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ENID MACROBBIE

Throughout her career, Enid MacRobbie has been at the forefront of studies of ion transport in plants, addressing fundamental questions in plant nutrition and cell signalling. She pioneered the use of radiotracers to measure ion fluxes, identified active and passive transport processes and their regulation in giant algae, and unravelled the transport events involved in stomatal movement in higher plants. She has trained a succession of outstanding Ph.D. students, who have gone on to become influential scientists in their own right, and has won worldwide recognition and honors for her research. There is no doubt that her career has helped change conditions for women scientists, to the benefit of those who have followed.

Enid was born in Edinburgh, Scotland in 1931 and attended high school and university in that city. She studied physics for her B.Sc. degree and was awarded a 1st class honors in 1953. She stayed at the University of Edinburgh for her Ph.D. becoming the first graduate student in Jack Dainty's new biophysics research group. The group was part of the Department of Physics, but, characteristically in those post-war years, was accommodated in a converted chicken house behind the Department of Genetics. In her Ph.D. project, Enid made the first use of radioisotopes to measure ion fluxes in plants. Her initial work was with the seaweeds Rhodymenia



palmata and Ulva lactuca, but she subsequently moved to the conceptually simpler system of the giant internode cells of the alga Nitellopsis obtusa. Her thesis work established the theoretical framework for, and practical application of, isotope efflux analysis-a technique that had been developed in animal cells, but which was made more complicated in plants because of the presence of the large central vacuole. The resulting papers were pioneering and immediately established Enid's reputation in her chosen field.

At the end of her Ph.D. research in 1957, Enid moved to a postdoctoral position with Professor H. H. Ussing at the Institute of Biological Isotope Research in Copenhagen where she studied ion transport in frog skin. After one year there, she secured a Research Fellowship at Girton College in Cambridge and moved back to the United Kingdom. Enid's initial hope had been to work with Nobel Laureate Alan Hodgkin in the Department of Physiology but, given her interests, he suggested that it might be better if she joined George Briggs, Professor of Botany, who was interested in the ionic relations of plant cells. Thus began her association with the Botany School (now Department of Plant Sciences) in the University of

Cambridge where she has been an inspirational colleague for more than 40 years. Briggs gave Enid freedom to follow her instincts, and she began using isotopes to measure fluxes of K+, Na+ and Cl- in the giant alga Nitella translucens. Her main aim was to establish which fluxes at the plasma membrane and tonoplast were active and which were passive, and how they were regulated, information that was essential to establish the molecular mechanisms of ion movement in plants. The work was outstandingly successful. It secured her international reputation and helped establish a more quantitative and biophysical approach to studies of plant transport systems.

Professor Briggs retired in 1960 and teaching quantitative plant physiology was taken over by Enid, Michael Pitman, and Martin Canny. When, in 1962, Michael Pitman left Cambridge for the University of Adelaide, Enid was recruited to the Demonstratorship (Cambridge's equivalent of a non-tenured Assistant Professorship) he vacated. Her research was given a major boost when, in 1964, she, Jack Dainty (by then the inaugural Professor of Biophysics at the newly-opened University of East Anglia), and Charles Whittingham (at Imperial College, London) were awarded a substantial 5-year grant by the Nuffield Foundation. This allowed Enid to build a group quickly and to establish strong links with the Dainty group in Norwich. The latter brought the additional benefit of contacts with a number of talented Australian biophysicists, including Alex Hope, Alan Walker and Geoff Findlay, who

ASPB Pioneer Member

became life-long scientific friends and collaborators. The Nuffield grant was doubly useful because it came with no strings attached, and Enid could spend with complete flexibility, a sharp contrast with the limitations placed on modern grants in these days of accountability! This period also saw the start of Enid's role as an inspirational Ph.D. supervisor when F. Andrew Smith joined her in 1962 as her first Ph.D. student. A year later, John Raven and John Cram were recruited, and the group quickly grew to ten, including Roger Spanswick, who was a postdoctoral associate.

From 1962 to the mid-1970s, the group was concerned mainly with characterizing ion fluxes at the plasma membrane and tonoplast of giant algae, but in 1978, Enid made a major change in research direction when she decided to begin studying the mechanism of stomatal guard cell movement, the fundamental process by which plants regulate the uptake of gases and the loss of water. The switch to stomates was driven by the realization that the nature of the fluxes underlying changes in ion content during opening and closing were largely unknown. Enid began studying this problem using her established methods, but adapting them to the more challenging guard cell system. She received her first grant for this work in the early 1980s and it has remained the mainstay of her research since then. As with her work on giant algae, Enid has made an important contribution to our understanding of the control of stomatal closure and her research has provided important quantitative flux information that complements

studies done by other means, such as patch clamping.

Enid's laboratory has been the incubator for the fledgling career of many now-distinguished plant physiologists. These include F. Andrew Smith, John Raven, John Cram, Roger Spanswick, Mel Tyree, Richard Williamson, Dale Sanders, Roger Leigh, Carol Shennan, Mike Blatt, Mark Tester, Mary Beilby, and Gerhardt Thiel, to name just a few. Enid's input to the work of her colleagues is always constructive. She is able to identify and focus on the key issues, and through this, draw the best out of others. Her positive outlook on the work of her colleagues remains the abiding memory of many of her former students and postdocs. As one former postdoc put it: "Some of my fondest memories of my time in Cambridge are of sitting with Enid talking through data or ideas and coming away knowing that I've been 'stretched' and have enjoyed the experience."

An unusual feature of Enid's approach is that she has actively encouraged the majority of the people who have worked with her to publish papers without her name on them. Thus only about 25% of the papers published by her colleagues during their time in her lab have included her as a co-author. Therefore, any literature search using her name as key words will substantially underestimate the full extent of the output of her laboratory. This has been a remarkably selfless approach to science that has given added impetus to the careers of those whom she has mentored. It is unlikely that, in these days of

citation analyses, present or future scientists will feel willing or able to make such a magnanimous gesture. As a result of her unselfish approach, it can be guaranteed that the papers with Enid's name on them indicate that she made a real and important practical contribution to the work. Throughout her career, she has always conducted her own experiments and all her free time is spent at the bench. Even now, following her official retirement in 1999, and at the start of her eighth decade, she remains active and can daily be seen performing flux measurements, reviewing papers, or offering advice to younger colleagues who regularly seek her counsel.

Enid's influence extends well beyond her own research laboratory. In her role as a teacher, she has influenced generations of Cambridge undergraduates to consider a career in research. Together with the late Tom ap Rees, she revolutionized the content of botanical courses in Cambridge in the 1960s and 1970s by introducing more cell biology and biochemistry, and emphasising quantitative approaches and analytical thinking. She was particularly effective in the smallgroup tutorial teaching that is a special part of teaching in Cambridge, and it is not uncommon to meet former undergraduates for whom Enid's teaching has been a life-long inspiration. Girton College, where she has been a Fellow since 1958, was the first women's college in Cambridge and has an outstanding record of promoting equal opportunities for women in higher education. In her role as a teacher at the College, Enid influenced many women undergraduates to pursue

ASPB Pioneer Member

science as a career and many of them have gone on to gain international recognition.

Enid's career has resulted in many honors and measures of esteem. although often these came scandalously late considering the influence she has had on her field, possibly because she was a woman in a male-dominated environment and because of her policy of letting students and postdocs publish without her. She was appointed to a permanent Lectureship in 1966, was promoted to a Readership in 1972, and to a Personal Professorship in 1987, the first woman scientist in Cambridge to be awarded a Personal Chair. A year later, she was awarded a Doctor of Science (Sc.D.) by the University. She was elected a Fellow of the Royal Society of London (the highest honor in U.K science) in 1991, is a Fellow of the Royal Society of Edinburgh (elected 1998), and a Foreign Member of the National Academy of Sciences of the USA (since 1999). She is also a Corresponding Member of the American Society of Plant Biologists. Her 40 years of service to Girton College were recognized by her election to a Life Fellowship in 1999. In her spare time, which even in retirement is not abundant, Enid amuses herself with gardening, walking, and trout fishing. The latter is mainly done when she escapes to her holiday house in Kilchoan on the Ardnamurchan Peninsula, the most westerly point on mainland Scotland.

Throughout her career, Enid MacRobbie has sought to make biologists think quantitatively. Often she has had an uphill struggle

because most consider themselves mathematically inept and unable to use equations. Enid's aim has been to show them that they can, and that their scientific understanding is enhanced as a result. Her own work more than adequately demonstrates how a quantitative approach can enlighten, and her outstanding achievements as a scientist, teacher. and unselfish individual will have influence on plant physiology for many years. Her legacy will be both an outstanding research record and a cohort of talented individuals who have gone on to make their own mark on plant biology.

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