patent. His original papers and reviews were published in high-impact journals, such as *Cell*, *Nature*, *Nature Biotechnology*, *Science*, *Proceedings of the National Academy of Sciences USA*, *Plant Cell*, *EMBO Journal*, *Journal of Biological Chemistry*, *Plant Journal*, and *Plant Physiology*. Autar Mattoo is a highly cited scientist with an h-index of 65, an i10-index of 198, and over 16,000 citations on *Google Scholar*. His national and international stature is apparent



Fig. 3. A 1988 group photograph at the Weizmann Institute of Science. *Left to right*: Massimo Cripa; unidentified (partly hidden); Hillel Fromm; Pierre Golobinoff; Esra Galun; Marvin Edelman; Adi Avni; and Autar Mattoo. Note: Autar Mattoo had written a comment on this photograph "How the time has flown!" This photo includes the 'PhD cream' who are now at the helm in their sciences around the world. Source: Adi Avni.

by invitations to deliver numerous lectures at international symposia, and to chair sessions in many (~30) countries throughout the world. In addition, he had been on the editorial boards of several scientific journals. Dr. Mattoo was a prodigious mentor, having guided more than 50 graduate students and over 60 postdoctoral fellows and visiting scientists from the U.S. and many other countries. In the following paragraphs, we summarize some of his accomplishments and contributions to science.

Research contributions

Dr. Mattoo pioneered investigations that provided fundamental new knowledge and novel concepts in plant physiology, biochemistry, and molecular biology. His early research led to several new concepts including the presence and the function of ATP citrate lyase in fruit metabolism (Mattoo and Modi 1970); establishing metabolic and regulatory cross-talk between polyamine and ethylene biosynthetic pathways (Mehta *et al.* 1997); ethylene biosynthesis induction by a fungal protein; influence of light, ethylene, and fruit development on wound-regulated gene expression; the role of ethylene as a cue for female moths to recognize host plants for mating (Mattoo and Suttle 1991); and unraveling the regulatory steps (Mattoo *et al.* 1981) and the life history of the PSII reaction center protein D1 (initially referred to as the 32,000 dalton or 32 kDa protein based on its molecular mass).

Identification and characterization of PSII reaction center proteins and their functions

Autar Mattoo, in long-term collaboration with Marvin Edelman, developed creative approaches to dissect the PSII reaction center that led to many novel concepts



Fig. 4. Two group photographs. *Top*: At the 1988 2nd International Symposium, International Society for Plant Molecular Biology, Jerusalem, Israel. The joint Edelman/Mattoo Duckweed research team; *left to right*: Frank Calahan, Marvin Edelman, Autar Mattoo, Victor Gaba, Jonathan Marder, Bruce Greenberg. *Bottom*: At the 1991 NATO Advanced Research Workshop, Regulation of Chlorophyll Biogenesis, Crete, Greece; *left to right*: Autar Mattoo, Charles Arntzen, and Marvin Edelman. Source: Marvin Edelman.

(Mattoo *et al.* 1989). He was the first to identify the 32kDa-D1 membrane protein as a component of photosynthetic electron transport and demonstrated its post-translational processing, including phosphorylation and acylation, in its function. He further demonstrated that 32kDa-D1 protein turnover is modulated by light intensity (Mattoo *et al.* 1981, 1984). He demonstrated the physical intramembrane translocation of the 32kDa-D1 protein within the chloroplast membrane system and isolated the PSII reaction center particle from stromal lamellae (Mattoo and Edelman 1987). He showed that post-translational modification of 32kDa-D1 protein by far-red light plays an essential role in its degradation and identified its primary degradation products (Gaba *et al.* 1987). Furthermore, his research demonstrated that two distinctly different photosensitizers, chlorophyll, absorbing in the visible and far-red regions, and plastosemiquinone, in the UV region, are involved in the degradation of 32kDa-D1 protein (Greenberg *et al.* 1989).

Mattoo's other contributions in the chloroplast function include the demonstration (i) that *in vivo* oxidative condition stimulates cross-linking of ribulose-1,5-bisphosphate carboxylase to the thylakoid



Fig. 5. A 1989 photograph of Autar Mattoo (*on the extreme left*) at the dedication ceremony of the Plant Molecular Biology Laboratory on the USDA (United States Department of Agriculture) campus in Beltsville, Maryland (MD). Autar had played a major role in planning the new facility, and in organizing the dedication ceremony. Others are members of USDA administration, a representative of the state government of MD, and Charles Arntzen (5th from the left, then the Deputy Chancellor for Agriculture at the Texas A&M University, who spoke in the symposium at the event). Source: Personal collection of Charles Arntzen.

membrane *via* cys247 resulting in its rapid degradation; (ii) of the presence of a distinct protein-foldase, peptidyl prolyl cis trans isomerase, in plant organelles; and (iii) of *in vivo* dephosphorylation of PSII core proteins by light absorption (Mehta *et al.* 1992). Further, his research has unequivocally established that environmental extremes such as drought, high light, and UV-B irradiation prompt changes in the PSII reaction center and that a circadian clock regulates 32kDa-D1 phosphorylation (Booij-James *et al.* 2002).

Making crops more nutritious

Autar Mattoo, in long-term collaboration with Avtar Handa, pioneered research to increase the levels of human health-associated antioxidants and other metabolites in fruits and vegetables (Kaur *et al.* 2017). He established the concept that polyamines regulate ethylene production and delay fruit ripening. Using molecular engineering to enable the accumulation of higher polyamines, spermidine, and spermine, in a ripening-specific manner, he has demonstrated that elevated levels of polyamines increase fruit shelf life, fruit juice quality, and anti-cancer lycopene levels by 300% (Mehta *et al.* 2002). The follow-up transcriptomic and metabolic characterization of engineered fruits delineated, for the first time, that putrescine, spermidine, and spermine have differential effects on metabolism, hormone production/signaling, and even fruit quality (Handa and Mattoo 2010). Higher spermidine/spermine-activated gene expression of many biochemical pathways led to a dramatic increase in metabolites, providing a novel strategy to generate added-value food (Mattoo *et al.* 2006). These results provided the first direct evidence for a physiological role of polyamines in plants, advanced scientific knowledge in this field, and opened new vistas for enhancing quality attributes of fruits and vegetables, none of which could have been achieved using the traditional breeding methods. Dr. Mattoo's research also provided a scientific basis for a linkage between the beneficial aspects of sustainable agriculture systems and distinct activation of select



Fig. 6. A 2006 photograph of Autar Mattoo, the Chef, behind the dishes he had cooked for his guests, at his home, in Laurel, Maryland, USA. Source: Marvin Edelman.



Fig. 7. Autar Mattoo floating in the Dead Sea, sometime in 2010; behind are Marvin Edelman and Barat Chatoo. Source: Marvin Edelman.



Fig. 8. Autar Mattoo at the Washington National Arboretum, in 2012, enjoying nature. Source: Marvin Edelman.

genes/proteins that provide more growth, higher disease resistance, and tolerance for abiotic stress.

Leadership

Dr. Autar Krishen Mattoo was appointed Research Leader of the newly created USDA's Plant Molecular Biology Laboratory in 1988. During his nine years of

tenure until 1997, he guided the focus of this laboratory, while supervising nine highly productive research scientists, mentoring numerous postdoctoral fellows, and collaborating with many visiting scientists covering a broad range of plant science projects. These projects included genetic engineering of cereals and soybeans for nutritional improvement, resistance to environmental stresses, and to microbial pathogens, as well as to altered ripening and organ abscission in soybeans and tomatoes. His efforts created a center of excellence in molecular biology and biotechnology research; his laboratory obtained significant extramural funds from BARD (US-Israel Binational Agricultural Research and Development Fund), USDA/National Research Initiative, North Atlantic Treaty Organization and the Foreign Currency Research Program, U.S. Embassy in India, and Foreign Agricultural Service, Washington, D.C. These awards allowed the training of many local and overseas postdoctoral research associates, and graduate students, for the emerging science and application of molecular biology to plant biology. Additionally, high-quality publications from Mattoo's laboratory led to solid partnerships with several institutions in the US and overseas, giving it the international recognition and visibility it now enjoys. Collectively, science resulting from his leadership led to a deeper fundamental understanding of many concepts in the research areas mentioned above.

As Research Leader of the Vegetable Laboratory, Dr. Mattoo was charged with reviewing and reorganizing this laboratory to enhance sustainable vegetable crop production. His leadership efforts bridged the interface between traditional breeding and genetic engineering programs to solve horticultural problems for the benefit of world agriculture. His leadership attracted many established scientists from all over the world to work in the Vegetable Lab. Dr. Mattoo's stellar contributions were recognized through the ARS Distinguished Senior Scientist of the Year Award in 1998, and the USDA Secretary's Honor Award for his Personal and Professional Excellence in 1999.

Outreach: bringing science to the public

Dr. Autar Mattoo's commitment to the advancement of science is evident from his outreach activities, including the pioneering of the widespread use of genetic engineering, the science involved, and its importance for feeding a growing world population – supported by being an advisor/expert in plant biotechnology, food security, biochemistry, and molecular biology. Further, Dr. Mattoo was widely sought out to explain, in a layperson's language, the basic science behind genomics and transgenic plants. In 2002 and 2004, he was selected as the US Department of State International Speaker to make presentations on biotechnology to varied groups in the Philippines (which included Congressional Staffers for the Philippine Senate), Thailand, Malaysia, and India. His deliberations with the Philippine Senate convinced them to allow the testing of genetically engineered food in their country. Similarly, Bangladesh's acceptance of genetically engineered crops

was heralded because of Dr. Mattoo's in-depth interactions with the scientific community at Dhaka University and the Agricultural University at Mymensingh. Further, Dr. Mattoo hosted over 150 delegations of scientists, scientific academics, administrators, state ministers, congressional staff, State Department personnel, foreign embassy public affairs staff, university teachers and students, and journalists, from over 30 countries. Dr. Autar K. Mattoo was a great spokesperson for the positive implications of molecular biology and biotechnology for agricultural sustainability and world agriculture.

In summary, throughout his life, Dr. Autar Krishen Mattoo, an outstanding scientist, remained an enthusiastic, passionate, and avid researcher with a deep commitment to excel in science. His contributions to science, leadership in science, and to worldwide outreach were truly remarkable, for which we have not seen any parallels yet. We now present below some of the Reminiscences and the messages received.

Reminiscences

1. William W. Adams III and Barbara Demmig-Adams (e-mail: william.adams@colorado.edu & barbara.demmig-adams@colorado.edu; University of Colorado at Boulder, USA)

Our collaboration with Autar Mattoo was prompted when Dr. Volker Ebbert, after completing his PhD under Professor Doris Godde (Bochum, Germany), joined our laboratory as a postdoc in the late 1990s, bringing his expertise in the extraction, separation, and characterization of chloroplast proteins. Prior to Volker's arrival, we had focused on photosynthesis and photoprotection through measurements of oxygen evolution, chlorophyll fluorescence, and pigment composition. After adding Volker's expertise, we were able to include assessment of thylakoid proteins for a more complete understanding. Given his deep expertise and perspective on the D1 (or 32 kDa) protein of Photosystem II, we also reached out to Autar. The common interpretation of D1 removal at the time (and to this day) was as unfortunate damage to the plant, *i.e.*, that D1 is damaged in response to high light or light in combination with stress and the plant consequently suffers (*see below* for our alternative interpretation based on decades of work with plants under physiologically relevant conditions). However, in their original characterization, Autar and his collaborator Marvin Edelman described the removal and replacement of D1 as a manifestation of protein turnover [for a review of their pioneering work, *see Edelman and Mattoo (2006)*], with the exceptional rapidity of this process positioning D1 as a candidate for highly sensitive regulation. After John Ellis suggested (Ellis 1981) that D1 turnover may be a protective mechanism, Mattoo and Edelman (1985) wrote: "The coordination in the rates of synthesis and breakdown of this regulatory protein may be one of the mechanisms by which plants adapt to changing light conditions."

In response to our proposed collaboration, Autar generously shared antibodies to the D1 protein with us.



Fig. 9. Autar Mattoo (on the left) with Marvin Edelman, in 2017, at the 4th International Duckweed Conference, Kerala, India. Source: Marvin Edelman.

We were working with several non-model species, and while these antibodies did not cross-react with D1 from all species, they did so with two species [*Monstera deliciosa*, Ebbert *et al.* (2001); *Pseudotsuga menziesii* (Douglas fir), Ebbert *et al.* (2005)]. We shared these findings at several meetings, such as the 13th International Congress on Photosynthesis (Demmig-Adams *et al.* 2004). Antibodies, provided by Autar, were particularly helpful in characterizing phosphorylated and nonphosphorylated forms of D1 and identifying a sustained form of D1 phosphorylation associated with continuous maintenance of zeaxanthin during cold spells in conifers that return to photosynthetic activity during milder periods in the winter (Ebbert *et al.* 2005). This contrasts with a more extreme syndrome in evergreens that suspend growth for the whole winter season at high-altitude sites, where the virtual absence of the D1 protein is associated with negligible photosynthetic oxygen evolution and Photosystem II photochemical capacity as well as continuous, season-long maintenance of exceptionally high zeaxanthin levels. In contrast to damage, our interpretation is that D1 removal during winter is an active process that stifles the production of superoxide and this is coupled with sustained engagement of zeaxanthin in photoprotective energy dissipation preventing formation of singlet excited oxygen, *i.e.*, the plants are in a highly photoprotected state awaiting environmental conditions in the spring when D1 is replaced and zeaxanthin become disengaged, reactivating the process of photosynthesis as frozen soil transitions and liquid water becomes available. Soon after publishing our work with Autar, the two of us proposed a book on Photoprotection and Photoinhibition for the series "Advances in Photosynthesis and Respiration" and Autar joined us as an editor, resulting in the publication of Volume 21 (Demmig-Adams *et al.* 2006) and its paperback version (Demmig-Adams *et al.* 2008).

We were saddened to see our friend Autar distressed about his separation from his beloved Kashmir and its



Fig. 10. *Left:* Autar Mattoo lecturing at the 5th International Duckweed Conference, Rehovot, Israel, held in 2019. *Right:* Autar with several others at the same conference – holding court – so-to-say. Source: Marvin Edelman.

repression. Autar was a kind human being and a gentle soul, and the world is a poorer place in his absence. During a week-long trip (in March 2001) to Washington, D.C. to participate in a United States Department of Agriculture panel meeting, one of us (William) gave a seminar in Beltsville, Maryland, and worked with Autar in his lab to use a portable chlorophyll fluorometer that we had loaned to his group for assessing the status of one of his favorite plants, the duckweed *Spirodela*. In a curious twist, our lab has had a major focus on duckweeds for the past half decade, bringing our connection to Autar full circle. We fondly remember Autar and are grateful for his insight, inspiration, and generous gift of his antibodies, which enabled progress that would not otherwise have been possible.

2. Ravinder Goyal (e-mail: Ravinder.goyal@agr.gc.ca; Agriculture and Agri-Food Canada, Lacombe Research and Development Center, Lacombe, Alberta, Canada)

I wish I had some photos of Dr. Autar Mattoo mentoring me, especially during my time in his lab between 2000 and 2004. I still vividly remember when he refused to let me perform an experiment involving a high dose of sulfur-35 (S^{35}), telling me I was too young to be exposed to such dangerous radiation. Instead, he took it upon himself, putting on his lab coat and conducting the experiment while instructing me to observe. Back then, cell phones weren't as common, and I never had the chance to capture those moments while he was in action.

Our conversations always revealed the depth of his commitment to science. Dr. Mattoo's insatiable curiosity drove him to contribute to a wide array of plant science disciplines. His grasp of diverse scientific fields was truly remarkable. To illustrate the breadth of his interests, we explored topics ranging from the relationship between polyamines and ethylene in fruit development under extreme climate conditions (Goyal *et al.* 2016), to plant defense mechanisms through basal immunity distinct from traditional resistance genes (Goyal and Mattoo 2014), and strategies for enhancing agricultural sustainability through improved nitrogen fixation (Goyal *et al.* 2021).

Now, all my memories with Dr. Mattoo live in the conversations we had, right up until a few weeks before his

passing. His passion for science was truly unparalleled; he continued discussing research even while battling cancer. Every time we spoke, he reassured me that he was getting better and that the doctors were adjusting his treatment. Not once did he reveal the true extent of his illness.

On 29 September 2024, he messaged me in response to my missed call, “*Ravinder, I have made up my mind that I will say goodbye to Beltsville at the end of this year.*” Looking back, perhaps he was also subtly hinting at saying goodbye to life itself. My last call to him on 18 December 2024 went unanswered. Little did I realize that he was pausing the science to prepare for his final journey. I cannot express how much I regret not seeing him one last time. Dr. Mattoo will always hold a special place in my heart, and he will be missed forever!

3. Govindjee Govindjee (e-mail: gov@illinois.edu)

I am extremely sad to learn that my dear friend of many years, Autar Krishen Mattoo, is no more with us. I miss his phone calls when he would start the conversation by saying, in Hindi: “Govindjee Saheb Kaisey Ho”, *i.e.*, How was I doing? Although I knew Autar for years, the only thing we published together was a Tribute to a friend, Ravinder Kaur Sawhney (1931–2020) from Allahabad University (Govindjee *et al.* 2021); it was Autar who understood and had written about her research (Mehta *et al.* 2002) as his own research was closely related to hers. In addition, Autar co-edited, with William Adams and Barbara Demmig-Adams, a highly challenging and up-to-date book dealing with photoprotection, photoinhibition, and more in the “Advances in Photosynthesis and Respiration” series (Demmig-Adams *et al.* 2006) for which I was the Series Editor at the time.

I have highly appreciated all of Autar's research over the years, but I was particularly interested in his outstanding discoveries related to the function and regulation of several proteins in the two photosystems. Below, as examples, I refer to just some of his selected papers, which include those on the D1 protein of Photosystem II. Chronologically, those, not mentioned thus far, are: Gaba *et al.* (1987), Elich *et al.* (1993), Sopory *et al.* (1993), Giardi *et al.* (1996), Booi *et al.* (1998), Koblizek *et al.* (1998), Mattoo *et al.* (1999), Edelman and Mattoo (2008), and Krol *et al.* (2009).

All in all, Autar Mattoo has contributed tremendously to the overall area of the physiology of plants – with the goal of increasing plant productivity for the benefit of us all. May his soul rest in Peace.

Messages

1. Enzo Agostinelli (*Department of Sensory Organs, Faculty Medicine and Dentistry, SAPIENZA University of Rome, University Hospital Policlinico Umberto I, Viale del Policlinico 155, I-00161 Rome, Italy and International Polyamines Foundation 'ETS-ONLUS'*)

Dear Polyamigos, Dearest Friends, I am deeply saddened by the passing of my friend Dr. Autar Mattoo. Autar was a sincere friend, always kind and generous since our first meeting over 35 years ago. During the exchange of visits to our laboratories, I had the opportunity to learn about his deep knowledge and preparation in the field of polyamines in plants. I would like to thank Autar for always encouraging me to continue with the International Polyamines Foundation, declaring that it will be a reference for the new generations of Polyamigos.

I express my deepest condolences to the Mattoo family for the loss of such a dear person. Dearest Autar, we will miss you – Enzo.

2. Susan Gilmour (e-mail: gilmours@mlhs.org; *Lankenau Institute for Medical Research, 100 Lancaster Ave., Wynnewood, PA 19096*)

I am very sad to hear of Autar's passing, who really knew all about polyamines. I'll miss his insights into polyamines and plants – and gardening, especially the importance of polyamines in the ripening of tomatoes. Rest In Piece (RIP), my fellow Polyamigo!

3. Otto Phanstiel IV (e-mail: Otto.Phanstiel@ucf.edu; <https://med.ucf.edu/person/otto-phanstiel-iv-ph-d-2/>)

Thank you for sharing this Tribute to Autar Mattoo, a very special person. I am very sad upon hearing this news. He was a special person, so friendly and he will be missed by many. Best wishes to all.

References

Booij I.S., Callahan F.E., Jansen M.A.K. *et al.*: Photoregulation and photoprotection of the Photosystem II reaction center heterodimer. – In: Singhal G.S., Renger G., Sopory S.K. *et al.* (ed.): *Concepts in Photobiology: Photosynthesis and Photomorphogenesis*. Pp. 549-571. Springer, Dordrecht 1998.

Booij-James I.S., Swegle W.M., Edelman M., Mattoo A.K.: Phosphorylation of the D1 Photosystem II reaction center protein is controlled by an endogenous circadian rhythm. – *Plant Physiol.* **130**: 2069-2075, 2002.

Demmig-Adams B., Adams III W.W., Mattoo A.K. (ed.): *Photoprotection, Photoinhibition, Gene Regulation, and Environment. Advances in Photosynthesis and Respiration*. Vol. 21. Pp. 380. Springer, Dordrecht 2006.

Demmig-Adams B., Adams III W.W., Mattoo A. (ed.):

Photoprotection, Photoinhibition, Gene Regulation, and Environment. Advances in Photosynthesis and Respiration. Vol. 21. Pp. 380. (Paperback Edition) Springer, Dordrecht 2008.

Demmig-Adams B., Ebbert V., Zarter C.R. *et al.*: Multiple mechanisms of zeaxanthin function in thermal dissipation, photoinhibition, and signal transduction. Oral presentation at the 13th International Congress on Photosynthesis, Montréal, Canada, 29 August to 3 September, 2004.

Ebbert V., Adams III W.W., Mattoo A.K. *et al.*: Up-regulation of a Photosystem II core protein phosphatase inhibitor and sustained D1 phosphorylation in zeaxanthin-retaining, photoinhibited needles of overwintering Douglas fir. – *Plant Cell Environ.* **28**: 232-240, 2005.

Ebbert V., Demmig-Adams B., Adams III W.W. *et al.*: Correlation between persistent forms of zeaxanthin-dependent energy dissipation and thylakoid protein phosphorylation. – *Photosynth. Res.* **67**: 63-78, 2001.

Edelman M., Mattoo A.K.: Future perspectives. – In: Demmig-Adams B., Adams III W.W., Mattoo A.K. (ed.): *Photoprotection, Photoinhibition, Gene Regulation, and Environment. Advances in Photosynthesis and Respiration*. Vol. 21. Pp. 23-38. Springer, Dordrecht 2006.

Edelman M., Mattoo A.K.: D1-protein dynamics in Photosystem II: the lingering enigma. – *Photosynth. Res.* **98**: 609-620, 2008.

Elich T.D., Edelman M., Mattoo A.K.: Dephosphorylation of Photosystem II core proteins is light-regulated *in vivo*. – *EMBO J.* **12**: 4857-4862, 1993.

Ellis R.J.: Chloroplast proteins: synthesis, transport and assembly. – *Annu. Rev. Plant Physiol.* **32**: 111-137, 1981.

Gaba V., Marder J.B., Greenberg B.M. *et al.*: Degradation of the 32 kDa herbicide binding protein in far red light. – *Plant Physiol.* **84**: 348-352, 1987.

Giardi M.T., Cona A., Geiken B. *et al.*: Long-term drought stress induces structural and functional reorganization of photosystem II. – *Planta* **199**: 118-125, 1996.

Govindjee G., Sawhney B., Mattoo A.K.: Ravindar Kaur Sawhney (1931–2020): An innovative plant physiologist. – *Plant Physiol. Rep.* **26**: 1-3, 2021.

Goyal R.K., Fatima T., Topuz M. *et al.*: Pathogenesis-related protein 1b1 (PR1b1) is a major tomato fruit protein responsive to chilling temperature and upregulated in high polyamine transgenic genotypes. – *Front. Plant Sci.* **7**: 901, 2016.

Goyal R.K., Mattoo A.K.: Multitasking antimicrobial peptides in plant development and host defense against biotic/abiotic stress. – *Plant Sci.* **228**: 135-149, 2014.

Goyal R.K., Mattoo A.K., Schmidt M.A.: Rhizobial–host interactions and symbiotic nitrogen fixation in legume crops toward agriculture sustainability. – *Front. Microbiol.* **12**: 669404, 2021.

Greenberg B.M., Gaba V., Canaani O. *et al.*: Separate photosensitizers mediate degradation of the 32-kDa photosystem II reaction center protein in the visible and UV spectral region. – *PNAS* **86**: 6617-6620, 1989.

Handa A.K., Fatima T., Mattoo A.K.: Polyamines: bio-molecules with diverse functions in plant and human health and disease – *Front. Chem.* **6**: 10, 2018.

Handa A.K., Mattoo A.K.: Differential and functional interactions emphasize the multiple roles of polyamines in plants. – *Plant Physiol. Biochem.* **48**: 540-546, 2010.

Kaur B., Handa A.K., Mattoo A.K.: Genetic engineering of tomato to improve nutritional quality, resistance to abiotic and biotic stresses, and for non-food applications. – In: Mattoo A.K., Handa A.K. (ed.): *Achieving Sustainable Cultivation of Tomatoes*. Pp. 229-282. Burleigh Dodds

- Science Publishing, Cambridge 2017.
- Koblizek M., Masojidek J., Komenda J. *et al.*: A sensitive photosystem II-based biosensor for detection of a class of herbicides. – *Biotechnol. Bioeng.* **60**: 664-669, 1998.
- Krol M., Ivanov A.G., Booi-James I. *et al.*: Absence of the major light harvesting antenna proteins alters the redox properties of photosystem II reaction centers in the *chlorina F2* mutant of barley. – *Biochem. Cell Biol.* **87**: 557-566, 2009.
- Mattoo A.K., Edelman M.: Photoregulation and metabolism of a thylakoid herbicide-receptor protein. – In: St. John J.B., Berlin E., Jackson P.C. (ed.): *Frontiers of Membrane Research in Agriculture*. Pp. 23-34. Rowman & Allanheld, Totowa 1985.
- Mattoo A.K., Edelman M.: Intra-membrane translocation and posttranslational palmitoylation of the chloroplast 32-kDa herbicide-binding protein. – *PNAS* **84**: 1497-1501, 1987.
- Mattoo A.K., Giardi M.-T., Raskind A., Edelman M.: Dynamic metabolism of photosystem II reaction center proteins and pigments. – *Physiol. Plantarum* **107**: 454-461, 1999.
- Mattoo A.K., Hoffman-Falk H., Marder J.B., Edelman M.: Regulation of protein metabolism: Coupling of photosynthetic electron transport to *in vivo* degradation of the rapidly metabolized 32-kilodalton protein of the chloroplast membranes. – *PNAS* **81**: 1380-1384, 1984.
- Mattoo A.K., Marder J.B., Edelman M.: Dynamics of the photosystem II reaction center. – *Cell* **56**: 241-246, 1989.
- Mattoo A.K., Modi V.V.: Citrate cleavage enzyme in mango fruit. – *Biochem. Bioph. Res. Co.* **39**: 895-904, 1970.
- Mattoo A.K., Pick U., Hoffman-Falk H., Edelman M.: The rapidly metabolized 32,000-dalton polypeptide of the chloroplast is the "proteinaceous shield" regulating photosystem II electron transport and mediating diuron herbicide sensitivity. – *PNAS* **78**: 1572-1576, 1981.
- Mattoo A.K., Sobolev A.P., Neelam A. *et al.*: Nuclear magnetic resonance spectroscopy-based metabolite profiling of transgenic tomato fruit engineered to accumulate spermidine and spermine reveals enhanced anabolic and nitrogen-carbon interactions. – *Plant Physiol.* **142**: 1759-1770, 2006.
- Mattoo A.K., Suttle J.C. (ed.): *The Plant Hormone Ethylene*. Pp. 347. CRC Press, Boca Raton 1991.
- Mehta R.A., Cassol T., Li N. *et al.*: Engineered polyamine accumulation in tomato enhances phytonutrient content, juice quality and vine life. – *Nat. Biotechnol.* **20**: 613-618, 2002.
- Mehta R.A., Fawcett T.W., Porath D., Mattoo A.K.: Oxidative stress causes rapid membrane translocation and *in vivo* degradation of ribulose-1,5-bisphosphate carboxylase/oxygenase. – *J. Biol. Chem.* **267**: 2810-2816, 1992.
- Mehta R.A., Handa A.K., Mattoo A.K.: Interactions of ethylene and polyamines in regulating fruit ripening. – In: Kanellis A.K., Chang C., Kende H., Grierson D. (ed.): *Biology and Biotechnology of the Plant Hormone Ethylene*. Pp. 321-326. Springer, Dordrecht 1997.
- Roberts D.P., Mattoo A.K.: Sustainable agriculture – enhancing environmental benefits, food nutritional quality and building crop resilience to abiotic and biotic stresses. – *Agriculture* **8**: 8, 2018.
- Sopory S.K., Ghirardi M.L., Elich T. *et al.*: Regulation of the 32k Da-D1 Photosystem II reaction center protein. – In: Abrol Y.P., Mohanty P., Govindjee G. (ed.): *Photosynthesis: Photoreactions to Crop Productivity*. Pp. 131-156. Springer, Dordrecht 1993.
- Wang K., Handa A.K., Mattoo A.K.: Understanding and improving the shelf life of tomatoes. – In: Mattoo A.K., Handa A.K. (ed.): *Achieving Sustainable Cultivation of Tomatoes*. Pp. 315-342. Burleigh Dodds Science Publishing, Cambridge 2017.