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I am writing this near the end of October 2020. The historical circumstances we are in, with societal divides in the United States laid bare by events during the COVID-19 pandemic, have persuaded me to write about my experiences from the fringe of the academic environment that nurtured and shaped my career. If hindsight has any value and a reflection of my observations resonates with a few young students who are anxious about penetrating this profession, it is perhaps good enough to share.

How did you spend your career?

I consider my education and a career in academia to have been an inevitable journey, but my career in plant biology was accidental. Born and raised in Hong Kong, I grew up in an oasis filled with adult discussions in literature, history, social, and political issues, something rare and totally irrelevant to a society built on material realities. Uprooted from their own relatively privileged but socially principled upbringing, my parents had prepared my brother and me for an education in the United States. The reason was not only the quality, opportunities, and seeming equality for everyone who tried what the United States had to offer, but also the social and political appeal of what the country stood for at the time (it is poignant at this moment to recollect such a moment in history). This background pretty much set the course for me until I completed my PhD.

Many chance encounters, and perhaps my always viewing the grass as greener on the other side, rendered my career in plant biology an accidental journey. As a PhD student, I studied the genetic and biochemical regulation of aminoacyl-tRNA synthetases. In hindsight, I believe my PhD training benefited from having taken place in a period when the traditional stringency of biochemical studies still prevailed while molecular biology was taking center stage in the lab. More importantly, opportunities for molecular investigations were opening up for many complex biological systems. Perhaps around 1980, when I attended a large society meeting the name and location of which I do not recall, a talk by Eugene Nestor on emerging knowledge about Agrobacterium–plant cell interaction and the Ti plasmid T-DNA inspired an instant interest in me to learn more about this system, though without any expectation that it would be the turning point of my career to plant biology.

My postdoctoral work, thanks to an adviser who was always eager to try a new thing, provided a golden opportunity to work in the Jeff Schell/Marc Van Montagu lab in Belgium for several short durations and gain experience in the Agrobacterium system as it was being built from the ground up. During this time, as I was learning and becoming interested in the chloroplast–nuclear interaction, two lectures among many at the Harvard BioLabs stand out as having an extraordinary impact on me for their biological elegance. One, by Adrienne Clarke, was on the *Nicotiana alata* self-incompatibility system; the other, by June Nasrallah, was on the *Brassica* self-incompatibility system. These lectures sowed the seeds for my interest in plant reproduction, though without the specialized knowledge or genetic resources, it was far from my mind that it would be something I could study.

An interesting and provocative paper published by Elizabeth Lord in 1989 ("Directed movement of latex particles in the gynoecia of three species of flowering plants," in *Science*) was probably the defining encounter with plant reproduction for me. This study, and her advocacy for the need to understand how compatible pollination is achieved, suggested to me that even for someone without a classical botany background, plant reproduction might indeed be something I could study and find room to develop. I took the rudimentary approach of looking for flower-, pollen-, and pistil-specific genes in tobacco. We published several papers based on this approach

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between 1992 and 1995, including our first paper in *The Plant Cell* in 1993. This laid the groundwork for a pair of back-to-back papers in *Cell* in 1995, an NIH grant the same year, and a DOE grant the following year. More importantly, these works cemented my commitment to research in plant reproduction, in particular how the pistil and pollen interact.

From an uncertain start, we built a relatively strong foundation of results for further development. Unfortunately, and to my surprise, my experience as a graduate student in the Molecular Biophysics and Biochemistry Department at Yale and four years as a postdoc in the Harvard BioLabs had not prepared me for the culture shock I would experience as a faculty member in the Yale Biology Department. I never adjusted to it, finding the environment hard to cope and impossible to align with. I left Yale in 1997. The experience taught me how the inflated personalities of a few and the complacency of some in the comfortable majority can very easily create an inhospitable environment for those seeking an entry, especially those who in one way or another, or even in ways hard to pin down, are different. That was more than 20 years ago. In hindsight, it did not take long for me to realize that it was a good thing to leave behind; this was a rare moment that I look back and reflect upon.

The year 1997 was an important turning point in my career because of my growing realization of the need to add cell biology to my research toolbox. I moved to the University of Massachusetts Amherst (UMass), just a few miles away from Smith College, where I had received my bachelor's degree. It is an area of which I was very fond. UMass provided an excellent cell biology research environment and the opportunity to collaborate with Peter Hepler, whose work with pollen tubes opened my eyes to the beauty of that system. It made me realize that I needed to understand how the pollen tube grows before I could truly explore how the pistil influences pollen tube growth and how pollination can lead to fertilization.

A period of intense cell biological research occupied the bulk of my attention at this time. We published four papers on our cell biology work in *The Plant Cell* between 2002 and 2003. One of these contributed to establishing the central importance of RAC GTPase (ROP in most plant literature) in polarized cell growth, and another described the first observation of auxin activation of these cell membrane–associated molecular switches, a discovery at the fringe of a very deep auxin biology field. These studies occurred during a time when the toolbox for plant research was filling up rapidly, and the phrase "the sky is the limit" seemed to ring true.

It was also during this period that I found myself answering questions from students during seminar visits about how and why I did what I did by saying, "This is exactly what I want to do, and there are these questions I want to answer" rather than giving my typical earlier answer, which was "I just tried my best and landed where life led me, and I am still looking for somewhere to fit in." After my move to UMass, I very quickly realized that the research environment and the accomplishments of its faculty were way underappreciated, and there were many examples of excellent research on campus. These qualities have only improved since then, thanks to the tireless efforts of many senior faculty members and the infusion of many excellent junior faculty.

From an upbringing in a family that was considered "out-of-province folks," a term locals use for people from outside of a province (in Hong Kong, that would be Guangdong province; almost like "foreigners" in the homogeneity of a Chinese society, but without the curiosity that word arouses), to becoming a relatively confident presence in my field, I feel my meandering career journey was traveled almost always on the fringe of the environment in which I found myself. It was traveled often without the passport of formal credentials or visas to scientific fraternities, and perhaps also without my willingness to spend the time and effort needed to apply for them. This could not be helped. However, along the way, the combination of reaching out to learn from others and the generosity of many people, and in turn my willingness to share with others what I had learned and help make their path easier, allowed me to forge many friendships and liaisons. These relationships have made the journey not only possible but also fruitful and enjoyable.

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My meandering scholastic journey was shaped by several unchanging principles I had learned: from my parents, the social responsibility to be a conscientious citizen and ease the path for others; from my doctoral adviser, Dieter S**ö**ll at Yale, the demand for quality in scientific details; from my postdoctoral adviser, Lawrence Bogorad at Harvard, his exuberant optimism in science; and from both of them, the devotion and dedication to work. Though I am sure I did not realize this at the time, in hindsight I am eternally gratefully for the environments they created, and for the friends I was able to make at every step along the way, some of whom I still remain close to. I was fortunate to have an important constant during my academic journey, a husband, Hen-Ming Wu, whose curiosity, imagination, and creativity are still inspiring after so many years, as much as they were exhausting to keep up with. His optimism and insistence on never giving up have sustained me in many of my doubtful moments during a journey that seemed to be constantly changing course, although the possibilities were always exciting to consider.

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

I will leave this for others to consider, but I hope my most important contributions are still in the making. I would, however, relate a few moments in our research that I consider memorable for me. Finding a protein-associated glycosylation gradient in the transmitting tissue of the tobacco pistil and a pollen tube–derived deglycosylation activity that theoretically could generate a self-sharpening gradient at every step of the pollen tube growth process was an intellectually stimulating discovery. This work, reported in 1995, also revived a forgotten assay of semi–in vivo pollen tube growth that displays the pollen tubes in a manner pretty enough to challenge a Christmas card (see picture). The method was tailored by others to suit various plant systems, particularly by Ravi Palanivelu for Arabidopsis, which led to many groundbreaking works in reproduction biology. Observing how the expression of a regulatory protein in a pollen tube can impact its growth led to the exciting realization that we had an in vivo test tube system allowing mechanistic dissection of a complex growth process. Since that report in *The Plant Cell* in 2003, the system has been used in many studies of pollen tube growth regulation.

Seeing actin cables assembled by the actin-nucleating protein formin emanating from the pollen tube cell surface (reported in a 2004 *The Plant Cell* paper) and their incorporation into the hallmark subapical actin structure in growing pollen tubes (reported in 2010) were truly pulse-quickening moments. Our discoveries in the early 2000s that auxin and pollen hydration activate RAC/ROPs in seedlings and pollen, respectively, led to our efforts that identified a receptor kinase, which we called RK10 at the time, as an upstream regulator for these small GTPases. Learning that RK10 was the "goddess" FERONIA and a key regulator of the pollen tube–ovule interaction described earlier by Ueli Grossniklaus's and Fred Berger's labs was more exciting than I could have anticipated. We had planned for the work with seedling root hairs to lead us back to pollen tubes, given the analogy between the two. But it was like a dream come true when it actually connected us back to pollen–pistil interaction. The finding of the FERONIA-to-RAC/ROP linkage, reported in 2010, also informed the broader involvement of FERONIA in plant growth and development, which has become an area of intense research activity by many groups.

It has been an extremely rewarding decade since 2010 as we worked to unfold the mechanisms behind how the signaling capacity of FERONIA is enabled by a glycosylphosphatidylinositol-anchored protein (2015), how in the female gametophyte FERONIA induces pollen tube disintegration to release sperm for fertilization (2014), how its pollen counterparts act in an almost antagonistic way to prevent the pollen tube from precociously bursting during its journey in the pistil (2017, 2019), and how FERONIA prevents supernumerary pollen tube entrance to ovules to avert polyspermy (2020). Gathering and putting the results together were exhilarating moments for the conceptual novelty they revealed and also the technical challenges we had to overcome to get there. We continue to decipher the signaling mechanisms surrounding "FERONIA and her pals" (*Plant Physiology,* 2016), and I hope we still

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will have many exciting findings to report.

So I have to say that the career I accidentally embarked on and the trepidations I felt along the way did have many rewarding moments that made all the efforts worthwhile.

When did you become a member of ASPP/ASPB? How did the Society impact your career, and what was your motivation for becoming a Founding Member of the Legacy Society?

I probably joined ASPP the first year *The Plant Cell* was published (1989), and I had those first issues until very recently. I don't remember being active in the Society during my early career years, probably because of my unfamiliarity with the field. *The Plant Cell* was always a top-quality journal that I aspired to publish in. Later, with growing appreciation of many interesting phenomena in plants, I came to regard *Plant Physiology* as the venue for promoting the breadth of plant biology and facilitating the depths of its understanding. I believe the knowledge disseminated in these two journals has considerably influenced my learning process.

I appreciate the tremendous learning opportunity, for more than 10 years now, of serving as a monitoring and then associate editor for *Plant Physiology* and being able to communicate with and meet many colleagues from rather distant areas in plant biology. The ASPB annual meetings are also great venues to learn about topics beyond my immediate knowledge base. The opportunities to serve on various ASPB awards committees over the years deepened my appreciation of the inspiring accomplishments of many plant scientists from different career stages. I remember when Brian Larkins first contacted me about the Legacy Society; my first thought was what a great opportunity it is for members to show their appreciation for ASPB, the science it represents, and the environment it cultivates for generations of plant biologists. Its vibrancy will be important for the future of plant biology, and who but its own members should help foster that?

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

I really don't think I can add to the wisdom that has been shared in other essays on the Legacy Society webpage. At this time, when many young students find themselves working on the fringe of their academic environment facing forces that seem insurmountable, I hope my experience and perspective as a more or less accidental participant in the plant biology field may help ease the anxiety that they might have while wondering how they will fit in. It's OK to be a bit, or even very, "foreign" to your environment, even when you have actually become very much a part of its core. Always support your environment and be interested in your colleagues, but don't be complacent and afraid to differ when there are justified and critical needs. Have your own compass, observe, and let sincerity and honesty guide you to those colleagues who are willing to get to know you; they will be your friends and allies for the long and exciting journey ahead.

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