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Understanding Abscisic Acid

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The name "abscisic acid" (ABA) was proposed in 1968 for the sesquiterpenoid hormone previously known as "dormin" or "abscisin II," which had been isolated from several higher plants (Addicott and others 1968). In early studies its functions appeared mostly negative inasmuch as ABA treatments reduced growth and inhibited germination. However, it became clear that ABA was essential for normal growth and development, and we now know that ABA produces a huge range of both short-term and long-term changes in cellular metabolism and processes. It has been estimated that 8–10% of *Arabidopsis* genes are ABA-responsive (Finkelstein and others 2002). As analytical methods improved, ABA was detected in algae, fungi, and liverworts in addition to higher plants (Hartung and Gimmler 1994). In this special issue, our progress toward understanding how ABA functions in higher plants is presented via reviews of selected topics.

For many years the biosynthetic origin of ABA in higher plants was obscure. Although fungal pathways to ABA via farnesyl diphosphate were identified, these pathways could not be convincingly demonstrated in higher plants. Traditional tracer experiments to identify pathway intermediates were plagued by low incorporation rates. It became apparent that the biosynthetic route in fungi was quite different from that in higher plants. It is now accepted that ABA is produced by an "indirect" route via carotenoids. Ian Taylor, Tineke Sonneveld, Tim Bugg, and Andrew Thompson review our current understanding of ABA biosynthesis, describing how the application of genetic methods has helped reveal the overall pathway and its regulation.

The pathways by which ABA is catabolized have been the subject of much less attention than biosynthesis. A recent upsurge in interest has revealed increasing complexity. Irina Zaharia, Mary Walker-Simmons, Carlos Rodriguez, and Sue Abrams describe two new catabolic pathways and note that the hydroxylated intermediates of ABA metabolism may themselves have hormonal roles. These recent studies of ABA metabolism have been facilitated by the application of high-resolution mass spectrometry, allowing sensitive detection and quantitation of endogenous hormones and hormone metabolites. Zaharia and colleagues also describe the uses of chemical analogs of ABA in research. These uses include identifying ABA-binding proteins and probing their structure-function requirements.

To understand how any hormone works, it is necessary to know how it is transported throughout the plant. Current studies are revealing large amounts of information about where ABA is produced, but the movement and transport of ABA are surprisingly poorly understood. These aspects of ABA are the subject of investigation by relatively few research groups. Perhaps this arises in part because movement and transport are less amenable to the genetics-based research strategies that predominate today. However, both are subjects of enormous potential significance. Understanding auxin transport has been essential for understanding how auxin regulates developmental processes and tropic responses. By analogy, we cannot fully comprehend

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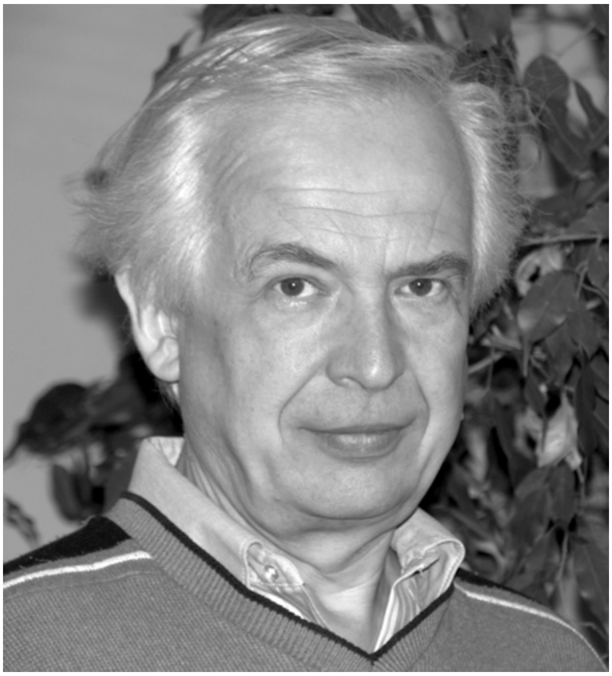

Figure 1. Adrian Cutler.

how ABA works until we understand how, when, and in what form it is transported between cells and tissues. The current state of knowledge is reviewed by William Davies, Guzel Kudoyarova, and Wolfram Hartung. An important theme is the interaction of ABA with other hormone signaling cascades and with pH. One interesting aspect relates to the ABA glucose ester (ABA-GE), which until recently was considered to be a dead-end catabolite. Unlike some auxin conjugates, ABA-GE did not appear to act as a hydrolysable source of free ABA. However, Davies and colleagues review evidence that the ABA glucose ester is a transported form of ABA from which free ABA can be released in ''target'' tissues.

A primary target for ABA action is guard cells, and Zhen-Ming Pei and Kazayuki Kuchitsu review the rapid events that occur after ABA binding to guard cell ABA receptors, which remain unidentified. After receptor activation, reactive oxygen species are produced, and changes in membrane polarization, cytosolic pH, free calcium levels, and ion channel activity occur over a period of about 15 minutes. Nitric oxide seems to be involved as a signaling intermediate and may function to modulate calcium levels. Pei and Kuchitsu point out that although ion channels have been studied in detail by means of electrophysiology, the genes coding for many of them have not yet been identified.

The best-known effects of ABA in vegetative tissue relate to abiotic stress responses, and there is an extensive literature related to this, especially with respect to adaption to dehydration and soil salinity. In this issue, Larry Gusta and Russell Trischuk focus on the role of ABA in relation to low temperature acclimation. They emphasize the pitfalls of convenient laboratory protocols for inducing stress. These protocols are sometimes very drastic and entirely unrelated to conditions that occur in the field. Data from these studies may be quite different from data obtained from studies in which plants are grown under realistic conditions. The acclimation effects of ABA are produced by changes in gene expression modulated by interaction with light (via phytochrome) and sugars.

The role of ABA in maintaining seeds in the dormant state is reviewed by Allison Kermode. Dormancy is a crucial adaptive trait that prevents seeds from germinating in unfavorable seasons and conditions. In this context ABA acts antagonistically to gibberellins, and the multi-level interaction of these growth regulators is crucial for determining whether dormancy is maintained or germination occurs. Kermode reviews the signaling process and transcription factors involved in dormancy regulation and the changes that occur upon termination of dormancy.

The articles in this issue reveal a huge increase in the amount of information related to how ABA works in plants. However, as with all other plant growth regulators, the effects of ABA are modulated by interaction with numerous other signaling pathways, producing a web of interactions of remarkable complexity and subtlety. In other words, our recent progress has revealed new layers of complexity, and an overall model of how ABA functions remains elusive. Much hard work remains before we can realistically ''understand'' how ABA works in any process.

I must thank all of the authors for their contributions to this thematic issue. I hope that the range of topics and depth of coverage in these articles will provide a useful resource for plant biologists, and perhaps inspire new ideas and new contributions to this field.

REFERENCES

Hartung W, Gimmler H. 1994. A stress physiological role for abscisic acid in lower plants. Progress Botany 55:157–173.

Addicott FT, Lyon JL, Ohkuma K, Thiessen W. E, Carns H R, and others. 1968. Abscisic acid: a new name for abscisin II (dormin). Science 159:1493.

Finkelstein RR, Rock CD. 2002. Abscisic acid biosynthesis and response. The Arabidopsis Book. (C. R. Somerville and E. M. Meyerowitz, Eds.), American Society of Plant Biologists., Rockville MD USA. (online) doi/10.1199/tab.005.