

John C. Cushman

How did you spend your career?

I studied biology as an undergraduate at Ursinus College, a small, private liberal arts college in Pennsylvania. I then moved to the Waksman Institute of Microbiology at Rutgers University to do my MS and PhD degrees in microbiology. During my college years, I was originally interested in microbiology and the discovery of antibiotics and their impact on human health and society. However, I became interested in plant biotechnology and ended up studying chloroplast development in *Euglena gracilis* in the laboratory of Carl Price, thus leading to my later studies in plant biology.

Near the end of my PhD studies, I was fortunate to be awarded a National Science Foundation Fellowship in Plant Biology and worked in Hans Bohnert's laboratory in the Department of Biochemistry at the University of Arizona, Tucson. My project was to investigate the molecular basis of crassulacean acid metabolism (CAM) induction by salinity or water-deficit stress in the common ice plant (*Mesembryanthemum crystallinum*), a process originally discovered by Klaus Winter. I have continued working on various aspects of this process for most of my career. After my fellowship ended, I was awarded my first USDA grant to



continue this work and was promoted to Research Assistant Professor at the University of Arizona.

I then moved to Oklahoma State University to join the Biochemistry and Molecular Biology department and manage their recombinant DNA/protein resource facility, while doing research on ice plant. We continued to characterize many of the genes involved in the C₄ metabolism of CAM and investigated the signaling mechanisms involved in CAM induction. At that time, I was awarded a National Science Foundation CAREER Program grant to investigate the genetic basis of CAM, and we isolated the first ice plant CAM mutants.

After promotion to Assistant and then Associate Professor in Biochemistry and Molecular Biology at Oklahoma State University, I moved my laboratory to the University of Nevada, Reno, to join the Biochemistry and Molecular Biology Department. After three years, I was promoted to Professor and was able to expand my research program to

different model systems. I moved to Nevada because it is the driest state in the USA and the College of Agriculture, Biotechnology, and Natural Resources proved to be an excellent environment to develop crops with greater drought and salinity tolerance. I was also awarded a University of Nevada Foundation Professorship in 2011. During my nearly 25 years in Nevada, my research program continued to work to more fully understand CAM induction in ice plant, while also expanding work in several other model systems, including halophytic algal species, alternative oilseed crops, such as *Camelina* and *Brassica* species, C₄ grass species such as teff, and obligate CAM species such as *Agave* and *Opuntia*. I served as the Biochemistry graduate program director for 17 years (2005-2022) and developed and taught several undergraduate and graduate courses in molecular genetics, functional genomics, plant molecular biology and biotechnology, grant writing for molecular biosciences, sustainable human ecosystems, and scientific communication. I was fortunate to be elected as a fellow of the American Association for the Advancement of Science (AAAS) in 2022.

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

Some of my most important contributions have centered on understanding the functional genomics of CAM and the signaling mechanisms that result

in CAM induction in facultative CAM plants. In research initiated at OSU in the late 1990's, with Tahar Taybi, we showed that CAM can be induced by osmotic, ionic, and abscisic acid treatments using a detached ice plant leaf assay. We later showed that the process required elevations in cytosolic calcium concentrations, protein synthesis, and might also occur by an ABA-independent signaling pathway. During this same time, in collaboration with Ray Chollet's laboratory in Nebraska, Tahar isolated and characterized the regulatory kinase that controls phosphoenolpyruvate carboxylase activity. In the 2000's, I developed a screening method using a simple colorimetric assay using a pH indicator dye to identify CAM mutants in ice plant. These mutants, which were characterized in collaboration with Anne Borland's laboratory in Newcastle, are defective in starch biosynthesis, which proved essential for the nocturnal production of malic acid and vacuolar acidification. The genetic screens also resulted in some very interesting ice plant mutants, including one characterized by Sakae Agarie, that lacked epidermal bladder cells, which are likely to participate in water and ion storage and homeostasis but have more recently been shown by Micheal Palmgen's lab in Denmark to play a role in herbivore defense.

During the next dozen years, in collaboration with Grant

Cramer's lab at the University of Nevada, Reno, my lab conducted extensive work into the drought and freezing stress responses of wine grape and the resultant effects on wine quality. We developed the first Affymetrix gene chip for wine grape, which revolutionized transcriptome profiling prior to the advent of RNA-seq technology. We also generated a more freezing-tolerant winegrape variety. My lab also continued characterizing CAM induction in ice plant, culminating in detailed 'omics analyses and genome sequencing. In collaboration with Won Yim's lab at the University of Nevada, Reno, we have also sequenced the genomes of several crop species including Saharan mustard, a drought-tolerance teff accession, and a diploid *Opuntia* species.

During the last ten years, my laboratory, in collaboration with Anne Borland at Newcastle University, James Hartwell at Liverpool University, and a large team at the Oakridge National Laboratory including Xiaohan Yang, have laid the groundwork for an ongoing project to engineer CAM into target crops to improve their water-use efficiency and yield stability under hotter, drier conditions. Tissue succulence, a related trait to CAM, was also engineered successfully by Sung Don Lim, now at Sangji University in South Korea, which resulted in improved salinity and drought stress tolerance in *Arabidopsis*. We have also continued our work, in

collaboration with Mel Oliver at USDA-ARS and the University of Missouri, Columbia, to understand how resurrection plants survive and recover from desiccation of vegetative tissues, with the goal that aspects of the desiccation tolerance trait might improve drought-resilience of crops in the face of the global climate crisis. Much of this work would not have been possible without the help of a dedicated team of undergraduates, graduate students, and postdoctoral scholars.

When did you become a member of ASPP/ASPB?

I became an ASPB member in 1985, when I was a graduate student in Carl Price's laboratory at Rutgers University. Around that time, I went to my first regional ASPP meeting at the University of Connecticut and presented a poster about my research.

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

I published one of my first papers in *Plant Physiology* in 1986 and published a paper in the first volume of *The Plant Cell* in 1989. So, from early on I had a strong affinity towards the Society for its publication opportunities at a time when there were relatively few outlets for plant-oriented research. I also served as an ASPB Education Committee member (2007-2013), which involved conducting outreach

ASPB Legacy Society Founding Member

events at several meetings throughout the USA. I also served as session chair and co-organizer for the Western Regional Meeting of the American Society of Plant Biologists. (2003-2004), and as the ASPB Western Section Chair (2013-2014). I was elected an ASPB fellow in 2013. All of these experiences and connections emphasized the importance of the Society in showcasing the role of plants in promoting science education in high school and college curricula and the role of basic plant research in improving crop production through biotechnology.

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

In terms of having a successful career in the plant sciences, the best advice I would give to students is to focus on one area of research and become the world's expert in that area early on, as this will help build a solid foundation for the rest of your career. Once established, one can branch out and follow multiple themes of plant research. The other important piece of advice is to follow your passion for plant research, work hard, be persistent, and stay curious, so that one might continue to pursue the kind of research that brings about genuine change to the planet.

Academic Family Tree

Few of my students have stayed

in academia, so my academia tree has few branches for me.

Ph.D. Advisor: Carl A. Price

Graduate Students:

Ilka Emig (Visiting, 1996)
Kang-Min Kim (1996-2001)
Rahul Patharkar (1998-2001)
Ananda Chandrasekaran (Rotation 1998)
El-Amir Wassim Chehab (1998-2003)
Anamika Ray (1999-2000)
Antony Dodd (Visiting, 1999)
Yongil Yang (2001-2004)
Richard Tillett (2003-2011)
Abou Yobi (2005-2013)
Katia Silvera (2005-2010)
Chong (Leo) Tong (Rotation 2006)
Matthew Wheatley (2007-2011)
Leticia Rodriguez (2007-2008)
Mark Lemos (2009-2010)
Tapas Acharjee (2010-2011)
Bahay Gulle Bilgi (2008-2013)
SangHo Kang (2008-2013)
Jeremiah Smith (2013-2014)
Sarah Fox (2015-2016)
Jesse Mayer (2012-2018)
Richard Lohaus (2012-2019)
Brittany Blair (2018-2019)
Travis Garcia (2013-2021)
Mitiku Mengistu (2015-2022)
Nicholas Niechayev (2016-2021)
Charli Faris (2020-2021)
Arely Viridiana Pérez López (2021-2021)
Gabriel Angres (2021-2022)
Johnathan Lomas (2021-present)
Nathan King (2022-2023)
Trevor Lewis (2023-present)
Elijah Holschbach (2023-present)
Monica Carey (2024-present)

Postdoctoral Research Associates:

Dr. Niranjana Maitra (1993-1995)
Dr. Holly Schaeffer (1993-1995)
Dr. Tahar Taybi (1996-2000)
Dr. João Maroco (1998-1999)
Dr. Sakae Agarie (1999-2001)
Dr. Shin Kore-eda (1999-2001)
Dr. Hans Gehrig (1999-2001)
Dr. James Hartwell (2001-2003)
Dr. Yuichi Uno (2001-2003)
Dr. M. Charlotte Bohlman (2003-2004)
Dr. Miguel Rodriguez (2003-2005)
Dr. Laurent Deluc (2004-2009)
Dr. Jerome Grimplet (2005-2008)
Dr. Gouthu Satyanarayana (2005-2009)
Dr. Mustafa Morsy (2005-2007)
Dr. Sage Hiibel (2009-2012)
Dr. Richard Tillett (2011-2012)
Dr. Matthew Wheatley (2011-2013)
Dr. Bernard Wone (2012-2015)
Dr. Won C. Yim (2013-2018)
Dr. Jungmin Ha (2013-2016)
Dr. Sung Don Lim (2013-2018)
Dr. Pradeep Yerramsetty (2016-2017)
Dr. Paula Pereira (2018-2019)
Dr. Dhurba Neupane (2019-2023)
Dr. Arely Viridiana Pérez López (2021-2023)
Dr. Monirul Islam (2024-present)