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EDITORIAL

Plant hormone functions and interactions in biological systems

Plant hormones are signal molecules that are synthesized *de novo* in plants. They are conserved in the plant kingdom and regulate diverse processes in plant growth and development and in acclimation responses to abiotic and biotic stresses. They also serve as communication tools between plants, as well as between plants and other surrounding organisms, such as microbes and insects. Plant hormones include auxins, cytokinins (CKs), gibberellins (GAs), abscisic acid (ABA), ethylene, jasmonates, salicylic acid (SA), brassinosteroids, peptide hormones, and strigolactones (SLs). Key players functioning in biosynthesis, catabolism, transport, perception, and signaling of plant hormones are steadily being identified and their molecular and physiological functions characterized. Usually, plant hormones are not solo players, but act together with each other or with other signal molecules in a synergistic, antagonistic, or additive manner. These interconnections contribute to the tight relations that exist between different biological plant processes, exemplified by the trade-off between stress responses and plant growth, but also by higher order growth regulations such as apical dominance and growth control between shoots and roots. Current plant hormone research has improved our understanding of molecular mechanisms underlying hormone interactions in signaling networks from a single cell to communication between proximal and distal cells. The exciting progress that has been made during recent years on complex hormone networks in different biological systems and the challenges that remain are reflected in the compilation of review articles in this Special Issue.

Hormone networks are activated by the recognition of hormone molecules. The receptors of all classical plant hormones have now been identified. Takeuchi *et al.* (2020) summarize structural studies of plant hormone receptors, showing the atomic-level of receptor–hormone binding, which triggers immediate primary responses. The hormones either act as a molecular glue for the interaction between receptors and target proteins, or function as allosteric regulators that cause conformational changes in the receptors, which enables binding to the target proteins. Molecular identification of individual hormone perception is essential to understand the activation and regulation of complex hormonal networks in different biological contexts.

Stomata are the primary structures to control the transpiration rate, thus multiple signals, in concerted action with the key hormone ABA, play important roles in regulating stomatal closure through controlling ion channels. Stomatal signaling has been used as a model system to understand plant signaling at the single-cell level. Hsu *et al.* (2020) provide an update on the current knowledge of ABA and other stomatal signaling pathways. They discuss the evolutionary aspect of stomatal ABA signaling and emerging regulators of core signaling components. They also discuss stomatal basal ABA signaling under non-stress conditions, such as influenced by CO_2 and low humidity.

SLs regulate plant growth and development but also act as communication tools between plants and other organisms, such as parasitic plants and microbes that reside in the rhizosphere. Aquino *et al.* (2020) provide an up-to-date review of the functions of SLs as endogenous and exogenous signal molecules in the direct and indirect regulation of plant growth and development. They also discuss the roles of SLs in the regulation of colonization of moss. Mashiguchi *et al.* (2020) focus their review on the molecular underpinnings of the biosynthesis, perception, and transportation of SLs.

Beside classical plant hormones, additional metabolites have been recognized as signal molecules in plants. Moreno *et al.* (2020) summarize the biological functions of carotenoid-derived molecules, including the well-known plant hormones ABA and SLs, but focus their review on the recently characterized apocarotenoid signals such as blumenols, mycorradicins, zaxinone, anchorene, β-cyclocitral, β-cyclogeranic acid, β-ionone, and loliolide. These apocarotenoids act in plant physiology, development, and interactions with other plants and microbes. Melatonin is another metabolite with a signaling function. It is a tryptophan-derived metabolite that functions as a hormone in animals, but also plants synthesize this molecule, and our understanding of its importance in plant physiology is recognized more in recent days. For example, melatonin auxotroph mutants of rice (*Oryza sativa*) show various phenotypes in growth, stress responses, and senescence. In this issue, Back (2020) summarizes the current knowledge of melatonin metabolism, signaling, and physiology in plants. The author discusses the control of melatonin levels by the catabolic pathway(s) and the potential roles of melatonin-binding proteins in signaling.

Growth regulation is fundamental in plant physiology and development. Environmental factors strongly influence plant growth via modulation of multiple hormone pathways. Favero *et al.* (2020) explain how plant hormone signaling is integrated into developmental and environmental signaling networks, thereby mediating plastic growth regulation of Arabidopsis hypocotyls and petioles under different light, circadian clock, and temperature conditions. The efficient use of soil nutrients is also essential for successful plant growth. The key role of growth-promoting CKs that are transported from root to shoot, and *vice versa*, in local and systemic nitrogen signaling and the different molecular components that are involved in this CK signaling mechanism are summarized by Sakakibara (2020).

Flowering, the phase transition from vegetative to reproductive growth, is a well-recognized important trait in agriculture. Elucidation of molecular mechanisms underlying this transition revealed that flowering is controlled by environmental, developmental, and hormonal signals, like GAs, that, among others, influence DELLA proteins that control flowering. Izawa (2020) gives an up-to-date summary of the current knowledge on the regulatory effects of this molecular network on the flowering process. Following fertilization comes fruit development and ripening, which are important agronomic traits that have attracted both fundamental and agronomical scientists. In addition to the well-understood role of ethylene in climacteric fruit ripening, other plant hormones are involved in the regulation of fruit development and ripening. Fenn and Giovannoni (2020) provide an update on the current knowledge of the integration of hormone signaling during fruit set initiation, growth, and ripening.

Plants need to deal with adverse conditions, such as imposed by diverse abiotic stresses. Devireddy *et al.* (2020) provide an overview of the interplay between hormone and reactive oxygen species (ROS) signaling, which orchestrates the (systemic) acclimation response of plants to the exemplified single stresses drought, salt, heat, or cold, or combinations of different abiotic stresses. In the review by Yoshida *et al.* (2020), recent progress in our understanding of long-distance stress, developmental signals, and their association with plant hormone pathways is described. Diverse stress-responsive peptide signals are highlighted, but special attention is paid to the root-to-shoot peptide signals, such as CLE25, which induces ABA accumulation in leaves under drought stress conditions.

Plant immunity relies heavily on plant hormones. Aerts *et al.* (2020) emphasize the complexity of the hormone interactive immune network that regulates plant defenses to pathogens and insects. They discuss the different levels at which crosstalk between different hormones in this network is regulated, from the level of whole-genome or -phenome responses, to the molecular level of protein, gene expression, or hormone homeostasis. Sun and Zhang (2020) review how a local infection by a pathogen can lead to the production of short- and long-distance defense signaling molecules. These include damage-associated molecular patterns, phytocytokines, SA, and *N*-hydroxypipecolic acid. The authors describe which regulatory proteins are involved in their production, as well as in their perception and in their induction of hormone-mediated defense responses. Eichmann *et al.* (2020) describe the role of plant hormones in shaping of the microbiome around and in plant roots. Hormones derived from plants and microbes contribute to the diversity of the microbial community in/around roots, which in turn is crucial for plant resilience.

Finally, to increase our understanding of hormone signaling, it is important to determine with high sensitivity, and in a non-invasive manner, the distribution and the concentration of plant hormones *in planta* under different conditions. Elucidation of the spatiotemporal nature of the hormone network can be accomplished by using genetically engineered biosensors. Isoda *et al.* (2020) describe the latest developments in this field, where biosensors are based on fluorescence of transcriptional reporters, degron-based sensors, or receptor-based sensors.

This Special Issue addresses novel aspects of our knowledge on plant hormones. The recent developments in the research on network functioning of hormones are covered by the reviews. The molecular functions of hormone pathways in local and systemic tissue, the transportation of systemic signals, and the integration of hormone pathways with other each other and other molecular signals are topics of many of the reviews in this issue. These aspects are covered for many different biological processes in growth, development, and stress responsiveness. Moreover, this issue includes reviews on metabolites with emerging hormone functions, as well as on non-invasive techniques to report hormones *in planta*. We believe it provides a wide and up-to-date perspective on a subject that is so central in plant biology.

Eiji Nambara[1] and Saskia C. M. Van Wees[2]
[1]Department of Cell & Systems Biology, University of Toronto, Toronto, ON, Canada (Email: eiji.nambara@utoronto.ca); and
[2]Plant-Microbe Interactions, Department of Biology, Utrecht University, Utrecht, the Netherlands (Email: s.vanwees@uu.nl)

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