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THEMATIC ARTICLES

Tribute to Folke Skoog: Recent Advances in our Understanding of Cytokinin Biology

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This issue is presented as a tribute to Folke Skoog, who recently passed away at the age of 92. Folke was a central figure in the field of plant hormones. He played a central role in research in a wide variety of areas, but is perhaps best known for his discovery of cytokinins in the 1950s. Therefore, it is fitting that this special tribute issue focuses on advances in the elucidation of the function of this phytohormone. Recently, there have been a series of remarkable breakthroughs in our understanding of cytokinin action, based largely on molecular genetic studies in *Arabidopsis*. These breakthroughs are discussed in the papers that follow.

Don Armstrong, a close friend of Folke, provides an overview of Folke's life and career. His article provides insight into the forces that shaped Folke's career and summarizes his major contributions to plant biology. We have also presented a list of Folke's extensive publications, highlighting his productivity and range of research areas, from plant hormones to plant morphogenesis to algal biology, and spanning five decades of research.

One of the primary problems in unraveling the biology of a signaling compound is understanding how that signal is produced by the organism. The search for the plant enzyme that catalyzes the key step in cytokinin biosynthesis, the attachment of the isoprenoid side chain to adenine, has been arduous and at times frustrating. The prior inability to identify this isopentyl transferase or IPT enzyme led to the suggestion that perhaps plants did not even synthesis cytokinin, but rather they might have relied on microbial symbionts to supply the hormone. Recent work from two labs (Sakakibara and co-workers and Kakimoto and co-workers) has finally identified a family of genes from *Arabidopsis* that encode IPT enzymes, demonstrating unequivocally that plants encode the capacity to synthesis their own cytokinin. This identification of IPT genes was made possible by the completion of the sequencing of the *Arabidopsis* genome and by the sequence similarity of these cytokinin biosynthetic enzymes to enzymes from both plants and animals that catalyze the conversion of a residue in tRNA to cytokinin. Sakakibara and Takei present an overview of this work and discuss some surprising properties of these enzymes.

In addition to biosynthesis, the inactivation of a signal is equally important in regulating its level. Cytokinins are modified in numerous ways, especially through conjugation to glucose to various positions and by interconversion among the free base, riboside and ribotide forms. Carol Auer pre-

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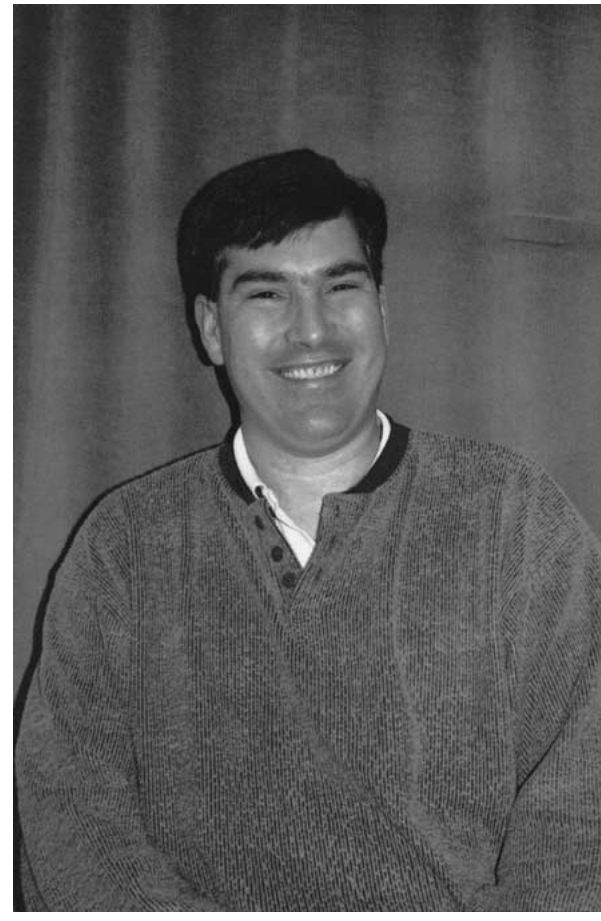
sents a summary and a discussion of the implications of recent findings regarding this metabolism of cytokinin.

In addition to understanding how the levels of a signal are regulated, it is crucial to determine how the signal is perceived and transduced by the target cells to understand the function of that signal. Remarkable progress has recently been achieved in understanding how cytokinin is perceived by a plant cell, and how that signal is then transmitted to the nucleus. Deruère and Kieber discuss these recent studies, and they suggest a model for cytokinin signaling that is similar to the bacterial two-component signaling paradigm.

Perhaps, ultimately, the most interesting aspect of cytokinin biology, and arguably the least well understood, is exactly what role this hormone plays in plant growth and development. The tools that have been assembled, including the cloning of genes that encode proteins involved in cytokinin biosynthesis, metabolism, perception and signal transduction and the identification of mutants disrupted in many of these processes, should allow this question to be addressed rigorously in the near future. Indeed, we already have exciting insights into some aspects of cytokinin function derived from studies using such tools, and these have been reviewed in the paper by Thomas Schmülling.

Although a multitude of questions remain, the articles presented herein provide a glimpse into the remarkable advances that have enriched our understanding of cytokinin biology. This field has come a long way from the seminal discovery of this hormone by Folke and his co-workers in the mid 1950s and their subsequent early work on cytokinins and auxin. I expect this fast pace of discovery to continue into the future, a fitting legacy to Folke and his founding contributions to the field.



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