

## Auxin and DORNRÖSCHEN joint force in the shoot apex

Xiuwei Cao<sup>1,2</sup> & Yuling Jiao<sup>1,2\*</sup><sup>1</sup>State Key Laboratory of Plant Genomics, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, and  
National Center for Plant Gene Research, Beijing 100101, China;<sup>2</sup>College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China

Received May 17, 2018; accepted May 18, 2018; published online June 5, 2018

**Citation:** Cao, X., and Jiao, Y. (2018). Auxin and DORNRÖSCHEN joint force in the shoot apex. *Sci China Life Sci* 61, 867–868. <https://doi.org/10.1007/s11427-018-9317-2>

Auxin is a classical phytohormone that is involved in various developmental processes. A striking example of auxin action is the promotion of shoot organogenesis. In the shoot apex, the shoot apical meristem (SAM) maintains a mass of stem cells in the central region, termed the central zone (CZ). Stem cells in the CZ divide slowly to replenish themselves and to provide cells to the surrounding peripheral zone (PZ), where cells divide rapidly to form lateral organs. The CZ also provides cells to the underneath rib meristem (RM), which forms the internal tissue of the stem. The organizing center (OC) harbors a small group of quiescent cells located in between of the CZ and the RZ, and maintains the stem cell niche in the above CZ (Figure 1). The homeodomain transcription factor WUSCHEL (WUS) is expressed in the OC to maintain stem cells in the CZ. WUS migrates to the CZ to activate the expression of the negative regulator *CLAVATA3* (*CLV3*). *CLV3* encodes a secreted peptide, which activates the transmembrane repeat receptor kinase CLV1 in the OC to inhibit *WUS* expression. Thus, the WUS-CLV feedback loop forms a self-correcting mechanism that maintains a stem cell pool of constant size (Sassi and Vernoux, 2013).

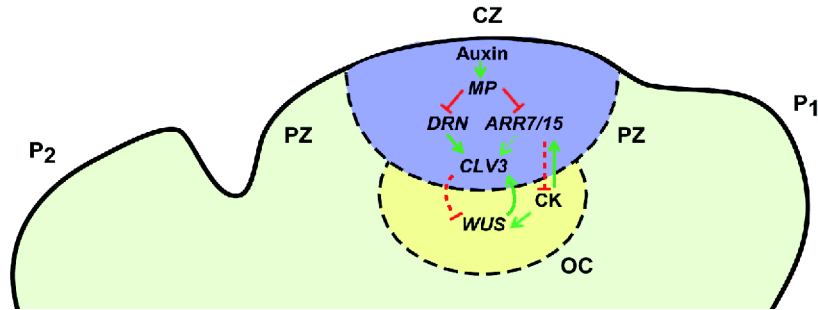
Auxin promotes primordium formation in the PZ, either leaf primordia during the vegetative stage or floral primordia during the reproductive stage. In this process, auxin regulates gene expression, at least in part, through the versatile MONOPTEROS (MP, also known as AUXIN RESPONSE FACTOR 5) transcription factor (Sassi and Vernoux, 2013).

In other domains of the SAM, it is less clear how auxin exerts its function. High level of auxin signaling accumulates in the CZ harboring stem cells (Vernoux et al., 2011). However, the function of auxin in the CZ remains to be fully resolved. A recent article from the group of Zhong Zhao fulfils this gap and describes surprising findings on auxin's function in shoot stem cells maintenance (Luo et al., 2018).

It was previously reported that the stem cell maintenance modulated by auxin is also mediated by MP, which has weak expression in the CZ and strong expression in the PZ (Zhao et al., 2010). MP directly inhibits the expression of two A-type arabidopsis response regulator (*ARR*) genes, *ARR7* and *ARR15*, which are negative regulators of cytokinin signaling. These *ARR* genes in turn negatively regulate the SAM size. In the new study, the authors reported that MP also directly repressed the transcription *DORNRÖSCHEN* (*DRN*, also known as ENHANCER OF SHOOT REGENERATION 1 or *ESR1*), encoding of an AP2/ERF family transcription factor. Furthermore, the authors reported that *DRN* activated *CLV3* expression in the CZ, thus indirectly repressing the expression of *WUS* in the OC. In double mutants of *drn* and *drnl*, the *DRN* homologous gene *DORNRÖSCHEN-LIKE* (*DRNL* also known as *ESR2*), *CLV3* expression is reduced, *WUS* expression is enhanced, and the SAM size is enlarged. Thus, *DRN* mediated stem cells homeostasis by interfering with the classical WUS-CLV feedback loop (Figure 1).

Taken together, the authors revealed a new branch of auxin signaling in the regulation of stem cell maintenance in the CZ. This new branch parallels the previously reported MP

\*Corresponding author (email: [yljiao@genetics.ac.cn](mailto:yljiao@genetics.ac.cn))



**Figure 1** A conceptual model showing MP-mediated auxin signaling controls stem cell homeostasis in the SAM. In the SAM, MP-mediated auxin signaling inhibits *CLV3* expression in the CZ to promote stem cell activities. Additional feedback loops contribute to the homeostasis of the SAM.

activation of A-type ARRs in the CZ, which indirectly affects the WUS-CLV feedback loop (Zhao et al., 2010). The role of MP in transcriptional regulation in the CZ appears to be distinct from its role in the PZ. In the PZ, where lateral organs initiate, MP recruits the SWI/SNF chromatin remodeling ATPases BRAHMA (BRM) and SPYLED (SYD) to increase the accessibility of target loci and to promote gene expression (Wu et al., 2015). It remains to be addressed how the context-dependent transcriptional activity of MP is achieved, especially given that both BRM and SYD are enriched in the CZ. Furthermore, high auxin levels negatively affect SAM size by promoting CZ cell transition into the PZ (Shi et al., 2018). Given that auxin promotes both the CZ and the PZ functions, it would be essential to further understand how auxin modulates the CZ/PZ balance. In addition, *DRN* and *DRNL*, although highly homologous to each other, have distinct expression profiles in the SAM. In fact, *DRNL* is excluded from the CZ but expressed in floral primordia and floral organ primordia (Chandler et al., 2011). Thus, the function of *DRNL* on the CZ is likely cell non-autonomous. It would be interesting to address if protein movement, which is common in the shoot apex, exists in this case.

Although extensive efforts have been devoted to studying stem cell homeostasis in the SAM, we are still blind men trying hard to learn and conceptualize what the elephant is like. Most likely, we currently have incomplete pieces of a

puzzle, which includes multiple positive and negative feedback loops. The current work certainly provides one important piece, and additional pieces are still awaiting us to accumulate.

**Compliance and ethics** The author(s) declare that they have no conflict of interest.

- Chandler, J.W., Jacobs, B., Cole, M., Comelli, P., and Werr, W. (2011). DORNROSCHE-LIKE expression marks *Arabidopsis* floral organ founder cells and precedes auxin response maxima. *Plant Mol Biol* 76, 171–185.
- Luo, L., Zeng, J., Wu, H., Tian, Z., and Zhao, Z. (2018). A molecular framework for auxin-controlled homeostasis of shoot stem cells in *Arabidopsis*. *Mol Plant* in press doi: 10.1016/j.molp.2018.04.006.
- Sassi, M., and Vernoux, T. (2013). Auxin and self-organization at the shoot apical meristem. *J Exp Bot* 64, 2579–2592.
- Shi, B., Guo, X., Wang, Y., Xiong, Y., Wang, J., Hayashi, K.I., Lei, J., Zhang, L., and Jiao, Y. (2018). Feedback from lateral organs controls shoot apical meristem growth by modulating auxin transport. *Dev Cell* 44, 204–216.e6.
- Vernoux, T., Brunoud, G., Farcot, E., Morin, V., Van den Daele, H., Legrand, J., Oliva, M., Das, P., Larrieu, A., Wells, D., et al. (2011). The auxin signalling network translates dynamic input into robust patterning at the shoot apex. *Mol Syst Biol* 7, 508–508.
- Wu, M.F., Yamaguchi, N., Xiao, J., Bargmann, B., Estelle, M., Sang, Y., and Wagner, D. (2015). Auxin-regulated chromatin switch directs acquisition of flower primordium founder fate. *eLife* 4, e09269.
- Zhao, Z., Andersen, S.U., Ljung, K., Dolezal, K., Miotk, A., Schultheiss, S.J., and Lohmann, J.U. (2010). Hormonal control of the shoot stem cell niche. *Nature* 465, 1089–1092.