

Topic #3: Angiosperm Anatomy and Selected Aspects of Physiology

REQUIREMENTS: Powerpoint Presentations.

Objectives

1. How do parenchyma cells, collenchyma cells, and sclerenchyma cells differ? (Thickness and chemical properties of cell wall? Cell function? Living at maturity? Location?)
2. What are tracheary elements? In which group of plants are vessel elements found? Which of the two types of tracheary elements is most primitive? How are tracheids distinguished from vessel elements? Distinguish bulk movement of water from diffusive movement of water. Do living plant cells have internal positive pressure? Can liquid water be under negative pressure? . . . gaseous water? Explain the cohesion theory of sap ascent. Which tracheary element is more specialized for transport? . . . for support?
3. What is auxin? Name some plant developmental processes that it affects. Where is auxin made? Describe the potential mechanisms for auxin action in cell expansion.
4. What are sieve-tube elements? What is their function? Describe their relationships with companion cells. Describe the structure of a sieve-tube element. Explain in detail the mass flow mechanism for phloem transport. Define apoplast, symplast.
5. Draw a cross-section of a typical dicot leaf. Label the different cell types. Where is the phloem, xylem?
6. What are stomata? Describe the mechanism of opening and closing. What is ABA? How does it function mechanistically? Describe several physiological processes in which it is involved.
7. How do dicots and monocots differ in overall root morphology? (What is a taproot, fibrous root system?)
8. What is (are) the function(s) of a root cap? Where is it? Do stems have an analogous tissue?
9. Draw a longitudinal section of a dicot root. Label the root cap, apical meristem, epidermis, cortex, endodermis. Where is the vascular tissue?

10. What is the function of the endodermis? Show how this function is made possible by the presence of Casparian strips. What is root pressure? How can it be generated?
11. Contrast lateral-root origin and development to those of a lateral shoot.
12. Draw a cross-section of a root vascular cylinder. Label xylem, phloem, pericycle, endodermis.
13. Contrast the vascular bundle arrangement in a dicot stem to that in a monocot stem.
14. Make a list of differences between primary dicot roots and primary dicot shoots. (Hints: covering of meristem? . . . presence of collenchyma? . . . nodes? . . . vascular arrangement? . . . origin of lateral appendages?)
15. Distinguish between primary growth and secondary growth. Describe the transition from primary to secondary growth in a dicot root, shoot.
16. What are mycorrhizae? Name the types. Which organisms are involved? How do these associations promote plant growth? Discuss the host specificity relative to that of pathogenic fungi.
17. Distinguish between monocots and dicots on the basis of the following characteristics: (a) number of cotyledons, (b) function of cotyledon, (c) endosperm persistence, (d) number of flower parts, (e) root system, (f) presence of secondary growth, (g) arrangement of vascular bundles in stem, (h) leaf venation pattern.

Lecture

Today, we will begin coverage of the internal structure of angiosperms. We will do so by surveying three levels of organization. First, I will provide an overview of the three major classes of plant cells; second, we will see how these cells are organized into tissues, and third, the arrangement of tissues into organs and ultimately the whole plant will be presented.

POWERPOINT SLIDE: Anatomy Preview.

POWERPOINT SLIDES: Series of slides on organization of the plant body.

POWERPOINT SLIDES: Root and shoot apical meristems (photomicrographs and illustration).

Three Major Generalized Plant-cell Types.¹

Parenchyma

(A) Parenchyma is made up of common undifferentiated cells; it is the main “ground” tissue system. Specialized tasks depend on location (e.g., parenchyma in stem may serve a storage function, as in the common “Irish” potato, whereas parenchyma in a leaf is usually specialized for photosynthesis).

(B) Commonly, parenchyma cell walls are thin and can be primary or secondary, terms that will be explained later. They may contain hydrophobic (“water fearing”) material.

(C) Parenchyma is living at maturity and has a complete complement of organelles. (As we move through the slides, we will see many examples of parenchyma.)

(D) Adjacent parenchyma cells, like virtually all other types of living plant cells, are connected by plasmodesmata. At its simplest, a plasmodesma is a membrane-bound tube that joins adjacent cells and permits movement of certain substances between cells without crossing a membrane.

POWERPOINT SLIDES: The plant cell in outline—primary wall, secondary wall, plasmodesmata, , concept of the symplast and apoplast.

Collenchyma (“coll-” means “glue”; the name comes from the appearance of the cell wall)

(A) Collenchyma is closely related to parenchyma but is commonly elongated (whereas parenchyma is more or less isodiametric). Intermediates exist between these two extremes.

(B) Collenchyma has a support function and thick cell walls (i.e., the chief difference between collenchyma and parenchyma is wall thickness). Importantly, collenchyma cell walls are unevenly thickened and contain no lignin (lignin is “water repellent”); thus, collenchyma cell walls are “rich” in water.

(C) Cell walls of collenchyma are primary only (for reasons not discussed here, this is a restatement of the fact that they contain no lignin).

(D) Collenchyma cells are complete and, like parenchyma, are capable of resuming meristematic activity.

(E) The peripheral location of collenchyma is highly characteristic. It is found adjacent to or just a few cell layers from the epidermis. Collenchyma is rarely found in roots.

¹In turn, I will discuss parenchyma cells, collenchyma cells, and sclerenchyma cells. It is also correct to refer to parenchyma tissue, collenchyma tissue, and sclerenchyma tissue when a pure assemblage of a respective cell type functions as a unit.

POWERPOINT SLIDE: “Strings” of celery petiole, a rich source of collenchyma (north Leon County).

POWERPOINT SLIDE: Collenchyma—location, irregular wall thickening (Fig. 5.5 of Esau).

Note (A) the unevenly thickened cell walls of collenchyma, (B) its location near the epidermis, and (C) that it commonly occurs in bundles (as here and in the “strings” of celery) but does not necessarily do so.

Sclerenchyma (“scler-” means “hard”)

(A) Sclerenchyma refers to either fibers (very long and often associated with vascular tissue) or sclereids (shorter and located throughout the plant body).

(B) Sclerenchyma has primary and very thick secondary walls.

(C) Sclerenchyma walls are often lignified.

(D) Sclerenchyma lends hardness and rigidity, whereas collenchyma is flexible and provides support for growing areas,

(E) Sclerenchyma may or may not be living at maturity. Even living sclerenchyma is incapable of dedifferentiating (by, e.g., removing wall thickness as collenchyma can do).

(F) Sclerenchyma fibers are important commercially, each individual cell being up to 250 μ m in length. They are used for rope, textiles, and paper.

POWERPOINT SLIDE: Microscopic view of phloem fibers of *Linum*.

Note that the walls are evenly thickened.

POWERPOINT SLIDE: Phloem fibers of *Linum*² (flax, used to make linen, “Old Salem,” North Carolina).

(G) Common examples of sclereids are the “grit” in pears, shells of nuts, stones of stone fruits.

²Linen was the first textile made by man, and artifacts from Switzerland date to 8,000 B.C.E. The versatility of this fiber lends itself to a range of products, from delicate laces to strong sailcloth and conveyor belts. As further examples, the fibers have been used to make fabric for wrapping mummies, for making Greek togas, and for making Phoenician armor (as a lighter substitute for chainmail). Flax seeds are also important, as they yield linseed oil, which has some direct applications (to protect wooden handles such as gunstocks) and serves as a feedstock for manufacture of other products such as linoleum, varnish, and soap. The residue from pressing the seeds is a high-protein cattle feed. This important plant, as expected, has left prints in our culture (white linen is a symbol of purity) and language (linen, distaff (“pertaining to women”), the mildly pejorative word spinster, and the color flaxen). For a quick overview, see T. A. Keegan (1996) “Flaxen fantasy: the history of linen.” *Colonial Homes*, August.

POWERPOINT SLIDE: Selection of fruit of Asian pear³ (also called pear-apple) (north Leon County, Florida).

POWERPOINT SLIDE: Cross-section of black walnut. (Nashville, Georgia).

Vascular tissues—the context

POWERPOINT SLIDE: . . . more on organization of the plant body, including stylized cross-section of dicot shoot, primary growth.

POWERPOINT SLIDE: Cross-section of the dicot shoot (primary growth) with focus on vascular bundles.

POWERPOINT SLIDE: Cross-section of the monocot shoot with a focus on vascular bundles.

Tracheary Elements

(A) Tracheary elements are the chief water-conducting elements and also provide support. Tracheary elements and other cells, parenchyma or sclerenchyma, make up a tissue system, the xylem⁴. As you will see elsewhere, wood results from secondary growth and is xylem.

(B) Tracheary elements have highly thickened and irregular walls, lignified.

(C) At maturity, tracheary elements are always dead, as indicated in this slide.

POWERPOINT SLIDES: Model of programmed cell death, explanation of positive hydrostatic pressure of symplast and negative hydrostatic pressure of apoplast (transpiring conditions).

POWERPOINT SLIDES: Models of symplastic and apoplastic movement of water and solutes, including membrane transport for movement from apoplast to symplast.

(D) Two types of tracheary elements exist:

(1) Tracheids are found in gymnosperms and angiosperms. Their end walls are **not** perforated.

(2) Vessel elements are the major water-conducting cells of angiosperms; for our purposes up to this point, we may say that vessels are not found in gymnosperms. Their end walls are perforated.

³ The Asian pear is harvested when it is fully ripe; it has a crunchy, succulent texture, and at its best, is quite good. The common pear is picked when it is mature (the lenticels darken and are surrounded by a halo of chlorophyll) and it is then ripened off the tree; the common pear is melting in texture and can be excellent. Not unlike many other fruits, pears cover a gamut of quality, from insipid, mushy, hard to wonderful.

POWERPOINT SLIDES: Tracheary elements, distinction of tracheids and vessel elements.

The vessel elements are stacked up end to end to form a pipe⁵ (panel A, the rims delineate each original cell; panel B, the arrow points to the boundary between two elements).

POWERPOINT SLIDES: Cohesion theory: concepts of negative pressure, driving forces, water potential.

Water transport from the roots to the aerial transpiring organs, such as leaves, is explained by the cohesion theory of sap ascent.^{6,7} (This theory is the only that provides a universal explanation of sap

⁴“xylos” (Greek), meaning wood, is seen in other English words such as xylophone.

⁵ We teach that these pipes are open and free for transport, but as Malpighi described in 1675 (see *Journal of Agricultural Research* 1: 445 (1914)), adjacent parenchyma cells may grow through the walls of the tracheary elements and partially occlude them. These ingrowths are called tyloses (Greek, “sacks”) or Füllzellen (German, “filling cells”).

⁶ Stephen Hales (b. 1677 in Bekesbourne in Kent) is regarded as the “Father of Plant Physiology.” He wrote: “Since we are assured that the all-wise Creator has observed the most exact proportions, *of number, weight and measure*, in the make of all things; the most likely way therefore, to get any insight into the nature of those parts of the creation, which come within our observation, must in all reason be to number, weigh and measure.” He, therefore, studied the ascent of sap in plants (and of fluid flow in animals, but who cares?). Although Hales did not know that water moved in the xylem, he did prove the existence of root pressure (discussed in the text later) and he quantified transport. A person of good sense, Hales worked with fruit trees (apple, lemon—certainly a novelty in Europe at that time—and banana (“*Musa Arbor*, or *Plantain-tree* of the *West-Indies*”).

Many of his contributions were published in his book *Vegetable Staticks*, which still is interesting reading. As perspective, even in the post-Newton age, algebraic signs were relatively new, requiring Hales to explain: “Whereas some complain that they do not understand the signification of those short signs or characters, which are here made use of in many of the calculations, and which are usual in Algebra; this mark + signifies more, or to be added to. Thus page 18, line 4, 6 ounces + 240 grains, is as much as to say, 6 ounces more by, or to be added to 240 grains. And in line 16, of the same page, this mark x or cross signifies multiplied by; the two short parallel lines signify equal to; thus $1820 \times 4 = 7280:1$, is as much as to say, 1820 multiplied by 4 equal to 7280 is to 1.” All this is not silly—the basic route to understanding anything is to quantify it; relationships hitherto unseen may flash before your eyes. (You need look no further than the work of the botanist Greg Mendel, who could not have intuited segregation and independent assortment of traits without quantifying them.)

An interesting aside: Hales not only made his mark in the new field of plant physiology but was also active in politics. He was one of the 20 charter members of the philanthropic company that sent Oglethorpe to found the colony of Georgia in 1732. In one fell swoop, when Oglethorpe negotiated the purchase of some land from Tomichichi on the Yamacraw Bluff, the displacement of Native Americans from Georgia (which then extended westward to the Mississippi) began in earnest, and the older colonies were buffered from the Spanish to the south. The situation did not stabilize for more than 100 years, longer to the south (1850s in Florida) and west (1870-1880s).

⁷As the late Martin Zimmerman (*Xylem Structure and the Ascent of Sap*, 1983, Springer-Verlag, Berlin) tells us, Hales was not the first person of note who was interested in sap flow in plants. Leonardo da Vinci drew several sketches of tree architecture, and he showed that the trunk cross-sectional area was equal to the sum of the cross-sectional areas of the branches at any of several levels in the canopy. da Vinci’s observations are generally true. This was a remarkable insight, because, at the time of da Vinci, basic physical phenomena like the trajectory that a cannonball takes were unknown, although the practical uses of the cannonball were raised to a fine art. It appears that da Vinci could have made at least a middling plant scientist, but regrettably, he dithered away his time at painting and such like.

ascent, one that is sufficient to explain this process in tall plants. At another time, I will discuss an auxiliary mechanism operative in some plants at some times. Although the cohesion theory has come under attack periodically,⁸ supporters rally and provide counterbalancing evidence.) An understanding of sap ascent will come more easily if you first reflect on how a plant is constructed. Individual cells, with few exceptions (e.g., mature guard cells) do not exist in isolation. Recall that cell connections, the plasmodesmata, exist. Thus, cell 1 is connected to cell 2, cell 2 to cell 3, and so forth. The space delimited by the plasma membrane is, thus, continuous from one end of a plant to the other (or at least certain domains comprise connected cells). The membrane-bound space is called the symplast; cell walls, air spaces, the lumina of dead cells (like mature tracheary elements) comprise the apoplast⁹. Thus, a potential transport path (which will not be discussed in my rendition of this course) from any one area of the plant to another is via the intercellular connections. Except as qualified later, the apoplast is also continuous from one area of the plant to another. Thus the walls and lumina of tracheary elements in the root (ultimately, the ordinary source of water) and the leaf (ultimately, the ordinary site of water loss from the plant) are continuously connected. Under most conditions, the air around a plant is not saturated with water vapor. Even if the air is 90% saturated (i.e., at 90% RH), it is exceedingly “dry” compared with a leaf. The relatively low water content of the air provides for a strong driving force (“tendency”) for net diffusive movement of water from the leaf to the atmosphere. This loss of water vapor (primarily through stomata, as discussed later) drives the whole process of sap ascent: the loss of water from the leaf creates a deficiency there. Actually, the whole column of water in the tracheary elements is under *negative* pressure (tension, modern sense.¹⁰) Were it not for the extreme cohesive force of water, the column would break. (When you have tried to separate two microscope slides stuck together, you were observing the cohesiveness of the thin water layer that held them together.) Were it not for the strong walls of the tracheary elements, they would collapse. In a transpiring plant, the water pressure in the tracheary elements of leaves is more negative than that in the tracheary elements of roots. This pressure difference causes the bulk flow of water from the root to

⁸Arguments are briefly summarized in the October 2001 issue of *Trends in Plant Science*.

⁹The definition of apoplast that I have given is correct as used by anatomists, but originally apoplast meant only the cell walls and water spaces outside the membrane. Sometimes, the word apoplasm is used to refer to the aqueous space. Unfortunately, these words have been used without precision so often that they are losing their scientific utility.

¹⁰ An interesting thing about language is that it changes. The archaic meaning of tension is *positive* pressure. Thus, hypertension means abnormally high arterial blood pressure. My favorite example is egregious; this word is derived from *e*, meaning “out of,” and *greg*, meaning “herd.” (*Greg* is the root for many words such as segregate, congregate.) One old dictionary indicates that the meaning is literally “towering above the flock.” The definitions were: 1. Prominent, projecting. 2. Of persons and personal qualities: Distinguished, eminent, excellent, renowned. or Of things: remarkably good or great. Of events and utterances: striking, significant. As late as 1855, we see “When he wanted to draw some one splendid and egregious, it was Clive he took for a model.” Now, of course, egregious still means “out of the herd,” but it means outstandingly bad, flagrant.

the leaf. The water-transporting cells (i.e., the tracheary elements) are dead and devoid of internal structure.

Both types of tracheary elements, of course, serve to transport water and provide support, but their relative efficacy differs. Whereas vessels are more efficient at water transport, the water column in them is much more easily broken.

POWERPOINT SLIDES: Bulk flow vs. diffusion; application of the flux equation.

POWERPOINT SLIDES: Review of basic osmometer; application to plant cells: osmotic generated pressure.

POWERPOINT SLIDES: Explanation of negative pressure in walls.

POWERPOINT SLIDES: The Cohesion Theory¹¹.

Sieve-tube elements and Companion Cells, and some comments on auxin

The bark of a tree is of a tree is obviously important, as this slide indicates:

POWERPOINT SLIDE: Girdled loblolly pine tree (*Pinus taeda*), dying (north Leon County, Florida). This photograph was taken about 3 years after girdling, and isolated roots in the soil may live much longer.

Food moves from its primary site of synthesis, the leaves, to the roots via the phloem, which is located in the bark of woody plants. (We will study particularly the location of phloem in other plants and so will defer that discussion at the present.) When the root is deprived of a source of carbohydrate, its respiratory functions halt, and the roots are no longer able to acquire nutrients and water. The tree therefore dies.

In this introductory course, our focus will be on the translocation of sugars via the phloem from sources (usually leaves) to sinks (such as roots or developing fruits). Horticulturists have long known, however, that other substances, such as a potent growth inhibitor of latent buds, also move in the bark. This inhibitor is made in the very tips of shoots and in leaves and moves downward. (As alluded to briefly later, auxin is also made in other locations in the plant, such as seeds, where it sustains fruit development.) As the following slide shows, interruption of the bark

¹¹ Of course, it is important to keep in mind the vast amount of water used in agriculture. (About 85% of consumed water is by agriculture.) Obviously, water is limiting in many agricultural ecosystems as well as natural ones. For a 2004 overview of “Water-saving Agriculture,” see *J. Exptl. Bot.* 55 (407) (a one-topic Special Issue)

POWERPOINT SLIDE: Strategically “scored” central leader of Mutsu (Crispen)¹² apple tree (*Malus domestica*) (north Leon County, Florida). Note that buds have grown where the bark above was cut away, but buds with intact bark above them did not grow and remained latent.

cuts off the supply of the inhibitor to the bud, and it grows. As a second example, observe that, in the following slide, the rootstock has put out a new bud. Generally, rootstock budding indicates that the scion has not knitted well with the rootstock¹³ and that the “abundant” and continuous supply of the plant growth regulator from the apex, the forming leaves, and mature leaves has been interrupted. Somewhat counterintuitive in the context of the previous discussion, the plant growth regulator is auxin,¹⁴ the most abundant natural form of which is indole acetic acid. (Your text is wrong on this point.)

(As a matter of completeness, auxin moves not only in the phloem, where it is passively swept along, but also from parenchyma cell to parenchyma cell in the vascular bundles at a much greater rate than diffusion alone would allow. Consensus is lacking on the relative importance of these two pathways. This cell-to-cell movement is in a polar fashion, in our example case, in the same direction as phloem transport, but further discussion is beyond the scope of this course. The second caveat, also along the line that things are often more complicated than they first seem, is that other growth regulators (cytokinin or unknown?) might also be involved in the maintenance of lateral-bud dormancy.)

POWERPOINT SLIDE: Ichang Lemon¹⁵ (*Citrus ichangensis*) budded onto ordinary trifoliolate orange (*Poncirus trifoliata*) (north Leon County, Florida). Note that cutting off the top of the plant removed the source of auxin that suppressed lateral bud growth.

¹²Robert A. Nitschke (Southmeadow Fruit Gardens, Birmingham, MI) described this cultivar, thus, in 1976: “In 1928 the breeding of varieties (of apples) was commenced in Japan at the Aomori Apple Experiment Station. Out of some 5,000 seedlings, 14 were named in 1948–1949 of which one, Mutsu (named after the Bay of that name at the northern tip of Honshu), has found recognition in many countries as a superior new apple variety. Mutsu is a cross of Yellow Delicious and Indo. It is very large, round in shape, colors pure yellow here at Southmeadow and has yellowish white, slightly coarse, but crisp, juicy flesh of a distinctive delicate spicy flavor—faintly anise-like, of completely first rank dessert quality. In addition it does not shrivel in storage, keeps exceedingly well, is highly resistant to spray and frost injury and produces uniformly beautiful unblemished fruits. Ripe middle to late October.” “Mutsu” does not have a pleasing sound to English ears, so it was imported into England as Crispin (or Crispin) and goes by this name in the supermarkets in Tallahassee. Unfortunately, as far as I can tell, this cultivar will not produce in Tallahassee. I have eliminated the tree in the photo, as I did in another experimental planting of a Mutsu a few years back. I will not try it again.

¹³Again, this is only a general rule. Some rootstocks, e.g., apple M7, are notoriously bad about forming root sprouts and have to be trimmed back each year to prevent overgrowth of the scion.

¹⁴“auxein” (Greek) meaning, “to increase” or grow.

¹⁵ In my opinion, the Ichang lemon is one of the finest of the cold-hardy citrus. It can withstand the mid teens easily (F scale) and provides a nice lemon-like juice earlier and an acceptable dessert fruit later, if a sweetener is added and if one doesn’t object to seeds.

POWERPOINT SLIDE: Satsuma (*Citrus unshui*) cv Silverhill budded onto trifoliolate orange (*Poncirus trifoliata*) cv. Flying Dragon.¹⁶ (north Leon County, Florida). Note that the rootstock (three-leaved) has budded out at the bottom.

Auxin plays many different roles in growth. The effect depends on the target tissue, on the auxin concentration, and on the concentration of other plant growth regulators.¹⁷ As an example, one concentration of auxin will cause stem elongation (a primary auxin effect), and a higher concentration will inhibit elongation. Other auxin-promoted effects are the production of adventitious roots,¹⁸ and fruit development. As a rule,¹⁹ a seed will not develop without a viable embryo, and fruit will not develop without a certain number of seeds—the source of auxin.

Like many potent developmental regulators, auxin appears to have several modes of action. As an example, cell expansion is stimulated by auxin. Cell expansion requires that cells release a so-called wall-loosening factor, which has been identified as protons. In one model, auxin enhances the transcription of a rapidly turning-over proton-extruding ATPase, which is delivered to the plasma membrane via the endomembrane system. Independently, a different stimulator of proton release (fusaric acid, the fungal toxin) or even auxin itself may act more or less directly to activate the H⁺-ATPase already in the membrane. Further discussion of the ubiquity and importance of the H⁺-ATPase will be found in our discussion of stomatal physiology and phloem transport, which we return to now.

(A) Sieve-tube elements are elongated cells specialized for conduction of food and other material. Sieve-tube elements and associated companion cells, along with parenchyma and

¹⁶Flying Dragon is finding service here as a rootstock, but it is grown also as an ornamental in its own right. Description from Oregon Exotics Rare Fruit Nursery: “A wildly mutated form of the Trifoliolate Orange. Contorted branches and thorns twisting at every inch. Cultured in China for many hundreds of years, this variety is very ornamental, especially when barren of leaves. Trees are dwarf in size and very hardy to about -15° below zero. They have a heavy bloom of fragrant white flowers and are followed by colorful yellow fruits that hang on into the Winter. The fruit yield (sic) small amounts of juice that may be used as a spicy lemon seasoning. After two weeks of refrigeration fruits yield higher juice content. The dried fruits are used in Chinese medicines. Trees prefer full sun and a well drained soil. They make a nice potted plant or bonsai.” Ignore the part about the juice being edible—it’d take the enamel off your teeth!

¹⁷Indeed, auxin will kill a plant. The synthetic auxins, 2,4-D and 2,4,5-T, preferentially kill dicots and were the active ingredients in Agent Orange, the controversial herbicide used in Vietnam. Unfortunately, during the synthesis of these auxins, dioxins are formed. Thus, the final herbicide product contains potent carcinogenic contaminants. As an aside, the U.S. efforts to destroy hiding areas and crops of the Viet Cong and the North Vietnamese troops destroyed 30% of Vietnam’s commercially important forests and the food supply for 600,000 people per year.

¹⁸The commercial rooting substance Rootone (a product of Amchem Products and sold nationwide) contains a mixture of four auxins and a fungicide.

¹⁹We all are, of course, familiar with exceptions. Some fruits, such as banana, seedless grapes, seedless citrus, and seedless cucumbers, develop without seed maturation.

schlerenchyma, make up a tissue system, the phloem²⁰. As implied in the above introduction to this topic, the inner layer of bark is phloem, but bark can be a very complex tissue, and an accurate description of it is outside the scope of this course.

POWERPOINT SLIDE: Sieve element, differentiation series (Fig. 11.5 of Esau) and structure.

(B) At maturity (right panel) one (sometimes two) companion cell (the more slender and darker cell) is associated with each sieve-tube element. The sieve-tube element and associated companion cell were derived from the same original mother cell. (As an aside, it is interesting to know that the food-conducting cells of gymnosperms function and look like those of angiosperms, but those of gymnosperms develop differently, so the same vocabulary is not used.)

(C) Along the path of transport (e.g., the petiole), the sieve-tube elements are much larger than the companion cells. Where transport originates (the source) and where transport terminates (the sink), the companion cell(s) is the larger.

(D) Transport is through the sieve-tube elements; companion cells serve for maintenance and for loading and unloading of transported substances into and out of sieve-tube elements.

(E) At maturity, the sieve-tube element lacks a tonoplast, a nucleus, the endomembrane system, and ribosomes. A few plastids and mitochondria remain. (As elsewhere in these notes, these descriptions are general.)

(F) Transport is by “mass flow”²¹ along the sieve tube—meaning that the pores of active sieve-tube elements are open. (A description of this process follows the slides.)

POWERPOINT SLIDE: Apoplastic phloem loading. (Symplastic phloem loading will be not discussed in this course.)

We will now examine “mass flow” through the sieve tubes from a source (usually a leaf) to a sink (e.g., a root). Sucrose (common table sugar) is the typical mobile transport species, and it is the terminal product of photosynthesis made in the same leaf cells that harvest light (i.e., chloroplast-containing cells). Depending on the species²² and the temporal physiological demands, sucrose may have several fates, and only one is outlined here: Recently photosynthesized sucrose is released from

²⁰“phloos” (Greek), meaning bark.

²¹ “Bulk flow,” “mass flow,” and “plug flow” are synonyms.

²² A gentle reminder that these notes are not comprehensive and cannot serve as a reference. This description applies to an “apoplastic phloem loader.” Many plants (particularly woody plants as well as some common herbaceous plants like cucumber) export photosynthate differently. Thus, one means of exporting photosynthate is described as a means of describing how it may occur, while introducing secondary active transport.

the cell into the cell wall (. . . or transported to adjacent cells symplastically, but still released into the apoplast before the companion-cell/sieve-tube-element (CC/STE) complex²³). As you have seen in the many slides, walls of adjacent cells are in contact. The cell-wall space is hydrated, so an external aqueous continuum extends from one cell to the next and so forth. Sucrose expelled from one leaf cell therefore diffuses externally to the next cell until it is in the cell wall of the companion cell, which is usually no more than a few cell diameters away from the producer cell. (Over these short distances, diffusion is an efficient transport mechanism, but it would be woefully inadequate as an explanation for long-distance transport such as that from a leaf to a root of even a modest-sized plant like maize.) The companion cells in a source are specialized for uptake of sucrose against a sucrose concentration difference. Plants (and fungi) have a H^+ -extruding ATPase embedded in the plasma membrane. (This pump and the associated secondary active-transport processes are analogous to the animal Na^+/K^+ ATPase that powers, e.g., glucose uptake via a Na^+ :glucose symporter.) Simply stated, the ATPase couples the energy of hydrolysis of ATP ($ATP \rightarrow ADP + Pi$) to the energetically uphill excretion of protons. (Excretion of protons is energetically uphill for two reasons: (a) protons have a positive electrical charge, and the cell interior is negative with respect to the exterior, and (b) the proton concentration outside the cell is 100–1000x higher than that inside the cell.) All plant cells, and especially companion cells, also have a protein transporter that allows the inward permeation of sucrose if (and only if) this transporter concomitantly transports a H^+ inward. For obvious reasons, the protein is referred to as a H^+ :sucrose cotransporter. Because H^+ and sucrose are transported in the same direction (here, inward), it is also called a symport. To recap: H^+ 's “want” to come into the cell more strongly than sucrose “resists” coming into the cell, so the inward cotransport of these species is energetically downhill. Of course, continual operation of the ATPase is required to maintain the membrane potential and proton-concentration asymmetry. The described mechanism causes the concentration of sucrose to become very high in the companion cell/sieve-tube element complex, which functions as one unit. The high inside concentration of sucrose lowers the chemical activity of water, and water therefore moves osmotically from the cell exterior to the interior (in the vernacular, high solute concentration “draws” water in). (Although it is beyond the scope of our coverage, most water permeates the plant membrane not by direct passage through the lipid bilayer per se; instead, there are water channels, or aquaporins, which may be regulated too.) Consider now that the stack of sieve-tube elements comprises the closed pipe-like sieve tube, many of which connect the source to the sink. As the water moves into the sieve tube in the source, high pressure there ensues. Concomitantly, sucrose release from sieve tubes in the sink causes osmotic water efflux, lowering the pressure. The key point is that the internal pressure in the sieve tube is higher in the source end than in the sink end.

²³Remember to treat these two cells as a functional unit.

This pressure differential causes bulk flow of water and the dissolved solutes from the source to the sink.

POWERPOINT SLIDES: H^+ -suc uptake by companion cells, stressing the thermodynamics and mechanisms.

POWERPOINT SLIDES: Mass Flow and anatomical limitations.

POWERPOINT SLIDES: Transport summary.

Angiosperm Organs and Tissues

As I pointed out in the first lecture on angiosperms, parts of the angiosperm body are specialized for (A) photosynthesis (usually the leaf), (B) support (stem, petiole, and trunk), and (C) anchorage (usually the root). Having discussed xylem and phloem transport (which occurs in all these organs), I will now focus on some specific and unique features of the various parts of the angiosperm body.

Root (anatomy, types)

POWERPOINT SLIDES: Dicot root cross-sections and stylized longitudinal section, orientation.

Note the pericycle, which lies just inside the endodermis. The pericycle gives rise to branch roots.²⁴ In contrast, the origin of lateral appendages on shoot is not deep within the shoot but is near the surface.

POWERPOINT SLIDES: Pericycle, as site of origin of lateral roots + adventitious roots (which don't arise from root and thus pericycle) of black mangrove trunk (*Avicennia germinans*) (the Everglades).²⁵

As you saw in the last topic, the first root develops from the apical meristem of the root (hypocotyl of embryo). In gymnosperms and dicots, this first root becomes the tap root, and it and its branch roots penetrate the soil rather deeply²⁶ or until O_2 becomes limiting, at the water table²⁷. In

²⁴The general truth is that roots arise from the pericycle, but you know of exceptions already. Adventitious roots must always arise from some tissue, usually of vascular or near-vascular origin, other than the pericycle (found only in roots). Commercial propagation of many plants is by development of adventitious roots from stem or leaf cuttings (ornamental example, African violets; row-crop example, sugar cane; root-stock example, MM 106 (or EMLA 106, its virus-free descendent); horticultural example, all rabbiteye and highbush blueberries.)

²⁵I wish to acknowledge with profound gratitude the excellent informative tour of the Everglades that was given to me by Dr. Tom Davenport (Tropical Research and Education Center, Homestead, Florida).

²⁶This is a general statement, of course, and there are examples of gymnosperms (spruce) and of dicots (beech) that do not produce deep tap roots.

contrast, the first root of a monocot usually dies rather soon, and the monocot root system consists of adventitious roots. (Literally, adventitious simply means arising from an unexpected location.) You have probably noticed adventitious roots that develop above ground on maize plants. Let us compare the outside appearances of two types of root systems.

POWERPOINT SLIDE: Fibrous roots and taproot (Fig. 22.2 of Raven, Evert, and Curtis).

POWERPOINT SLIDE: Adventitious roots emerging from the base of a small palm seedling, maybe *Butia capitata* (from the late Christine Outlaw's garden, south Georgia).

POWERPOINT SLIDE: Maggie points to adventitious roots on maize (north Leon County, Florida).

POWERPOINT SLIDE: Daikon radishes grown in water-logged soil (north Leon County, Florida).

POWERPOINT SLIDES: Primary vascular differentiation (Fig. 14.16 of Esau) of root plus other important attributes of roots.

This slide is a diagrammatic representation of a root tip. Note the following points on the slide (ignore all else right now):

(A) The tip of the root is covered by a root cap, a small mass of cells that protects the meristem and aids in the root's penetration of the soil. Cells of the root cap are sloughed off as the root penetrates the soil. New cells are added by the activity of the meristem. Interestingly, a slimy substance is secreted by the root-cap cells to aid in penetration; as you would expect, this secretory function is carried out by Golgi vesicles. The shoot meristem does not have a covering analogous to the root cap.

(B) The meristem is at the root tip, but this region is not homogeneous; some cells are relatively "inactive" mitotically. We might say that rapid cell division takes place over the first 0.5 mm and that cell elongation occurs over the next, say, 1–1.5 mm. An important difference between roots and shoots is that roots elongate only very near the tip, as stated. (On reflection, one realizes that elongation very far from the tip would tear the root apart as it "snaked" through the soil.)

(C) Note the three basic tissue systems: (1) the epidermis, (2) the cortex, and (3) the vascular tissue.

(D) The vascular tissue is contained within a ring of cells.

²⁷Tallahassee is an excellent locale to observe the effect of water-logged soils on root morphology. After a "good" hurricane, one will notice uprooted live oaks in swampy regions. These uprooted trees have "pancake"

Leaf

POWERPOINT SLIDES: Real and stylized cross-sections of leaf, and a little fun.

This slide is a schematic of a generalized mesomorphic (“average-shaped”) dicot leaf, such as that of bean.

(A) Essentially, the leaf comprises photosynthetic parenchyma²⁸ or mesophyll (“middle of leaf”). Toward the upper surface are the palisade (“columnar”) cells, and toward the bottom are the spongy cells. Both palisade cells and spongy cells carry out photosynthesis in a normal fashion, but palisade cells (toward the sun) probably do the bulk of it. There are no general biochemical differences between these two types of cells.

(B) Vascular tissue. The water supply (including necessary dissolved substances, generally minerals) is delivered via the xylem, whereas carbohydrates formed during photosynthesis are carried by the phloem. Of course, sieve-tube elements and companion cells are the primary cell types of interest in the phloem, whereas tracheary elements comprise the water-conducting cells in the xylem. Note that the xylem is on the adaxial (“top”) side of the vascular bundle, whereas phloem is located toward the abaxial (“bottom”) side. This orientation results from the orientation of vascular tissue in stem. Leaves show many variations, some of which will be pointed out during our discussion of angiosperm adaptations.

(C) The epidermis (“outer skin”). The epidermes have a special coating, the cuticle, through which water vapor and CO₂ gas cannot pass. These gases therefore enter and exit the leaf through pores (stomata; singular, stoma). In broad terms, we may say that it is disadvantageous for the plant to lose water²⁹ (losing too much would result in desiccation). At the same time, the plant must admit

roots. Live oaks growing up on a hill have substantially deeper roots and are less likely to be blown over.

²⁸ **It is very important to remember that** the prerequisites of this course include treatments of photosynthetic electron transport and photosynthetic CO₂ fixation. You may need to review on your own. These topics are found in all introductory, cell biology, and biochemistry texts. You can cut to the essence of what you need to know by going to a link on my webpage (http://bio.fsu.edu/~outlaw/courses/BSC_3402L/) and select “Scientific Background”).

²⁹ “Water scarcity is now holding back growth in food production on every continent.” (Lester R. Brown (1995), *Who will feed China? Wake-up Call for a Small Planet*. The World Watch Environmental Alert Series (L. Starke, Series Editor), W. W. Norton and Company, New York).

It is too simple to say only that the plant must conserve water. Although that is important, it is also important for the plant to lose water! Water loss has two major advantages. First, as water is lost, more water moves up the xylem and transports mineral elements from the soil. Several physiological disorders (such a tomato blossom-end rot) may result during periods of uneven transpiration (e.g., rainy humid weather). Because of the high CO₂ concentration during the time that plants invaded land and the sparse and patchy distribution of stomata on the first land plants, some (see *Journal of Experimental Botany* 49: 255) believe that the evolutionary

CO₂, to use as a substrate for photosynthesis. Therefore, the aperture size of stomata is adjusted from moment to moment by the swelling and shrinking of the subtending pair of guard cells. Although these cells represent perhaps only 0.1% of the leaf volume, their function is critical to the performance of the entire plant. To fulfill their special role, they have evolved special biochemical attributes. Two sausage-shaped guard cells lying parallel and joined at the ends define the stoma between them. Because of the radial micellation of the cellulose microfibrils of the guard-cell walls, an increase in turgidity causes cell deformation. At high internal pressure, the guard-cell pair resembles a pair of opposing kidneys (or, more appealingly, a doughnut). In such an open state, a stoma has a high nonselective conductance for gases. When the guard cells lose turgidity (“become flaccid”), the aperture size of the stoma is diminished (the stoma “is closed”), and the resistance to gaseous effusion is high.

POWERPOINT SLIDE: Principles of gas exchange.

POWERPOINT SLIDE: Open and closed stomata, composite images (FSU lab).

POWERPOINT SLIDE: Basic outline of stomatal opening and closing mechanisms.

The crux of the issue, then, resides in an explanation of the physiological fluctuations between the relatively turgid and flaccid states. An overview, reduced to the essence, follows: (1) A physiological condition (e.g., low internal (CO₂), sufficient water) is sensed, and a signal cascade to open the stoma is initiated. (2) The proton pump—this is the same universal pump that we discussed during the explanation of mass flow in the phloem—is activated. (3) Proton extrusion causes the inside of the guard cell to become more negative, which creates a driving force for K⁺ (a positive ion) to move into the cell. (4) The accumulation of K⁺ and other solutes lowers the chemical activity of water in the guard cell, and water flows into the cell osmotically. (5) The water influx distends the cell, opening the stoma.

driving force for stomatal development was to drive the transpiration stream upward to deliver nutrients. Second, water loss cools the plant (by means of the latent heat of vaporization).

Why not take advantage of the cooling power of water evaporation from plants? My colleague at NASA, Ray Wheeler, states in a grant proposal we coauthored: “Closed environment studies with plants have shown canopy transpiration rates up to 10 L m⁻² d⁻¹ (10 mm d⁻¹) (Monje and Bugbee, 1993), which equates to a nearly 300 W m⁻² of continuous heat movement through the system by latent transfer (Wheeler et al., 1995).” Plants have a large heat capacity, in addition. Thus, having a shade tree over your home is a very inexpensive way of cooling—Uno et al. (2001, *Principles of Botany*) equate a large tree to five air conditioners! Of course, there’s no free lunch—branches fall and high humidity around a home encourages mold.

The sensors that “tell” the stomata to open or closed are many, and they provide inputs that result in an integrated response. Speaking broadly, the plant must prevent excessive water loss, even if that means that the stomata are closed and the plant cannot take up CO₂ for photosynthesis. For our purposes, the “water deficient” signal is abscisic acid, usually known by its shorter moniker, ABA (say aye bee aye). This hormone is formed by all parts of the plant. E.g., when a leaf is excised, it makes ABA and its stomata close; when roots penetrate dry soil, they make ABA, which can be transported to leaves for an action there.

How ABA acts biochemically is a matter of considerable current interest; we know that it affects ion channels directly and indirectly and it also affects levels of certain proteins. (The five major plant growth regulators—auxin, cytokinins, ethylene, abscisic acid, and gibberellins—all affect gene expression, which, of course, is an expectation.) Whereas all these ABA actions are known for guard cells, ABA has many other effects. It was named *abscisic acid* because it was discovered as a plant-growth regulator, or hormone, that is involved in excision of leaves from a plant that is water stressed³⁰. (As discussed in the previous topic, ABA is also important to seed development—seeds naturally dry out during development, and accumulation of ABA is necessary for this process. The presence of high concentrations of ABA prevents seed germination, and ABA acts antagonistically with gibberellin. Thus, a high gibberellin-to-ABA ratio favors germination, and a high ABA-to-gibberellin ratio favors continued dormancy. For more information on seed development and germination, refer back to the previous unit.³¹)

POWERPOINT SLIDES: Membrane transport aspects of stomatal opening and closing.

Root (endodermis and root pressure)

POWERPOINT SLIDES: Schematics and real view of the endodermis, with transport steps.

POWERPOINT SLIDE: Function of the root as an osmometer because of apoplastic discontinuity.

Think of the endodermis (“inside skin”) as a cylinder of cells resembling a smokestack (each cell corresponds to brick). The wall of each cell is impregnated with a fatty substance, the Casparian strip

³⁰ Although this role is responsible for the name ABA, we now know that ABA’s role in this process is minor. The primary stimulus for leaf excision is ethylene, a simple volatile gaseous hormone that is involved in fruit ripening also. Indeed, producers pick some fruits green (such as tomatoes and bananas) and hold them until the market is right, and then treat them with ethylene to ripen them before moving them to the grocery shelf.

(comparable to the mortar in the smokestack analogy), that prevents the flow of water (and dissolved minerals) around the protoplasm. This cylinder of cells separates the xylem from the solution bathing the roots—the solution can reach the xylem only by passing through living protoplasm. Therefore, we say that the Casparian strip confers specificity on xylem transport.

The apoplast is interrupted by the endodermis. Imagine what would happen if the endodermal cells pumped solutes (e.g., mineral nutrients) across them, into the root xylem (interior apoplast). The higher internal solute concentration causes the osmotic influx of water, thereby creating positive pressure in the xylem. This pressure, higher in the root than in the leaf, causes the bulk flow of water from the root to the leaf. The water transudes through special leaf structures, a process called guttation. Root pressure is real³², and in some species is an explanation for sap ascent, but it is not the typical mechanism, and it is never sufficient to push water very high. Again, the universal explanation of sap ascent is the cohesion theory, which invokes negative pressure inside tracheary elements.

POWERPOINT SLIDE: Dew-covered leaves of strawberry with marginal droplets of water formed by guttation (north Leon County, Florida).

POWERPOINT SLIDE: Broccoli seedling with marginal droplets of water formed by guttation (north Leon County, Florida).

Root (mycorrhizae)

As discussed earlier, root hairs—modified epidermal cells—absorb water and dissolved substances. Root hairs are near the tips (just back of the elongation zone) of roots. Their penetration of the soil increases the surface area. As a rule, increased transport is indicated by surface proliferation, whether in the lung or in the folded membranes of the mitochondrion.

A discussion of roots and the absorption of water and dissolved substances would be incomplete without a discussion of the associations between plant roots and other organisms, particularly fungi. Perhaps the single most important function of mycorrhizae is to facilitate nutrient acquisition, particularly phosphate, which is often limiting in soils and for which plants have a major requirement.³³ This slide shows plants that were grown under phosphorus limitation with and without the fungal association:³⁴

³¹ Or, an especially interested student can consult a review of this important subject (*Seed Science Research* 5: 61 (1995)).

³² Indeed! Root pressure, a result of a sugary apoplastic solution in maple, causes the rise of the sap, a fact not overlooked by American Indians. These people manufactured sugar from the maple sap in pre-Columbian days.

³³ Phosphate mining for fertilizer production is a major industry. Florida has large deposits, and overall, the U.S. produces on the order of 100 billion pounds each year. (That's about 40 pounds for each man, woman, and

POWERPOINT SLIDE: Western cedar (*Thuja plicata*) responds to mycorrhizae (Fig 6-14 of Berg).

Approximately 80-90% of the investigated angiosperms have a mutualistic relationship between a fungus (or fungi) and their roots. All investigated gymnosperms have such a relationship. The general term for the fungus-root association is mycorrhiza (plural, mycorrhizae). This term literally means “fungus” + “root,” but it is also applied to other fungus-plant associations such as with gametophytes of primitive plants, which lack roots, or even to aquatic fungal-plant associations. So, you must consider mutually beneficial relationships between fungi and plants as well as pathologic relationships. As you will see later, some pathogenic attacks by fungi on plants display a high specificity between the pathogen and the host (i.e., one strain of a particular fungal species will successfully penetrate the defenses of one cultivar of a plant species), and some are nonspecific. The same situation holds for mycorrhizal associations. Indeed, the associations are even dynamic—the species and the numbers of fungi may shift temporally as a tree ages. Complicating matters, the fungal morphology is also variable—in one plant, the fungus may take one shape, and in another plant, the fungus may take another shape. Mycorrhizae can be classified into several types. The two major ones are: (a) ectomycorrhiza, in which the fungus surrounds the root and grows into the intercellular regions between cells. As examples, 98% of the species in the pine family and in the oak family have such associations. (Pine is a gymnosperm and oak is an angiosperm. Most mycorrhizae in both gymnosperms and in angiosperms are endo-, not ectomycorrhizae.) The usual fungal partner is a basidiomycete (“club” fungus—see the topic on fungi), but many ascomycetes (“sac” fungi) and occasionally a zygomycete (alga-like fungus) may be involved. The ectomycorrhizae, as a broad rule, are more likely to display species specificity.³⁵ (b) endomycorrhiza, by far the most common type of

child!) When the U.S. mines play out, quality deposits in North Africa are expected to yield supplies for the growing world demand. For exact figures and tables, see http://minerals.usgs.gov/minerals/pubs/commodity/phosphate_rock

Carrol Vance (Professor, University of Minnesota) tells me that the world's supplies of mineable phosphate are expected to be exhausted by about 2030–2050. Most of you will still be living then, so you might want to think about what your alternatives are.

³⁴ I would like to inspire at least one student to consider mycorrhizal research, and Dirac Library has a number of quality references. First, mycorrhizae are endlessly fascinating—consider the germinating and nonphotosynthetic orchid seed, which is colonized by a fungus. In this case, the orchid actually receives its sustenance from the fungus, which, being heterotrophic itself, must acquire its C from another plant! Second, for the ecologist—consider the large amounts of phosphates applied to soils, which wash off to ruin lakes. Third, for the biochemist—consider the chemical signaling and the trafficking of substances between the fungus and the plant. Fourth, for the cell biologist or molecular biologist—consider the suite of molecular changes that occur during formation of the symbiosis. . . . and the list could go on.

³⁵As a means of emphasizing this point, I quote from the father-daughter team Weber and Smith ((*A Field Guide to Southern Mushrooms*, University of Michigan Press (1985)), “The association of certain species of mushroom with particular kinds of trees is so predictable that a mushroom hunter looking for a particular kind of mushroom

association. The partners are, as a general rule, rather promiscuous (i.e., a fungus species may associate with one of several plant species, and a plant species may associate with one of several fungi). In this case, the fungus—only four genera from zygomycete-related fungi—penetrates the root cortical cells and forms an intracellular hyphal coil (first slide) or a bushy structure (second slide), both of which provide for enhanced surface area for exchange of nutrients between the fungus and the plant:

POWERPOINT SLIDE: The pawpaw, *Asimina triloba* + young fruit (north Leon County, Florida).

POWERPOINT SLIDE: Endomycorrhiza in *Asimina triloba*³⁶ root. (specimen from north Leon County, Florida). The fungus has been stained by analine blue. (FSU lab).

The fungus does not penetrate the plasma membrane of the root cell, however. We will not distinguish the several subcategories of endomycorrhizae.

In brief, the fungus acquires the nutrient³⁷ and infected cells acquire the nutrient from the fungus. For this purpose, the infected cell has altered its biochemistry (abundance of transporters on the plasmalemma appressing the fungal hypha) and cytology (20x increase in cytosol, decrease in vacuole, increase in plasmalemma surface area). The chemical messages produced by the plant and the fungus coordinate the establishment of the symbiosis, but these aspects are beyond the scope of this course, and we return to the root *per se*.

should first locate the appropriate tree then look for the mushroom. Trees are easier for most of us to find than mushrooms.” But, to remind you that the question of specificity is relative, I note that *Pinus* spp. are known to form mycorrhizal associations with 74 species of fungi (D. Arora 1986 *Mushrooms Demystified*. Ten Speed Press, Berkeley, CA).

³⁶*Asimina triloba* is the pawpaw (or papaw) tree (JINGLE: “Where, oh where, is dear little Nellie? . . . way down yonder in the pawpaw patch . . .”). (The papaya (*Carica papaya*) is also called papaw (derived from a Cariban word) and it produces a large yellow fruit, which explains how the pawpaw obtained its English name.) *A. triloba* produces the largest edible fruit of any native north American tree. Interestingly, we believe that its large “native” range is a result of its intentional propagation and distribution by Amerinds. Although it is a little-known plant today, it has played an interesting role in American folklore (e.g., in the Hatfield-McCoy feud three McCoy brothers were executed while being tied to a pawpaw tree, and an entry dated 18 September, 1806, in the Lewis-Clark journal records how they were saved from starvation by the pawpaw (“our party entirely out of provisions subsisting on poppaws. We divided the buiskit which amounted to nearly one buiskit per man, this in addition to the poppaws is to last us down to the Settlement’s, which is 150 miles. The party appear perfectly contented and tell us that they can live vey well on poppaws.”)).

Some effort is being made to revive an interest in pawpaws. Neil Peterson founded the PawPaw Foundation, which spearheaded the collection of superior clones and generally promotes pawpaws. Brent Calloway is the coordinator of the Pawpaw Interest Group of NAFEX, and Dr. Pomper manages the pawpaw germplasm collection at KSU (Visit <http://www.pawpaw.kysu.edu>). Meanwhile, some Purdue chemists have isolated compounds with insecticidal and pharmaceutical properties from pawpaws.

For more about this all-American fruit, see *Hortscience* 77: 777 and the *Fruit Gardener* 28 (3): 12, and 28 (4): 6.

Primary and Secondary Growth

Primary growth results from activity of apical (“at the tip”) meristems of roots and buds whereas secondary growth results from cell division of the vascular cambium.

POWERPOINT SLIDE: Tree trunk with carved initials (Colonial Williamsburg, Virginia).

As a matter of emphasis, this slide shows that any particular vertical position on a plant is “locked” in place: the mature portion of a plant does not elongate. Secondary growth is a thickening of stem or root that results from meristem activity in the vascular tissue within the stem, root, or trunk.

Gymnosperms and many dicots exhibit secondary growth; *for our purposes*, we may generalize and say that monocots do not have secondary growth.³⁸ Therefore, as an oak (a dicot) ages, its trunk thickens.

POWERPOINT SLIDE: Young and old oak (FSU campus, present site of the Biomedical Research Facility).

In contrast, the trunk of a palm, a monocot, does not thicken except very near the apex as it ages. Its girth comes from division and enlargement of ground parenchyma cells near the apical meristem. One observes that the thickness of a palm trunk varies along its height, because of “good” and “bad” years. The key point is that once growth has occurred in monocots like the palm, future growth in girth does not take place.

POWERPOINT SLIDE: Short and tall palms (FSU campus, near Chemistry building).

³⁷In a recent paper (*Nature* 410:651 (2001), it was reported that ectomycorrhizal fungi are predators of soil-inhabiting invertebrates, and transfer some of the nitrogen to the host tree. This article indicates that up to 25% of the tree nitrogen may be derived from this mycorrhizal activity!

³⁸This is the correct canned answer, good for a standardized test, but the statement that monocot *shoots* never have secondary growth is only true in a strictly technical sense. A few woody monocots like palms have special cells very near the growing tip that contribute to girth. As those of you from south Florida know, royal palm (*Roystonea regia*) has a remarkable (and beautiful) increase in girth near the base of the plant. The *roots* of some monocots do have secondary growth.

This brief mention of royal palm provides another opportunity to mention the hazards of monoculture (= “growing one crop”). In a previous unit I pointed out the heavy dependency of mankind on a few species. As you will see later, when one species (in this case, man) depends so heavily on a second, obviously, failure of the second dooms the first. The signature of south Florida, as revealed by the images on old post cards before the 1970's, was the coconut palm. This tall slouching tree lined many main streets, and its demeanor seemed to fit the image of its place of residency. In brief, a disease, lethal yellows, struck down about 97% of the coconut palms. (. . . and the stately royal palm has been planted to some extent as a replacement for the coconut palm).

The internal structure of a dicot shoot in primary growth is relatively simple:³⁹, as this slide reminds one:

POWERPOINT SLIDE: Primary and secondary growth of dicot shoot.

Note the three basic tissue systems (viz.: epidermis, cortex, and vascular tissue = stele), which we have already discussed.

This slide shows a primary dicot root with (1) central core of xylem with arm-like ridges (here four ridges, but the number is variable), (2) phloem positioned between the ridges, and (3) cambium separating xylem from phloem.

The vascular anatomy of the dicot root is not like that of the dicot shoot, but it is like that found in plants that evolved earlier and that we will study later. On this basis, the dicot-shoot anatomy is a more advanced characteristic. Roots, which evolved later than shoots, are, by definition, more advanced. From this brief discussion, one sees that “primitive” or “advanced” should be applied to individual characteristics, and it is hazardous, if not incorrect, to say that an organism is more advanced than another, as an organism is a composite of characteristics. (As a matter of example, again, the gut bacterium *E. coli* exhibits primitive characteristics, but it did not appear until after the evolution of the mammalian gut.)

POWERPOINT SLIDE: Primary and secondary growth of dicot root.

During maturation, the cambium becomes continuous, and xylem is differentiated to the inside and phloem to the outside.

As we discussed, in the typical dicot root (primary growth), the vascular tissues form a solid core. Although this anatomy is also true of some monocots (e.g., *Lilium*), the typical monocot root has a pith or may be hollow in the center with the vascular tissue loosely arranged in the cortex. Regardless of the taxonomic group, the root anatomy is more simple than that of the shoot (no nodes)

Of course, the subtext is that if the coconut palm had been essential to the residents of south Florida, the outcome would have been devastating.

³⁹ This is a true and accurate representation of the root of many dicots. It is somewhat simpler than the structure of most, however, which have another barrier, the exodermis. For convenience, we will follow the convention of most introductory courses and general standardized exams and ignore the exodermis.

and is phylogenetically more primitive. Also as discussed earlier, some monocot roots do have secondary growth, whereas monocot shoots “never” do.

A Collection of Differences between Monocots and Dicots

Throughout our coverage of angiosperms, I have pointed to differences between monocots and dicots. For your convenience, I have summarized and expanded these differences and placed them in a chart at the end of this topic. Please use that chart as a study guide.

Monocot	Dicot
single cotyledon	two cotyledons
function of cotyledon is to absorb food from endosperm (when the cotyledon is specialized for this function, it's called a scutellum, Greek for “small shield”)	function of cotyledons is to store food; often expand and become photosynthetic
endosperm a large portion of seed at maturity	endosperm does not persist at maturity
flower parts (especially petals and sepals) in 3's	flower parts in 4's or 5's
fibrous root system arises adventitiously	tap root persists and gives rise to laterals
secondary growth absent	secondary growth may be present
vascular bundles “diffuse” in roots	tracheary elements form a core in root (primary growth)
scattered vascular bundles in stem	vascular bundles form ring in stem
parallel venation in leaf	net venation in leaf

N.B. As indicated in the text, angiosperms cannot accurately be divided into simply monocots and dicots, so this table is a simplification that eliminates perhaps 10% of diversity. As stated throughout, these notes cannot be imagined as a comprehensive reference. Real complexity has been eliminated for the sake of painting a broad general picture for an introductory course with limited time.

Summary of Some Roles of the Five Major Plant Growth Regulators (“Hormones”)⁴⁰

T. Jiang, Y. Kang, F. Meng & D. Sherdan collected this information from a variety of resources.

⁴⁰ Standardized exams often include questions about the roles of plant growth regulators. This material may appear in bonus questions.

Regulator	Examples of Biological Functions	Commercial Applications⁴¹
Absciscic Acid	Stress adaptation (e.g., stomatal closure) Seed development and maintenance of dormancy Inhibition of elongation growth	Component of tissue culture medium Seed coating to regulate dormancy Potato treatment to increase shelf life
Auxin	Fruit development Apical dominance and tropisms Root initiation	Herbicide (high concentration) Spray to induce flowering (pineapple) Dip for rootings Spray to prevent fruit drop or to induce thinning
Cytokinin	Cell division Organ initiation and development Inhibitor of senescence	Agent to improve needle growth in Christmas trees
Ethylene	Fruit maturation Senescence	Agent to ripen fruits (e.g., bananas, tomatoes) Treatment to induce senescence in tobacco leaves
Gibberellin	Seed germination Inhibition of senescence Flowering Cell division and elongation	Agent to induce flowering w/o cold/photoperiod treatment Spray to thin grapes and increase fruit size Agent to regulate bolting Treatment to speed malting

⁴¹ Application may be stable analog of hormone or inhibitor of regulator.