Indra K. Vasil

How did you spend your career?

I grew up in a small village in one of the poorest regions in northeastern India, located just a few miles from the border with Nepal and within sight of the mighty snow-clad Himalayas. My parents encouraged, motivated, and supported my brother and me to get as much education as possible. Some of my motivation also came from reading the hundreds of books in my father's personal library, which gave me a glimpse of the wider world, with all of its wonders and opportunities.

After graduating from high school in 1948 (a year after India gained independence from colonial rule), I left home at age 16 and enrolled at Banaras Hindu University (BHU) for a bachelor of science degree, majoring in botany, geology, and zoology. BHU, in contrast to other Indian universities, was a truly national university as it had a very diverse faculty and a student body representing all regions of the country. It has been consistently ranked among the top universities in India. It is situated on the banks of the river Ganges in Varanasi, a large and one of the oldest inhabited cities in the world.

At the time of my graduation from BHU, I was considering pursuing further studies in fish biology or paleobotany, but I changed my mind after taking a course on sexual reproduction in angiosperms by Y. S. R. K. Sarma. In July 1952, I joined the master of science program in botany at the University of Delhi (DU) under the leadership of P. Maheshwari,



one of the foremost plant embryologists in the world, and his close associate B. M. Johri.

For my doctoral work I switched to the emerging field of experimental embryology to study the physiology of anther and pollen development. Because neither of my advisers had any practical experience in these areas, I had to rely entirely on extensive reading of the literature and correspondence with experts abroad, including R. A. Brink (University of Wisconsin, Madison; UW), Hans F. Linskens (University of Nijmegen), Arnold Sparrow (Brookhaven National Laboratory), and J. Herbert Taylor (Columbia University). O. J. Eigsti, an American geneticist visiting Delhi, showed me how to collect fresh pollen and introduced me to the hanging drop culture technique. Kenneth V. Thimann (Harvard University), who was spending a sabbatical at Delhi, became interested in my work on the role of boron and various sugars in pollen

germination and provided valuable guidance, and he helped in the preparation of my manuscripts for publication.

I obtained excellent growth of pollen of many dicot species but found pollen of cereals, except pearl millet (Pennisetum americanum), nearly impossible to culture. Sugars, which play a metabolic as well as an osmotic role, and boron are both required for pollen germination and pollen tube growth. Gibberellic acid and cytokinin (then known as kinetin) had just been discovered and were not commercially available, so I wrote for them to P. W. Brian (Imperial Chemical Laboratories), and Folke Skoog (UW), respectively. I found that both of these new hormones supported development of early meiotic anthers, at least up to microspore formation.

The results of this early work were published as single-author papers in Science, Nature, Journal of Experimental Botany, American Journal of Botany, and other journals (including a major invited review with B. M. Johri in Botanical *Review*). This helped me gain some recognition among my peers. Philip R. White (Roscoe B. Jackson Laboratory), a legendary and revered figure in experimental plant biology, wrote to me after reading my papers in Science and offered suggestions and encouragement for further work. Later I had the great pleasure of meeting him several times and found him to be exceptionally kind and supportive of young scientists.

Soon after receiving my PhD in 1958, I was appointed lecturer

(assistant professor) in botany at DU. At the time I earned tenure, I was considering going abroad on sabbatical and had received offers from Linskens and Herbert Stern (University of Illinois at Urbana-Champaign). At the same time, I was awarded a Fulbright scholarship. Vimla Negi, a fellow botanist whom I had met at Delhi and married in 1959, and I left Bombay in the summer of 1962 with our infant daughter on a P & O Liner to join Stern's group to work on the molecular biology of meiosis. Air travel was not yet very common, and traveling by sea gave us the opportunity to visit famous historical and architectural sites in Aden (now Yemen), Alexandria, Cairo, Naples, Pompei, and Rome.

I was fascinated by the exciting advances in cell culture research being made in the laboratories of Albert C. Hildebrandt (UW), Skoog, and White, as well as other luminaries such as John Pierre Nitsch (Gif-sur-Yvette, France), Jacob Reinert (Berlin, West Germany), F. C. Steward (Cornell University), and Herbert E. Street (Leicester, U.K.) whom I had met at a symposium in Delhi in 1961, where Nitsch and Steward led a toast and cheers to Vimla and me on our becoming first-time parents. I joined Hildebrandt's laboratory in June 1963 after talking to him at a meeting organized by White; he also offered a position to Vimla.

Our time in Madison was most enjoyable, rewarding, and productive. I worked on photoautrophic growth of plant cell cultures. This work was supported by the U.S. Army and was a prelude to current

research supported by NASA and others as a possible source of food during space travel. My other project was on induction and analysis of somatic embryogenesis in Petroselinum hortense and *Cichorium endivia,* the latter being the first example of in vitro somatic embryogenesis outside the umbellifer family. The results were reported in American Journal of Botany, Planta, and Science. Vimla's work, published in two papers in Science and another in *Planta*, provided the long-elusive proof of the totipotency of plant cells by documenting the growth of isolated single cells obtained from tobacco cell suspension cultures into mature plants.

I found the bureaucracy and rigidity of working conditions in India to be dispiriting and resigned from DU. I was surprised and impressed by the merit-based academic system in the United States and wondered why the same could not be done in India. Soon after returning to India late in 1965, I received offers of senior positions in national laboratories in Bombay, Pune, and New Delhi, as well as a university faculty position at the University of Punjab (Chandigarh). They all offered a comfortable life, but none provided any opportunities for continuing my research.

Afraid of losing my academic relevance by remaining inactive for a long time, I accepted the position of associate professor of botany at the University of Florida (UF) and returned to the United States in 1967 on an immigrant visa. It was one of the most difficult and consequential decisions of my life. Vimla and I have thrived in our personal and professional lives with the freedoms and opportunities guaranteed to all Americans. None of this would have been possible had we stayed in India.

At UF I built my research program from scratch and was frustrated by the time it took to have a functional laboratory and accept graduate students. Concurrently, I also developed and taught two new graduate courses (Developmental Biology of Flowering Plants and Plant Cell Culture and Biotechnology) and an undergraduate course (Plants in Human Affairs). In the early 1970s, there was much excitement about the isolation, culture, and fusion of plant protoplasts, along with uncritical speculation that such methods could be used to produce useful hybrids that were unattainable through conventional breeding. Although all of the early work involved two model species (tobacco and petunia) that were easily manipulatable in vitro, there was the assumption—in spite of a long history of failed attempts with important food crops—that success with them could be extended to important crops.

At conferences and in publications, I highlighted the experimental challenges being faced in the application of the new methods to cereals and legumes and urged more sustained and focused efforts to overcome them. In 1974, Vimla joined my laboratory supported by grant funds and later as a research faculty member. To practice rather than just preach, we started culture of maize and sorghum tissues in

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an attempt to regenerate plants as well as establish cell suspension cultures that could be used to obtain protoplasts. Predictably, the experiments were frustratingly unsuccessful.

Then I remembered that in my earlier work, pearl millet had proved to be an exception among cereals. Fortunately, Stan Schank, a colleague in agronomy, had some young plants growing in a small plot on campus. We placed small segments of young inflorescences in culture and were excited to observe the development of regenerable embryogenic callus, and we were soon able to grow adult plants from the somatic embryos that were strikingly similar to sexual embryos. Our training in plant embryology at Delhi was valuable in identifying the embryogenic nature of the cultures and early-stage somatic embryos. Not long after that, we also obtained stable embryogenic cell suspension cultures.

Critics of the work countered that these results were limited to a single species. Yet in a long series of publications between 1979 and 1990, we described similar results with cultured immature embryos, young inflorescences, and bases of young leaves in several species of Pennisetum and Panicum and in maize, rice, rye, sorghum, sugarcane, and wheat. These provided the first clear and unambiguous structural, anatomical, and ultrastructural evidence of the formation of somatic embryos. We also successfully regenerated plants from cell suspension cultures as well as protoplasts. These results

have been widely cited and emulated and led to my being included in the original member group of the most highly cited researchers in plant biology.

We fused protoplasts isolated from cell suspension culture lines to obtain somatic hybrid tissues in several combinations, but none of these gave rise to plants. Indeed, the promise of producing useful somatic hybrids by protoplast fusion has proved to be largely elusive. We obtained transient expression of electroporated DNA into protoplasts in several species of cereals. This method has been used extensively for rapid molecular analysis of gene function. Next, we used the newly invented biolistics method to introduce genes for herbicide resistance, insect resistance, and improved bread quality into embryogenic callus and immature embryos of wheat and genes for herbicide resistance into immature embryos of rye, and we obtained transgenic plants stably expressing the transgenes.

I was proud to receive a letter from Norman Borlaug, father of the Green Revolution and Nobel Peace Prize laureate, offering congratulations and encouragement. I had first met him after my presentation on somatic embryogenesis in cereals at a small private meeting in Orlando, Florida, in 1983. He showed great interest in our work and visited my laboratory several times, and he always took the time to talk to everyone in our group, a real treat for everyone. Another valued colleague was Jeff Schell, who was most supportive and visited us several times and hosted

Vimla and me at the Max Planck Institute in Cologne, Germany.

Somatic embryogenesis has been a uniting theme during much of my research career, beginning with the early work in Wisconsin and later throughout my tenure at UF. Our more than two decades of experience with cereals and grasses showed that the type and quality of the explant are critical for the production of embryogenic cultures. The explants (immature embryos, segments of young inflorescences, and basal parts of young leaves) must be obtained from healthy and vigorous plants, at precise morphological and physiological stages of development when they contain developmentally uncommitted and mitotically competent cells. The window of opportunity is narrow and declines sharply. Embryogenic ability of the explants is closely associated with the type and level of endogenous plant growth substances. Like their zygotic counterparts, somatic embryos develop from single cells and give rise to nonchimeric plants that show little to no somaclonal variation because there appears to be a strong selection in favor of genetically normal cells.

In keeping with my long-held commitment to maintaining worklife balance, I had planned to retire in 1997, at age 65, but delayed it by two years to finish our final major project on transgenic wheat. On the eve of my retirement in 1999, UF and Monsanto established an endowed chair in plant molecular biology. I was delighted that my large laboratory with all of its equip-

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ment was inherited by Mark Settles, who was appointed the first Vasil-Monsanto Professor of Plant Cell and Molecular Biology. In my desire to have ready access to books and journals that I needed to consult for teaching, research, and writing, I had collected about 3,000 books and complete sets of about 20 journals going back to the early 1950s. This entire collection was gifted to UF and is housed in the Vimla and Indra Vasil Library and Reading Room.

I kept my office after retirement and remained active until 2012, when we moved to the Silicon Valley in the San Francisco Bay area to be near our daughter and her family and our only grandchild. I keep up with the literature and new developments by regularly reading Science, Nature, Plant Physiology, The Plant Cell, and about 20 other journals. I am delighted to see the progress that is being made, and proud to come across the names of many of my former students and postdocs who now lead their own prominent groups at universities in the United States, Austria, Canada, Germany, New Zealand, and elsewhere, as well as many new promising scientists.

What do you consider your most important contributions to plant science?

Until about 1980, there was much pessimism and disagreement about the possibility of in vitro genetic manipulation of cereals owing to their perceived recalcitrance to in vitro culture. It had been suggested that such recalcitrance might be genetic in nature and insurmountable. I firmly opposed this proposition. Our work demonstrated that

cereals are not inherently different from other plant species in their competence for totipotency, and our success encouraged many others to begin work on cereals. The theoretical framework and experimental strategies that we developed have withstood the test of time, and their utility has been amply demonstrated with the production of transgenic plants with many useful agronomic traits in all of the economically important cereal and grass species, some of which are now grown on large acreages in many countries. Indeed, all of the transgenic cereals, as well as other transgenic crops such as soybean, cotton, and tree species, are also derived from embryogenic cultures.

I have had the good fortune of having an excellent international group of talented, motivated, and highly productive graduate students, postdoc and research associates. None of what I have described would have been possible without them, and without Vimla's long association with my laboratory. To them all I owe a deep sense of appreciation and gratitude. Furthermore, I have always been very conscious of the kindness and encouragement I received from many giants of plant biology and have endeavored throughout my career to repay at least some of this debt by being helpful to young scientists.

In 1987, a small group of colleagues and I spearheaded the establishment of UF's Interdisciplinary Center for Biotechnology Research. In addition, I led the founding of the highly rated campuswide Graduate Program in Plant Molecular and Cell Biology in 1989 and the Florida Genetics Symposium held annually since 2007. The graduate course in plant cell culture and biotechnology that I introduced at UF was the first of its kind in the country. From 1968 to 1974. I served on the Education Committee of the Tissue Culture Association (now the Society for In Vitro Biology [SIVB]), which was tasked with building the new W. Alton Jones Cell Science Center in Lake Placid, New York, and developing that society's education program. In 1971, I organized and directed the first international training course at the center soon after its opening and did so again in 1973 and 1978.

As convener of the Panel on Plant Cell Biology and Biotechnology of the International Cell Research Organization from 1982 to 1996, and as founding director of the Biotechnology Action Council (BAC) of UNESCO from 1990 to 2001, I organized and codirected with a local host more than a score of advanced training courses in Santiago (Chile), Shanghai (China), Cali (Colombia), Turrialba (Costa Rica), Godollo (Hungary), Irapuato (Mexico), Rabat (Morocco), Ibadan (Nigeria), Pretoria (South Africa), Madrid (Spain), Kiev (then in the USSR), and Caracas (Venezuela). A number of international faculty participated in each course. Students were recruited from around the world, preferably from developing countries, and bore no costs except for their travel. Under the auspices of BAC, we

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awarded nearly 500 fellowships to students from the developing world to work in any laboratory of their choice for up to three months, and opened Biotechnology Education and Training Centers in Bethlehem (Palestinian Territories), Godollo, Irapuato, Pretoria, and Qingdao (China) for regional scientists. The training courses and fellowships provided hundreds of international students the rare and unique opportunity to meet and learn directly from some of the best minds in plant biology.

Early in my career I had become aware of the discrimination faced by women in academia. To address this injustice, I deliberately accepted equal numbers of men and women for graduate studies or postdoctoral work in my laboratory, in the training courses I organized, and in the hundreds of fellowships offered under the auspices of BAC. It is gratifying to see that discrimination against women in academia has now attracted national and international attention and that steps are finally being taken to redress this grave injustice.

When did you become a member of ASPP/ASPB? 1989.

How did the Society impact your career, and what motivated you to become a Founding Member of the Legacy Society?

When I came to the United States, I knew hardly anyone in the scientific community except eminent plant biologists such as James Bonner (Caltech), Arthur Galston (Yale), F. C. Steward, and Ken Thimann, whom I had met in Delhi. I had corresponded with a few, and I knew some through their publications. I joined the Botanical Society of America, ASPP, and SIVB, and I attended and made presentations at their meetings, which were valuable in making professional and personal contacts and in networking.

Learning from history and awareness of the historical context are important for our personal as well as professional lives. ASPB continues to contribute to the professional development of thousands through its superb journals and annual meetings. The Legacy Society will complement this by being a valuable repository of historical knowledge that can provide useful guidance to the younger generation.

What important advice would you give to individuals at the start of their career in plant science?

To them I commend the following two quotations:

"If I have seen further it is only by standing on the shoulders of giants." (Isaac Newton)

"Research is to see what everybody has seen and think what nobody has thought." (Albert Szent-Györgyi)

Finally, I repeat what I have written before: Be bold, think outside the box, and challenge conventional wisdom. Learn from and respect history, and be a kind and giving mentor.

Academic Family Tree

https://academictree.org/plantbio/ tree.php?pid=803782