Gerald E. Edwards

How did you spend your career?

Careers evolve over time and, to some extent, are unpredictable. I grew up on a farm in Virginia and was interested in agriculture through activities in the Future Farmers of America. It was fortuitous that I had experience at six land grant universities—Virginia Tech, University of Illinois, University of California (UC), Riverside, University of Georgia, University of Wisconsin, and Washington State University (WSU)—during my college training and as a faculty member. With colleges of agriculture, these universities are noted for having a large group of plant scientists, so the knowledge gained is made accessible to benefit society.

My strong interest in plant science and physiology developed in the 1960s through interactions with an excellent group of professors, Fred Slife, Richard Hageman, and Jack Hanson, during my master's studies in the Agronomy Department at the University of Illinois. During my PhD studies at UC Riverside, I did research on photosynthetic bacteria with Carlton Bovell and was introduced to research on crassulacean acid metabolism (CAM) with Irwin Ting. Mack Dugger, a member of my committee, recommended me for a postdoctoral position with Clanton Black at the University of Georgia in 1969. This was very timely, as the field of C_4 photosynthesis was emerging, and there were debates as to whether some species had a different mechanism of assimilating atmospheric CO_2 with C_4 acids as initial products, as opposed to initial synthesis of C_3 acids by the conventional Calvin–Benson cycle.

During my postdoctoral experience, I gave three presentations on research about C_4 plants by our group at my first ASPP meeting, where I met Martin Gibbs, who chaired the session. My dream was to have a faculty position at a land grant university, but there were few openings. I applied to positions at UC Berkeley, which soon notified me the search was cancelled, and the University of Wisconsin, where in 1971 I joined the faculty in the Horticulture Department. Key to early establishment of a research program was having Steve Huber, Maria Gutierrez, Maurice Ku, and Ryuzi Kanai join my lab. It was a stimulating environment, as there was a strong group of plant scientists on campus, and I had good administrative support.

I never thought I would consider administrative experience or relocate to another campus. However, in 1980 a colleague invited me to apply for chair of botany at WSU. I moved there in 1981 and was chair of the Botany Department for five years. It was ideal, as we had a small faculty engaged in both teaching and research in different botany disciplines, and it gave me a broader perspective on service and interactions with students, faculty, and administrators. I also had time to establish my research program, which was facilitated by having a small teaching load. Maurice Ku, who had been a PhD student with me at Wisconsin and a USDA employee in Georgia, joined our department. He was an excellent faculty member and collaborator in research, teaching, and mentoring. During my tenure at the University of Wisconsin and WSU, I conducted research on the mechanisms of photosynthetic carbon assimilation in C_4, C_3, C_3–C_4 intermediates, and CAM plants and their responses to climate conditions, and I taught courses on plant physiology, plant stress, and photosynthesis.

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

In the late 1960s, results with a few species suggested that both PEP carboxylase (PEPC) and Rubisco function in CO_2 assimilation, but their compartmentation and functions in carbon assimilation were not clear. The anatomy showed these plants had two distinctive photosynthetic cell types, mesophyll and bundle sheath (BS) cells. In my postdoctoral research I

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developed a means of mechanically isolating and purifying intact mesophyll and BS cells from a C_4 plant, *Digitaria sanguinalis,* which I knew as crabgrass on the farm (and wondered why it was so prevalent in our crops). The mesophyll cells had PEPC and fixed CO_2 in the light when provided with pyruvate, whereas the BS cells had Rubisco and fixed CO_2 in the light when provided with ribose-5-P (published in 1970 and 1971 in *Plant Physiology*). The two photosynthetic cell types in Digitaria can be isolated by mechanical grinding, whereas in most other species (e.g., maize, sorghum, sugarcane) the mesophyll cells readily break.

In the 1970s, Ryuzi Kanai from Saitama University in Japan was a major collaborator in our research on C_4 photosynthesis, which also led to future collaborations with Japanese scientists. In our research at Wisconsin, he developed a technique using a combination of cellulase and pectinase (which he brought from Japan) to enzymatically digest, isolate, and purify mesophyll protoplasts and BS strands from various C_4 species (and in some species' BS protoplasts). This was published in initial research with maize (1973 citation classic in *Plant Physiology*), which was a breakthrough for subsequent studies. It settled disputes on partitioning of PEPC and Rubisco based on mixed reports with mechanical grinding procedures.

With the enzymatic technique, we conducted studies on the intercellular compartmentation of enzymes involved in carbon assimilation between the two cell types, the intracellular compartmentation of enzymes within photosynthetic cells by gentle breakage of protoplasts with an osmoticum to keep organelles intact, and the light-dependent functions of the cells. From these studies, schemes were developed showing how photosynthesis functions in three C_4 subtypes based on C_4 decarboxylases (NADP-malic enzyme type, NAD-malic enzyme type, and PEP-carboxykinase C_4 species).

During my career, this methodology was used in studies on the intracellular compartmentation and function of photosynthesis in C_4, CAM, C_3–C_4 intermediates, and C_3 species. This research included studies on CAM plants in the 1980s, when there were uncertainties about the compartmentation and means of carbon assimilation during synthesis of atmospheric CO_2 into malate in the dark, and its feeding of CO_2 to the C_3 pathway by decarboxylation in the light. Using protoplasts to isolate intact organelles, the intracellular pathways for day–night carbon metabolism were elucidated for representative species of malic enzyme and PEP carboxykinase-type species. In 1983, David Walker (University of Sheffield) and I published a book titled *C_3, C_4: Mechanisms and Cellular and Environmental Regulation of Photosynthesis,* which was recognized as a valuable synthesis of information on carbon assimilation in these different forms.

For decades, all C_4 plants discovered among grasses, dicots, and sedges had Kranz-type anatomy, consisting of mesophyll and bundle sheath cells. This was considered a diagnostic criterion essential for C_4 to function by separating the synthesis of atmospheric CO_2 with formation of C_4 acids in mesophyll cells and donation of CO_2 to the C_3 pathway in BS cells. It was thus surprising when C_4 photosynthesis without Kranz anatomy was discovered in a few species in the family Chenopodiaceae, a dicot family with great diversity in forms of C_4. In this family, Helmut Freitag in Germany found some species having C_4-type isotope composition, whereas light microscopy showed absence of Kranz anatomy and unusual chlorenchyma cells.

In research on these species initiated at WSU with Elena Voznesenskaya and Vince Franceschi, we showed that C_4 functions by developing two cytoplasmic domains with dimorphic chloroplasts within individual chlorenchyma cells that function analogous to the chloroplasts in the dual-cell Kranz-type system (initial publication 2001 in *Nature*). During the latter part of my career, a major focus was on characterizing this mechanism of C_4 photosynthesis by biochemical, microscopic, and gas exchange analyses in the two single-cell C_4 subtypes based on the intracellular compartmentation of the two cytoplasmic domains.

There are differences in how C_3, C_4, and CAM plants perform in assimilating CO_2 depending on environmental conditions and climate. In this respect, in climates with high temperature or limited water, C_4 photosynthesis is more efficient than in C_3 plants that have high losses of CO_2 because of photores-

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piration. With current interests in engineering C_4 photosynthesis in C_3 crops like rice, these single-cell C_4 species demonstrate that structurally there is an alternative form of C_4 that functions without requiring development of Kranz anatomy.

When did you become a member of ASPP/ASPB?

In 1966 I entered the PhD program at the University of California, Riverside, and I became a member of ASPP in 1967. This occurred as I was attracted to the field of plant physiology through my training and interactions with professors of plant biology at the University of Illinois and UC Riverside. I became a member before attending my first ASPP annual meeting.

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

Over the years, a strong group of scientists in the field of photosynthesis has been affiliated with the Society. Annual and regional meetings have provided opportunities to personally interact with researchers in the field, to present results of our work (posters and oral presentations), and to interact with colleagues through service in the Society (editorial boards and committees). Among 400 papers I published with colleagues, 77 were published in the Society's journal *Plant Physiology*. I attribute this to my association with the Society, to our collaboration with many colleagues, and to my late wife Sandy, who coordinated and helped visitors to our lab and provided extensive editing. Finally, the ASPB meetings provided me with up-to-date information to support teaching courses in plant physiology, plant stress, and photosynthesis. The benefits I received from my affiliation with ASPP/ASPB were my motivation to become a Founding Member of the Legacy Society.

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

Pursuing a successful career in plant science requires dedication, time, and curiosity about the subject in graduate school, in postdoctoral studies, and in a future career in research, teaching, and/or service in the field. This must be foremost in your mind. In research, develop a broad understanding of the field of interest and the unresolved problems and questions. Focus on one query of interest; develop hypotheses, experiments, and results; and take it to completion through writing and publication. Persistence is also required in seeking grant support for your research. Early in my career, I was disappointed in not initially having an NSF proposal funded; encouragement I received from an experienced senior scientist, Martin Gibbs, made a difference.

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