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THEMATIC ARTICLES

Gibberellin Signaling: How Do Plant Cells Respond to GA Signals?

Makoto Matsuoka*

BioScience Center, Nagoya University, Chikusa, Nagoya 464-8601, Japan

The gibberellins (GAs) are a large family of tetracyclic diterpenoid plant growth substances which are associated with various plant growth and development processes such as seed germination, stem and hypocotyl elongation, leaf expansion, floral initiation, floral organ development, fruit development, and induction of some hydrolytic enzymes in the aleurone of cereal grains. Many GA-related mutants have been identified from plant species, and can be categorized as either GA-sensitive or GA-insensitive. GA-sensitive mutants respond to exogenous GA treatment to rescue their abnormal phenotypes. These kinds of mutations are usually caused by deficiencies in the genes encoding GA catalytic enzymes. Many genes encoding GA-catalytic enzymes have been identified using GA-sensitive mutants, enabling researchers to build a detailed picture of the GA biosynthesis process. By contrast, GA-insensitive mutants do not respond to exogenous GA treatment. The mechanism by which GA triggers signal transduction is currently poorly understood compared with the GA biosynthesis mechanism, but recent progress in molecular genetics and molecular biology have led to the identification of several important genes involved in the GA signaling pathway. These latest advances in understanding this pathway are reviewed in this thematic issue of *Journal of Plant Growth Regulation*.

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**Corresponding author; e-mail:* makoto@nuagr1.agr.nagoya-u.ac.jp

The eight articles in this issue have been arranged in logical order, from the perception of the extracellular GA signal to the transcription of GA-regulated genes. In making this arrangement, I wanted to start with an article on the GA receptor, but this was not possible because there is currently no clear information about the GA receptor, even though efforts have been made to isolate the GA receptor protein. It has previously been considered that there are two types of GA receptors in plant cells: (1) a plasma membrane-bound receptor that has been primarily studied for its role in the induction of α-amylase into the aleurone cells of cereal grains; (2) a cytoplasm-type receptor that has been considered to be mainly involved in shoot elongation. Candidate proteins that can interact with GA (GA-binding protein) have successfully been isolated, but these have not been identified as receptors. Molecular genetics offers another possible approach. When a GA-receptor loses its function, the plant should exhibit a recessive GA-insensitive phenotype. However, such a loss-of-function mutant has not been reported, suggesting that they might be difficult to obtain because GA receptors may present themselves in a redundant manner, as is the case for ethylene receptors. Irrespective of these considerations, the isolation and characterization of the GA receptor(s) is one of the most important targets in this research area.

The α subunit of the heterotrimeric G protein (Gα) should be located as a neighboring factor to the membrane-bound GA receptor, as is the case in the

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analogous animal Gα proteins. Based on observations of the rice knock-out Gα mutant, *d1*, Gα is thought to function as a positive regulator of GA signaling. However, the most recent studies have revealed that the function of Gα is not only limited to GA signaling but is also involved in other signaling pathways. Iwasaki and colleagues have summarized the current understanding of Gα function in plant cells.

At present, we can consider DELLA proteins to act as a molecular switch in the GA signaling pathway of both monocot and dicot plants, although the situation is much simpler in the former. In rice, for example, loss-of-function of the DELLA protein SLR1 (rice has only one DELLA protein) induces a constitutive GA-response phenotype, and production of the protein truncated with the DELLA domain induces severe dwarfism without GA-responsiveness. Ashikari and colleagues describe the molecular function of SLR1 in rice. In contrast, *Arabidopsis* has five DELLA proteins, all of which are negative mediators of GA signaling with different expression patterns. Hussian and Peng review the function of these DELLA proteins in *Arabidopsis*. Current debate concerning the DELLA proteins is focused on how and why they are degraded by the upstream GA signal. Some recent studies have revealed that the proteasome pathway is involved in the degradation process of DELLA proteins. Ashikari and colleagues have found that loss-of-function of the rice *GID2* gene, which encodes a putative F-box protein, a component of an SCF complex (the E3 ubiquitin-ligase complex), causes a severe GA-insensitive mutation with a correspondingly high level of accumulation of the SLR1 DELLA protein in the mutant. They discuss the degradation process of SLR1 as mediated by the SCF^{GID2} complex.

Arabidopsis spindly (*spy*) was first identified as a resistant mutant against a GA biosynthesis inhibitor, paclobutrazol (PAC): it can germinate in the presence of PAC, which blocks the germination of the wild-type. Further analyses of *spy* have shown that this mutation induces a GA-hypersensitive response phenotype in a recessive manner and that the *SPY* gene encodes a homologous protein to *O*-GlcNAc transferase. Filardo and Swain review the recent progress of research on SPY and its related proteins. Monte and colleagues review the function of PHOR1, with particular attention to the U-box domain, which is implicated in ubiquitin-dependent protein degradation. They discuss the possibility that DELLA proteins might be ubiquitinated to be targets of the proteasome by the PHOR1 ubiquitin ligase enzyme. In support of this idea, the antisense PHOR1 plants show a reduced response to GA application; conversely, its PHOR1 overexpressors are slightly resistant to PAC.

GAMYB is a positive transcription regulator for α-amylase expression in barley aleurone cells. Woodger and colleagues summarize the properties of GAMYB and describe new results concerning the proteins that interact with GAMYB, in addition to the function of GAMYB outside the aleurone cells. The phenotype of the transgenic barley plants overexpressing *HvGAMYB* supports this idea. David Ho and colleagues also describe GA signaling in cereal aleurone cells, but their article is focused on crosstalk between GA and ABA. It is well known that GA and ABA function in an antagonistic manner. Ho and others discuss the importance of an ABA-related protein kinase (PKABA) in the crosstalk between GA and ABA.

The topic of the final article by Takahashi and colleagues is slightly different from the others. They began their studies with a tobacco clone encoding a putative transcriptional activator containing a bZIP domain, RSG ('repression of shoot growth'). Through the phenotypic analysis of the transformants carrying its dominant negative construct, they have demonstrated that RSG is a positive transcriptional regulator for the expression of the gene

encoding *ent*-kaurene oxidase, a member of the GA biosynthesis pathway. Furthermore, they found that a 14-3-3 protein interacts with RSG and regulates its intracellular localization. Strictly speaking, this topic should not be categorized along with GA signal transduction but instead, as the regulation of GA biosynthesis. However, Takahashi and others' findings could provide us with some hints on how to study feedback regulation of the expression of GA20 oxidase or GA3 oxidase through GA signaling. In fact, the feedback regulation of the expression of these genes is one of the most reliable events controlled by GA signaling. Consequently, it should be an important cue for further studies of GA signaling.