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Embryology of flowering plants: Then and now – A Tribute to Professor Panchanan Maheshwari on his Birth Centenary

Panchanan Maheshwari chaired the Department of Botany at the University of Delhi from 1950 until his demise in 1966. In his book *An Introduction to the Embryology of Angiosperms* which became a classic, he synthesized the descriptive and phylogenetic aspects of plant embryology. Importantly, he articulated the value of experimental embryology. He trained a large number of research scholars who have contributed significantly to the advancement of this subject. Maheshwari was the first to initiate the integration of analytical and plant cell and tissue culture techniques to embryological processes. This approach has helped plant scientists in understanding the causal aspects as well as in applying the results to crop improvement. Maheshwari could be justifiably considered the father of 'experimental embryology of flowering plants'.

With advances in molecular biology and the availability of a model system such as *Arabidopsis thaliana* (aptly called the *Drosophila* of plant biology), experimental embryology has become a frontline area of research and is being actively pursued in several laboratories in the world. The effective integration of electron microscopy, protoplast technology, genetics, and cell and molecular biology has given answers to long standing questions and has opened up new challenges to be pursued.

The year 2004–2005 marked the birth centenary year of P. Maheshwari. We had not originally planned to bring out a special section in *Current Science* for Maheshwari. A few articles were published remembering him. It dawned on us later that we should honour him for his originality, and for stimulating research to pursue a whole line of work. The most fitting way was to take stock of the developments in embryology by bringing out reviews by leading scientists. We invited leading authorities in the field to contribute to the special section. The response was overwhelming, in spite of the shortage of time. We extend our gratitude to all of them. Unfortunately, the first review by Peter Endress entitled 'Links between embryology and evolutionary floral morphology' was published in a regular issue of this journal (*Curr. Sci*., 2000, **89**, 749–754).

We are hopeful that these papers would benefit students, researchers and teachers of embryology and encourage those specializing in integrative biology, notably molecular biology in India, to study embryological problems.

In the introductory article (**page 1820**) we have traced the origins of experimental embryology in P. Maheshwari's school. The pioneering studies made on *in vitro* culture of ovaries, ovules, embryo and endosperm, and those dealing with the analytical and applied aspects of the control of fertilization, adventive embryony and androgenic haploids have been recapitulated and linked to subsequent developments.

The seat of sexual reproduction in angiosperms is the flower, a modified shoot. Embryology begins with the initiation of the floral meristem. During Maheshwari's lifetime there was hardly any information on the controlling factors that determine the differentiation and development of floral organs, although a hypothetical graft-transmissible substance, florigen, had been proposed. In recent years, an enormous amount of knowledge has accumulated on genetic control of flowering in *Arabidopsis.* Usha Vijayaraghavan *et al.* (**page 1835**) have presented the interplay of environmental factors and endogenous cues that trigger the initiation of floral meristem. They have described the role played by regulatory genes which activate or repress floral initiation. Further, they have emphasized that a balance between floral repressors and floral activators fine-tune the temporal and spatial control of floral meristem specification, its maintenance and determinate development.

In the article that has already appeared (*Curr. Sci*., 2005, **89**, 749–754), Endress has analysed the links between embryology and evolutionary floral morphology based on molecular developmental genetic studies during the past 15 years and on comparative investigations made on the diversity of extant and fossil plants. He has given particular attention to ovules, embryo sac and stamens in the discussion. He has emphasized the need for interdisciplinary collaboration for further advances in this area.

The female gametophyte (embryo sac) contains a small number of cells and develops inside the sporophytic tissues of the ovule in a coordinated way; it provides an ideal system to study critical events in development. In the light of lack of information on the mechanisms which determine the development of female gametophyte, it had been termed the 'forgotten generation'. The situation has changed considerably in recent years. Brukhin *et al.* (**page 1844**) explain the recent investigations carried out on molecular and genetic aspects of embryo sac. These include identification of gametophytically acting genes, documentation of gametophytic mutants at different stages of embryo sac development and some of the new approaches which can be profitably used in further studies. Thus the female gametophyte is no longer the 'forgotten generation'.

Pollen grains have been used for analytical studies for several decades. Extensive data have been gathered on their structure and function. One area that has shown remarkable progress only in the past 10–15 years has been on the cytoskeleton elements which play a crucial role in pollen function. Cai *et al.* (**page 1853**) report on the assembly and organization of actin filaments and microtubules during pollen germination and pollen tube growth. They have also highlighted the function of cytoskeleton elements and their associated proteins in the movement of organelles and the tip growth of pollen tubes. On the basis of available evidences these authors have presented an integrated model.

Double fertilization is an exclusive feature of the flowering plants. It has been a difficult problem to investigate because it occurs in the embryo sac, deeply embedded in the tissues of the ovule and the ovary. A beginning was made to overcome the accessibility problem by Maheshwari and his associates by eliminating the stigma, style and the ovary and bringing the ovule and pollen grains together on the nutrient medium. It is now possible to effect the two fertilization processes *in vitro* using isolated sperm, egg and central cell protoplasts and promote the growth of the embryo and endosperm. Okamoto and Kranz (**page 1861**) highlight the progress made with this technology in elucidating the mechanism of early embryonic patterning in higher plants. They have outlined a series of experiments which have enabled them to detect and isolate up- or down-regulated genes in the two-celled embryo, apical cell, basal cell, and multicellular embryo and have highlighted the potential of *in vitro* fertilization technology in unravelling the mysteries of double fertilization and embryo development.

Haploids have immense potential in both fundamental and applied areas of crop improvement programmes. However, because of their rare occurrence in nature and uncertainty of their induction, their application could not be exploited until recently. The induction of androgenic haploids in cultured anthers of *Datura* by Guha and Maheshwari at the Delhi school changed the haploid scenario completely. The progress made since then has been phenomenal. Many improved cultivars have been developed in a number of crop species through the haploid pathway. Datta (**page 1870**) has briefly reviewed the progress made, especially the role of several important factors that influence haploid induction. He has also discussed the advances made and prospects of haploids related to artificial seeds, marker-assisted selection, genomics and transgenesis.

Apomixis, although known since long, has largely remained an academic curiosity. The success of hybrid seed technology in increasing crop productivity and the possibility of fixing hybrids through induction of apomixis (which would enormously simplify hybrid seed technology) has greatly stimulated research on apomixis. Bhat *et al.* (**page 1879**) discuss the potential strategies for transmitting apomictic genes to crop plants through the techniques of molecular biology and biotechnology.

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Modelling of methane emissions

Indian scientific research on rice cultivation has been targeted primarily at enhancing crop productivity for the wide range of soil and climate conditions across India. With the understanding that rice paddies are a major source of atmospheric CH_4 and N_2O, there is a need for careful evaluation of the source strength of this ecosystem, and of the influence of soil, water and crop management practices on both grain yield and greenhouse gas (GHG) fluxes. A major challenge in meeting this objective lies in reducing the large uncertainties associated with regional and global level estimates of GHG emissions. From last few years data from field measurements and laboratory incubations have been accumulated. Advances are necessary to meaningfully upscale measurements to a regional or global scale. The DNDC model was calibrated and tested against the experimental data on CH_4 emission from rice fields of CRRI, Cuttack (**see page 1904**). Simulated seasonal CH_4 flux sensitivities were evaluated for air temperature, soil pH, soil texture, and soil organic carbon content. The sensitivity was also tested to management parameters, viz. the amount and type of fertilizer applied and degree of flooding/draining.