Christoph Benning

How did you spend your career?

I started my career working on auxin transport at the University of Freiburg in Germany, mentored by Rainer Hertel. As fortune had it, in 1985 I had just received a 10-month international travel fellowship from the German Scholarship Foundation when Winslow Briggs and Hans Kende visited Rainer on their way to the International Conference on Plant Growth Substances in Heidelberg. I had a chance to meet them both and was invited to visit their labs.

I ended up joining the Michigan State University (MSU) DOE Plant Research Laboratory in 1986, rotating through the labs of Hans Kende, Ken Poff, and Chris Somerville. The latter became my PhD adviser on a pretty esoteric but fascinating topic, the biosynthesis of sulfolipid, a lipid specific to photosynthetic membranes that was discovered by Andrew Benson. While everyone around me isolated mutants of Arabidopsis and tried to map the mutations, I used a bacterial genetics approach to identify the genes for sulfolipid biosynthesis in a purple bacterium. This was done the Somerville way, by brute force, screening about a thousand mutagenized bacterial colonies by thin-layer chromatography (TLC) to find mutants, and then thousands more after the introduction of wild-type cosmids into the mutant to find the genes. I must credit John Browse, who was visiting the lab and taught me everything he knew about lipid analytics.

After I received my PhD in 1991, I hung around waiting for my spouse, Susanne Hoffmann-Benning, to finish her PhD work with Hans Kende. During that time, I finally started to screen Arabidopsis mutants, focusing on those with reduced seed oil content. One of them was the *wrinkled1* mutant, which is deficient in a key transcription factor now used for engineering oil content in many different crop plants. At that time, I also suggested to Chris Somerville to do a TLC screen for Arabidopsis membrane lipid mutants. His response was, "We are not quite ready for that yet."

Well, there always comes a time in young scientists' career when they should stop listening to their mentor. After I moved in 1993 to a five-year group leadership position at the Institute for Gene Biology Research in Berlin-Dahlem, Germany, headed by Lothar Willmitzer, we did screen for Arabidopsis lipid mutants by TLC and came up with the *dgd1* mutant, which is deficient in one of the major chloroplast lipids. Mapping that gene was a monumental task pre–Arabidopsis genome sequence, and a concerted effort among Ilse Balbo, Peter Dörmann, and me took three years; we succeeded only after I had moved back to MSU in 1998 as assistant professor in the Department of Biochemistry and Molecular Biology, where I am still affiliated today.

Over my many years at MSU, I had a close relationship with John Ohlrogge, my faculty mentor, whom I credit for bringing me back to MSU as a faculty member. We had a great collaboration and published many papers together. In 2015, I became director of the MSU–DOE Plant Research Laboratory, where I had started out as visiting scholar 30 years earlier.

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

Over the years, we identified a lot of genes and explained their functions in Arabidopsis, photosynthetic bacteria, and algae. Based on the number of citations alone, the discovery of the Arabidopsis *AGO1* gene and its mutant, involved in RNA-mediated posttranscriptional gene silencing, stands out. Notably, this work was born of a side project by my graduate student Karen Bohmert, who had T-DNA tagged this gene in an effort to redirect carbon from storage proteins to oil in Arabidopsis seeds. The mutant had an interesting developmental

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phenotype, and we pursued its characterization and the isolation of the gene based on the T-DNA tag. Keep in mind, this was before the time of sequence-tagged T-DNA mutants.

The discovery of the WRINKLED1 transcription factor has become an important tool for many interested in engineering oil content in plants. This has likely been the most important translational work I was involved in, and in the long run it may contribute to the advancement of food and fuel security. We also found, in a roundabout way, the chloroplast lipid import machinery, which consists of the TGD proteins. During my time in Chris Somerville's lab, this was a hotly debated topic with no real solution in sight.

The recognition that photosynthetic bacteria, algae, and plants remodel their membranes in response to phosphate deprivation, replacing phospholipids with nonphosphorus lipids and sending some of them outside the plant chloroplast, is something I think was an important contribution to science. Many years after I started to develop this concept toward the end of my PhD, I was still in doubt whether this happened in nature and not just in my petri dishes. Then one day I was contacted by Woods Hole scientist Benjamin Van Mooy, who had discovered that photosynthetic marine plankton is rich in nonphosphorus lipids, and much more so in places where the phosphate concentration in the ocean drops. This confirmed the phospholipid–nonphosphorus lipid substitution hypothesis on a global scale.

During my time in Chris Somerville's lab, we wondered how plants could survive freezing, with the idea that membrane lipids must play a role in this resilience process. In the 1980s, Peter L. Steponkus had shown that lipid phase transitions during freezing make plants vulnerable to membrane disruption and ultimately death by cell leakage. But a biochemical mechanism for how plants could prevent this was not known. Fast forward to 2010, when we were looking for a mysterious processive galactosyl transferase that shuffled galactose residues between galactolipids, an activity first described over 30 years ago by Johan W. M. Heemskerk and Jef F. G. M. Wintermans. It turns out that the two phenomena are connected: we discovered that the Arabidopsis gene *SENSITIVE TO FREEZING 2,* which was first described by Garry Warren just before his untimely death, encodes this activity. This allowed us to come up with an elegant model of lipid remodeling that explains how fusion of organelles is prevented during severe dehydration, as encountered when plants freeze. Connecting these two basic processes is one of the scientific advances I found most gratifying. This discovery also shows how one stands on the shoulders of others who came before.

When did you become a member of ASPP/ASPB?

I recall giving my first presentation in English in 1986 in front of a big audience at the ASPB meeting in St. Louis, Missouri, where I reported my findings on auxin transport, work I had done in Rainer Hertel's lab in Germany. Rainer could not be there, but he had a lot of friends and had introduced me to them in advance, which made this big, scary event less intimidating.

Ever since, the ASPB meetings have become an event for my family and me to reconnect with friends. Our kids (now budding scientists!), who came along for many years, had an opportunity to explore different locales in the United States, as everything was new to us coming from Europe. Over the years, this meeting became the opportunity to introduce my students and postdocs to my network of friends and colleagues and help them advance their careers. In fact, a large community of MSU–DOE Plant Research Laboratory alumni meets every year during these meetings; the ASPB meeting has always been an outstanding venue to maintain these connections.

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

Aside from being a great platform to connect with colleagues and friends, the Society, with its two primary publications, has been an important medium to publish and promote our scientific findings. Some of our most significant and in-depth papers have been published either in *Plant Physiology* or in *The Plant Cell*. It was Natasha Raikhel, then editor-in-chief of *Plant Physiology,* who first introduced me to editorial work. I then realized

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how important it is to provide expedient and fair reviews, especially to young scientists, and how editors can make a difference for better or worse. Ever since, I have focused much of my service to the plant science community on editorial work.

Harry Klee, then editor-in-chief, asked me to become a handling editor for the Society of Experimental Biology's publication *The Plant Journal,* which I served over much of my career, ultimately as editor-in-chief. During this time, I was graciously invited by my ASPB colleagues at the annual meetings to join the editors' dinner, and we worked together on many issues, some of them taking us deep into the trials of publication ethics. After I stepped down from the editorial board of *The Plant Journal,* I served on the ASPB Ethics Review Committee to help quietly resolve some of the most difficult ethics issues the editors at *Plant Physiology* and *The Plant Cell* came across.

ASPB has been part of my circle of friends, mentors, and colleagues over many years, and being a Founding Member of the Legacy Society just feels right to me. Having been asked to join this effort has been a great honor.

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

To all graduate students and postdocs, I must say that one of the most important turns in your career occurs when you stop taking for granted everything senior scientists or your mentors say. You will arrive at a point in your life when you must be confident enough to go your own way en route to becoming a successful scientist. Never be intimidated by dogmatic senior colleagues. As a young assistant professor, I was told during an international meeting, where I presented data showing that under phosphate limitation galactolipids show up outside the chloroplast, "Mr. Benning needs to learn how to purify chloroplasts." Of course we were right; our work was published with high impact, and our findings were confirmed many times over by others.

I have also learned never to stop a young scientist from pursuing an unusual approach or project or to discourage a person who shows up in my office with a hard-to-explain result. Nine times out of 10 they are on the way to discovering, or have already discovered, the next big thing on the way to a paradigm shift in the field. I have given you a few examples above.

My career has benefitted from the extraordinary generosity of my mentors, especially Rainer Hertel, who helped me pursue my scientific career in the United States, and Chris Somerville, who let me and others take great projects from his lab to start our own careers. I have been inspired by their mentorship to do the same and have taken great delight in the subsequent success of the scientists I have trained.

Finally, look for great collaborators. I had many, especially when I started to work on algae and collaborated with Sabeeha Merchant, Kris Niyogi, and Arthur Grossman. Nothing advances scientific progress more than being generous with your colleagues and mentees, and in the end, this is what enriches your professional life the most.

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