William John Lucas

Life has unpredictable events

I was fortunate to grow up in a farming community in South Australia, where I had opportunities from an early age to gain experience with family farms involving crops, horticulture, and livestock. My early formal education in the field of agriculture was in Adelaide at the Urrbrae Agricultural High School, where the curriculum provided a balance between theory and hands-on training. In this setting, gifted teachers opened doors to a wide range of knowledge in agricultural sciences. In parallel, an uncle provided me a unique opportunity to gain experience converting scrubland into pastureland for sheep and cattle. This involved many aspects: land clearing, soil preparation, soil sampling to determine fertilizer composition, development of irrigation systems, and finally pasture establishment. This combination of theory and practice established what I had imagined would be a solid foundation for a rewarding life as a farmer.

My first unpredictable event was conscription into the Australian Army, under the National Service Act, for military service in Vietnam. During basic training, I applied for assignment to the Engineering Corps, as I reasoned skills learned there would be beneficial to farming. Much to my surprise and clear disappointment, I was assigned to the Royal Australian Army Education Corps, and after a few misadventures, I was posted to an Education Unit within a Recruit Training Battalion located outside Wagga Wagga in New South Wales. This unlikely posting changed the direction of my life. Although I had no credentials as a teacher, one of my roles was to instruct trainee National Service conscripts on a range of topics relating to their new life in the army. This proved to be an amazing experience, as to my surprise I found these teaching activities to be stimulating and enjoyable. In addition, I gained new insights and became troubled by an apparent very broad spectrum of regional inequalities in educational quality within Australia. It appeared many rural schools could benefit by an influx of qualified instructors.

The second unpredictable event

Upon being discharged from the army, my mind was in a quandary: return to farming or follow the path to becoming a teacher. I had recently married, and my wife, Diana, was beginning her career as a very talented high school mathematics teacher. As we discussed these paths, the question uppermost in our minds was how I could gain teaching credentials. Then a letter arrived from the Australian Army, informing me that, based on my National Service record, I was being offered a full fellowship to the Adelaide Teachers College at the University of Adelaide!

In the fall of 1968, I enrolled in a B.Sc. degree program, and as I wanted to be able to teach a range of high school science subjects, I applied for permission to enroll for both biological and physical sciences majors. After a few interviews, my petition was approved thanks largely to one committee member, Prof. Barry Steele, who went on to become my academic mentor. So began a wonderful journey that is still unfolding!

The third unpredictable event

After graduation I was ready to begin my teaching career. However, based on my First-Class Honors, I received a letter from the government offering support for a Ph.D. program at an Australian university. I was not interested in doing another degree, as teaching with Diana in a rural high school was our goal. Well, Diana's mother had another idea. On an unforgettable Saturday, she arrived to discuss my future options. She argued that my destiny was to "teach the teachers." Some eight hours later, she invited us out for dinner to celebrate my decision to pursue a Ph.D. at the University of Adelaide; that part of my journey was completed in 1975.

I then spent two years on a postdoctoral appointment in the group of Professor Jack Dainty, Chair of Botany at the University of Toronto, where I continued to work on biophysical aspects of plant membrane transport. Jack was a wonderful mentor. Besides his advice and counsel, he provided me many opportunities to meet with numerous distinguished visiting scholars. And, when Jack was unable to accept invitations to give seminars, he sent me in his place, thereby providing great opportunities to meet with colleagues in Canada and the US.

The fourth unpredictable event

Before departing for Canada, Sir Rutherford (Bob) Ness Robertson offered me a faculty position in the Research School of Biological Sciences at the Australian National University in Canberra - the position would be held for the period of my postdoctoral time in Jack Dainty's group. Unfortunately, just prior to our return to Australia, I received a letter from Bob telling me he was sending "a most difficult letter to write," as the open position had been frozen!

What to do? Should I apply for a faculty position elsewhere? Soon after receiving Bob's letter, Nancy Dengler (then Vice Chair of Botany at the University of Toronto) told me the Department of Botany at the University of California Davis (UCD), her alma mater, was recruiting for an Assistant Professor position and strongly encouraged me to apply. Diana and I had never considered living and working in the US, but the unpredictable turn of events and a timely opportunity altered our plans. So, I applied, interviewed, and was offered the position! But then UC Berkeley called, asking me to interview for their open position. That interview was most interesting – famous campus, distinguished faculty – but the farm boy in me was drawn to UC Davis as an equally famous agricultural campus. So, I came to UCD, and stayed for my entire academic career – I made the right choice.

During my career, I was most fortunate to have an amazing group of students, postdoctoral scholars, and visiting scientists work in my laboratory. In parallel, I was able to teach undergraduate and graduate classes in collaboration with great, dedicated, faculty. Who could ask for anything more?

To explore the mechanism involved in bicarbonate uptake for photosynthesis in aquatic algae, we developed a range of new methods, including motorized extracellular vibrating ion-specific and voltage electrode probes, in conjunction with a plasma membrane voltage clamp system. Using these tools, and mathematical modeling, we mapped the spatial organization of transport domains and subdomain formation in the Chara plasma membrane. We then established that in Chara light activates a plasma membrane two-cycle H+-transport system that can reverse its direction to allow a passive H+ influx back into the cell.

Root and phloem biology

As a condition of my employment at UCD, I had agreed to expand my research program beyond algal systems into crop plants. To this end, projects were initiated on both membrane transport in maize roots and phloem biology, with a focus on photosynthate loading and long-distance control over resource allocation. Some major findings from these early projects were that K+ uptake into maize roots occurred through the action of a two-component kinetic system functioning at the root periphery, and that phloem loading involved a sucrose-H+ cotransporter, with sugar being retrieved from the apoplast.

During this same period, various international groups sought ways to identify genes encoding plant plasma membrane transporters. At a NATO conference in Spain, I learned of yeast strains incapable of growing on a low K+ medium, and this presented a molecular pathway to screen for genes encoding for K+ transporters. Indeed, screening of an Arabidopsis cDNA library within such a mutant yeast strain allowed us to identify the first plant membrane transporter, KAT1, a member of the Shaker family of K+ channels. This yeast screen was subsequently used by the plant membrane biology community to identify a broad array of plant transport systems.

Plasmodesmata and control of symplasmic transport

A project on plasmodesmal (PD) biology was initiated as a direct outcome from my 1984/85 sabbatical at the University of Göttingen in Germany. My sabbatical project was to develop an electrophysiological system to analyze the response of the phloem, specifically the sieve tube system, to application of exogenous sugars. To this end, we developed an aphid feeding system that, after the stylet was severed, afforded direct electrical access to the "cytoplasm" of mature phloem sieve elements (SEs). Using this model system, we established a strong electrical response to the application of exogenous sucrose. However, our controls provided evidence for direct electrical coupling between the SEs and the ground tissue, including mesophyll cells!

These findings were most perplexing, as the current model for phloem loading was consistent with sucrose uptake from the SE apoplast, and PD symplasmic continuity, between the SEs and the surrounding cells, would short circuit this loading process. In my attempt to understand this conundrum, I made a visit to Katherine Esau, an international authority on phloem biology. Dr. Esau met with me for two days, and in our final meeting she suggested, based on her pioneering work on the role of PD in viral infection, that I develop a viral system to explore this "very interesting problem." Based on her sage advice, I researched articles on plant-infecting viruses and consulted with my plant pathology colleagues at UCD.

During this same period, we had installed a photon-counting VIM Hamamatsu system for real time analysis of gene expression, using luciferase as a reporter. The remarkable sensitivity of this camera meant that by using this system we could monitor, in real time, the presence of a fluorescent dye after it was microinjected into a mesophyll cell within a mature leaf. These assays clearly revealed dye movement from the mesophyll into and along the phloem! This result also offered support for the hypothesis that PD can provide a symplasmic path from the mesophyll all the way to the functional SEs, consistent with the above-described finding of electrical coupling between the SE and ground tissues.

PD as intercellular organelles

Fortunately, earlier work on plant-infecting viruses, performed in other laboratories, had identified viral proteins, termed viral movement proteins (vMP), as being essential for local infection. Our experiments with transgenic tobacco expressing the vMP of Tobacco mosaic virus revealed the properties of mesophyll PD were altered, such that molecules 10 – 15 kDa in size were able to spread between cells, whereas in control leaves only molecules ¬< 1 kDa could move. Thus, we demonstrated that a viral MP could interact with and modify the size exclusion limit (SEL) of mesophyll PD. Our physiological studies performed with TMV vMP transgenic tobacco plants also revealed this vMP could modify both carbon partitioning and source-sink allocation, leading to a change in root-to-shoot ratio.

These important findings led to experiments with both RNA- and DNA-infecting viruses that revealed vMPs could bind and mediate cell-to-cell transport of their cognate vRNA/vDNA. As cell-to-cell movement of the viral nucleoprotein complexes occurred in a millisecond timeframe, it implied the machinery for such movement preexisted within the PD. Strong support for this notion was gained through microinjection studies with the maize Knotted1 (KN1) protein. Here, we demonstrated that KN1 engages in selective trafficking through PD, taking along its mRNA! Although the results of these pioneering studies on vMPs and KN1 took some time before acceptance by our colleagues, it is now well known that a broad spectrum of plant proteins/mRNAs function non-cell-autonomously.

Phloem functions as an information superhighway

To further explore the "electrical coupling conundrum", we developed a system to study the contents of the phloem translocation stream. To this end, we collected phloem exudates from which we identified and characterized a broad range of proteins, with many being established as graft transmissible. Our initial studies on pumpkin phloem exudates revealed these proteins have the capacity to increase PD SEL, traffic through PD, and exhibit very high affinity for interacting with the PD cell-to-cell trafficking machineries. Cellular, biochemical, and molecular studies established that the entry of specific proteins into the phloem could be regulated by phosphorylation and/or glycosylation recognition motifs. Proteins that mediate selective trafficking of non-cell-autonomous proteins into the sieve tube system were also characterized.

The vMPs and certain plant proteins, such as the maize KN1 protein and many other phloem proteins, have the capacity to transiently dilate PD during their cell-to-cell movement. Their trafficking activities, for example those taking place between mesophyll, bundle sheath and phloem cells, would also permit transient movement of small molecules, such sucrose, and ions like K+. Such PD-mediated ionic leakage currents resolved our "electrical coupling conundrum".

Long-distance signaling proteins were also identified, with perhaps the most important being Flowering Locus (FT), which acts as the long-distance florigenic signal – here, our phloem data provided the first direct evidence for FT entry into the phloem and movement through the sieve tube system to the vegetative apex for floral induction. Other phloem mobile proteins were shown to be involved in photosynthate partitioning and yield, as well as regulation of the shoot to root ratio by mediating an auxin response in distant organs.

A phloem proteome, built from pumpkin and cucumber exudates, revealed the presence of a full complement of proteins required for a functional 26S proteosome, along with the attendant machineries associated with ubiquitination, consistent with protein turnover in the phloem translocation stream. In addition, our phloem proteomics and metabolomics analyses revealed the cucurbit sieve tube system functions as a complex metabolic space. Next, we identified all the proteins necessary for functional ribosomes within mature enucleate sieve elements, which suggested translation of the imported mRNA. In this regard, we identified a plant paralog of a viral movement protein that mediates transport of mRNA into the phloem, and a 50 kDa protein that forms the basis of a phloem ribonucleoprotein complex; phosphorylation of this 50 kDa protein is essential for assembly of a stable phloem-mobile high-affinity ribonucleoprotein complex.

The phloem sap-based transcriptome identified a large population of endogenous mRNAs, many of which were shown to be graft transmissible, and, further, were targeted to specific sink tissues. In terms of the phloem as a signaling pathway for delivery of environmental-related stresses, we identified a vascular-mediated mRNA signaling system involved in an early phosphate stress response. Relevant to plant development, we established that phloem-mobile Aux/IAA transcripts are targeted to the root tip, where they modify root architecture.

Gene silencing was known to be transmitted to distant plant tissues, and we identified the presence of siRNAs in the phloem, along with PHLOEM SMALL RNA-BINDING PROTEIN 1, which functions in systemic delivery of siRNAs in the form of ribonucleoprotein complexes. Our further studies revealed the presence of a surveillance system that regulates selective entry of RNA into the shoot apex. Collectively, these findings established the angiosperm phloem system functions both as protein and an RNA-based information superhighway.

How did the Society impact your career?

I joined the American Society for Plant Physiology in 1976, and attended the annual meeting, held that year in Madison, WI. This was a truly memorable experience, with many exciting presentations, "enormous" poster sessions, and so many colleagues with whom I had an opportunity to chat about research, collaborative possibilities, and academic life as experienced by participants from around the word! I was "hooked", and after I joined the Botany Department at UC Davis, attendance at these annual meetings was strongly encouraged for members of my laboratory.

During one such annual meeting, I had the pleasure to meet Martin Gibbs, then Editor-in-Chief of Plant Physiology, and I was delighted to be invited to join his Editorial Board. My experience as an editor provided new insights into both the world of scientific publishing and my colleagues. I was also fortunate to have an opportunity to serve the Society in various roles, including memberships on the Planning Committee for annual meetings, various other administrative committees, Society-sponsored teaching events, and as a Senior Editor for The Plant Cell.

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

We are presently in the “century of biology”, and my advice to someone considering a career in the plant sciences is to identify a field of endeavor that excites them, establish a rigorous understanding of the existing knowledge in their chosen specialty, and then develop a vision for the future of this area of plant science. Next, maintain a passion for learning new pathways/technologies that enhance their capacity to push forward the frontiers of knowledge. Collaborations will be necessary; establishment of clear ground rules, responsibilities and expectation are vital for success. Finally, be passionate about your science, but maintaining a work-life balance is also important. And always be prepared for unpredictable events, i.e., expect the unexpected!