NEWS AND VIEWS

Fleeting hormone cues get stabilized for plant organogenesis

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Unlike animals, plants continue to develop their body plan postembryonically and add organs such as leaves or flowers throughout their life. In the shoot apex, a central group of stem cells continuously proliferates and displaces older cells to the periphery, where they differentiate and new organs are initiated. It is known that local maxima of the plant hormone auxin coincide with the sites of new organs (Benková et al., 2003) and there is good evidence that the local accumulation of auxin acts as a trigger for organogenesis (Dubrovsky et al., 2008). Extensive studies during the last decade revealed that these local auxin maxima are the result of a coordinated and highly dynamic directional cell-to-cell transport of auxin by specialized transport proteins (Petrašek et al., 2006). However, it is poorly understood how these rather dynamic changes in auxin concentration are translated into stable developmental decisions. In a recent article published in Molecular Systems Biology, Vernoux et al. (2011) undertake the herculean task of comprehensively analyzing the vast auxin signaling network with over 50 interacting players and come to some surprisingly simple conclusions regarding how auxin signaling is fine tuned to allow for robust patterning in the shoot apex.

The basic building blocks of the auxin signaling network are few: auxin response factors (ARFs) bind a conserved motif in the promoter of auxin responsive genes and either activate or repress their activity. Aux/IAA proteins interact with activating ARFs and render them transcriptionally inactive when auxin concentrations are low. High auxin concentration leads to degradation of Aux/IAAs, mediated by an SCF-type E3 ligase complex, in which the F-Box TIR1 (or AFB homologs) act as auxin coreceptors. Upon release from Aux/IAAs, activating ARFs are able to induce effector gene expression. Independently of auxin levels, they compete with repressing ARFs for the promoter motif. This conceptually simple system is greatly complicated by the sheer number of ARFs and Aux/IAAs.

Figure 1 Two different auxin signaling sensors. (A) The DII box is fused to the yellow fluorescent protein variant VENUS and constitutively expressed. High auxin levels stabilize its interaction with the auxin coreceptors TIR1/AFB, leading to polyubiquitination and degradation, thus providing an inverted image of an early step of auxin signaling. (B) Auxin-dependent degradation of Aux/IAA repressors liberates activating ARF transcription factors (+ARF), which then compete with ARF repressors (−ARF) for the conserved binding motifs present in the synthetic DRSrev promoter. The DRS activity, thus, monitors the final transcriptional output of the auxin signaling pathway.
In Arabidopsis, there are 23 ARFs and 29 Aux/IAAs identified to date and there are sufficient differences in the protein sequences to presume different binding and signaling activities (for a review, see Calderon-Villalobos et al., 2010). Depending on where and when individual components are expressed, auxin sensitivity can be modulated by different combinations of ARF–Aux/IAA interactor pairs (Parry et al., 2009). Because all studies so far focused on only a few components of the network, the broad picture of auxin signaling has not yet been drawn.

Vernoux et al. (2011) have used an interesting, global approach to better understand auxin signaling. Combining expression with interaction data in a mathematical model allowed them to make predictions about transcriptional output as a function of auxin input. They were able to test these predictions with a newly designed reporter for transcriptional auxin signaling, which measures auxin input in the system, and comparing these results with established reporters for transcriptional output.

Expression analysis by in situ hybridization of all ARFs, Aux/IAAs and TIR1/AFBs that occur in the shoot apex revealed that it can be divided into two distinct zones, without undue over-simplification: the center, in which expression of auxin signaling components is generally low, and the periphery, where their expression is high. To identify the structure of the signaling network, Vernoux et al. (2011) employed a large-scale yeast two-hybrid assay to test the >1200 possible interactions among ARFs and Aux/IAA proteins. A clustering analysis revealed a surprisingly simple topology of the >400 positive interactions: Aux/IAAs interact with each other and with activating ARFs, whereas repressive ARFs generally do not interact with other proteins. Thus, activating ARFs are not only controlled by Aux/IAAs in an auxin-dependent manner, but also compete with repressive ARFs, whose expression and stability seems unaffected by auxin.

Based on these data, a mathematical model was devised that describes the effect of varying auxin concentrations on the expression of auxin-regulated genes, taking into account the abundance of signaling components. This model proved robust over a wide range of tested conditions and predicts that the balance of activating and repressing ARFs is decisive for generating different auxin sensitivities and a robustly buffered system.

To confirm these predictions, it is necessary to distinguish between auxin input and transcriptional output in the system. To this end, a novel auxin reporter termed DII-Venus based on auxin-dependent degradation of Aux/IAAs was developed (Figure 1A). 35S::DII-Venus monitors an early step of auxin signaling when compared with the tried and proven DR5rev::GFP reporter (Friml et al., 2003) that basically is a synthetic auxin responsive gene and monitors the overall transcriptional output of auxin signaling (Figure 1B). In the periphery, input (DII) and output (DR5) sensors coincide, however, in the central zone only auxin input is observed, implying a less sensitive auxin signaling there. Moreover, the DII signal is much more dynamic than DR5, indeed indicating that the signaling network has the buffering and stabilizing properties that are required to create stable expression patterns.

Although DII is a more dynamic auxin reporter than DR5, it still depends on the activity of the semi-constitutive 35S promoter controlling its expression and is an indirect auxin sensor that depends on availability and sensitivity of auxin perception, ubiquitination and proteolysis components in a given cell. Nonetheless, clearly, DII-Venus is superior to DR5 in terms of dynamics of the response. The combination of DII-Venus and DR5 (with their inherent strengths and weaknesses) promises to provide new insights into the auxin-mediated processes where rapid changes in cellular auxin levels occur. These include, besides organogenesis (Heisler et al., 2005; Moreno-Risueno et al., 2010) and embryogenesis (Friml et al., 2003) mainly growth responses to light and gravity, which has been shown to rapidly remodel auxin fluxes and distribution (Kleine-Vehn et al., 2010; Ding et al., 2011).

Conflict of interest

The authors declare that they have no conflict of interest.

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