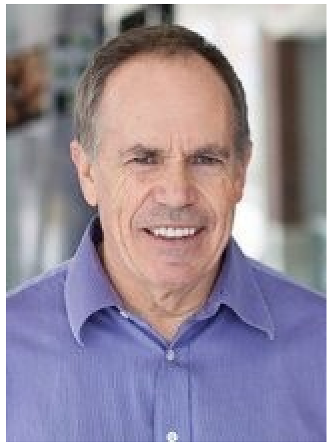
ASPB Pioneer Member

Stephen Long

How did you spend your career?

To understand how I spent my career, or rather how I am spending it, I had first to consider how I arrived here. My parents were both keen gardeners, and we often visited gardens around England on our summer holidays. Even though we had a small garden of 70 x 20 feet in the London suburb of Pinner, my parents managed to pack a lot of diversity in terms of flowers, fruit bushes and vegetables into that space. Watching David Attenborough's "Zooquest" on our black and white TV in the early 60s awoke my interest in biology, but by the age of 14 my ambition was to become an aircraft engineer. That all changed through inspiring biology teachers. Muriel Hosking, the biology teacher for my last two years in high school, showed me just how fascinating plants were; I was hooked and have been ever since. Muriel's classes on biochemistry, function, evolution, and genetics inspired me to read more on these topics. However, as an idealistic teenager I wanted to make a difference in the world, and I did not see then how studying botany could do that. Muriel's solution for me was to study Agricultural Botany, and she encouraged me to apply to Reading, the leading Agriculture school in Britain at that time. Spencer Barrett, a plant evolutionary biologist and currently Emeritus Professor at the University of Toronto, had been one of her students. Spencer had entered



Reading the year before, and on a return visit to Pinner he showed me notes from his plant physiology discussion classes. Fascinated, I was convinced that Reading was where I needed to go. Luckily, I was accepted. Besides learning the practicalities of agronomy, breeding, pests and diseases, the degree required that I also took all the courses of a standard botany degree. While I did not appreciate this extra course load at the time, that part of my education has been invaluable to me throughout my career. A couple years before I started at Reading, C4 photosynthesis was discovered. Learning of this more efficient form of photosynthesis, associated with some of the most productive crops, was captivating. Our Head of Department at Reading, Hugh Bunting, initiated an opportunity for us to spend an optional year in a research laboratory before our senior year. Knowing my interests, he arranged for me to spend a year as a research assistant at Tate & Lyle's Research Centre, working on C4 biochemistry in sugarcane. Many of the greats of photosynthesis research visited the lab while I was there, and I knew at the end of the year this was what I wanted for my future. At that time, C4 photosynthesis was considered exclusive to warm climates, but from my classes at Reading it appeared to me that some plants of the northern European flora should be C4, based on evolutionary relationships. I wanted to study this for graduate school, and again with Hugh Bunting's advice I found an adviser at Leeds who would entertain the idea, Harold Woolhouse .

My graduate education was strongly influenced by two quite different individuals. Harold Woolhouse, my Ph.D. advisor, was an exceptional visionary unafraid to take on major projects, as he demonstrated later as Director of the John Innes Institute, transforming it into the world-leading plant molecular biology institute it is today. He read broadly, could identify emerging developments across plant sciences, and he brought together disparate areas to develop unique and powerful insights. He had great analytical ability, and was quick to see flaws in reasoning, as many speakers were unfortunate to discover at meetings. When I came to him with the idea of C4 species in the British flora, he supported what most would have viewed as a naïve and fruitless idea at that time. Lynton Incoll was a research scientist working with Harold, and effectively my lab supervisor. Lynton was highly practical and inventive, and devised innovative ways to measure and analyze photosynthesis and transpiration. He also taught me the importance of, and approaches to, precision and accuracy of measurement in the lab and field, as well as scientific writing. Combined, the two gave me an exceptional graduate education that has been with me throughout my career. The first paper from my Ph.D. was published in Nature, which seemed easy then, but something I have never been able to repeat.

I had planned to go abroad for post-doctoral research, but when I was finishing my Ph.D., Harold encouraged me to apply for a tenure track lectureship (= Assistant Professor in the US system) at the University of Essex. To my surprise, I was offered the position as the first plant biologist in the then new Biology Department. So, I had the opportunity to determine the plant biology curriculum and research direction.

Photosynthesis is the most important process on the planet, it is the source, directly or indirectly, of all of our food, the oxygen we breath, and the process which drives all ecosystems and removes carbon dioxide from the atmosphere. So, my seemingly then naïve vision as an idealistic 24-year-old, was that Essex would become a world leader in researching and improving this process for global food and energy security. That is exactly what Essex is today, with a group of six faculty focused on photosynthesis. However, I was told on appointment that I would be the only plant biologist. However, the next year there was a vacancy for a biophysicist, and the best candidate by far was, now emeritus, Professor Neil Baker, who just happened to be working on photosynthesis. Photosynthesis had to that point been studied as two very separate disciplines. The light reactions encompass how sunlight energy is trapped and transduced through the splitting of water to release oxygen and generate reducing power. Subsequently, the dark reactions use the reducing power to remove carbon dioxide from the atmosphere and produce carbohydrate and everything else that makes up the plant, including, directly or indirectly, all of our food. Neil worked on the light reactions and I on the dark. Further, most work was in single celled algae, isolated spinach chloroplasts, and chloroplast fragments. We could see that individually we could not compete with the big photosynthesis research groups of the time, which were either light or dark reaction research groups. However, we saw that by collaborating on the linkages between light and dark reactions, and focusing on intact leaves, we could do something unique and important. It worked, and we won some good financial support from research councils, industry and even the United Nations Environment Program (UNEP). And, most importantly, we had fun doing it. We collaborated on investigating why C4 photosynthesis in maize and sorghum collapsed under cool conditions, but not in Spartina, which had been the subject of my Ph.D. This led to the discovery that an Asian C4 grass, commonly grown as an ornamental and related to sorghum, Miscanthus, was remarkably cold tolerant. In the early 1980s in collaboration with Mike Jones at Trinity College, Dublin, this led to the first agricultural trials of Miscanthus x giganteus as a potential biomass and bioenergy crop in the EU. It resulted in the highest productivities so far recorded in Britain and Ireland, and 40 years later in M. x giganteus being a major bioenergy/biomass crop on both sides of the Atlantic. In parallel, as part of a UNEP project investigating biodiversity resources, I was able to search for exceptionally productive C4 species in the tropics. In collaboration with INPA in Manaus, Brazil, we identified the natural monocultures of the C4 grass Echinochloa polystachya on the Amazon floodplain that are exceptional. We showed this grass produced over 100 tonnes of dry matter per hectare per year, which remains a world record for natural terrestrial vegetation. At Essex, I progressed to become full Professor and Director of its growing Photosynthesis Group.

I became curious about the direct effects of rising CO2 in the atmosphere on photosynthesis initially through mechanistic modeling. Dr. Bert Drake had established one of the first long-term field experiments exposing natural vegetation to elevated CO2 and invited me to test my ideas on a sabbatical at his field site on the Chesapeake Bay. The successes there excited my interest in looking more deeply at food crops. A further spell with the Free-Air CO2 Enrichment (FACE) facilities developed by Brookhaven National Lab and implemented by Bruce Kimball in wheat fields in Arizona took my interest further – in particular, how photosynthesis acclimated to these changes. During this time, it also appeared to me that biology was being by-passed as part of climate change, because the research focus was primarily the physical sciences. With help from Prof. Harry Smith, I was able to launch a journal, Global Change Biology, to provide a focus for promoting the key position of biology in impact, adaptation, mitigation, and the Earth System. Today the journal is a key resource used in the reports of the Intergovernmental Panel on Climate Change.

My interests now focused on developing hypotheses at the plant and crop level from ever more complex mathematical models of photosynthesis, and then testing them in the field. In 1999, the University of Illinois had the most powerful public domain computer in the world, the largest photosynthesis research group anywhere, and about six square miles of adjacent experimental farm. When offered a position there, it was my obvious next career move. With the help of Don Ort, Evan DeLucia, and some exceptional graduate students, we were able to establish a FACE facility on the farm. Today, and now led by my former student, Lisa Ainsworth, it is the largest open-air facility in the world for testing the impacts of atmospheric and climatic change on crops. As more data on crops under elevated CO_2 from FACE became available, two things became evident. In the absence of other changes, elevation of CO_2 consistently increased C3 crop photosynthesis throughout the growing season, and this in turn corresponded to increased crop yield, especially in more modern cultivars and in root crops with large sinks. That is not to say rising CO_2 is good for crops, it is not, since it drives rising temperature, water loss and extreme events that more than cancel any direct gain. However, it did show us that if we could increase photosynthesis by genetic means, we would gain more yield. In parallel, we developed a digital twin of the photosynthetic process in crop leaves, which then allowed us to numerically optimize the system. This indicated a number of bottlenecks in the process amenable to transgenic modification. Three of these have now been successfully implemented, as evidenced in replicated field trials. The fact that photosynthesis is not already optimized in crops appears to result largely from the rapid changes in atmospheric $[CO_2]$, a limiting substrate for C3 photosynthesis, and the light environment of the dense canopies of modern crop fields, which contrast greatly with the largely open environment in which their ancestors evolved. I was also able to show, again with the work of some remarkable graduate students, that Miscanthus x giganteus was particularly productive in the Midwest, 60% more so than our best corn crops, as a result of its ability to produce photosynthetically competent leaves earlier in the season and maintain them well into the Fall.

All of the above were not achieved by me alone, but through collaborations with generous faculty colleagues, exceptional graduate students and post-doctoral fellows, and dedicated support staff. In considering how I have spent and will spend my career – it is in collaborations.

What do you consider your most important contribution to plant science research?

I would like to think that my greatest contribution has been through mentoring and encouraging the next generation of students. It is so very pleasing to see that almost all of my past graduate students and post-doctoral research fellows have remained in plant science research, many assuming leadership positions and exceeding myself. In terms of research findings, I see three contributions that I have made with collaborators: 1) Demonstrating that the benefits of C4 photosynthesis can extend into cooler climates and cooler parts of the year, which led to identifying Miscanthus x giganteus as a key and highly sustainable bioenergy crop; 2) Showing through elevated CO_2 field experiments and transgenic manipulations that photosynthesis can be increased in crops to result in substantial yield benefits; and 3) Finally, showing the means to improve photosynthetic efficiency in current and future conditions through in silico engineering, and in turn actual bioengineered improvements.

When did you join ASPP/ASPB and how did it affect your career?

As a graduate student, Plant Physiology was my go-to journal and has been key throughout my career. I joined ASPP, as it was then, in the late 80s. Although based in Britain, increasingly I saw the need to network with ASPP members. Soon after moving to Illinois, I joined the Meetings Committee, which included building a Major Symposium on plant physiology and climate change.

Soon after, Sally Assmann, Keith Mott, and I organized an ASPB specialist meeting, "The Biology of Transpiration: From Guard Cells to Globe"' at Snowbird Utah. With Nick Carpita, then ASPB President, and international collaborators, we organized the first and ASPB sponsored Pan-American Congress on Plants and Bioenergy. These events, together with the regular ASPB Summer meetings, were critical to allowing me to form an enduring and ever-expanding network of collaborators and colleagues across the USA and beyond. Of course, being awarded the Society's Kettering Prize and elected a Fellow of the Society were and are key recognitions for my career. Perhaps the greatest value though has been through the multiple programs and opportunities that ASPB provides for early career scientists. These have been so valuable in helping to launch the careers of graduate students and post-doctoral fellows from my lab, while also supporting diversity.

What advice would you offer to young people contemplating a career in plant biology?

We are all different and there is no single manual of advice that can work for all. My career has seen so many revolutions in what is possible, from being able to sequence a few DNA bases on gels over weeks, to sequencing whole genomes in hours, from spending a year to build a system to measure CO_2 uptake by leaves under controlled conditions, to off the shelf commercial units, and from hours spent in the library researching a topic to a quick AI-driven summary and synthesis. This and many other innovations mean that opportunities have on the one hand never been greater, but also never more daunting. Surmounting this requires forming effective collaborations, so that the range of expertise needed can be brought to bear on a question. My observation is that those who are generous and share with their collaborators form enduring and successful partnerships, while those who insist on credit above others risk isolation. For me, discovery in and of itself has never been enough, as I have wanted to see how it could be beneficial and potentially make a difference to the many challenges we have in global food supply and reducing greenhouse gas (GHG) emissions. I hope the next generation will share this and increasingly move to apply the amazing advances in plant biology to field situations. Plant biology has never been more important or more able to address some of our pressing global problems, so consider being a part of the solution. But most of all, find something you are passionate about, and like me you can spend your career being paid to pursue your hobby.

Academic Family Tree: https://academictree.org/plantbio/tree.php?pid=754145