On the Inside

Enhanced Suc Loading Improves Grain Size in Rice

Yield in rice (*Oryza sativa*) is a complex trait that is directly associated with grain size, panicle number, and the number of grains per panicle. Identifying and characterizing unique genes or targets that regulate yield traits would improve our understanding of the molecular mechanisms that regulate yield traits and facilitate the breeding of new rice varieties with higher yields. The carbohydrates in rice grains originate from photosynthesis that is carried out predominantly in leaves (sources). Therefore, grain filling and rice yield depend on the efficient transport of carbohydrates from the leaves to seeds (sinks). In most plants, Suc is the main carbohydrate transported long distance in the veins to support the growth and development of roots, flowers, fruits, and seeds. Suc is synthesized in leaf mesophyll cells and diffuses from cell to cell through plasmodesmata until it reaches the phloem parenchyma cells. Suc transporters mediate Suc efflux from the phloem parenchyma cells into the apoplast, where Suc is subsequently loaded into the phloem sieve element-companion cell complexes. AtSUC2 is a phloem-specific Suc transporter that is expressed specifically in companion cells. AtSUC2 plays an essential role in phloem Suc loading and is necessary for efficient Suc transport from source to sink tissues in Arabidopsis (*Arabidopsis thaliana)*. The *atsuc2* mutants show stunted growth, retarded development, and sterility. Furthermore, these mutants accumulate excess starch in the leaves and fail to transport sugar efficiently to the roots and inflorescences. **Wang et al. (pp. 2848–2862)** report that transgenic rice plants expressing the Arabidopsis phloem-specific Suc transporter, AtSUC2, showed an increase in grain yield of up to 16% relative to wild-type plants in field trials. Compared with wild-type plants, the transgenic plants had larger spikelet hulls and larger and heavier grains. Grain filling was accelerated in the transgenic plants, and more photoassimilate was transported from the leaves to the grain. Thus, enhancing Suc loading represents a promising strategy to improve rice yield.

Fungal Protein Alters Apical Dominance in Host Plants

Pathological changes in the developmental programs of plant hosts are often caused by infection with biotrophic pathogens. *Sporisorium reilianum*, a biotrophic fungal pathogen of maize (*Zea mays*) and sorghum (*Sorghum bicolor*), interferes with the regular development of inflorescences of host plants and leads to phyllody that is caused by changes in floral organ identity, floral meristem identity, and floral meristem determinacy. In addition, the fungus triggers suppression of apical dominance, which leads to a higher number of female inflorescences (ears) of maize and increased tillering of sorghum. By deletion analysis of the largest genomic divergence cluster in *S. reilianum*, **Ghareeb et al. (pp. 2789–2804)** have identified a secreted fungal effector responsible for *S. reilianum*-induced loss of apical dominance, which they have named SUPPRESSOR OF APICAL DOMINANCE1 (SAD1). *SAD1* transcript levels were highly upregulated during biotrophic fungal growth in all infected plant tissues. SAD1-GFP fusion proteins expressed by recombinant *S. reilianum* localized to the extracellular hyphal space. Transgenic Arabidopsis-expressing *GFP-SAD1* displayed an increased number of secondary rosette leaf branches. This suggests that SAD1 manipulates inflorescence branching architecture in maize and Arabidopsis through a conserved pathway. In wild-type plants, axillary meristem initiation is preceded by a depletion of auxin. After meristem initiation, the emerging axillary meristem is characterized by a local accumulation of auxin. Basipetal auxin transport from the apex toward the root suppresses axillary meristem outgrowth, leading to apical dominance, signaling, and nuclear processes. It is interesting, therefore, that the presence of SAD1 led to an increase of the transcript levels of the auxin transporter *PIN-FORMED1* in the root and a reduction of the branching regulator *TEOSINTE BRANCHED1* in the stalk. This indicates a role of SAD1 in regulation of apical dominance by modulation of branching through increasing transcript levels of the auxin transporter PIN-FORMED1 and derepression of bud outgrowth.

Leaf Attack Triggers Root Herbivore Avoidance

Insect herbivores constantly compete for plants as a primary terrestrial source of organic carbon and nitrogen. Consequently, resource competition is thought to be a major determinant of the distribution and abundance of insects in natural and agricultural systems. Although leaf feeders generally reduce the performance of root herbivores, little is known about the underlying systemic changes in root physiology and the associated behavioral responses of the root feeders. **Erb et al. (pp. 2884–2894)** have investigated the consequences of maize leaf infestation by *Spodoptera littoralis* caterpillars for the root-feeding larvae of the beetle *Diabrotica virgifera virgifera*, a major pest of maize. *D. virgifera* strongly avoided leaf-infested plants by recognizing systemic changes in soluble root components. The avoidance response occurred within 12 h and was induced by real and mimicked herbivory, but not by wounding alone. Roots of leaf-infested plants showed altered patterns in soluble free and soluble conjugated phenolic acids. Biochemical inhibition and genetic manipulation of phenolic acid biosynthesis led to a complete disappearance of the avoidance response of *D. virgifera*. The results provide a physiological mechanism for a behavioral pattern that explains the negative effect of leaf attack on a root-feeding insect. Furthermore, it opens up the possibility to control *D. virgifera* in the field by genetically mimicking leaf herbivore-induced changes in root phenylpropanoid patterns.

PTEN Regulates Cell Cycle Progression in Moss

Human Phosphatase and Tensin Homolog (PTEN) was first identified as a protein that is frequently disrupted in multiple tumor types. Its role as

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a tumor suppressor gene in human cancer is now firmly established. PTEN is a dual phosphatase that can act both on polypeptide and phosphoinositide substrates, with a high preference toward phosphoinositides, specifically the signaling molecule phosphatidylinositol (3,4,5)-trisphosphate, which it dephosphorylates to phosphatidylinositol (4,5)-bisphosphate. **Saavedra et al. (pp. 2572–2586)** have performed a genetic, biochemical, and functional characterization of the moss *Physcomitrella patens PTEN* gene family. *P. patens* has four *PTEN*s, which are ubiquitously expressed during the entire moss life cycle. All four genes are expressed in growing tissues, namely caulonemal and rhizoid cells. Analysis of single and double knockouts revealed no significant phenotypes at different developmental stages, indicating functional redundancy. However, compared with wild-type, triple, and quadruple *pten* knockouts, caulonemal cells grew faster, switched from the juvenile protonemal stage to adult gametophores earlier, and produced more rhizoids. Furthermore, analysis of lipid content and quantitative real-time PCR data performed in quadruple mutants revealed altered phosphoinositide levels and up-regulation of marker genes from the synthesis phase of the cell cycle. These results indicate that PpPTEN is a suppressor of cell growth and morphogenic development in plants.

Diterpenoid Biosynthesis in Stevia Leaf Tissues

Stevia (*Stevia rebaudiana*) is a perennial shrub belonging to the Asteraceae family and has been used for centuries in South America as a sweetener for herbal teas and foods. In addition to being a sweetening agent, Stevia has been used as a cardiotonic for hypertension and heartburn and also to lower uric acid levels. For reasons of food and medicine, there has been widespread cultivation of this plant throughout Europe, Asia, and North America. The sweetness of Stevia leaves is attributed to a group of diterpenoid derivatives known as steviol glycosides (SGs), which are 150 to 300 times sweeter than cane sugar (*Saccharum officinarum*). In contrast to artificial sweeteners, SGs are natural and can be used primarily as a noncalorie sweetener and/or flavor enhancer. Stevia accumulates SGs in its leaves to as high as 20% of the dry weight. In this issue, **Kim et al. (pp. 2462–2480)** integrate metabolomic and transcriptomic analyses of Stevia to explore the biosynthetic capacity of leaf tissues for diterpenoid metabolism. The biosynthesis and accumulation of many plant diterpenoids are restricted to specialized tissues or specific cell types, which enables plants to effectively synthesize specific natural chemicals and to avoid metabolic interference. Tissue-specific chemical analyses confirmed that SGs accumulate in leaf cells but not in trichomes. In contrast, Stevia leaf trichomes stored other labdane-type diterpenoids. Taken together, these results show that comparative transcriptomic analyses along with metabolite profiling provide useful information on the distinct biosynthetic pathways for specialized diterpenoids that preferentially accumulate in different tissues of Stevia leaves.

Metabolism Switch in Oleaginous Microalgae

Chlorella spp. are among the most widely cultivated freshwater microalgae. *Chlorella* spp. have served as a popular food supplement and animal feed in Asia, the United States, and Europe for centuries because of their high protein, lipid, and chlorophyll content (the highest amount among known plants). However, the improvement of industrial *Chlorella* spp. strains has been hindered by the lack of genomics research models. One important feature of *Chlorella* spp. is their ability to support high biomass productivity under both autotrophic and heterotrophic culture modes. Under photoautotrophic conditions, most *Chlorella* spp. produce abundant proteins and lipids, but 1 to 2 weeks of cultivation is usually required from inoculation to harvest. Such a relatively long production cycle often results in low productivity and vulnerability to changes in the weather. However, when cultivated heterotrophically, they reach much higher biomass productivity while accumulating significant levels of starch and much lower levels of lipids and proteins. Remarkably, when cells are shifted from heterotrophic to photoautotrophic conditions, a short duration (1–2 d depending on the weather) of illumination induces a prominent change in the intracellular profile, with marked decreases in starch and 70% to 120% increases in lipids and proteins, resulting in both high-target product contents (lipids and proteins) and high biomass productivity. Such a controlled switch that exploits the advantages of both autotrophy and heterotrophy shows potential in large-scale food and biofuel production. To probe this mechanism, **Fan et al. (pp. 2444–2461)** sequenced the 56.8-Mbp genome of *Chlorella pyrenoidosa* FACHB-9, an industrial production strain that has the capacity to produce high levels of protein, starch, and lipids. By tracking transcriptome dynamics during the transition from heterotrophy to photoautotrophy at six time points along the complete process of the metabolic switch from starch-centric to lipid-centric production, they revealed the underpinning molecular machineries and mechanism. The authors also demonstrated the first genetic transformation of an industrial oleaginous *Chlorella* spp., showing that introducing an NAD(H) kinase gene into FACHB-9 increased the lipid content by 45.3% to 110.4% but did not affect the growth rate of the host cells under either heterotrophic or photoautotrophic conditions. These findings provide a foundation for exploiting the metabolic switch in microalgae for improved photosynthetic production of food and fuels.

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