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TRIBUTE

Vallabhaneni Sita Rama Das, 1933–2010: teacher and mentor

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Abstract We present here the life and research of V. S. Rama Das, a distinguished Indian botanist who specialized in photosynthesis. He was the first to purify chloroplasts that were free of mitochondrial contamination. He then studied C_4, C_3–C_4 intermediate and CAM pathways, as well as their taxonomic distribution in tropical climates. His most valuable legacy is that he, as a philosopher, inspired and guided many students to pursue their research career in India. Also see Narayana and Pullaiah (Eminent Indian Botanists: Past and present: Biographies and contributions, pp 394–401, 2010) and Raghavendra and Reddy (Curr Sci 101:798–799, 2011) for further information on Rama Das.

Keywords C_4 metabolism · C_3–C_4 intermediate pathway · Taxonomy · Light response · Daniel Arnon · W. O. James

This manuscript was read by two anonymous reviewers, and edited by William Adams III, and Barbara Demmig-Adams before it was accepted for publication. Barbara, who serves on the Editorial Board of *Photosynthesis Research* wrote: "This tribute should serve as an inspiration for young scientists and show them that innovative science tends to be done by well-rounded people, as was the case with V. S. Rama Das."

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Early life and education

Vallabhaneni Sita Rama Das was born on February 5, 1933 in Gudlavalleru, a village in Andhra Pradesh, India. His father (Venkatappayya) and mother (Ratnamma) were from a family of farm owners who took great pride in respecting land resources. We note that in the tradition of this part of India, he grew up with his surname (family name) Vallabhaneni written before his given name Sita Rama Das, but that in his published work Vallabhaneni Sita Rama has always been used as initials, V.S.R., before Das. When we talk about him, we always call him "Rama Das". [See footnote[1] for a similar case for one of us (SVE).]

Rama Das' interest in unraveling mysteries of natural processes led him on a journey, during 1949–1951, to do his B.Sc. at the Hindu College in Machalipatnam, Andhra Pradesh (AP). He received a University medal for standing first among several thousand students. He was soon married, on June 22, 1951, to Ahalya, daughter of Vemuri Venkataratnam, the then President of the rice millers association of AP. He then went to Delhi, obtaining his M.Sc. in Botany from Delhi University in 1953.

Later, Rama Das went to Sweden and worked with the renowned mycologist Elias Melin at the Institute of Physiological Botany, University of Uppsala. Melin and Das (1954) concluded that the growth-promoting root metabolites (known then as the M factor) were not specific to one plant species, but occurred in a great number of unrelated plants. Thereafter, Rama Das became fascinated with the process of photosynthesis.

[1] SVE's surname (family name) Mantha was written first followed by Sailaja in all her publications with Rama Das; now her last name is changed to Elchuri, and her given name (Sailaja) precedes the family name in all her recent publications.

To fulfill his fascination for photosynthesis, Rama Das went to the laboratory of William Owen (W. O.) James at Oxford University, Oxford, UK (Fig. 1), earning a D. Phil. in Botany in 1957. In James' laboratory, he isolated, for the first time, chloroplasts (from broad bean and sugar beet plants) without any mitochondrial contamination (James and Das 1957). Since this isolate did not consume oxygen nor produce Krebs cycle acids, it proved the absence of mitochondria. The first author of the present tribute (Sailaja) remembers that Rama Das considered his days at Oxford to be the most intellectually memorable time of his life. In the tradition of Oxford, he inspired all his students in India by encouraging discussions on various aspects of research. Rama Das had helped other students at Oxford emulate his method of chloroplast isolation, where he had used sucrose density gradient centrifugation (Ellis 2004).

After returning to India, he served for 2 years (1957–1959) as a Lecturer in the Department of Botany, University of Allahabad, Allahabad, Uttar Pradesh, where the co-author of the present tribute (Govindjee) had been a B.Sc. and M.Sc. student (1950–1954), and then a Lecturer (1954–1956). After Allahabad, Rama Das accepted an appointment at Sri Venkateswara (SV) University Tirupati, after which he went to the University of California, Berkeley (1959–1960) to work with Daniel (Dan) I. Arnon. They established culturing conditions for the anoxygenic photosynthetic bacterium *Chromatium* and studied the effect of metabolites on its growth and photosynthetic properties (Arnon et al. 1963). Idupulapati Madhusudana (I. M.) Rao told us that Rama Das considered his interactions with Dan Arnon and Melvin Calvin at the University of California (UC), Berkeley as the best time of his life in the USA; Rao added that Rama Das has indeed inspired students to think originally and to ask penetrating questions. Sailaja, the last doctoral student guided by Rama Das, had the opportunity of working on Photosystem II (PSII) acclimation to limiting light in *Amaranthus hypochondriacus* L; this work was published in a special issue of *Photosynthesis Research*, dedicated to Dan Arnon (Sailaja and Das 1995a). This acclimation involved increases in the amount of light harvesting complex, decreases in the PsbA gene expression and in D1 protein assembly in thylakoid membranes.

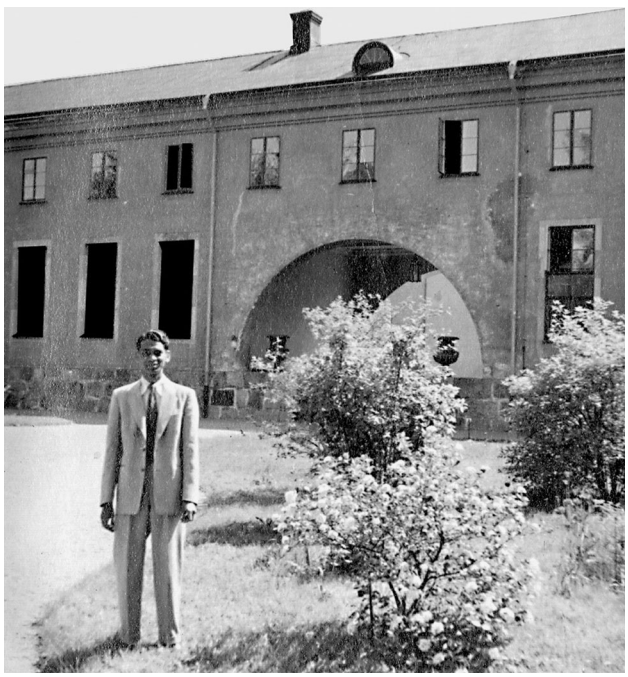

Fig. 1 Rama Das at Oxford University; date unknown; photograph provided by Vallabhaneni Ravi

Research at Sri Venkateswara (SV) University, Tirupati

Rama Das returned to India from UC Berkeley and continued working at the SV University, Tirupati (AP, India) as a Lecturer (1960–1966) and then Reader starting in 1967. During 1967–1969, he worked at the Memorial University, Newfoundland, Canada, as an Associate Professor. He later returned to SV University, where, during 1969–1988, he served first as a Reader, then a Professor of Botany, Head of the Department of Botany, Dean of the School of Biological and Earth Sciences, and finally as a Rector of the University. He was also a Professor at the University of Hyderabad (U of H), Hyderabad, AP, now Telangana, during 1978–1980, and again during 1988–1993. One of Rama Das' major accomplishments was that he established the Center for Photosynthesis Research in India at SV University, Tirupati, and also later at U of H.

Students of Rama Das

He guided many PhD students, and published over 200 research papers. His former students include: Agepati S. Raghavendra and Attipalli Ramachandra Reddy (both at the University of Hyderabad), the late Gedupudi Rajendrudu (SV University, Tirupati), I. M. Rao (International Center for Tropical Agriculture, Cali, Colombia, South America), Rathnam Chaguturu (SRI International, USA), Ramamurty Naidu (Vignan University, Guntur, AP), Veeranjaneyulu Konka (Miami, USA), Prasada Rao Allu (Koneru Lakshmaiah University, & Education Foundation, Guntur, AP), C. V. S. Bhaskar (Venkatagiri Raja's College, Nellore, AP), and Audipudi Amruthavalli (Nagarjuna University, Guntur, AP).

Research contributions of V.S.R. Das

We present below some selected research contributions of Rama Das.

Phenolic acids

Rama Das initially worked on liverworts; Das and Rao (1963) reported the presence of mannuronic acid for the first time in several liverworts including *Riccardia*. He had been a great taxonomist in his early life; he had a keen interest in identifying plants and in also classifying them. Initially, he and his students worked on the determination of phenolic acids in various families. Das et al. (1965) studied phenolic acids in Pedaliaceae, and proposed the separation of *Martynia* from this family, placing it in the Martyniaceae. Further, Das and Rao (1966) proposed placing the genus *Nyctanthus* in Oleaceae, instead of Verbenaceae, after examining its phylogenetic origin and phenolic content.

Stomata

Rama Das was also interested in studying stomatal dynamics; he and his students studied the role of chemical herbicides, plant hormones (abscisic acid and benzyl adenine) as well as the ability of morphactins to regulate stomatal opening (Das and Santakumari 1975; Das et al. 1976a, b). We note that soon thereafter, Das et al. (1977) published a comment on the phenomenon of stomatal movement in the journal *Nature*. In this paper, an involvement of photosynthetic/respiratory electron transport-mediated H^+/OH^- efflux for stomatal opening was elucidated. Further, he and coworkers proposed an active transport of K^+ for guard-cell energy metabolism.

C_4 metabolism

The main thrust of Rama Das' research, however, was on several different C_4 pathways. His group focused on these pathways in several plants, characterizing aromatic grasses, identifying novel C_4-containing families, and plants with unusual C_4 characteristics, as well as localizing C_4 pathway enzymes (Das and Raghavendra 1973, 1976; Rathnam et al. 1976; Raghavendra and Das 1976, 1977a, 1978a; Rajendrudu and Das 1981). Raghavendra and Das (1977b) discovered that the C_4 pathway was developmentally regulated and also showed that it was an energy-intensive process (Raghavendra and Das 1978b). Furthermore, Rama Das' group perfected methods for chloroplast isolation from C_4 plants to understand the division of labor in the C_4 pathway (Rathnam and Das 1975; Raghavendra and Das 1978c, d; Rajendrudu et al. 1979; Rajendrudu and Das 1982).

C_3-C_4 intermediates

Plants with intermediary features between C_3 and C_4 are termed C_3-C_4 plants. Interestingly, although young leaves of *Mollugo nudicaulis* exhibit C_3 metabolism, older leaves have C_4 metabolism (Raghavendra et al. 1978). Rajendrudu et al. (1986) studied C_3–C_4 intermediate pathways in *Alternanthera tenella* and *A. ficoides;* the activities of the key enzymes of C_4 photosynthesis and photorespiration were low in these species. Furthermore, Rajendrudu and Das (1990) reported a C_3-like carbon isotope (^{13}C) discrimination accounting for only the activity of RuBP carboxylase and not **p**hosho-**e**nol-**p**yruvate (PEP) carboxylase in *A. ficoides*. Rajendrudu et al. (1987) showed that many C_4 and C_3–C_4 weeds exhibit high foliar dark respiration rates compared to C_3 plants. These plants are predominantly adapted to the tropics and do poorly under temperate conditions (Das and Rao 1980; Raghavendra and Das 1993).

Crassulacean acid metabolism (CAM) pathway

CAM is an adaptation to conserve water found in many succulent plants. Reddy and Das (1978) classified them into three sub groups: NADP-Malic Enzyme (ME), NAD-ME and PEP-carboxykinase, based on the presence of different decarboxylating enzyme activities. However, Rao et al. (1979) found CAM behavior in non-succulent plants growing in the semi-arid tropical climate of India. Further, they (Santakumari et al. 1979) found similar features in the legume chickpea. Reddy and Das (2000) proposed that such plants in the semi-arid tropics, using CAM-like features, could adapt to their environment, minimizing water loss and maximizing photosynthetic carbon fixation for improved productivity.

Rubber synthesis

Rama Das and his associates elucidated pathways for the synthesis of rubber in Guayule, (*Parthenium argentatum*) under standard conditions (Reddy and Das 1986, 1987; Reddy et al. 1987) and under water stress (Reddy and Das 1988). They demonstrated the utilization of photosynthate for isopentenyl diphosphate (IDP) synthesis, a crucial precursor for rubber biosynthesis in Guayule. Attipalli R. Reddy and Rama Das suggested, for the first time, the possibility of using Guayule as a source of natural rubber in India. However, due to lack of proper Guayule germ plasm, this project could not take off. Reddy told us that establishing the CAM pathway in several higher plants other than the traditional Crassulacean plants for his Ph.D. thesis was a real inspiration from Rama Das who said "*no plant is useless and we have to establish its potential for its adaptive characteristics as a physiologist*". Reddy also recalls certain highly valuable *dictums* from Rama Das during his long association with him: *Every minute is precious in your research career*; *spend at least 12 h per day in the lab to get the best fruits with your work*; *no spoon feeding and be innovative!* Reddy told us that the

Fig. 2 Rama Das with others at Palampur, 1992; photograph provided by Vallabhaneni Ravi

most memorable quote that inspired him a lot was "*As a plant science researcher do not only look at the plant but look into the plant; you have a fascinating machinery*."

Low-light stress in C_4 plants

Rama Das and his coworkers studied the effects of suboptimal light on photosynthesis in C_4 plants. At high light intensity, there was a good correlation between the composition of the reaction center of Photosystem I (PSI), P700, and of cytochrome f, but at low intensities the amount of electron carriers and the reaction centers were found to be independent of each other (V.C.Reddy et al. 1983; Bhaskar and Das 1987). Structural and functional alterations in isolated PSI complex was observed in *Sorghum* (Amruthavalli et al. 1989) under different light intensities; there was an increase in LHCP1 complex to maximize light harvesting capacity of PSI. In *Amaranthus hypondriacus* L., PSI centers decreased in the mesophyll chloroplasts in plants grown at limiting light (200 µmol photons m^{-2} s^{-1}). However, the plants retained their PSI centers intact to operate energy-intensive C_4 pumps in the bundle-sheath chloroplasts. Acclimation to limiting light was achieved by modulating the amount of cytochrome b_6/f complex (Sailaja and Das 1996a). This acclimation process to limiting light was found to be dependent on the C_4 metabolism existing in C_4 plants (Sailaja and Das 1995b, 2000).

Evolution of C_4 plants

During 1991–1992, Rama Das was Director of the Council of Scientific and Industrial Research (CSIR)-Institute of Himalayan Bioresource Technology, Palampur, Himachal Pradesh. Here, he was a great inspiration to his colleagues (see a group photograph in Fig. 2). Das and Vats (1993) documented the presence of numerous C_4 grasses in the Himalayan region and attributed this to the presence of low ambient atmospheric CO_2 concentration in that region. This work provides a clue for the understanding of how low atmospheric CO_2 levels during the Palaeocene and Miocene could have resulted in the evolution of C_4 grasses (Moore 1994).

Solar tracking

Beginning in 1993, Rama Das became a CSIR Emeritus Scientist at U of H. He studied the solar-tracking ability (heliotropism) of leaves in novel, unreported plant families. Sailaja and Das (1996b) proposed that leaf movement helps plants to attain a higher degree of intrinsic PSII photochemical efficiency at midday. Rama Das and his last research associate, Prasad Rao (1995–1998), worked on the mechanism of heliotropism in numerous C_3, C_4 and C_3–C_4 tropical plants. Prasad Rao told us that his beloved teacher Rama Das was his motivation to pursue a research career.

Rama Das finally moved to Nagarjuna University as a Indian National Science Academy honorary scientist and Visiting Professor; there, he taught several students and published a book for their benefit (Das 2004). However, there were issues with the published version. Govindjee (2006) wrote a review of this book. He praised it, but he was very concerned about the errors in the book. He wrote: "Rama Das deserves our appreciation for writing this book for the use of students and researchers alike. However, the lack of appropriate "proof-reading' is a serious concern for the current version. To help him produce a revised version of this book, I enumerate below some of the types of problems that exist in the present version." He provided a long list and added: "When the author and the publisher would produce a version of this book that is free from format concerns, typographical and other errors, only then I would have no hesitation in recommending it to all the libraries and the students around the world". Although Rama Das wanted to bring out a revised version, he, unfortunately, became busy with administrative duties and this did not happen.

Awards

Rama Das received many prestigious awards and honors that include: Outstanding Achievement Award in Biological Sciences (Federation of Indian Chamber of Commerce and Industries, 1978; see his photo with his wife at that time: Fig. 3); J. J. Chinoy Memorial Medal from the Indian Society for Plant Physiology (1979); Birbal Sahni Gold Medal from the Indian Botanical Society (1985); Sir J. C. Bose Award from the University Grants Commission of India (1991); and the Professor S. B Saksena Memorial Award from the Indian National Science Academy (1996). In addition, Rama Das served as President of the Indian Society for Plant Physiology (1973), as Editor-in-chief of the Indian Journal of Plant Physiology during 1977–1978, and as an Executive committee member of the Indian Science Congress, 1983–1984.

The family

Members of Rama Das' family organized his 60th birthday celebration at Vijayawada, AP, on February 5, 1993. In the Indian tradition, the 60th birthday is known as "*Shasthi-purthi*", when friends and family celebrate the couple's wedding again. Figure 4 shows Sailaja, then a graduate student, with Rama Das at that function.

Ahalya, wife of Rama Das, passed away on February 8, 2014. They are survived by their daughter Kausalya and son Vallabhaneni Ravi. Ravi wrote to us: "Writing a few words cannot do justice to all the years of love and strength

Fig. 3 Rama Das and his wife Ahalya, 1978. This photograph was taken when Rama Das received an outstanding achievement award in Biological Sciences from the Federation of Indian Chamber of Commerce and Industries; photograph provided by Vallabhaneni Ravi

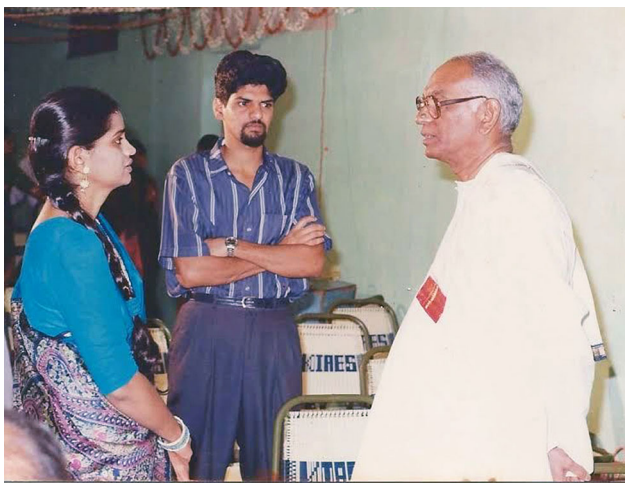

Fig. 4 Rama Das at his 60th Birthday, February 6, 1993, with the author Sailaja Elchuri and her brother Sinivas Peri

that my Dad gave me". V. S. R. Bhupal, grandson of Rama Das, who is soon to become a cardiologist, wrote: When grandpa talked about "recognition by others", he would say, "*Don't bother about the recognition you get, but serve your country before self*".

Last public appearance

Rama Das was felicitated, during March 7–9, 2008, by the Department of Botany of the SV University, Tirupati, for his valuable services to the university; he was affectionately remembered by his students and staff of the SV University (see http://svubotanyhome.blogspot.in/p/phddegrees.html). Rama Das gave the inaugural address at this

Fig. 5 The authors: Govindjee (*left*) and Sailaja V. Elchuri (*right*)

celebration, which was held as an international seminar on Medicinal plants and Herbal products.

We end this Tribute with a picture of the two of us (Fig. 5).

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