March 12 – Secondary growth/secondary tissues

Before we explored the mechanics and structure of 2° growth, we pondered the evolutionary advantages vs. disadvantages for plants when it comes to being herbaceous and short lived vs. woody and (potentially) long-lived. Remember, everything in biology is best understood in the evolutionary context of survival and reproduction!! (Get those genes to the next generation…!!)

Perennial plant: a plant that lives for multiple years. Most perennials are **woody**.

Annual plant: a plant that germinates from seed, reproduces sexually, and then dies in a single year (growing season). Annuals are **herbaceous** (lack wood).

Biennial plant: A plant that requires two years (growth seasons) to germinate from seed, reproduce sexually, and then die. Biennials often have bulb or corm as the overwintering structure. We did not discuss biennials in today's lecture, but we discussed bulbs and corms during our lab on stems.

Herbaceous and annual:
Advantages: reproduce quickly without making a large investment in parent plant – no huge loss if a single plant is eaten, dies due to disease, etc.
Disadvantages: seeds must successfully find open space and germinate every year (or every few years)

Woody and perennial:
Advantage: Large and occupy space from year to year, grow tall and shade competitors, deeper roots for water, produce many offspring over many years.
Disadvantages: every year must "defeat death" (!) herbivory, disease, wind, etc. Large investments of energy into non-reproductive tissues

Secondary growth: growth in woody plants that results from activity (cell divisions) of lateral meristems. 2° growth causes thickening of stems or roots. 2° tissues are wood and bark. There are two lateral meristems: **vascular cambium** and **cork cambium**.

Vascular cambium: The meristem that produces 2° vascular tissues: 2° xylem (wood) and 2° phloem (inner bark)

Wood: 2° xylem (produced by the vascular cambium)

Consider a stem cross section in which 1° tissues are present (see Figure 1). Between the 1° xylem and 1° phloem in the vascular bundles, and continuing between them, a band of cells exists – this is the young vascular cambium. Cells of the vascular cambium divide and give rise to 2° xylem (wood) and 2° phloem. 2° xylem is deposited to the inside of the V.C., whereas 2° phloem is deposited to the outside of the V.C. The result is a thickening of the stem in which the oldest xylem (the 1° xylem) is interior to the new xylem, and the oldest phloem (1° phloem) is the outermost phloem and is outside the 2° phloem (see Figure 2).

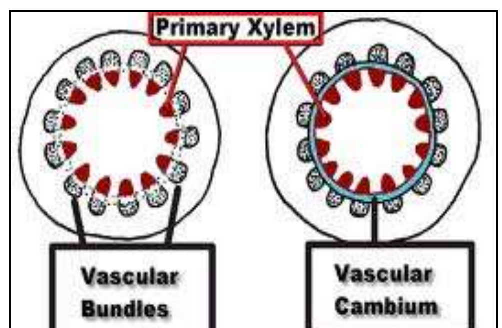

Figure 1

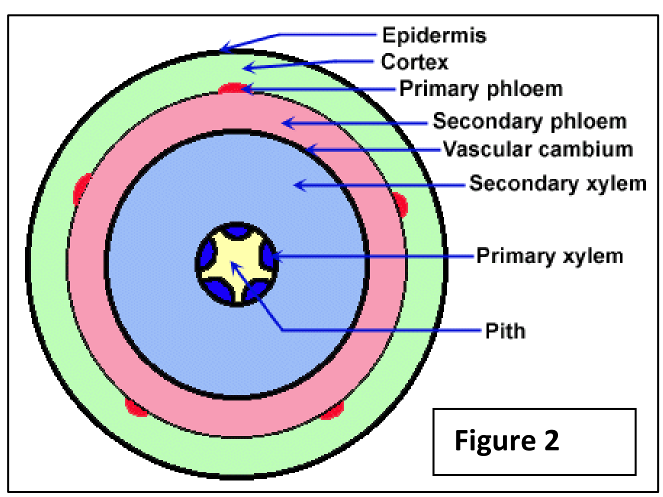

Figure 2

Wood produced by the vascular cambium contains some or all of the following cells, and their ratio varies greatly by species and growing conditions:

- **Tracheids**
- **Vessel elements**
- **Fibers**
- **Parenchyma cells**
- **Ray cells**

Rays: conduct fluids radially (from inside to outside, and vice-versa) across the 2° xylem and phloem.

Hardwood: A term applied to dicot flowering trees/shrubs and their wood. The wood of many dicot trees/shrubs is hard because of the high density of fibers. Hardwoods may have vessels, but softwoods have only tracheids.

Softwood: A term applied to conifers (e.g., cone-bearing and non-flowering trees such as pines, firs, spruce, etc) and their wood. They are relatively "soft" because the wood has few fibers (unlike many hardwoods). Conifers contain no vessels – all water transport in xylem is via tracheids.

Wood that is formed early in a growth season (i.e., in the spring) typically contains lots of vessel elements (and the vessels they form) or large-diameter tracheids and this wood is therefore relatively light in color, it is called early wood (spring wood). This wood has lots of water-conducting cells in order to deliver H_2O to newly emerging leaves that require lots of water to form, and which lose lots of water through transpiration because their epidermal layers and cuticles may be incompletely formed. Wood that is formed later in the season has a relatively lower proportion of vessels elements and tracheids, but a higher proportion of fibers. These fibers are added to reinforce the trunk. This late-season wood is darker in color due to the high density of fibers, it is called late wood (summer wood).

Early wood (aka spring wood): 2° xylem (wood) formed early in the growth season, typically contains a high proportion of vessels or larger diameter tracheids, and a lower proportion of vessels, and thus appears lighter in color than late wood

Late wood (aka summer wood): 2° xylem (wood) formed later in the growth season, typically contains a low proportion of vessels or larger diameter tracheids, but a higher proportion of fibers, and thus appears darker in color than early wood

A single year's growth of early wood and late wood form an easily recognizable ring, and over many years of growth these rings are easily identifiable in areas with strongly seasonal weather. These rings are the basis for ageing trees and dendrochronology ("counting tree rings").

Annual ring (aka tree ring, growth ring): 2° xylem (wood) produced in one year and which contains a clear ring of annual growth formed by early wood and late wood.

Heartwood: The darkly-colored, innermost (relative to sapwood), aromatic, and typically chemically defended 2° xylem (wood) towards the interior of a tree; these cells are filled with material and thus no water conduction occurs through these cells. May contain tannins (we'll discuss tannins in the secondary metabolite lecture) and other compounds that resist decay by bacteria/fungi.

Sapwood: 2° xylem (wood) that is outermost xylem of a trunk or branch – these xylem cells are hollow and conduct water & nutrients – it is light in color.

> Although flowering trees/shrubs are referred to as "hardwoods", and conifers are referred to as "softwoods", the actual "hardness" of the wood in both groups is highly variable. Many "hardwoods" have wood that is actually quite soft (e.g., balsa wood). Similarly, many softwoods have wood that is relatively hard (e.g. bald cypress). In general however, most hardwoods (dicot flowering trees/shrubs) have wood that is harder than softwoods (conifers). For this reason, the density of hardwood is preferred for many woodworking applications, and in general hardwoods are a superior firewood (for this reason oak firewood is much more expensive that pine or fir).

As the vascular cambium produces 2° xylem (wood) and 2° phloem, these expanding tissues cause a stem and/or trunk to increase in diameter most quickly at its outer diameter. In order to help the outer diameter of the tree keep pace with inner diameters, and to help provide additional protection for the considerable investment that the tree has made in its secondary tissues, trees produce protective coating of outer bark. The meristem that produces bark is the cork cambium. Ultimately, the epidermis and cortex are so reduced that they may become practically and functionally absent/insignificant.

Cork cambium (aka 'phellogen', but no need to know)**:** A meristem that produces the cork cells of bark
Bark: 2° phloem and cork

- **Inner bark**: All tissues between the cork cambium and the vascular cambium; mostly 2° phloem (note that 2° phloem is produced by the *vascular cambium*!). Inner bark is where phloem is found.
- **Outer bark**: All tissues outside the cork cambium; mostly cork cells. Outer bark protects trees against the environment (cold, heat, insects, fungi, etc…)

Cork cell: A cell of the outer bark that has walls encrusted with suberin; cork prevents water loss and entry of bacteria, fungi, insects, and other pathogens

Periderm: *Cork cambium and cork cells (also includes the phelloderm, which is produced in a few species as 1-2 layers of cells just inside the cork cambium). (You don't need to know the term periderm)*

Outer bark is a protective layer that can resist herbivory, heat stress, and even fire. Many large trees in fire-prone areas have thick bark. In California, prime examples include redwoods, including both the coast redwood (*Sequoia sempervirens*) and giant redwoods (*Sequoiadendron giganteum*), as well as oaks such as the coast live oak (*Quercus agrifolia*).

The bark of some trees is commercially important. Examples we discussed included:

- Cork oak (*Quercus suber*): outer bark can be removed without killing the tree, and the outer bark is regenerated in less than a decade in ideal growing locations.
- Cinnamon (*Cinnamomum* spp., especially *Cinnamomum verum*). There are two general types of cinnamon – Ceylon and cassia, but we skip that here. Cinnamon is native to SE Asia and India. Cinnamon as we know it is the inner bark of cinnamon trees. The bark is harvested in the

following manner: 4-6 year-old trees are cut down to stump level, and this causes many new shoots to emerge from the stump. This process is known as **coppicing**. 1-4 years after the shoots emerge from the stump, they are harvested and the outer bark is removed. The inner bark is then peeled off with a knife, and the long strips curl (as they dry) into the characteristic "cinnamon stick" shape with which we are so familiar.

Girdling: removal of a strip of inner and outer bark (consisting of cork, cork cambium, 2° phloem, vascular cambium and ….sometimes going into the xylem) from around the circumference of a tree trunk or branch.

Girdling is an effective way to kill trees because it cuts of sugar transport via the phloem, and if the girdling is deep enough, it cuts off water transport through the xylem. An injury or cut that results in girdling need not cut deeply into tree tissue – because the phloem is a thin layer directly underneath the outer bark. Girdling is an efficient strategy for killing trees in situations such as thinning forests or other places where felling the trees is not desirable. Girdling can also happen quite by accident, and it can be a very injurious result of improperly staking a tree or otherwise injuring the bark.

We discussed sapsuckers – a group of birds that resemble woodpeckers but have a much different feeding ecology. Many woodpeckers collect acorns and drill strorage galleries deep into the 2° tissues (phloem and xylem) of trees. Sapsuckers drill small holes into the phloem of tress, and the sap that leaks out attracts insects that are then eaten by the sapsuckers – genius!! Although the drill holes of sapsuckers can be quite dense – they seldom result in death by girdling (though they must certainly result in infection due to bacteria and fungi). Why do you suppose sapsuckers have "learned" through evolution not to girdle trees when they drill their sap holes?

IF WE DID NOT COMPLETE OUR DISCUSSION OF DENDROCHRONOLOGY AND ESTABISHMENT GROWTH IN LECTURE, THEN WE COVERED THIS MATERIAL IN LAB DURING WEEK 8

Dendrochronology: scientific method of dating based on the analysis of patterns of tree rings (annual rings, growth rings). Dendrochronolgy is useful for many scientific investigations:

1) Botanical – age the trees/plants themselves
2) Climate science – reconstruct past climate and weather patterns based upon growth patterns
2) Fire Ecology – reconstruct fire frequency in forests
3) Archaeological – estimate dates of construction of human dwellings where wood is used
4) C14 dating – used to calibrate, or "ground-truth" C14 dating methods. C14 is in turn used to date materials up to ~70,000 years old. *(no need to know how C14 dating works)*

Here in California, we have the oldest living tree species on Earth, the **Bristlecone pines (*Pinus longaeva*)**. These exist in dry, cold, high elevation habitats in the White Mountains of eastern California. Remember that one of the disadvantages to getting big and attempting to live a long time is that a plant must continually defend itself against attack from disease (bacteria and fungi) and herbivory. The bristlecone pines avoid these threats in part by living in an habitat that is too dry and cold for many insects, fungi and bacteria – and if those organisms are present they themselves grow and function very slowly due to the cold temperatures.

Thus, bristlecones live to very old ages – many have been dated using **dendrochronology** at well over 4,000 years old! The oldest specimen measured (and published) to date is 5062 (Tom Harlan in 2012). Other notable specimens are the *Methuselah* tree (~4862 years old) in the White Mountains of CA (~) and *Prometheus* (~4862 years old) of the Great Basin National Park in Nevada. The oldest known trees these days are not labeled in the field due to fears of vandalism.

Dendrochonolgy researchers have combined overlapping growth rings in bristlecones trees in three different stages: 1) live trees, 2) dead but standing ("snags"), and 3) dead and on the ground bristlecones. By overlapping these trees of different ages, researchers have established a dendrochronological record that stretches back nearly 10,000 years!

Establishment growth: 1° growth in palms by which adventitious roots are established around the base of the stem and increase stem width. **Palms are monocots** (yes they are flowering plants!) and monocots do not have true 2° growth (they lack a vascular cambium).

Vocabulary and concepts to ***ignore*** *while reading Chapter 8 in Mauseth or otherwise studying this material:*
Fascicular vs interfascicular cambium ; Fusiform initials vs ray initials ; Perclinal vs anticlinal walls/divisions
Storied vs nonstoried cambium; Upright vs procumbent ray cells