

On the Inside

A Novel Form of Crosstalk between GA and ABA

The negative interaction between GA and the stress hormone abscisic acid (ABA) has been studied for many years in numerous plant species. These studies suggest that GA and ABA negatively affect each other's biosynthesis and signaling. The nuclear DELLA proteins suppress almost all GA responses by interacting with various transcription factors. ABA plays a central role in the regulation of stomatal closure under water-deficit conditions. Previously, **Shohat et al. (pp. 518–528)** demonstrated that a gibberellin response inhibitor in tomato (*Solanum lycopersicum*), the DELLA protein PROCERA (PRO), promotes ABA-induced stomatal closure and gene transcription in guard cells. Their attention has now turned to the question of how PRO affects stomatal closure. PRO does not affect ABA accumulation in leaves, suggesting that it affects ABA signaling or uptake into guard cells via transcriptional regulation of unidentified ABA signaling components or transporter genes. To examine these possibilities, the authors performed RNA-sequencing analysis of isolated guard cells. They have identified ABA-IMPORTING TRANSPORTERS (AITs) as being upregulated by PRO. Tomato has four *AIT1* genes, but only *AIT1.1* and *AIT1.2* were upregulated by PRO, and only *AIT1.1* exhibited high expression in guard cells. The functional analysis of *AIT1.1* in yeast (*Saccharomyces cerevisiae*) confirmed its activity as an ABA transporter. An *ait1.1* mutant exhibited increased transpiration, larger stomatal apertures, and a reduced stomatal response to ABA. Moreover, *ait1.1* suppressed the promoting effects of PRO on ABA-induced stomatal closure and gene expression in guard cells, suggesting that the effects of PRO on stomatal aperture and transpiration are *AIT1.1*-dependent. Although many previous studies have revealed negative crosstalk between gibberellin and ABA that is mediated by changes in hormone biosynthesis and signaling, the results of this study suggest that this crosstalk can also be mediated by changes in hormone transport.

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Villin and GLABRA2 Regulate Root Hair Growth

The enhanced elongation of root hairs in response to mild water deficiency permits more effective water and nutrition uptake. The growth of root hairs is regulated in part by actin dynamics. Thick actin-filament bundles in the apical and subapical area of root hairs inhibit root hair growth. Actin-binding proteins, including villins (VLNs), are believed to be major organizers of the thick bundles in root hairs. Additionally, a series of key transcription factors have been identified as key regulatory factors that influence root hair growth. The transcription factor GLABRA2 (GL2) in particular plays an important role in the initiation and growth of root hairs in Arabidopsis (*Arabidopsis thaliana*). Several *gl2* mutants, for example, have significantly longer root hairs than the wild type. GL2 directly suppresses the function of positive hair growth regulators, including several transcription factors, thus negatively regulating root hair cell growth. **Wang et al. (pp. 165–175)** now show that *vlm1* mutants display significantly longer hairs, with longer hair growing time and defects in the thick actin bundles and bundling activities in the subapical and apical regions. The authors show that *VLN1* overexpression suppresses the *gl2* mutant phenotypes with regard to hair growth and actin dynamics. Moreover, GL2 directly recognizes the promoter of *VLN1* and positively regulates *VLN1* expression in root hairs. The GL2-mediated *VLN1* pathway is also shown to be involved in the root hair growth response to osmotic stress. These results demonstrate that the GL2-mediated *VLN1* pathway plays an important role in the root hair growth response to osmotic stress and suggest a transcriptional mechanism that regulates actin dynamics and hence cell tip growth in response to environmental signals.

Biosynthesis of Montbretin, an Antidiabetes Drug

Diabetes and obesity are major health challenges. Diabetes alone affects over 422 million people worldwide and is among the top ten leading causes of

death. Type-2 diabetes is characterized by the body's inefficient use of insulin, which leads to elevated blood Glc levels with detrimental effects on different organs and increased risk of dying prematurely. The plant metabolite montbretin A (MbA) is being developed as an antidiabetes and anti-obesity treatment due to its potent and specific inhibition of the human pancreatic α -amylase. MbA is a complex acylated flavonol glycoside formed in small amounts in the corms of montbretia (*Crococsmia* \times *crococsmiiflora*), a member of the iris family, during the early summer. Unfortunately, the spatial and temporal patterns of MbA accumulation limit its supply for drug development and application. **Irmisch et al. (pp. 97–109)** are exploring MbA biosynthesis with the aim of enabling metabolic engineering of this rare and valuable compound. Genes and enzymes for the first four steps of MbA biosynthesis, starting from the flavonol precursor myricetin, have recently been identified. Now, the authors describe the gene discovery and functional characterization of the remaining two enzymes of MbA biosynthesis. The authors reveal that two UDP-glycosyltransferases, CcUGT4 and CcUGT5, catalyze consecutive reactions in the formation of the disaccharide moiety at the 4'-hydroxy position of the MbA flavonol core. Both enzymes are specific for flavonol glycosides and their respective sugar donors. This study completes the discovery of the MbA biosynthetic pathway and provides the complete set of genes to engineer MbA biosynthesis. Indeed, the authors announce their successful reconstruction of MbA biosynthesis in *Nicotiana benthamiana*.

The Regulation of Cuticle Biosynthesis

The outer surface of the aerial parts of land plants is covered by the cuticle, a waxy layer that provides a barrier against damage caused by environmental factors, as well as protection against nonstomatal water loss. **Castorina et al. (pp. 266–282)** now show that both cuticle deposition and cuticle-dependent leaf permeability during the juvenile phase of plant development are controlled in

maize (*Zea mays*) by the transcription factor ZmFUSED LEAVES-1 (FDL1). Lack of ZmFDL1 activity in the *fused leaves1-1* (*fdl1-1*) mutant specifically affects seedling development at early developmental stages and results in organ fusions due to the lack of cuticular material in the boundary between organs and irregular distribution of wax crystals on young leaf epidermal surfaces. To gain further insight into the role of ZmFDL1, the authors compared the cuticle composition of mutant and wild-type seedlings and analyzed the impact of the mutation on the transcriptome during early phases of seedling development. They also investigated ZmFDL1 involvement in controlling cuticular permeability and in mediating the drought stress response in maize seedlings. Their biochemical analyses reveal that among cutin compounds, ω -hydroxy fatty acids and polyhydroxy-fatty acids were specifically affected, while the reduction of epicuticular waxes was mainly observed in primary long chain alcohols and, to a minor extent, in long-chain wax esters. Transcriptome analysis allowed the identification of candidate genes involved in lipid metabolism and a hypothetical construct of a proposed pathway for cuticle biosynthesis in maize. Lack of ZmFDL1 affects the expression of genes located in different modules of the pathway. Overall, their results indicate that the response to water stress involves activation of wax biosynthesis and involvement of both ZmFDL1 and ABA regulatory pathways. The functional characterization of the ZmFDL1 regulatory gene presented here sheds light on the molecular mechanisms underlying cuticle-mediated drought stress tolerance in maize.

Sphingolipids and Plasmodesmata

Plasmodesmata are cytoplasmic channels that physically connect the cytoplasm

and endoplasmic reticulum of adjoining plant cells. These intercellular channels play important roles during plant development by allowing the molecular exchange of signaling molecules such as transcription factors, RNAs, and growth regulators. Interestingly, the plasma membrane (PM) of plasmodesmata is distinct from the general cellular PM and is enriched in sterol and sphingolipid (SL) species. The domains enriched with these special lipids are referred to as lipid rafts. Perturbation of sterol biosynthesis affects plasmodesmatal connectivity by changing the subcellular localization of two glycosylphosphatidylinositol (GPI)-anchored plasmodesmata proteins, namely plasmodesmata callose binding-1 (PDCB1) and plasmodesmata-associated β -1,3-glucanase-2 (PdBG2); this, in turn, results in the accumulation of plasmodesmata-associated callose, with the consequence that the exclusion limit of plasmodesmata is lowered. **Iswanto et al. (pp. 407–420)** now turn their attention to the other class of lipids enriched in the PMs of plasmodesmata, the SLs. By way of SL pathway inhibitors and two distinct SL pathway mutants, the authors report that they were able to modulate callose deposition to control symplasmic connectivity through perturbations of SL metabolism. The alteration of glucosylhydroxyceramide levels in particular disturbed the secretory machinery for the GPI-anchored PdBG2 protein, resulting in an overaccumulation of callose. In summary, this study reveals that changes in the composition of SL species and related compounds are important for the regulation of plasmodesmatal transport via their effects on PdBG2 and callose.

A Molecular Determinant of Rice Plant Architecture

Plant architecture is a major determinant of rice (*Oryza sativa*) productivity. Rice plant architecture is mainly

defined by plant height, the spatial pattern of leaves, and tiller and inflorescence branching patterns. Plant height and tiller branching determine the biomass and harvest index, while the spatial pattern of leaves, including leaf shape and angle, influences the photosynthesis rate and therefore the accumulation of carbohydrates. GROWTH-REGULATING FACTORS (GRFs), proteins specific to plants, participate in reproductive and vegetative development, senescence, and stress tolerance. In rice, there are 12 GRFs, but the role of the miR396-OsGRF7 regulatory module remains unknown. **Chen et al. (pp. 393–406)** now report that OsGRF7 shapes rice plant architecture via the regulation of auxin and GA metabolism. OsGRF7 is mainly expressed in lamina joints, nodes, internodes, axillary buds, and young inflorescences. The overexpression of OsGRF7 causes a semidwarf and compact plant architecture with an increased culm wall thickness and narrowed leaf angles mediated by shortened cell length, altered cell arrangement, and increased parenchymal cell layers in the culm and adaxial side of the lamina joints. Knockout and knockdown lines of OsGRF7 exhibit contrasting phenotypes with severe degradation of parenchymal cells in the culm and lamina joints at maturity. Further analysis indicated that OsGRF7 binds a specific motif in the promoters of a *cytochrome P450* gene and *AUXIN RESPONSE FACTOR12*, which are involved in the GA synthesis and auxin signaling pathways, respectively. Correspondingly, OsGRF7 alters the contents of endogenous GAs and auxins and sensitivity to exogenous phytohormones. This study demonstrates that OsGRF7 is a key regulator of the shaping of plant architecture through its effects on GA and auxin signaling networks.

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