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Insight

The role of WOX1 genes in blade development and beyond

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This article comments on:
Wang C, Zhao B, He L, Zhou S, Liu Ye, Zhao W, Guo S, Wang R, Bai Q, Li Y, Wang D, Wu Q, Yang Y, Yan J, Liu Yu, Tadege M, Chen J. 2021. The WOX family transcriptional regulator SLAML1 controls compound leaf and floral organ development in Solanum lycopersicum. Journal of Experimental Botany 72, 1822–1835.

WOX1 genes have been identified in several eudicot species as important regulators of lateral organ development, and were found to control outgrowth of the blade along the mediolateral axis. However, the role of WOX1 genes in species that have compound leaves remained to be further investigated. Using a reverse genetics approach, Wang et al. (2021) analyzed WOX1 function in tomato and found that SILAML1 loss-of-function mutants exhibit defects in leaflet development and leaf complexity. This reveals that SILAML1 also plays a critical role in the initiation and growth of leaflets, in addition to its conserved role in blade outgrowth. Interestingly, SILAML1 function appears also to be critical for fruit size.

Final three-dimensional leaf shape depends on the coordinated growth of the leaf primordium along the abaxial/adaxial, proximal–distal, and medio-lateral axes (Fig. 1), and different classes of genes required for the establishment and/or growth along any of these polar axes have been identified (reviewed in Du et al., 2018). Formation of the leaf blade requires growth along the medio-lateral axis, and WOX1 genes, comprising a distinct subfamily of the Wuschel-like homeobox family (Haecker et al., 2004), were found to be specifically involved in this process in diverse eudicot species (Vandenbussche et al., 2009; Tadege et al., 2011; Nakata et al., 2012; Zhuang et al., 2012; Niu et al., 2018; Wang et al., 2021). Mutations in WOX1 genes typically result in a reduction of the leaf blade, but without significantly affecting proximal-distal growth, or abaxial/adaxial polarity. During leaf development, WOX1 genes exhibit a very localized expression pattern restricted to the middle domain region of the leaf primordium, identifying this region as a center that organizes the outgrowth of leaf blades (Nakata et al., 2012). On the other hand, Poaceae such as maize, rice, and barley do not possess WOX1 genes, and blade outgrowth in these species fully depends on the activity of members of the WOX3 subfamily (Nardmann et al., 2004; Cho et al., 2013; Ishiwata et al., 2013; Yoshikawa et al., 2016).

Studies of WOX gene function in various species identify the WOX gene family as particularly dynamic (in part reviewed by Costanzo et al., 2014), and therefore as an interesting target for further comparative (evo-devo) studies. Wang et al. (2021) have analyzed the role of WOX1 in tomato, a species with compound leaf development. Comparison of the results obtained in this study with those of other species further enhances our understanding of the functional diversification of the WOX family and, in the long term, of the evolutionary diversification of the gene regulatory networks in which they are embedded.

Variations in the phenotypic severity of WOX1 mutants in diverse species

When comparing WOX1 mutants in different species, the degree of leaf blade reduction varies significantly. At one end of the spectrum, there is the tobacco lam1 mutant (Tadege et al., 2011) with virtually no blade tissue remaining, and a similar severe blade reduction was also found by Wang et al. in tomato SILAML1 mutants (Wang et al., 2021). Arabidopsis is positioned at the other end of the spectrum, as single AtWOX1 mutants have no obvious phenotype (Vandenbussche et al., 2009). However, leaf blade reduction is observed in wox1 prs (wx3) double mutants (Vandenbussche et al., 2009; Nakata et al., 2012), indicating that blade expansion in Arabidopsis is redundantly encoded by members of the WOX1 and PRS (WOX3) subfamilies. Despite this, leaf blade reduction in Arabidopsis wox1 prs mutants is clearly less severe compared with the single WOX1 mutants in tomato and tobacco. This indicates
the presence of other factors that can partially compensate for the loss of WOX1/PRS function in Arabidopsis, but apparently not in Solanaceae species such as tobacco and tomato. This suggests that at least part of the molecular network controlling blade development has diverged during evolution of the eudicots. Future understanding of this will require a more integrated view of WOX1 function in the molecular network controlling blade development in diverse species.

Another obvious question that rises from the available comparative data concerns the functional conservation of WOX3 members. The severe blade reduction in SILAM1 and lam1 mutants demonstrates that in contrast to Arabidopsis, WOX3 genes in tobacco and tomato are not capable of compensating for loss of WOX1 function, possibly suggesting a different role. The analysis of WOX3 function in these species will be required to validate this hypothesis. Thus far, WOX3 function in dicot species other than Arabidopsis has been analyzed only in Medicago truncatula (Niu et al., 2015), showing that loss of function of the WOX3 ortholog LFL (LOOSE FLOWER) affects floral development, but not leaf blade outgrowth. In addition, the leaf blade phenotype of stf lfl double mutants was found to be similar to that of stf [STENOFOLIA (WOX1 ortholog)] single mutants, indicating that LFL/MtWOX3 has no overlapping function with STF in blade development (Niu et al., 2015).

An unexpected result from the study of tomato WOX1 mutants (Wang et al., 2021) is that SILAM1 plays a critical role not only in leaf blade development, but also in the initiation and growth of leaflets in compound leaf development. Earlier studies in other species with compound leaves showed that WOX1 function is required for blade development but does not affect leaflet initiation, as illustrated by the maintenance of trifoliate identity in slf (Tadege et al., 2011) and multifoliate identity in lath (Zhuang et al., 2012). Tomato and pea/Medicago are representatives of the Asterids and Rosids, respectively, which constitute the two largest clades within the core eudicots. These two major clades are thought to have diverged >100 million years ago (Moore et al., 2010). Therefore, differential recruitment of WOX1 function in leaflet initiation might reflect basic differences in the evolutionary changes that led to compound leaf development in distant species. Indeed, a systematic comparison of the molecular players known to regulate compound leaf development in four model organisms (tomato, Medicago, pea and cardamine) indicated already that although some mechanisms are clearly conserved, other components of the compound leaf regulatory network may have diverged significantly (reviewed in Bar and Ori, 2015).

Transcriptional networks regulated by WOX1 genes in diverse species

In recent years, several genome-wide datasets have become available aimed at the elucidation of the transcriptional network regulated by WOX1 transcription factors (Tadege et al., 2011; Nakata et al., 2018; Niu et al., 2018), including the study discussed here in tomato (Wang et al., 2021). RNAseq analysis comparing the slwox1 mutant with the wild type revealed a large number of differentially expressed genes (DEGs), of which the large majority are up-regulated in the slwox1 mutant background. This is consistent with previous studies and further supports that WOX1 transcription factors act mainly as transcriptional repressors (Lin et al., 2013; Zhang et al., 2014). A further commonality in these studies is the strong enrichment of DEGs belonging to plant hormone signal transduction pathways, of which of particular interest is the auxin pathway. Furthermore, it was recently found in Arabidopsis that MONOPTEROS (MP) [also called AUXIN RESPONSE FACTOR5 (ARF5)] can directly up-regulate WOX1/PRS expression while ARF2/3/4 act as negative regulators, and that the adaxial/abaxial distribution of these ARF factors together with auxin collectively defines WOX1 and PRS expression (Guan et al., 2017). This suggests that in Arabidopsis at least part of the leaf developmental defects observed in various arf mutants can be attributed to deregulation of WOX1/PRS expression. Furthermore, using an inducible Arabidopsis WOX1 expression system combined with indole-3-acetic acid treatments, Nakata et al. (2018) found, among others, that WOX1 positively regulates MP expression and that WOX1 and auxin additively influenced common downstream target genes. Together, this suggests that WOX1 function and the auxin (signaling) pathway are tightly intertwined through complex feedback loops.

A bright future for comparative evo-devo studies

Since the beginning of the 1990s, tremendous progress has been made in the understanding of the molecular mechanisms that underlie plant development. For obvious reasons, most advance has been made in Arabidopsis, for which detailed gene
regulatory networks have emerged covering a wide variety of developmental processes. We are, however, still very far from understanding how evolutionary variations in these networks have shaped the astonishing morphological diversity in the plant kingdom. Indeed, this requires that a wide range of detailed gene functional studies of key developmental regulators in species with contrasting architecture become available. The recent technological revolutions in next-generation sequencing methods (e.g. RNAseq) and gene functional analysis [clustered regularly interspaced palindromic repeats (CRISPR)/CRISPR-associated protein 9] will strongly accelerate this process and will deliver robust datasets required for comparative studies. The study of SILAM1 function by Wang et al. is a perfect illustration of this. They analyzed WOX1 function in a different developmental context (compound versus simple leaf development), and characterized the gene regulatory network downstream of tomato SlWOX1 function, allowing comparison with other datasets obtained in different species.

Keywords: Blade development, fruit development, leaflet initiation, mediolateral polarity, WOX1.

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