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OBITUARY

Clarence A. "Bud" Ryan (29.09.1931–07.10.2007)

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The plant community has lost one of its pioneer researchers. Clarence A. "Bud" Ryan died suddenly and unexpectedly on October 7th at age 76. For more than 40 years Bud was a member of the Institute of Biological Chemistry at the Washington State University in Pullman where he worked on plant-herbivore interactions. In the early 1970s he discovered that plants induce the synthesis of proteinase inhibitors after herbivore attack. Proteinase inhibitors are natural insecticides that prevent digestion of plant material in the insect gut. The accumulation of proteinase inhibitors in leaves distant from the site of herbivore feeding let Bud to postulate the existence of a chemical signal that moves throughout the plant to activate expression of PIN genes. He pursued this signal for 20 years when in 1991 his persistence paid off. Bud together with his senior technician Greg Pearce isolated a short peptide from 2 kg tomato leaves, which they called systemin and which was the first signaling peptide isolated from plants. In addition to his pioneering work that followed on the wound signaling cascade and isolation of the systemin receptor, Bud was also interested in signaling peptides in solanaceous species and other plant families. This work led him to the discovery of hydroxyproline-rich glycopeptides (HypSys peptides) in tomato, petunia and tobacco. Similar to tomato systemin, all HypSys peptides turned out to be processed from a single polypeptide precursor. Since the HypSys peptides differed from systemin in sequence and signaling properties, Bud realized that there was considerable specificity in peptide signaling between species. Later Bud discovered the rapid alkalization factors (RALFs), which comprise a family of 5 kDa proteins. At the age of 75, Bud identified the Arabidopsis systemin homologs and their receptor(s). He was able to demonstrate their function in plant innate immunity. This tremendous success in plant peptide research even after his retirement in 1999 demonstrate that Bud remained fully engaged at the frontiers of plant science research. His tireless pursuit of problems central to plant defense was exemplary but also characteristic of his dedication to excellent research.

With one of his last manuscripts published in this issue of Plant Molecular Biology, Bud returned to his initial question on systemic wound signaling. Using transgenic tomato lines that ectopically express sense and antisense constructs of the tomato HypSys precursor or prosystemin, Bud could provide proof that their expression in response to wounding is necessary for systemic signaling. His paper shows for the first time that the two plant peptides cooperate in systemic wound signaling. The results provide evidence that the peptides amplify both the local and systemic response through a feedback loop, which generates jasmonate that activates defense gene expression. Bud's demonstration of the cooperative action of two peptides upstream of jasmonate significantly sets another milestone in our knowledge of wound signaling mechanisms. The postulated role of jasmonates in systemic wound signaling has now been elegantly demonstrated by Gregg Howe, one of Bud Ryan's former post docs, who used tomato mutants affected in jasmonate biosynthesis and signaling.

For the last two decades, Bud's pioneering work has opened an exciting new field in plant research—peptide signaling. His work will continue in many laboratories around the world, including the groups of his former postdocs such as C. Nelson (Des Moines, Iowa), E. Farmer (Lausanne, Switzerland), G. Howe (East Lansing, Michigan), J. Stratmann (Columbia, South Carolina), or A. Schaller (Stuttgart-Hohenheim, Germany). Bud has left us, but his legacy will live on.

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