CHAPTER 4

Tissues

OVERVIEW

A discussion of meristems (apical meristems, vascular cambium, cork cambium, intercalary meristems) and non-meristematic tissues (parenchyma, collenchyma, sclerenchyma, secretory tissues, xylem, phloem, epidermis, periderm) forms the body of this chapter.

Some Learning Goals

1. Know the meristems present in plants and where they are found.
2. Learn the conducting tissues of plants and the function of each cell component.
3. Learn tissues of plants that are neither meristematic nor function in conduction at maturity.

once was privileged to have a new house constructed for me on a vacant lot. I followed the stages of construction with considerable interest. First, a foundation was laid; then, trucks arrived with various building materials, and construction of a frame began. This was followed by the installation of plumbing, electrical wiring, windows, heating and air-conditioning units, vents, and various other devices. Finally, waterproof walls and a roof were added, and, upon occupation, food and other materials were stored in their appropriate niches.

In a sense, the growth of a plant from a seed is something like the construction of a house. Using raw materials from the soil and a superb manufacturing process, each plant develops a framework, “plumbing,” a waterproof covering that includes “windows,” vents, means of waste disposal, and food-storage areas. Even a form of air--conditioning, which enables plants to survive and thrive in the hottest summer sun, is included in each mature plant package. The building components of the framework, plumbing, and related features of plants form the body of this chapter.

There are many interesting modifications of higher plants discussed in the three chapters that follow this one, but, regardless of the outer form, most plants have three or four major groups of organs—**roots, stems, leaves,** and in some instances, **flowers.** Each of these organs is composed of tissues, which are defined as “groups of cells performing a similar function.” Any plant organ may be composed of several different tissues; each tissue is classified according to its structure, origin, or function.

Three basic tissue patterns occur in roots and stems (see *woody dicots, herbaceous dicots,* and *monocots,* discussed in Chapters 5 and 6). The following are major kinds of tissues found in higher plants. The specific types of cells associated with each tissue, as well as illustrations of them, are included in the discussions that follow the classification.

MERISTEMATIC TISSUES

Unlike animals, plants have permanent regions of growth called **meristems,** or *meristematic tissues,* where cells actively divide (Fig. 4.1). As new cells are produced, they typically are small, six-sided, boxlike structures, each with a proportionately large nucleus, usually near the center, and with tiny vacuoles or no vacuoles at all. As the cells mature, however, they assume many different shapes and sizes, each related to the cell’s ultimate function; the vacuoles increase in size, often occupying more than 90% of the volume of the cell.

Apical Meristems

Apical meristems are meristematic tissues found at, or near, the tips of roots and shoots, which increase in length as the apical meristems produce new cells. This type of growth is known as *primary growth.* Three *primary meristems,* as well as embryo leaves and buds, develop from apical meristems. These primary meristems are called **protoderm, ground meristem,** and **procambium.** The tissues they produce are called **primary tissues.** Note their locations in Figure 4.1; they are discussed in Chapters 5 and 6.

Lateral Meristems

The *vascular cambium* and *cork cambium,* discussed next, are **lateral meristems,** which produce tissues that increase the girth of roots and stems. Such growth is termed *secondary growth.*

Vascular Cambium

The **vascular cambium,** often referred to simply as the **cambium,** produces *secondary tissues* that function primarily in support and conduction. The cambium, which extends throughout the length of roots and stems in perennial and many annual plants, is in the form of a thin cylinder of mostly brick-shaped cells. The cambial cylinder often branches, except at the tips, and the tissues it produces are responsible for most of the increase in a plant's girth as it grows. The individual remaining cells of the cambium are referred to as *initials,* while their sister cells are called *derivatives.* The cambium and its cells and tissues are discussed in Chapters 5 and 6.

Cork Cambium

The **cork cambium,** like the vascular cambium, is in the form of a thin cylinder that runs the length of roots and stems of woody plants. It lies outside of the vascular cambium, just inside the outer bark, which it produces. The cork cambium is discussed in Chapters 5 and 6. The tissues laid down by the vascular cambium and the cork cambium are called *secondary tissues,* since they are produced *after* the primary tissues have matured.

Intercalary Meristems

Grasses and related plants have neither a vascular cambium nor a cork cambium. They do, however, have apical meri-stems, and, in the vicinity of **nodes** (leaf attachment areas), they have other meristematic tissues called *intercalary meristems.* The intercalary meristems develop at intervals along stems, where, like the tissues produced by apical meristems, their tissues add to stem length.

TISSUES PRODUCED BY MERISTEMS

After cells are produced by meristems, the cells assume various shapes and sizes related to their functions as they develop and mature. Some tissues consist of only one kind of cell, whereas others may have two to several kinds of cells. Simpler, basic types of such tissues are discussed first, followed by those that are more complex.

Simple Tissues

Parenchyma

Parenchyma tissue is composed of *parenchyma cells* (Fig. 4.2), which are the most abundant of the cell types and are found in almost all major parts of higher plants. They are more or less spherical in shape when they are first produced, but when all the parenchyma cells push up against one another, their thin, pliable walls are flattened at the points of contact. As a result, parenchyma cells assume various shapes and sizes, with the majority having 14 sides. They tend to have large vacuoles and may contain starch grains, oils, tannins (tanning or dyeing substances), crystals, and various other secretions.

More often than not, parenchyma cells have spaces between them; in fact, in water lilies and other aquatic plants, the intercellular spaces are quite extensive and form a network throughout the entire plant. This type of parenchyma tissue—with extensive connected air spaces—is referred to as *aerenchyma.*

Parenchyma cells containing numerous chloroplasts (as found in leaves) are collectively referred to as **chlorenchyma** tissue. Chlorenchyma tissues function mainly in photosynthesis, while parenchyma tissues without chloroplasts function mostly in food or water storage. For example, the soft, edible parts of most fruits and vegetables consist largely of parenchyma.

Some parenchyma cells develop irregular extensions of the inner wall that greatly increase the surface area of the plasma membrane. Such cells, called *transfer cells,* are found in nectaries of flowers and in carnivorous plants, where they apparently play a role in transferring dissolved substances between adjacent cells. Many parenchyma cells live a long time; in some cacti, for example, they may live to be over 100 years old.

Mature parenchyma cells can divide long after they were produced by a meristem. In fact, when a *cutting* (segment of stem) is induced to grow, it is parenchyma cells that start dividing and give rise to new roots. When a plant is damaged or wounded, the capacity of parenchyma cells to multiply is especially important in repair of tissues.

Collenchyma

Collenchyma cells (Fig. 4.3), like parenchyma cells, have living cytoplasm and may remain alive a long time. Their walls generally are thicker and more uneven in thickness than those of parenchyma cells. The unevenness is due to extra primary wall in the corners. Collenchyma cells often occur just beneath the epidermis; typically, they are longer than they are wide, and their walls are pliable as well as strong. They provide flexible support for both growing organs and mature organs, such as leaves and floral parts. The "strings" of celery that get stuck in our teeth, for example, are composed of collenchyma cells.

Sclerenchyma

Sclerenchyma tissue consists of cells that have thick, tough, secondary walls, normally impregnated with **lignin.** Most sclerenchyma cells are dead at maturity and function in support. Two forms of sclerenchyma occur: **sclereids** and **fibers.** Sclereids (Fig. 4.4) may be randomly distributed in other tissues. For example, the slightly gritty texture of pears is due to the presence of groups of sclereids, or *stone cells,* as they are sometimes called. The hardness of nut shells and the pits of peaches and other stone fruits is due to sclereids. Sclereids tend to be about as long as they are wide and sometimes occur in specific zones (e.g., the margins of camellia leaves) rather than being scattered within other tissues.

Fibers (Fig. 4.5) may be found in association with a number of different tissues in roots, stems, leaves, and fruits. They are usually much longer than they are wide and have a proportionately tiny cavity, or *lumen,* in the center of the cell. At present, fibers from more than 40 different families of plants are in commercial use in the manufacture of textile goods, ropes, string, canvas, and similar products. Archaeological evidence indicates that humans have been using plant fibers for at least 10,000 years.

Complex Tissues

Most of the tissues we have discussed thus far consist of one kind of cell, but a few important tissues are always composed of two or more kinds of cells and are sometimes referred to as *complex tissues.* Two of the most important complex tissues in plants, *xylem* and *phloem,* function primarily in the transport of water, ions, and soluble food (sugars) throughout the plant. Some complex tissues are produced by apical meristems, but most complex tissues in woody plants are produced by the vascular cambium and are often referred to as *vascular tissues.*

The *epidermis,* which forms a protective layer covering all plant organs, consists primarily of parenchyma or parenchyma-like cells, but it also often includes specialized cells involved in the movement of water and gases in and out of plants, secretory glands, various hairs, cells in which crystals are isolated, and others that greatly increase absorptive parts of roots. Accordingly, the epidermis and tissues with secretory cells are discussed in this section.

Periderm, which comprises the outer bark of woody plants, consists mostly of cork cells, but it is included in this discussion because it contains pockets of parenchyma-like cells.

Xylem

Xylem tissue is an important component of the "plumbing" and storage systems of a plant and is the chief conducting tissue throughout all organs for water and minerals absorbed by the roots. Xylem consists of a combination of parenchyma cells, fibers, *vessels, tracheids,* and *ray cells* (Fig. 4.6). **Vessels** are long tubes composed of individual cells called **vessel elements** that are open at each end. As each vessel element develops, the perforation plate, in some instances, can become barlike strips of wall material that extend across the openings. However, the flow of fluid through the vessels is not blocked by the strips.

Tracheids, which, like vessel elements, are dead at maturity and have relatively thick secondary cell walls, are tapered at each end, the ends overlapping with those of other tracheids. Tracheids have no openings similar to those of vessels, but there are usually pairs of *pits* present wherever two tracheids are in contact with one another (Fig. 4.7). Pits are areas in which no secondary wall material has been deposited and, as indicated in Chapter 3, they allow water to pass from cell to cell. Figure 4.8 illustrates how, in some plants, pit pairs function in regulating the passage of water between adjacent cells.

In cone-bearing trees and certain other non-flowering plants, the xylem is composed almost entirely of tracheids. The walls of many tracheids, as well as vessel elements, have spiral thickenings on them that are easily seen with the light microscope (Fig. 4.9). Most conduction through xylem is upward, but some is lateral (sideways). The lateral conduction takes place in the **rays.** Ray cells, which also function in food storage, are actually long-lived parenchyma cells that are produced in horizontal rows by special *ray initials* of the vascular cambium. In woody plants, the rays radiate out from the center of stems and roots like the spokes of a wheel (see Figs. 6.6 and 6.8).

Phloem

Phloem tissue (Fig. 4.10), which conducts dissolved food materials (primarily sugars) produced by photosynthesis throughout the plant, is composed mostly of two types of cells without secondary walls. The relatively large, more or less cylindrical **sieve tube members** have narrower, more tapered **companion cells** closely associated with them. Phloem is derived from the parent cells of the cambium, which also produce xylem cells; it often also includes fibers, parenchyma, and ray cells. Sieve tube members, like vessel elements, are laid end to end, forming **sieve tubes.** Unlike vessel elements, however, the end walls have no large openings; instead, the walls are full of small pores through which the cytoplasm extends from cell to cell. These porous regions of sieve tube members are called **sieve plates.**

Sieve tube members have no nuclei at maturity, even though their cytoplasm is very active in the conduction of food materials in solution throughout the plant. Apparently, the adjacent companion cells form a very close relationship with the sieve tubes next to them and aid in the conduction of the food.

Living sieve tube members contain a polymer called *callose* that stays in solution as long as the cell contents are under pressure. If an insect such as an aphid injures a cell, however, the pressure drops, and the callose precipitates. The callose and a phloem protein are then carried to the nearest sieve plate where they form a *callus* plug that prevents leaking of the sieve tube contents.

Sieve cells, which are found in ferns and cone-bearing trees, are similar to sieve tube members but tend to overlap at their ends rather than form continuous tubes. Like sieve tube members, they have no nuclei at maturity, but they have no adjacent companion cells. They do have adjacent *albuminous cells*, which are equivalent to companion cells and apparently function in the same manner.

Epidermis

The outermost layer of cells of all young plant organs is called the **epidermis.** Since it is in direct contact with the environment, it is subject to modification by the environment and often includes several different kinds of cells. The epidermis is usually one cell thick, but a few plants produce aerial roots called **velamen roots** (e.g., orchids) in which the epidermis may be several cells thick, with the outer cells functioning something like a sponge. Such a multiple-layered epidermis also occurs in the leaves of some tropical figs and members of the Pepper Family (Piperaceae), where it protects a plant from desiccation.

Most epidermal cells secrete a fatty substance called **cutin** within and on the surface of the outer walls. Cutin forms a protective layer called the **cuticle** (Fig. 4.11). The thickness of the cuticle (or, more importantly, wax secreted on top of the cuticle by the epidermis) to a large extent determines how much water is lost through the cell walls by evaporation. The cuticle is also exceptionally resistant to bacteria and other disease organisms and has been recovered from fossil plants millions of years old. The waxes deposited on the cuticle in a number of plants (see Fig. 7.7) can reach the surface by diffusion, migrate between cells, or travel through microscopic channels in the cell walls. The susceptibility of a plant to herbicides may depend on the thickness of these wax layers. Some wax deposits are extensive enough to have commercial value. Carnauba wax, for example, is deposited on the leaves of the wax palm. It and other waxes are harvested for use in polishes and, in the past, for phonograph records. In colonial times, a wax obtained from boiling leaves and fruits of the wax myrtle was used to make bayberry candles.

In leaves, the epidermal cell walls perpendicular to the surface often assume bizarre shapes that, under the microscope, give them the appearance of pieces of a jigsaw puzzle. Epidermal cells of roots produce tubular extensions called *root hairs* (see Fig. 5.4) a short distance behind the growing tips. The root hairs greatly increase the absorptive area of the surface.

Hairs of a different nature occur on the epidermis of above-ground parts of plants. These hairs form outgrowths consisting of one to several cells (Fig. 4.12). Leaves also have numerous small pores, the **stomata,** bordered by pairs of specialized epidermal cells called **guard cells** (see Figs. 7.8 and 9.13). Guard cells differ in shape from other epidermal cells; they also differ in that chloroplasts are present within them. The stomatal apparatus is discussed in Chapters 7 and 9. Some epidermal cells may be modified as **glands** that secrete protective or other substances, or modified as hairs that either reduce water loss or repel insects and animals that might otherwise consume them (Fig. 4.13).

Periderm

In woody plants, the epidermis is sloughed off and replaced by a **periderm** after the cork cambium begins producing new tissues that increase the girth of the stem or root. The peri-derm constitutes the outer bark and is primarily composed of somewhat rectangular and boxlike **cork** cells, which are dead at maturity (see Fig. 4.14). While the cytoplasm of cork cells is still functioning, it secretes a fatty substance, **suberin,** into the walls. This makes cork cells waterproof and helps them protect the phloem and other tissues beneath the bark from drying out, mechanical injury, and freezing temperatures. Some cork tissues, such as those produced by the cork oak, are harvested commercially and are used for bottle corks and in the manufacture of linoleum and gaskets.

Some parts of a cork cambium form pockets of loosely arranged parenchyma cells that are not impregnated with suberin. These pockets of tissue protrude through the surface of the periderm; they are called **lenticels** (Fig. 4.14) and function in gas exchange between the air and the interior of the stem. The fissures in the bark of trees have lenticels at their bases. The various tissues discussed are shown as they occur in a woody stem in Figure 6.6.

Secretory Cells and Tissues

All cells secrete certain substances that can damage the cytoplasm, if allowed to accumulate internally. Such materials either must be isolated from the cytoplasm of the cells in which they originate or moved outside of the plant body. Often, the substances consist of waste products that are of no further use to the plant, but some substances, such as nectar, perfumes, and plant hormones (discussed in Chapter 11), are vital to normal plant functions.

Secretory cells may function individually or as part of a **secretory tissue.** Secretory cells or tissues, which often are derived from parenchyma, can occur in a wide variety of places in a plant. Among the most common secretory tissues are those that secrete nectar in flowers; oils in citrus, mint, and many other leaves; mucilage in the glandular hairs of sundews and other insect-trapping plants; latex in members of several plant families, such as the Spurge Family; and resins in coniferous plants, such as pine trees. Latex and resins are usually secreted by cells lining tubelike ducts that form networks throughout certain plant species (see Fig. 6.11). Some plant secretions, such as pine resin, rubber, mint oil, and opium, have considerable commercial value.

Summary

1. A group of cells performing a common function is called a tissue.
2. Apical meristems are found in the vicinity of the tips of roots and stems; the vascular cambium and the cork cambium occur as lengthwise cylinders within roots and stems; intercalary meristems occur in the vicinity of nodes of grasses and related plants.
3. Tissues produced by meristems consist of one to several kinds of cells. They include parenchyma, collenchyma, sclerenchyma, epidermis, xylem, phloem, periderm, and secretory tissues.
4. Parenchyma cells are thin-walled, while collenchyma cells have unevenly thickened walls that provide flexible support for various plant organs.
5. Two types of sclerenchyma occur—fibers (which are long and tapering) and sclereids (which are short in length); both types have thick walls and are usually dead at maturity.
6. Complex tissues have more than one kind of cell. The principal types are xylem, phloem, epidermis, and -periderm.
7. Xylem conducts water and minerals throughout the plant. It consists of a combination of parenchyma, fibers, vessels (tubular channels), tracheids (cells with tapering end walls that overlap), and ray cells (involved in lateral conduction).
8. Phloem conducts primarily dissolved sugars throughout the plant. It is composed of sieve tubes (made up of cells called sieve tube members), companion cells (that apparently regulate adjacent sieve tube members), parenchyma, ray cells, and fibers. Callose aids in plugging injured sieve tubes. Sieve cells, which have overlapping end walls, and adjacent albuminous cells take the place of sieve tube members and companion cells in ferns and cone-bearing trees.
9. The epidermis is usually one cell thick, with fatty cutin (forming the cuticle) within and on the surface of the outer walls. The epidermis may include guard cells that border pores called stomata; root hairs, which are tubular extensions of single cells; other hairs that consist of one to several cells; and glands that secrete protective substances.
10. Periderm, which consists of cork cells and loosely arranged groups of cells comprising lenticels involved in gas exchange, constitutes the outer bark of woody plants.
11. Secretory tissues occur in various places in plants; they secrete substances such as nectar, oils, mucilage, latex, and resins.

Review Questions

1. What is the function of meristems? Where are they located?
2. How are parenchyma, collenchyma, and sclerenchyma distinguished from one another?
3. Distinguish between epidermis and periderm.
4. What are the functions of xylem and phloem? What cells are involved in their normal activities?
5. What types of substances do secretory cells secrete?

Discussion Questions

1. Most plant meristems are located at the tips of shoots and roots and in cylindrical layers within stems and roots. What could happen if they were present in leaves?
2. The cambium produces xylem toward the center of a tree and phloem toward the outside. Do you think it would make any difference if the positions of the xylem and phloem were reversed? Why?

Additional Reading

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A heliconia (*Heliconia* sp.), native to the New World tropics. There are about 200 known species of these striking plants, many of which are becoming increasingly popular as ornamentals in tropical and subtropical areas.

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Figure 4.1 A diagram of the longitudinal axis of a plant, showing the location of meristems. Note that in most microscope slides used in botany laboratories, meristems are normally stained green.

Figure 4.2 Parenchyma cells. They are more or less spherical when first formed, but as their walls touch other parenchyma cell walls, the cells end up with an average of 14 sides at maturity. ×100.

Figure 4.3 Collenchyma cells. Note the walls are unevenly thickened at the corners. ×100.

Figure 4.4 *A.* Sclereids (stone cells) of a pear in cross section. ×1,000. *B.* Sclereids in the leaf of a wheel tree (*Trochodendron aralioides*). ×1,000. *(B. Photomicrograph by G. S. Ellmore)*

Figure 4.5 Fibers. *A.* A cross section of a portion of stem tissue from a linden tree (*Tilia* sp.). ×1,000. Note the thickness of the walls of the darker fibers. *B.* A longitudinal section through fibers in a *Welwitschia* leaf. ×1,000. *(B. Photomicrograph by G. S. Ellmore)*

Figure 4.6 *A.* Tracheids. ×200. *B.* Vessel elements. ×200.

Figure 4.7 Pits. Pits are depressions in cell walls where the secondary wall does not form. There may be from one or two to several thousand in a cell. They often occur in pairs, with one on each side of the middle lamella. Some, called *bordered pits* (right), bulge out from the wall and resemble doughnuts in surface view, while others, called *simple pits* (left), do not bulge.

Figure 4.8 How water flow is controlled in adjacent pairs of bordered pits. The pits are separated by a *pit membrane* consisting of the middle lamella and two thin layers of primary walls. *A.* Water moves relatively freely through the pit openings and pit membrane when the torus (a thickened region of the pit membrane) is in the center. *B.* If the flexible pit membrane swings to one side so that the torus blocks an opening, water movement through the pit pair is restricted.

Figure 4.9 Spiral thickenings on the inside walls of vessel elements. ×400.

Figure 4.10 Longitudinal view of part of the phloem of a black locust tree *(Robinia pseudo-acacia).* ×1,000.

Figure 4.11 A portion of a cross section of a kaffir lily (*Clivia*) leaf, showing the thick cuticle secreted by the epidermis. ×1,000.

Ecological Review

The first point of contact between plants and the environment is a surface layer of cells called the epidermis. The structure of the epidermis, particularly the thickness of waxes on its surface, determines the potential rate of water exchange between a plant and the environment. The resistance of the epidermis to water loss is generally higher in the plants of arid environments. A second critical ecological function of the epidermis is a barrier to attack by pathogens. Pathogens, which may restrict the distribution of plant species and strongly influence plant population size, are an important part of a plant's biological environment. The extent of development of a plant's xylem and sclerenchyma cells also is related to the plant's environment, with, for example, aquatic plants having weakly developed xylem, large trees having well-developed xylem, and fire-resistant trees, such as redwoods, having thick bark.

Figure 4.12 Hairs on the surface of an ornamental mint plant. ×50.

A.

B.

Figure 4.14 Periderm and a lenticel. A cross section through a small portion of elderberry (*Sambucus*) periderm, showing a large lenticel, ca. ×250.

Figure 4.13 *A.* Tack-shaped glands and epidermal hairs of various sizes on the surface of flower bracts of a western tarweed. Scanning electron micrograph ca. ×200. *B.* Hairs on the surface of a tomato plant stem. Note the raised stoma to the right of center. Scanning electron micrograph ca. ×300. *(A. Courtesy Robert L. Carr and Charles Sternburg; B. Courtesy Dr. Tahany H. I. Sherif)*