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REVIEW ARTICLE

A tribute

Ravindar Kaur Sawhney (1931-2020): An Innovative Plant Physiologist

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A 1998 portrait of Ravindar Kaur-Sawhney

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Ravindar Kaur's research at the University of Allahabad demonstrated basic understanding of how certain hormones break dormancy in potato tubers, which was of significance to potato farmers. Later, at the Yale University her work with a renowned plant biologist Arthur (Art) Galston brought out important information about the role polyamines play in plants. Another key discovery dealt with her work on senescence (aging) in plants, which led to the in vitro production of ripe tomatoes from thin layer explants of flower pedicels. She authored or coauthored over 100 publications in peer-reviewed journals, review articles and book chapters.

Ravindar Kaur was born in Burma (March 9, 1931) where her father was a general surgeon for the government. During the Japanese invasion of Burma (1940), the family, literally, fled on foot through jungles of Burma to reach India. After schooling, she joined the University of Allahabad for her B.Sc. (Chemistry, Botany and Zoology) and M.Sc., specializing in Plant Physiology (1949) under the mentorship of Shri Ranjan (1899–1969; see: Laloraya 1970).

Ravindar used the variety *Phulwa* of potatoes for respiratory studies and growth response to dormancy-breaking hormones (Kaur 1952; Ranjan and Kaur 1954) and discovered a correlation between the rate of respiration and dormancy. She also found that N-ethylene chlorhydrin was effective in breaking dormancy. Further, she established the prerequisite of high respiration for bud growth. Her work with Shri Ranjan had practical applications, and she received the Empress Victoria Reading Award for this outstanding research.

Ravindar Kaur's keen interest in plant physiology research brought her to the USA (1957) on a Fulbright fellowship and a travel grant from the American Association of University Women (AAUW). After spending a year at the University of California at Los Angeles (UCLA), she joined the Biology Department at Yale University, working with Art Galston (1920–2008; https://news.yale.edu/2008/07/18/memoriam-arthur-galston-plant-biologist-fought-use-agent-orange; also see Chou 2017). Prof. Galston was interested in unraveling the function of positively charged molecules called polyamines, in particular, putrescine, spermidine and spermine. Ravindar pioneered research on several key aspects of plant physiology and was particularly involved in determining the role(s) polyamines play in different physiological and development processes in plants. Kaur-Sawhney and Galston (1979) provided an understanding of how polyamines delay dark induced leaf senescence via a time dependent phenomenon: RNAse increases first, then the proteases increase, and finally chlorophylls are degraded. The in vitro work that was carried out by Ravindar in Galston's's lab led to the suggestion that polyamines be regarded as plant hormones, although the data on which this concept was based was mostly indirect. Polyamines and ethylene, the ripening hormone, share methionine as a precursor and their pathways separate out from SAM (S-adenosylmethionine) to form ACC (1-aminocyclopropane-1-carboxylic acid) that feeds into the ethylene pathway while decarboxylation of SAM feeds into making polyamines spermidine and spermine (see Suppl. Fig. S1). That polyamines indeed function as hormones was proven by the demonstration via genetic engineering that ripening-specific expression of polyamines spermidine and spermine in tomato fruit positively impacts the fruit quality and vine life of tomatoes in addition to a very high accumulation of lycopene, an important carotenoid for human health (Mehta et al. 2002). In 2003, Kaur-Sawhney et al. (2003) reviewed, in depth, the role of polyamines in plants. Through excellent experiments, Kaur-Sawhney et al. (1996) found that isatin (an auxin precursor) was an effective source of auxin for bud formation, while zeatin (a cytokinin) was best for growth and development of buds; the two together were best for tomato development—giving also nice color and flavor. For her extensive research contributions, see: https://www.researchgate.net/scientific-contributions/3993027_Ravindar_Kaur-Sawhney.

During her tenure at Yale, Ravindar helped a large number of international graduate students and post-docs, including many from India, to settle in the new environment away from their homes. It was no surprise that she acquired the loving nickname of "Mother Hen" of the Department of Biology at Yale. The same was true earlier when she was at Allahabad. We refer the readers to the 'Supplementary Information' (https://doi.org/10.1007/s40502-020-00554-0) where wonderful reminiscences are available from her time at Allahabad from Rajni Govindjee (USA); Manmohan Laloraya (India); Sirajul Hasan (France); Raghubir Raj Prasad (Canada); one of us (Brij Sawhney); and Sushila Narsimhan (India). They provide a glimpse of Ravindar's special personal qualities: a loving, helpful, and an extremely caring human being. In the words of many "She was a most loving, polite, caring, giving, and elegant person and a highly accomplished scientist of her time."

Dr. Ravindar Kaur Sawhney left behind her husband, Brij Sawhney, their son, Rajiv Sawhney and his wife Anjali, and her two beloved grandchildren Jai and Aanika.

Authors' contributions All authors have contributed equally in providing information included in the paper except that the corresponding author Govindjee Govindjee has prepared the final copy of the manuscript.

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Supplementary Information
for
Ravindar Kaur-Sawhney (1931—2020): An Innovative Plant Physiologist
by
G. Govindjee, B. Sawhney and A. Mattoo

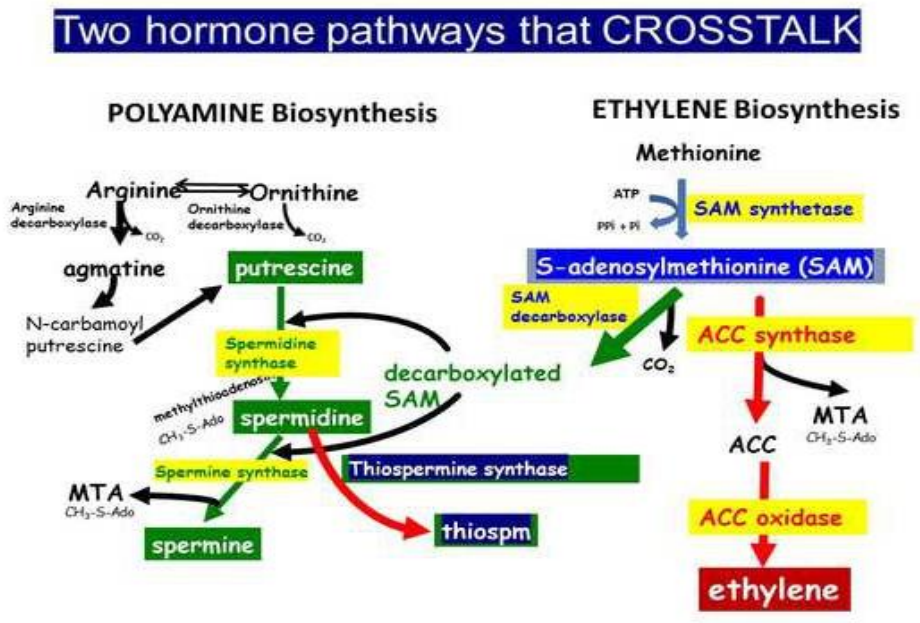

Fig. S1. A schematic of interactive two hormone pathways that crosstalk, showing common features of the biosynthesis of polyamines and ethylene. *Left panel:* Arginine (Arg) and ornithine (Orn) produce diamine putrescine, involving specific decarboxylases. Then, putrescine is converted to spermidine (SPD) via SPD synthase, involving decarboxylated S-adenosylmethionine (SAM). This is followed by SPD being converted to spermine (SPM), or to thiospermine (thiospm), catalyzed by their specific synthases, both requiring decarboxylated SAM. *Right panel*: Ethylene biosynthesis is initiated via conversion of methionine to SAM, catalyzed by SAM synthetase. SAM is then converted to 1-aminocyclopropane-1-carboxylic carboxylic acid (ACC), catalyzed by ACC synthase, and to methyl thio adenosine (MTA). Finally, ACC is converted to ethylene (C_2H_4) via ACC oxidase. We note that MTA is also produced during catabolism of putrescine to SPD and that of SPD to SPM. Original provided by Autar Mattoo.

Reminiscences

Rajni Govindjee (University of Illinois at Urbana-Champaign, Urbana, Illinois, USA; e-mail: rajni_govindjee@yahoo.com)

I am deeply saddened to learn of Ravindar's death; she was a very kind and gentle person. I met her for the first time when I joined B.Sc., in 1951, at the University of Allahabad, as a beginning undergraduate student. One day she invited me to her room (lab; Wahal Hall) and we chatted for a while (see **Fig. S2**). She very graciously allowed me to park my bicycle in her room, not outside in the usual bicycle stand, as she feared that I might encounter harassment from rowdy boys. She helped me enormously in my student life, both in B.Sc. (1951-1953) and in M.Sc. (1953-1955) days. Her guidance and help continued even during the initial stages of my research life, in Shri Ranjan's Lab in the Department of Botany (1955- 1957).

I also have very fond memories of our visits (1970s—1980s) to the home of Ravindar and her husband Brij, in New Haven, Connecticut; this was when she had been working in the

laboratory of the late Arthur (Art) Galston already for several years. They welcomed us (Govindjee and me) and our children (Anita and Sanjay) in their home and were very gracious hosts; we indeed had a very nice visit with them. I had a great desire to meet her again, but, alas, we never made it. I will always cherish her kindness and friendly help in the early days of my student life in the Department of Botany at the University of Allahabad. Ravindar Kaur-Sawhney was a wonderful role model to me; I will miss her.

Fig. S2. A photograph of Wahal Hall where Ravindar Kaur did her research in the Department of Botany at the University of Allahabad. Source: Harbans Kaur Kehri

Manmohan Manohar Laloraya (Devi Ahilya Vishwavidyalaya, Indore; e- mail: mmlaloraya@gmail.com)

Dr. Ravindar Kaur-Sawhney's passing away has been a personal loss to me. Affectionately known to some of us as Minnie, she was a charm to younger research scholars, always willing to help in whatever manner she could do to cheer them up whenever they faced any hurdle in their research work. During the 1950s, she was the first woman research scholar of the Department of Botany at the University of Allahabad. Her thesis advisor was Shri Ranjan, a leading plant physiologist of India. She sat alone in a large Lab named Wahal Hall (see Fig. S2) -- on the back of the large Blackman air commutator, table laid down, with several Pettenkoffer (absorption) tubes for continuous measurement of respiration by plant tissues.

I can never forget Ravindar Kaur's kindness and concern about us when we were appearing in M.Sc. Final Practical Examination during the hot summer days. She organized for us to have fresh orange juice during the examination, which no one could have ever done. After the

examination, when we went to thank her, she just smiled and simply said "*it's so hot and you will get it every day*".

Ravindar Kaur's research work on the "Dormancy of Potato Tubers" required some field experiments; our department had its own agricultural farm in Allahabad. Sometimes, students were taken to the farm to help cut the 'eye' region of a large quantity of potato tubers and the rest was used to prepare cutlets on the experimental farm itself! A sort of picnic was organized and another professor in the department, Dr. S.P. Naithani, would get the tea prepared for all of us; it was a lot of fun and both our teachers Shri Ranjan and S.P. Naithani would join us in all the activities.

In 1958, when Minnie was in New Haven in Art Galston's laboratory at Yale University, I had joined as a Post-Doctoral Fellow at Harvard University to work with Professor Kenneth V. Thimann. Then, we met again. She came to Harvard for a day and discussed lots of things including the idea of her getting married. She said 'Manmohan, I have a conundrum; the person I want to marry is not from my religious community, and, thus, I need to find a way to convince my family in India'. She was a strong person; she went to India, convinced first her brothers, and then the parents. The rest is history. She was happily married to Brij Sawhney in 1962-- a very happy couple, indeed. I am glad I had several occasions to meet her since-- whenever I was invited to give a seminar in the Department of Biology, at Yale, I would visit her and enjoy their hospitality. We all shall miss Minnie; her nobility and love shall always be there to remind us of her kindness.

Sirajul Hasan (Montpellier, France; e-mail: siraj.hasan@aliceadsl.fr)

I am extremely saddened to hear that Dr. Ravindar Kaur-Sawhney has passed away. I have vivid memories, from the 1950s, of receiving kind and generous help from her, while I was a student of M.Sc. in Botany at the University of Allahabad. This was, especially, the case when Prof. Shri Ranjan, the Head of the Department, was away. At that time, Ravindar Kaur was doing her D.Phil. in Plant Physiology, working on the role of plant growth substances (auxins) in potatoes. She had a graceful personality, and a very kind attitude towards all the MSc. students of our group. I still clearly remember her highly friendly attitude towards all the students whenever we discussed anything concerning our subject or even personal problems. From Allahabad, I went to Dacca and then to Montpellier (France), where I worked on a totally different area: microbial control of weeds and other pests of agricultural farms and forests. In spite of this long gap of time, and different areas of our research, I still remember that she was a wonderful mentor. I am very proud of being helped by her, especially when I needed it the most, i.e., when I was a student. May her soul rest in peace!

Raghubir Raj Prasad (Forestry Department of Canada, Victoria, British Columbia, Canada; e-mail: arailprasad@gmail.com)

I am extremely sad to hear that Ravinder Kaur-Sawhney is no more. I met her first during my M.Sc. Ag (Bot) days (1954-1956) in the Department of Botany at the University of Allahabad. She was working, with Shri Ranjan, on the role of Plant Growth Substances (Auxins) on potatoes. I was inspired and enthused by her research and chose to work on the "Role of Auxins in Sugarcanes". She was a very kind and knowledgeable person and helped me even when we would visit the nearby University farm, where both potatoes and sugarcanes were grown; there, we would not only tend to our plants, but would discuss general problems in plant physiology. After attending a symposium, in 1974, on "Dutch Elm Disease" at the University of Maine, I visited Ravindar Kaur at Yale University, when she was working with Arthur (Art) Galston

(coauthor, with James Bonner, of the most popular “Plant Physiology” book of the 1960s). I vividly remember and enjoyed the most wonderful dinner, at their home. We reminisced about the “good old days” and about all those who had left Allahabad and were doing great research in USA or Canada. We all will miss Ravindar Kaur- Sawhney.

Brij Sawhney (Connecticut Experimental Station, New Haven, CT, 06511, USA; e-mail: brijsaw1@gmail.com)

I describe here the peaceful and saintly manner my wife Ravindar passed away—She passed away as peacefully as she had led her life. She and I had led a married life together since 1962. On May 31, 2020, we were getting ready for breakfast when she said, "I am not feeling well, call somebody for help." I called our son, Rajiv, who lives only a 2-3-minute drive from our home (in Tiburon, near San Francisco, CA), and told her so. She said "good." She laid down on the bed and asked me to put my hand on her head, which I did, and she said, "It Feels Good", and then I put my second hand under her head, and she said, "Oh It Feels Good." Immediately after that, she took her last breath and departed from this World, with me holding her head in both my hands. Indeed, Ravindar was a very gentle soul. In a Zoom memorial for her attended by a very large number of relatives and friends, many remarked "She was a most Loving, Polite, Caring, Giving, and Elegant person." We all miss her.

Sushila Narsimhan (Department of East Asian Studies, University of Delhi, Delhi, India; e-mail: sushila@narsimhan.com)

I had met Ravinder only once; I still remember her regal looks and charming smile. When a person is so kind and so good, as Ravinder was, they can never be forgotten; they will always stay in your heart and be a part of your life. Ravinder was one such person. I present here my painting of ‘Apple Blossoms’—a fragrant memory (see **Fig. S3**) -- since, to me (and many others), she was like an apple blossom who spread her rich fragrance all around!

Fig. S3. Photograph of a 2020 painting by Sushila Narsimhan

Sushila Narsimhan describes the painting for Ravindar as:

When a sudden breeze from hills
Blowing through the orchard trees,
Fills the air with a rich fragrance
We know it's springtime.
It's time to enjoy the while Apple Blossoms
Delicately colored with a pinkish tinge,
Dainty pink buds and serrated leaves
Look so attractive -a sheer delight.