



Review

Surfing along the root ground tissue gene network

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ABSTRACT

Organization of tissues in *Arabidopsis thaliana* root is made of, from outside in, epidermis, cortex, middle cortex, endodermis, pericycle and vascular tissues. Cortex, middle cortex and endodermis form the ground tissue (GT) system. Functional and molecular characterization of GT patterning mutants' properties has greatly increased our understanding of fundamental processes of plant root development. These studies have demonstrated GT is an elegant model that can be used to study how different cell types and cell fates are specified. This review analyzes GT mutants to provide a detailed account of the molecular network that regulates GT formation in *A. thaliana*. The most recent results indicate an unexpectedly complex network of transcription factors, epigenetic and hormonal controls that play crucial roles in GT development. Major differences exist between GT formation in dicots and monocots, particularly in the model plant rice, opening the way for evo–devo of GT formation in angiosperm. In rice, adaptation to submergence relies on a multilayered cortex. Moreover, variation in the number of cortex cell layers is also observed between the five root types. A mechanism of control for cortical cell number should then exist in rice and it remains to be determined if any of the *Arabidopsis thaliana* identified GT network members are also involved in this process in rice. Alternatively, a totally different network may have been invented. However, first available results suggest functional conservation in rice of at least two transcription factors, SHORT ROOT (SHR) and SCARECROW (SCR), involved in ground tissue formation in *Arabidopsis*.

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Introduction

The root anatomy of *Arabidopsis thaliana* is simple; the roots contain several concentric layers of cells, each of which assumes a specific role in the root's function (Dolan et al., 1993; Scheres et al., 1994). The function of the root epidermis, for example, involves nutrient uptake and the differentiation of root hairs, which are specialized cell structures that increase water uptake (Waisel et al., 2002). The root cap protects the growing root tip and facilitates soil penetration by secreting specific compounds. In a mature *A. thaliana* root, the radial anatomy of the root (from the outside in) consists of the epidermis, cortex, middle cortex (MC), endodermis, pericycle and vascular tissues (Fig. 1a). The cortex, MC and endodermis form the ground tissue (GT) system. The GT system and the two other tissues systems, the dermal (epidermis) and the vascular system (including the pericycle), converge to four cells in the root apical meristem (RAM) that are nearly mitotically inactive and are called the quiescent center (QC) (Evert and Esau, 2006). Each tissue system is produced following stereotypical cell divisions by an initial cell (Evert and Esau, 2006). The initial cells regenerate by first asymmetrical division and produce daughter cells that will also divide and differentiate to form

root tissues. Four types of initial cells exist in the *A. thaliana* root; one population of initial cells produces the columella cells, one produces the vascular tissue, a common initial cell produces the lateral root cap and epidermis, and a common initial cell produces all of the tissues that form the GT. These initial cells surround the QC and divide less frequently than their immediate daughter cells (Campilho et al., 2006; Dolan et al., 1993). The QC forms an organizing center that is required for stem cell maintenance (Aida et al., 2004; van den Berg et al., 1997). In the 1990s, several experiments demonstrated that position but not lineage was crucial for cell fate and cell patterning (van den Berg et al., 1995, 1997). Laser ablation of all of the initial cells in contact with a QC cell induces premature differentiation of these cells (van den Berg et al., 1995). Therefore, the role of the differentiated tissue is to maintain the QC in an undifferentiated stage.

As in almost all vascular plants, *A. thaliana* contains a single endodermis layer that is characterized by the presence of Casparian bands in the radial and transverse walls of the cells (Enstone et al., 2002). The appearance of an endodermis was a key event in the evolution of land plants, and its essential function is to prevent the apoplastic passage of ions from the cortex to the stele. It is essential for the selective uptake of ions, nutrients and water, and it also has other specialized functions, such as graviperception in shoots (Tasaka et al., 1999). The function of the endodermis in apoplastic ion movement is evidenced by the multilayered endodermis that is found in several

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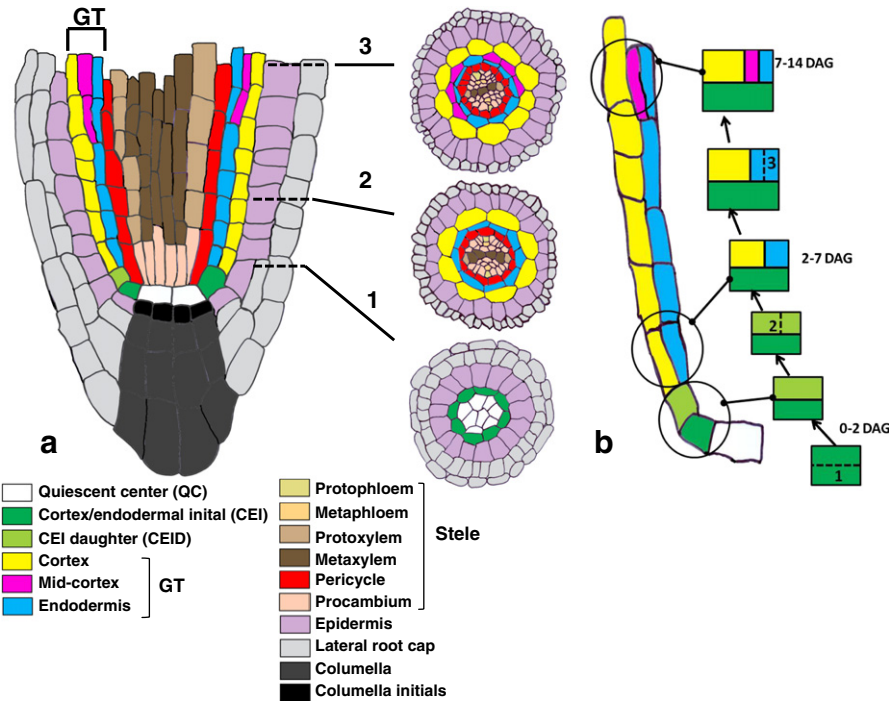


Fig. 1. *A. thaliana* root meristem structure and GT cell fate. (A) *A. thaliana* RAM structure and cell fate. Left: Longitudinal sections of the *A. thaliana* RAM. All of the cell files converge into four mitotically inactive cells, which are called the quiescent center (white). Four distinct zones of initials are present and produce all of the root tissues: vascular, including the phloem, protoxylem, metaxylem and pericycle; the lateral root cap/epidermis, with a common initial; the columella initials and the GT-containing endodermis, cortex and middle-cortex. Right: Serial root radial sections of an *A. thaliana* root at increasing distances from the QC. (1) A radial section at the QC level with the CEI visible around the QC. (2) A radial section just up to the procambium zone, which shows separate cortex and endodermis initials. (3) A radial section further from the QC in the basal meristem, where the last GT has started to appear. The middle cortex is visible between the cortex and endodermis. (B) Schematic representation of GT cell fate. The first anticlinal division ($n^{\circ}1$) regenerates the CEI (dark green) and gives rise to the CEID (light green) during or soon after germination. The asymmetrical division of the CEID ($n^{\circ}2$) separates the cortex (yellow) and endodermis (blue) between 2 and 7 days after germination (DAG). The late asymmetrical periclinal division of the endodermis ($n^{\circ}3$) and the formation of the last GT layer, the middle cortex (pink), occur between 7 and 14 DAG. All of the tissues in the figure are color-coded. Adapted from Baum et al. (2002), Dolan et al. (1993), Paquette and Benfey (2005), and Petricka et al. (2009).

halophyte species. Presence of a multilayered endodermis represents an anatomical adaptation to high salt stress (Inan et al., 2004). The number of cortex cell layers is considerably larger in numerous species. These layers differentiate into more specialized tissues that reflect specific plant adaptations (Evert and Esau, 2006). In rice, a multilayered cortex differentiates into a gas-containing tissue, called the aerenchyma, which is visible in roots and represents an anatomical adaptation to water submergence (Coudert et al., 2010; Rebouillat et al., 2009). Rice can also develop a specialized GT layer, called the exodermis, that is a water barrier with a function similar to that of the endodermis (Enstone et al., 2002); this feature is shared by most vascular plants but is absent in *A. thaliana* (Enstone et al., 2002).

A fundamental problem in plant development is understanding how different cell types and cell fates are specified. GT is an elegant model that can be used to study these fundamental questions in plant roots. Identifying the mutations that affect cell fate and cell patterning is a powerful method for isolating the genes that are involved in this process. They can be identified by taking advantage of the simple and hierarchical fates of the cells that form the GT in the RAM. Numerous mutants have been isolated over the last 10 to 20 years, and characterizing their functional and molecular properties has greatly increased our understanding of the fundamental processes of plant root development. This review analyzes GT mutants to provide a detailed account of the molecular network that regulates GT formation in *A. thaliana*. The most recent results indicate an unexpectedly complex network of genes that play crucial roles in root tissue cell identity, division and differentiation and in RAM maintenance.

Ground tissue formation involves a complex interplay of transcription factors

The initial divisions that form the GT can be determined simply by looking at root anatomy (Fig. 1b). GT cell patterning has also been confirmed using ^3H -thymidine labeling of actively growing roots and time-lapse analyses of transgenic reporter lines (Campilho et al., 2006; Dolan et al., 1993). Cortex endodermis initials (CEIs) are formed early after seed germination. The CEIs first divide anticlinal to regenerate themselves and produce proximal daughter cells, which are called cortex endodermis initial daughter cells (CEIDs). The CEIDs divide periclinal and asymmetrically to form separate cortex and endodermis cell layers (Dolan et al., 1993). During the later root growth, at 7 to 14 days after germination (DAG), additional asynchronous asymmetric periclinal divisions occur in the endodermis to generate the MC, which is a cortical tissue (Baum et al., 2002; Paquette and Benfey, 2005). The MC appears near the protoxylem pole and progresses as a one-gyre helix (Baum et al., 2002). The identification and characterization of several GT mutants has helped to elucidate a complex genetic GT formation network that involves several transcription factors and hormonal and epigenetic control.

Transcription factors involved in cortex and endodermal identity and formation

Mutations in the *SHR* and *SCR* genes (two members of the plant-specific GRAS transcription factor family) were first identified as causing shorter roots compared to in wild type (WT) plants (Benfey

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