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How did you spend your career?

My first exposure to research in plant biology was as an undergraduate at Purdue University, in the lab of Mike Forman, with my own project on auxin transport in roots. I had the good fortune to also meet Carl Leopold, who took me under his wing and showed me how to work with labeled indole-3-acetic acid (IAA). After getting my BSc in biological sciences, I headed west to Colorado State, where I studied the growth physics of phytochrome-mediated seed germination in the lab of Murray Nabors, one of only two graduate students who worked with Anton Lang, a world authority on the physiology of flowering. I was also guided, usually late into the night, by wonderful discussions on plant physiology and biochemistry with Cleon Ross, who worked on nucleotide synthesis in plants, and John Hendrix, who studied carbon partitioning.

It was Cleon who directed me to the DOE (at that time the Energy Research and Development Administration) Plant Research Lab at Michigan State for a postdoc in the lab of Debby Delmer. Debby had quickly become established as the premier researcher in cellulose synthesis. She had improved protocols to culture unfertilized cotton ovules that produce cellulose fibers *in vitro*, and we used this system to establish the first kinetic data that UDP-Glc is the actual substrate for cellulose synthase. It is hard to believe today, but at that time GDP-Glc was thought to be the



substrate—and to this day GDP-Glc persists erroneously on many metabolic pathway wall charts as the substrate for cellulose synthesis!

Debby always had a grand challenge for everyone in the lab, and mine was to determine the largest molecule that could freely pass through the cell wall. One Friday afternoon, before joining cohorts at a local pub, we plated some sycamore maple cells in liquid culture and plasmolyzed them with mannitol solutions. When I added polyethylene glycol, an osmoticum I used in graduate school to mimic drought, the cell walls collapsed around the plasmolyzed membrane, indicating that the molecule could not pass through—that is, that the wall was acting like a membrane. In the next months, we narrowed down the size range of dextrans that just began to collapse the walls, thus defining the pore size—the freely diffusible space in the wall—to be on the order of 4 nm in diameter, a

value much smaller than expected.

Debby also encouraged us to explore individual projects that we could take with us when we launched our independent careers. My interests from my undergraduate days were focused on how auxin causes growth, and after my experience in Debby's lab, the question was refined to how auxin alters cell wall structure and composition during growth. I chose to use the classic grass coleoptile system, and Debby let me purchase some labeled arabinose and xylose to study their uptake and incorporation into cell walls. I started with oat coleoptiles but found them too small for my clunky paws, so I switched to maize coleoptiles, which were far easier to handle. I found that over 80% of the labeled arabinose became incorporated into the cell wall, whereas label from xylose ended up everywhere. These were really puzzling data to me, but Debby was amused and advised that maybe I should read the well-established literature on the arabinose salvage pathway in plants.

I brought these studies with me to my first and only faculty position at Purdue University, where I have spent the remainder of my professorial career. I'm indebted to Tom Hodges, who discovered the K^+ -activated ATPases involved in ion uptake in roots, for hiring me. One useful skill I picked up in Debby's lab is how to do methylation analysis and gas chromatography mass spectrometry determination of sugar linkage groups. I spent a great deal of my early years at

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Purdue refining and making high-throughput chemical protocols and the use of deuterium labeling to define subtle features of polysaccharide structure and dynamics in grasses.

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

Probably, it is the understanding that flowering plants make two distinct kinds of primary cell walls. My early work on grass cell walls showed that they are completely different from those of dicots. From surveys describing the rich history of research on cell wall structure and synthesis, my postdoc David Gibeaut and I developed models to illustrate the fundamental components and structures of the xyloglucan-rich Type I walls of dicots and some monocots compared with those of the glucuronoarabinoxylan-rich Type II walls of grasses and commelinid monocots. We showed the tremendous dynamics of wall polymers and the recycling of their sugars during growth and development. These findings contributed to reversing the concept of the cell wall as a static box surrounding the cell to that of a dynamic and responsive matrix that is the cell's "sensory panel" of the environment. Grasses uniquely make a (1→3),(1→4)-β-D-glucan during certain stages of development, and David and I demonstrated its full-length synthesis in isolated Golgi membranes. A life-long colleague from Brazil, Marcos Buckeridge, and an undergraduate student, Breeanna Urbanowicz, characterized several features of

the synthesis of mixed-linkage glucan, including its topology on the surface of the Golgi.

Although the mixed-linkage glucan synthase is interesting in its own right, I never lost interest in the structure of cellulose synthase. Another longtime colleague, Catherine Rayon, had cloned and expressed the catalytic domain of a rice CesA8 protein. Together with Lee Makowski, we solved the solution structure of the catalytic domain by small-angle X-ray scattering and showed it to be a two-domain structure, with the class-specific regions, one of two plant-unique sequences inserted in the catalytic core, forming the dimer. Today, we continue to probe the structure of the large, multi-subunit cellulose synthase complex at its site of assembly in the Golgi.

I began a collaboration with Maureen McCann about 25 years ago when she was in the lab of Keith Roberts at the John Innes Center in the United Kingdom. This collaboration has continued since 2003, when she took a faculty position at Purdue. Maureen brought Fourier-transform- and near-infrared microspectroscopy to bear on the structure of plant cell walls, and together with Arabidopsis geneticists Sara Patterson and the late Tony Bleecker and maize geneticists Karen Koch and Don McCarty, we launched a genome-wide research program to characterize mutations in cell wall biosynthetic genes in Arabidopsis and maize. Maureen and I have continued our teamwork both inside and outside the lab (we married in 2011). We have characterized more than 1,200 genes of

Arabidopsis and maize that function in cell wall biology, and we have defined the biochemical function of many of them. Our most recent work was to characterize the expression of these genes in the maize stem during development.

When did you become a member of ASPP/ASPB?

I became a member of ASPP in 1975, mainly to publish my first scientific paper in *Plant Physiology* and to register for my first annual meeting at Oregon State University. I was immediately struck by the sheer number of famous plant scientists at that meeting. I had read many of their papers, but I never dreamed I would actually meet them. Imagine the doors of a hotel elevator opening and being met by Anton Lang, Hans Kende, Jan Zeevaardt, Russell Jones, and Joe Varner, and then Anton asking in his seemingly austere Russian accent, "I understand you have something to tell me about lettuce seed germination?" (My adviser had put him up to it.) Gulp! I gave my first ASPP talk at that meeting. I remember the stress of that experience as I waited my turn to speak in a room full of these stars of plant biology.

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

The terror of giving my first talk at an ASPP meeting gave way to euphoria afterward, when so many of these famous scientists came up to talk with me about the work I

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presented. I learned that the “stars” were not austere and unapproachable, but really cared about the next generations of plant biologists. We had great discussions and even “arguments,” but we had great fun as well. I had found my scientific home, and I couldn’t wait until the next meeting.

I published quite a lot of my lab’s research in *Plant Physiology* and *The Plant Cell*, as these are the best journals in plant biology, but I didn’t think about involving myself in leadership until 2000. I served as elected member of the Executive Committee, then as secretary, and finally as president of ASPB. While I was serving on the Executive Committee, we were confronted with the challenge of maintaining a Society that is funded primarily by its journal subscriptions in the age of open access publication. It was then that we began thinking of developing a foundation to increase

the ASPB endowment and ensure the financial security of the Society while expanding its good works, including fellowships, travel awards, and other means of support for young plant scientists.

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

First, attend ASPB annual meetings. Relish the larger community of plant biologists and the close friendships that come with it. Far too many people tell me that they get so much more out of smaller, specialty meetings of their discipline. You need to network with the broader community of plant biologists through presentations of posters, symposium talks, and workshops that enhance your visibility outside your specialty. Don’t be afraid to ask a question in a symposium. Get involved in region-

al ASPB meetings—this is likely the venue for your first scientific talk.

Second, read the “old” literature. Hans Kende once said that we fool ourselves in thinking that “photocopying is knowledge.” Too often, we download what we think are key articles to search for what are supposed to be the original works, but then never really read the articles. If we did, we might discover that the cited works often don’t actually show what is reported. Try to locate and read the “ur-references” by digging as deep as you can. Don’t rely on others’ citation of previous works. That said, reading can be overrated compared with the knowledge gained from a simple experiment, regardless of whether or not it has been done before.

Academic Family Tree

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