

In Memoriam

Tadimeti Raja Rao (1930-2022): A Superb Plant Physiologist and Wonderful Mentor

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We honour here Tadimeti Raja Rao (1930-2022), a wonderful human being – who was a friend to many and a superb plant physiologist of our time. His research began with discoveries in organic acid metabolism in plants, and on the effects of virus infection on nitrogen metabolism. Raja Rao (also spelled as ‘Rajaroo’) followed this research by providing novel and practical information on the effects of several growth regulators (hormones) on the physiology of many plants, particularly sugarcane, guava, Indian gooseberry, and gladiolus, among others. During his later academic life, he gave unique and valuable guidance to many for the improvement of ‘crop production’ which was vital for *plant biotechnology*. We end this tribute to Raja Rao with *Reminiscences* from his family (Sarada, his wife, and Visweswara Rao and Srinivasa Rao, their sons); his friends from Allahabad (Rajni Govindjee and Raj Prasad), and two of the co-authors (Sheo Mohan Prasad and G. S. R. Murti[#]).

[#]Note that G. S. R. stands for ‘Gummadi Sri Ramachandra’, where Gummadi is the family name, and ‘Sri Ramachandra’ is a part of his given name, that goes with ‘Murti’; a caveat to this note is that the another way his name has been written is: ‘Sriram Chandra Murti’.

Keywords: Plant Biotechnology, Shri Ranjan, Guava, Mango, Sugarcane.

PERSONAL AND EARLY ACADEMIC LIFE

Tadimeti Raja Rao was born on July 30, 1930, in Rajahmundry, Andhra Pradesh (AP, India), and passed away on Feb 14, 2022, in Bangalore (now Bengaluru, Karnataka, India). His father was T. Visweswara Rao, and his mother T. Durgavathi. Raja Rao obtained his B.Sc., in 1951, from Andhra University, Visakhapatnam, AP; M.Sc., in 1953 from Birla College, Pilani, Rajaputana University, Rajasthan; and Ph.D. (in Plant Physiology), in 1957 from Allahabad University, Allahabad (now Prayagraj). He leaves behind his dear wife Sarada, and two fine sons Vishy (Visweswara Rao Tadimeti) and Sri (Srinivasa

Rao Tadimeti). Figure 1 shows two portraits of Raja Rao – one from the late 1950s and the other from the early 2000s.

We provide below a glimpse of Raja Rao’s research legacy, followed by a few reminiscences, for the benefit of the future generation of plant physiologists.

RESEARCH, PERSONAL, AND ACADEMIC LIFE

At Allahabad University

During his days as a graduate student in the Department of Botany at Allahabad University, Raja Rao worked on ‘Organic acid metabolism of *Coleus*



Fig. 1: Photographs of T. Raja Rao. Left: At the time of his Ph.D. graduation from the University of Allahabad (1957); Right: At his home in Bengaluru (~2000). Source: Archives of Raja Rao's family.

aromaticus' under the mentorship of a topmost plant physiologist of India, Shri Ranjan (1899-1969; see Laloraya, 1970; cf. (<https://www.life.illinois.edu/govindjee/ranjan.html>), who, himself, was a student of the eminent Frederick Frost Blackman (1866-1947; https://en.wikipedia.org/wiki/Frederick_Blackman). Raja Rao's original organic acid research was presented at conferences (see e.g., Ranjan and Rao, 1958); and recognized by many (see e.g., Sen et al., 1971).

Together with Govindjee and Manmohan (MM) Laloraya, Raja Rao did interesting research on changes in amino acid composition of several virus-infected plants: *Abelmoschus esculentus*; *Acalypha indica*; *Carica papaya*; and *Trichosanthes anguina* (see Govindjee et al., 1956; Laloraya et al., 1955; Laloraya et al., 1956; Raja Rao et al., 1956; for a brief historical account, see Govindjee, 2019). In addition, during his PhD days, Rajarao (1956) described, for the first time, metabolic disorders that a mosaic virus caused on the leaves of an important plant, the castor bean, *Ricinus communis*. Here, he clearly showed that the virus causes large increases in many free amino acids and amides (including glutamic acid, aspartic acid, and asparagine); these observations were important for the future understanding of the overall biochemistry

of virus infection (see Govindjee, 2019, for citation to the 2014 reviews by Fernández-Calvino and Maukand their co-workers).

We note that it was Rajarao who made the key suggestion for a simple but elegant way of measuring many (up to 16) samples, at one time, using circular paper chromatography, as was acknowledged by Ranjan et al., (1955) when they wrote: "We are deeply grateful to Mr. T. Raja Rao for his suggestion of radial cut and to Dr. (Miss) Ravindar Kaur for reading the manuscript" (For a tribute to Ravindar Kaur, see Govindjee et al., 2021). Furthermore, Ranjan and Rao (1955) described this method in the following words: "A circular piece of (27 cm diameter) Whatman No. 1 filter paper was cut out and small circles of radii 4 cm and 3×5 cm were drawn from the centre. 16 points were made on the outer circle at equal distances and 16 small circles with the radii of 5 mm were drawn at those points. From the outer circle (4 cm diameter). 16 radial fins $2 \text{ mm} \times 9.5 \text{ cm}$. were made at equal distances in between the smaller circles (5 mm diameter). These were then clipped off to separate each radial sector, comprising all sixteen sectors. Perforations were also made in between the outer (4 cm diameter) and inner (3.5cm diameter) circles in between the 16 small radial circles."

We remember Raja Rao, particularly, for his time in the Botany Department at Allahabad University as shown below in the photograph with three others

(Govindjee and Laloraya, mentioned above, and Rajni Varma, mentioned below), all in Shri Ranjan's laboratory (see Figure 2).



Fig. 2: A 1956 photograph of T. Raja Rao (extreme left) with Rajni Varma (later Rajni Govindjee), Manmohan Laloraya, and Govindjee discussing their results; a 16-sector filter-paper chromatogram is on the table.

Source: <https://www.life.illinois.edu/govindjee/>

Figure 3 shows a 1956 photograph of a chromatogram dealing with the effects of the *Carica-Curl* virus on the amino acids of papaya leaves. This

was taken from the memorable research of Raja Rao done jointly with others.



Fig. 3: A 1956 chromatogram of standard amino acids and samples extracted from virus-infected and healthy leaves of *Carica papaya* leaves, showing increased amount of free amino acids, especially asparagine, in virus-infected plants (cf. 3rd and 5th sectors with 2nd and 4th sectors from the left).

Source: Laloraya et al., (1956), and personal collection of Rajni Govindjee.

At the Sugarcane Research Institute, and at NBRI, in Lucknow, India

Sugarcane Research. After his Ph.D., Raja Rao worked at the Indian Institute of Sugarcane Research, Lucknow (Uttar Pradesh, UP). Here, two of his research areas were (1) After preventing, by using atmospheric force, loss of moisture from the cut-ends and the internodal surface of the sugarcane “setts”, Raja Rao showed that the sugarcane buds still grew, although slowly, for 2-3 months and produced new leaves (cf. Panje and Raja Rao, 1964)—using the ‘moisture’ in the setts. This simple, but elegant, trick led later to a useful method to transplant sugarcane. This method is being used not only in India but in many countries around the world. (2) After preventing flowering by a defoliation technique (Panje and Raja Rao, 1962), Raja Rao successfully showed that it had a beneficial effect on the yield and the quality of sugarcane juice (Panje et al., 1968).

Research on Many Other Plants. After working on the physiology of sugarcane, Raja Rao moved to the National Botanical Research Institute (NBRI) in Lucknow. Here, he exploited the use of plant growth hormones, which included gibberellins to understand their role in the fruiting of Indian gooseberry (*Embllica officinalis*; also known as *Phyllanthus emblica*) and the common guava (*Psidium guajava*; see Raja Rao and Nagar, 1973a for method, and Raja Rao and Nagar, 1973b, for results). In this research, Raja Rao deciphered the roles of growth hormones in fruit setting and fruit development of guava and gooseberry. For details on endogenous auxins in guava, see Nagar and Raja Rao (1983). Furthermore, Raja Rao focused on the gibberellins—separating them on the columns of silicic acid and celite^{##} (see Ram and Raja Rao, 1978) on the properties of *Gibberella fujikori* in so-called ‘still’ cultures; and, from these cultures, he isolated gibberellic acid in crystalline form. For the current status of this field, see e.g., Cen et al., (2020). However, we note that Raja Rao’s first love with

sugarcane and, thus, sugars, has come to be more important than auxins as far as apical dominance is concerned (see e.g., Mason et al., 2014).

At the Indian Institute of Horticultural Research, Bangalore

After working in U. P. (Uttar Pradesh) for ~30 years, Dr. Raja Rao moved to Bangalore (Karnataka) to work at the Indian Institute of Horticultural Research. At that time, the institute was at a formative stage, with no building and laboratory facilities. He held multiple key responsibilities as the Head of the Division of Plant Physiology, Biochemistry and Microbiology; Processing in-charge of technical work; and Chief of the Plant Hormones Laboratory at the institute. Through his perseverance, he helped setup laboratory facilities of the entire research institute and organized the division, bringing in a new concept of divisional laboratories. For details of his research on the dormancy mechanism in *Gladiolus* corms, and on the role of cytokinins in it, completed at this institute, see the reminiscence by one of the authors (G. S. R. Murti) as well as their published papers (Rajarao et al., 1983; Murti and Raja Rao, 1984).

Visiting Kenya and Guiding Others in Manjari, Maharashtra

In Kenya. Rajarao took a break from doing research in India by going to Kenya—where he was a Research Advisor, dealing with projects in plant physiology and even agronomy, at one of Kenya’s National Sugarcane Research Stations. He provided guidance to their ongoing research on sugarcane growth and yield as affected by transplantation, climatic cycles, and inter row spacings—all highly practical information for the benefit of all countries.

Back in India. After returning from Kenya, Raja Rao served, during 1987-1989, as Emeritus Professor in Plant Physiology at Vasantdada

^{##}Unfortunately, Sant Ram (born 1941), a close collaborator of Raja Rao (see Ram and Raja Rao, 1978), passed away in 2003; his son Vijay Yadav and a faculty member Sudhir Kumar Guru wrote: “We pay tribute to the late Sant Ram; with a PhD, in 1971, in Horticulture, he had served on the faculty at the Govind Ballabh (G.B.) Pant University, from 1964 till 2003, and mentored, with great love, more than 35 graduate students there. He was a leading authority on the horticultural and physiological aspects of many fruit trees (e.g., Litchi, Mango, and Amla), having published many original papers and books.” We all miss him.

Sugarcane Research Institute, in Manjari, Maharashtra. Here, he focused on guiding research on improving productivity of sugarcane by various means – considering different local climate and soil conditions. Then, from 1990-1993, he served as a consultant to Vasantdada Sugar Factory at Sangli, where he continued to give advice on practical aspects of crop production—something he considered important for the growing human population at a time of facing global climate changes. (See the **Appendix** for a partial list of their cognition and the Awards Raja Rao received in his lifetime). We now provide a few selected reminiscences by others.

REMINISCENCES

1. Sarada (Raja Rao's wife) and his sons Visweswara Rao and Srinivasa Rao (e-mail of V. Rao: tadi@hotmail.com)

Dr. T. Raja Rao was a practical, strict yet inspirational and encouraging father, professionally focused, hardworking, and committed to his research work. A gifted counsellor to us and anyone who approached him, a patient empathetic listener, extending his well-honed Scientist's single, focused, analytical, and objective mind, distilling and laying out the pros and cons of any situation, leaving one much more clear-headed about the issue, energized and motivated at the end of the long engaging session.

We also fondly recall him as a family man. We remember some of his favourite things, especially his enduring love for sweet foods any time of the day! We remember his dotting love for his four grandchildren, and a competitive love for *Bridge*, which he played every day without fail with his regular friends at the neighbouring Bridge club. Even in frail health he was mentally active. In his late 80s, he was self-teaching—picking up bridge chat acronyms, and etiquettes online, while playing with people from all over the world; and keeping mentally occupied, solving *Sudoku* puzzles. Even when confined to bed his enduring interests remained a part of his life.

To his large number of friends including neighbours, relatives, and acquaintances, he was a highly personable, social, and engaging person, who had a wide and diverse circle of friends and through

which he inspired and touched many lives. He was everyone's friend regardless of age, relationship, education or social standing; not even the absence of a common lingua franca was a barrier to prevent him from connecting at a human level and communicating with anyone whom he got acquainted with and whose well-being he cared for. We all miss him.

2. Rajni Varma Govindjee (e-mail: rajni_govindjee@yahoo.com)

I knew Raja Rao quite well, during 1955-1957, when we were graduate students in the Department of Botany at Allahabad University, Allahabad (now Prayag)—working in Shri Ranjan's Plant Physiology laboratory. Raja Rao was a wonderful person friendly and sincere—always willing to help others. Regarding his research, he was thorough and hard-working, staying in the lab sometimes all night long. I participated in joint experiments with him, Manmohan Laloraya, and Govindjee, including one experiment on the effect the Carica-curl virus had on the amino acids in papaya leaves. We discovered, among many things, that virus infection caused a large increase in asparagine (see Laloraya et al., 1956; see Fig. 3). I want to share two interesting stories: one has to do with the difference in one's tolerance for 'hot' (spicy) food. Raja Rao once gave us some pickles that had come from his home in Andhra Pradesh. While he enjoyed these in his lunch, the pickles were so hot for me that my mouth was burning, and I had to keep drinking water for a very long time to cool off! The second story has to do with the fact that Raja Rao did not speak Hindi (his mother tongue was Telugu), and he was describing an incident where a cow was eating away his experimental plants, and he wanted the other lab members to help him. So, he excitedly said "A big *safediwala*" (one who is white) is eating all my plants." To describe the "big white animal" he was using both his hands to describe the horns! We found this hilarious; we did not immediately react to the danger of the horns. Instead, we laughed for a while! (The "animal" was a 'stray' big white cow, and a couple of students then went out to "shoo" away the cow—saving some of his experimental plants.) I always had great respect for Raja Rao's ingenuity and integrity in science and in his daily life. Long after

we became residents of the United States, Govindjee and I visited him in Bangalore (Bengaluru) and had the privilege of receiving great hospitality from him and his dear wife Sarada. Our heartfelt condolence to Sarada, their two sons Vishy and Sri and the rest of the family. We miss Raja Rao and his unmatched generosity to others –no matter who they were.

3. Raj (Raghubir) Prasad (e-mail: arailprasad@gmail.com)

I am extremely sad to hear that Dr. T. Raja Rao is no more with us. I express my heartfelt condolence to his wife Sarada and the rest of the family. I remember him as a very kind, gentle and humble person. I overlapped with him, during 1954-1956, in the Department of Botany at the University of Allahabad. I had highly useful discussions with him when I was doing my M.Sc. (Agriculture Botany) research on the 'Role of Auxins in Sugarcane'; both of us were working under the mentorship of Prof. Shri Ranjan. Later, I read Raja Rao's pioneering research on the growth of sugarcane (*Saccharum officinarum* L), while he worked in Lucknow (see Panje and Rao, 1964; Panje et al., 1968); I pay special homage to Raja Rao for this valuable research. We know that sugarcane is a native plant of India, now grown in the tropical and sub-tropical parts of the world. Sugarcane gives us sugar (called 'sharkara' in Sanskrit) that we love so much; sugar (or its products) is/are used widely all over the world. We also know that sugarcane is an efficient photosynthesizer, being a C-4 plant, and sugar from it is widely used all over the world. Raja Rao's early work has had an unsaid but key impact on current sugarcane research. For information on sugarcane, see e.g., Cock (2003); Figueroa-Rodríguez et al., 2019; and for a website on sugarcane breeding institutes in India, see <https://sugarcane.icar.gov.in/index.php/en/front-page>. We all miss our good friend Raja Rao.

4. Sheo Mohan Prasad (e-mail: profsmprasad@gmail.com)

I feel proud that Dr. Tadimeti Raja Rao spent many years in the Department of Botany, University of Allahabad. He, along with Mannohan Manohar Laloraya, Govindjee and Rajni Varma Govindjee,

worked as graduate students of Prof. Shri Ranjan and are credited with the innovative use of the circular paper chromatographic technique which successfully separated large number of amino acids in plant extracts. Dr. Laloraya retired as a professor emeritus, from the Devi Ahilya Vishwavidyalaya in Indore, with his major contributions on the effect of light responses and hormones in plants. Additionally, Dr. Govindjee (one of the authors of this Tribute to Raja Rao) is a pioneer of photosynthesis—still working and studying as he approaches his 90th birthday. I hasten to add that the Ranjan laboratory is still contributing dynamic research related to Photosystem II photochemistry and signalling and oxidative stress regulation in the field of physiology and biochemistry in plants and cyanobacteria under my guidance in the "Ranjan Plant Physiology and Biochemistry Laboratory" named in honour of Prof. Shri Ranjan—the mentor of Raja Rao and the others mentioned above.

All the past and the present members of this laboratory dearly miss Raja Rao.

5. G. S. R. Murti (e-mail: gsr_murti@yahoo.com)

I begin my reminiscence by showing a 2016 photograph of Raja Rao with his wife Sarada, seated with me and my wife Sailarani (see Figure 4).

I recall my association with Dr. Rajarao (Dr. Tadimeti Raja Rao) with a deep sense of pride and sorrow. Our journey started in 1979, when I joined his team of researchers at the Indian Institute of Horticultural Research (IIHR), Bangalore (now Bengaluru), India; he was then the Head of the Division of Plant Physiology, Biochemistry, Microbiology and Processing there. Together, we studied the dormancy mechanism in *Gladiolus* corms and the role of cytokinins in it. We note that *Gladiolus* is propagated through its underground modified shoots, the corms and cormels; further, at high temperatures (e.g., 25°C), the germination of cormels is low. *The dormant cormels contain a high amount of ABA (abscisic acid), but with treatment with BAP (benzyl amino purine), we could break dormancy in the cormels stored at the high temperature.* When others questioned Raja Rao about the need for research on a minor crop like *gladiolus*, he was



Fig. 4: Left to right: T. Sarada (wife of Raja Rao), T. Raja Rao, G. S. R. Murti (one of the authors) and his wife Sailarani. *Source:* Archives of Murti's family.

steadfast in his conviction that the physiological problem was of greater importance than the precise plant that was being used. Our findings were subsequently published in the 'Annals of Botany' (Raja Rao et al., 1983). Thus, a role for endogenous ABA and cytokinins in dormancy regulation was postulated. Then, Raja Rao and his group tentatively identified zeatin, and a few other components in corms, that were higher in non-dormant corms; these compounds behaved as cytokinin glucosides; further, these nucleotides were higher in dormant corms. [Interested readers are welcome to write to me for details.]

Together with Raja Rao, I investigated the important role of xylem sap in the development of crop plants (see Murti and Raja Rao, 1984). Since root tips are important sources of cytokinins, the naturally occurring cytokinins in the xylem sap of brinjal (eggplant) were studied. Here, we identified, using sephadex column chromatography and high-performance liquid chromatography (HPLC), ribosyl zeatin (ZR) and zeatin (Z) as the principal forms of cytokinins in the xylem sap of the eggplant at the flowering stage. Further investigations were also carried out on cytokinins in *Dioscorea floribunda* (see Leela and Raja Rao, 1986). In addition, during his stay in Bangalore, Raja Rao's love for mango and its physiology again surfaced in his efforts on the physiology of

flowering of this plant; he spent much time in understanding the biennial fruit-bearing habit in certain prominent mango varieties—much of this was to satisfy his curiosity of Nature; he was indeed a visionary!

Tadimeti Raja Rao was a man with an unwavering dedication to plant physiology and an authority on methodology for plant hormones in India; he built a world-class plant hormones laboratory, while serving as the head of the above-mentioned division. To further research (in India in the 1980's), he equipped the lab with state-of-the-art equipment such as High-Performance Liquid Chromatography (HPLC), Gas Liquid Chromatography (GLC), Freeze dryer, Fraction collector, N₂ evaporator, Set up for bioassay facilities, and Sterile inoculation (for hormonal estimation). Dr. T. Raja Rao was instrumental in establishing the infrastructure for IIHR, which is today a leading horticultural research organization in the Indian sub-continent (www.iihr.res.in).

Somewhere between the shared lunches, the late-night conversations at our homes, the regular debates on science and listening to his life's lessons as unforgettable quotes, he became a member of our family and we of his. We continued to stay in touch after his departure from IIHR, through his engagements in Kenya and Maharashtra (India) and eventually through his and my retirement.

CONCLUDING REMARKS

All the authors end this “*In Memoriam*” with a heavy heart for this wonderful friend of all of us and the entire plant physiology and horticulture community of the Indian subcontinent. Included is a recent photograph of his with one of us (GSRM). In his passing, we have lost not only a learned scientist and

an institution builder, but a kind teacher. He was indeed someone we could look up to get advice and to overcome our own frailty (see Figure 5).

Lastly, we end our Tribute by citing what Bhaskara and Usha Yelamanchili, Champaign-Urbana friends of Govindjee, gave him, after learning about



Fig. 5: Left to right: G. S. R. Murti, Sailarani (wife of Murti), Sarada (wife of Raja Rao), and Tadimeti Raja Rao at Raja Rao’s residence, ~ 2021.

Source: Archives of Raja Rao’s family

the life of Raja Rao.

“This is a dedication to a sweet person with tears

With dedication he worshipped his passion

Gave immense value to friendship

*Shared and treated family with immense love and
left this place.*

Final goodbyes to a dear friend, our Raja Rao.”

Appendix

Service and recognition of T. Raja Rao: A partial list

1977 (Dec 17-22): Convener of the session on growth regulators in citrus product at international symposium on citriculture by the Horticultural society of India in Bangalore; **1979** (March 5-9): Chairman: of session on Plant Physiology at the All India coordinated vegetable improvement workshop, Tamil Nadu Agricultural University Coimbatore; **1980** (Dec. 14-18): Chairman of a session at the symposium

on “Photosynthesis and Plant Productivity” Indian Institute of Science, Society of Biological Chemists, second FAOB Congress and Golden Jubilee meeting of the society.

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USDA) for reading and making suggestions for improvement, Sanjay Govindjee for his help in translating Rajarao (1956) from German into English, and Bhaskara and Usha Yelamanchilli for the ending quote.

Contributions of the authors

All the authors had equal contributions except that G. S. R. Murti provided a detailed description of his research with Raja Rao, and the manuscript was drafted and finalized by the first author (G. G.).

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