On the Inside

Strigolactone-Gibberellin Cross Talk

Root parasitic weeds, such as broomrape (Orobanche spp.) and witch weed (Striga spp.), are harmful plants in sub-Saharan Africa, the Middle East, and Asia that maintain seed dormancy in the absence of a host plant. Both parasitic plant species require germination stimulants released from the host plant. Strigolactones (SLs) are the major group of germination stimulants effective for almost all Orobanche and Striga spp. It has been reported that approximately 300 million people are affected economically by Striga spp. in Africa, with estimated losses of $US 7 billion. SLs also regulate diverse physiological processes in plants in general, including shoot branching and root development. They also act as rhizosphere signaling molecules to stimulate the germination of root parasitic weeds and the branching of arbuscular mycorrhizal fungi. Although various types of cross talk between SLs and other hormones have been reported in physiological analyses, the cross talk between gibberellin (GA) and SLs is poorly understood. Ito et al. (pp. 1250–1259) screened for chemicals that regulate the level of SLs in rice (Oryza sativa) and have identified GA as a novel SL-regulating molecule. The regulation of SL biosynthesis by GA is dependent on the GA receptor GID1 and F-box protein GID2. GA treatment also reduced the infection of rice plants by Striga. The authors found that GA is a regulator of SL biosynthesis, and that GA signaling controls the biosynthesis of SL by regulating the expression of SL biosynthesis genes. Moreover, GA-treated rice showed reduced Striga infection. These data not only demonstrate cross talk between SL and GA, but also suggest that GA might be used to control parasitic weed infections.

A Flavone Synthase That Alters Lignin

Lignin, a ubiquitous phenylpropanoid polymer found in the cell walls of vascular plants, is derived primarily from oxidative couplings of monolignols (p-hydroxycinnamyl alcohols). By filling up spaces between cell wall polysaccharides (cellulose and hemicelluloses), lignin confers increased mechanical strength, imperviousness, and resistance to pathogens. Lignin biosynthesis bioengineering has long been a major research focus, particularly because of its economic importance associated with agroindustrial uses of biomass. Lignin has traditionally been viewed as an impediment to chemical pulping, forage digestion by livestock, and cellulose bioethanol production. Recently, it was discovered that many grasses, including cereals, utilize a member of the flavonoidic, tricin (3’,5’-dimethoxyflavone), as a natural co-monomer with monolignols for cell wall lignification. Cytochrome P450 93G1 is a flavone synthase II (OsFNSII) indispensable for the biosynthesis of soluble tricin-derived metabolites in rice (Oryza sativa). Lam et al. (pp. 972–985) have examined the involvement of OsFNSII in lignification and alterations in cell wall properties upon tricin deficiency. A rice fnsII mutant was subjected to a series of analyses for the assessment of growth phenotypes, gene expression, as well as lignin structure. The mutant is similar in growth to wild-type control plants with normal vascular morphology. Chemical and NMR structural analyses demonstrated that the mutant lignin is completely devoid of tricin, indicating that FNSII activity is essential for the deposition of tricin-bound lignin in rice cell walls. The mutant also showed substantially reduced lignin content with decreased syringyl/guaiacyl lignin unit composition. Interestingly, the loss of tricin in the mutant lignin appears to be partially compensated by incorporating naringenin, which is a preferred substrate of OsFNSII. Such lignin alterations resulted in enhanced cell wall digestibility without negative impact on growth and development. Thus, grass biomass utilization may potentially be enhanced by manipulation of the flavone biosynthesis pathway.

Folate, DNA Methylation, and Flowering Time

Tetrahydrofolate (THF) and its derivatives, collectively termed folates, are a group of essential B-complex vitamins that have long been recognized as necessary nutrients to support normal cell differentiation and growth. Folates function as coenzymes in one-carbon transfer reactions and play a central role in synthesis of nucleotides and amino acids. Dysfunction of cellular folate metabolism leads to serious defects in plant development; however, the molecular mechanisms of folate-mediated cellular modifications and physiological responses in plants are still largely unclear. Wang et al. (pp. 1274–1284) now report that THF controls Arabidopsis (Arabidopsis thaliana) flowering time by adjusting DNA methylation-regulated gene expression. Changes in chromatin structure due to altered DNA methylation patterns have previously been implicated in the transition to flowering. One gene in particular, Flowering Wageningen (FWA), has been extensively studied since it was originally characterized from epigenetic mutants displaying a heritable late-flowering phenotype. To initiate normal flowering process, FWA expression is required to be silenced by methyltransferase1 (MET1)-mediated cytosine methylation to release its interfering effects on the function of the key flower-promoting gene FLOWERING LOCUS T. The authors report that seedlings supplied with THF as well as the high endogenous THF content mutant Atdfb (for dihydrofolate synthetase fopoly-Glu synthetase homolog B), showed dramatically induced effects on the release of MET1-mediated chromatin silencing and gene expression activity in a genome-wide scale, including the flowering regulation gene FWA. With elevated folate conditions, FWA constantly displayed transcription activity leading to retarded floral transition in a dose-dependent manner. Moreover, the loss of function of MET1 dramatically impaired THF-mediated flowering responses. These studies reveal a fundamental role of folate homeostasis in epigenetically controlled gene expression.

Light Direction, Absorption, and Photosynthesis

Plant photosynthesis generally increases with irradiance until light saturation occurs. The directional quality of light, however, can affect its penetration and absorption within a leaf. For
example, increasing the angle of incidence (from perpendicular) at which light intersects the leaf surface decreases penetration depth and, ultimately, absorption. Although studies at the individual leaf level are few, several lines of evidence suggest that the leaf’s developmental environment underlies internal light absorption and subsequent photosynthetic responses to diffuse versus direct light. Thick, sun-grown leaves show lower photosynthesis under diffuse relative to direct light, whereas thin, shade-grown leaves show no advantage. Despite its potential impact on agricultural and ecosystem productivity, the effect of diffuse light on photosynthesis at the leaf level is not well understood. Earles et al. (pp. 1082–1096) have investigated whether the spatial distribution of light absorption relative to electron transport capacity in sun- and shade-grown sunflower (Helianthus annuus) leaves underlies its previously observed diffuse light photosynthetic depression. Using a new one-dimensional porous medium finite element gas-exchange model parameterized with light absorption profiles, they found that weaker penetration of diffuse versus direct light into the mesophyll of sun-grown sunflower leaves led to a more heterogeneous saturation of electron transport capacity and lowered its CO₂ concentration drawdown capacity in the intercellular airspace and chloroplast stroma. This decoupling of light availability from photosynthetic capacity under diffuse light is sufficient to generate an 11% decline in photosynthesis in sun-grown but not shade-grown leaves, primarily because thin shade-grown leaves similarly distribute diffuse and direct light throughout the mesophyll.

**Vitamin B₆ Is Essential for Maize Embryogenesis**

Vitamin B₆ is synthesized de novo in plants, fungi, archeae, and most eubacteria, but not in animals, including humans, which have to obtain it from dietary sources. Vitamin B₆ is an essential cofactor for a range of biochemical reactions and a potent antioxidant. In plants, it plays important roles in plant growth and development, and stress tolerance. Although vitamin B₆ biosynthesis is essential for embryogenesis in Arabidopsis, the roles of vitamin B₆ in embryogenesis and endosperm development in grasses have not been addressed. Whereas Arabidopsis seeds develop transient endosperm that is quickly consumed by the developing embryo leaving a single layer of aleurone cells in mature seeds, endosperm is a major component of the mature grass seed. By means of a molecular characterization of the small kernel2 (smk2) mutant in maize (Zea mays), Yang et al. (pp. 1127–1138) reveal that vitamin B₆ has differential effects on embryogenesis and endosperm development. Vitamin B₆ levels are decreased dramatically in both the endosperm and embryo of the smk2 mutant, indicating that embryogenesis is more sensitive to reduced vitamin B₆ levels than endosperm development. In particular, a vitamer having some potential role in embryogenesis but has a reduced role in endosperm development in maize.

**Solar UV-B Inhibits Growth of Maize Leaves**

Growth inhibition is one of the most consistent plant responses to UV-B exposure, both as part of the solar spectrum in the field and from UV-B lamps in controlled environments. Fina et al. (pp. 1110–1126) demonstrate that the UV-B levels present in solar radiation inhibit maize leaf growth without causing any other visible stress symptoms, including the accumulation of DNA damage. So how does UV-B inhibit leaf growth? To answer this question, the authors conducted kinematic analyses of cell division and expansion to understand the impact of UV-B radiation on these cellular processes. Their results demonstrate that the decrease in leaf growth in UV-B-irradiated leaves is a consequence of a reduction in cell production and a shortened growth zone. To determine the molecular pathways involved in UV-B inhibition of leaf growth, they performed RNA sequencing on isolated growth zone tissues of control and UV-B-exposed plants. Their results show a link between the observed leaf growth inhibition and the expression of specific cell cycle and developmental genes, including growth-regulating factors (GRFs) and transcripts for proteins participating in different hormone pathways. Interestingly, the decrease in the growth zone size correlates with a decrease in the concentration of GA₁₉, the immediate precursor of the active gibberellin GA₁ by UV-B in this zone. This decrease is regulated, at least in part, by the expression of GRF1 and possibly other transcription factors of the GRF family.

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