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Shaping a root system: regulating lateral versus primary root growth

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Primary and lateral roots comprise root systems, which are vital to the growth and survival of plants. Several molecular mechanisms associated with primary and lateral root growth have been described, including some common regulatory factors for their initiation and development. However, in this opinion article, we discuss the distinct growth behavior of lateral roots in response to environmental cues, such as salinity, gravity, and nutrient availability, which are mediated via specific regulators. We propose that differential growth dynamics between primary and lateral roots are crucial for plants to adapt to the ever-changing environmental conditions.

Root growth plasticity

The root system is important for a range of processes, such as anchoring, nutrient and water uptake, storage, and as the main interface between a plant and its soil environment. Root growth plasticity determines the survival of plants to continuously changing environmental conditions [1]. In *Arabidopsis* (*Arabidopsis thaliana*), the primary roots and individual lateral roots are the basic components of its taproot system architecture [2]. In crops, such as maize (*Zea mays*) or rice (*Oryza sativa*), the fibrous root system comprises embryonic primary and seminal roots, and postembryonic shoot-borne and lateral roots. The embryonic roots are important for the early growth and development of the seedlings, whereas the postembryonic roots, especially shoot-borne roots, have an important role in the later stages of growth and development [2–4]. Understanding how root systems develop holds potential to increase plant yield and optimize agricultural land use. For example, diversified root growth angles and root growth depths are intimately correlated with the uptake of natural nutrients distributed in soil [5], and alteration of root system architecture improves drought avoidance in rice [6].

The mechanisms that control the development and growth of primary and lateral roots have mainly been explored separately [7–9]. The comparison between lateral and primary roots is rarely made, and it has always been assumed that a lateral root is similar to the primary root in all aspects. However, recent observations from different labs showed that primary and lateral roots have differential growth dynamics in responses to environmental cues, such as gravity, salt, and nitrate [10–12]. In this opinion paper, we mainly use knowledge from *Arabidopsis* to illustrate that, although there are common regulatory factors for primary and lateral root initiation and development, lateral roots display distinct growth responses that are mediated through endogenous signals (e.g., plant hormones) in response to external environmental cues.

Root system architecture

Embryonic primary root initiation

The *Arabidopsis* primary root is initiated during embryogenesis via the specification of a single extra-embryonic suspensor cell, called the hypophysis. This upper suspensor cell generates the quiescent center, following an asymmetric cell division, and leads to the generation of the primary root meristem [13]. This primary root meristem is a population of cells at the primary root tip that divide to form postembryonically all the cells and tissues that comprise the root. Cell division, combined with elongation and differentiation, is responsible for the continuously growing and developing primary root [14]. The quiescent center, a small group of cells that rarely divide, is surrounded by the stem cells [14,15]. These stem cells divide asymmetrically to give rise to various cell types and tissues in the primary root [16] (Figure 1A,C).

Postembryonic lateral root initiation

In contrast to primary roots, which are initiated during embryogenesis [13], lateral root initiation is a postembryonic process and largely determines root system architecture. The *Arabidopsis* lateral root initiates in the pericycle, which represents a heterogeneous tissue comprising cells at the phloem poles and cells specified to form lateral root primordia opposite the xylem pole [17]. The

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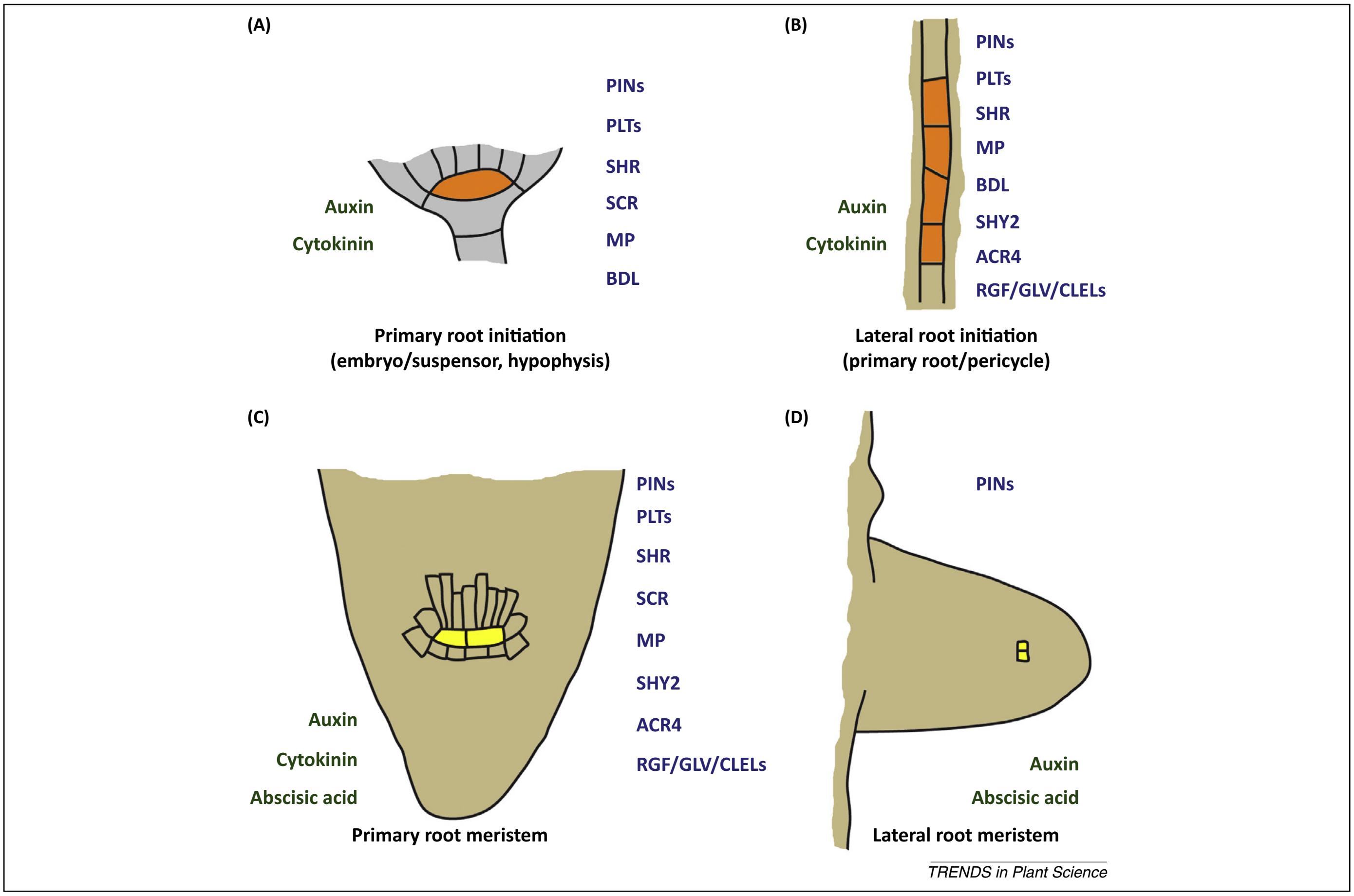

Figure 1. Key common players in primary and lateral root initiation, growth, and maintenance. A selection of common hormones (green) and key molecular components (blue) are indicated. Orange in **(A,B)** indicates the small daughter cells following asymmetric cell division. Yellow in **(C,D)** indicates the quiescent center. Abbreviations: ACR4, ARABIDOPSIS CRINKLY4; BDL, BODENLOS; CLEL, CLE-LIKE; GLV, GOLVEN; MP, MONOPTEROS; PIN, PIN-FORMED; PLT, PLETHORA1; RGF, ROOT GROWTH FACTOR; SCR, SCARECROW; SHR, SHORTROOT; SHY2, SHORT HYPOCOTYL 2.

process of lateral root initiation requires tightly coordinated asymmetric cell divisions, followed by further divisions to generate a lateral root primordium that develops into a mature lateral root emerging from the primary root [8,9] (Figure 1B,D).

Key players in primary root growth and development also act in lateral roots

The initiation of primary and lateral roots is different with respect to origin (embryonic versus postembryonic) and tissue (suspensor versus pericycle). However, there are similarities at the mechanistic level (asymmetric cell division, see above) and with respect to key players involved in primary and lateral root initiation and development (see below). In this section, we illustrate these communalities with some examples (Figure 1).

Auxin transport and core auxin response regulators

Auxin is required for both primary and lateral root initiation [9,18–20]. It regulates embryonic primary root initiation through the action of the AUXIN RESPONSE FACTOR 5 (ARF5)/MONOPTEROS (MP) transcription factor and its auxin-labile inhibitor IAA12/BODENLOS (BDL) [21,22]. MP, through positively regulating the expression of *PIN-FORMED 1* (*PIN1*), an auxin efflux carrier, promotes auxin transport from the embryo to the hypophysis precursor, thereby providing positional signals for root hypophysis specification [23,24]. In addition, the basic helix–loop–helix (bHLH) transcriptional regulator TARGET OF MP7 (TMO7), which is transcriptionally controlled by MP, has to move from the hypophysis-adjacent embryo cells, where it is synthesized, to the hypophysis, as such contributing to MP-dependent primary root initiation [25]. In the mature primary root tip, MP and PIN3, another auxin efflux carrier, also have a role in regulating stem cell differentiation [26,27].

PIN1-dependent auxin transport is also essential for lateral root initiation. There is a coordinated rearrangement of PIN1 polarity in lateral root primordia correlating with DR5-visualized auxin response gradients and correct primordium development [23]. PIN3 is also involved in lateral root initiation via regulation of auxin reflux between the endodermis and pericycle in the primary root [28]. Numerous core auxin response-related molecular components are involved in lateral root initiation [8]. Interestingly, the MP–BDL auxin response module also has a central role in regulating divisions during early lateral root development [18].

Cytokinin

Cytokinin also has a critical role in primary and lateral root initiation. It controls root stem cell specification via antagonizing the function of auxin. Loss of function of *ARABIDOPSIS RESPONSE REGULATOR* (*ARR*) genes