SPLICEd in the Seeds: Integration of Abscisic Acid and Light Signaling in Arabidopsis

Plant development and adjustment to the environment require not only tight regulation of core signaling pathways but also their integration in a time- and context-dependent manner. For example, seed germination and seedling development are coregulated by endogenous hormonal cues such as abscisic acid (ABA) and by external environmental stimuli such as light (Lau and Deng, 2010). ABA inhibits seed germination, and light subsequently modulates ABA balance for photoautotrophic seedling establishment (Chen et al., 2008). The molecular players governing core ABA and light signaling pathways are regulated by alternative or precursor mRNA splicing, a posttranscriptional mechanism by which a single gene is transcribed into various mRNA isoforms. Nonetheless, how such regulation integrates ABA and light signaling pathways is still something of a mystery.

In this issue of *Plant Physiology*, Punzo et al. (2020) report that DNA-DAMAGE REPAIR/TOLERATION PROTEIN111 (DRT111) links ABA- and light-regulated pathways to negatively control seed germination sensitivity to ABA through specific splicing events (Fig. 1). DRT111 is a protein related to human SPLICING FACTOR45 and was first identified as SPLICING FACTOR FOR PHYTOCHROME SIGNALING (SFPS) in light-regulated development of Arabidopsis (*Arabidopsis thaliana*; Xin et al., 2017). DRT111/SFPS promotes photomorphogenesis by interacting with the photoreceptor phytochromes (phyB) and regulating precursor mRNA splicing of genes involved in light signaling (Fig. 1).

In a previous study, the authors had identified genes up-regulated in potato (*Solanum tuberosum*) cells adapted to long-term exposure to osmotic stress and ABA (Ambrosone et al., 2017). In their new study, they use bioinformatic analysis to identify Arabidopsis orthologs of the potato genes along with DRT111. The ABA-dependent expression of DRT111 was confirmed by real-time PCR and promoter-GUS assays. Mutation of DRT111 resulted in hypersensitivity to ABA in seed germination and seedling root growth assays and reduced sensitivity to ABA in stomatal responses, typical phenotypes of ABA-signaling mutants. When overexpressed, DRT111 reversed a subset of these mutant phenotypes. The authors further characterized the role of DRT111 in seed germination through transcriptome sequencing of *drt111* seeds and found that the negative influence of *DRT111* on germination was partly due to its effect on the expression and splicing of genes involved in not only ABA-dependent but also light-dependent control of germination. In the *drt111* mutant, they found that several Arabidopsis *HDzip* genes, the targets of ABA INSENSITIVE3 (ABI3), PhyA, PHYTOCHROME INTERACTING FACTOR1 (PIF1), and PIF6, were all up-regulated, whereas the *drt111* mutant led to a down-regulation of PhyE, PhyD, and PIF7.

The authors next examined the splicing of seed-specific mRNAs likely to affect seed germination. They found, in *drt111* seeds, substantial alterations in splicing pattern in the mutant, with a majority of the affected genes related to germination and mRNA metabolism. Among these genes, they noticed a defective splicing of ABI3 in *drt111* seeds, consistent with the deregulation of ABI3 target genes in *drt111* RNA sequencing. ABI3 is a key player determining ABA sensitivity at the seed stage and is under the control of another splicing factor, SUPPRESSOR OF ABI3-5 (SUA; Sugliani et al., 2010). Through double and triple mutant analyses, they confirmed that DRT111 and SUA likely...
work in the same pathway to control ABI3 splicing during seed germination. As it was known that DRT111/SFPS modulates PIFs to promote photomorphogenesis (Xin et al., 2017), the authors hypothesized that DRT111 marks a major point of convergence between ABA and light in the control of seed germination. The SOMNUS (SOM) gene is an important target for ABI3-PIF1 transcriptional activation that normally inhibits seed germination (Park et al., 2011). Punzo et al. (2020) found that mutating DRT111 resulted in SOM expression in seeds. Conversely, mutation of PIF1 alone or with additional PIFs, which decrease SOM expression, led to ABA insensitivity in seed germination.

The model that emerges is one in which DRT111 modulates the splicing of ABI3 (and additional factors), in turn targeting the expression of ABA/light signaling genes to regulate seed germination (Fig. 1). Such a splicing module adds an additional level of regulation for flexible integration of hormone and environmental cues to coordinate growth and stress responses. This model fits with the ABA hypersensitivity of phyB mutants in seed germination, which implies a role for light in regulating DRT111-dependent splicing events, an interesting possibility that has yet to be experimentally tested.

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