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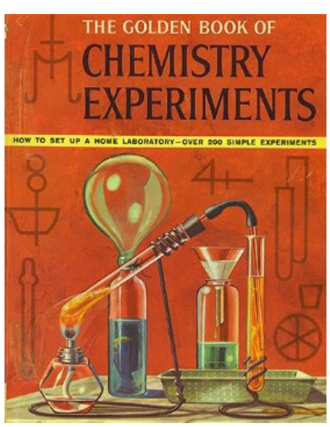
How did you start your career in plant science?

My trajectory into a STEM field probably started when I was nine, with a birthday gift from my parents. It was a book entitled *The Golden Book of Chemistry Experiments* written by Robert Brent and published in 1960. In it were scores of simple experiments that a kid could do with at-home supplies. As inspiring as the book was, I now appreciate the irresponsibility of the author; in fact, the book has been banned from most libraries. Using its protocols, you could make gunpower and rockets, strong acids and bases, and hydrogen balloons, and even manufacture chlorine gas, which I did in my sandbox. From then on, I wanted to be a chemist and continued to perfect my pyrotechnics.

Fast forward to college and my first biology class at the University of Connecticut, which was taught by an inspiring botanist, Terry Webster. I grew up in a rural setting, so I always appreciated gardening, agriculture, and plants in general, but seen through Terry's eyes, that realm was far more complex than I ever imagined. Given my allergy to the sight of blood, the green world was my new focus.



After graduation in 1976, I headed off to DOE (then the U.S. Atomic Energy Commission and later the Energy Research and Development Administration) Plant Research Laboratory (PRL) at Michigan State University (MSU) for my PhD. What a fantastic time! The lab was full of kindred (geek) spirits, and the generous funding at the time allowed us to pursue nearly any experiment, regardless of cost. I ended up completing my thesis work under the direction of Kenneth Poff, who studied light perception, which has been one of my lab's foci to this day. Those four years were some of the best times of my life, and I made many long-lasting friends. I even "helped" MSU win the national championship in basketball in 1979, but that's another story.

Finally, as a postdoc I joined the lab of Peter Quail at the University of Wisconsin–Madison to uncover the mode of action of phytochromes. I guess my claim to fame was the discovery that most phytochrome preparations were actually degraded and that a larger, nonproteolyzed form existed. Through a number of biochemical and spectroscopic approaches, I showed that the missing pieces were actually critical, thus laying the groundwork for all subsequent studies on these photoreceptors.

Then in 1984 I had the good fortune to land a faculty position at Wisconsin. Now with my wife Karen and three kids in tow, it was a special time for the family and me. I don't think there is anything more exciting than becoming an independent investigator and charting your own path—right or wrong. I decided to study how cells break down proteins, using phytochromes as the example given that Peter was still on campus with a lab of 10 postdocs. The novelty of phytochromes was their "in planta" stability as Pr but rapid degradation as Pfr, thus allowing me to uniquely regulate turnover by short flashes of light. From an important tip provided by Joe Varner, an icon of plant biology at the time, I anticipated that the recently discovered ubiquitin/26S proteasome system (UPS) might be involved, and with tireless work by my graduate student John Shanklin and postdoc Merten Jabben, they proved it so. At the time, phytochromes were the first example of a real-life substrate for the UPS, and hundreds of others then followed.

This discovery led me down the paths of trying to understand how the UPS works and understanding what was different about the Pr

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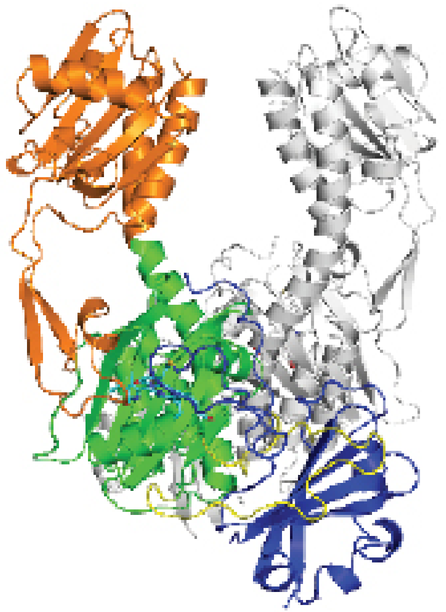
and Pfr conformations that allowed the UPS to distinguish them. Fast-forward 30 years and many papers on the topic, and what we learned is that the UPS is one of the most complex processes in plants: it engages over 6% of the genes in plants such as Arabidopsis, many of which are ubiquitin ligases (or E3s) that identify which proteins should be ubiquitylated. In fact, the system became too complex to study any substrate one at a time, so I transitioned to proteomic analysis of ubiquitylated proteins to look at substrates in bulk and decipher how plants use the UPS to maintain protein homeostasis.

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

I have been fortunate, mainly through the tireless efforts of numerous graduate students, postdocs, and staff scientists, to have participated in a number of influential studies. Besides the breakthroughs mentioned above, key advances were the connections of the UPS to ethylene signaling, the roles of SUMOylation in plant stress responses, and an improved understanding of autophagy. Autophagy, in combination with the UPS, is now considered among the cornerstones for avoiding proteotoxic stress, which is central to both agriculture and medicine. Owing to this importance, the first scientists who unearthed autophagy and the UPS won Nobel Prizes. In recent studies, a talented postdoc, Richard Marshall, single-handedly showed that autophagy might rival the UPS in depth and breadth of influence.



My fondest contributions are related to our lab's understanding of how phytochromes work at the atomic level. Realizing that our discovery of phytochromes in bacteria might facilitate their recombinant assembly, we went without hesitation to exploit these prokaryotic versions for various structure-based techniques, including x-ray crystallography, 2D nuclear magnetic resonance spectroscopy, and later cryogenic electron microscopy (cryo-EM) approaches that were clearly foreign to me. Our advances included the first crystal structures of the photosensory module as Pr and Pfr by Jeremiah Wagner and Sethe Burgie, respectively, and more recently the first full structure of the phytochrome dimer by cryo-EM in collaboration with Huilin Li. I remember Jeremiah showing me his first electron density map of Pr, which allowed him to position the bilin chromophore buried within the apoprotein. I remember thinking I was now "seeing god."

When did you become a member of ASPB?

I joined ASPP in 1977, after my first year in graduate school. Although such an early commitment might now seem odd to many young scientists, we at the MSU–DOE PRL were inculcated with the fact that your participation in graduate school was part of a long-term professional career. So to best forward your career, you needed to join its main professional society—ASPB. I attended not only the national ASPB meetings but also the Midwest Section meetings. A seminal moment at one sectional meeting was me being awarded the "best presentation by a graduate student," which enhanced my confidence and affirmed by career choice.

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

During the early parts of my career, the annual ASPP/ASPB meetings were the best place to hear about breakthrough science and network with others in my field and beyond. Like other ASPB members, I used *Plant Physiology* and *The Plant Cell* as vehicles to publish our work, and I was on the editorial board of *Plant Physiology* for a number of years. Later, when I began to understand that the ability to fund my science was determined by federal granting agencies such as NSF and USDA, I realized that ASPB was intimately connected to my success as much as my lab's progress was. So getting involved in the machinery of ASPB

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was a necessity. Since then, I have served on the Program Committee, numerous awards committees, the Executive Council, the Board of Directors, and the Board of Trustees, and I even was treasurer in 2017–2019. Support for the Legacy Society seemed only natural as a way to pay back and, hopefully, pay forward to future generations.

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

First off, be dedicated to your work and the quality of your science. There are really no shortcuts to having a successful career. Second, having confidence in your approach is nice, but being prepared for alternative outcomes is way better. Science is not often linear. Sometimes the fork in the road provides the most exciting revelations, so be open to the unexpected. And third, the key is asking the right questions and then choosing the best avenue to answer them, even if the approach or technique is unfamiliar.

Having advised graduate students and postdocs on various career pathways, I have found that there are many tracks possible (e.g., research, teaching, policy, industry). Your challenge is to figure out which one best fits your talents, disposition, and personal and family goals. During my time as a graduate student, I once asked Anton Lang, director of the DOE–MSU PRL, what the challenges are in landing a faculty position, which was my goal at the time. He answered, in his famous gravelly voice, “There is always room for great scientists; your job is to become one!”

Academic Family Tree

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