

VII. PRIMARY ROOT STRUCTURE AND DEVELOPMENT

Bot 404—Fall 2004

A. Root System

1. True root system

- in a true root system all roots are ultimately derived from the primary root
- radicle of the seedling gives rise to the primary root, which then continues to grow and rebranch to form most or all of the lateral roots
- true roots mainly in gymnosperms, dicots
- generally two categories recognized but distinction can be tenuous:
 - a) when the primary root is prominent and remains so, called a taproot; but there are smaller branches extending outward that are fibrous
 - b) the root system may be entirely fibrous (primary root is there but not dominant)

2. Adventitious root system

- the seedling root is the first root (seminal root), but never develops into a primary root in plants that have adventitious systems—often dies relatively soon
- defined as a root which does not arise from another root or the embryo, usually arises from stem tissue; do not undergo secondary growth (relatively narrow definition)
- either additional roots are derived from stem tissue, or, in grasses, the seminal root is also interpreted as adventitious
- characteristic of monocots, pteridophytes, with scattered occurrence in dicots (e.g., white clover, strawberry), absent from gymnosperms
- adventitious roots overcome limitations of not having secondary growth in the stem in monocots
- monocot trees (e.g., palms) sometimes do have a little secondary growth, but without this (as in most arborescent monocots) they must have support for the stem, either with sheathing leaf bases or prop roots (which are adventitious); in addition to support, the prop roots provide a way to bypass areas of the stem that cannot carry more water (volume)

B. Primary Root Structure

- axial structure, no nodes and internodes (no leaves or leaflike structures)
- primary root actually refers to a limited area fairly near the root tip, at least in roots with secondary growth
- will start off with dicot roots to discuss major structural features (DIAGRAM)

1. Longitudinal section

a. root cap

- made of parenchyma cells involved in physical protection of apex and also secretion of a mucilage (young epidermis does too) called mucigel
- preparations are usually made from roots obtained from moist chambers or water, and thus not exactly as in nature
- mucigel coats young, growing part of root; functions as a lubricant, probably other functions too
- as cells are sloughed off of the root cap, new ones are produced so it is continually renewed
- only stimulus for root orientation is gravity
- starch grains are numerous in cells, particularly of central column, called statoliths (= balancing stones)
- statolith theory says that starch grains sense gravity and control root orientation; when starch removed enzymatically, roots lose sense of direction
- problems: if true, what signal do starch grains send to cells and root cap as a whole?; only works for primary roots
- lateral roots have the same structure as the primary root, including starch

grains; if take seedling and place it on its side, the primary root goes down, but the others continue growing in their original directions

b. subapical meristem

- zone of meristematic tissue at the apex of the root
- usually referred to as a “subapical” meristem because of its position relative to the root cap
- will discuss this in more detail under root development

c. elongation zone (part of meristematic region)

- area beyond the meristem where cells are elongating
- procambium is differentiating in this zone

d. root hairs (part of the epidermis)

- constant root hair zone, a few mm long about 2 mm from the root tip
- root hairs increase surface area
- primary vascular tissue is mature here
- most roots have root hairs, small extensions from certain epidermal cells (an underground trichome); cell that produces a root hair = trichoblast; may be in a regular pattern or not
- both root hairs and roots must pass around obstructions, so tend to be irregular in appearance
- in natural environments, root hairs live for about 2-3 weeks, but new ones are formed as the root grows
- supposedly root hairs actively take up water and dissolved minerals BUT evidence doesn't really support this: e.g., 1) water enters a hairless epidermal cell just as rapidly as an epidermal cell with a hair; 2) phosphate and potassium enter older (suberized) portions of roots; 3) some plants do not have root hairs; 4) development of root hairs differs in a given species depending on environment, etc.
- root hairs may 1) alter rhizosphere conditions, 2) permit exploitation of soil pores that the main root can't reach

2. Transverse section

a. Epidermis

- cuticle is thin if it occurs at all on the root surface
- found in the younger part of the root
- older parts may become suberized or lignified
- velamen = multilayered (multiseriate) epidermis of dead cells found on roots of orchids and certain other tropical plants, mostly epiphytes; presumed to be absorptive but more likely serve as mechanical protection and reduction of water loss

b. Cortex

i) exodermis

- one (or more) layers just below the epidermis that are sclerified
- cells initially have delicate Casparian strips but suberin layer deposited quickly, and then layers of cellulose laid down; lignin may also be deposited
- conspicuous exodermis common in monocots—related to lack of secondary growth; this becomes the protective layer
- becomes the outermost protective layer if the epidermis disappears

ii) mid-cortex

- storage parenchyma, often develops large intercellular spaces or air passages (aerenchyma)
- often disproportionately large, can usually see starch grains
- basically for storage
- usually long-lived, but may degenerate quickly (e.g., some grasses and dicots) leaving endodermis or pericycle as surface

iii) endodermis (DIAGRAM)

- innermost layer of the cortex (usually only one layer)
- radial and transverse walls of cells are impregnated with a strip of suberin, like a ribbon wrapping around the cell; shared by adjacent cells
- known as the Casparian strip—usually visible as a red-staining area—it effectively seals the walls (apoplast), so that all solutes (water, minerals, etc.) must pass through the protoplast of the endodermal cells
- water and minerals go through the apoplast in cortex (path of least resistance), but at the endodermis, the Casparian strip is a selective filter
- under conditions when water might be lost, the Casparian strip prevents water from going back out
- can be a Casparian strip in the exodermis as well as the endodermis
- the Casparian strip really functions only in the root hair zone where water and minerals are taken up; up higher where the vascular cylinder is mature, more heavily suberized (except for plasmodesmata) and higher still, layer of cellulose between suberin and plasmalemma + lignification
- in the endodermis opposite the phloem are groups of endodermal cells lacking suberization or cellulose layer (opposite the xylem the endodermis is normal) called passage cells; hypothesized that these are transfer cells but no experimental evidence
- root pressure builds up in xylem due to active transport of ions into the stele—allows repair of small embolisms; suberized mature endodermis retains water in stele and pushes it upward (leading to guttation), otherwise cortical tissues could become waterlogged

c. Vascular cylinder (stele)

i) pericycle

- ring of tissue just inside the endodermis, but can be interrupted by xylem or phloem in some groups
- primarily of parenchyma but can contain sclerenchyma
- in contact with both the phloem and protoxylem
- it becomes the meristematic layer in roots with secondary growth, contributing to both vascular cambium and periderm
- usually uniseriate but may be multiseriate
- new roots (lateral roots) are initiated here

ii) vascular tissue

- no practical distinction between proto- and metaxylem in roots
- protoxylem poles occur on the points (in 3-D, ridges); usually don't find secondary wall thickenings in protoxylem comparable to those in the stem tissue; usually no annular or helical tracheary elements in xylem of roots
- protostele, no pith region (no discrete vascular bundles) except in some monocots (eustele or atactostele)
- phloem is in several discrete strands between protoxylem ridges, in contact with the pericycle but always separate from the xylem by parenchyma

iii) parenchyma

- may become sclerified in roots that lack secondary growth
- will become meristematic and form part of the vascular cambium if secondary growth occurs

iv) vascular patterns in dicots and gymnosperms (DIAGRAM)

- the different patterns may reflect differences among species, but sometimes they reflect vigor of different roots on the same plant
- conifers mostly diarch; dicots mostly triarch to pentarch

3. Monocot roots (DIAGRAM)

- more complex than in dicots
- often a central pith, or the center is occupied by a single metaxylem vessel (esp. in annual monocots, e.g., wheat), or other variations are known
- generally polyarch (with five or more, in some up to >100) protoxylem poles; reflecting the lack of secondary growth and the atactostele
- metaxylem may form horseshoe-shaped areas (other variations too)
- endodermis tends to develop an asymmetrical wall thickening (this covers the Casparian strip)
- if the exodermis develops a thick wall, this becomes a mirror image of the endodermis
- pericycle is multiseriate in some monocots

C. Primary Root Development

1. Subapical meristem (DIAGRAM)

- organized around a single subapical mother cell in some ferns and other pteridophytes
- seed plants have a group of central initials (quiescent center = actual meristem) around which there are varying numbers of organized layers of meristematic cells
- closed type: distinct layers are distinguishable, and vascular cylinder, cortex, rootcap are traceable to those layers (Fig. 14.12 A-D; also seen in *Zea*)
- open type: no distinct layers, basically one group of transversely oriented cells (Fig. 14.12 E, F; also seen in *Pisum*) giving rise to the root cap and root proper
- other plants fall between these extremes; usually see root cap derived from one layer, but other distinctions may be difficult; organization may change during development
- quiescent center is variable in volume, but located at the apicalmost (distalmost) portion of the root; mitotic divisions occur within the QC but much less frequently than in the area basal (proximal) to the QC (see Fig. 14.14)

- greatest mitotic activity occurs in the proximal meristem where the cortical and vascular initials are dividing and in the calyptrogen where the rootcap initials are active (i.e., in the meristematic region)
- calyptrogen divides once in 12-40 hours; proximal meristem 20-35 hours; QC 150-500 hours
- why does QC exist? 1) geometric argument—must have an area that divides less in its center, or else the root would not have any functional shape; 2) physiological argument—QC secretes hormones that stimulate cell division, too high at source so suppresses division, but with dilution it stimulates; 3) constitutes a reserve of genetically healthy cells

2. Vascular cylinder

- procambium develops in an uninterrupted acropetal (toward the apex; least mature cells are closer to the apex) direction
- phloem is next, also continuous and acropetal
- xylem matures last, after the phloem
 - a) metaxylem cells enlarge first, but do not lay down secondary wall until later
 - b) protoxylem lays down secondary wall only when elongation of a portion of root is almost complete, so wall thickenings and distortions are not as conspicuous as in stems
 - c) secondary wall formation in metaxylem

3. Lateral (branch) roots

- initiated endogenously by periclinal divisions in local areas of the pericycle and just to the outside of the protoxylem ridges; may also include cell layers from the endodermis
- after initiation, a subapical meristem similar to that in the parent root soon forms
- pressure is exerted on the endodermis and cortex of the parent root as the lateral root expands; endodermis may expand by anticlinal divisions for a short time, and cortical cells of parent root are destroyed
- lateral root emerges by rupturing epidermis of parent root
- connection of xylem and phloem of lateral and parent roots is by differentiation of cells produced by pericycle and sometimes adjacent parenchyma (not well studied)
- all vascular plants show endogenous origin of lateral roots
- no particular pattern with reference to the main axis (e.g., not spiral, opposite etc.); probably a function of growing in soil which is heterogeneous