Root apical organization in *Arabidopsis thaliana* ecotype ‘WS’ and a comment on root cap structure

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**Abstract**

*Arabidopsis thaliana* roots have closed apical organization with three initial tiers. The dermatogen/calyptrogen tier consists of two parts - the central initials form the columella root cap, and the peripheral initial cells form the protoderm (epidermis) and the peripheral root cap. These peripheral initials divide in a sequence to form a root cap consisting of interconnected cones. The periblem initial tier forms the ground meristem (cortex). For the first week after germination the periblum consists of one layer of initial cells. The peripheral cells of the tier divide periclinally and then anticlinally (a T-division) to form the two-layered cortex (outer cortex and endodermis). After about one week, all the peripheral cells have divided periclinally forming two initials; the outermost produces the outer cortex while the inner initial produces the endodermis and middle cortex layer. The latter two cells arise via a periclinal division. During this time, other cells within the tier divide periclinally to form a two-layered tier. The plerome forms the cells of the procambium (vascular cylinder) by simple anticlinal divisions followed by longitudinal divisions to fill out the cell files of the vascular cylinder. A survey (27 dicot species in 17 families) of roots with closed apical organization revealed that there are three different types of root cap - concentric cylinders of cells (e.g. *Linum*), interconnecting cones (e.g. *Arabidopsis*) or overlapping arcs (e.g. *Gossypium*).

**Introduction**

Root apical organization patterns have been studied for over one hundred years by Hanstein (1870) and others. Janczewski (1874) published a scheme to categorize root apices into different types based on cellular patterns. Popham (1966) further configured this into eight distinct root apical organization patterns. In its simplest form there are two basic types - open and closed. Open root apical organization means that all cell files in the root body converge on a zone between the root cap and body, but, that there are no discernible initial cells; the pea root (*Pisum sativum*) is a good example of this type. Closed root apical organization refers to the pattern where all cell files in the root body can be traced directly to tiers of initial cells; *Arabidopsis thaliana* is an example. Scheres et al. (1994) and Dolan et al. (1993) have reported on the closed apical organization structure in *Arabidopsis thaliana* ecotype ‘Columbia’. Unfortunately, Dolan et al. (1993) used incorrect terms for the histogen layers (e.g. periderm instead of periblem and protoderm instead of dermatogen/calyptrogen) and their analysis did not follow the cell lineages. This paper is one of a series on the apical organization in *A. thaliana* (Baum and Rost, 1996). In this paper we will describe the activity of all three histogen layers, and report some preliminary observations on the diversity of root cap structure in roots with closed apical organization.

**Apical organization in Arabidopsis thaliana**

The root apex of *A. thaliana* is closed with three tiers of initial cells: (1) dermatogen/calyptrogen (protoderm → epidermis / root cap), (2) periblem (ground meristem → cortex), (3) plerome (procambium → vascular cylinder) (Figures 1, 2). The root cap/epidermis has been fully described (Baum and Rost, 1996) so will
Figure 1. A. Median longitudinal section of a primary root apex in a one week old *Arabidopsis thaliana* cv WS seedling. (CRC-columella root cap, PRC-peripheral root cap, PC-procambium, GM-ground meristem, P-protoderm, 1-dermatogen / calyptrogen initials, 2-periblem initials, 3-plerome initials; Bar = 20 μm) B. Transverse section of *A. thaliana* root taken near the root cap/protoderm initial tier. The peripheral root cap cells are organized in an obvious two-dimensional spiral. The arrow shows the direction of the spiral; Bar = 25 μm. C. A clay model of the dermatogen / calyptrogen from a two week old *A. thaliana* root illustrating the spiral pattern of periclinal and anticlinal divisions of the root cap/protoderm (RCP) initials. The 'r' marks the youngest RCP initial. The next anticlinal division, which will regenerate a new RCP initial will occur in the cell to the right of the 'r'. The development of the RCP initial in this clay model begins with the cell marked with an 'r' and proceeds in a clockwise direction. The RCP initials first expand. This is followed by a periclinal division forming a protoderm initial (PI) to the inside and a peripheral root cap cell (RC) to the outside. The cell labeled with a star is the first RCP initial to divide periclinally. Cells continue to expand until such time that an anticlinal wall is formed producing two root cap cells (RC) to the outside, a protoderm cell (P) to the inside and proximal to the protoderm cell a regenerated RCP initial. The curved arrow on the right indicates the direction of the next youngest RCP initial due to an anticlinal division of the protoderm initial. The curved arrow on the left indicates the direction of periclinal divisions forming a peripheral root cap initial and a protoderm initial.