BOT 4503
2.5 hour
Essential review of plant anatomy and plant-cell structure.

Objectives

1. Review the following lecture notes to make sure that you know all the vocabulary and technical terms.

2. Name the three vegetative organs of plants and give a generalized description of the function of each.

3. What is primary growth, secondary growth?

4. Describe differences between the root and the shoot.

5. Describe a plant in terms of source, path, and sink.

6. Draw an outline of a root tip and a shoot tip.

7. What are meristems? Locate those involved in the primary growth of a dicot.

8. Write an essay on the development of the primary-plant body.

9. What is phloem? Where is phloem? What is the function of phloem? Which are the transporting cells of the phloem? How are these cells physiologically and developmentally related to companion cells? Name a special cytological attribute of sieve-tube elements. What is xylem? Where is it located? Which cells are involved in transport? What do phloem and xylem transport? What are tracheary elements? Are they living at maturity? Contrast the pressures inside functioning sieve tubes with those in tracheary elements.

10. Describe, differentiate parenchyma, collenchyma, sclerenchyma. Which have secondary walls? Name functions of each. Describe typical locations. Which might be dead at maturity? What is the relationship between secondary wall deposition, lignin, and the ability to dedifferentiate? Give some examples of redifferentiation of parenchyma cells to assume new physiological roles.

11. Draw and label a cross-section of a dicot root and of a dicot shoot (both, primary growth).

12. Briefly discuss the constraints on root elongation, compared with shoot elongation.

13. Draw and label a typical plant cell.

14. Describe the relative abundance, the absolute abundance, the variable abundance, and the localization of DNA in plant vs. animal cells.
15. Name an obvious difference between mitosis in plant and animal cells.

16. Describe the chemical organization of the plasmalemma. What are transporters? What is the significance of the electrical potential across biological membranes?

17. What are vacuoles? How may they arise? Name some functions.

18. Review the differences between prokaryotic cells and eukaryotic cells.

19. Name three differences between plant and animal mitochondria.

20. What are microbodies? Name the two types that can be biochemically described in plants. What are their functions?

21. What are microtubules? Name some general functions, as well as a uniquely "planty" function.

22. Briefly contrast protein synthesis and targeting of vacuolar protein and chloroplast (or mitochondrion) protein.

23. What is the ER? What are Golgi bodies? How do these interrelate dynamically and functionally? What is the endomembrane system? Name one uniquely planty secretory function of the Golgi.

24. Distinguish symplast, apoplast.

Lecture

Our first goal is to review plant cell structure and anatomy. Of course, you have covered these topics in BOT 3015 and perhaps in a cell biology course as well. Some of these topics were also covered in BSC 2010. Nevertheless, it is easy to forget, and I want to make sure that all of you are getting off in the course on equal footing. It is extremely important that you become conversant with all the general terminology and the basic concepts, as we will return—without explanation—to much that will be said in the next 2.5 hours. Please do stop me, if need be.

For the most part, the scope of this course will be limited to angiosperms (the flowering plants), which comprise monocots and dicots. Thus, our review will be limited to these organisms, with only passing comments made with regard to gymnosperms, the other category of seed plants.

Overhead 1: Schematic representation of the body of a seed plant.

In general, three vegetative organs are recognized: the leaf, the stem, and the root. (Often, the aerial portion of the plant—the stem plus leaves—is referred to as the shoot; occasionally, the words "shoot" and "stem" are used interchangeably.) The representation shown on the overhead is a mesomorphic dicot in primary growth. (At the moment, consider primary growth to be the growth that occurs before there is a thickening of the stem; in many plants—such as a bean—there is no secondary growth (increase in girth); however, in other plants, such as the oak, secondary growth is predominant.)

The root is specialized for anchorage, absorption of water and minerals, and storage. Aside from the fact that stems are generally above ground and roots are generally below ground, there are many differences in these organs. (1) The root is covered by a root cap, which is a small "hood" over the tip of the root that is involved in geotropism (sensing of gravity), that provides mechanical protection as the tip of the root is pushed forward in the soil, that provides lubricant. There is no analogous structure on the stem. (2) Root-epidermal cells often develop long extensions—root hairs—that increase the surface area and facilitate uptake from the soil. There are also, in some cases, outgrowths of leaf or stem epidermal cells, but these outgrowths are fundamentally different, e.g., hairs that increase the layer of unstirred air around the leaf and, therefore, slow the loss of water. (3) Lateral roots arise within the root (in the pericycle, a tube of cells that surrounds the vascular tissue). Lateral shoots arise surficially. (4) The stem, but not the root, is divided into nodes (the point at which lateral appendages [leaves, secondary shoots] arise) and internodes. (5) The vascular arrangement is also different, and we will return to this point later. Collenchyma, a type of cell involved in support, is also generally absent in the root. (6) Roots generally lack a surface layer of wax, the cuticle, that prevents water loss.

The stem is specialized for support and transport. Food, usually carbohydrate, is synthesized in leaves (commonly called "sources") and transported to user regions that are incapable of sustained photosynthesis; these user regions (e.g., developing leaves, fruits, roots) are commonly called "sinks." On the other hand, nutrients such as phosphate or nitrate are often transported up to leaves, where they are utilized. In this terminology, the stem is a "path" for transport. It is important to recognize that sunlight itself can be a limiting resource for plants; a plant's stem can posit the leaves more competitively in this regard.

The leaf, of course, is the photosynthetic factory. This organ is specialized to harvest light, to convert that harvested light into usable chemical energy. There are two basic intermediate energy-transduction steps, first, the phosphorylation of ADP to ATP, and second, the reduction of $NADP^+$ using electrons extracted from water. There are two primary end products: the reduction of CO_2 to carbohydrate and the reduction of nitrate to the level of amine. The former is approximately 4x the latter.

Plant growth is considerably different from that of animals. There are perpetually embryonic regions in plants. These clusters of cells are called meristems.

Overhead 2: Longitudinal section of root and shoot tips.

Thus, there is an apical meristem, located at the shoot apex. The progeny of these cells cause elongation growth (or, as said earlier and more formally, "primary" growth). Although the exact pattern of cell division is somewhat different from species to species, one can discern early on that the daughter cells can be classified into either (1) dermal tissue, (2) ground tissue (aka "fundamental tissue"), or (3) vascular tissue. Once you recognize that an epidermal cell ("dermal tissue") is not ontogenetically related to the underlying palisade parenchyma cell ("ground tissue"), but it is related ontogenetically to the adjacent guard cell, you are well on your way to understanding pattern formation in plants. In particular, the apical meristem is interesting because it may give rise to continuous vegetative growth, or given the appropriate physiological or environmental signal, the result can be a flower! There are many kinds of meristems. We will note only two more now that you should remember. There is, of course, the apical meristem of the root, and there is a latent meristem located in each leaf axil. If the suppression of the axillary meristem or bud is relieved—for example, by removing the shoot apical meristem— a side shoot will develop. (From your experience, you probably can imagine other meristems—e.g., after you mow, the grass blade seems to elongate, growth that results from a so-called intercalary meristem. The cell division that gives increase in girth (recall, secondary growth) happens in two other kinds of meristems, one located in the vascular tissue and another that gives rise to bark.

(return to 1st overhead: schematic representation of the body of a seed plant.)

Dermal tissue, as implied, is the skin of the plant. (Later the epidermis may be supplanted by even more durable cells, e.g., those that comprise the bark.) The epidermis of aerial portions of the plants is usually covered with a waxy material, which retards water loss. This waxy layer, the cuticle, is not present on roots.

Vascular tissue comprises two subtypes of tissues. The phloem transports various salts and plant growth substances, but we usually think of it with regard to the transport of carbohydrate produced by photosynthesis. The particular cells that actually transport in the phloem are sieve-tube elements, which are stacked end-to-end to form a pipe. A sieve-tube element is always associated with one or more companion cells, which are derived from the same mother cell. The sieve-tube elements and associated companion cells are embedded in a matrix of parenchyma cells. (As will be discussed later, parenchyma cells are generalized cells—e.g., palisade cells in a leaf or the unremarkable cells of mammalian liver.) The second subtype of vascular tissue is xylem. The conducting cells of xylem are tracheary elements—either tracheids or vessels. These cells are dead in their mature and functioning state, and, in the most advanced types, are stacked end-to-end to form a more-or-less open pipe.

The ground or fundamental tissue serves many functions, e.g., food storage in the carrot root or in the potato tuber, which is actually a modified underground stem. In the example shown on the overhead, the photosynthetic leaf cells (palisade parenchyma and spongy parenchyma) are ground tissues. Cells of the ground tissue usually can be identified as one of three generalized types of cells: (1) as mentioned, parenchyma cells, which may serve many functions, which are living at maturity, and which may dedifferentiate (e.g., a cell specialized for photosynthesis may change into a cell specialized for food storage) if a second cell-wall layer has not been laid down. (2) Collenchyma cells have thick cell walls; they are specialized for support during growth—elastic support. They are found in groups (e.g., capping a vascular bundle), near the epidermis of stems, but almost never of roots. (In some cases, collenchyma may even form a ring well nigh the periphery of the stem. The hallmark of collenchyma is that the cell walls are irregularly thickened. Collenchyma cells are related to parenchyma and there are intergradations between the two prototypes. Collenchyma cells are always living, and only have primary walls; they—like the parenchyma cells that lack a secondary wall—can dedifferentiate. Collenchyma is most important in young shoots. (3) Sclerenchyma cells are supportive, and often they occur in groups. They may be dead at maturity, and the presence of a secondary wall prevents even the living ones from dedifferentiating. Based on their shape, they are subdivided into two categories.

The final point to be taken from the overall representation of the plant body is to notice that the vascular tissue is arranged differently in the stem and in the root. In the primary root of dicots, the xylem occupies a central core with two-to-several “arms,” between which lies the phloem. This arrangement contrasts with that in the stem, where there are discrete vascular bundles. In both cases, the phloem lies to the outside generally, whereas the xylem is more centrally localized. (For the sake of clarity, it should be noted that the dicot root anatomy actually resembles the stem anatomy of some primitive plants. It should also be noted that other plants (e.g., monocots) have different vascular anatomy.)

(So far, this general overview of the organization of a plant has been intended to jog your memory. Intentionally, I have not shown various slides of types of cells, &c., because, so far, I want your focus to be on the overall picture. Later, as a matter of detail and reinforcement, I will provide graphic examples.)

Slide: Typical plant cell.

Because almost any biological curriculum focuses on animals, I like to start a plant-cell-biology or plant-biochemistry lecture by remarking that plants and animals are really very much alike, so much so that there is the quip that “once you grind the head of a king and that of a cabbage, you can't tell them apart.” There is a great deal of truth in that statement, despite some rather obvious unique attributes of plants (and of animals).

This slide is of a bundle-sheath cell of maize. The purpose of its presentation is to give you a grand overview of the cell and to give you perspective concerning size. This could be “any” plant cell, because the major differences among various cells are quantitative—e.g., how many ribosomes, how much activity of such-and-such enzyme, how large the vacuole is. While this statement is something of an oversimplification, it is a good starting concept.

As a generality, plant cells, like animal cells, have a single nucleus. This organelle, or little organ, is generally the most conspicuous one in the cell, and, save the vacuole, is usually the largest organelle. Whereas there are some differences—e.g., the microtubule organizing center (the site of spindle microtubule formation) in plants does not include a pair of centrioles (structures similar to basal bodies associated with flagella)—for our physiological interpretations, the nuclei of plants and animals are the same. As a means of emphasis, the cell biology (e.g., cytoplasmic factors and proteins that lead to mitosis) is the same, and the molecular biology is the same (e.g., alternative splicing of mRNAs, promoter and enhancer regulation of transcription). [These last comments are made with something of an apology, but with many people, plants might seem inanimate, no pun intended.] The nucleus is the single most important repository of DNA in animals and in plants, but there are two differences that you may wish to note: (1) Animals contain DNA in only two organelles, viz., the nucleus and the mitochondrion, whereas plants also have DNA in plastids. In some cases, a trait may be inherited only through the maternal parents, since usually eggs, but not sperm (“bare” nuclei) will transmit plastidic DNA. (2) The mammalian genome size does not vary much, ca. 3 x 10^9 base pairs per haploid genome. On the other hand, some plants have a small genome (e.g., *Arabidopsis* with ca. 7 x 10^7 bp—which is the reason that it is a favored genetic model) whereas some plants have a truly staggering amount of DNA (up to 2 x 10^{11} bp)[1]. Even within closely related members of the genus *Vicia*—which is the prime physiological model in our lab—the DNA content can vary by 20-fold! The variation in genome size is mirrored by vast differences in the number of chromosomes found in various plants. E.g., the fern *Ophioglossum* is estimated to have a diploid chromosome number of ca. 1250, whereas the desert annual *Haplopappus* has only four chromosomes per cell.

An invariant feature of organisms is the plasma membrane, which is the limiting barrier for cells[2]. In plants, usually the specialized name, plasmalemma, is used. (The other essential feature of "all" cells is the genetic material. Whereas this course will go into detail with regard to membrane function, other courses focus on genetics and plant development.) The plasma membrane is differentially permeable; some substances are retained within the cell against a free-energy gradient, whereas others are excluded. Simply put, the plasmalemma maintains the chemical and ionic environment that favors the chemistry required for life. First, the membrane is composed of (liquid) lipids that have a charged end and a hydrophobic end. Recall that most biological membranes are bilayers of these lipids, prototypically phospholipids, that assemble with the hydrophilic "heads" exposed on either side, where they interact with the aqueous phase whereas the nonpolar "tails" point inward and interact with each other. Thus, the membrane is an effective barrier to water-soluble substances that are found in the cytosol, such as ions, sugars, acids, and so forth. Second, floating in this so-called "sea of lipids"are proteins. These proteins have various functions (e.g., recognition, biosynthesis of cell wall, structural [as attachments to cell wall, e.g.]), but our focus will be on those that are transporters, e.g., of protons, potassium ions, and sugars. The combination of the basic impermeability of the lipid bilayer to water-soluble substances and selective transport (either up or down a free-energy gradient) confers the special and necessary attributes of the membrane. It can not be overemphasized that there is an electrical potential across biological membranes, and that this potential represents a form of energy storage that can be interconverted with the free energy increase associated with the phosphorylation of ADP.

Immature plant cells, or those of meristematic tissue such as the tip of the root, contain many small vacuoles, which are sometimes called provacuoles or vacuolules. (The membrane that limits the vacuole is

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[1] Wheat, rice, and maize are the most important plants in meeting the caloric requirements of man. The genome sizes are, respectively, 1.5 x 10^{10}, 2.7 x 10^9, and 4.5 x 10^8. A large genome size is one factor that contributes to difficulty in molecular biological studies.

[2] The word cell itself originated with a botantist (Hook, late 1600's) and the initial observations that led to the cell theory were made by a botanist (Schleiden, 1838).

called the tonoplast.) At least in some immature cells, these small vacuoles are not discrete entities, as would be suggested by the cross-section. Instead—at least in some cases—they are actually a reticulum (or network). Imagine a cross-section taken through the knuckles of your extended fingers—were you to view this cross-section, you might conclude that “fingers” are round and not connected to one another. This is the basic dilemma often faced in the interpretation of thin sections in electron micrographs. At any rate, it thought they are derived from the Golgi apparatus, a membranous system that will be discussed later. Indeed, many of the membranes within a eukaryotic cell are connected in time or space, as we briefly digress to show:

Overhead 3: Endomembrane system.

Mature plant cells are usually highly vacuolate—indeed, up to 90% of the volume of the cell will often be occupied by a single large central vacuole. What does the vacuole do? (1) By occupying the central portion of the cell and containing within an “inexpensive” solution of salts, sugars, and organic acids, the water-accumulating ability of the vacuole maintains the cell's turgidity; in fact, if a young plant (primary growth) is deprived of water, it will wilt. The central position of the vacuole also pushes the cytoplasm to the periphery of the cell, which, e.g., would expose the chloroplasts more directly to incident radiation. (2) The vacuole is a “dumping ground,” a place to rid the cytoplasm of noxious substances, which explains, at least in part, why leaves are periodically shed, even in evergreens. Accumulation of certain noxious compounds in vacuoles also provides some protection against herbivory. 3) As the vacuole is metabolically inaccessible, storage products such as protein can be maintained. (4) As the vacuole contains many enzymes involved in breakdown of organics, it may have a digestive role, similar to that of the animal lysosome. (5) Pigments accumulate in the vacuole in some instances. In some cases, vacuolar pigments direct pollinators to flowers; in other cases, pigments accumulate in the vacuole and absorb deleterious UV light and even PAR (which prevents over-reduction of the photosystems when the temperature is too cold for the “dark” reactions).

Briefly, while this slide remains, note the (1) cell wall, which lies external to the plasmalemma; (2) chloroplasts, distinguishing features of eukaryotic photosynthetic cells; (3) mitochondria, which are much smaller than chloroplasts.

(off slide)

Because chloroplasts and mitochondria are so similar, they will be discussed at the same time. Both these organelles are sites of energy conversion; both are endosymbiotically derived (i.e., they are prokaryote—like in organization of DNA, in the type of ribosomes, in the chemical composition of the lipid components of the membrane, &c); both have a relatively permeable exterior membrane and a selective interior membrane; both reproduce by fission but they must import many of their proteins from the cytosol during organellar "assembly;" as implied, both are semi-autonomous; and, both are involved in photosynthesis, which is probably a new fact for you. In addition to the involvement of plant mitochondria in photosynthesis, they have other unique biochemical attributes (such as an alternative method of oxidizing malate), but structurally, plant mitochondria resemble other mitochondria, so this slide will just refresh your memory:

Slide: Mitochondrion, chloroplast, peroxisome, glyoxysome.

Adjacent to and functionally related to the mitochondrion is a chloroplast, which is one kind of plastid. Other types of plastids are chromoplasts (which give carrots their color), amyloplasts (which are specialized for starch storage, and found, e.g., in a potato tuber), &c. Plastids develop from proplastids and may interconvert—you have probably noticed the undesirable trait of "green shoulders" on carrots; if the shoulder of the root is exposed to light, the chromoplasts will convert to chloroplasts. Similarly, amyloplasts of potato tuber will convert to chloroplasts if the tuber is exposed to light. (This greening of potatoes is unpredictably associated with an unhealthy increase of alkaloids.) In addition to formation by conversion, plastids regularly develop from proplastids, which are in meristematic cells. Again, at the expense of redundancy, the mere fact that plastids contain information in the sequence of DNA implies that plastids must arise from pre-existing plastids. (Even more generally, all membranes grow by expansion of existing membranes and not by de novo "creation," thus all membrane-bound organelles are formed by division of previously existing organelles, or are constructed from membrane formed elsewhere.)

A major focus of this course is photosynthesis. As form and function are intimately related, we will delay a detailed review of chloroplast structure until the beginning of carbon metabolism.

A microbody is also shown on this slide and it is in functional proximity to the chloroplast. "Microbody" is a morphological term, but there are two types of plant microbodies that can be distinguished biochemically. One, the peroxisome—which I can infer because it is present in this photosynthetic cell—is similar to the animal peroxisome in that it is specialized for detoxification. As you will learn, H_2O_2 is an inevitable byproduct of photosynthesis. This highly active oxygen species (or the hydroxy radical it forms) must be degraded to avoid cellular damage. Thus, the reaction that forms peroxide is localized in the peroxisome and, therefore, the formed peroxide is sequestered there as it is immediately converted to harmless water and molecular oxygen. The second type of microbody is the glyoxysome, which does not have an animal equivalent. This type of microbody is found in germinating seeds, and is involved in the conversion of stored lipid to carbohydrate. As we alluded to, the "food" transport system is aqueous, and, therefore, lipid cannot be readily solubilized, so the evolved solution is to convert the lipid to sugars. (For absolute accuracy, means have evolved to transport hydrophobic molecules in an aqueous medium by association with macromolecules—the cholesterol transport system in mammals is an example.)

In brief summary, nominal figures are, say, 700 mitochondria and 100 chloroplasts per cell (compared with, e.g., 500 000 ribosomes). However, mitochondria are smaller—say, 0.5-2 µm; animals have small mitochondrial genomes (17-80 x 10^3 bp vs. 100-150 x 10^3 bp for chloroplasts, which are up to 5 µm in "length"). In sharp contrast, plant-mitochondrial genomes can be large and variable—15 to 150 x the 17 kb in humans! As an example, Cucurbits (melons, squash, &c.) have a mitochondrial genome size of 2 400 kb. The large plant-mitochondrial genome has arisen in many ways (integration of RNA viral sequences, direct and inverted repeats, integration of plastid (in *Arabidopsis*, 1.2 % of mtDNA) and nuclear in *Arabidopsis*, 5 % of mtDNA sequences). Whereas plant mitochondria do encode for more genes than your mitochondria, the large genome size does not encode for a proportionately larger number of genes. As an example, the *Arabidopsis* mtDNA is 367 kb and encodes 58 genes (cf. 13 in *Homo)*. However, as I said earlier, cell-types differ primarily by the amount of constituents, so obviously the quoted values must be used for perspective, and not as absolute measures.

Overhead 4: Mitochondrion, chloroplast, and cyanobacterial genes.

Slide: Microtubules

Microtubules are a varied collection of dynamic 24-nm, polar, hollow cylinders that are polymers of two types of tubulin, each about 50 kD. (In addition, there are other smaller amounts of so-called microtubule-associated protein. One view is that these different proteins give the microtubules specific attributes that permit them to function in the diverse roles they play. In addition, there are various isoforms of the two types of tubulin and specific microtubules have a particular isoform.) In broad terms, these microtubules function in movement and structure; the specific function is highly contextual. Some animal microtubules are found in flagella; angiosperms lack flagella (an absence complementary to the noted absence of centrioles). Some functions are ubiquitous in eukaryotic cells, e.g., facilitating the movements of chromosomes during karyokinesis or providing guidance for the movement of Golgi vesicles, which will be covered later. Still other functions are uniquely "planty," as shown in this slide, which portrays the orderly deposition of cellulose (a plant-cell-wall polymer), which is guided by microtubules.

(Two parenthetical statements are added to complete the brief sketch and to provide an interesting observation. First, in most eukaryotic cells, the most abundant single cytosolic protein is actin. The major component of microfilaments is actin. These microfilaments in plants mediate cytoplasmic streaming. Second, as implied, microtubules are not in prokaryotes. Interestingly, microtubule-like structures are observed in some plant chloroplasts, which—as mentioned—are prokaryotic in character.)

Slide: Golgi

Eukaryotic cells have an elaborate network of internal membranes, as shown on a previous overhead. The endoplasmic reticulum (usually, simply ER) is a series of flattened sacs that are interconnected. The inside of the ER—usually called by the general name, lumen—constitutes a space distinct from the cytosol *per se*. Whereas proteins destined for import into mitochondria, chloroplasts, the nucleus and microbodies are synthesized on "free" ribosomes in the cytosol, proteins of other organelles and those that will be secreted or inserted into the plasma membrane are synthesized on the ribosomes of the ER. The nascent peptide chain is either incorporated into the ER membrane, or into the lumen of the ER. The vesicles bleb off and these vesicles coalesce to form the cis (forming) face of the Golgi body. (Each individual collection of sacs is called a Golgi body, or and only in plants, a dictyosome, whereas, collectively, the Golgi bodies of a cell are called the Golgi apparatus.) "Maturation" of the protein occurs over time, when new cis membranes are laid down and older trans membranes break away. As implied, when the secretory product, organellar protein or plasma membrane protein is processed, the oldest membrane sac of the Golgi body breaks into vesicles, which fuses with the target membrane. Thus, over time, there is continuity between the outer envelope of the nuclear membrane, the ER, the Golgi apparatus, the plasma membrane, and all other cellular membranes except those of the chloroplasts and mitochondria. Collectively, these membranes are called the endomembrane system. It is important to appreciate that these structures are dynamic, and not static, as one sees in a fixed preparation.

The default pathway for ER-synthesized Golgi-processed proteins is secretion. A specific peptide sequence—either a signal peptide or non-contiguous amino acids that form a 3-D structure—directs the protein away from the default pathway to the vacuole. (In some specific cases, the process is somewhat different, but the preceding is a general rule.)

The previous description focussed on the processing of protein, but the Golgi has broader functions in secretion. A specific planty example is the delivery of certain cell-wall components. Non-cellulosic polysaccharides and some glycoproteins are synthesized in the Golgi and delivered into the cell wall by exocytosis. (As you will see later, the synthesis of cellulose, a hallmark component of plant cell walls, is synthesized by macromolecular machinery that floats in the cell membrane.)