Life and work of an Indian botanist (1904–1966) of the 20th century

Ramesh Maheshwari

In an e-mail dated 21 November 2010, P. Balaram said 'It would be wonderful to have a scholarly, yet personal, biography of your father'. Though it seemed odd to write a biography of one's father, nonetheless here was an opportunity to review and learn about a discipline of botany that is assuming increasing importance for generating the next-generation inter-generic hybrid crops producing high-quality seeds by overcoming incompatibility barriers between parents. Having grown up in P. Maheshwari (hereafter PM) household, I had the fortune of some plant embryology rubbed onto me although I went on to specialize differently. Googling led to an article by PM himself[1] published in *Nature* way back in 1952. This article tells about a sensational claim made by a Russian agricultural botanist of conversion of seeds of one plant species into that of another species merely by a change in environment (temperature)[2].

A voracious reader, a hard worker and a master in laboratory skills with scientific temper, the insight and ability to identify promising research topics, PM was a multitasker and a stickler for punctuality. Although always immersed in work, he was generous with his time for any research worker who wished to show and tell microscopic observations. He was the founder-editor of an international journal, *Phytomorphology*; served on the editorial boards of some international journals; edited biology textbooks for the higher secondary students; corrected theses and manuscripts of his Ph D students; frequently accompanied research students on botanical forays; contributed articles for *BOTANICA* – an in-house journal of the Delhi University Botanical Society – that he had founded; organized national and international symposia; workshops for high-school biology teachers; trained Ph D students in all-round abilities; and when called upon to do so advised the Government on science policy matters; and played host to out-of-station colleagues and visitors at his home. Following the publication in 1950 of his highly successful book on embryology of angiosperms[3], PM was working on his second book, *Morphology of Gymnosperms*. Both the angiosperms and the gymnosperms produce seeds, whereas the seeds in the former are enclosed inside the ovary (e.g. mango, papaya), the seeds in the latter are not, as for example, the cycads and the pines. Rather, in the latter group of plants the seeds are borne on the surface of scales, not enclosed inside the fruit. The latter book was to deal with the morphology of the reproductive structure and seed development in species of Gymnosperms, chiefly the species found in the Himalayan mountain ranges. Unfortunately this work remained unpublished as PM died a couple of weeks prior to the submission of the manuscript to the publisher.

Tall, broad-shouldered, always well-dressed and generally sporting a stern look, PM worked from pre-dawn to sunset all seven days in the week, at home or in his office (Figure 1) in the Botany Department of Delhi University. One of his former students described him as a 'karmayogi'[4]. Though a strict disciplinarian, PM was a kind-hearted person who enjoyed telling jokes and humorous anecdotes. His large personal library comprised of original and rare titles acquired during his several visits abroad. The collection of books and reprints served as a valuable resource not just for his own research students, but also for out-of-station faculty and students from other parts of India in need to access to the literature. Some of his former students have written remembrance articles on him in this very journal[5–8]. He gave talks and wrote newspaper articles on various topics in botany. He gave talks on topics such as the life and work of Sir J. C. Bose, Nature or Nurture? Among the popular articles written by him were 'The plants that India gave to the world', 'What seeds must be preserved in the event life is destroyed by a holocaust?', 'Botany in ancient India', 'Plants, history and politics'. He was a complete botanist.

Professional development

PM was born in 1904 in Jaipur, Rajasthan, where his father was an office superintendent in the SMS Medical College. His father had wished that his only surviving son would enter the medical profession. However, since PM wore thick glasses, he was denied admission in the medical programme. PM took up botany instead. Who mentored him in specializing in plant embryology is not known. Some of his clan was seed or grain merchants; perhaps the seeds sprouting during the monsoon rains aroused his curiosity to dissect the seeds to find out which parts emerge and grow as the root and the shoot axes. After a D Sc from the Ewing Christian College in Allahabad, under an American missionary teacher Dr Winfield Dudgeon,

Figure 1. P. Maheshwari at about 1960 in his office room in Delhi University. A major effort was collection of scholastic reference material through postal exchange with scientists. These were classified and stored in reprint boxes in the background. From *Curr. Sci.*, 2004, **87**, 1738.

PM taught botanical disciplines at the universities in Agra, Lucknow and Allahabad, where he established himself as an innovative and committed teacher who inspired and aroused curiosity of students. He was a born teacher. Using the reverse psychology method he gave popular talks such as 'How to give a poor lecture?', 'How to write a research paper for outright rejection by the journal' and the 'Ten commandments for bad writing'. These were among the most hilarious talks in the department. He wrote articles on a variety of botanical topics for *BOTANICA* under the pseudoname IDLER.

A highly cited textbook

Since during PM's early days the scientific literature was almost wholly in German, there was an acute need of scientific literature in English for the research workers. Recognizing this, with the aim of bringing out a textbook on plant embryology in English, at the age of 34 PM undertook visits to Kiel and Vienna where he became fluent in German and worked with German experts. He discussed the scope of embryology and its interfaces with cytology, taxonomy, genetics and plant physiology. During 1945–1947, he worked at Harvard University in Cambridge. He visited several laboratories in USA, met a number of botanists, did intensive library work for rare literature and finalized the manuscript for publication by the McGraw-Hill Book Company, New York. In his seminal work[3], *An Introduction to the Embryology of Angiosperms*[3] (hereafter referred to as the 'book'), he stated the scope of plant embryology as the study of embryo and endosperm and the development of the male and female structures that participate in fertilization resulting in seed formation. Stated thus the 'book' created an entire new field of enquiry with focus on the fine events in seed development. The book met with immediate success throughout the world, including USSR, where it was quickly translated into Russian, as *Embriologia pokritocemmenikh rastenii* or the 'Embryology of the covered seeded plants'. The 'covered seeded plants' are the Angiosperms in the original book title.

Impact of the 'book'

Publishing a book may seem a small thing, but PM's book had wide implications. It opened an entire new field of research that investigated the correlations between sex in plants and seed development. In 1980, in an editorial Eugene Garfield (ISI) ranked the book as among the 20 biology texts most quoted in the century! With the current emphasis on reproductive structures, the last ten years have seen resurgence in plant embryology using the tools of modern molecular biology. PM's book continues to be cited more than 50 years after its publication.

A discipline which has simple research requirements is likely to take roots and flourish in India where the facilities for research are rudimentary or even nonexistent, Plant embryology offered a field of enquiry in which India could become a leader. With its diversity of exotic plants, modest requirements of a microtome for serial sectioning of wax-embedded flowers, ovaries or ovules, and staining of sections, followed by their light microscopic examination and the camera-lucida sketches would provide research results of adequate quality and quantity and be a competitive area of scientific research. Botanical material could be collected from different climatic regions, fixed and brought to the laboratory for histochemical processing and microscopic examination of embryological oddities. This would allow a steady publication of papers, earn the research workers recognition, and give them a feeling of accomplishment leading to growth of science in general and botany in particular. PM and/or his research students undertook regular forays for collection of botanicals and their processing in the laboratory. Careful examination and documentation of embryological features led to the discovery of different types of embryo sacs, variations in the number and the distribution of nuclei in them, intercarpellary pollen grains, multiple embryos, modified suspensor cells, endosperm haustoria, polyembryony and apomictic plants, enabling observations to be published in high-ranking journals (see Selected bibliography). He investigated embryological features of doubtful taxa and showed that in conjunction with morphology, and anatomy, embryology could be useful in identification of taxa and phylogeny of taxa with uncertain affinities.

The plant embryo develops rapidly following fertilization of the egg cell and becomes differentiated into a suspensor cell and conspicuous cotyledon. It prompts how a single fertilized egg cell is converted into a mass of cells organized into a basal and apical pole that differentiate into the root and the shoot? This is the fundamental problem of polarity or the establishment of a basal and an apical end. PM recognized that embryology and morphogenesis are linked and should be studied together. With the major events in seed development – from the time pollen grains land and germinate on stigma identified, and new examples discovered wherein for one or the other reason seed development fails, practical solutions could be conceived for overcoming the bottlenecks under controlled conditions using the emerging technique of organ and tissue culture, or experimental embryology. Around 1950, PM embarked on 'experimental embryology'. This work involved the aseptic culturing of excised reproductive parts on chemically defined nutrient media for determining the nutritional and hormonal substances that the globular or the pre-globular embryo receives from the maternal (female) ovarian tissue for them to grow and develop into plantlet. With the enthusiastic support of his former student and later a

Box 1. Plants named after Panchanan Maheshwari.

P. Maheshwari has been commemorated by naming plants after him:

Panchanania jaipuriensis, a hypomycetous fungus; *Isoetes panchananii*, a new species of quillworts; *Maheshwariella bicornuta,* a Palaeozoic seed from the lower Gondwanas of Karaharbari coal field, India; and *Oldenlandia maheshwarii*, a new rubiaceous taxon are some examples. Names of up to 10 taxa ranging from microbes to angiosperms commemorate his interest in several fields of botanical research.

From: Rangaswamy[4]

colleague, B. M. Johri, who had received training in plant tissue culture in the UK, laboratories were set up at Delhi for plant cell and tissue culture. Plant embryos from a variety of flowers of parasitic and non-parasitic plants, of terrestrial and aquatic plants were cultured and their chemical requirements for growth determined. With experimental and descriptive studies side by side, the Delhi school established itself as the leading centre of research on plant reproductive biology. It began attracting research scholars from all over the world. Reminiscing about this period, a former student, Guha-Mukherjee[7], a co-discoverer of androgenic haploids[9,10], said:

> 'My major inspiration came from Prof. P. Maheshwari, a world-renowned plant embryologist, who headed the department. P. Maheshwari made it his mission to inculcate students' interest in Botany by applying various teaching innovations. The whole department was in the birth pangs of the plant tissue culture. The intellectual ferment had a major effect on all of us.'

Today, with finer and finer techniques this area of botanical science is increasingly gaining importance, offering new challenges for fundamental research and opportunities for breeding new varieties of crop plants.

Debunking Lysenko

Prior to 1950, PM was at the University of Dacca (now Dhaka, Bangladesh), where he founded the Department of Biology. In 1949, Maurice Gwyer, the Vice-Chancellor of Delhi University, invited PM to Head the new Botany Department.

Soon after taking charge, a situation developed in the department that required to be expertly tackled. A faculty member with a formidable personality had returned from visits to USSR and had begun teaching Michurin biology, which is essentially the discredited Lamarck's 'theory of inheritance of acquired characters'. Ivan Michurin (1855–1935) had propounded his view that the genotype of a plant can be changed by the variation of environmental condition. This view was vigorously championed by his disciple Trofim Denisovitch Lysenko[2] (1898–1976), who claimed that some grains in the spikes of the spring-planted crop of rye (*Secale cereale*) are converted into wheat (*Triticum vulgare*) and wheat into rye and barley (*Hordeum vulgare*) by exposing the plants to near freezing temperatures at the time of inflorescence development (flowering). Lysenko called the low temperature-induced phenotypic change in plants as 'jarovization'. If a species of plant could be converted into a different species simply by a change in the environment, then this could be translated into practical agriculture for solving the problem of food shortage that was plaguing Russia. Lysenko shot into fame. A web photo shows Lysenko giving a speech at the Kremlin with Joseph Stalin on the dais, suggesting that Lysenko had the backing and support of Stalin. Lysenko's challengers lived in fear.

Since Lysenko's claims were against the tenets of plant embryology and genetics, PM considered Lysenko's data as faked or false. How could a plant species distinguishable on the basis of the number of its chromosomes – the bearer of DNA – the chemical substance determining heredity – be converted into some other species? Lysenko's 'discovery' found way in the newspapers. PM felt that teaching of Lysenkoism to young research students would not be acceptable. He published a strong scientific criticism of Lysenko in a widely read journal[1] that circulates internationally (Figure 2), drawing the curtain on Lysenko.

Impact of the 'book'

The *Nature* article[1] must have created confusion among the minds of the botanists in Russia as to how to react to PM's criticisms of Lysenko, who had dominated the Russian botanical and agriculture scene. Not very long after, PM was invited to visit Russia, perhaps at the stance of the academicians who wished to express their appreciation and gratitude to him for his campaign against Lysenko's pseudoscience.

PM welcomed the opportunity to visit USSR, but for a different reason as well. In 1898, a Russian botanist, Sergius Nawaschin, had made an epochal discovery. This discovery, called 'double fertilization', is a crucial event in the life of seed-formng plants. It is unique to flowering plants (in botanical terminology called the angiosperms). The embryo sac (a cell in an ovule formed by meiotic division) has two female cells of which one is the egg cell attached at one end of the embryo sac, whereas another female cell called the secondary cell is positioned at the centre of the embryo sac (Figure 3). In plants, fertilization entails a pollen grain germinating on the stigma of the ovary bringing in two male nuclei (cells) through the pollen tube inside the embryo sac. Whereas one male cell fuses with the egg cell to produce the zygote and embryo, the other male cell fuses with the secondary cell to form endosperm – a cellular tissue which accumulates starch, lipids and proteins filling the embryo sac. Until when the mature seed falls on the ground and the seedling turns green and is able to synthesize its own food by the chemical process of photosynthesis, the endosperm provides the food to the developing embryo. The embryo and the endosperm are the basis of our dependency on the plant seeds as a source of nutrition. It is remarkable that a Russian plant embryologist, Sergius Nawaschin, had at about 1898 seen the nuclei in the act of fusion in whole mounts of ovules or fine serial sections, and reconstructing the picture from careful examination of the sections of the embryo sac. A photograph of Nawaschin is given in PM's book.

Unique features of embryo development in plants

To recapitulate, in plants, the development of a seed involves two separate male nuclei (cells) fusing with two separate female nuclei (cells) inside the embryo sac. This unique event of double fertilization was discovered by Nawaschin. Perhaps, as said above, one of PM's interests in visiting Russia was to pay homage to the memory of Nawaschin for his epochal discovery of double fertilization in the 19th century.

Although PM did not get to meet Lysenko in USSR, he had the opportunity to visit a few research institutions in Moscow, Leningrad and Kiev. A Russian botanist, V. Poddubnaya-Arnoldi (see her contributions to plant embryology in the 'book') fluent in English, offered to the Academy to serve as PM's official interpreter during his entire visit. During this visit a surprised PM was presented a Russian translation of his own book – titled *Embryologia pokritocemmenikh*

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LYSENKO'S LATEST DISCOVERY—THE CONVERSION OF WHEAT INTO RYE, BARLEY AND OATS

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A FEW months ago Academician T. D. Lysenko produced an interesting paper entitled "New Developments in the Science of Biological Species", an English translation of which has been recently published by the Foreign Languages Publishing House, Moscow[1].

The first half of the paper is devoted to a consideration of the concept of genus and species. In the latter half Lysenko first refers to V. K. Karapetian's[2] observation of 1948 that if 28-chromosome durum wheat (*Triticum durum*) is sown late in the autumn some of the plants are converted in two or three generations into 42-chromosome soft wheat (*T. vulgare*). This prompted Russian workers "to search for grains of soft, 42-chromosome wheat in the spikes of experimentally grown durum wheat. As a result, individual grains of soft wheat were quite easily observed in the spikes of durum wheat, i.e., *grains of one botanical species were found in the spikes of another species*" (italics mine)....

Academician Lysenko thinks that so far as plants are concerned the problem of speciation has therefore been solved, and a change in environment is the key to its solution. With regard to animals also he is quite hopeful as the following quotation will show: "We do not yet have the data essential to demonstrate how species are formed in the animal world. But we may rest assured that before long the development of the theory of Michurinist biology will make it possible to accumulate data also for zoological objects analogous to the data taken from the world of plants"....

... Thomas Johnson[3] in 1633 reported the occurrence of a grain of oat in an ear of wheat, and Ole Worm[3] in 1655 claimed to have seen a rye grain in an ear of barley.

Most botanists outside the U.S.S.R. are inclined to dismiss all such reports as errors of observation or as faked. Judging from the exaggerated nature of Russian reports and the lack of proper data for an evaluation of their claims such a surmise is not unnatural. However, if rye grains do occasionally occur in wheat spikes, the only possible explanation is that the stigmas of some of the wheat flowers become pollinated by rye pollen. In most cases, perhaps, such pollen tubes would fail to reach the ovules. If they did it is possible that either the eggs may be stimulated to develop parthenogenetically; or there is a fusion of the female nucleus belonging to the wheat parent with the male nucleus contributed by the rye parent, resulting in hybrid progeny; or the male gamete develops 'androgenetically' inside the embryo sac, seed coat and pericarp of wheat. In the third case the offspring would be a haploid rye, but if chromosome doubling took place at some stage in embryogeny the mature grain would produce a normal diploid rye plant. The so-called 'conversion' of wheat into barley or oats could also be understood as occurring in the same manner.

Such 'androgenesis' is already known to occur in *Nicotiana* and *Crepis* (see Maheshwari[4] for references; also Darlington and Mather[5]), and the work on *Crepis* was done by a Russian botanist, Helen Gerassimova[6]. Lysenko is either not acquainted with the literature on cytology, embryology and genetics or is unable to take this into account because of a blind faith in environment.

It is hoped that other botanists who see this note will express their opinions on this wheat–rye conversion and that meanwhile Russian botanists will themselves present a cytological analysis of the converted wheat or rye plants.

1 Lysenko, T. D., *Agrobiologia*, **6** (1950); English translation, "New Developments in the Science of Biological Species", Foreign Languages Publishing House, Moscow (1951).
2 Karapetian, V. K., *Agrobiologia*, **4** (1948).
3 Dunn, L. C., "Genetics in the Twentieth Century" (1951).
4 Maheshwari, P., "An Introduction to the Embryology of Angiosperms" (1950).
5 Darlington, C. D., and Mather, K., "The Elements of Genetics", p. 168 (1949).
6 Gerassimova, H., *Planta*, **25** (1936).

Figure 2. Excerpts from an article questioning the claims of T. D. Lysenko on conversion of wheat grains into rye, barley and oats.

rastenii. In scientific English, '*pokritocemmenikh rastenii*' refers to the angiosperms which comprise the large group of plants in which the seeds are covered (in contrast to the group gymnosperms in which the seeds are not covered by integument).

With a reference book on plant embryology available, it entered into the curricula of botany in all universities, at home as well as in countries where English is spoken. In the preface of the 'book', PM defined the scope of embryology as: 'In a strict sense, embryology is confined to a study of the embryo, but most botanists also include under it events which lead on to fertilization. I am in agreement with this wider comprehension of the subject and have therefore included in this volume not only an account of the embryo and endosperm, but also an account of the development of the male and female gametophytes and fertilization.' PM recognized that smaller structures would offer greater chance of discovering microscopic structures that are new to science and their characterization would yield academic satisfaction. Indeed, more than any other branch of botany, descriptive plant embryology entered into the curricula in all institutions in India and became popular. The embryological findings from studies of the diversity of the extant flora by the botanists attracted international acclaim.

Though small to be seen by the unaided human eye, the embryo is a miniature plant, differentiated into a micropylar or the root end, and a chalazal or the shoot end. This is a classic example of 'polarity' or a 'top and bottom' axes in plants. A plethora of fascinating questions came to the fore: how does fertilization occur of two female cells inside the embryo sac by two male cells brought inside the embryo sac by the pollen tube? The male cells were originally inside the pollen grain that germinated on the stigma of the ovary in the flower. The germinating pollen grain produces a tube that works its way through the stylar tissue to (chemotropically?) enter into the embryo sac contained in the ovule wherein the two male (nuclei) cells are discharged. While one male cell fuses with the female egg cell, the other male cell fuses with a secondary cell inside the embryo sac. Several figures in the 'book' illustrate that polarity in the zygote cell is established after the first cell division which is invariably in the transverse direction. Thus the central question: what rules of shape or size, i.e. geometry account for the plane of cell division or the localization of the new cell wall?

The side of the zygote cell attached to the embryo sac at the micropylar end develops into a root, whereas the opposite chalazal end develops into a shoot. Further, the embryo has symmetry, viz. root and shoot are alike on either side of a vertical plane of symmetry. The embryo sac is mostly a seven-celled, eight-nucleate structure, comprising one egg cell, two synergid cells, three antipodal cells, and two polar nuclei that fuse to form one $(n + n)$ diploid nucleus in the central cell (Figure 3). Why a plant embryo sac needs this cellular organization is unknown. Neither is it known if the extant primitive plants have a seven-cell organization of the embryo sac?

Descriptive embryology

PM greatly encouraged collections, observations and descriptions of botanical materials from different countries. He recognized that morphology would offer the chance of discovering structures that are new to science and their characterization would, as said before, provide academic satisfaction. Indeed, more than any other branch of botany, plant embryology became popular in almost all teaching and research institutes in India. Several botanists, notably B. G. L. Swamy, M. A. Rau, B. M. Johri, H. Y. Mohan Ram and S. C. Maheshwari, to name just a few, made important contributions to the embryology of exotic plants.

As was said before, the original work in plant embryology was in Germany and the literature was in German. Among the names of prominent embryologist cited in the 'book' is that of Karl Schnarf about whom PM commented as: 'Among the modern students of the subject, the name of the late Karl Schnarf of Vienna stands preeminent. His two works entitled *Embryologie der Angiospermen* (1929) and *Vergleichende Embryologie der Angiospermen* (1931) are the most important and exhaustive treatises in the field, and still serve as valuable works of reference.' A handwritten letter by Schnarf in his calligraphic handwriting in German was the only memorabilia at home. The handwriting was so beautiful that the publisher is said to have accepted Schnarf's entire hand-written manuscripts without requiring a typed copy.

Two slogans – descriptive and experimental – embryology have come in vogue. The former is the description of all the various ways and contrivances that occur in a flower from the time the egg cell is fertilized by a male cell brought in by a pollen germinating on the stigma, with the pollen tube working its way inside the tissue of the style to reach the egg cell for discharging the male cells (pollen contains two male cells) inside the embryo sac to produce a zygote. The zygote (or the fertilized egg cell) then undergoes cell divisions, the first division is almost always in a transverse direction that results in asymmetric segregation of cytoplasm into a large basal cell and a small apical cell, and each time the cell divides the rule of segregation in specific planes apply, forming a species-specific embryo. That seeds produce recognizable species-specific plants implies that the embryo – a structure comprising thousands of cells – has emergent patterns of shoot and root that divide mitotically and enlarge to form the shoot and root (Figure 4).

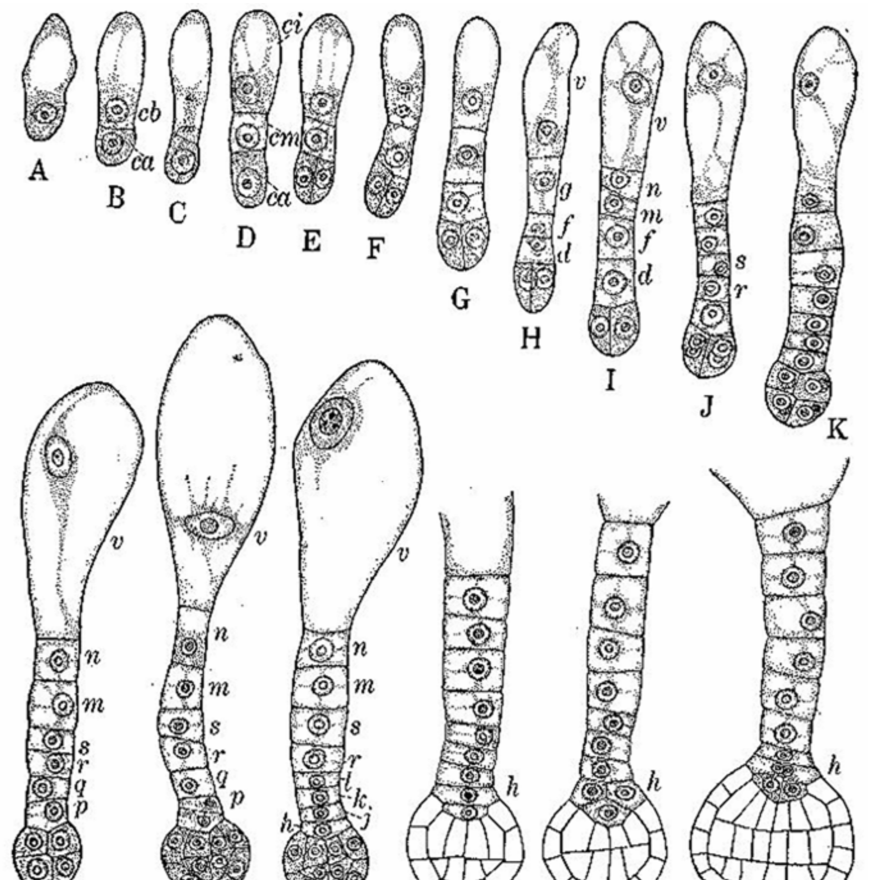

Figure 3. Camera lucida drawings of stages in embryo development in the plant *Capsella bursa-pastoris* following fertilization of egg cell. Note that the first division in the transverse direction with the basal cell *cb* larger and showing vacuolation. The polarity and body plan of the embryo of a flowering plant are established during early embryogenesis, but the rules controlling the order of cell divisions are not known. Drawing made in 1914 by C. R. Soueges, University of Paris, shows highly ordered sequence of invariant cell divisions to generate a multicellular embryo with differentiation of two cotyledons.

Experimental embryology

Experimental embryology is cell and development biology encompassing the mechanisms by which pollination occurs, the biochemical conditions that control pollen germination on stigma and the mechanisms by which the pollen tube grows through the style and finds the female cell inside the embryo sac for discharging the two free male cells inside the embryo sac. Further, what mechanisms determine that only one of the two male nuclei (cells) fuses with the egg cell, whereas the second male nucleus fuses with two polar nuclei in a central cell in the unique process of double fertilization? What signalling events occur for triple nuclear fusion inside the embryo sac for formation of a nutritive tissue called the endosperm which surrounds the growing embryo until it is consumed by the embryo? Embryology thus has great relevance to the science of improving the nutritional quality of crop plants – not by Lysenko's 'jarovization' method, but through sexual crosses between selected parents.

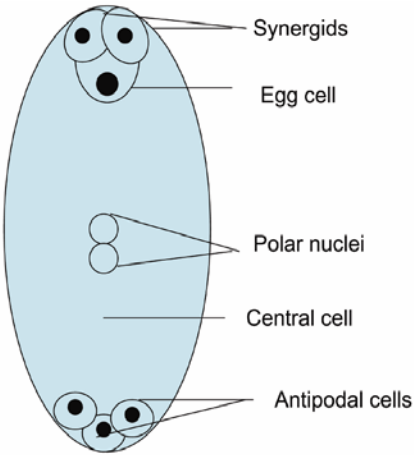

Figure 4. Diagram of a seven-celled, eight-nucleate embryo sac of a flowering plant (angiosperm). The egg apparatus consisting of two synergids and one egg (*n*) cell is towards the upper (micropylar) pole of the embryo sac. The chalazal pole contains three ephemeral antipodal cells. Fertilization involves the fusion of one male cell brought in by pollination to form diploid embryo. Double fertilization involves fusion of one (*n*) of the two haploid male cells brought in by pollen tube with the two haploid polar nuclei ($n + n$) in the centre of embryo sac fusing with one male cell to effect triple fusion, producing triploid endosperm tissue. Apparently triple fusion of nuclei signals the female plant to accumulate food material as a source of nutrition for the developing embryo. The mechanism of cell signalling resulting in triple fusion is not known. The mature seed containing a diploid embryo, a triploid multicellular endosperm tissue is surrounded by a hard seed coat for protection from infection by microorganisms in soil. The synergid cell presumably guides the pollen tube towards the egg apparatus. The function of antipodal cells is not known. The embryo sac and the endosperm are surrounded by maternal tissue which hardens into a protective covering as the mature seed falls on the ground to begin new growth.

In his 'book' PM discussed examples where inter-generic or inter-specific crosses for creating new varieties of crops had failed – either because of the failure of pollen to germinate on foreign stigma, or the failure of pollen tubes to grow in the foreign style of the ovary, or the failure of pollen tube to enter into the ovule through the micropyle (an opening), or the abortion of embryo following fertilization? Identifying the precise block and carrying out remedial operation might help circumvent the problem.

The plant embryo is formed inside an embryo sac (Figure 4) is attached to maternal tissue by a long suspensor cell. This raises the question about what chemical substances does the embryo receive from the maternal tissue until it can grow independently into an adult plant by absorption of mineral nutrients from the soil and carbon dioxide fixation by photosynthesis? This study required that smaller and smaller embryos be manually dissected out from the ovules and cultured in nutrient media of defined chemical compositions. Requiring keen eyes, immense patience and steady hands for dissecting out the minute embryos from flowers under a dissecting microscope a new research worker was quickly transformed into a scientist having patience, precision and determination. The results caught the imagination of new workers entering into botany[8].

With tissue culture laboratories established, the Delhi School expanded research on plant embryology. Experimental embryology with its modest research requirements caught on at several places in India and even displaced descriptive embryology. With proximity to a diversity of native flora, the workers chose and collected different plant materials for *in vitro* cultivation and examined their potentialities for regenerating into complete plants. Overall, the results strengthened the concept of totipotency of plant cells, i.e. virtually any cell of plant from almost any part, diploid or haploid, will develop into embryo. By comparison, totipotency of animal cells is not yet demonstrated. The animal scientists have coined a term 'pluripotency' which is defined as the potential of a cell to develop into more than one type of mature cells, depending on the environment (http://groups.molbiosci.northwestern.edu/holmgren/Glossary/Definitions/Def-P/Pluripotency.html). The numerous figures in the 'book' depict development of embryos from single fertilized cells, establishing the tenet that plant embryology is about what determines the plane in which the cell wall is laid down after each cell division to form a species-specific embryo. Published in 1950, two generations of botany students have read the 'book'.

Seeds formed without fertilization

Tuned to the knowledge that a seed is formed by the fertilization of gametes involving fusion of male and the female nucleus, one of PM's students, Prem Murgai, discovered a herbaceous plant *Aerva tomentosa* growing in the botanical research garden of Delhi University that surprisingly produced seeds even though the male plants were *not* found[11]. Neither pollen grains were seen on the stigma, nor pollen tubes in longitudinal sections of the style. It was inferred that this plant is an apomict – the embryo arises without fertilization. Identification of apomicts is important, for if the genes controlling this trait can be transferred by genetic transformation technique into a crop plant the transformed plant can produce generations of genetically identical plants without forming seeds.

Artificial induction of fruiting

Since seed development is at the core of embryology, PM was always thinking of the ways in which embryology could be put into practical uses. His 'book' gives examples of plants where inter-generic or inter-specific crosses for creating new varieties of crops had failed for lack of precise knowledge of embryology. Where exactly is the embryological block – in pollen germination on foreign stigma, or the failure of pollen tubes to grow in the foreign style of the ovary, failure of pollen tube to enter into the ovule through the micropylar opening, or the abortion of embryo following fertilization? Guided by the precise understanding of the block in embryogenesis, corrective operations could be devised to circumvent the problem. For example, one of PM's students, Kusum Kanta, circumvented incompatibility and achieved seed set by intraovarian pollination in some plants belonging to the family Papaveraceae[12,13]. In this technique a suspension of pollen grains is directly injected into the ovary using a hypodermic syringe. The technique is analogous to artificial insemination (AI) in which semen is directly installed in the uterus. This work underscores that knowledge of the diversity of plants, and thoughtful choice of a plant material for experiments, is very important for success. It also reminds us that excessive dependency on a model plant such as *Arabidopsis thaliana* which is widely used today, may not answer all questions in biology. Diversity of plant life must at least dimly reflect the diversity of research problems.

Because the plant embryo is attached to the maternal plant tissue by a long suspensor cell, an unanswered question is what chemical substances does the embryo receive from the plant until the seed falls on the ground and the embryo can grow independently? This investigation required that smaller and smaller embryos be manually dissected out from ovules and cultured in nutrient media of defined chemical composition[14]. With expertise gained in designing nutrient media, the work on culturing a variety of tissues from plants was expanded with rewarding results. I select two examples: Culture of anthers of a weed *Datura innoxia* growing in the campus resulted in production of haploid embryos[9,10]. The culture of floral buds of another weed *Ranunculus scleratus* gave crop of embryos arising from the epidermis of the explants[15]. These observations reinforced the concept of totipotency of plant cells.

A vision for the future

In the 1960s, biology was becoming molecular. Traditional plant embryology required a paradigm shift to answer outstanding questions, for example, would the seed germinate without double fertilization and the formation of endosperm? How does double fertilization reprograms cellular biochemistry and trigger the developing seed to accumulate nutrients (that is, become a 'sink')? Clearly the traditional botany will have to be reoriented towards physiology and biochemistry and genetics and the new students will have to be given practical experience in techniques of biochemistry and molecular biology. With his personal contacts, PM helped young colleagues to secure postdoctoral research fellowships abroad with scientists doing cutting edge research in plant embryology. He maintained contacts and invited some scientists to visit India and give lectures, and stay for short periods to hold workshop and demonstrate new techniques to the research workers.

One of the problems that fascinated and challenged PM was to extract a live plant egg from the embryo sac, fertilize it in a test tube with a sperm cell extracted from a pollen grain, the two mixed on some artificial medium, and the zygote reared into a complete plant! Recently (2010), R. G. Edwards (b. 1925) and Patrick Steptoe were awarded the Nobel Prize in Physiology or Medicine for successful creation of the world's first test tube baby. The similarity in the aims of both human and plant embryology is striking, although in the plants the presence of a cell wall that binds the adjacent plant cells together, making manipulations of separating live gamete cells very difficult if not impossible. Recently, live egg cells and zygotes were isolated using microcapillary connected micropump from enzyme-treated ovule of *Alstroemeria*[16]. Kranz and Lorz[17] in Germany isolated single sperm and egg cells from maize embryo sac and fused these cells *in vitro* by applying an electric shock. Following fusion, the *in vitro*-produced embryo underwent similar pattern of embryogenesis and produced multicellular embryo just as in the normal maize plant. Plant embryology is poised for exciting advances.

Accolades

Following a visit to Delhi, the Caltech plant biochemist, James Bonner, known for his researches on chromatin biology in plants visited the Delhi School. Bonner wrote an article[18] in which he summarized his impressions:

> 'Each time I go to a meeting of botanists and hear the many things they are finding out, I begin to worry that everything about botany will be known, and then what will botanists do? Anyone who has visited the University of California at Davis in the past few years knows the sense of excitement which pervades the anatomy laboratories, as Katherine Esau, Vernon Cheadle, and their allies work out in detail the anatomical facts of plant development. The same may be said of Professor Maheshwari's group in Delhi and of other groups throughout the world.'

And, an English biophysicist R. D. Preston, FRS, Professor of Plant Biophysics and Head of the Astbury Department of Biophysics at University of Leeds (author of *Physical Biology of Plant Cell Walls*) who had reviewed some published work by PM commented as[19]:

> 'One of the most remarkable developments of our time in plant sciences has been the way in which hitherto purely observational regions are progressively becoming experimental or even mathematical. One case of the former is the remarkable developments in embryology at the hands of Professor Maheshwari and his colleagues and students.'

Honours and awards

PM rarely, if ever, talked of the honours and awards bestowed upon him. We learned about these only through reports in the newspapers. During the International Botanical Congress held at Paris in 1954, PM was conferred the Honorary degree of Doctor of Science. Five years later, in 1959, the McGill University in Montreal honoured him for his contributions to plant embryology. In 1966, PM was elected a Fellow of the Royal Society, London. He died shortly thereafter.

Concluding remarks

Plant embryology developed from observations by the ancient naturalists that a non-fruit bearing female date palm would set seeds only if dusted by the inflorescence from a male palm. This observation led to the discovery of sex in plants, of fertilization of gametes, of the formation of an embryo with a root and a shoot end, and the formation of nutrient-rich endosperm tissue by the unique process of double-fertilization. The core of plant embryology encompasses knowledge of the male and the female gametophytes, of the process by which fertilization occurs to produce single-celled zygote, of the programmed cell divisions that occur to form a multicellular species-specific embryo. Today, with the basic events in seed development elucidated[17,21,22], plant research has entered into a new era in which genetics, molecular and cell biology approaches offer guidance for developing crops producing better quality seeds. P. Maheshwari was ahead of his time.

Glossary

Androgenic haploids: Haploid embryos produced from microspore mother cell by culturing anthers.
Angiosperm: Plants producing seeds covered by integuments that harden to form the seed coat.
Apomixis: Formation of seeds by a process not involving fertilization of egg cell.
Chromosomes: Condensed form of chromatin visible under microscope. Contain DNA.
Descriptive embryology: Study of developmental processes that take place in a plant from the initiation of sex organs to the maturation of embryo.
Double fertilization: The act of fusion of one of two male gametes (cell) brought inside the embryo sac by pollen tube with the egg and the second male gamete with the fused polar nuclei, resulting in the formation of endosperm.
Embryo culture Growth of excised globular embryos on artificial nutrient medium.
Embryo sac: A cell in the developing seed containing the egg apparatus, the central cell containing polar nuclei and the antipodal cells.
Endosperm: The nutritive tissue in a seed for the developing embryo formed as a result of double fertilization. The endosperm id formed by multiple divisions of primary endosperm nucleus.
Experimental embryology: In vitro modification of processes underlying the development and differentiation of the embryo.
Gymnosperm: A group of plants in which the seeds are not enclosed inside the seed coat.
Haploid: A plant containing half the number of chromosomes (n) in each nucleus of the cell than normal diploid ($2n$).
Intraovarian pollination: Injection of pollen grains suspended in a suitable liquid nutrient medium into the ovary and achieving pollen germination, pollen tube entry into ovule and fertilization.
Male cells: Male gametes formed in pollen and transmitted into embryo sac through pollen tube.
Nucellus: The central portion of a seed in which embryo sac develops.
Pollen tube: A tubular structure formed by the germinating pollen that penetrates into stylar tissue for delivery of male gametes inside embryo sac.
Seed: Propagule of a flowering plant containing an embryo, endosperm and the seed coat.
Somatic embryo: Embryo (as opposed to zygotic embryo) produced from any cell other than egg cell without involving fertilization.
Zygote: Fertilized egg cell.

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