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THEMATIC ARTICLES

Ethylene Biosynthesis, Perception, and Response

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This thematic issue surveys our current understanding of ethylene biosynthesis, perception, and response. Tremendous progress has been made in elucidating how this gaseous hormone functions from the molecular level to the whole-plant level. At the same time, a number of questions are unanswered and new questions are being raised, making ethylene a fascinating hormone for which much remains a mystery. Classically considered the ripening or stress hormone, ethylene is known for its dramatic and diverse effects on plant growth and development. Numerous processes involve the action of this volatile hormone, including fruit ripening, senescence, abscission, and adaptive responses to biotic and abiotic stresses. Many of ethylene's effects have been known for nearly a century, yet responses to this simple hydrocarbon continue to be uncovered and examined from new perspectives, as illustrated by several articles in this issue.

Many important advances have been made in our understanding of both ethylene biosynthesis and ethylene signaling. Although the enzymatic steps of ethylene biosynthesis are well understood and form a simple biochemical pathway, it is now known that the regulation of this pathway is highly complex, involving multigene families activated by diverse stimuli and controlled at different levels. In ethylene signal transduction, the foundation for the molecular dissection of the pathway has been the isolation of mutants in *Arabidopsis* that display an altered seedling ''triple-response'' phenotype in response to ethylene treatment. The first few mutants led to the identification of key components of the signaling pathway in fairly rapid succession. These components formed a linear pathway starting with ethylene binding to the receptors and leading to the regulation of gene expression. While thus it appeared early on that the ethylene-signaling pathway was largely solved, exactly how the proteins in this unique collection signal to one another remains an important question. Recent discoveries in ethylene signaling have created a more complex picture by introducing genes and processes that regulate the pathway. In addition, the integration of ethylene biosynthesis and ethylene response into larger signaling networks involving cross-talk with numerous other signals (for example, jasmonic acid, gibberellic acid, abscisic acid, auxin, glucose, and light) is just beginning.

The nine articles in this issue highlight many of the advances and novel insights attained in recent years and suggest future directions and challenges. The articles cover a range of topics and reflect the diverse roles that ethylene plays in plant growth and development. Because of the scope of this issue,

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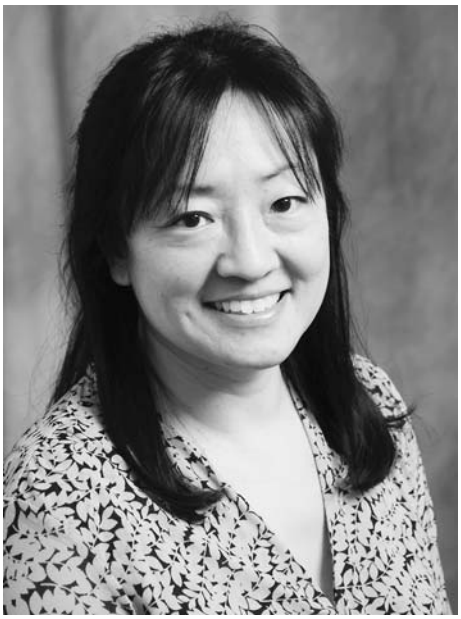

Figure 1. Caren Chang, guest editor.

other topics such as the many practical applications of ethylene are touched on only briefly. I (Figure 1) thank all of the authors who contributed to this issue and I apologize to those whose work could not be included here.

In the first article, Cristiana Argueso, Maureen Hansen, and Joseph Kieber review the intricacies behind the regulation of ethylene biosynthesis. Ethylene biosynthesis is activated by diverse stimuli, including a wide array of abiotic and biotic stresses, leading to temporal and spatial patterns of ethylene production. These complex patterns of synthesis involve two key enzymes: 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (which catalyzes the rate-limiting step) and ACC oxidase, both encoded by multigene families. One level of regulation, which has been extensively documented, is the differential transcriptional activation of the genes for ACC synthase. Recently, an important second level of regulation has been uncovered that involves post-translational control of ACC synthase stability, which is regulated by phosphorylation. The topic of ethylene biosynthesis is also addressed by several other articles in this issue in the context of fruit ripening, plant defense, and crosstalk

In the next article, Hongjiang Li and Hongwei Guo review our current understanding of the ethylene signal transduction pathway in *Arabidopsis*. As with ethylene biosynthesis, significant progress has been made with respect to how a key component of the pathway is regulated. The key component in this case is the transcription factor, EIN3, which was recently found to be regulated by protein degradation mediated by two F-box proteins. The latest discovery in this story is that these F-box proteins themselves are regulated at the level of RNA turnover involving the 5′–3′ exoribonuclease XRN4. At the other end of the pathway, a novel predicted membrane protein (RTE1/GR), which is highly conserved in metazoans and protozoans, was identified as a positive regulator of ethylene receptor function. Such additions to our understanding of the ethylene-response pathway are in keeping with the eclectic character of the pathway's components. Li and Guo provide a nice overview of the ethylene signaling pathway and then discuss the emerging data on interactions between ethylene signaling and auxin, light, gibberellin, jasmonic acid, and glucose.

The article by Brenda Hall, Samina Qureshi, and G. Eric Schaller focuses on the structure and function of the ethylene receptors. Many aspects of the receptors have been studied extensively, including ethylene binding, protein kinase activity, membrane topology, and subcellular localization. Although the ethylene receptor was the first plant hormone receptor to be identified, the biochemical mechanism of receptor signaling has remained elusive, and current evidence indicates that kinase activity plays only a minor role in ethylene signaling. The authors provide a thorough discussion of the existing data (primarily based on studies in *Arabidopsis*) and synthesize the findings into a mechanistic model for how the ethylene receptor family transmits the signal.

Next, Brad Binder reviews the use of high-resolution time-lapse imaging to examine short-term kinetic growth responses of dark-grown *Arabidopsis* seedlings either treated with ethylene or recovering from ethylene treatment. High-resolution time-lapse imaging has allowed ethylene responses to be described at a striking new level of detail and has led to the discovery of ethylene-dependent nutation in *Arabidopsis* seedlings. Whereas dissection of the ethylene response pathway has relied exclusively on end-point (static) mutant phenotypes, the examination of short-term kinetic responses, including nutation, now allows for greater analysis of mutants in the pathway.

Of the many responses to ethylene, fruit ripening is probably the most extensively studied. The wealth of information on this topic is evident in the article by Cornelius Barry and Jim Giovannoni, who provide a comprehensive review of ethylene biosynthesis and signaling in the context of fruit ripening, particularly as elucidated in tomato. Tomato is an excellent genetic model for studying fruit ripening, and, as shown by this article, tomato has

been important in providing both contrast and confirmation for molecular data derived from *Arabidopsis*. While it is well established that ethylene is involved in the ripening of climacteric fruits, the authors also present accumulating evidence for ethylene having a role in the ripening of fruits that are classified as nonclimacteric.

Ethylene also plays a pivotal role in plant defense, acting in a complex signaling network, together with jasmonic acid, salicylic acid, and abscisic acid, to orchestrate responses to biotic stress. In the next article, Bruce Adie, José Manuel Chico, Ignacio Rubio-Somoza, and Roberto Solano provide a comprehensive review of ethylene's involvement in defending against pathogen and insect attack. The authors review the induction of ethylene biosynthesis, ethylene-induced defense responses (including xylem occlusions, cell wall strengthening, production of phytoalexins, and induction of pathogenesis-related proteins), the transcriptional regulation of defense-related genes, and cross-talk.

The interplay between ethylene and other growth regulators occurs in many processes besides defense. Filip Vandenbussche and Dominique Van Der Straeten review the current evidence for cross-talk in various growth processes (germination, stomatal closure, differential growth, and elongation), describe interactions between ethylene and other growth regulators (for example, abscisic acid, gibberellic acid, auxin, brassinosteroids, and glucose), and present known and hypothesized mechanisms of cross-talk.

In the next article, Ronald Pierik, Rashmi Sasidharan, and Laurentius A. C. J. Voesenek discuss the opposing inhibitory and stimulatory effects of ethylene on plant growth that occur in response to various environmental challenges, such as flooding, drought, light conditions, nutrient availability, and mechanical stress. The authors discuss what is known about the mechanistic basis for these striking effects and present a model by which the opposing growth effects can be understood.

In the final article, Caroline von Dahl and Ian Baldwin discuss ethylene's role in plant-herbivore interactions. It is well established that herbivory stimulates ethylene production, but it is less clear to what extent ethylene-dependent responses influence herbivore performance and plant fitness. Ethylene may modulate plant interactions with herbivores via jasmonic acid-dependent responses that are either direct (such as secondary metabolites that act against the attacker) or indirect (such as the emission of volatile organic compounds that attract predators and parasitoids to the attacker). In addition, ethylene might well function as a direct mediator with potential ecologic consequences.

Last, but not least, I dedicate this issue to the late Tony Bleecker, a dear friend and colleague to many. Tony graced the ethylene community with his insight, wisdom, generosity, and humor, and his landmark discoveries and numerous contributions leave a lasting impact on the field. This issue is a tribute to Tony as so many of the articles bear his footprints.