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Current Opinion in Plant Biology

From signals to stem cells and back again

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During plant development, organ morphology and body architecture are dynamically adjusted in response to a changing environment. This developmental plasticity is based on precisely controlled maintenance of primary, as well as programmed initiation of pluripotent stem cell populations during secondary- and *de novo* meristem formation (reviewed in [1–3]). Plant stem cells are found exclusively in specific locations that are defined by relative position within the growing tissue. It follows that stem cell fate is primarily instructed by endogenous signals that dynamically define the stem cell niche in response to tissue topography [4]. Furthermore, plant stem cell activity is strongly dependent on developmental stage, suggesting that they are sensitive to long range signaling from distant organs, including the root [5,6••]. And finally, environmental signals exert a major influence allowing plants to cope with the plethora of highly variable environmental parameters during their life-cycle [7]. Integrating tissue level positional information with long range developmental cues, as well as environmental signals requires intricate molecular mechanisms that allow to filter, classify, and balance diverse inputs and translate them into appropriate local cell behavior. In this short review, we aim to highlight advances in identifying the relevant signals, their mode of action, as well as the mechanisms of information processing in stem cells of the shoot apical meristem (SAM).

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Current Opinion in Plant Biology 2018, **45**:136–142

This review comes from a themed issue on **Cell signaling and gene regulation**

Edited by **Jorge Casal** and **Javier Palatnik**

https://doi.org/10.1016/j.pbi.2018.06.005

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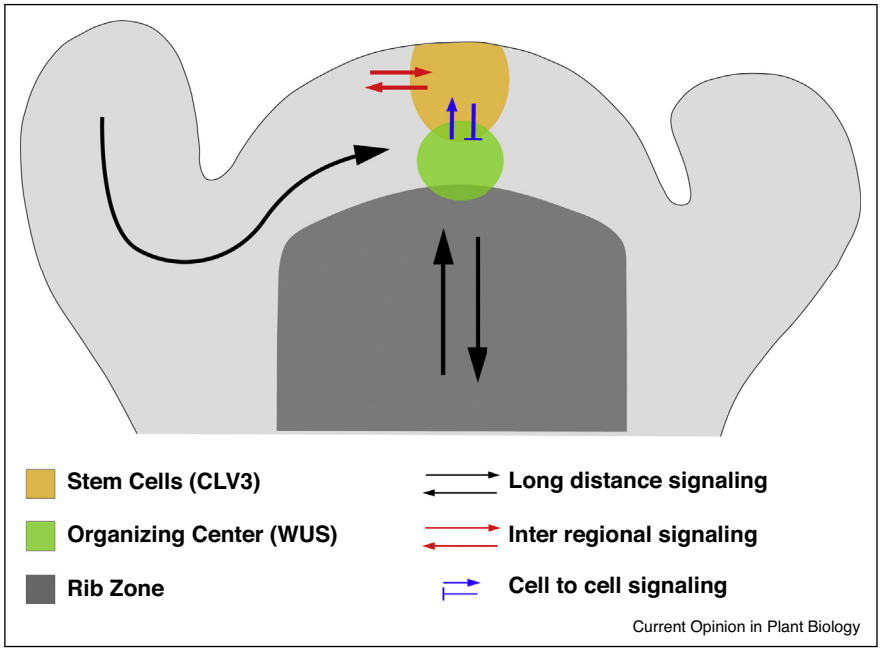
Tissue level signaling: transcription factors, ligand-receptors systems and the cell wall

The molecular basis for stem cell identity and maintenance in the shoot is composed of a negative feedback loop between the homeodomain transcription factor WUSCHEL (WUS) and the peptide signaling factor CLAVATA3 (CLV3) (Figure 1) [1,4,7]. *WUS* mRNA is exclusively expressed in the stem cell niche in the deeper layers of the SAM, termed the Organizing Centre (OC). From these cells, WUS protein migrates apically via cytoplasmic bridges, called plasmodesmata, to induce stem cell fate [8–10]. Stem cells in turn express the CLV3 precursor, which is processed into a small peptide and secreted to the extracellular space [11], from where it represses *WUS* expression through stimulation of receptor kinase complexes (Figure 2).

Several receptors have been identified to function in CLV3 signaling to limit stem cell fate. The leucine-rich repeat receptor kinases (LRR-RKs) CLV1, the related BARELY ANY MERISTEM 1, 2 and 3 (BAM 1, 2, and 3) and the more distant RECEPTOR-LIKE-PROTEIN KINASE 2 (RPK2) receptors all function in stem cell fate restriction [12] (Figure 2). Furthermore, the heterodimer between the LRR non-kinase CLV2 and the pseudo-kinase CORYNE (CRN) is required for stem cell signaling. Redundancy between these receptor complexes is demonstrated by the ability of BAM1 to partially compensate for the loss of CLV1 although *BAM1* is usually repressed by CLV1 signaling [13], demonstrating substantial cross regulation between the different signaling modules. Apart from the core stem cell signaling receptors, the ERECTA (ER) family and ARABIDOPSIS HISTIDINE KINASEs (AHKs) receptors are required for proper SAM morphology by tuning cellular sensitivity to cytokinin (Figure 2). While AHKs promote cytokinin perception, ER receptors appear to restrict signaling output to deeper layers of the SAM, thus collectively defining the organizing center (OC) [14,15,16•].

Importantly, CLV2 and ER receptors appear to have additional roles in immune signaling [17,18] and BAM receptors are required to control molecular trafficking through plasmodesmata [19••], suggesting that RLKs have not only functionally diverged, but are able to execute multiple context dependent roles. The fact that more than 600 RLKs are encoded by the *Arabidopsis* genome [20], and because many of them act in immune signaling via the recognition of defined Pathogen Associated Molecular Patterns (PAMPs), which include small peptides [21], makes it likely that additional 'dual use receptors' with roles in stem cell control may exist. The observations that MAPK and Ca^{2+}-signaling are putative downstream effectors of CLV signaling also supports this hypothesis [22,23], since they are important downstream effectors in immune signaling as well. Taken together these observations imply that in addition to CLV3, other molecules might be sensed by stem cell regulatory

Figure 1



Signal integration in the shoot apical meristem (SAM). The stem cell niche in the organizing center (OC) and the stem cells are positioned and regulated by multiple layers of signaling. Cell to cell signals instruct and maintain stem cell fate, inter-regional signals position the stem cell domain and tissue architecture, while long distance signals from root and leaves regulate stem cell activity in response to the environment.

receptor complexes. This would allow for signal integration at the receptor level by diverse mechanisms, including spatial partitioning, co-receptor interaction or control of receptor abundance. The idea of information processing at the receptor level is supported by several independent findings: First, CLV3 signaling is buffered through internalization of CLV1 upon ligand exposure and different *clv1* and *crn* alleles have divergent, yet additive effects on carpel development and *BAM* repression, respectively [24,25••]. Second, FEA2, the CLV2 orthologue in maize, can sense multiple ligands and confers downstream signaling specificity by differential interaction with either ZmCRN or the alpha subunit of the heterotrimeric G-protein COMPACT PLANT 2 [26••]. And third, RLKs are differentially recruited into microdomains upon stimulation [27].

In addition to mechanisms acting on the level of the receptor molecule, regulation of the apoplastic space, or extracellular matrix, is important for receptor–ligand interactions. The cell wall is the outermost interface for signal perception and integration for all plant cells. It acts as a selective barrier to many biomolecules and it confers mechanical strength, while at the same time preventing migration of cells within or between tissues. Therefore, in developing tissues like the SAM, mechanisms are required that enable coordinated remodeling of the cell wall to maintain tissue and cell-integrity. Since differentiation of plant cells is usually accompanied by changes in cell wall composition and mechanical properties [28], it is not surprising that these aspects seem to be intimately linked with cell fate decisions, as demonstrated by the ability of cell wall remodeling enzymes to induce organ initiation in the periphery of the SAM [29]. Strikingly, even the expression domain of the stem cell factor *SHOOT MERISTEMLESS* (*STM*) is controlled by mechanical forces present at the boundary of the dome shaped SAM [30,31]. STM is an important regulator of meristematic cell identity by activating expression of enzymes for CK biosynthesis in the center of the SAM [32] promoting proliferation, while at the same time suppressing differentiation through repression of *ASYMMETRIC LEAVES1* [33]. In addition, cell wall synthesis is highly controlled in the SAM [34] leading to differential stiffness of cells even within the meristem [35]. The coupling of cell fate progression and cell wall remodeling, implies a feedback regulatory mechanism between the molecular networks controlling stem cell fate and the signaling modules controlling cell wall integrity (CWI). With regard to CWI, the methyl-esterification status of the cell wall molecule pectin, which is the major component of primary walls, seems to be actively sensed by several plasma-membrane localized receptor complexes [36–38]. Galacturonic acid oligomers, a class of cell wall derived molecules and major constituent of pectin, inhibits the developmental transition from skotomorphogenesis to photomorphogenesis [39••] which is accompanied by SAM activation [40••]. While most studies on cell wall

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