Plant Tissues

Plant tissues form three distinct major groups, as follows:

1. **Ground tissues** include three basic kinds of cells that differ mostly by the nature of their cell walls.
    ¥ **Parenchyma** cells, the most common component of ground tissue, have thin walls and serve various functions including storage, photosynthesis, and secretion.

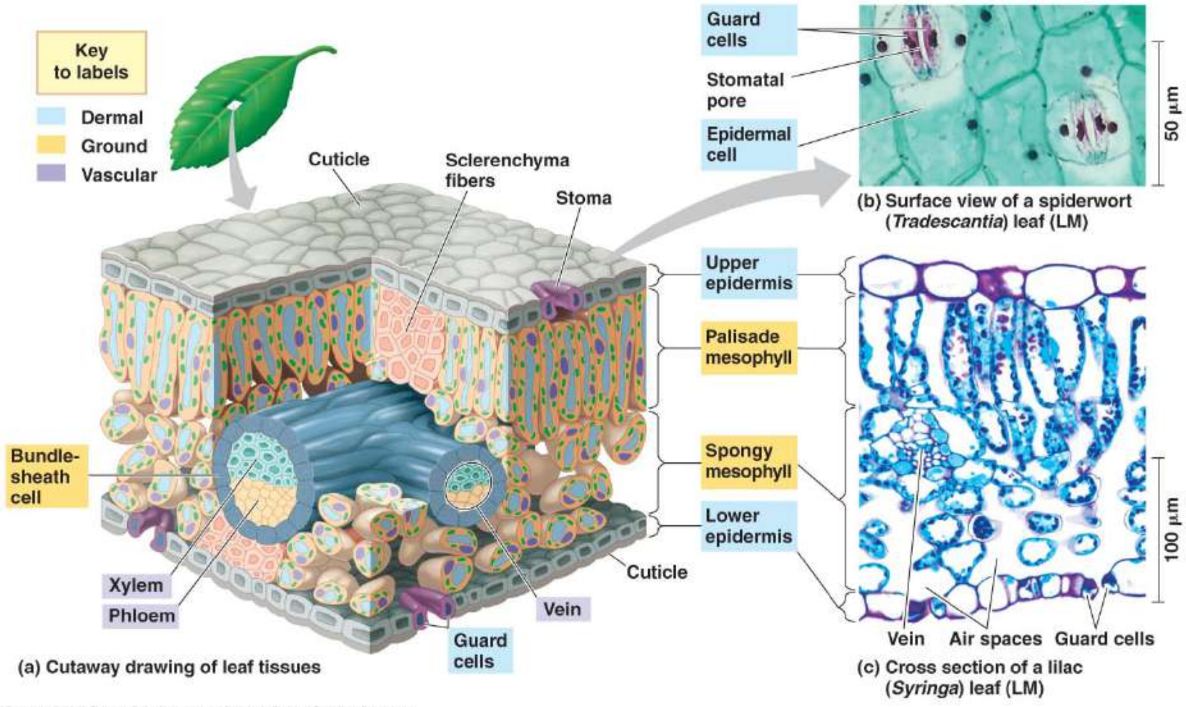
    ¥ **Collenchyma** cells, which have thick but flexible cell walls, serve mechanical support functions.

    ¥ **Sclerenchyma** cells, with thicker walls than collenchyma, also provide mechanical support functions.
2. **Dermal tissue** consists of epidermis cells that cover the outside of plant parts, guard cells that surround stomata, and various specialized surface cells such as hair cells, stinging cells, and glandular cells. In aerial portions of the plant, the epidermal cells secret a waxy protective substance, the **cuticle.**
3. **Vascular tissue** consists of two major kinds of tissues, **xylem** and **phloem.** The two usually occur together to form **vascular bundles.**

    ¥ **Xylem** functions in the conduction of water and minerals and also provides mechanical support. In addition to the **primary cell wall** that all plants have, xylem cells have a **secondary cell wall** that gives them additional strength. Sometimes, the walls of xylem cells have **pits,** or places where the secondary cell wall is absent.
    Most xylem cells are *dead* at maturity, that is, they are essentially cell walls, completely lacking cellular components, and contain only the material being transported. There are two kinds of xylem cells, **tracheids** and **vessel elements** (or **vessel members**). In tracheids, which are long and tapered, water passes from one tra-cheid to another through pits on the overlapping tapered ends of the cells. Vessel members are shorter and wider than tracheids, and have less or no taper at their ends. A column of vessel members is called a **vessel.** Water passes from one vessel member to the next through areas devoid of *both* primary and secondary cell walls. These areas are called **perforations** and are literally holes between cells. Because of the perforations, water movement through vessel members is more efficient than through tracheids. As a result, vessels are con-sidered a more evolutionarily advanced feature. They are found most prominently among the flowering plants.

    ¥ **Phloem** functions in the conduction of sugars. Phloem is made up of cells called **sieve-tube members** (or **sieve-tube elements**) that form fluid-conducting columns called **sieve tubes.** Unlike mature xylem cells, sieve-tube members are *living* at maturity, although they lack nuclei and ribosomes. **Pores** on the end walls of sieve-tube members form **sieve plates,** areas where the cytoplasm of one cell makes contact with that of the next cell. Sieve tubes are associated with **companion cells,** living parenchyma cells that lie adjacent to each sieve-tube member. Companion cells, connected to adjacent sieve-tube members by thin tubes of cytoplasm called **plasmodesmata,** maintain physiological support to the nuclei-lacking sieve-tube members.

STRUCTURE OF LEAF



(a) Cutaway drawing of leaf tissues

(b) Surface view of a spiderwort (*Tradescantia*) leaf (LM)

(c) Cross section of a lilac (*Syringa*) leaf (LM)

1. The **epidermis** is a protective covering of one or more layers of cells. As in other aerial portions of the plant, the

epidermis is covered by the **cuticle,** a protective layer consisting of the waxy material **cutin.** The cuticle reduces **transpiration,** or the loss of water through evaporation. Specialized epidermal cells may bear trichomes (hairs, scales, glands, and other cell outgrowths).

2. **The palisade mesophyll** consists of parenchyma cells equipped with numerous chloroplasts and large surface areas, specializations for photosynthesis. Photosynthesis in leaves occurs primarily in this tissue. The parenchyma cells are usually tightly packed in one or more layers at the upper surface but can occur at both surfaces of vertically oriented leaves of plants adapted to dry habitats.
3. The **spongy mesophyll** consists of parenchyma cells loosely arranged below the palisade mesophyll. The numerous intercellular spaces provide air chambers that provide CO_2 to photosynthesizing cells (and O_2 to respiring cells).
4. **Guard cells** are specialized epidermal cells that control the opening and closing of **stomata.** Stomata are open-ings in the epidermis that allow gas exchange between the inside of the leaf and the external environment.
5. **Vascular bundles** consist of xylem and phloem tissues. Xylem delivers water for photosynthesis, while phloem transports sugars and other carbohydrate by-products of photosynthesis to other areas of the plant. There are usu-ally specialized mesophyll cells called bundle sheath cells that surround the vascular bundles in such a way that no vascular tissue is exposed to intercellular spaces. In this way, air bubbles cannot enter vessels where they could impede the movement of water. In addition, bundle sheath cells provide the anaerobic environment for CO_2 fixation in C_4 plants.

Transport of Water

Water and dissolved minerals enter the roots through root hairs by osmosis. There are two pathways by which the water moves toward the center of the root, as follows.

1. Water moves through *cell walls* and intercellular spaces from one cell to another without ever entering the cells. This pathway is called the **apoplast** and consists of the ÒnonlivingÓ portion of cells.
2. Water moves from one cell to another through the **symplast,** or ÒlivingÓ portion of cells. In this pathway, it moves from the cytoplasm of one cell to the cytoplasm of the next through **plasmodesmata,** small tubes that connect the cytoplasm of adjacent cells.

When water reaches the endodermis, it can continue into the vascular cylinder only through the symplast pathway. The apoplast pathway is blocked by the suberin that permeates the casparian strips. The endodermal cells allow water to enter the stele (vascular cylinder) but are selective as to which minerals are allowed to enter. For example, potassium (K^+), an essential mineral, is allowed to pass, while sodium (Na^+), common in soils but unused in plants, is blocked. Once through the endodermis, water and minerals continue by the apoplast pathway to the xylem. The xylem tissue, consist-ing of tracheids and vessels, is the major conducting mechanism of the plant.

Three mechanisms are involved in the movement of water and dissolved minerals in plants. These mechanisms are described in the following:

1. **Osmosis.** Water moves from the soil through the root and into xylem cells by osmosis. A concentration gradient between the soil and the root is maintained in two waysÑby the continuous movement of water out of the root by xylem and by the higher mineral concentration inside the stele maintained by the selective passage of ions through the endodermis. To a certain extent, the movement of water into the root by this concentration gradient forces water up the xylem. This osmotic force, called **root pressure,** can be seen as **guttation,** the formation of small droplets of sap (water and minerals) on the ends of leaves of grasses and small herbs in the early morning. Under most envi-ronmental conditions, however, the forces generated by root pressure are too small to have a major effect on the movement of water in plants, especially large plants such as trees.
2. **Capillary action. Capillary action** or **capillarity,** is the rise of liquids in narrow tubes. It also contributes to the movement of water up xylem. Capillary action results from the forces of **adhesion** (molecular attraction between *unlike* substances) between the water and the capillary tube (a tube with a narrow bore). These forces combine to pull water up the sides of the tube. As a result, a **meniscus,** or crescent-shaped surface, forms at the top of the wa-ter column. In active xylem cells, however, water forms a continuous column without menisci. Thus, the effect of capillary action is minimal, confined to minute cavities in the cellulose microfibrils of the cell wall.
3. **Cohesion-tension theory.** Although root pressure and capillary action may make minor contributions to water movement under special conditions, most water movement through xylem is explained by **cohesion-tension theory.** The major concepts of this theory are as follows:

   ¥ **Transpiration,** the evaporation of water from plants, removes water from leaves, causing a **negative pressure,** or **tension,** to develop within the leaves and xylem tissue.

   ¥ **Cohesion** between water molecules produces a single, polymerlike column of water from roots to leaves. Cohesion is the molecular attraction between *like* substances. In water, cohesion results from the polarity of water molecules, which causes hydrogen bonding to occur between adjacent water molecules. As a result, the water molecules within a series of xylem cells (vessels or tracheids) behave as a single, polymerlike molecule.

- **Bulk flow** of water through xylem cells occurs as water molecules evaporate from the leaf surface. When a water molecule is lost from a leaf by transpiration, it pulls up behind it an entire column of water molecules. In this way, water moves by bulk flow through the xylem by a pulling action generated by transpiration. Since transpiration is caused by the heating action of the sun, the sun, then, is the driving force for the ascent of sap through plants.

Control of Stomata

The opening and closing of the stomata influence gas exchange, transpiration, the ascent of sap, and photosynthesis. When stomata are closed, CO_2 is not available, and photosynthesis cannot occur. In contrast, when stomata are open, CO_2 can enter the leaf, but the plant risks desiccation from excessive transpiration. A mechanism that controls the opening and closing of stomata must, therefore, balance these two states and provide a means to optimize photosynthesis while mini-mizing transpiration.

Each stoma is surrounded by two **guard cells.** The cell walls of guard cells are not of uniform thickness. Instead, the cell wall that borders the stomata is thicker than the rest of the cell wall. In addition, the cellulose microfibrils are arranged radially, that is, they encircle the guard cell from the stoma side to the outside. When water diffuses into a guard cell, the guard cell expands. But because of the nonuniform and radially constructed cell wall, the expansion is distorted in such a way that most of the expansion is realized by the bulging out of the thinner wall, the wall away from the stoma. The overall effect is to produce two kidney-shaped guard cells that create an opening, the stoma, between them. When water diffuses out of the guard cells, the kidney shape collapses and the stoma closes. The opening and closing of the stomata, then, is controlled by the movement of water into and out of the guard cells.

Many factors seem to be involved in the mechanism that controls opening and closing of stomata. The following obser-vations have been made:

1. Stomata close when temperatures are high. This reduces loss of water (but shuts down photosynthesis).
2. Stomata open when CO_2 concentrations are low inside the leaf. This allows active photosynthesis, since CO_2 is required.
3. Stomata close at night and open during the day. This may be in response to CO_2 fluctuations caused by photosyn-thesis. During daylight hours, CO_2 is low because it is used by photosynthesis, but at night, CO_2 levels are high because of respiration.
4. Stomatal opening is accompanied by a diffusion of potassium ions (K^+) into the guard cells (from surrounding subsidiary cells). An increase in K^+ creates a gradient for the movement of water into the guard cell, which, in turn, results in guard cell expansion and the opening of the stomata.
5. When K^+ enter a guard cell, they create an unbalanced charge state. In some plants, the charge is balanced by the movement of chloride ions (Cl^D) into the guard cells along with the K^+. In other plants, H^+ are pumped out of the cell. The H^+ originate from the ionization of various organic substances within the cell.

Transport of Sugars

Translocation is the movement of carbohydrates through phloem from a **source,** such as leaves, to a **sink,** a site of carbohydrate utilization. Translocation is described by the **pressure-flow** hypothesis, as follows:

1. **Sugars enter sieve-tube members.** Soluble carbohydrates, such as fructose and sucrose, move from a site of pro-duction, such as the palisade mesophyll, to phloem sieve-tube members by active transport. This develops a con-centration of solutes (dissolved substances, sugars in this case) in the sieve-tube members at the source that is higher than that at the sink (a root, for example).

2. **Water enters sieve-tube members.** As a result of the movement of solutes into the sieve-tube members, the con-centration of water inside the cell becomes less than in the area outside the cell. As a result, water diffuses into these cells, moving down the water concentration gradient.

3. **Pressure in sieve-tube members at the source moves water and sugars to sieve-tube members at the sink through sieve tubes.** When water enters the sieve-tube members in the leaves (or other source), pressure builds up because the rigid cell wall does not expand. As a result, water and sugars move by bulk flow through sieve tubes (through sieve plates between sieve-tube members).

4. **Pressure is reduced in sieve-tube members at the sink as sugars are removed for utilization by nearby cells.**

   As water and sugars move by bulk flow from source to sink, pressure begins to build at the sink. However, a sink is an area where carbohydrates are being utilized. Thus, sugars are removed from the sieve-tube members (by active transport), which increases the concentration of water within the sieve-tube members. Water then diffuses out of the cell (moving down the water concentration gradient), relieving the pressure.

There is a physiologically important result when sugars are stored as starches. Starch is essentially insoluble in water. Thus, any cell can act as a sink if it removes soluble sugars from its cytoplasm by converting them to starch. Doing so would have the same effect as breaking down the sugars for energy. Similarly, any cell can act as a source if it breaks down starch into soluble glucose molecules. For example, when photosynthesis activity is low (during nights or cold winters), roots in plants can act as a sugar source when stored starches are broken down to sugars.

Plant Hormones

Hormones are substances that are produced by specialized cells in one part of an organism that influence the physiology of cells located elsewhere. They are small molecules, capable of passing through cell walls, that affect the division, growth (elongation), or differentiation of the cells. Very small quantities of hormones are required to alter cell physiology. However, the specific effect of a hormone depends upon the particular hormone, its concentration, the target cell, and the presence or absence of other hormones. A description of the five classes of plant hormones follows:

1. **Auxin,** or **IAA** (indoleacetic acid), promotes plant growth by facilitating the elongation of developing cells. Auxin does this by increasing the concentration of H^+ in primary cell walls, which, in turn, activates enzymes that loosen cellulose fibers. The result is an increase in cell wall plasticity. In response, turgor pressure causes the cell wall to expand, thus generating growth. Auxin is produced at the tips of shoots and roots, where, in concert with other hormones, it influences plant responses to light (**phototropism**) and gravity (**geotropism**). In addition, auxin is active in leaves, fruits, and germinating seeds. Structurally, auxin is a modified tryptophan amino acid. After synthesis from tryptophan, it is *actively* transported (using ATP) from cell to cell in a specific direction (**polar transport**), by means of a chemiosmotic process.
2. **Gibberellins** are a group of plant hormones that, like auxin, promote cell growth. The more than 60 various related gibberellins are abbreviated GA1, GA2, GA3, etc., for **gibberellic acid.** They are synthesized in young leaves, roots, and seeds but are often transported to other parts of the plant. For example, gibberellins produced in the roots and transported to shoot tips interact with auxins to stimulate shoot growth. Gibberellins are also involved in the promotion of fruit development and of seed germination, and the inhibition of aging in leaves. High concentrations of GA can cause the rapid elongation of stems (called **bolting**). For example, bolting occurs in rice plants when a fungus that produces GA attacks the plant.
3. **Cytokinins** are a group of hormones that stimulate cytokinesis (cell division). Structurally, they are variations of the nitrogen base adenine. They include naturally occurring **zeatin** and artificially produced **kinetin.** Cytokinins are produced in roots (and perhaps elsewhere) and are transported throughout the plant. They have a variety of effects depending upon the target organ and, sometimes, the presence (and concentration) of auxin. In addition to stimulating cell division, cytokinins influence the direction of organ development (organogenesis). For example, the relative amounts of cytokinins and auxin determine whether roots or shoots will develop. Cytokinins stimulate the growth of lateral buds, thus weakening **apical dominance** (the dominant growth of the apical meristem). Cytokinins have been found to delay **senescence** (aging) of leaves and are often sprayed on cut flowers and fruit to prolong their usefulness.
4. **Ethylene** ($H_2C = CH_2$) is a gas that promotes the ripening of fruit. During the later stages of fruit development, ethylene gas fills the intercellular air spaces within the fruit and stimulates its ripening by enzymatic breakdown of cell walls. Ethylene is also involved in stimulating the production of flowers. In addition, ethylene (in combination with auxin) inhibits the elongation of roots, stems, and leaves and influences **leaf abscission,** the aging and dropping of leaves.
5. **Abscisic acid** (**ABA**) is a growth inhibitor. In buds, it delays growth and causes the formation of scales in preparation for overwintering. In many species of plants, ABA maintains dormancy in seeds. Dormancy in these seeds is broken by an increase in gibberellins or by other mechanisms that respond to environmental cues such as temperature or light. In some desert species, seed dormancy is overcome by the leaching of ABA from seeds by rains. Although ABA is named for the process of abscission, its influence on the abscission of leaves, flowers, and fruits is controversial.

Plant Responses to Stimuli

Since plants are anchored by their roots, they cannot move in response to environmental stimuli. Instead, they change their growth pattern. A growth pattern in response to an environmental stimulus is called a **tropism.** Three tropisms are described below:

1. **Phototropism,** the response to light, is achieved by the action of the hormone auxin. The process is described as follows:

   ¥ Auxin is produced in the apical meristem, moves downward by *active transport* into the zone of elongation, and generates growth by stimulating elongation.

   ¥ When all sides of the apical meristem are equally illuminated, growth of the stem is uniform and the stem grows straight.

   ¥ When the stem is *unequally* illuminated, auxin moves downward into the zone of elongation but concentrates on the *shady* side of the stem. Auxin that would have normally accumulated on the sunny side ends up on the shady side.

   ¥ The higher concentration of auxin in the shady side of the stem causes *differential growth;* that is, since auxin generates growth by stimulating elongation, the *shady side grows more* than the sunny side. When the shady side grows more than the sunny side, the stem bends toward the light.

2. **Gravitropism** (or **geotropism**), the response to gravity by stems and roots, is not well understood. In general, both auxin and gibberellins are involved, but their action depends on their relative concentrations and the target organ (root or stem). The role of auxin appears to agree with the following:

   ¥ If a *stem* is horizontal, auxin produced at the apical meristem moves down the stem and concentrates on its lower side. Since auxin stimulates cell elongation, growth of the lower side is greater than that of the upper side, and the stem bends upward as it grows.

   ¥ If a *root* is horizontal, auxin is produced at the apical meristem (root tip), moves up the roots, and, as in stems, concentrates on the lower side of the root. However, in roots, auxin *inhibits* growth. This is because concentrations of auxin are higher in roots than in stems.

Dissolved ions, auxins, gibberellins, and other hormones do not respond to gravity. They remain evenly distributed in a solution, regardless of the presence or directional pull of gravity. Therefore, auxins do not concentrate in the lower parts of stems or roots in *direct* response to gravity. Starch, on the other hand, is insoluble in water and does respond to gravity. It is believed that specialized starch-storing plastids called **statoliths,** which settle at the lower ends of cells, somehow influence the direction of auxin movement.

3. **Thigmotropism** is a response to touch. When vines and other climbing plants contact some object, they respond by wrapping around it. The mechanism for this kind of differential growth is not well understood.

Photoperiodism

Photoperiodism is the response of plants to changes in the **photoperiod,** or the relative length of daylight and night. To respond to changes in the photoperiod, plants maintain a **circadian rhythm,** a clock that measures the length of daylight and night. The mechanism is **endogenous**; that is, it is an internal clock that continues to keep time (although less accurately) even if external cues are absent. External cues, such as dawn and dusk, reset the clock to maintain accuracy.

The mechanism for maintaining the circadian rhythm is not well understood. **Phytochrome,** a protein modified with a light-absorbing chromophore, seems to be involved. There are two forms of phytochrome, P_r (or P_{660}) and P_{fr} (or P_{730}), depending upon which wavelengths of light the phytochrome absorbs, red (wavelength 660 nm) or far-red (730 nm). The two forms are photoreversible; that is, when P_r is exposed to red light, it is converted to P_{fr}; when P_{fr} is exposed to far-red light, it is converted back to P_r. The following observations have been made for many plants:

1. **P_{fr} appears to reset the circadian-rhythm clock.** P_{fr} is the active form of phytochrome and appears to maintain photoperiod accuracy by resetting the circadian-rhythm clock.
2. **P_r is the form of phytochrome synthesized in plant cells.** P_r is synthesized in the leaves of plants.
3. **P_r and P_{fr} are in equilibrium during daylight.** During daylight, P_r is converted to P_{fr}, since red light is present in sunlight. Some far-red light is also present in sunlight, so some of the P_{fr} is converted back into P_r. In this manner, an equilibrium between the two forms of phytochrome is maintained during *daylight.*
4. **P_r accumulates at night.** At night, the levels of P_{fr} drop. This is because there is no sunlight to make the conversion from P_r to P_{fr}. Also, P_{fr} breaks down faster than P_r, and in some plants, P_{fr} is metabolically converted back into P_r. Furthermore, the cell continues to make P_r at night. Thus, P_r accumulates at *night.*
5. **At daybreak, light rapidly converts the accumulated P_r to P_{fr}.** An equilibrium between P_r and P_{fr} is again attained.

6. **Night length is responsible for resetting the circadian-rhythm clock.** If daylight is interrupted with a brief dark period, there is no effect on the circadian-rhythm clock. In contrast, flashes of red or far-red light during the night period can reset the clock. If a plant is exposed to a flash of red light during the night, P_r is converted back to P_{fr}, a shorter night period is measured, and the circadian rhythm is reset. If a flash of far-red light follows the red light, then the effect of the red light is reversed, and the night length is restored to the night length in effect before

the far-red flash. In a series of alternating flashes of red and far-red light, only the last flash affects the perception of night length. Thus, red light shortens the night length and far-red restores the night length.

Many flowering plants initiate flowering in response to changes in the photoperiod. Flowering plants can be divided into three groups, as follows:

1. **Long-day** plants flower in the spring and early summer when daylight is *increasing.*
2. **Short-day** plants flower in late summer and early fall when daylight is *decreasing.* These plants flower when daylight is *less than* a critical length (or when night *exceeds* a critical length).
3. **Day-neutral** plants do not flower in response to daylight changes. Some other cue, such as temperature or water, triggers flowering.

When the photoperiod is such that flowering is initiated, it is believed that a flowering hormone is produced. There is evidence that this hormone, called **florigen,** is a protein produced in leaves that travels to shoot tips.

Phytochrome also seems to be involved in other light-related functions. For example, many seeds require a minimum exposure to light before germinating. The phytochrome system detects changes in the amount of light, and when the critical exposure is exceeded (and when other factors, such as water, are present), production of gibberellins (or destruc-tion of abscisic acid) begins. Germination follows.

By measuring the red to far-red light ratio, the phytochrome system evaluates the quality of light reaching the plant. In this manner, it is able to determine shade from sun. As a result, it can stimulate growth when a shade-intolerant plant is suddenly shaded by other plants.