

H. Y. Mohan Ram (1930–2018)

India lost one of its most distinguished botanists, Professor Holenarasipur Yoganarasimham Mohan Ram, on 18 June 2018. He was born on 24 September 1930 to illustrious parents at Mysore, Karnataka. His father was a great Sanskrit scholar and distinguished musician. Mohan Ram's elder brother, H. Y. Sharada Prasad was an eminent journalist and Press Advisor to four Prime Ministers of the country.

Professor Mohan Ram, fondly referred to as HYM by his peers and students, obtained B Sc degree from the University of Mysore and M Sc from Agra University. While working as a Lecturer in the Department of Botany, University of Delhi, he did Ph D under the supervision of the world renowned embryologist, P. Maheshwari, FRS, and continued his long career in the same Department as Lecturer (1953), Reader (1961), Professor (1968–1995), and Head of the Department and Director, Centre of Advanced Studies in Botany (1973–1976). He continued his academic activities as INSA Senior Scientist (1996–2001), INSA Honorary Scientist (2006–2010), INSA Jawaharlal Nehru Birth Centenary Visiting Fellow (1997) and Srinivasa Ramanujam Professor (2011–2016). He remained academically active until a few weeks before his demise. In these days of specialization in every discipline of science, HYM was one of the critically endangered true botanists with vast knowledge in all areas of botany. Although he used to mention his specialization as plant growth and development, it included practically all aspects of structural and functional botany.

HYM worked at Cornell University, Ithaca, NY, as a Fullbright and Smith-Mundt Fellow (1958–1960) with F. C. Steward, internationally famous for demonstrating the totipotency of plant cells (each cell has the potential to develop into a complete plant under suitable conditions) for the first time, which revolutionized plant tissue culture studies. He was introduced to the technique of plant tissue culture at Cornell University where he worked on banana tissue culture, for the first time, besides writing a critical review with Steward on 'Determining factors in cell growth'. Subsequently one of HYM's students, R. Dore Swamy, who worked at the Indian Insti-

tute of Horticultural Research, Bengaluru, standardized the technique for commercial propagation of banana plants through tissue culture technique; nowadays banana plantlets produced through micropropagation are routinely used in our country to raise banana plantations. He later worked in the laboratory of J. P. Nitsch CNRS (1970–71) at Gif-sur-Yvette, France, as UNESCO Senior Fellow on developmental biology and flowering in *Utricularia*.



Mohan Ram's research contributions are so massive and cover such a wide area of plant growth and development, it is difficult to do justice here. Several areas of investigations were initiated for the first time in the country. I shall try to highlight some of his major contributions with particular emphasis on recent researches. His own work during his Ph D programme was on seed development in Acanthaceae. Initial studies of his group include effects of plant growth regulators on vegetative and reproductive growth of *Kalanchoe*, wheat and linseed, development of true seeds in potato, induction of pollen sterility by application of growth regulators, role of sucrose and gibberellic acid on flower development and prolongation of vase-life of flowers of *Gladiolus*, effects of a number of chemicals such as cobalt chloride, silver nitrate and malic hydrazide in extending the shelf-life of flowers of several ornamental species, and floral and pollen biology of *Cassia fistula*.

Endosperm is a unique tissue in flowering plants. Although it is a product of double fertilization, it lacks the capacity

to differentiate organs but accumulates reserve material to nurse the embryo. It has been a challenge to culture and induce organogenesis in cultured endosperm. A casual observation by one of HYM's students on proliferation of the endosperm when de-coated castor seeds (*Ricinus communis*) soaked in 2,4-D, were allowed to germinate, led to *in vitro* culture of castor endosperm in his laboratory. Although continuously growing callus cultures were realized, the callus failed to differentiate organs. Subsequently Johri's students continued the work on endosperm culture of several other species and were able to induce organogenesis from endosperm cultures.

Potato is traditionally propagated vegetatively by seed tubers. Because of the transmission of viral diseases, and the problems of storage and transportation associated with tuber propagation of potato, propagation by true seeds is a desirable alternative. However, true seed production in potato has many practical problems. One of HYM's students carried out detailed studies on reproductive biology of potato and standardized the methodology to obtain true seeds.

Induction of male sterility through gametocides was attracting considerable attention around the world since 1960s because of their potential in the production of hybrid seeds. HYM's group was the first in our country to initiate studies on these lines and carry out extensive studies on wheat and linseed (*Linum usitatissimum*). Their intensive studies on the effects of three of the gametocides, Mendok, Dalapon and Morphactin, indicated that although these gametocides may induce pollen sterility to a limited period, none of them was effective as a commercial gametocide to induce male sterility for hybrid seed production. Even with the enormous amount of subsequent work around the world on induction of male sterility, the situation has remained the same; no chemical agent has been found as yet that is effective for commercial application.

Another important study initiated in HYM's laboratory has been on *in vitro* culture of insectivorous plants. Insectivorous plants generally grow in nitrogen-deficient habitats and have evolved various adaptations to catch insects and digest them. It was believed that

insectivorous plants are dependent on insects as the source of organic nitrogen. *In vitro* studies in his laboratory showed that one of the aquatic insectivorous species, *Utricularia inflexa*, can grow and also flower on a medium containing inorganic nitrogen. Subsequently studies were carried out on pollination biology of the species both *in vivo* and *in vitro* cultures. Pollen grains germinate *in situ* inside the anthers; following anther dehiscence, pollen grains are deposited *en masse* on the stigma because of the close positioning of stigma with anthers. Thus the species exhibits autogamous pollination. As there was no pollination limitation, fruit set both *in vivo* and *in vitro* was almost 100%. These studies showed that *U. inflexa* can complete its life cycle *in vitro* without the source of organic nitrogen in the medium. This work received a special mention by P. R. White, considered the father of plant tissue culture, when the paper was presented in a symposium. On the basis of the studies by HYM's group it appears that the requirement of organic nitrogen from insects may not be obligatory for the insectivorous plants when their habitat contains adequate inorganic nitrogen source.

Cannabis sativa (hemp or marijuana) is a dioecious species with separate male and female plants. One of HYM's students studied the role of different growth substances on the sexuality of hemp flowers. Treatment of plants with ethephon (2-chloroethyl phosphonic acid), an ethylene-releasing compound, induced female flowers in genetically male plants and a treatment of genetically female plants with gibberellic acid induced male flowers. Further studies showed that treatment with ethylene antagonists such as silver nitrate and cobalt chloride induced male flowers not only in female plants of *Cannabis* but also in female line of *Ricinus communis*. These studies indicated that the sex expression in flowers is regulated by a balance of endogenous hormones.

When HYM's group initiated work on tissue culture of legumes, they were considered to be refractory and not readily amenable for regeneration from the callus. His students were able to induce regeneration of plantlets in cultures of a number of legumes such as red gram and winged bean paving the way for using the technique of plant tissue culture for economic benefit in these important crop species.

The contributions of HYM's group in advancing the biology of aquatic angiosperms are outstanding. Apart from *Utricularia*, other aquatic species studied include *Ceratophyllum*, *Limnophila*, *Trapa* and several members of Podostemaceae. *Ceratophyllum* is monoecious and the plants bear both male and female flowers. Interesting studies were made on the pollination biology of two species of *Ceratophyllum* under *in vitro* conditions. Mature stamens abscise from the male flowers and rise to the surface of the liquid medium *in vitro*. Pollen grains germinate inside the anthers; following anther dehiscence the germinated pollen grains are released on to the surface of the liquid culture medium and gradually sink through the medium and come in contact with the stigma of submerged female flowers, thus bringing about pollination.

Podostemaceae is the largest fresh water aquatic family with 48 genera and about 270 species. It is one of the most interesting families in morphology, ecology and embryology. The plants are thalloid without differentiation into roots and shoots and grow submerged in fast flowing rivers attached to the rocks through holdfasts and adhesive hairs. The plants emerge partially during the reproductive phase when the water level recedes, thus exposing the flowers. Most of the Indian species are narrow endemics (18/20) and several of them are endangered. The members lack many embryological features such as antipodal cells, double fertilization and endosperm. HYM's group was able to germinate the seeds of seven members of Podostemaceae using ingenious methods and studied a number of developmental features of the embryo for the first time and interpreted the plant body as dorsiventrally flattened stem that arises endogenously as a lateral primordium with stem-like apex and internal structure. Embryological studies revealed that mature female gametophyte lacks the central cell; out of the two male gametes released in the embryo sac, one fuses with the egg cell resulting in syngamy whereas the other male gamete degenerates, confirming the occurrence of single fertilization. Their studies on pollination biology showed that both autogamy and xenogamy are prevalent. In *Griffithella hookeriana*, the pollination is cleistogamous (occurs in bud stage). Fruit development is rapid and is completed within 4–5 days.

Another notable contribution from HYM's group has been on the biology of bamboos and their mass multiplication through tissue culture technology. Most of the bamboos flower gregariously once in their life time producing enormous amount of seeds and die. Bamboo flowering is generally associated with huge increase in rat population due to unlimited availability of food in the form of bamboo seeds. His group studied reproductive biology of some Indian bamboos in Mizoram to understand the relationship between bamboo flowering and rodent population. They showed that flowering of *Bambusa tulda* is accompanied by a staggering enhancement in the population of the rodent, *Rattus rattus brunneusculus*. They studied the biology of the seeds of some bamboos for the first time and incorporated these characters to describe the species, which was earlier based only on vegetative features. They also standardized the technology for mass scale production of bamboo plantlets through tissue culture and were able to successfully transfer a large number of *in vitro* raised plants to the forests. This technology has been transferred to The Energy and Resources Institute (TERI), Gurgaon.

Although India is one of the megadiversity countries with varied habitats with a large number of endemic species, our knowledge on the details of their reproductive biology, particularly pollination biology and breeding system, are very limited. Such information is very important for effective management of our biodiversity, particularly the endemic and endangered species and sustainable exploitation of economically important species. Realizing the importance of such studies, Mohan Ram initiated studies on these lines and a number of his students carried out detailed studies on the reproductive biology of many species. These include *Dalbergia sissoo* and several gum- and gum-resin yielding species – *Butea monosperma*, *Acacia senegal* (the source of gum arabic), *Commiphora wightii* (the source of guggul), *Sterculia urens* (the source of gum karaya) and *Boswellia serrata* (the source of salai guggul) – on which no information was available. I have been fortunate to have had collaboration with HYM on some of these studies. One of the major limitations of earlier studies on pollination biology has been that most of the papers did not distinguish pollinators from floral

visitors. All floral visitors may not be pollinators; some of them may be the predators on other floral visitors and some may rob the pollen and/or nectar without effecting pollination. Confirmation of a floral visitor as pollinator has to be on the basis of pollen transfer to the stigma following the visit of the visitor to virgin flowers. But this takes a lot of time and efforts with the result that very few investigators carry out such detailed studies, and consider all the floral visitors as pollinators. All the papers of HYM's group on pollination biology are unique in that the pollinators have been confirmed on the basis of pollen transfer.

D. sissoo is the source of an important timber; detailed studies on its reproductive biology showed that *Apis dorsata* is the main pollinator. Unlike earlier reports that *D. sissoo* is an inbreeder, studies of HYM's group showed that the species is self-incompatible and predominantly an outbreeder. Most of the gum- and gum-resin yielding species are overexploited and there is a need to conserve their germplasm. *Acacia*, *Butea* and *Boswellia* bear bisexual flowers. *Sterculia* produces male and apparently bisexual flowers; however, the bisexual flowers are functionally female as their stamens are sterile. However, the brightly coloured sterile stamens serve as attractants for floral visitors; emasculated flowers do not attract any floral visitors. Flowers of *Acacia*, *Sterculia* and *Boswellia* are of generalized type and are pollinated by several species of which honey bees, particularly *Apis dorsata* and *A. cerana indica* are the dominant pollinators. Flowers of *Butea* show typical bird pollination syndrome and are visited by a number of bird species and also by three-striped squirrel. Out of seven species of birds that visit *Butea* flowers, only the purple sunbird (*Nectarinia asiatica*) is the effective pollinator; other bird visitors rob the nectar without effecting pollination. For the first time, the squirrel has been shown to be an effective pollinator. Flowers of *Acacia* also attract a wide variety of insects but the honey bee, *Apis dorsata*, is the most effective pollinator. Under natural conditions, fruit set is very low (<1%), manual pollination improves the fruit set to 30%. Thus, pollination limitation is one of the main reasons for low fruit set recorded in *Acacia* under natural conditions. *Boswellia* and *Butea* show typical self-incompatibility with inhibition of pollen

tubes in the stigma/style. *Acacia* and *Sterculia* exhibit late-acting self-incompatibility; although the pollen tubes reach the embryo sacs following self-pollination, no seeds develop. Late-acting self-incompatibility is rather a rare phenomenon in flowering plants. Pollination by a snail is another first record from HYM's group in *Volvulopsis nummularia* (Convolvulaceae), a prostrate herb that occurs in Delhi area during the rainy season.

One of the interesting studies on pollination biology from HYM's laboratory has been on *Lantana camara*. The freshly opened flowers are yellow; as the flowers age, their colour changes to orange, scarlet and magenta. Fresh yellow flowers offer pollen and nectar as rewards to pollinators, but the older flowers, although retain on the plant for many days, do not offer rewards. Thrips are the major pollinators and detailed observations showed that pollinators visit only the fresh yellow flowers but not the older flowers. The colour change is triggered by pollination; even pollen extracts are effective in changing floral colour; the change is so sensitive that the presence of merely one pollen on the stigma is sufficient to trigger the change. Retention of non-rewarding flowers on the plant is an effective adaptation to increase the plant's attraction to pollinators from a distance, but when they come nearer the flowers, pollinators can discriminate the rewarding and the rewardless flowers and visit only the rewarding fresh flowers.

In *Commiphora wightii*, natural populations comprise exclusively or largely of female individuals, but they set fruits and seeds normally irrespective of the absence or presence of male plants. No floral visitors were observed in any of the populations and thus no pollination occurred under field conditions. Manual pollinations resulted in germination of some pollen grains on the stigma, but none of the pollen tubes reached the ovary. Intensive studies on the reproductive biology on *C. wightii* demonstrated, for the first time, that the species is an obligate apomict; apomicts are plant species in which seed development occurs without fertilization. Unlike many other apomictic species which require pollination, in *Commiphora* apomictic seed development is independent of pollination. The egg degenerates and multiple embryos develop from the surrounding

nucellar tissue. Endosperm, in most of the other apomictic species, develops as a result of semigamy (one of the two sperms delivered by the pollen tube fuses with the polar nuclei resulting in endosperm development and the other sperm degenerates); but in this species endosperm develops autonomously and nurtures the embryos. As this species is obligately apomictic, clones can be raised from elite plants from the seeds. Protocol for achieving optimal seed germination was also standardized.

Commercial tapping of gum and gum-resins from the trees of natural populations is done generally by making deep cuts in the stem. This crude and injurious and unscientific method of tapping results in the death of trees after some years of tapping. Because of the use of crude methods for tapping and overexploitation to satisfy the increasing demands, the populations of gum- and gum-resin yielding species have declined and there is hardly any regeneration of new adults. HYM's group has carried out intensive experimental studies to devise refined techniques of tapping in a few of these species particularly on guggul and gum karaya trees. They showed that making small holes of a few mm in the stem and loading the holes with ethephon (2-chloroethyl phosphonic acid) not only increased the yield about 20 times over the control but also healed the wounds early. These studies showed the potential of ethephon, a non-toxic, environment-friendly, inexpensive plant growth substance, in obtaining sustainable yield of gum and gum-resin without causing too much of injury to the plant.

HYM mentored 32 research scholars, and published nearly 250 research and review papers, and edited four books. He always had close association with his students. He considered all the students of the Botany Department, Delhi University, as his own students; he was available to them all the time, and they could always rely on him and his wife, Mrs Manasi Ram for advice and help whenever needed. When hostellers fell sick, his house used to be a temporary nursing home. There are innumerable instances of his extraordinary and unique help rendered to his students and colleagues. Although he had a large number of students who got M Phil and/or Ph D under his supervision, he kept in touch with all his students and colleagues. He made it a point to attend their marriages and other

important functions in their families. Whenever his students and colleagues discussed their work with him, he listened to them with lot of patience and invariably gave them encouragement and inspiration. Manasi Ram ably supported him in all his academic and other pursuits. He is survived by his son Rahul Ram, daughter Sushmita, and two grandchildren.

HYM made profound contributions to the promotion of teaching and research in India. His efforts to popularize science among young students are well known. He had a knack of communicating science to school children. Whenever he got an opportunity to address youngsters, he accepted them with full of enthusiasm and impressed them enormously with his speeches. He taught physiology and economic botany to the undergraduate and post-graduate students of botany. He was one of the most popular teachers and made the subjects most interesting for students. His lectures, both popular and technical, in the meetings of Science Academies and Conferences used to attract a large number of participants. Anyone who met him and spent some time with him, or attended any of his lectures would be overwhelmed by his depth of knowledge, ability to communicate, simplicity and humility, they would remember him for ever.

HYM played a significant role in establishing the Department of Genetics and Department of Environmental Studies, both in Delhi University, CSIR-Institute of Himalayan Bioresource Technology at Palampur, and the National Science Centre at New Delhi. Presently, they are amongst the foremost University Departments and Institutions in the country. He served as the Chairman of the Governing Body, Birbal Sahni Institute of Palaeobotany, Lucknow (1987–1993); Member SERC and Programme Advisory Committee on Plant Sciences of DST (1988–1990, 1995–1998); MAB Committee of the Ministry of Environment and Forests (1990–1996); Member Advisory Council, Centre for Ecological Sciences, IISc, Bangalore (1985–2006); Member, BRPC of the Department of Biotechnology (1988–2006); and several

others. He was the Chairman of the Biology Text Book Development Committee for Higher Secondary Schools of the National Council of Education, Research and Training. Four volumes of Biology text books for XI and XII standard were produced under his Chairmanship. They turned out to be very popular and authentic books giving integrated account of modern biology and served for a number of years not only for schools but also for graduate students. He was a Trustee of Children's Book Trust (since 1980). He used to be a Member of Selection Committees of a number of educational and research institutions and strived to recruit competent people for both teaching and research positions. He always looked for merit. He used to identify outstanding teachers and researchers wherever he went and nominate/recommend them for suitable Awards, Fellowships and Honours. He was closely associated with Phytomorphology, an international journal started in the Department of Botany, Delhi University, by his Guru, the late P. Maheshwari, and served as the Secretary-Treasurer (1964–1988) and President (1988–1992) of the International Society of Plant Morphologists, which publishes the journal.

HYM participated in a number of international conferences; to mention a few: IX International Congress held at Montreal (1969) and XI International Congress held at Leningrad (1975), VIII International Congress on Plant Growth Substances held at Tokyo (1973), Indo-Soviet Symposium held at Leningrad (1977) and First International Symposium on Reproduction in Flowering Plants held at Christchurch, New Zealand (1979). He chaired several technical sessions in these meetings.

Mohan Ram was the recipient of a number of awards and honours. Some of the noteworthy ones are: J.C. Bose Award of UGC (1979), P. Maheshwari Medal of the Indian Botanical Society (1980), President, Botany Section of Indian Science Congress Association (1980), UGC National Lecturer (1980), Om Prakash Bhasin Award (1986), Sergei G. Navashin Medal, USSR (1990), Saxena Memorial Award of INSA

(1990), Birbal Sahni Birth Centenary Medal, ISCA (2001), Gregor Johannes Bruhl Medal, Asiatic Society (2002), Jawaharlal Nehru Birth Centenary Award, ISCA (2004), VASWIK Award (2008), Aryabhata Medal (2009), Lifetime Achievement Award, Indian Botanical Society (2012). Besides, HYM delivered a number of Award/Memorial lectures. He was on the Editorial Boards of a number of journals.

HYM was elected Fellow of Indian Academy of Sciences (1974), Indian National Science Academy (1978), National Academy of Sciences, India (1977) and National Academy of Agricultural Sciences (1991). Also he served as Editor of Publications (1979–82), Secretary (1985–88) of INSA and co-edited several INSA publications: *Science in India, 50 years of Indian National Science Academy, Profiles of Scientific Research: Contributions of Fellows of INSA*, and *Pursuit and Promotion of Science: An Indian Experience*. He also served as the Vice-President of the Indian Academy of Sciences (1988–1990).

HYM's main hobbies were photography, Indian classical music and cricket. He was a passionate photographer. He has left thousands of transparencies and digital photographs in his collections mostly on nature and interesting plants, animals and people. I hope that some organization would be able to maintain them in good condition, and allow their use freely for educational and research purposes. HYM had in depth knowledge on Indian classical music. He used to remember most of the names of Indian and international cricketers and their contributions.

With Mohan Ram's passing away, the community of botanists will miss an extraordinary and exemplary family member but his contributions and legacy will live forever.

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