## Focus on Ethylene

First discovered as a plant growth regulator over a century ago, ethylene continues to be a focus for research worldwide due to the many roles it plays in growth, development, and adaptive responses to biotic and abiotic factors. Ethylene is frequently manipulated for agricultural purposes, with both the inhibition and induction of ethylene responses being of commercial value. Ethylene is removed during the storage of fruit and vegetables by scrubbers and absorbants, its biosynthesis inhibited by aminovinylglycine, which targets the enzyme 1aminocyclopropane-1-carboxylic acid synthase, and its perception blocked at the receptor level by silver or cyclopropenes. Conversely, ethylene treatment, often applied in the form of ethephon, is used to regulate ripening, flowering, abscission, and even the flow of latex from rubber trees.

Ethylene was previously featured in a 2004 Plant Phys*iology* Focus issue edited by Caren Chang and Anthony Bleecker. We contributed research articles to the 2004 Focus issue, and there is a symmetry to our now taking on the editorial role for this 2015 Focus issue on the same subject. There have been substantial advances in our understanding of how ethylene functions in the decade since the previous Focus issue, and a comparison of the research articles found in the two issues provides a snapshot of which aspects of the field have changed and which have remained the same. For example, in the 2004 Focus issue, four studies employed Arabidopsis (Arabidopsis thaliana), two studies employed tobacco (Nicotiana tabacum), and the remaining three studies employed petunia (Petunia spp.), oak (Quercus ilex), and marsh dock (Rumex palustris). By comparison, in this issue, 10 studies employed Arabidopsis, two studies each employed rice (Oryza sativa) and maize (Zea *mays*), and the other studies employed pea (*Pisum sativum*), tobacco, apple (Malus domestica), the legume Medicago truncatula, and the moss *Physcomitrella patens*. Although both issues feature a diversity of experimental subjects, Arabidopsis is the most prominent of these, emphasizing the continued utility of Arabidopsis for mechanistic studies. Perhaps the most significant change in terms of experimental subjects is the presence of four articles in this issue that explore ethylene function in monocots, no such studies being present in the earlier issue.

There has been a change in the overall research focus of the articles between the two issues. In the 2004 issue, five articles, representing over half the issue, explored molecular mechanisms of the ethylene signal transduction pathway, analyzing the roles of receptors, the transmembrane protein ETHYLENE INSENSITIVE2 (EIN2), and the EIN3 family of transcription factors. In this issue, there are three articles that emphasize the study of primary pathway elements. Bakshi et al. (2015b) explore a

diverging role of the receptor receiver domain in transmitting the ethylene signal; Yasumura et al. (2015)take an evolutionary approach to characterize the role of CONSTITUTIVE TRIPLE RESPONSE1 in ethylene signaling; and Yang et al. (2015) characterize the function of the EIN3 transcription factor family in rice. There are also two articles that focus on novel signaling elements, which interact with and regulate the response from the primary signaling pathway. Shi et al. (2015) provide evidence that members of the ARGOS gene family, which encode short transmembrane proteins, regulate ethylene signaling, whereas Tao et al. (2015) identify a protein that interacts with and stabilizes the receptor against degradation. Interestingly, three of these articles address, although in different ways, cross talk between the ethylene and abscisic acid hormonal responses (Bakshi et al., 2015b; Shi et al., 2015; Yasumura et al., 2015).

A major area of interest in this Focus issue is how ethylene regulates specific aspects of growth and development. In the 2004 issue, two articles focused on specific downstream ethylene responses of shade avoidance and hyponastic growth. This issue features studies on aerenchyma formation (Yamauchi et al., 2015), root growth (Street et al., 2015), hypocotyl growth (Sun et al., 2015), hyponastic growth (Polko et al., 2015), abscission (Eccher et al., 2015), leaf senescence (Ueda and Kusaba, 2015), and the interaction of ethylene with light to regulate development (Weller et al., 2015). Of note, three articles in this issue emphasize a previously unheralded role for ethylene as an inhibitor of cell proliferation in both the shoot and root of Arabidopsis (Polko et al., 2015; Street et al., 2015; Tao et al., 2015).

Another major area of interest in this Focus issue is in the roles that ethylene plays in mediating plant responses to their environment. In the 2004 issue, abiotic interactions of shade, flooding, heat, and drought stress were represented, but biotic interactions were conspicuously absent. In this issue, four articles analyze the role of ethylene in nodulation (Larrainzar et al., 2015) and in defense responses against Pseudomonas syringae (Zhang, 2015) and aphids (Casteel et al., 2015; Louis et al., 2015). Three other articles explore abiotic interactions, analyzing the role of ethylene in response to drought (Shi et al., 2015), salt (Yang et al., 2015), and osmotic (Dubois et al., 2015) stresses. Although the focus has shifted away from the mechanistic analysis of pathway elements, mutants of these pathway elements serve prominently as genetic tools in the Arabidopsis articles as a means to decipher the role(s) of ethylene in its diversity of downstream regulation.

Commensurate with the diversity of roles for ethylene in plant physiology, this Focus issue features Update articles that illuminate how ethylene is synthesized (Booker and DeLong, 2015), its signal transduced (Ju and Chang, 2015), and the roles it plays in development (Van de Poel et al., 2015), microbial interactions (Gamalero

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and Glick, 2015), and abiotic stress responses (García et al., 2015; Gibbs et al., 2015; Müller and Munné-Bosch, 2015; Sasidharan and Voesenek, 2015; Thao et al., 2015).

Just months after the 2004 Focus issue, Tony Bleecker passed away from cancer. His significance to the field was commemorated in a 2006 piece by Edgar Spalding (Spalding, 2006) and more recently in a broad historical perspective on the history of ethylene studies written by Brad Binder, Caren Chang, and members of their laboratories (Bakshi et al., 2015a). Tony's presence is strongly felt in this Focus issue through the contributions of Chang, Binder, and Schaller, whose studies on ethylene were launched as a result of their interactions with Tony. Chang collaborated with Tony on the cloning of the ethylene receptor gene ETHYLENE RESPONSE1 of Arabidopsis while a postdoc in the laboratory of Elliot Meyerowitz, and Binder and Schaller studied ethylene signaling as postdocs in the Bleecker laboratory. In addition to establishing a family of ethylene researchers, one of Tony's enduring legacies is the infectious intellectual joy he brought to scientific study. For these reasons, we dedicate this Focus issue to the memory and legacy of Tony Bleecker.

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## **Guest Editors**

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