New Interacting Partners of BLADE-ON-PETIOLE in Regulation of Plant Development

Organ boundaries are junctions that separate initiating lateral organs from the meristem or other plant parts. Cells at the boundary often exhibit slow growth rates and morphology distinct from that of the surrounding cells, and their development is controlled by complex gene networks. Lateral organ boundary marker genes BLADE-ON-PETIOLE1 (BOP1) and BOP2 are two closely related members in the Broad Complex, Tramtrack and Bric-a-brac/POX virus and Zinc finger domain family, encoding plantspecific transcriptional coactivators. As indicated by the gene name, a dominant negative mutant of bop1 was first identified with ectopic leaf growth on petioles from an ethylmethane sulfonate mutant screen in Arabidopsis (Arabidopsis thaliana). Ectopic outgrowth also occurs in the stem and at the base of floral organs due to ectopic meristematic activities in these tissues (Ha et al., 2003). In addition, BOP1 and BOP2 function redundantly in various aspects of lateral organ and boundary development, including leaf, stem, and flower patterning, and abscission zone development (Khan et al., 2014). Broad Complex, Tramtrack and Bric-a-brac/POX virus and Zinc finger domain proteins lack a DNA binding domain and interact with the TGACG-motif binding (TGA) class of basic leucine zipper transcription factors (TFs) for DNA binding (Khan et al., 2014). Previous analysis showed that BOP1 and BOP2 physically interact with PERIANTHIA (Fig. 1), a class V TGA, to regulate flower development, particularly sepal numbers (Hepworth et al., 2005). In this issue of Plant Physiology, Wang et al. (2019) demonstrate that BOP1 and BOP2 and two clade I TGA proteins, TGA1 and TGA4, together regulate meristem maintenance and inflorescence architecture.

Wang et al. (2019) use yeast two-hybrid and bimolecular fluorescence complementation assays to show that TGA1, TGA4, BOP1, and BOP2 physically interact. Promoter-β-glucuronidase assays show that TGA1, TGA4, BOP1, and BOP2 are all referentially expressed at organ junctions, although TGA1 and TGA4 are also expressed in roots and vascular tissues of leaf and stem. tga1, tga4, or tga1 tga4 mutants do not show a bop1 and bop2 phenotype; however, TGA1 and TGA4 are required for BOP2 promotion of stem elongation, as the shortstem phenotype in BOP2 overexpression lines is diminished in the tga1 tga2 mutant background. TGA1, TGA4, BOP1, and BOP2 also share the same upstream regulators of paralogous BEL1-like homeodomain TFs, PENNYWISE and POUND-FOOLISH, which regulate shoot apical meristem maintenance and inflorescence development (Wang et al., 2019). Moreover, chromatin immunoprecipitation assays revealed that TGA1, TGA4, BOP1, and BOP2 associate with the same promoter region of ARABIDOPSIS THALIANA HOMEBOX GENE1 (ATH1), which encodes another BEL1-like homeodomain TF that regulates boundary development of shoot organs (Gómez-Mena and Sablowski, 2008). BOP1 promoter of ATH1 expression in an ATH1pro:β-glucuronidase assay was abolished in the tga1 tga4 background, confirming the role of BOP1, BOP2, ATG1 and ATG4 as transcriptional coactivators of ATH1 expression (Fig. 1; Wang et al., 2019).

The nonoverlapping phenotypes of the bop1/2 and tga mutants indicate additional players in the BOP1 and BOP2 pathway. Indeed, BOP1 forms a complex with two master regulatory TFs in brassinosteroid (BR) signaling, BRZ-INSENSITIVE-LONG HYPOCOTYL1/BRASSINAZOLE-RESISTANT1 and BRI1-EMS-SUPPRESSOR1, and inhibits their transport from cytosol to nucleus to suppress their activation of BR signaling (Shimada et al., 2015). BOP2 also interacts with the CULLIN3 ubiquitin ligase and recruits PHYTOCHROME INTERACTING FACTOR4...
(Zhang et al., 2017) or LEAFY TFs (Chahtane et al., 2018) as ubiquitination substrates for degradation, to modulate photomorphogenesis/thermomorphogenesis or flower identity, respectively (Fig. 1).

Taken together, these results suggest that BOP1 and BOP2 regulate lateral organ and boundary development by interacting with different partners to modulate gene transcription or mediate protein degradation. It would be interesting to study further how different interactors coordinate in BOP signaling.

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