VIII. SECONDARY ROOT DEVELOPMENT AND ROOT SPECIALIZATIONS

Bot 404—Fall 2004

A. Secondary Root Growth

-absent from most monocots and pteridophytes
-present in all gymnosperms and most dicots
-if root is going to operate for more than one season, must increase vascular system
-initiation of cambial activity is indicated by periclinal divisions

1. Vascular cambium (DIAGRAM)
   a) develops from meristematic activity of undifferentiated procambium (or dedifferentiated parenchyma) cells between xylem and phloem (strips of tissue) (**E**, Fig. 15.1)
   b) meristematic activity of pericycle around the protoxylem ridges occurs
   c) meristematic areas are joined to form a vascular cambium

2. Secondary vascular tissue

-vascular cambium produces secondary xylem to the inside, secondary phloem to the outside; vascular cambium is one layer, cells divide relatively slowly; additional faster-dividing layers occur in the cambial zone on either side

-early vascular cambium has most of its activity between protoxylem poles, eventually giving it a symmetrical shape (**E**, Fig. 15.1) with original shape of primary xylem visible in the center (DIAGRAM)

-then secondary xylem and phloem are laid down evenly around the root; primary phloem pushed to outside and eventually crushed or lost; primary xylem eventually becomes inactive

-always more xylem than phloem is produced, about 5:1; why? Xylem also contains non-conducting support elements, especially in stems but also in roots;

also, generally not as much food storage (except for specialized storage roots), so don't need as much phloem

3. Periderm
  -secondary protective tissue that replaces the epidermis in stems and roots
  -after secondary growth of vascular tissue is initiated, cells of the pericycle undergo both periclinal and anticlinal divisions
  -increase in number of layers radially, forcing the cortex outward
  -eventually cortex ruptures and is sloughed off
  -another lateral meristem, the phellogen (cork cambium), arises in the outer part of the proliferated pericycle
  -phellogen produces phellem (cork cells) to the outside, protective tissue, nonliving, suberized cells
  -phellogen may produce phelloderm to the inside, resembles cortical parenchyma

  -functions of pericycle: 1) produces new (lateral) roots; 2) contributes to vascular cambium; 3) produces the phellogen (cork cambium)

4. Anomalous secondary growth
  -variations in the manner of secondary growth occur
  -one example is sugar beets, which generate multiple concentric cambia

B. Root Specializations

1. Specializations not involving other organisms (four examples)
   a) Storage roots
      -swollen portions of primary root or lateral roots, and often the hypocotyl as well
      -usually involves secondary growth in which the vascular cambium produces numerous parenchyma cells in the secondary xylem/phloem which become filled with food reserves

   b) Contractile roots
      -common feature of bulb- and corm-bearing monocots, also known in herbaceous perennial dicots

-a poorly known phenomenon; inner cortical cells change shape (expand radially and contract longitudinally)
-pulls bulbs or corms deeper into the ground, lateral movement may also occur

c) Aerial roots
-more common in tropics
-function as prop roots or anchorage in epiphytic plants
-in tropical orchids, frequently green and photosynthetic, lack root hairs but have a velamen

d) Proteoid roots
-were first discovered in the dicot family Proteaceae, hence the name
-now known also from some legumes and a sedge
-locally on the root dense clusters of short lateral roots emerge all around, appearing like a bottle brush; these roots lack root hairs
-some evidence indicates that this is related to PO_4 uptake in extremely phosphorous-poor soil

2. Specializations involving fungi
a) Mycorrhizae ("fungus root")
-symbiotic association of fungi with roots
-thought to be a normal feature of all perennial plants; approx. 80% of plants have mycorrhizal associations
-also widespread among gametophytes of bryophytes and pteridophytes; also known from fossils dating back 400 mya or more
-plants benefit by increased accessibility of minerals and organic materials (through conversion by fungi); fungi benefit by receiving photosynthate and other compounds (e.g., amino acids) produced by host
-plant hosts are photosynthetic with functional roots

i) ectomycorrhizae (ectotrophic)
-commonest type in dicots and gymnosperms, especially in trees and shrubs
-fungus forms a mantle on specialized side root which is determinate, short, and lacks a root cap and root hairs
-hyphae grow between, but do not penetrate, epidermal and outer cortical cells to form "Hartig net"
-association tends to be very host specific
-fungus is a basiomycete

ii) endomycorrhizae (endotrophic) (**M**, Fig. 13.21)
-commonest in monocots and pteridophytes
-fungus lives within cortical parenchyma cells, but not in direct contact with the plant cell cytoplasm

-as fungus invades new tissue, it dies off behind and is absorbed by the host plant (tolypophagy)
-not much host specificity involved
-fungus is a zygomycete; known as vesicular-arbuscular mycorrhizae (VAM)

b) Saprophytes
-known in about 15 families of plants
-non-photosynthetic and dependent on their symbiotic fungi
-root system is reduced and replaced physiologically by fungal hyphae, which penetrate surrounding organic material and break it down into simpler compounds
-probably endomycorrhizal

3. Specializations involving bacteria
a) Root nodules of legumes (**M**, Fig. 13.22)
-root hairs penetrated by *Rhizobium*, soil-inhabiting, nitrogen-fixing gram-negative rodlike bacteria
-root hair tips invaginate and form a tube, which extends into the cortex, then branches (DIAGRAM)
-bacteria within tube form an "infection thread" and penetrate certain cortical cells, causing them to divide
-cortical cells divide and resulting cells enlarge until a prominent nodule can be seen (a nodular meristem usually forms)
-this involves some stimulation of the vascular tissues to surround the infected area (need to bring nutrients and carry away nitrates)
-invaded cells are stuffed with bacteria, yet remain alive for a time
-nuclei of infected cells become much larger and polyploid
-host cells and bacteria fix nitrogen although neither can do so alone

4. Parasitism (presence of haustorial roots—DIAGRAM)
    -threadlike cells (searching hyphae) grow between or through host cells until xylem or phloem is reached
    -searching hyphae differentiate into xylem or phloem cells and remove host plant's water, minerals and photosynthates
    -e.g., dodder
    -obtaining the photosynthates against a gradient and without disturbing the STM is difficult

   a) Hemiparasites
      -green plants with some roots that invade roots of neighboring plants to tap phloem
      -only partly parasitic
      -35 families of angiosperms and 1 gymnosperm

   b) Holoparasites
      -mostly non-photosynthetic plants entirely dependent on xylem and phloem of host plant
      -may never have a connection with the soil