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Toward a Molecular Understanding of Plant Hormone Actions

Plants rely on a diverse set of small-molecule hormones to regulate every aspect of their biological processes including development, growth, and adaptation. Since the discovery of the first plant hormone, auxin, hormones have always been at the frontier of plant biology. Although the physiological functions of most plant hormones have been studied for decades, the last 15–20 years have seen dramatic progress in our understanding of the molecular mechanisms of hormone actions. The publication of the whole-genome sequences of the model systems of *Arabidopsis* and rice, together with the advent of multidisciplinary approaches, has opened the door to successful experimentation on plant hormone actions.

To discuss the latest advances and future frontiers in hormone biology, almost 10 years ago, a group of young Chinese talent, mainly recruited overseas scientists, organized the 286th Xiangshan Science Conference on Plant Hormones and Green Revolution on October 18–20, 2006, in Beijing, China. One of the fruitful achievements of this milestone meeting was a consensus that Chinese plant biologists should carry out interdisciplinary cooperation and integrated studies on the molecular mechanisms of hormone actions. Consequently, a proposal entitled “Molecular Mechanisms of Plant Hormone Actions” was submitted to the National Natural Science Foundation of China (NSFC) on November 4, 2006. After several rounds of discussions and consultations, NSFC granted a 10-year-funded Major Research Program on April 3, 2007. This is actually the first Major Research Program to be granted to the life sciences by the NSFC.

A long-term goal of the Plant Hormone Program is to achieve integrated understanding, at the molecular level, of the mechanisms of hormone actions in regulating plant growth, development, and responses to environments. This will be carried out in rice and the reference species of *Arabidopsis* using recently developed tools and the philosophy of systems biology. Initially, the research funded by this Program is focused on the following six scientific issues: (1) the molecular basis of hormone biosynthesis, metabolism, and its regulation; (2) hormone perception and signal transduction; (3) signal crosstalks in hormone actions; (4) hormonal regulation of organ patterning, development, and outgrowth; (5) hormonal regulation of plant responses to biotic and abiotic stresses; and (6) hormone analysis. After the mid-term evaluation by the NSFC in 2011, the Program entered its second stage, which mainly funded Integrated Projects focusing on (1) hormone homeostasis, modification, and their biological effects; (2) hormonal regulation of organ patterning and development; (3) hormonal regulation of abiotic stress responses; and (4) hormone analysis. Up to now, 63 Fostering Projects, 30 Key Projects, and 57 Integrated Projects have been funded by this Program. The major accom-

plishments of the Program are training talent in the field of hormone biology, establishment of hormone analysis platforms, and deeper understanding of the molecular basis of plant hormone actions.

This special issue of *Molecular Plant*, organized by Jiayang Li, Kang Chong, Klaus Harter, Youngsook Lee, Jeffrey Leung, Chuanyou Li, Enrico Martinoia, Makoto Matsuoka, Remko Offringa, Lijia Qu, Julian Schroeder, and Yunde Zhao, includes two spotlights, seven review articles, six research articles, and three Letters to the Editors contributed by global plant biologists, some of which are funded by the Plant Hormone Program in China.

TECHNICAL ADVANCES AND NEW TOOLS FOR HORMONE ANALYSIS

Gibberellins (GAs) comprise at least 136 highly similar endogenous analogs but appear only at an ultra-trace level of femtomoles to picomoles per gram fresh weight in scientifically relevant parts of plants. In this issue, [Li et al. \(2015\)](#) describe the development of an ultra-trace method for quantitative analysis of ultra-trace GAs in single organs of plants. It is the first time that a separation method can quantify GAs in only a single flower and even a single stamen.

HORMONE HOMEOSTASIS AND TRANSPORT

Carrier proteins responsible for the subcellular partitioning of auxin can play a key role by increasing or decreasing the nuclear auxin signal. In this issue, [Kramer and Ackelsberg \(2015\)](#) show that tonoplast-localized permease transports auxin out of vacuoles, which supports the inverse relationship between vacuolation and auxin content ([Ranocha et al., 2013](#); [Rutschow et al., 2014](#)). This led to a hypothesis that auxin homeostasis is more robust than previously suspected. [Yu et al. \(2015b\)](#) provide evidence that clathrin regulates auxin maxima and hook formation through modulating PIN3 localization and auxin efflux, suggesting a novel mechanism that integrates developmental signals and environmental cues to regulate plant skotomorphogenesis and photomorphogenesis. [Han and Kim \(2015\)](#) highlight the role of plasmodesmata in integrating hormone- and micromolecule-mediated signaling by non-cell-autonomous intracellular and intercellular signaling micromolecules, which is pivotal for plant development, physiology, and defense.

HORMONE SIGNALING

Wei and Li (2015) review the current findings on the functions of brassinosteroids (BRs) in mediating root growth, development, and symbiosis. Wang et al. (2015) report the function of the PP2A regulatory B subunits in regulating the dephosphorylation of BRI1. They demonstrate that the subcellular localization of PP2A specifies its substrate selection and distinct effects on BR signaling. Kim et al. (2015) show that the PPKL (Protein Phosphatases with Kelch-Like repeat domains) family members form homo- and hetero-oligomeric association, which is required for effective BR signaling. Pekárová et al. (2015) discuss the recently solved crystal and nuclear magnetic resonance structures of proteins that act in cytokinin/ethylene-related multi-step phosphorelay signaling, and the functional aspects of available structural information. By using a comparative phosphoproteomics approach, Dautel et al. (2015) demonstrate that the AHK2/AHK3-dependent phosphorelay influences the modification state of many proteins, particularly those that are involved in calcium signaling, cellular organization, and transcription regulation.

Most of the molecular models tacitly assumed abscisic acid (ABA) as the determinant for stomata closure. In this issue, however, Leung et al. (2015) highlight that NATA1-mediated acetylation of 1,3-diaminopropane (DAP) evoked stomatal opening when there was no stress and can reverse the closing stimulatory effects of ABA. Qing et al. (2015) show that ethylene regulates water transport via the C-terminal phosphorylation of the *Arabidopsis* aquaporin PIP2;1, which contributes to our understanding of ethylene-regulated leaf wilting, which is commonly observed during postharvest storage of plant organs.

HORMONE CROSSTALK

A recurrent theme of hormone research is to understand the molecular mechanisms of hormone crosstalk. In this issue, Daviere and Achard (2015) review the rapidly expanding information on the mechanisms of DELLA actions, which is providing novel insights into how DELLAs may function as a central hub, integrating signals from multiple hormone pathways and environmental cues, and allowing fine-tuning of the tradeoff between growth/defense and phenotypic plasticity. Shu et al. (2015) summarize current understanding of the sophisticated molecular networks involving the critical roles of phytohormones in regulating seed dormancy and germination, and discussed the interactions of diverse hormonal signals in these important processes. Yu et al. (2015a) review the regulatory role of ubiquitination in many steps of ABA signaling, and the significance of ubiquitination in subtly regulating plant response to ABA and stresses that lead to ABA synthesis. Li and He (2015) identified a physical connection between the BR and light signaling pathways, which was mediated by the BR-regulated transcription factor BZR1 and light-regulated transcription factor HY5 in *Arabidopsis*. This work provides a molecular framework for coordination of BR and light signals in regulating cotyledon opening, an important process in photomorphogenesis in plants. Dong et al. (2015) report that ABA negatively regulates ethylene production through ABI4-mediated transcriptional repression of the ethylene biosynthesis genes ACS4 and ACS8 in *Arabidopsis*.

EPIGENETIC REGULATION AND PLANT HORMONE ACTIONS

Recent studies reveal an emerging relationship between the function of phytohormones and epigenetic modifications. Epigenetic modifications give us exciting prospects of considering the unexpected complex and layered but ordered regulatory mechanisms modulating hormonal actions at the epigenetic level. The competing or coordinating rewriting of epigenomes might be one crosstalk point among different plant hormones. In this issue, Yamamuro et al. (2015) give a detailed review on plant hormone-related epigenetic modifications. In addition, Peirats-Llobet et al. (2015) uncover a direct link between ABA sensing and the chromatin remodeling ATPase BRAHMA (BRM) via core ABA signaling pathway components. They show that BRM represses ABA response during germination and establishment. Genetic and biochemical studies reveal an ABA-dependent phosphorylation-based switch to control BRM activity. Thus, SnRK2-dependent phosphorylation of BRM leads to its inhibition, and PP2CA-mediated dephosphorylation of BRM restores its ability to repress ABA response (Peirats-Llobet et al., 2015).

This is an exciting time for researchers interested in plant hormones. We believe that this special issue brings us a fresh understanding of hormone biology, particularly molecular mechanisms driving plant hormone actions. We anticipate that our growing understanding of hormone biology will provide new outlooks on how we value and utilize the built-in potential of plants for improvement of crops in an environmentally friendly and sustainable manner.

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