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Push–pull strategy in the regulation of postembryonic root development

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Unlike animals, plants continue to grow throughout their lives. The stem cell niche, protected in meristems of shoots and roots, enables this process. In the root, stem cells produce precursors for highly organized cell types via asymmetric cell divisions. These precursors, which are "transit-amplifying cells," actively divide for several rounds before entering into differentiation programs. In this review, we highlight positive feedback regulation between shoot- and root-ward signals during the postembryonic root growth, which is reminiscent of a "push–pull strategy" in business parlance. This property of molecular networks underlies the regulation of stem cells and their organizer, the "quiescent center," as well as of the signaling between stem cell niche, transit-amplifying cells, and beyond.

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Introduction

Unlike animals, a distinctive property of plants is to set up their basic body plans as embryos and undergo postembryonic growth and development in an indeterminate manner, thereafter. The indeterminate growth involves both the growth of a single organ in apical and radial directions and the generation of new organs from pre-existing ones. These processes allow plants to survive under ever-changing environments, even if parts of their bodies are heavily damaged. Stem cell populations present in shoot and root play critical roles in these processes.

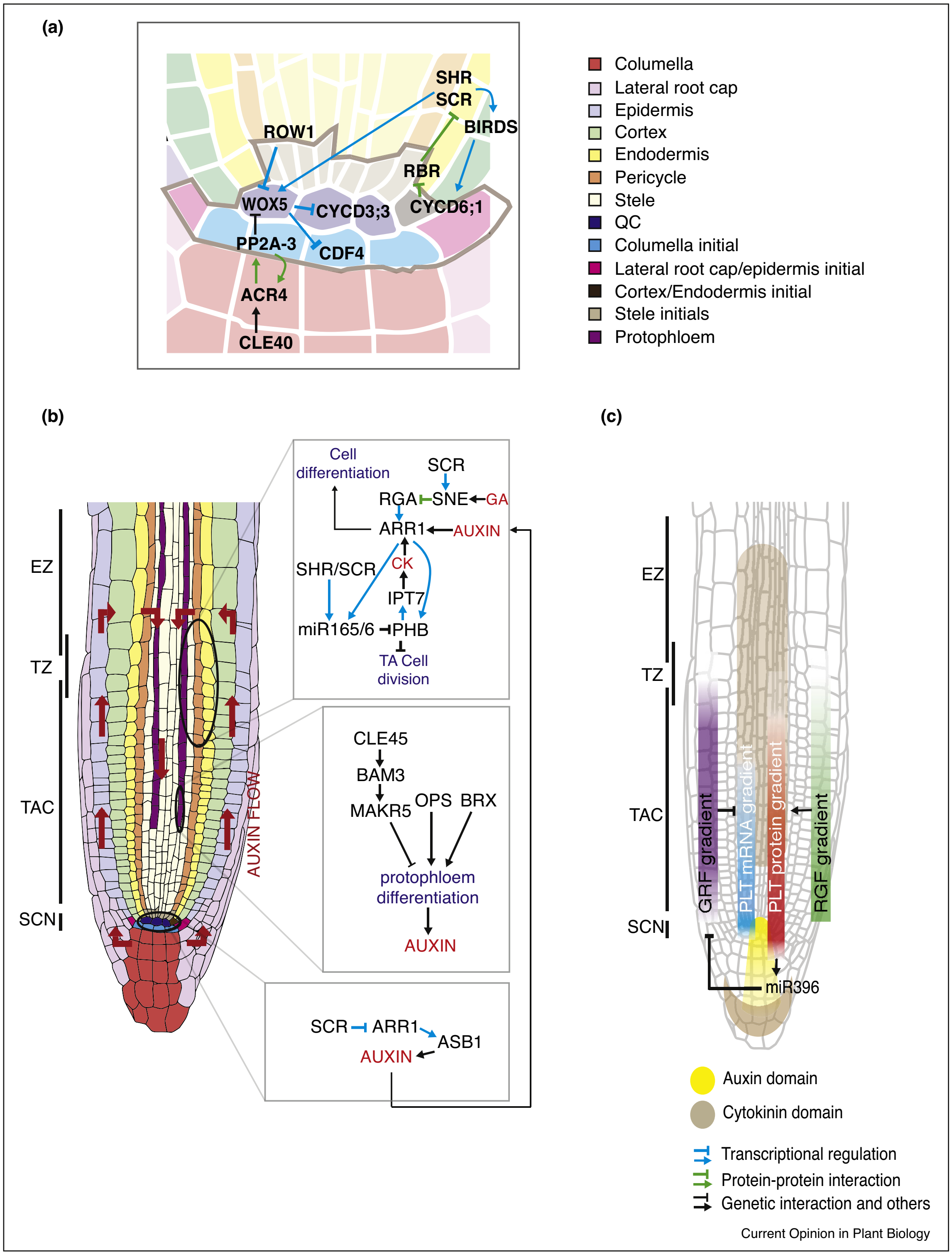
Roots have highly conserved tissue organization in radial direction, consisting of dermal, ground, and vascular tissues from the periphery to the center. As roots grow, cells constituting the radial tissues are constantly generated in the meristem through a combination of symmetric and asymmetric cell divisions. Undifferentiated cells that undergo asymmetric cell divisions are called "initials." In *Arabidopsis* roots, proximal stem cells are easily distinguishable as a single layer of cells, with the initials located in shoot-ward direction, right above the "quiescent center" (QC). "Columella initial cells," or "distal stem cells," are located in root-ward direction. "Cap cells" are generated from columella initials and "epidermal/lateral root cap initials" by asymmetric cell division for protection of root apical meristem, as the root grows through the soil. Proximal stem cells undergo asymmetric cell divisions in anticlinal direction; one daughter cell adjacent to the QC stays as a stem cell and the other undergoes another round of asymmetric cell division periclinally to generate progenitors for two different cell types. These progenitors actively undergo several rounds of division before entering the differentiation programs. A pool of these actively dividing cells is called "transit-amplifying cells." The transition from cell proliferation to differentiation in radial tissues occurs simultaneously with a clear shift of isodiametric cells to rapidly elongating cells (Figure 1b).

During postembryonic root growth, cell division activities of stem cells and transit-amplifying cells should be maintained for a long term. Laser ablation studies in 1990s [1,2] suggested that QC is required for maintaining the stemness of surrounding cells by sending out local signals. Therefore, the QC and surrounding stem cells are together considered as a stem cell niche. In the present review, we have introduced local regulatory programs in each root zone and have discussed how they coordinate the postembryonic root growth.

Local transcriptional networks and signaling that regulate the stem cell niche

Forward genetic studies of mutants that display short root phenotype revealed two key pathways for the formation of stem cell niche [3]. One is directed by PLETHORAs (PLTs) [4] and the other by SHORTROOT (SHR) [5] and SCARECROW (SCR) [6]. PLT1 and PLT2 are essential for QC specification and stem cell activity. They are expressed in a gradual manner, peaking around the QC and decreasing toward the transition zone between the meristem and elongation zones. *PLT1* and *PLT2* respond positively to auxin and auxin response factors (ARFs) [4], and their activity depends on the gene dosage [7], suggesting that PLTs have morphogenic

Figure 1



Local and intercellular regulatory networks underlying the postembryonic root development: **(a)** Local regulatory networks in the stem cell niche. Stem cell activities are regulated by the restriction of *WOX5* expression domains to the QC. SHR-SCR signaling pathway induces asymmetric cell division and tissue specification in the ground tissue through BIRD transcription factors. **(b)** Short- or long-distance crosstalk between the SCN and TAC. Root meristem size is determined by SCN and TAC activity and their coordinated regulation. Auxin reflux-loop regulates the establishment of SCN and TAC boundaries in the root meristem. Phloem, established by ACD of initial cells and enucleation program during differentiation, carries top-down signal. **(c)** Multiple pathways that modulate PLT gradient along the root. PLT gradient regulates stem cell maintenance and meristem boundaries. Auxin-cytokinin crosstalk provides spatial cues for zonal boundaries. SCN: stem cell niche, TAC: transit-amplifying cell, TZ: transition zone, EZ: elongation zone.