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IN BRIEF

Taking Hormone Crosstalk to a New Level: Brassinosteroids Regulate Gibberellin Biosynthesis

Given that both brassinosteroid (BR) and gibberellin (GA) phytohormones regulate plant growth (reviewed in Schwechheimer, 2011; Fridman and Savaldi-Goldstein, 2013), it is perhaps not surprising that there is extensive crosstalk between the BR and GA signaling networks, with DELLA proteins and the BZR1 transcription factor playing particularly important roles to integrate the signals. However, it had long been thought that the effects of BR were not mediated directly through GA, for instance, based on the inability of exogenous GA to rescue the phenotypes of BR mutants in various species. Recent findings have brought this question back to the forefront. Stewart Lilley et al. (2013) reported that expression of the GA biosynthetic gene *GA20ox* in *Arabidopsis thaliana* is responsive to exogenous BR, and Tong et al. (2014) found that GA biosynthesis is regulated by BRs in rice (*Oryza sativa*). Now, **Unterholzner et al. (2015)** have established that some downstream effects of BRs in Arabidopsis are in fact mediated by their function in GA production.

Unterholzner and coworkers found that GA was decreased in an Arabidopsis BR biosynthetic mutant (*cpd*) and in BR signaling mutants (including the receptor mutant *bri1-1*). These results were in striking contrast to the decade-old findings that GA levels are not changed in pea (*Pisum sativum*) BR mutants (Jager et al., 2005). To explore this potential interaction between BR and GA biosynthesis, Unterholzner et al. used *bri1-1* and the milder BR receptor mutant allele *bri1-301* as well as the BR biosynthesis mutant *cpd*. For each mutant, germination on water agar was reduced compared with that of the wild type. Importantly, germination of these BR mutants was rescued by exogenous GA and by stratification, which is known to induce GA biosynthesis. These results demonstrate that downstream effects of BR on germination in the wild type are mediated by GA. Furthermore, GA partially restored hypocotyl elongation and plant height phenotypes of the BR mutants. Growth conditions greatly influenced these effects of GA, which likely explains why they have not been observed previously.

Growth defects of the BR signaling mutant *bri1-301* can be rescued by targeted expression of the GA biosynthesis gene *GA20ox1*. Expression of the transgene is higher in 13.11 and 15.4 complementation lines than in lines 6.12 and 7.6. (*Adapted from Unterholzner et al. [2015], Figure 3F*.)

Unterholzner et al. went on to elucidate how the effects of BR on GA biosynthesis are mediated. They found that the expression of the GA biosynthetic genes *GA20ox* and *GA3ox* was reduced in BR biosynthetic and signaling mutants. Treatment with exogenous BR in the *cpd* background further demonstrated that BR regulates GA biosynthesis by influencing the expression of genes responsible for the rate-limiting step of GA production. The authors elegantly showed that defects in *bri1-301* could be rescued by expression of *GA20ox1* under the *BRI1* promoter (Figure 1), which indicates that a portion of the *bri1-301* phenotypes are related to GA deficiency.

They found that the BES1 and BZR1 transcription factors likely mediate this BR-responsive expression through binding a motif in the promoters of *GA20ox1* and other GA biosynthetic genes. This nice work from Unterholzner et al. establishes that BR influences GA biosynthesis in dicots as well as in monocots and that the two hormones function in the same pathway for at least some downstream effects. It also makes clear crosstalk between these phytohormones occurs not just at the level of signals converging on the same transcription factors, but also at the level of hormone biosynthesis.

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