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From receptors to responses

Editorial overview

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Zhi-Yong Wang's group is interested in elucidating the brassinosteroid signal transduction pathway and its interactions with other hormonal and light signaling pathways. The Wang lab uses proteomics and genomics approaches to dissect signal transduction pathways and transcriptional networks that control plant growth and development.

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Giltsu Choi works at KAIST in Daejeon, Korea. He has identified and characterized a number of phytochrome signaling components using Arabidopsis as a model plant. He is using genetic and genomic approaches to understand how phytochromes regulate various light responses through their interacting proteins. His works extend to identifying an intimate relationship between phytochrome signaling and plant hormone signaling in germinating seeds.

Signal perception, signal transduction, and gene regulation are fundamental mechanisms underlying plant development and adaptation to the environment. The first decade of the 21st century has been exciting time for the field of plant signal transduction and gene regulation, thanks largely to the use of diverse technologies and approaches, including chemical genetics, proteomics, structural biology, and computational biology. These new research tools have brought insights of new depth into molecular details, such as atomic-level structural basis of signal perception by receptor proteins, and new breadth of global views, such as transcriptional networks through which signals control physiology and development. This issue highlights recent progress in understanding the molecular mechanisms of signal perception, transduction, and crosstalk in the context of regulation by hormones, light, peptides, and nutrient signals.

The ability of plants to adjust growth and metabolism according to environmental changes is crucial for survival and presents some of the best examples of how signal transduction enables adaptation in plants. Bailey-Serres and Voesenek discuss how deep-water rice plants respond to flooding, submergence, and low-oxygen stress. Low-oxygen stress causes an energy and carbohydrate crisis that must be controlled through regulated consumption of carbohydrates and energy reserves. Different rice plants can survive flooding through two opposing adaptive strategies: elongation to escape submergence and inhibition of elongation (quiescence) to conserve energy and survive a period of submergence. Both strategies use related ethylene response factor (ERF) DNA binding proteins that act down stream of ethylene and modulate gibberellin-mediated shoot growth. This review discusses several components in a regulatory network that underlies plasticity in growth and metabolisms essential for the survival of distinct flooding regimes. It illustrates how hormones are recruited to help plants survive extreme environmental conditions.

How plants sense or perceive chemical and physical signals is one of the questions that capture much curiosity of scientists. Several articles in this issue focus on structural studies of soluble receptors. While identified only a year ago, the PYR/PYL/RCAR family of ABA receptors quickly became one of the best-understood hormone receptors. As Weiner *et al.* describe, following the discovery of the receptors by chemical genetics and protein interaction approaches, there has been rapid progress in understanding the structural mechanism of ABA perception and the downstream signaling pathway. The crystal structures of ligand-free and ABA-bound receptor reveal ligand-induced conformational changes that facilitate binding and inhibition of the PP2C phosphatases. Inhibition of PP2C releases its inhibition of the SnRK2 kinase, which phosphorylates numerous target proteins, such as the ABF transcription factors and anion channel SLAC1, to activate ABA responses.

Ueguchi-Tanaka and Matsuoka discussed the structure of gibberellin receptor GID1 and structural basis for GA recognition by GID1. GID1 has a structure of binding pocket with a lid. GA binding induces closures of the lid over the GA-binding pocket, and this closed state of GID1 favors interaction with the DELLA proteins, which lead to interaction with the GID2/Sly1 F-box E3-ubiquitin ligase and ubiquitination of DELLA proteins at Lys-29. Comparative analysis of GA receptor components of higher plants to their homologs in lower plants provides interesting clues about how evolution has increased the ligand-binding specificity. This article also compared the mechanistic similarities for perception of GA, auxin, and ABA. While binding of ABA and GA induces intra-molecular conformational changes that lead to binding to downstream effectors, auxin functions as an 'inter-molecular glue' between the TIR1 receptor and the Aux/IAA repressors.

Transmembrane receptor-like kinases (RLKs) play key roles in cell–cell communication and cell response to the environment. No three-dimensional structure has been solved for any RLKs in plants, but there has been major progress in understanding the mechanisms of receptor kinase activation. Jia Li describes recent insights into RLK activation by sequential trans-phosphorylation between the brassinosteroid receptor kinase BRI1 and its co-receptor kinase BAK1. While ligand-induced homodimerization or heterodimerization is considered a common mechanism for receptor kinase activation, the field was surprised to find that BAK1 function as co-receptors to help activate many RLKs that mediate diverse processes such as responses to hormones, pathogens, oxidative species, and developmental signals. While it remains unclear how widely this mechanism is used, it is obviously important to keep in mind the concept of co-receptor RLKs as we try to genetically dissect the functions of the hundreds of RLKs in plants.

The large numbers of RLKs encoded by the plant genomes suggest there are numerous extracellular signals that impact on plant cells through these RLKs. Many of these signals are peptide in nature, derived from interacting microbes or secreted by neighboring cells. Shinohara and Matsubayashi describe recent findings of posttranslational modification by hydroxyproline arabinosylation of the CLV3 and related peptide hormones. This article summarizes the research history of glycopeptide signals, the physiological functions of known glycopeptide hormones, the structural information about sugar linkage, and possible mechanisms of glycosylation.

Not all cell-to-cell communications are productive. Recognition of a peptide from self-pollen by the self-incompatibility receptor-like kinase (SRKs) leads to rejection of the pollen by stigma cells. Tantikanjana and Nasrallah describe introduction of self-incompatibility into self-compatible *Arabidopsis thaliana* by transforming a SRK and its ligand peptide from the self-incompatible *Arabidopsis lyrata*, and the use of it as a genetic system to dissect the SI signaling pathway. This review also discusses recent progress in understanding how signaling downstream of the SRKs leads to down regulation of localized exocytosis, which is one of many cellular events triggered by SRK signaling that contribute to various aspects of pollen rejection.

Phosphorylation is a common mechanism for intracellular signal transduction, but phosphorylation *per se* is often not sufficient to bring activity change to the modified protein. Phosphopeptide-binding proteins play important roles in reading the phosphorylation tags. Gokirmak *et al.* review recent advances in understanding the mechanisms of regulation by the 14-3-3 phosphopeptide-binding proteins. 14-3-3 proteins are highly conserved in eukaryotes and are usually highly abundant in cell, participating in many regulatory processes. While traditionally known as regulators of metabolic enzymes, recent studies revealed important roles of 14-3-3s in signaling pathways for hormonal, light, and stress responses.

Signaling pathways lead to regulation of transcription factors and gene expression. The articles of Argueso *et al.*, and Jianming Li describe how cytokinin and brassinosteroid, respectively, regulate the activities of transcription factors and orchestrate gene expression programs for development. Cytokinin signaling through the histidine kinase receptors activates the type-B response regulators, which transcriptionally regulate addition transcription factors specifically involved in either shoot apical meristem function, root apical meristem, or light-dependent development and chloroplast biogenesis. The mutual regulation of key factors of other signaling pathways also starts to elucidate the molecular mechanism underlying the inductions of shoot and root differentiation by balanced actions between cytokinin and auxin.

BR signaling through the BRI1 receptor kinase-mediated pathway activates the homologous BZR1 and BES1 transcription factors to modulate gene expression and plant growth. Jianming Li discusses recent findings of additional transcription factors and nuclear proteins as either interacting proteins or downstream transcriptional targets of BZR1 and BES1. These factors provide possible links from BR signaling to various cellular and developmental processes. For example, two families of antagonizing non-DNA-binding HLH and DNA-binding bHLH factors play a major role in regulating cell elongation downstream of BZR1 in both Arabidopsis and rice.

Development and cell differentiation requires actions and interactions of multiple signaling pathways coordinated in