A passion for plant life

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1. Introduction

I find it amusing when fellow scientists try to label me. An unsparing critic of mine, who is no longer alive, introduced me at a botanical meeting as a specialist in general botany. Being deeply interested in plant form and function, I am happy as I am: teacher and researcher, naturalist, author, editor, reviewer, adviser, promoter and popularizer of science, traveller, photographer, lover of music and cricket and a tolerably good cook. I would not have exchanged my job as a university professor with any other, either for prestige or money. My most precious experience has been interacting with students in the field and lab. I am least concerned about not being a narrow specialist; there is not much time left to become one even if I want to. S Mushtaq Ali, the unorthodox and dashing opening batsman who represented India in cricket from 1934 to 1949, was known to play any shot at any time. Pleasant and always smiling, with a red handkerchief tucked in his white trousers, he was hugely popular. When approached to give advice to youngsters, he is supposed to have said "Don't follow me". That sums up my opinion as well.

2. Roots and growing up

I was one of eight children born in a middle class family in Mysore. Having served as inspector of schools and Principal of Sanskrit colleges in Mysore and Bangalore, my father H Yoganarasimham retired as District Educational Officer. He was a scholar and self-trained musician of exceptional talent but chose not to become a performing artist; he took to serious composing after retirement. Gita Kusumanjali, a book of his compositions was published posthumously. What I cherished most as a child was singing sessions by my father on Saturday evenings attended by music lovers. B R Seshachar, our neighbour in Visweswarapuram (Bangalore) and later a well-known zoologist, was a regular attendee. My mother Saraswathy had studied only up to the fifth class in school but was a forceful writer in Kannada. She translated the autobiography of Parvati Bai Athawale and Bapi Needu's pictorial Telugu book on the Mahabharata for children into Kannada. She made no concessions to sons over daughters and expected us to sweep, mop, wash, iron and cook. She never depended on men to replace bulbs or fuses. We imbibed our love of plants from her.

I passed the Secondary School Leaving Certificate examination in 1946, missing a first class by 6 marks. After Intermediate College, disappointment awaited me as I could not make it to the Medical College. My early interest in botany was kindled by two great teachers, M A Rau and B N N Rao. I stood first among the successful candidates in B.Sc. and was appointed Demonstrator in Botany from 1950 to 1951 in my college, St. Philomena's. My teacher Varghese Chandy generously allowed me to lecture to the B.Sc. students. This experience not only gave me a good grounding in botany but also introduced me to the joy of teaching. My father told me that he could not support me further and I should find my own sources. When I broached the subject of pursuing my Master's with N K Anant Rao, a family friend who was teaching agronomy at B R College in Agra, he offered to speak to R K Singh, the Principal of the college. Singh, who had studied education under John Dewey at Harvard, was generous and offered me a part-time assistant lectureship in the college at 50 rupees a month for one year. My eldest brother supported me financially till I completed my M.Sc. R S Badami, a close friend and I went to Agra and joined the College (now renamed RBS College) in 1951. Later Badami went to the Rothamsted Agricultural Station in England and obtained a Ph.D. in Virology. He had a congenital heart problem and died in his 30s in Madras. I am yet to come across a noble person like him.

The change from life in a green and clean city to a semi-arid, dry city with dust storms and intense heat was drastic. I often wondered why the Taj Mahal could not have been built in Mysore. The college did not have the necessary infrastructure; our laboratory had a roof made of galvanized iron sheets. But the teachers were excellent, kind and devoted. I received my first introduction to research on the embryology of the blood flower *Asclepias curassavica* under the guidance of Professor Bahadur Singh, who taught me the value of academic rigour. Plants such as *Salvadora*, *Tamarix*, *Suaeda*, *Salsola* and *Capparis* were typical of the Agra region and tolerant not only to drought but also to high salinity. As students we made several field trips to wetlands and large water bodies at Bharatpur, Parkham and Keetham where many unknown aquatic plants came to my attention. S N Chaturvedi, my teacher who rose to the position of Professor and Head of the Department, continues to knit past students together. Standing first at the M.Sc. examination of the Agra University boosted my morale and charged me with fresh enthusiasm.

When I was a student at Agra, I was told that all the *Cycas revoluta* plants in the garden of the Taj Mahal were female and had not set seed due to the absence of male plants. These plants belong to a group of gymnosperms which formed the dominant vegetation in the Triassic period of the Mesozoic Era, about 190 million years ago and saw both the appearance of the dinosaurs and their extinction. Asked to bring a male cone from Mysore to effect pollination, I managed to steal one from the Palace Garden and covered it with several layers of sack cloth. While on the train to Agra with the parcel, my fellow-passengers, who could not stand its offensive stench, hurled it out of the window when I was fast asleep at night. The Taj cycads are quite old now but are still virgins.

3. Early years in the University of Delhi

To be selected as a Lecturer in Botany at the University of Delhi in October 1953, just a few months after receiving the M.Sc. degree, was a windfall. I came under the influence of Professor Panchanan Maheshwari, the internationally recognized plant embryologist, and accepted him as my Guru. He was a highly organized, assiduous and energetic scientist. After doing original work and reviewing world literature, he wrote the classical book "*Introduction to the Embryology of Angiosperms*", which is still studied by students and researchers all over the world. Maheshwari realized quite early the need for elevating the standard of general botany in India. He therefore read, supported and taught, and even guided, research in themes outside his specialization.

The Department of Botany was small but well integrated. The Professor selected teachers and scholars from various parts of the country after verifying their credentials. We had famous scientists visiting us from all parts of India and abroad. He organized national and international conferences and summer schools (figure 1). Maheshwari ran his Department like a regiment. His complete involvement in the subject and insistence on regularity and cleanliness are qualities rarely noticed among present day teachers. Quite a few found his demands formidable. He set a high priority on the training of research students. From his frequent overseas visits and through close contacts with world scientists, he was able to focus the direction in which educational progress should be attempted. While he encouraged original work, he stressed the importance of application, methodology, punctuality, neatness and accuracy. Himself a voracious reader, he kindled in all of us the value of learning and the need to acquire a broad-based knowledge to sustain high specialization. Finding that most research scholars were poor in general knowledge, he introduced a weekly seminar in which only non-botanical topics were presented. We thoroughly enjoyed the lively discussions which were like spices added to a dull life of sectioning, staining and drawing. His insistence that talks should be rehearsed before presenting them at important meetings set a high standard of scientific communication. Most useful were the classes he initiated in scientific writing. Two contributions of P Maheshwari which have had lasting impact were the forming of the International Society of Plant Morphologists and its journal *Phytomorphology* and the starting of Plant Tissue Culture Laboratory for the first time in India at Delhi for carrying out experimental embryology.

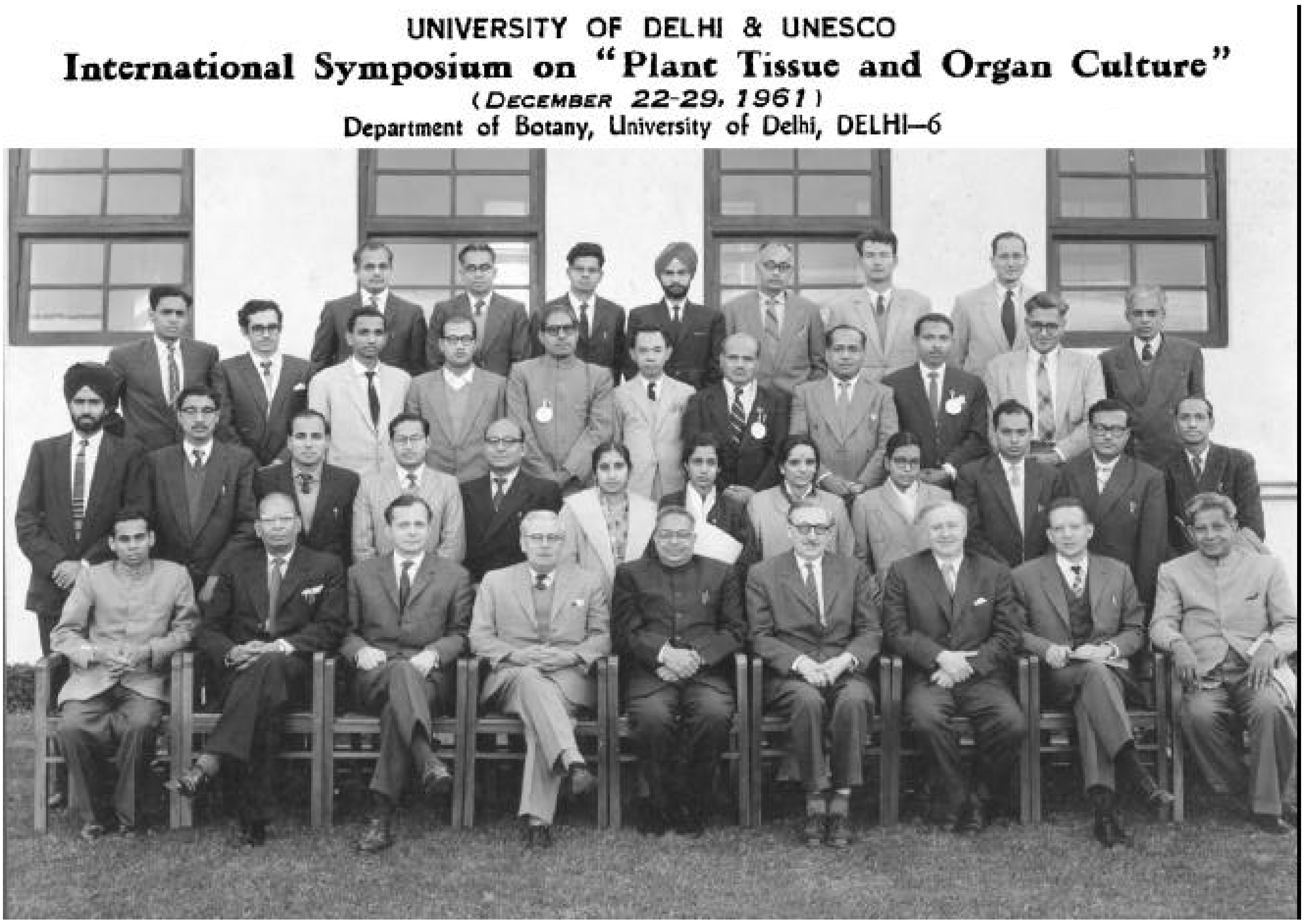
My commitment to pursue botany as a career was inspired by Maheshwari's example. I did my doctoral degree work under his supervision on the development of seeds in some Acanthaceae. In collecting the materials for my study I came in close contact with the lively Fr. Santapau, at that time Professor of Botany, St. Xavier's College, Bombay, and later Director of the Botanical Survey of India. Manasi Ghosh was another young research scholar in the department at the same time. She was working with B M Johri, a hard taskmaster. Manasi and I had decided to marry as soon as one of us submitted the Ph.D. thesis.

Looking back on my career, I see that I owe a perennial debt to her. Her curiosity about plants, sharp probing mind, deep love and trust enabled me to keep learning and working. In later years she became a mother figure to my research scholars, meeting their academic and emotional needs. As a scholar she studied the development of endosperm and embryo in three rare members of the Santalaceae using dissections – a technique followed by later students of B M Johri. She would have made a first rate researcher in a University set up. However, even in the early 1960s, heads of science departments were conservative and did not appoint women on the faculty.

4. Fulbright and Smith-Mundt Fellow

I was selected as a Fulbright and Smith-Mundt Fellow in 1958 to work for one year in the USA. My placement with F C Steward at Cornell University was finalized at the last moment. I submitted my Ph.D. thesis around noon and caught the train to Bombay the same afternoon along with my wife. Our group departed by the P & O Boat *SS Strathnaver*. An interesting incident took place at the dining table during our wonderful journey. A Lecturer in English from Kerala showed me a red, round fruit and asked me what it was. I told him, “It is A for apple”; evidently he had never seen an apple in his life. The orchardists of Himachal, Kashmir and Kumaon have produced such an enormous quantity of apples in recent years that you find them in every village in Kerala today. Very few people talk of the red revolution (apples and tomatoes).

Frederic Campion Steward was an outstanding plant physiologist. He was endowed with a rare blend of high intellect, plenteous energy and originality. The range of subjects in which he made substantial contributions was wide: cell physiology, ion uptake, metabolism, protein synthesis, respiration, morphogenesis, growth and development. He is best remembered for his research on cellular totipotency in plants using carrot root cultures and for his monumental work as editor and contributor to *Plant Physiology – A Treatise*, which runs into 10 volumes and 15 numbers. Cellular totipotency was reported from a wide range of sources, including haploid cells in the anther at the University of Delhi. The major outcome of these efforts was regeneration



A group photograph taken during the symposium shows, sitting from left to right: N S Rangaswamy (Convenor), B M Johri, J Reinert, F C Steward, P Maheshwari, J Swarbrick, H E Street, J P Nitsch and B Sen. The author is standing at the extreme left in the last row.

of full plants from cells, cloning and genetic engineering.

Steward wanted me to spend one more year and absorbed me as a Research Associate from 1959 to 1960. Manasi joined me as the recipient of a Fulbright travel grant. We studied the developmental morphology of the inflorescence and flowers of the banana and the anatomy of seeded and non-seeded banana fruits. I was the first to start tissue culture work in bananas and my experimental material was the unripe fruit. We procured a large number of genotypes from Honduras and Jamaica. I went to Kingston, Jamaica to collect tissues of banana varieties for biochemical studies by Steward's colleagues as well as carry out tissue culture work. This required frequent visits to Bodles, where the Banana Breeding Station was located. I took the opportunity to botanize in this beautiful Carribean island and saw the original bread fruit plants in Spanish Town brought by Captain Bligh from Tahiti on the historic ship 'Bounty'. After coming back, Steward and I went to work on preparing a critical review entitled 'Determining Factors in Cell Growth' for the first volume of *Advances in Morphogenesis* (Steward and Mohan Ram 1961). Steward would ask me to discuss with him the latest findings, absorb all my information and would dictate the draft of our review to a dictaphone machine non-stop, starting after dinner and going on till the early hours next day. He would then leave the tape on his secretary's desk, drop me home and ask me to read the typed material, fill up the blanks and add references. The speed with which he worked astonished me.

I packed as much as I could into my two-year life at Cornell and was looking forward to returning to Delhi with a new addition to our family. Unluckily for us, the baby girl died just after one day. It came as a bolt and the otherwise eventful stay ended as a bad dream. My wife and I learned the value of equanimity at an early age. From that time onwards nothing made us over-elated or deeply depressed. Back in India in August in 1960, I had to start my research and resume teaching. Within a year I was promoted Reader and accepted new Ph.D. scholars. The period between 1960–1968 was the most productive in my research career in morphogenesis and growth regulators. I was selected as Professor in 1968.

5. Research Fellow in France

When K N Raj, the renowned economist of the University of Delhi, was appointed Vice-Chancellor in 1969, he took me on his team as Proctor. I agreed to work for just one year. Dealing with errant students, hunger strikes, election to the Students' Union, transport problems, gheraos, etc., kept me busy 16 to 18 hours a day. Yet, that short period was a most educative one for me, as I came to learn how deeply complicated it was to manage the University. When Raj resigned after all his attempts to bring reforms failed, I also left the Proctorship and made use of a UNESCO senior fellowship to work with J P Nitsch at the Laboratoire de Physiologie Pluricellulaire in Gif-sur-Yvette, France from 1970–1971.

Jean P Nitsch was one of those rare plant scientists who had a broad range of interests in plants, notably in the problems of growth and development. Like F C Steward, Nitsch believed that applying findings of cell-free or bacterial systems to the whole plant would minimize the role of organization, characteristic of pluricellular systems. His well-known aphorism was "Single cells cannot tell the whole story". Nitsch's research on the hormonal regulation of the development of strawberry and tomato fruits, and flower sex-expression in cucurbits, was outstanding. His elegant demonstration of the role of seeds in the development of the strawberry fruit stimulated much interest among the young botanists at Delhi in the early 1950s; following his techniques, work on the excised reproductive organs was initiated by us. Nitsch was quick to grasp new lines of research. For instance, he recognized the importance of the production of haploid embryos from cultured anthers done at Delhi. Along with his wife Collette and students Bourgin and Brigit Norreel, Nitsch was able to produce haploid plants on a large scale from anthers belonging to several species of *Nicotiana*. Sipra Guha-Mukherjee, who was the first to discover androgenic haploids in *Datura* (and published her results with S C Maheshwari in 1964 and 1966) tells me that Nitsch and Nitsch (1969) did not refer to the pioneering work done at Delhi in their paper. I have confirmed this. Nitsch demonstrated spontaneous development of diploid clones in the cultured pith callus of haploid tobacco; buds originating from this callus could be made to develop into completely homozygous plants which would set seed.

While in Paris, I went to meet Roger Gauthérét, at the University of Paris (Sorbonne). He was a pioneer in plant tissue culture about whose inspiring life I had heard from Professor Johri. Born into an affluent family, the young Roger wanted to achieve something spectacular in life, as he had no need for money. His teacher the famous cell biologist Guilliermond, asked him to culture plant cells and regenerate whole plants. Gauthérét carried out monumental work on the methods of plant tissue culture (especially derived from cambium) and published numerous papers. These are embodied in his work *Lés Culture des Tissus Végétaux* (1959). Gauthérét knew Nitsch very well and was happy to personally show me around his laboratory. At the end of my appointment Gauthérét told me "I will show you some places which may be historically more valuable". We walked into an old, ill kept, nearly bare room. I wondered why he had brought me to this unimpressive place. Gauthérét let my dismay subside and whispered, much to my awe, "This is a part of the Radium Institute established by the University of Paris for Madame Curie".

The day I left Paris for India, on July 29, 1971, Nitsch went for a short vacation to the coast of Brittany and died of accidental drowning at the age of 50. My return to Delhi from Paris was eagerly awaited by my family and Ph.D. students and we plunged back into hectic activity. I have never taken sabbatical leave again.

6. Research contributions from Delhi

The work I did for my doctoral degree was on seed development in the Acanthaceae with special reference to the endosperm. Teaching and researching in embryology gave me a solid base for later work on growth and development. Only a few highlights of the research carried out over the years by our group, eventually consisting of over 35 students and post-doctoral fellows, are sketched below.

6.1 *Endosperm culture*

A publication that came out of an M.Sc. dissertation by my student Asha Satsangi was published in *Current Science* in 1963. It pertained to the induction of cell divisions in the mature endosperm of the castor seed. Endosperm is a triploid tissue in the seed, unique to flowering plants, resulting from the fusion of one of the male gametes (sperm) with two polar nuclei in the embryo sac (triple fusion). Recently some botanists have started questioning the concept of biparental endosperm. The embryo is diploid and is a product of syngamy. When it develops into a full plant after germination, the endosperm serves the embryo by supplying it with stored food reserves. Thus there is a clear-cut division of functions and morphogenetic fates between the embryo and the endosperm. It was important to ascertain what happens if the embryo growth is artificially suppressed by the herbicide 2,4-D (2,4-dichlorophenoxyacetic acid). To our surprise the cells of endosperm which would have never had a chance to divide showed meristematic activity. The other researchers in the Department continued the work on *in vitro* growth of excised endosperm of other Euphorbiaceae, *Santalum* and members of the Loranthaceae and even demonstrated the formation of shoot buds and somatic embryos (figure 2).

6.2 *Modification of sex expression*

Chemical manipulation of sex expression was investigated by V S Jaiswal and Rina Sett using the dioecious *Cannabis sativa*. One of the principal reasons why we chose *Cannabis* is that it grows abundantly and naturally in India. We have few competitors because western scientists might be behind bars if they cultivated it! The plants are morphologically alike at the vegetative stage and sex becomes distinguishable only when flowers appear; the male and female flowers look quite different (figure 3). Cytology indicated the absence of a heteromorphic pair or sex chromosomes, although *C. sativa* is listed in the literature as a plant in which a chromosomal basis of sex determination exists. Male flowers (functionally and morphologically identical to natural ones) can be induced

Figure 2. *Santalum album*. The left tube shows that decoated seed grown on MS medium with 2,4-D has proliferated into a callus. The culture tube in the middle shows the differentiation of somatic embryos. The tube on the right shows a shoot developing from a somatic embryo on a filter paper bridge in liquid medium without 2,4-D. From Rao and Raghava Ram (1983).

Figure 3. *Cannabis sativa*. Left, male plant with clusters of flowers at nodes. Right, female plant with 2 flowers at nodes.

in female *Cannabis* plants by the application of gibberellins (GAs) and antiethylene agents such as silver nitrate ($AgNO_3$), silver thiosulphate anionic complex (STS), aminoethoxyvinyl glycine (AVG) and cobalt chloride ($CoCl_2$). Fertile female flowers can be induced in male plants by ethephon (2-chloroethanephosphonic acid) and NIA 10637 (ethylhydrogen-l-propylphosphonate). Interestingly, stamens could be seen arising even from fruits. Stopping the application of growth regulators caused the plants to revert to their original sex. We hypothesized that in *Cannabis*, GA and ethylene act as male and female hormones respectively, and that the expression of sex is controlled by a balance between their endogenous levels. Abscisic acid (ABA) is able to overcome the GA-induced male flower formation (Mohan Ram and Jaiswal 1973; Mohan Ram and Sett 1985).

6.3 *Flower physiology*

Basic studies were carried out using excised inflorescences of lupine, gladiolus, chrysanthemum, marigold, lantana and flowers of rose. This work has not only given an insight into the mechanisms of flower opening, petal growth, petal colour and senescence but has also provided methods of prolonging vase-life. I V R Rao studied some aspects of this fascinating problem under my guidance. He obtained a large quantity of spikes of gladiolus through the generous help of T N Khoshoo and M A Kher of the National Botanical Research Institute, Lucknow. In gladiolus, the system of overlapping outer bracts (which completely enclose the flower buds) and their gradual separation represents a system programmed for sequential exposure of successive buds to light. The outer bract acts as a natural qualitative light filter and regulates the production of a-amylase and petal growth by a red/far-red control. a-Amylase is formed exclusively in the petal epidermis. On perception of light, the enzyme is transported to the ground parenchyma where it hydrolyses the extensive starch reserves. Sugars released through a-amylase activity are involved in petal growth through the development of an osmotic and sink potential. Rao showed that a critical stage in flower bud growth in the spike of gladiolus, which is initiated by gibberellic acid and sustained by sucrose, is when separation of the outer bract occurs (Mohan Ram and Ramanuja Rao 1984).

In a colour variant of *Lantana camara* selected for study by Gita Mathur, pink buds, yellow newly opened flowers (rich in b-carotene) and ageing orange, scarlet and magenta flowers are found in the same inflorescence. To a common observer it would appear that the plant bears flowers of different hues. Butterflies are seasonal pollinators (January–February and June–July), whereas thrips are regular pollinators and are attracted to yellow flowers; they avoid flowers of other colours because yellow colour is associated with the availability of food rewards. Pollination triggers rapid anthocyanin synthesis as confirmed by injecting pollen into unpollinated flowers. The post-pollination shift in petal colouration is caused by the masking of carotenoids by differential amounts of anthocyanin (delphinidine monoglucoside) (Mathur and Mohan Ram 1986).

6.4 *Biology of aquatic plants*

Nearly 50% of the aquatic plants of the world are recorded from the Indian subcontinent, but only a few have been studied in detail, probably because of inconvenience, inaccessibility or mere apathy. Our group took up the cultivation of aquatic plants in axenic cultures, as this technique provides unlimited opportunities for studying growth, nutrition, flowering and reproduction. Several bladderworts are aquatic insectivores (*Utricularia* sp.), endowed with special devices to trap insects. There have been claims that nitrogen derived from the insect prey is an obligate requirement for growth and flowering of these plants. Working with me, R Doreswamy showed that *Utricularia inflexa* var. *stellaris*, an aquatic bladderwort (figure 4), can grow, flower and set fruits and viable seeds even on a medium containing nitrate nitrogen. Flowering in this plant occurs under short days (20 cycles of 16 h dark 8 h light). Anita Sehgal has shown that the mature embryo of *Ceratophyllum* is unique among angiosperms in having as many as 12–14 whorls of leaves with a few lateral branches (Guppy calls it “a complete plant in miniature”). The oldest lateral branch bears 3–5 whorls of leaves. A radicle is absent. It appears that the theory of compensatory growth finds some validity in *Ceratophyllum*. The embryonic shoot grows at the expense of the root and perhaps also to secure its survival, especially in the absence of roots. Several plant hormones failed to stimulate meristematic activity in the radicular pole as also noted in the case of *Utricularia*, supporting the view that the genetic block to root development cannot be reversed by hormonal treatment. It remains to be seen whether there are specific genes that regulate root growth, using *Ceratophyllum*, which is one of the most ancient flowering plants.

6.5 *The Podostemaceae, an enigmatic family of aquatic plants*

Our group (Vidya Shankari, Anita Sehgal, P Uniyal, Charu Khosla, J R Bhatt, jointly with me and K R Shivanna) has carried out a considerable amount of research on the strange family of aquatic flowering plants, the Podostemaceae. This is a large family consisting of 48 genera and 270 species, invariably growing attached to rocks and boulders (haptophytes) in rivers and cataracts in the tropics and subtropics. The members have a thalloid plant body, usually dorsiventral, resembling an alga, a lichen or a liverwort (figure 5). They grow adhering firmly to the substratum (figure 6) by means of gum-secreting rhizoids and holdfasts. India has 10 genera and 23 species, of which 21 are endemic, largely confined to Kerala and Karnataka. The Podostemaceae exhibit such enormous phenotypic diversity and fuzzy morphology that the conventional distinction into root and shoot is absent. The nature of the plant body has not been understood and is interpreted as a root, stem or a combined-shoot (leaf-stem structure). Aerenchyma (a system of air spaces), typical of water plants, and xylem tissue are absent. They also lack vegetative propagation. The young plants are subjected to high water flow pressure, dim light, low CO_2 and high dissolved O_2. Embryologically also, podostemads are deviants with several remarkable features not known in such combination in any other angiosperm family. Among the interesting embryological features brought out by botanists of Mysore and Delhi University are the presence of a pseudo-embryo sac, lack of antipodals, triple fusion and endosperm, prevalence of single fertilization and the absence of plumule and radicle in the mature embryo and presence of suspensor haustoria. These characteristics not only make the Podostemaceae markedly distinct from other angiosperms but also evolutionarily enigmatic. The perplexing and diverse morphology of the Podostemaceae prompted Willis to disbelieve that Darwinian Natural Selection could provide an explanation for this existed within what he considered to be uniform conditions of rapidly flowing water in the warm tropics. In his opinion many of the characters were ‘unadapted’; he proposed that large mutations rather an accumulation of small ones accounted for the diversity observed (see Mabberley 1997). The unique combination of characters presented by this family is unparalleled among angiosperms, and has led to a recent resurgence of world-wide interest. A whole issue of the journal ‘*Aquatic Botany*’ has been brought out on Podostemaceae; we were invited to contribute a paper on *in vitro* studies on developmental morphology (Mohan Ram and Sehgal 1997).

The main reason for our poor understanding of the development of the podostemads is due to difficulties in tracing the germination of the minute seeds in flooded rivers. A method for *in vitro* cultivation from seed to vegetative stage of the plant was developed by Vidyashankari and Mohan Ram (1987). Polystyrene (thermocole) cubes (*ca* 1 cc) were used for supporting the seeds.

Figure 4. The insectivorous aquatic plant *Utricularia inflexa* var. *stellaris*. It has bladders to trap insects.

Figure 5. A dorsiventrally flattened vegetative thallus of *Polypleurum stylosum* var. *laciniata* collected from a river in Silent Valley (photo: Susindran).

When steam-sterilized thermocole cubes containing the seeds were inserted aseptically into liquid culture medium, the seeds not only clung to their surface but were also partially exposed to air. They germinated and developed into young plants *in vitro*. This simple and reproducible technique paved the way for detailed studies on the developmental biology of several Indian Podostemaceae. We have been able to cultivate mature plants of seven species and even induce flowering in two by subjecting them to stress (figure 7). Under natural conditions, the podostemads start their life cycle with the onset of monsoon. Their seeds are tiny (*Griffithella hookeriana* has 0·5 million seeds per one gram) and the mature embryo has two prominent cotyledons but is devoid of a plumule and a radicle. In members of the sub-family Tristichoideae, during germination, an ephermal primary shoot axis consisting of 15 ramuli is formed apically between the cotyledons and a few adventitious roots develop at the basal end which become compressed and grow horizontally and bear asymmetric root caps. They put out vertical, highly branched shoots.

Members of the other sub-family, the Podostemoideae, have a horizontally flattened plant body with secondary shoots on the dorsal margins. During germination a stemless tuft of alternately arranged leaves is formed. This represents the primary axis and is limited in its growth. It fails to develop flowers. The hypocotyl becomes swollen and gives rise to a conical protuberance below the level of the cotyledons. It subsequently progresses into a flat, green ovate thallus.

Our recent investigation of seedling histology of *Hydrobryopsis sessilis* (a highly crustose and endemic member of the Podostemoideae) has shown that a diminutive shoot apical meristem (SAM) is formed endogenously at the junction of the cotyledons. This meristem forms an apical determinate primary axis and a lateral indeterminate thallus primordium. The radicular pole does not give rise to a root. Further, the thallus in *Hydrobryopsis* can be interpreted as a flattened stem because it has a tunica corpus-like organization at its apex (Sehgal *et al* 2002). In our earlier papers (also see above), we were referring to the thallus as a lateral outgrowth of the hypocotyl. It is only gradually that we have been able to trace the origin of the thallus to the SAM. This calls for a re-investigation of the early histology of seedlings of other taxa of Podostemoideae.

In the Indian Podostemoideae flowers are differentiated when the plants are still submerged. The androecium is made up of a pair of laterally placed staminodes and generally two fertile stamens fused at the base. The entire flower bud is enclosed in a spathe (figure 8). Pre-anthesis cleistogamy has been observed in *Griffithella hookeriana* and *Hydrobryopsis sessilis*. In *Polypleurum stylosum* as the flowers reach the surface of water, one of the anthers gets clasped between the two stigmas, facilitating self-pollination. However, cross pollen can germinate on stigmas in petri plate pollinations. Pollination triggers enormous elongation of the flower stalk in some species (1 cm recorded in 24 h in *Polypleurum*).

6.6 *Tree biology*

Our research group is deeply concerned with the study of gross and time structure of wood, origin and

Figured 6. A crustose thallus of *Hydrobryopsis sessilis* growing on a pebble in the river Netravati in Killor, near Dharmasthala, Karnataka State. Note profuse branching and the resemblance of the plant to a lichen.

Figure 7. Profusely branched 110-day-old plant of *Indotristicha ramosissima* growing on the surface of agar in the flask. Note the pink colouration.

development of resin canals and gum secreting tissues. A recent paper that was published in *Current Science* (Nair and Mohan Ram 1992) was on the structure of sola wood. This is the traditional art material used for making intricate decorations for Durga, Saraswati and other Hindu idols; *mukut* or *topa* for brides and bridegrooms in Bengal; '*shera*', the bridal veil and tazias used in Muharram; garlands and ornaments worn by Odissi dancers; artificial flowers, hats (sola topi or sun hats), toys, etc. In Tamil Nadu sola is used for making replicas of temples and ships. We found that the material is technically wood, though spongy. It is the lightest wood in the world with a specific gravity of 0·04 and comes from the shrubs *Aeschynomene aspera* and *A. indica* that occur in wetlands. The stems are not more than 5–6 cm in diameter and enclose a marble white, soft wood. The wood is storeyed and is diffuse porous, with very few vessels, and is chiefly made of thin-walled fusiform cells, endowed with abundant simple pits on end walls. We have coined the term "fusiform wood cells" to demarcate them from other wood components. These cells eventually become filled with air to provide the wood its unusual properties.

Lately we have been studying the reproductive biology of trees. An important outcome of our study refers to *Commiphora wightii* (Burseraceae), a shrubby plant that occurs wild in the semi-arid regions of Madhya Pradesh, Rajasthan and Gujarat. It yields guggul, an important oleo-gum resin used as incense, fixative in perfumery and in Ayurvedic medicine since the time of Susruta. Its anti-arthritic, hypocholesterolaemic and hypolipidaemic properties have been re-established. A thorough study of six populations showed a predominantly large number of isolated groups of female individual plants and only one andromonoecious and two exclusively male plants. As female plants set seed, irrespective of the presence or absence of pollen, detailed embryological studies were made. It has been confirmed that the plant shows non-pseudogamous apomixis, nucellar polyembryony and autonomous endosperm formation (Gupta *et al* 1996).

Figure 8. Flowering thallus of *Polypleurum stylosum* var. *laciniata*. Note short and round secondary shoots, each bearing a sheath from which a flower has emerged. Flowers are at various stages of development (Photo: Susindran).

6.7 *Bamboos*

Bamboos are giant grasses that constitute a major non-timber forest product of India. The enormous diversity and design exhibited by the spectrum of their products reflect their indispensability for tribal and rural communities. Once embarrassingly abundant and aptly termed poor man's timber, bamboo has increasingly become a target of rich man's plunder. The unique assets of bamboos such as grace, beauty, renewability, strength, resilience and straightness have been disastrous for their survival. Growing demands, habitat destruction, over-exploitation by paper mills at highly subsidized rates, lack of adequate seed storage facilities and poor nursery techniques have imposed a check on the sustained availability of bamboos. Bamboos also play a protective role in the ecosystem and are an important feed material for wild herbivores.

Flowering in bamboos has been a matter of intense biological interest and speculation. There is wide diversity in the flowering and seeding cycle of bamboos. On the basis of flowering, bamboos have been categorised in three broad groups: (i) those that flower annually or nearly so (*Indocalamus wightianus*, *Bambusa atra*, *Ochlandra sivagiriana*), (ii) those that flower sporadically or irregularly (*Chimonobambusa* sp., *Arundinaria falcata*, *Dendrocalamus giganteus*, *D. hamiltonii*, *D. longispathus*) and (iii) those that flower gregariously or exhibit synchronized production of seeds at long intervals (*Bambusa bambos*, *B. polymorpha*, *B. tulda*, *Ochlandra travencorica*, *Dendrocalamus strictus*). A majority of bamboos belong to the third category. *Phyllostachys bambusodies* takes 120 years to flower (Janzen 1976). We know little about the mechanism responsible for determining when a given species of bamboo will flower.

Bamboos of the third category mentioned above generally die after gregarious flowering and production of an enormous quantity of seeds. With the availability of large amount of nutritious feeding material, there is a concomitant rise in the populations of squirrels, birds and notably rodents. After consuming the bonanza, the populations of rats turn to the standing crops and cause severe devastation, resulting in famine. In India, Mizoram has often experienced mass seeding of bamboos and resultant famines. Tribal lore and forest records indicate a regular cycle of about 48 years for *Bambusa tulda* and *Melocanna baccifera* in Mizoram (Mohan Ram and Hari

Gopal 1981). Flowering of *M. baccifera* causes a famine called 'mautam' and that of *B. tulda* brings about 'thingtam' famine. Whereas the gap between mautam and thingtam is 18 years, mautam follows thingtam by 30 years.

Conventional propagation of bamboos involves propagules such as rhizomes, suckers, culm cuttings and seeds. Propagation by seed is the most convenient method because a single seed will result in a whole clump. However, availability of seeds is problematic as gregarious flowering occurs after long intervals of time followed by mass seeding and death of entire populations. Sporadic flowering (out of step flowering) does occur but a large proportion of seeds may be sterile. Tissue culture offers special advantages as it ensures a continuous supply of planting material, helps in conserving wild germplasm and in scaling up of rare mutants or elite clonal materials. A large number of plantlets can be raised in a short span of time.

The first successful report on somatic embryogenesis and plantlet regeneration from the seed cultures of *Bambusa bambos* and *Dendrocalamus strictus* via a callus was made by our group (Mehta *et al* 1982) (figures 9, 10). Once the plantlets were differentiated from the developing somatic embryos a major hurdle was their transplantation for hardening. Reproducible procedures for rhizome initiation and acclimation to potted conditions were developed. Over 10,000 tissue culture raised plantlets have been introduced in various parts of the country with a high percentage of success in their establishment and performance in the field. Subsequently several successful reports on somatic embryogenesis and plantlet regeneration in bamboos have appeared. Micropropagation using explants taken from mature plants has now been reported. Reports on precocious flowering of bamboos in aseptic cultures from Delhi and Pune have been of special significance, because the requirement of several years of vegetative growth can now be curtailed (Rao *et al* 1988; Nadgauda *et al* 1990).

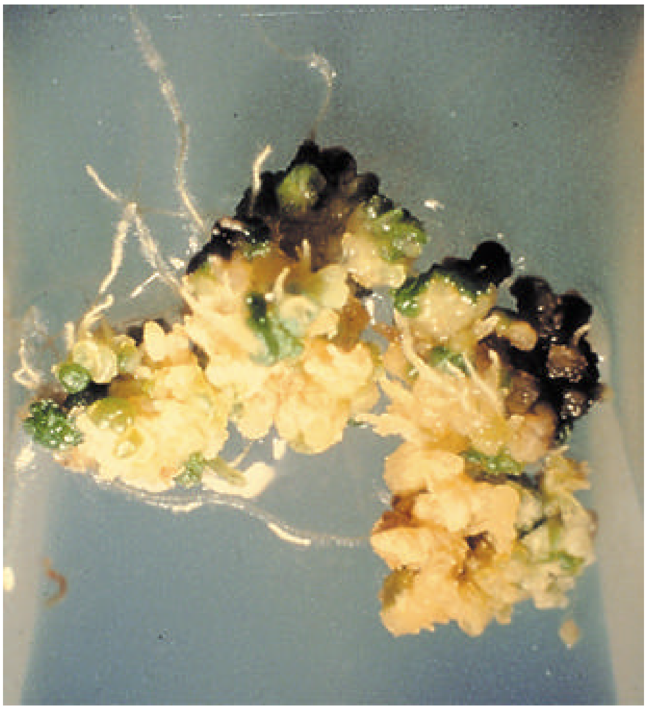


Figure 9. Seed cultures of *Bambusa arundinacea* (presently *B. bamboos*) callusing on modified N_6 basal medium + 2,4-D+ BAP+PVP, showing somatic embryogenesis. A few roots are also seen.

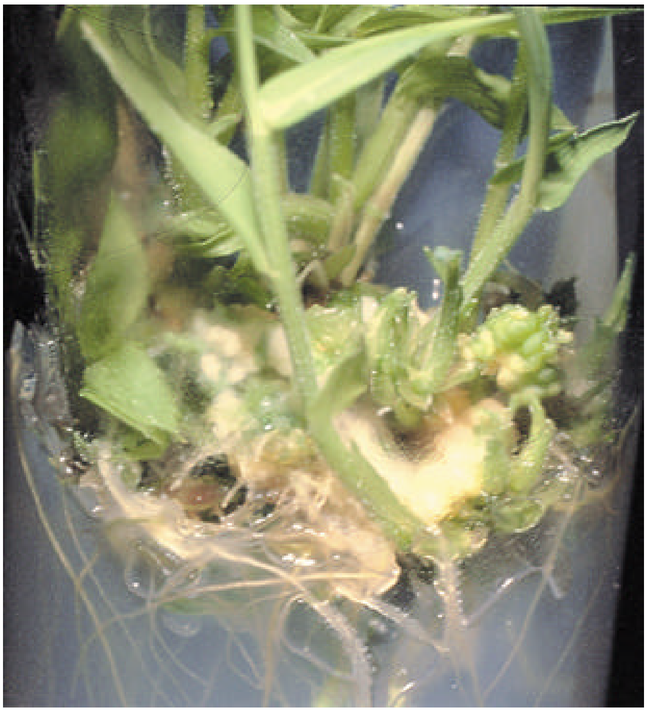


Figure 10. Plantlets developing from somatic embryos in the seed callus of *Bambusa* which can be hardened and transplanted.

7. Scientists I have admired

In sheer versatility, dedication to research, energy, wide interests, originality and productivity, the name of B G L Swamy (1916–81) stands out. Son of the illustrious scholar D V Gundappa, Swamy was recognized throughout the world for his contributions to plant structure and embryology. He joined as Professor of Botany, Presidency College, Madras in 1953 after returning to India from Harvard University, where he had worked closely with Irving W Bailey, the most respected plant anatomist of the time. Swamy investigated the embryology and anatomy of plants of the Magnoliales, especially belonging to families such as Austrobaileyaceae, Degenariaceae, Schisandraceae and Winteraceae which lack vessels in their wood. He was an inspiring teacher, thinker, art historian, epigraphist, musician, painter and above all an unusually gifted writer in Kannada. In my opinion no scientist has written on the biodiversity, morphology, taxonomy, domestication and introduction of plants in any Indian language, that too in an inimitable and delightful style, as Swamy has done in Kannada. His book '*Hasiru Honnu*' (green gold) is based on visits to the Western Ghats with students. It contains descriptions, uses, myths, conservation practices and references to plants in Kannada and Tamil literature. In using a story telling style with wit and humour, Swamy set a trend in popularization of science in Kannada.

An eminent scientist who generated in me a committed interest in ornamental plants and environmental issues was B P Pal, the renowned wheat breeder. He succeeded in breeding wheat varieties resistant to all the three major rusts and was an authority on roses and bougainvilleas. His refined culture and deep understanding of the arts were a rare combination. B P Pal was particularly happy that our group was working with flowers, although we were in a conventional university. Very few Indian agricultural scientists have spotted talent and promoted them to become established scientists as B P Pal and M S Swaminathan have done. Pal encouraged me to do fundamental research on floral crops and taught me the basics of judging roses. It is worth remarking that the movement to begin environmental awareness and action-oriented research related to the environment was initiated by generalist visionaries and not by specialists. No one who has known Dr Pal would forget his courteous manners, puckered sense of humour and vast collection of limericks. While we were interviewing candidates for a senior position, Pal lamented that there had been an overemphasis on formal degrees than actual research work. He narrated to me the story of B Viswa Nath who was a brilliant soil chemist. When Viswa Nath applied for the Directorship of the Imperial Institute of Agricultural Research (originally at Pusa, Bihar), with the Selection Committee consisting mostly of Englishmen, one member remarked "Mr Viswa Nath, you don't have a degree!" Viswa Nath, who had failed in the matriculation examination and vowed to become a top scientist without reappearing in the examination retorted: "But I have a pedigree". He was grilled for over two hours on various aspects of soils and agriculture. The Committee was unanimous in recognizing his merit and appointing him the first Indian Director of the Institute in 1935. B Viswa Nath was also one of the 65 Fellows who founded the Indian Academy of Sciences.

J Heslop-Harrison was a towering personality, both intellectually and physically. He was a complete botanist with an extraordinary capability in experimental taxonomy, developmental physiology, electron microscopy, conservation biology, reproductive biology and cell biology. Heslop-Harrison's reviews "*Experimental Modification of Flower Sex Expression in Flowering Plants*" (1957) and '*Sexuality in Angiosperms*' (in F C Steward 1972) are classics and have markedly influenced our own research. Heslop-Harrison came to Delhi University for two months in 1973 and delivered a series of 10 lectures. I have happy memories of accompanying him on a field trip to the Southern Alps in New Zealand with several international experts on reproductive biology.

T A Davis was a colourful scientist with a keen eye for detail. He had a perceptive and analytical mind and used it to seek the meaning of form and symmetry in nature. J B S Haldane had spotted Davis when he was a student and had awakened in him the zeal to explore the biological world, full of enigmatic phenomena. The tools Davis used were a camera, a notebook and a pencil. He did wonders with these, especially by capturing nature's intricate forms and colours through superb photographs. He was an authority on the coconut and other palms. We travelled to Leningrad to attend the International Botanical Congress in 1975. In the passport that Davis carried, the entry against his profession was 'palm specialist'. Somehow this came to be known to the officials of the Indian embassy and Davis was invited to dinner by a senior embassy official in Moscow. Davis had guessed the reason for being singled out for this honour and dragged me along. Several ladies crowded round Davis and stretched their palms to know their future. Without batting an eye, Davis performed the role of a fortune-teller and enjoyed the occasion immensely. He told me that it was not the first episode of its kind. Davis made a serious study of asymmetry in nature. He carried out a statistical study of left-handed and right-handed spirality in the arrangement of leaves in the coconut palm, and its possible significance for yield parameters. He had reported that as one moves towards the north of the equator, left handedness increases and the opposite occurs towards the south. He had noted that the left antlers of the caribou in Alaska were always shorter than the right ones, as they were used more frequently than the right ones to clear the snow to locate lichens, the main food of caribou during severe winters.

Davis studied the number of floral organs in different groups of plants and also the number of spirals of sporophylls in the cones of gymnosperms, and demonstrated the preponderance of the Fibonacci numbers (1, 1, 2, 3, 5, 8, 13, 21, 34 . . . etc.). The credit for solving the century-old problem of reconstructing the sunflower head goes to him. Davis truly fitted the Raman formula of catching young children's excitement for science. He had a strong background in mechanics, which enabled him to invent and fabricate gadgets such as a palm-climbing vertical bicycle, an electronic detector for insects, an angle measurer for sugarcane research, and a hardness tester. He loved travelling (he used to call himself Travelling Always Davis). He once reported the unusual case of the tribal women of Irian Jaya (Western New Guinea) who use kami bark (*Cinnamomum kami*) as a weapon against their husbands. When harassed, they would threaten to chew the bark and become sexually sterile. Tapping his head with his fingers, he once told me “No funding agency can provide the contents of the cranium”. Davis was an interesting person because he was interested in many things. He died in November 1989.

Two students of Panchanan Maheshwari – B M Johri and V Puri* – have completed 90 years and are continuing in their individual style as models of the botanical tradition in Delhi and Meerut respectively. B M Johri has made noteworthy and original contributions to embryology and has authored and edited numerous professional books exemplifying the adage that nothing succeeds in life as perseverance. His physical frame has become frail and his eyes have sunk. Yet poke him a little, the ash blows away and the fire begins to glow. He has not lost the determination and confidence which are characteristic of his personality. He has been a critical investigator, teacher, exacting guide, able administrator, analyser and synthesizer of knowledge and reviewer of botanical literature and chronicler of the history of Botany in India. In sheer productivity, there are few plant scientists who can match him. What might surprise youngsters is his immense academic output even after he retired formally from the University 28 years ago.

V Puri, an internationally acclaimed floral anatomist, has contributed richly to our understanding of the nature of the angiosperm carpel, origin of the inferior ovary, placentation and ovules, and their taxonomic and phylogenetic significance. His critical essays on these aspects have appeared in the *Botanical Review*. Puri founded the School of Plant Morphology at Meerut College and the Post-graduate Department of Botany at Meerut University.

What makes persons like them keep working beyond the limits of endurance from the rest of us? It is like asking why do men climb mountains? Out of the several probable explanations to this age-old question, to me it seems that obsession is the main force that drives them.

8. Visit to Brazil

The Jawaharlal Nehru Birth Centenary Visiting Fellowship (1997) which enabled me to go to Brazil was a dream come true. Brazil is a paradise for botanists, although massive destruction of the Atlantic Rain Forest has occurred causing irreparable loss of a large number of species. Having come to know that the only botanist in Brazil studying the taxonomy of Podostemaceae was Dr Aldalea Sprada Travares working at the National Institute of Amazonian Research (INPA) at Manaus in northern Brazil, I flew to that city, met her and saw her extensive collections – both pickled and pressed. She told me that as the rivers are generally in spate during May, the best time to visit to see live specimens and make collections would be September, which disappointed me. I learnt that there was a ban on giving any seed samples to foreign scientists unless they are part of a joint research project approved by the Brazilian Government. Although upset, I realized that Brazil might have come to this decision as it has been continuously exploited for over two centuries by European botanists (including Alexander von Humboldt). I was amazed at the large size of the podostemads of the Amazon region and curious to know whether they had any economic uses. Apparently the original inhabitants of the Amazon used the thalli of these plants as salad and also as a source of salt.

I felt that my life’s ambition was fulfilled when I saw the giant water-lily (*Victoria amazonica*) growing naturally in the Amazon river backwaters close to Manaus. The Amazon lily is a rooted plant with large floating leaves (often 1·5 m in diameter) with up-turned margins like frying pans (figure 11). The underside of the leaf is dark maroon–purple and has sharp spines and prominent veins starting from the middle and forking several times before reaching the periphery. A mature leaf can support the weight of a young adult. The first time I had seen this largest water lily in the world was in the glass house at Kew. It has also been cultivated in the Indian Botanic Gardens for many years and recently at the Tropical Botanic Garden and Research Institute in Kerala. Seeing such wonderful plants in their original habitat is a rare experience. I asked the boatman to take me close to the plant so that I could touch it. Curiously, on the surface of the leaves of this gigantic aquatic plant, there were fronds of what might be the smallest flowering plant (*Wolffia brasiliensis*, less than 1·5 mm long), swimming in a film of water.

It was an unforgettable experience to visit the immensely large and fascinating market (Vero-o-Peso) in Belem, capital of the state of Para. On sale were unusual vegetables, fruits, animal products and a wide variety of medicinal and magic potions from the jungles of Amazon, which I had never seen before.

9. Future of botany

Do subjects like botany and zoology have a place today? It is paradoxical that at a time when there is global concern for the conservation of biodiversity, India should face an acute shortage of experts who can study, evaluate and

*Professor V Puri passed away on 9th October, 2002. He would have crossed 93 on December 10, 2002.

Figure 11. *Victoria amazonica* growing in the back waters of Amazon near Manaus in Brazil.

explain the role of the wide variety of organisms that it has. A large number of bacteria, fungi, nematodes, insects and plants are waiting to be identified and studied. We need trained persons who can quantify biodiversity and determine the conservation status of species. More importantly, we need to equip them with modern methods of studying, analysing, storing and retrieving information. There has been an over-emphasis on areas such as molecular biology, biotechnology and genetic engineering. To assume that these subjects would replace the other well-established branches of biology appears illogical as they are all interconnected. Ernst Mayr (1997) has said that ' . . . . Even the most traditional branches of biology – systematics, anatomy, embryology and physiology – are still needed not just as data but also because all of them are endless unfinished frontiers and all of them are still needed to round out our view of the living world. Each discipline seems to have a golden period, and many of them have several. But even after the law of diminishing returns has taken over, there is no justification for abolishing a discipline that has become "classical". . .' .

10. Conclusions

An autobiographical essay should also bring out the deficiencies and failures of the author. My biggest flaw, pointed out by my wife, was a built-in incapacity to say "No". I accept assignments and squander away much time. I fit Lin Yutang's famous saying about the Chinese, that they are prompt provided they have plenty of time. I have too many interests. P Maheshwari's advice to 'close many windows and open a big door' has had little effect on me. I am like a *harikatha* artist still following the oral tradition of conversing, lecturing and storytelling and not putting down much on paper. My American friends think that I am foolish for giving advice without charging a consultation fee! Money is useful and necessary but as J C Bose said 'once you get into the trap there is no way out'. I wish I could be like a tree: deep rooted and firmly fixed, bearing a lofty bole and a broad canopy, continuously absorbing, synthesizing and renewing, bearing fragrant flowers and delicious fruits, unmindful of stresses and insults, resilient to changes and perpetually giving and not coveting. To this I must add tenacity, based on the remarkable example of a ginkgo tree, almost at the epicentre of the 1945 Hiroshima nuclear explosion, that sprouted from the root after its trunk had been completely demolished along with everything around it.

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