SPOTLIGHT

Ian Sussex: simple tools, clever experiments and new insights into plant development

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ABSTRACT

Ian Sussex, who began his career at a time when the most powerful tool available to plant developmental biologists was a scalpel, helped transform the discipline of plant developmental biology into the dynamic, sophisticated field that it is today. He did this through his own research, through an influential book that he wrote with his friend and colleague Taylor Steeves, and through his many students and post-doctoral fellows, to whom he gave the greatest gift a scientist can receive – the freedom to do whatever they wanted.

KEY WORDS: Developmental patterning, Plant morphogenesis, Claude Wardlaw

Ian was born and raised in New Zealand, and obtained his PhD from the University of Manchester in England, where he worked in the laboratory of Claude Wardlaw. As he described in a biography that he wrote for the *Annual Review of Plant Physiology and Plant Molecular Biology* (Sussex, 1998), Manchester was an exciting place to be at the time. Experimental analysis of plant morphogenesis was relatively new, and several groups at Manchester were pioneers in implementing new experimental strategies and devising new hypotheses. Wardlaw was conducting seminal work on the organisation of the shoot apical meristem, Eric Ashby was studying the regulation of leaf shape and shoot maturation, H. E. Street was using root culture to study plant metabolism, and Alan Turing was developing his reaction-diffusion model for pattern formation. Ian's experience at Manchester influenced the way he thought about plant development for the rest of his career. Although Ian was always among the first to try new experimental approaches, many of the questions he and his students explored were the same questions that motivated Wardlaw and his colleagues. How is the shoot apical meristem organised? Which aspects of its activity are determined by factors autonomous to the shoot apex and which by factors from outside the shoot apex? What is the role of the shoot apical meristem in the specification of lateral organ identity? How are the fundamental aspects of leaf morphology (polarity, shape, size) determined? Why do the character of the structures produced by the shoot meristem change during its development? And, how is the development of a plant embryo regulated *ab initio* before there are meristems?

These were not the kinds of questions that most plant biologists were asking in the 1960s and 70s, in the early part of Ian's career. During this period, plant biologists were primarily interested in discovering the roles of specific hormones in plant growth and development, and with characterising the effects of various environmental factors such as light on these processes. Research was focused on the cellular mechanisms by which these factors act, rather than on the mechanism of pattern formation and morphogenesis per se. This is not to say that Ian was uninterested in cellular or molecular mechanisms; his students were among the first to study the molecular basis of plant embryogenesis, and they also made important contributions to our understanding of the hormonal control of this process, as did Ian personally in studies of auxin-induced wound healing. However, these studies were motivated more by an interest in fundamental principles of development than by a desire to work out the detailed molecular mechanisms of a particular process.

The publication of *Patterns in Plant Development* in 1972 (Steeves and Sussex, 1972), and the 2nd edition in 1989, marked a turning point in plant developmental biology because it described a body of experimental work on plant morphogenesis that had been largely ignored, and drew attention to important developmental phenomena about which very little was known. Anyone looking for a research project now had a good place to start, and Ian's lab swelled with students and post-docs in the years following the publication of this book. At one point, there were a dozen or so people in his laboratory studying nearly as many different problems in nearly as many species. Students and post-docs expecting to be tutored in the mysteries of plant development from a founder of the field were in for a surprise, however. Although Ian was always willing to provide encouragement and advice, he expected the people in his laboratory to figure out what they wanted to do, and then do it more or less on their own. This approach was exhilarating to some, and nearly incapacitated others. It was unusual even then, and was only possible because Yale had funding for graduate students and plant growth facilities that – as far as we knew – were free.

As I alluded to above, Ian's research, and that of his students, spanned a wide variety of topics. The work for which he is most famous is his analysis of leaf polarity (see Kuhlemeier and Timmermans, 2016; also in this issue), which he conducted as a graduate student. Using microsurgery, he showed that the adaxial-abaxial polarity of a leaf depends on the physical continuity between the adaxial side of the leaf and the shoot apical meristem (SAM), suggesting that this polarity might depend on a diffusible substance from the SAM. This study was also the first to demonstrate that the lateral expansion of the leaf requires adaxial-abaxial polarity. In subsequent studies, Ian explored other aspects of leaf development, including the timing of leaf determination, and the role of nutrition in determining leaf shape.

Ian began working on embryo development in 1968, focusing on the kidney bean *Phaseolus vulgaris* and the scarlet runner bean *P. coccineus* because of their relatively large embryo, including the suspensor. In addition to demonstrating the existence of temporally regulated programmes that controlled patterns of gene expression and desiccation tolerance, these studies revealed that some aspects

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of embryo development – in particular, developmental arrest – were dispensable. This led to the idea that embryo development involves a series of overlapping, independently regulated programmes, rather than a linear series of dependent steps. His studies of the role of abscisic acid in embryo development demonstrated that it had both activating and repressive functions, and provided a completely new view of the activity of this plant hormone. The genetic analysis of embryo development in *Arabidopsis thaliana* performed in Ian's laboratory presaged the explosion of interest in this species as an experimental system. In addition to these studies of embryo development, Ian's lab resurrected the use of genetic mosaics as a tool for studying cell lineage patterns and for the analysis of cell and tissue interactions during morphogenesis. These studies provided a comprehensive, and sometimes unexpected, picture of the cellular processes of division and expansion that underlie organogenesis in plants.

Ian had a major hand in some of this work; in other cases, he was a supportive but largely uninvolved observer. However, none of these studies would have been performed had he not provided the intellectual environment in which independently minded junior scientists could flourish. His reward was not only new insights into the mysteries of plant development, but a generation of plant scientists who owe their success to his light touch and gentle encouragement, and their students, who have been the indirect beneficiaries of his intellect.

Some years ago, my wife and I were in Auckland, New Zealand, returning from a conference in Australia. I visited the library of the National Museum of New Zealand and asked to see the 1928 edition of the book *The Trees of New Zealand* by L. Cockayne, which includes descriptions of species that undergo vegetative phase change, a phenomenon for which the flora of New Zealand is famous. I sent Ian a postcard to tell him of my visit. Soon after we returned home, I got an email from Ian with a PDF attached. It was a scan of the title page of the 1928 edition of *The Trees of New Zealand*, which Ian had received in high school. On it was the inscription: 'To Ian Sussex, for excellence in science'. What more can be said?

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Competing interests
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