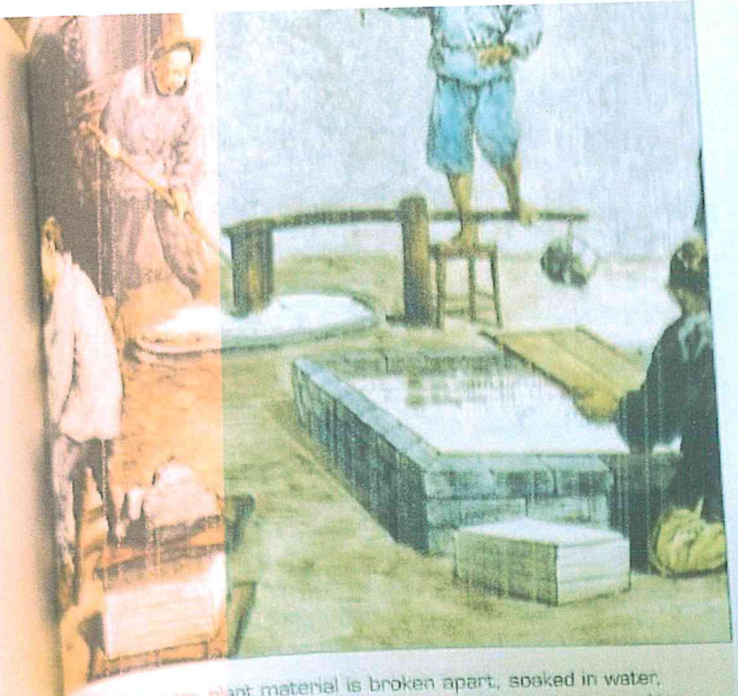


To make paper, plant material is broken apart, soaked in water, spread into sheets, and dried. The Chinese invented papermaking about 2,000 years ago.

Versatile Paper

Our uses of paper seem endless. We use it to package food, as currency, to communicate, to decorate walls, and even to mop up various bodily secretions. This versatile product consists of cellulose from plant cell walls, mixed with water and spread on a fine mesh. As the water drains, the fibers entangle, adjacent cellulose molecules bond, and paper forms.

Manufacturing paper today demands a constant supply of wood pulp from millions of trees. Over the centuries, however, paper has been made from cotton and linen rags, hemp, jute, bamboo, sugarcane, wheat, rice straw, aspen, beech, birch, fir, gum, oak, pine, hemlock, and spruce.

The word "paper" comes from "papyrus," which refers to the sedge plant *Cyperus papyrus*, which the ancient Egyptians used to make sheets of writing material. They took strips from the interiors of stems, flattened them, and arranged them crosswise. They added water, then pressed the material so that the fibers would adhere, and allowed it to dry. The sheets were smoothed and rolled up. About 500 B.C., the Greeks and Romans discovered the same use for papyrus. Then a Chinese man named Ts'ai Lun, who served in the emperor's court in A.D. 105, invented modern paper from the inner bark of the mulberry tree, *Broussonetia papyrifera*. He ground up the bark and spread it on a cloth mesh held between sticks of bamboo.

–continued

Plant Form and Function

26

This sheet of paper was handmade with paper mulberry (*Broussonetia papyrifera*). The long fibers are easily visible in the finished sheets.

Arabs who took Chinese prisoners learned from them the art of papermaking, and soon Baghdad had a thriving paper industry. Paper came to Japan in A.D. 610 and the Near East in 800. The Crusades and the Moorish conquest of north Africa and Spain brought papermaking to Europe, first in Spain in 1150. Meanwhile, the Aztecs and Mayans used fibers from native American plants tc make paper.

The first paper mill in the United States was built near Philadelphia in 1690. Paper for newspapers came from linen or cotton rags. Around 1800, machines took over the difficult task of making paper. In 1840, with the rag supply becoming depleted, attention turned to wood pulp in several nations.

To make paper, plant material is gently broken apart in water, forming a slurry of fibers. The material is compressed into a sheet, then dried. Several chemical steps are added to the process to improve the transformation of wood pulp into paper. For example, to make white paper, manufacturers treat wood fibers with strong chemicals to dissolve lignin, leaving cellulose behind. On August 23, 1873, *The New York Times* published its first all-wood issue. Today, each issue of the Sunday *Times* uses 150 acres (0.61 square kilometers) of trees. Currently, people in the United States use almost 200,000 tons of paper each day, despite increasing use of electronic communication.

To conserve wood resources, magazines and books are printed on recycled paper, and napkins, towels, and paperboard come from recycled paper. To recycle paper, old newspapers, magazines, and junk mail are placed into huge tanks called pulpers, to which solvents and detergents are added to remove inks. The fibers are then reassembled into new paper.

Another approach to preserving wood is to find alternative sources of paper. One jeans manufacturer converts leftover fabric to paper, which the company uses for stationery and labels. Hemp fibers make an excellent, long-lasting paper that doesn't require bleaching. Early drafts of government documents, including the Declaration of Independence and the Constitution, were written on hemp-based paper.

One large American publishing company took a clever approach to saving paper—it trimmed 2.5 centimeters from the width of toilet paper rolls in its building. The employees still used the same number of rolls each month. Trimming all rolls of toilet paper in the United States would save a million trees a year. Other inventive ideas could undoubtedly save millions more.

Other Plant Products
Food
Herbs and spices
Fossil fuels
Drugs
Textiles
Building materials
Houseplants and cut flowers
Landscape plants

26.1 Plant Tissue and Cell Types

Plant bodies consist of four basic tissue types. Cells in meristems divide, increasing the length and girth of the plant. Ground tissue is specialized for storage, photosynthesis, and physical support. Dermal tissue protects the plant, while allowing gas exchange and water and mineral uptake. Water and dissolved materials move within a plant in vascular tissue.

A cactus, an elm tree, and a dandelion look very different from one another, yet each consists of the same basic parts. Most people are familiar with the vegetative, or nonreproductive, plant organs—the roots, stems, and leaves that support each other. Through photosynthesis, the aboveground part of a plant, or **shoot,** produces carbohydrates. A portion of this sugar supply nourishes the **roots,** which are usually belowground. In turn, roots absorb water and minerals that are transported to the shoots.

The plant organs are composed of specialized tissues that make and store food, acquire and transport water and dissolved nutrients, grow, provide support, and protect the plant from predators. Specialized cells give these tissues their unique properties. This chapter begins by exploring the tissue and cell types that perform the functions of plant life, then describes how these cell and tissue types work together to produce the diversity of stems, leaves, and roots found in herbaceous (nonwoody) and woody plants. The emphasis is on flowering plants—angiosperms—the most diverse and abundant plants.

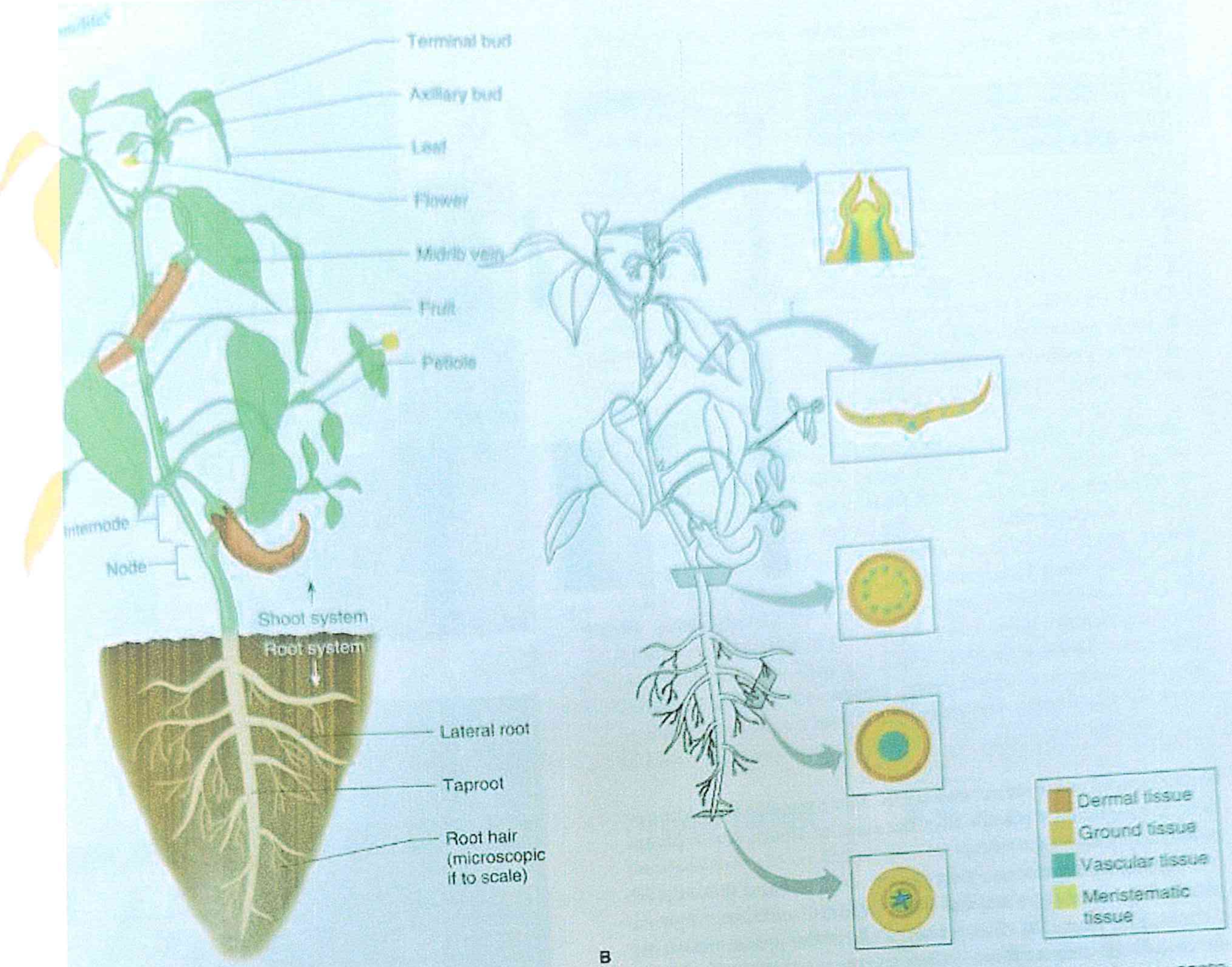


FIGURE 26.1 **Parts of a Flowering Plant.** (**A**) A plant consists of a root system and a shoot system. Roots, stems, and leaves are vegetative organs; flowers and fruits are reproductive structures. (**B**) Four tissue types build plant organs.

All the plant's organs consist of the same four basic tissue types (figure 26.1 and table 26.1). Meristematic tissue adds new cells that enable a plant to grow and specialize. Ground tissue makes up the bulk of the living plant tissue and stores nutrients or photosynthesizes. Dermal tissue covers and protects the plant, controls gas exchange with the environment, and, in roots, absorbs water. Vascular tissues, including xylem and phloem, conduct water, minerals, and photosynthate (sugars) throughout the plant.

TABLE 26.1

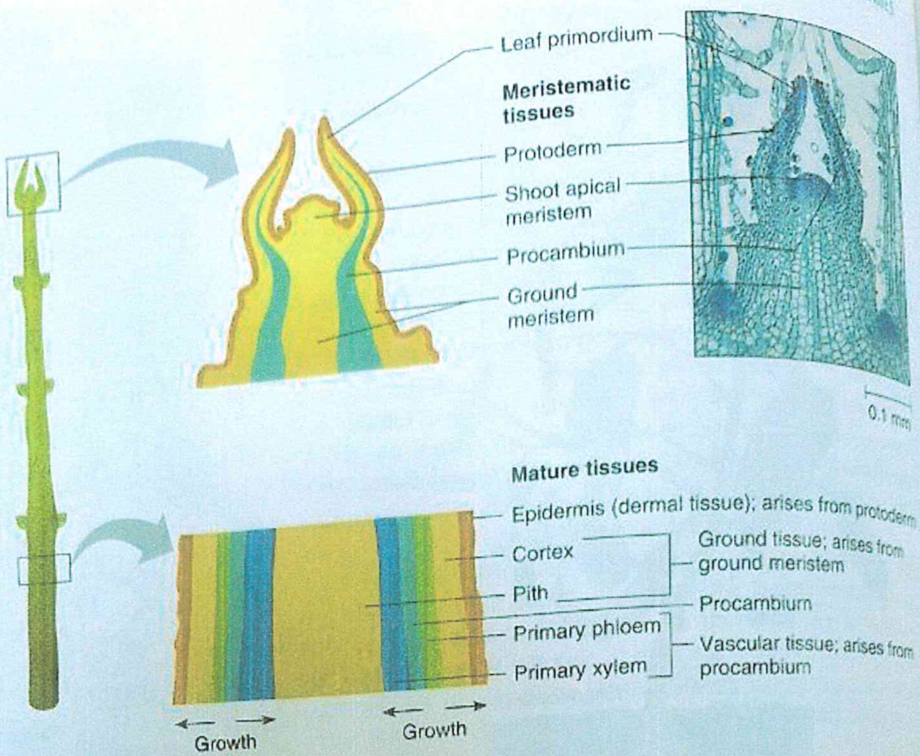
Tissue Types in Angiosperms

Tissue	Function
Meristem	Cell division and growth
Ground	Bulk of interiors of roots, stems, and leaves
Dermal	Protects plant; controls gas exchange; absorbs water
Vascular	Conducts water, dissolved minerals, and photosynthate

Meristems

Meristems are localized regions in a plant that undergo mitotic cell division and are the ultimate source of all the cells in a plant. These regions of active cell division account for the elongation of root and stem tips, the growth of buds, and the

FIGURE 26.2 **Primary Growth of a Dicot's Shoot.** Looking at the tissue layers that comprise the growing tip of a shoot reveals how apical meristems give rise to primary meristems, which form mature, specialized tissues visible in older parts of the shoot.



thickening of some stems and roots. Meristematic tissues function throughout a plant's life; because of them, some plants never stop growing.

Apical meristems are near the tips of roots and shoots in all plants. Figure 26.2 depicts the location of the apical meristem in a shoot, and figure 26.15 in a root. Cells in the apical meristems are small and unspecialized. When the meristematic cells divide, the root or shoot tip lengthens in what is called **primary growth.** Apical meristems give rise to three other types of meristems—the ground meristem, protoderm, and procambium—which produce ground tissue, epidermal tissue, and vascular tissue.

In contrast to apical meristems, which lengthen a plant, **lateral meristems** (also called cambia) grow outward to thicken the plant. This process, called **secondary growth,** does not occur in all plants. Wood forms from secondary growth, which is discussed at the end of this chapter.

In some plants, intercalary meristems occur between areas that are more developed. Grasses, for example, tolerate grazing (and mowing) because the bases of their leaves have intercalary meristems that divide to regrow the leaf when it is munched off. Table 26.2 summarizes meristem types.

Ground Tissue

Ground tissue makes up most of the primary body of a flowering plant, filling much of the interior of roots, stems, and leaves. These cells have many functions, including storage, support, and basic metabolism. Ground tissue consists of three cell types: parenchyma, collenchyma, and sclerenchyma.

TABLE 26.2

Meristem Types

Type	Function
Apical meristem	Growth at root and shoot tips
Lateral meristem	Growth outward, thickening plant
Intercalary meristem	In grass, allows rapid regrowth of mature leaves

Parenchyma cells are the most abundant cells in the primary plant body. They are structurally relatively unspecialized, although they can divide, which enables the tissue to become specialized in response to injury or a changing environment. These living cells typically have thin primary (outer) cell walls.

Parenchyma cells store the edible biochemicals in plants, such as the starch in a potato or a kernel of corn. These cells may also store fragrant oils, salts, pigments, and organic acids. Parenchyma cells of oranges and lemons, for example, store citric acid, which gives them their tart taste. These cells also conduct vital functions, such as photosynthesis, cellular respiration, and protein synthesis. Chlorenchyma cells are parenchyma cells that

26.4

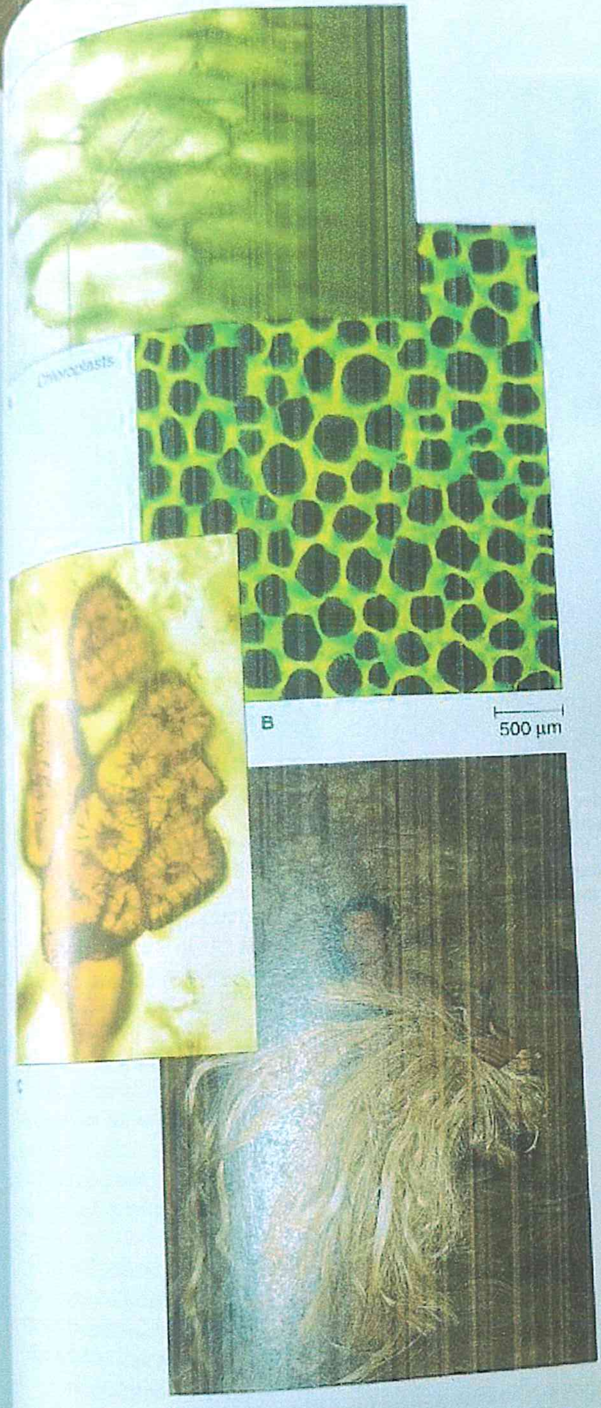


FIGURE 26.3 **Plant Cells.** (**A**) Parenchyma cells are usually structurally unspecialized and store carbohydrates and other important biochemicals. Chlorenchyma is a type of parenchyma that photosynthesizes. (**B**) Collenchyma differentiates from parenchyma and supports growing shoots with unevenly thickened cell walls. The collenchyma tissue pictured forms the "string" of a celery stalk. Sclerenchyma supports plant parts that are no longer growing. This cell type includes these sclereids (**C**), which provide the gritty texture of pear flesh, and long fibers (**D**), such as these from Manila hemp (*Musa textilis*), which is used to make rope.

photosynthesize. Their chloroplasts impart the green color to leaves (**figure 26.3A**). Other parenchyma cells, such as the "rays" in wood, are associated with vascular tissues.

Collenchyma cells are elongated living cells that differentiate from parenchyma and support the growing regions of shoots. Collenchyma cells have unevenly thickened primary cell walls that can stretch and elongate with the cells. As a result, collenchyma provides support without interfering with the growth of young stems or expanding leaves (figure 26.3B). **cell walls, p. 74**

Sclerenchyma cells have thick, rigid secondary cell walls (a trilayered structure inside the outer, or primary, cell wall). Lignin strengthens the walls of these cells, which are usually dead at maturity, supporting parts of plants that are no longer growing. Two types of sclerenchyma form from parenchyma: sclereids and fibers.

Sclereids have many shapes and occur singly or in groups. Small groups of sclereids create a pear's gritty texture (figure 26.3C). Sclereids may form hard layers, such as in the hulls of peanuts. Fibers are elongated cells that usually occur in strands that vary from a few to a few hundred millimeters long (figure 26.3D). Paper often includes wood fibers, and many textiles are also sclerenchyma fibers. Humans now cultivate more than 40 families of plants for fibers and have fashioned cords from fibers since 8000 B.C. The hard leaf fibers of *Agave sisalana*, commonly known as sisal, or the century plant, are used to make brooms, brushes, and twines. Linen comes from soft fibers from the stems of *Linum usitatissimum*, or flax.

Dermal Tissue

Dermal tissue covers the plant. The **epidermis**, usually only one cell layer thick, covers the primary plant body. Epidermal cells are flat, transparent, and tightly packed. Special features of the epidermis provide a variety of functions.

The **cuticle** is an extracellular covering over all the aerial epidermis of a plant; it protects the plant and conserves water (**figure 26.4A**). The cuticle consists primarily of cutin, a waxy material that epidermal cells produce. This covering retains water and prevents desiccation. As a result, plants can maintain a watery internal environment—a prerequisite to survival on dry land. The cuticle and underlying epidermal layer also are a first line of defense against predators and infectious agents. In many plants, a smooth white layer of wax covers the cuticle; when it is thick, it is visible on leaves and fruits. The layer on the undersides of wax palm leaves may be more than 5 millimeters thick. It is harvested and used to manufacture polishes and lipsticks.

An impermeable cuticle covers the tightly packed epidermal cells, but plants must exchange water and gases with the atmosphere. They do this through specialized pores, called **stomata** (singular: stoma) (see figure 6.7 and figure 26.4B). **Guard cells** surround the pores and control their opening and closing, which regulates gas and water exchange.

When a plant has sufficient water, potassium ions (K^+) move into guard cells. Because the concentration of K^+ becomes greater inside than outside the cells, water enters them by osmosis. This

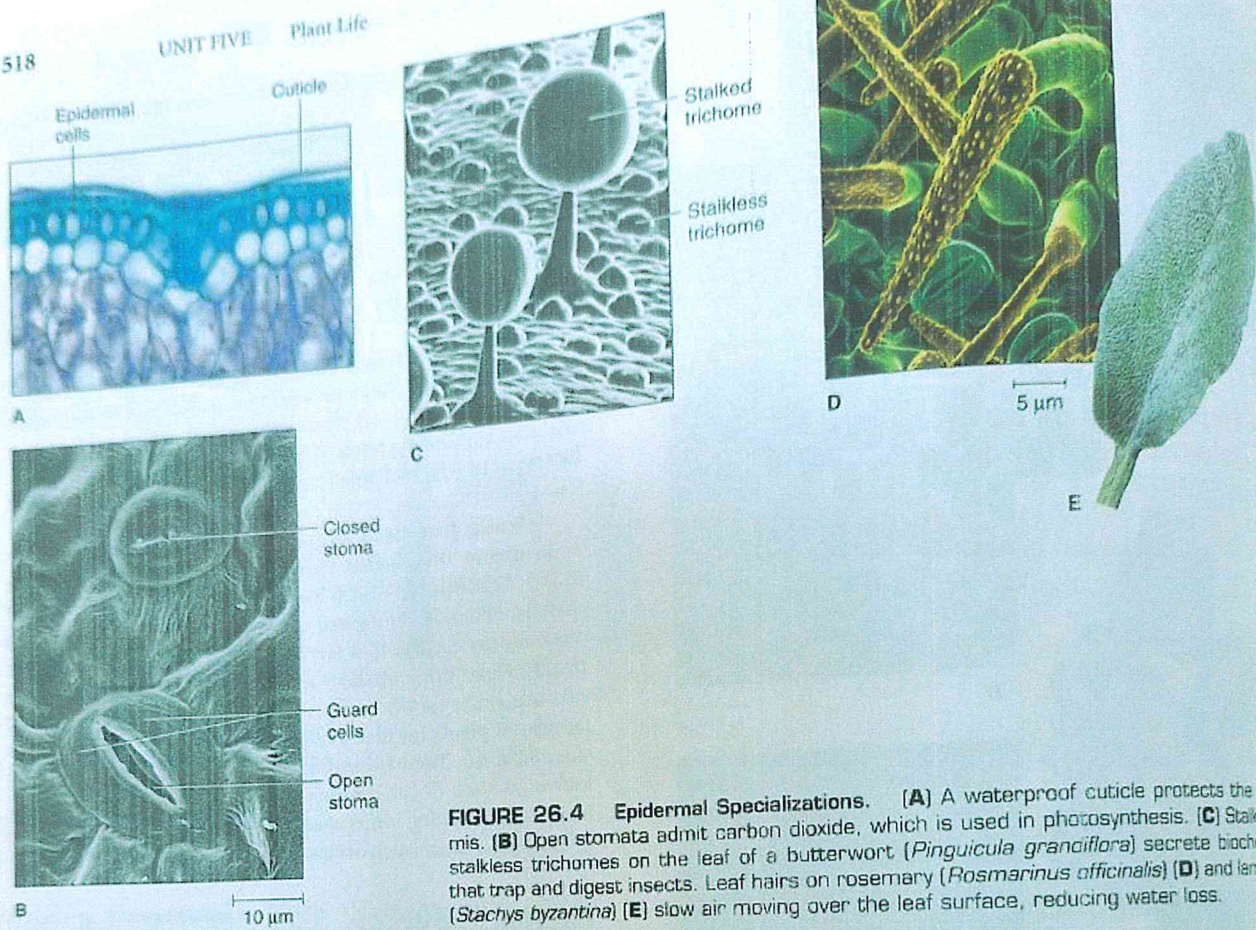


FIGURE 26.4 Epidermal Specializations. **(A)** A waterproof cuticle protects the epidermis. **(B)** Open stomata admit carbon dioxide, which is used in photosynthesis. **(C)** Stalked and stalkless trichomes on the leaf of a butterwort (*Pinguicula grandiflora*) secrete biochemicals that trap and digest insects. Leaf hairs on rosemary (*Rosmarinus officinalis*) **(D)** and lamb's ear (*Stachys byzantina*) **(E)** slow air moving over the leaf surface, reducing water loss.

swells the guard cells, which opens the stoma between them. When too much water evaporates from the plant, cells in the leaves lose turgor pressure, which causes release of a hormone, abscisic acid. This hormone ultimately lowers K^+ concentration inside the guard cells (**figure 26.5**). Water exits, the guard cells collapse onto each other, and the stoma closes. • **abscisic acid, p. 574**

Stomata regulate the amount of water that evaporates from leaves, a process called transpiration. Because stomata help plants conserve water, they are an essential adaptation for life on land. They are also the pores through which carbon dioxide diffuses into a leaf for photosynthesis. Stomata may be very numerous. The underside of a black oak leaf, for example, has 100,000 or so stomata per square centimeter! • **transpiration, p. 542**

Trichomes are outgrowths of the epidermis present in nearly all plants (see figure 26.4C–E). These structures have many functions, including deterrence of predators. Hook-shaped trichomes may impale marauding animals. In some plants, predators may inadvertently break off the tips of trichomes, releasing a sticky substance that traps the animal. For example, trichomes of the stinging nettle have spherical tips that break off and penetrate a predator's body, injecting their toxic contents into the wounds. Trichomes of carnivorous plants such as the Venus's flytrap secrete enzymes that digest trapped animals (see Investigating Life 22.1). These trichomes then absorb the digested prey.

Leaf hairs, a class of trichomes, are epidermal structures that slow the movement of air over the leaf surface (see figure 26.4D–E). This action reduces water loss. **Root hairs** are trichomes that increase the root surface area for absorbing water and minerals.

Many trichomes are economically important. Cotton fibers, for example, are trichomes from the epidermis of cotton seeds. Burrs, on which the fastener Velcro is based, are also trichomes. Menthol comes from peppermint trichomes, and hashish, a powerful narcotic, is purified resin from *Cannabis* trichomes.

Vascular Tissue

Vascular tissues are specialized conducting tissues that transport water, minerals, carbohydrates, and other dissolved compounds throughout the plant. The two types of vascular tissue, **xylem** and **phloem**, form a continuous distribution system that is embedded in the plant's ground tissues (see figure 27.1). Together, these primary vascular tissues make up a central cylinder, called the stele,

26.6

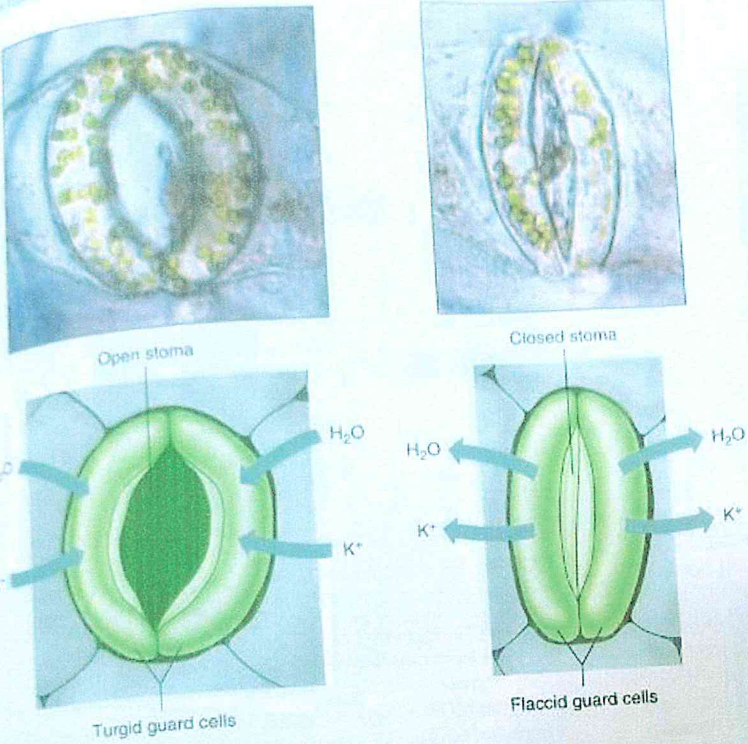


FIGURE 26.5 **Opening and Closing of Stomata.** Relative concentrations of potassium ions (K^+) in guard cells and adjacent cells determine whether the stoma is opened or closed. When concentrations in guard cells are high, water enters, and the guard cells swell, opening the stoma. When concentrations in guard cells are low, water leaves, and the stoma closes as the guard cells collapse.

in the stems and roots of the primary plant body. The cell types making up vascular tissue are described here, and their function is further explored in chapter 27.

Xylem Xylem, from the Greek for wood, transports water and dissolved minerals from the roots to all parts of the plant. This water replaces water lost in transpiration through stomata.

The two kinds of conducting cells in xylem are **tracheids** and **vessel elements** (figure 26.6). Both are elongated, dead at maturity, and have thick secondary walls. The fact that these cells are dead means that there are no organelles to block water flow. The thick, lignified cell walls prevent tracheids and vessel elements from collapsing as water rises through the plant under negative pressure. They also help keep the plant upright.

Tracheids, the least specialized conducting cells, are long and narrow, overlapping at their tapered ends. Water moves from tracheid to tracheid through thin areas in cell walls called pits. Water moves slowly because of the small diameter and end walls of the tracheids. Tracheids are probably ancient cells, because they are the only means of water conduction in most nonflowering vascular plants, which are more ancient than flowering plants.

Vessel elements are more specialized than tracheids. Unlike tracheids, vessel elements are short, wide, barrel-shaped cells. Vessel elements stack end to end, and their end walls disintegrate, forming hollow tubes, or vessels, that may extend from a centimeter to 3 meters long. Vessel elements are like cellulose pipes, and water in them moves much faster than in the narrower tracheids (see figure 26.6). The greater width of vessel elements and the fact that water can pass directly from one "cell" to another accounts for their more efficient water conduction.

Phloem Phloem transports dissolved organic compounds, primarily carbohydrates, throughout a plant. Phloem sap also contains hormones, alkaloids, viruses, and inorganic ions. Unlike xylem, which transports water upward under negative pressure, like a drinking straw, phloem transports substances under positive pressure, which is like water flowing through a hose when the spigot is turned on. Thus, water and dissolved sugars can move through phloem in all directions. Also, the conducting cells of phloem, unlike those of xylem, are alive at maturity. Their cell walls have thin areas perforated by many structures called sieve pores, through which the cytoplasm of adjacent cells connects. Solutes move through these pores from cell to cell.

Different vascular plants have different types of phloem cells. **Sieve cells** are long, tapering cells with overlapping ends that are usually found in gymnosperms and seedless vascular plants. Phloem sap moves from cell to cell through sieve pores, which permeate all walls of the sieve cells. **Sieve tube members** are mostly in angiosperms, and they are more specialized than sieve cells. In most sieve tube members, the pore areas are

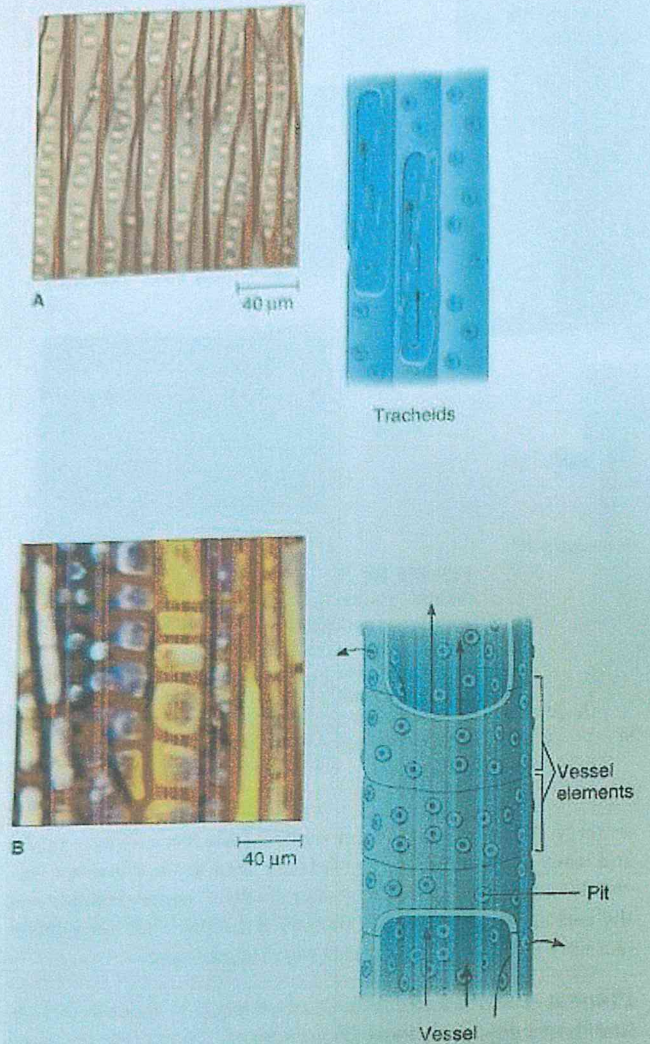


FIGURE 26.6 **Two Types of Xylem Cells.** Xylem transports water and dissolved minerals from roots to shoots. Tracheids (**A**) are long, narrow, and less specialized than the barrel-shaped vessel elements (**B**). Both types of xylem structures consist of dead cells.

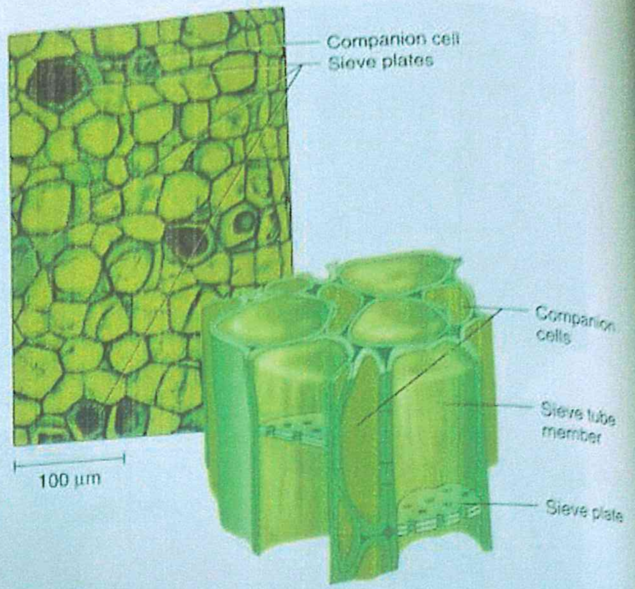


FIGURE 26.7 **Phloem Cells.** Phloem consists of living cells and transports an aqueous solution of carbohydrates, hormones, ions, and various other substances under positive pressure in all directions. In flowering plants, sieve tube members with perforated end walls form sieve tubes that carry phloem sap.

aggregated into **sieve plates,** usually at the ends of the cells (**figure 26.7**). Many sieve tube members aligned end to end comprise a single functional unit, the sieve tube, much as vessels in xylem are made up of vessel elements arranged end to end. Near sieve tube members are **companion cells,** which are specialized parenchyma cells that help transfer carbohydrates into and out of the sieve tube members. • **pressure flow theory, p. 545**

Table 26.3 reviews the major tissue and cell types in plants.

26.1 Mastering Concepts

1. What is the function of meristematic tissue?
2. What cell types make up ground tissue?
3. How does dermal tissue protect a plant and enable gas exchange to occur?
4. What are the functions of the two types of vascular tissue in plants?
5. What types of cells make up each of the two types of vascular tissue?

26.2 Anatomy of a Plant

A plant's tissues are organized into stems, leaves, and roots, each of which can be modified. These tissues and organs associate to produce a great variety of specialized body forms.

The organs of a plant are composed of meristematic, dermal, ground, and vascular tissues. Natural selection sculpts different organizations of these basic plant tissues as certain forms become adapted to particular environments. We look now at the basic parts of a flowering plant.

TABLE 26.3

Plant Tissue and Cell Types

Tissue Type	Cell Types	Function
Meristem	Undifferentiated	Produce new cells that add to plant's length or girth
Ground	Parenchyma	Photosynthesis, storage, respiration
	Collenchyma	Elastic support
	Sclerenchyma (fibers and sclereids)	Nonelastic support
Dermal	Epidermal	Protection, regulation of gas exchange in stems and leaves, absorption of water and minerals in roots
Vascular (xylem)	Tracheids or vessel elements	Water and mineral conduction
	Parenchyma	Storage
	Sclerencyhma (fibers and sclereids)	Support
Vascular (phloem)	Sieve cells or sieve tube members	Conduction of organic molecules
	Companion cells (specialized parenchyma)	Transfer carbohydrates to/from sieve tube members
	Sclerenchyma (fibers and sclereids)	Support

Stems

The central axis of a shoot system is the **stem.** Stems support leaves, produce and store sugars, and transport nutrients and water between roots and leaves. Stems may provide food for other species—asparagus, for example, is an edible stem.

Stems consist of **nodes** (areas of leaf attachment) and **internodes** (portions of the stem between the nodes) (see figure 26.1). The angle between the stem and leaf stalk (petiole) is the leaf axil. Axillary buds are undeveloped shoots that form in leaf axils. Although axillary buds can elongate to form a branch or flower, many remain small and dormant.

Stems grow and differentiate at their tips, with new cells originating at the shoot's apical meristem (see figure 26.2). The shoot elongates as cells divide, grow, and become specialized into ground tissue, vascular tissue, or dermal tissue.

In most plants, stems also elongate in the internodal regions, and separate nodes may be easily distinguished. However, some plants have stems called rosettes that elongate very little. Rosettes have short internodes and overlapping leaves. A cabbage head is a rosette made of large, tightly packed leaves.

The epidermis surrounding a stem is a transparent layer only one cell thick. It contains stomata, but fewer than are in a leaf's epidermis. The epidermis of a stem also may have protective trichomes.

Vascular tissues in the stems of nonwoody flowering plants are organized into groups called **vascular bundles** that branch into leaves at the nodes. Phloem forms on the outer portions of a bundle, whereas xylem forms to the inside. Often, thick-walled sclerenchyma fibers associate with vascular bundles and strengthen the vascular tissue. The flax fibers used to make linen are one example.

Vascular bundles are arranged differently in different types of plants. Consider the two groups of flowering plants: monocotyledons (monocots for short), which have one first, or "seed," leaf; and dicotyledons (dicots), which have two seed leaves (see figure 22.18). Monocots such as corn have vascular bundles scattered throughout their ground tissue, whereas dicots such as sunflowers have a single ring of vascular bundles (**figure 26.8**).

The ground tissue that fills the area between the epidermis and vascular tissue in a stem is called the **cortex.** This area is mostly parenchyma but may include a few supportive collenchyma strands. Some cortical cells are photosynthetic and store starch. The centrally located ground tissue in dicots is called **pith.**

Many plant stems are modified for special functions such as reproduction, climbing, protection, and storage (**figure 26.9**). Some specialized stems are listed in the following.

- Stolons, or runners, are stems that grow along the soil surface. New plants form from their nodes. Strawberry plants develop stolons after they flower, and several plants can arise from the original one.
- Thorns often are stems (branches) modified for protection, such as on hawthorn plants.
- Succulent stems of plants such as cacti are fleshy and store large volumes of water.
- Tendrils support plants by coiling around objects, sometimes attaching by their adhesive tips. Tendrils enable a plant to maximize sun exposure. The stem tendrils of grape plants readily entwine around anything they can touch. (Leaves may also be modified into tendrils.)
- Tubers are swollen regions of underground stems that store nutrients. Potatoes are tubers produced on stolons or underground stems called rhizomes.
- Rhizomes are underground stems that produce roots and new shoots. Ginger is a spice that is derived from a rhizome.

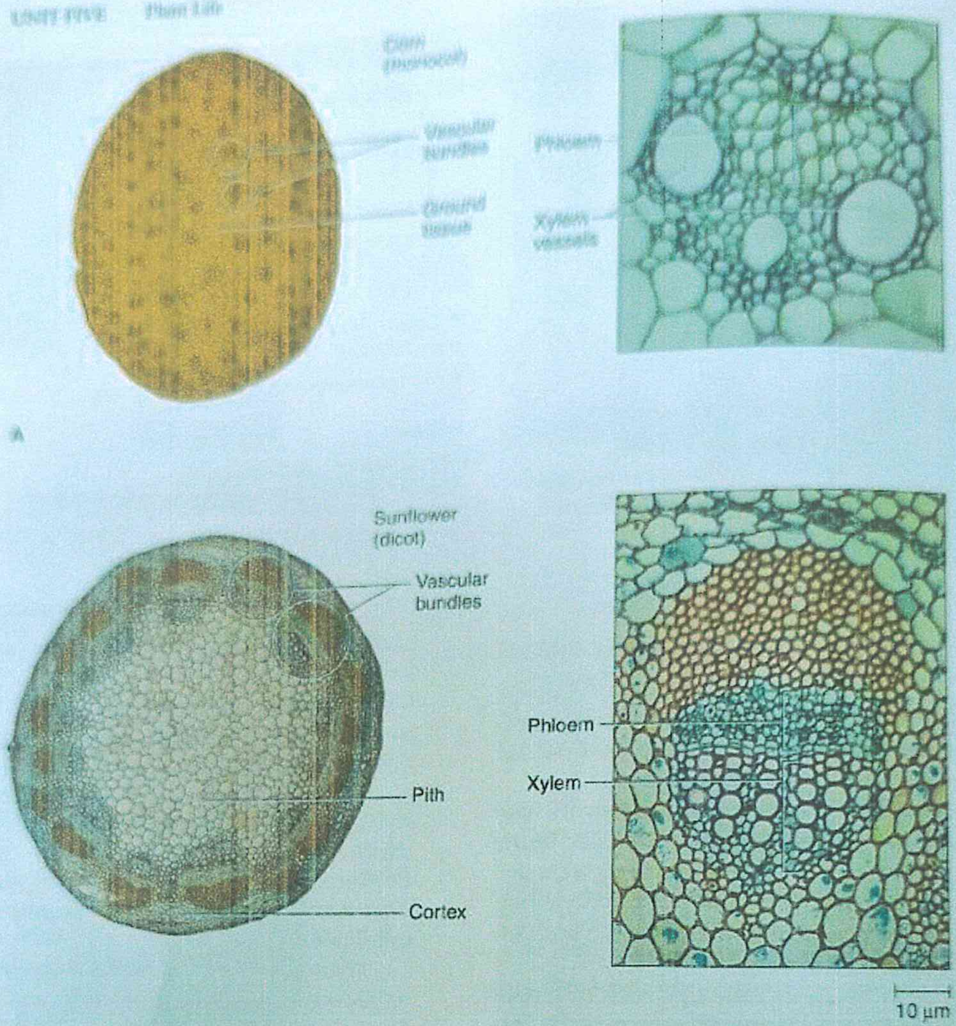


FIGURE 26.8 Stem Anatomy. Cross sections of **(A)** a monocot stem (corn) and **(B)** a dicot stem (sunflower) (×10). Notice the scattered vascular bundles in the monocot stem and the ring of vascular bundles in the dicot stem.

Leaves

In addition to the stem, a shoot system has **leaves.** Like stems, leaves consist of epidermal, vascular, and ground tissues. Leaves are the primary photosynthetic organs of most plants. They provide an enormous surface area for the plant to capture solar energy. For example, a large maple tree has approximately 100,000 leaves, with a total surface area that would cover the area of six basketball courts (about 2,500 square meters).

Leaves are extremely diverse in form. The leaves of some tropical palms may be 65 feet (20 meters) long, whereas the leaves of *Azolla,* an aquatic fern, are only millimeters long. A mature American elm may have several million leaves, whereas the desert gymnosperm *Welwitschia mirabilis* produces only two leaves during its entire lifetime. Leaves may be needlelike, feathery, waxy, or smooth.

Botanists categorize leaves according to their basic forms (**figure 26.10**). Most leaves consist of a flattened **blade** and a supporting, stalklike **petiole.** The large vein down the center is called the midrib. Leaves may be simple or compound. Simple leaves have flat, undivided blades. Elm, maple, and zinnia have simple leaves. Compound leaves are divided into leaflets and are further distinguished by leaflet position. Pinnate compound leaflets are paired along a central line and include ash, rose, walnut, and *Mimosa.* Palmate compound leaflets all attach to one point at the top of the petiole, like fingers on a hand, and include lupine, horse chestnut, and shamrock.

Leaf epidermis covers the leaf and consists of tightly packed transparent cells. With the exception of guard cells, the epidermis is usually nonphotosynthetic. It may contain many stomata—more than 11 million in a cabbage leaf, for example. Water loss is minimized in many species because stomata are most abundant on the shaded undersides of horizontal leaves. The floating leaves of lily pads are unusual in having stomata on the upper surface only. Vertical leaves, such as those of grasses, have equal densities of stomata on both sides.

26.10

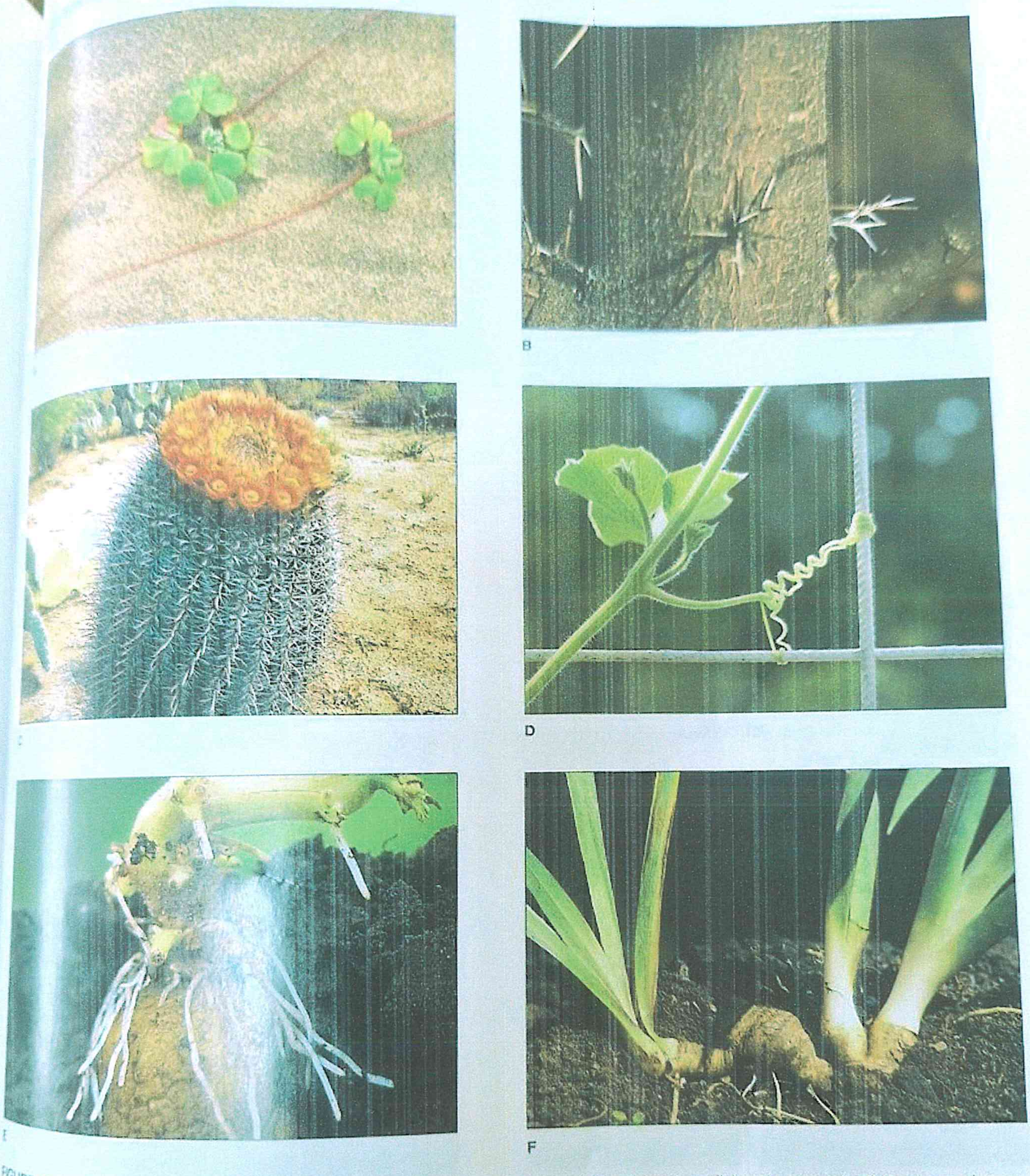
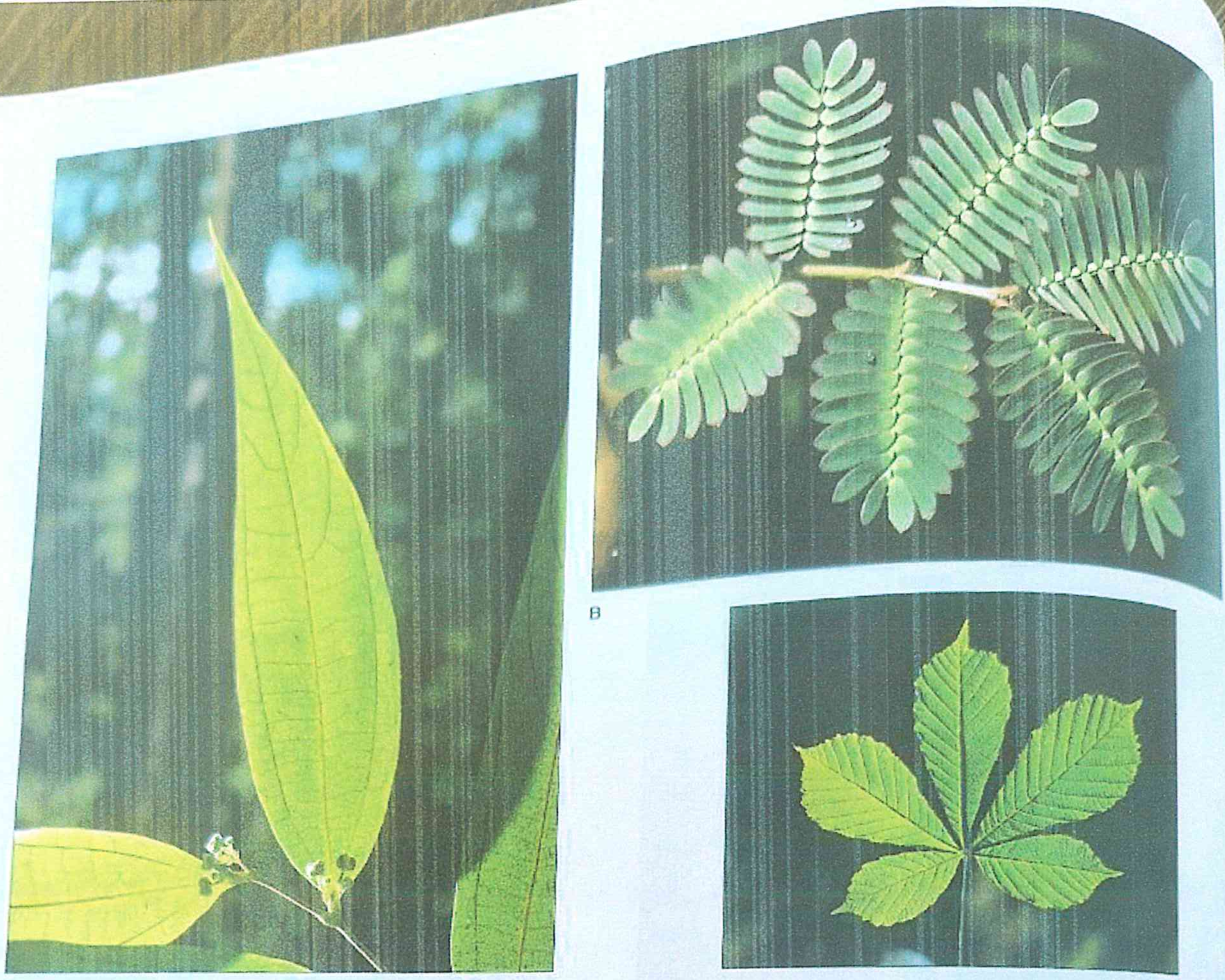
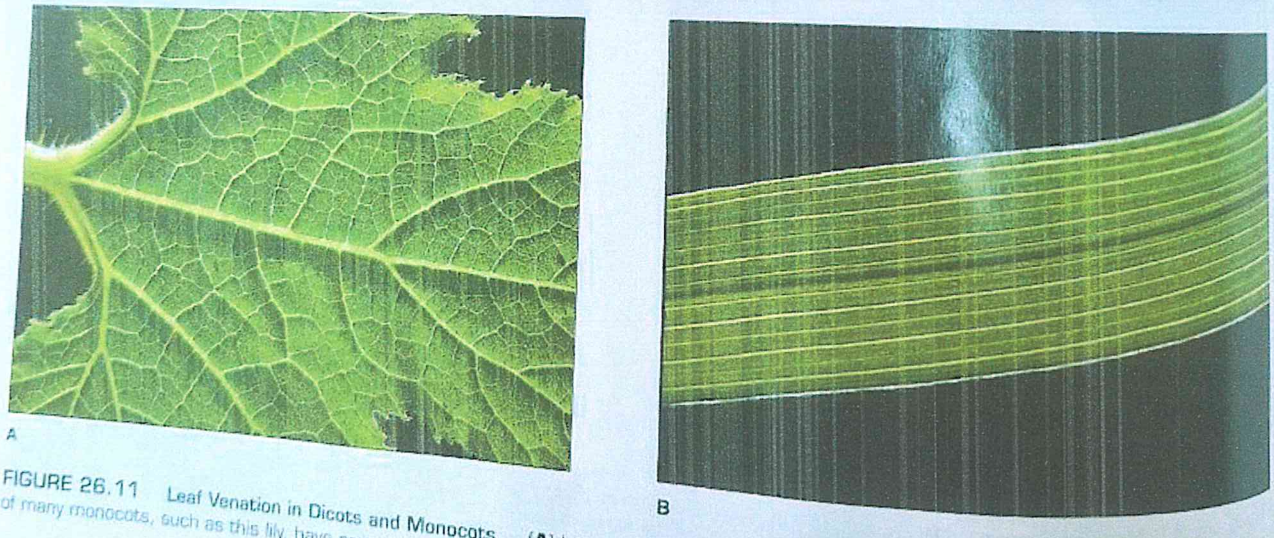


FIGURE 26.9 Modified Stems. (**A**) Stolons of the beach strawberry (*Fragaria chilensis*) run parallel to the ground. (**B**) The thorns that protect the honey locust are outgrowths of the stem. (**C**) The stem of the fishhook barrel cactus is highly modified to store water; its thorns are actually modified leaves. (**D**) Tendrils may be stems modified to coil around objects, supporting and anchoring plants. (**E**) The potato is a tuber. Sprouts grow from its "eyes" and form new plants. (**F**) The rhizome of an iris is an underground stem.



A B C

FIGURE 26.10 **Leaf Forms.** **(A)** This simple leaf of *Thottea* attaches to the stem by its short petiole. **(B)** This pinnate compound leaf of a *Mimosa* plant has many leaflets. **(C)** The horse chestnut plant has palmate compound leaves, with five leaflets. The stalk leading to the group of leaflets is the petiole.



A B

FIGURE 26.11 **Leaf Venation in Dicots and Monocots.** **(A)** Leaves of dicots, such as this pumpkin plant, have netted venation. **(B)** Leaves of many monocots, such as this lily, have prominent parallel veins interconnected by many tiny veins.

Xylem and phloem in leaves are connected to the stem's vascular tissue at the stem's nodes. Inside the leaves, the vascular tissue branches into an intricate network of veins. Sclerenchyma fibers and parenchyma cells support leaf veins. Leaf veins may be of two types: netted, with minor veins branching off from larger, prominent midveins, or parallel, with several major parallel veins connected by smaller minor veins (**figure 26.11**). Most dicots have netted veins, and many monocots have parallel veins. Vein endings are the blind ends of minor veins, where water and solutes move in and out of cells.

Leaf ground tissue, which is called **mesophyll**, is made up largely of parenchyma cells. Most of these cells are chlorenchyma and therefore photosynthesize and produce sugars. Horizontally oriented leaves have two types of chlorenchyma (**figure 26.12**). The long, columnar cells along the upper side of a leaf, called palisade mesophyll cells, are specialized for light absorption. Below the palisade layer are spongy mesophyll cells, which are irregularly shaped chlorenchyma cells separated by large air spaces. These cells are specialized for gas exchange and can also photosynthesize.

In addition to photosynthesizing, leaves may provide support, protection, and nutrient procurement and storage, with the following specializations:

- Tendrils are modified leaves that wrap around nearby objects, supporting climbing plants. Pea plants growing in a garden will "grab" a fence with leaf tendrils. (Both leaves and stems can be modified into tendrils.)
- Spines of plants such as cacti are leaves modified to protect the plant from predators.
- Bracts are floral leaves that protect developing flowers. They are colorful in some plants, such as poinsettia. Other floral parts, such as sepals and petals, are also modified leaves.
- Storage leaves are fleshy and store nutrients. Onion bulbs are the bases of such leaves.
- Insect-trapping leaves are found in about 200 types of carnivorous plants and attract, capture, and digest prey, as Investigating Life 22.1 explains.
- Cotyledons are embryonic leaves that may store carbohydrates, which supply energy for germination.

Leaves have a limited life span. Leaf abscission is the normal process by which a plant sheds its leaves, thus removing a large surface area from which water would otherwise be lost in cold, dry air. Deciduous trees shed leaves at the end of a growing season. Evergreens retain leaves for several years but shed some leaves each year.

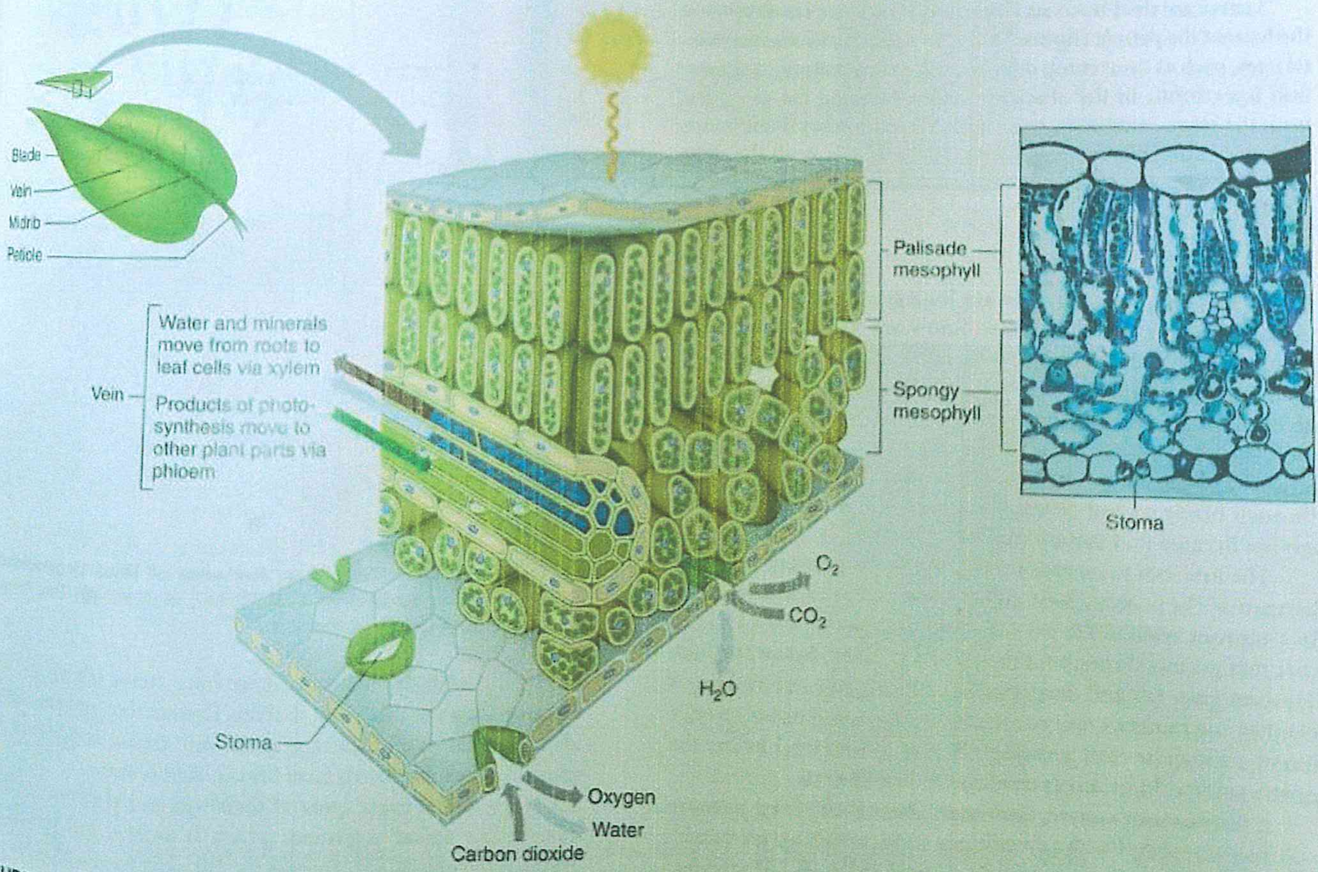


FIGURE 26.12 **Anatomy of a Leaf.** Leaf mesophyll consists of an upper palisade layer and spongy mesophyll below. Stomata are often concentrated on the lower leaf surface. Leaf veins deliver water and minerals and carry off the products of photosynthesis.

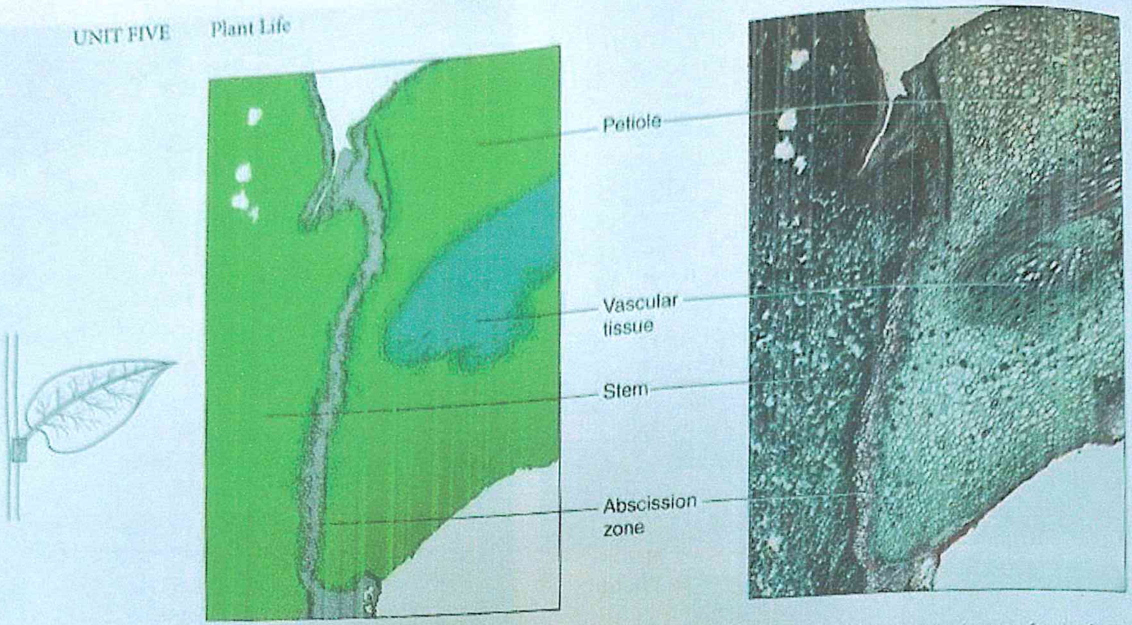


FIGURE 26.13 Leaf Abscission. The abscission zone is a region of separation that forms near the petiole base of a leaf. The protective layer that forms at this zone minimizes risk of infection and nutrient loss when the leaf is shed. Although not shown in this thin section, the vascular system is continuous between leaf and stem.

Leaves are shed from an abscission zone, which is a region at the base of the petiole (**figure 26.13**). In response to environmental cues, such as shortening days or cooler temperatures, a separation layer forms in the abscission zone, isolating the dying leaf from the stem. Eventually, wind, rain, or some other disturbance, such as a scurrying squirrel, breaks the dead leaf from the stem. The abscission zone remains visible as a leaf scar on the stem.

Roots

Plants are immobile, but they are biologically active, especially underground, where roots grow. Roots are so indispensable to plant growth and photosynthesis that annual root production often consumes more than half of a plant's energy and may account for a substantial portion of its bulk. Roots anchor plants and absorb, transport, and store water and nutrients. They absorb oxygen from between soil particles; roots pushing through firmly packed or water-logged soil may die from lack of oxygen because they cannot respire.

The first root to emerge from a seed is the primary root. The lifespan of the primary root differs in two types of root systems. In a **taproot system,** the primary root enlarges to form a major root that persists throughout the life of the plant (**figure 26.14A**). Taproots grow fast and deep, maximizing support and enabling a plant to use minerals and water deep in the soil. Engineers once found a mesquite root growing 174 feet (53 meters) below the earth's surface! Most dicots develop taproot systems.

A **fibrous root system,** conversely, has a short-lived primary root that is replaced with adventitious roots, which are roots arising from nonroot plant parts such as stems or leaves. (Many people grow new houseplants from stem or leaf cuttings, which quickly form adventitious roots.) In fibrous root systems, branching adventitious roots arise from stems (figure 26.14B). Because they are relatively shallow, fibrous root systems rapidly absorb minerals and water near the soil surface and prevent soil erosion. Most monocots have fibrous root systems.

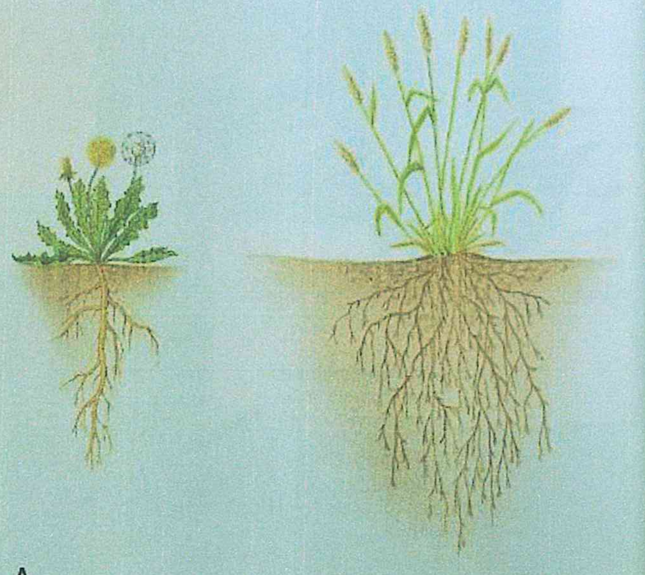


FIGURE 26.14 Two Main Patterns of Root Organization. **(A)** The taproot system of a dandelion, a dicot. **(B)** The fibrous root system of barley, a monocot.

Like stems, roots grow at their tips as a result of cell division at the apical meristem, which is located just behind the root tip (**figure 26.15**). Toward the tip, cells produced at the apical meristem differentiate into the **root cap,** whose cells slough off as the root grows through the soil. Root cap cells produce a

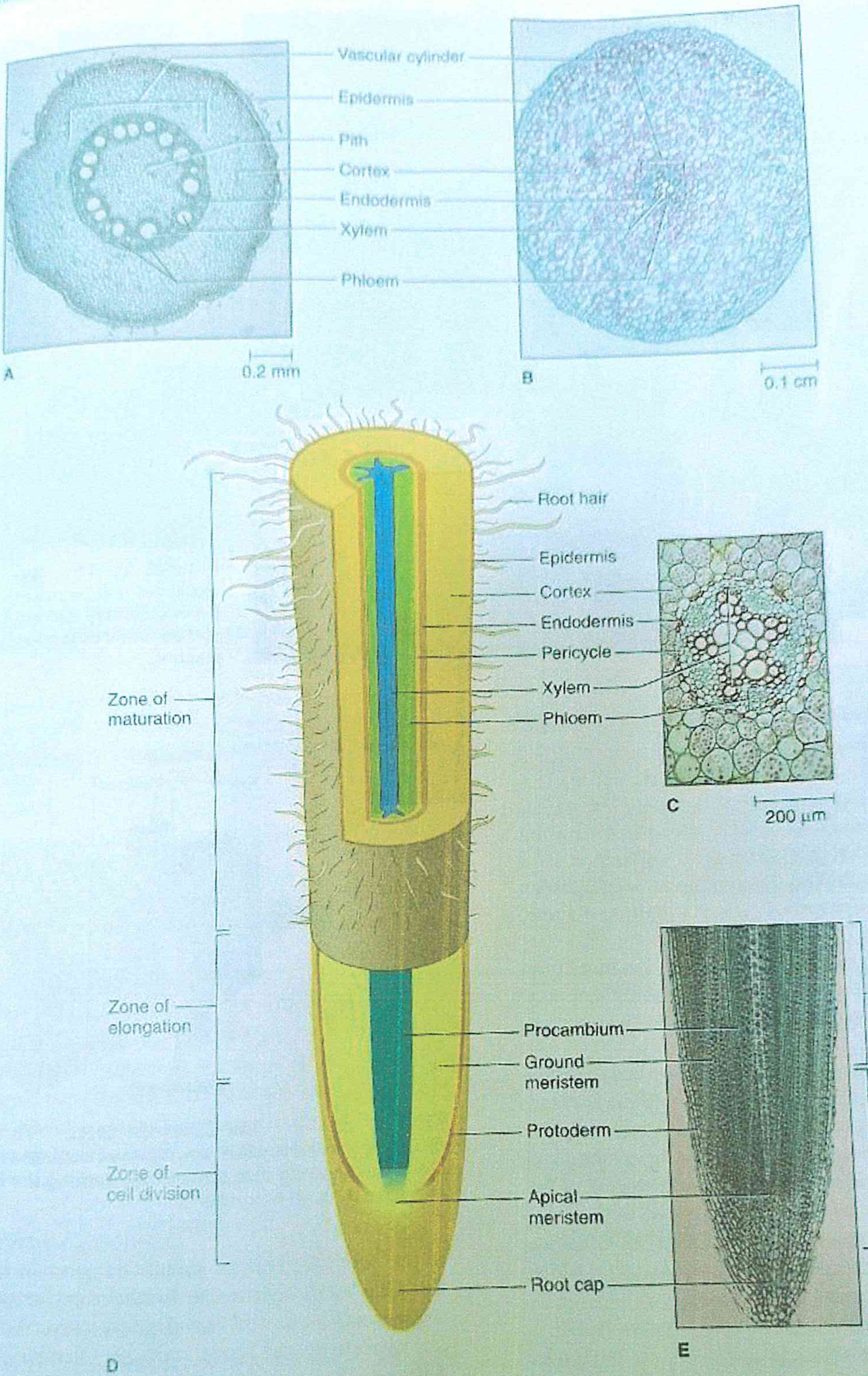


FIGURE 26.15 Anatomy of a Primary Root. Cross sections of (**A**) a monocot root (corn) and (**B**) a dicot root (buttercup). A close-u dicot's vascular cylinder appears in (**C**), along with a diagram of the root's internal structures (**D**). The apical meristem (**E**) produces root c toward the root tip and meristematic tissues just above the root cap. These meristems produce cells that mature into ground tissue, vasc sue, and the root epidermis.

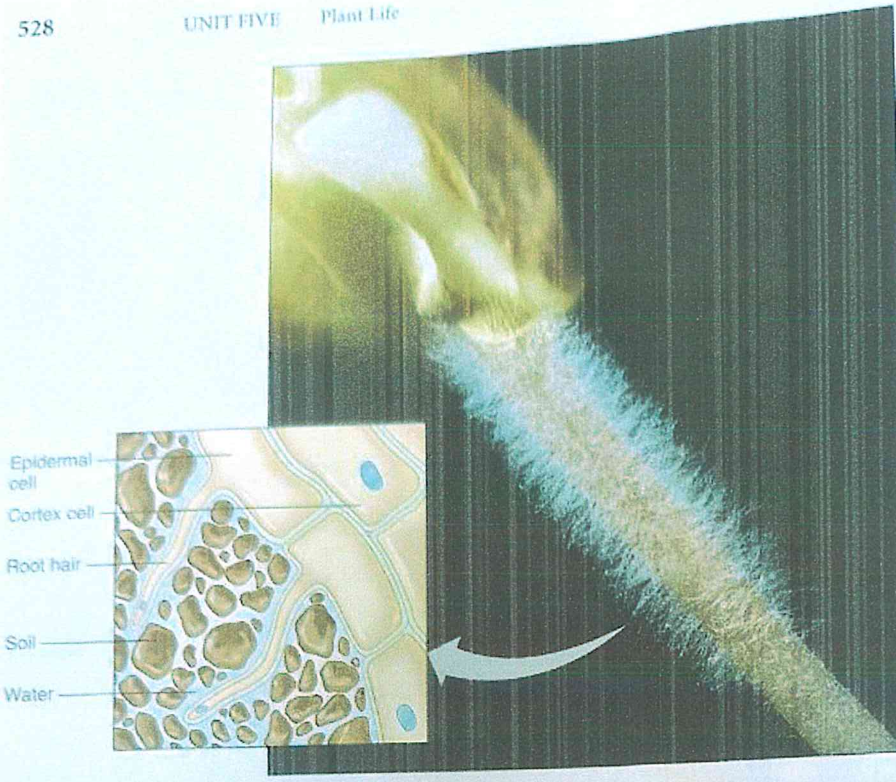


FIGURE 26.16 **Root Hairs.** These epidermal cell outgrowths extend through the soil, greatly increasing the absorptive surface area of the root. This is a corn seedling.

slimy substance, mucigel, which lubricates the root as it grows and protects the tip from abrasions. The root cap also plays a role in sensing gravity. Just above the root cap, the apical meristem produces cells that elongate and differentiate into xylem, phloem, and other root tissues. Root hairs, which are extensions of root epidermal cells, often give this zone of cell maturation a fuzzy appearance (**figure 26.16**). Figure 26.15D distinguishes the zones of cell division, elongation, and maturation of a root.

• **gravitropism, p. 575**

The root epidermis surrounds the entire primary root except the root cap. Root epidermal cells have a very thin cuticle or none at all and are thus well adapted for absorbing water and minerals.

• **root absorption, p. 544**

Interior to the epidermis is the cortex, which makes up the majority of the primary root's bulk. It consists of loosely packed, interconnected parenchyma cells that may store starch or other materials. The air spaces between the cells allow for aeration and water movement. The **endodermis** is the innermost ring of the cortex. It includes a single layer of tightly packed cells, whose walls contain a waxy, waterproof material called suberin. The waxy deposits form a barrier, called the **Casparian strip,** which ensures that all materials entering the vascular cylinder pass through the cytoplasm of endodermal cells first (**figure 26.17**).

Inside the endodermis is a layer of cells called the **pericycle,** which produces lateral roots that grow through the cortex and epidermis and extend into the soil. The pericycle is the outermost layer of the root's vascular cylinder. In many roots, the vascular cylinder consists of a solid core of xylem, with ridges that project

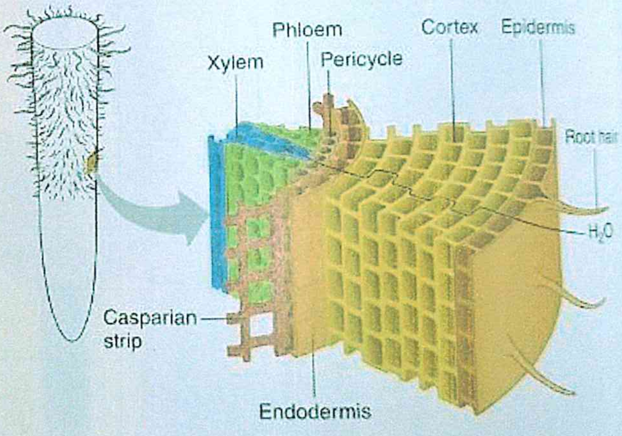


FIGURE 26.17 **The Casparian Strip.** The Casparian strip blocks movement of water and dissolved minerals between endodermal cells, ensuring that all materials entering the vascular cylinder first pass through living cells.

to the pericycle. Phloem strands are generally located between the "arms" of the xylem core. In other roots, a ring of vascular tissue surrounds a central core of parenchyma cells.

Like stems and leaves, roots are often modified for special functions (**figure 26.18**):

- Storage is a familiar root specialization. Beet, carrot, and sweet potato roots store carbohydrates, and desert plant roots may store water.

A B C

FIGURE 26.18 **Root Modifications.** **(A)** The banyan tree has aerial roots growing out of its branches. **(B)** This tropical fig tree has buttress roots so enormous they resemble a trunk. **(C)** Prop roots on corn arise from the stem and support the plant.

- Pneumatophores are specialized roots that form on plants growing in oxygen-poor environments, such as swamps. Black mangrove trees have pneumatophores. These roots form underground and grow up into the air, allowing oxygen to diffuse in.
- Aerial roots are adventitious roots that form from stems and grow in the air. Orchids have aerial roots.
- Thick, enormous buttress roots at the base of a tree provide support, as do prop roots that arise from the stem, as seen in corn.

A plant's roots may interact with other organisms. Recall from chapter 23 that many roots form mycorrhizae with beneficial fungi. The fungi absorb water and minerals from soil, while the plants provide carbohydrates to the fungi. Roots of legume plants, such as peas, are often infected with bacteria of genus *Rhizobium*. The roots form nodules in response to the infection. The bacteria function as built-in fertilizer, providing the plant with nitrogen "fixed" into compounds it can use.

26.2 Mastering Concepts

1. What are the parts and tissues of a stem?
2. What are the functions of stems?
3. What are the structures and functions of leaves?
4. How do the two types of root systems differ?
5. What are the regions and structures of a root?
6. What are some special modifications of stems, leaves, and roots?

26.3 Secondary Plant Growth

Wood and bark support and protect the stems, branches, and roots of many plants. These supportive tissues arise from two lateral meristems, the vascular and cork cambia, that allow the plant to grow outward.

The tallest plants can intercept the most light. However, continued elongation poses a problem, because primary tissues cannot adequately support tall plants. Lateral meristems, which increase the girth of stems and roots by secondary growth, address this problem. These meristems are called the vascular cambium and cork cambium.

Secondary growth can be impressive. A 2,000-year-old tule tree in Oaxaca, Mexico, is 148 feet (45 meters) in circumference and only 131 feet (40 meters) tall. A 328-foot-tall (100-meter) giant sequoia in California is more than 23 feet (7 meters) in diameter. To support all of this extra tissue, a plant's transport systems must also become more complex and powerful.

Vascular Cambium

The **vascular cambium** is a ring of meristematic tissue that produces most of the diameter of a woody root or stem. Generally, it forms only in plants that exhibit secondary growth—primarily woody dicots and gymnosperms.

In roots and stems that undergo secondary growth, the vascular cambium forms a thin layer between the primary xylem and phloem. In stems with discrete vascular bundles, the vascular cambium extends between the bundles to form a ring (**figure 26.19**).

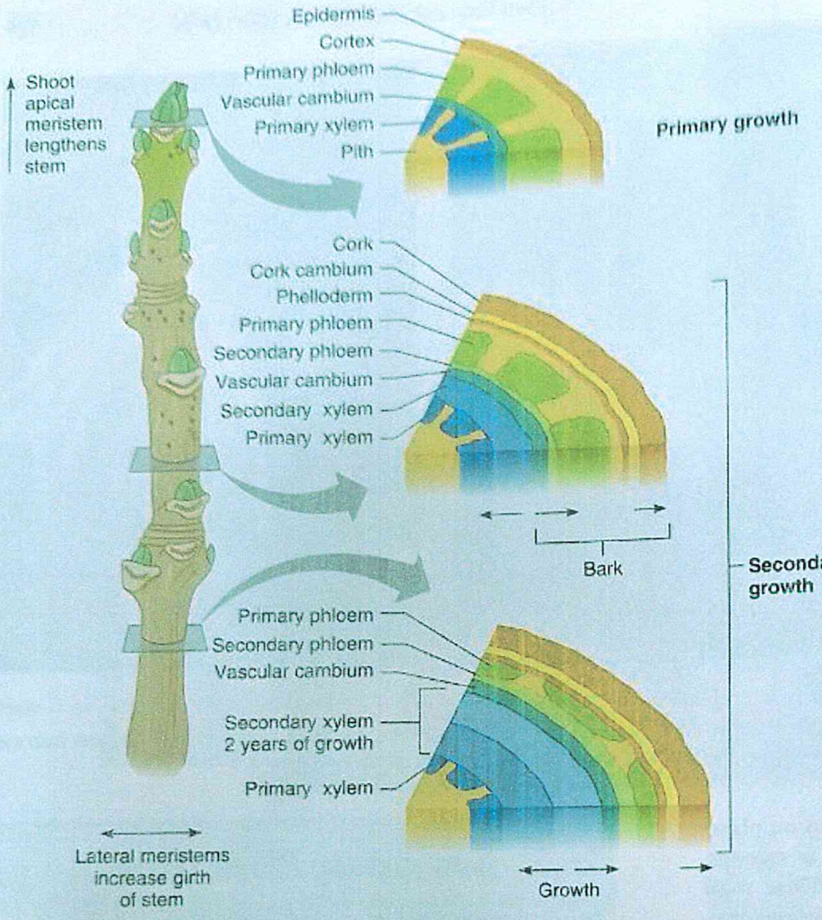


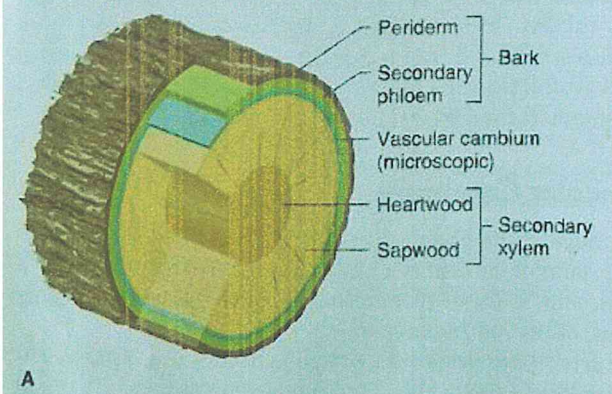
FIGURE 26.19 Secondary Growth Produces Wood. The secondary growth of a woody stem involves the activities of two types of lateral meristem—vascular cambium and cork cambium. In the top cross section, the microscopic vascular cambium has formed but not yet started producing secondary vascular tissue. The vascular cambium produces secondary xylem toward the inside of the stem and secondary phloem toward the outside, eventually crushing the primary vascular tissue, cortex, and epidermis. Although the two lower diagrams depict only one cork cambium, many trees have more than one.

The cells of the vascular cambium produce secondary xylem toward the inside of the cambium and secondary phloem on the outer side. Overall, the vascular cambium produces much more secondary xylem than secondary phloem.

Secondary xylem is more commonly known as wood. In temperate climates, cells in the vascular cambium divide to produce wood during the spring and summer. During the moist days of spring, wood is made of large cells and is specialized for conduction of water. During the drier days of summer, the vascular cambium produces summer wood that has small cells and is specialized for support. These seasonal differences in wood cell sizes generate visible demarcations called growth rings (**figure 26.20**). Secondary xylem can be used to measure the passage of time because the larger spring wood cells appear light colored, and summer wood cells are smaller and darker colored. The contrast between the summer wood of one year and the spring wood of the next creates the characteristic annual tree ring. The most recently formed ring is next to the microscopic vascular cambium. Tropical species, which have secondary growth all year long, do not have regular tree rings. Investigating Life 26.1 describes how tree ring data are aligned to correlate to historical events.

The older, innermost increments of secondary xylem gradually become unable to conduct water; this nonfunctioning wood is called **heartwood.** The **sapwood,** located nearest the vascular cambium, transports water and dissolved minerals.

Woods differ in hardness. Dicots such as oak, maple, and ash are often called hardwood trees, and gymnosperms such as pine, spruce, and fir are called softwood trees. Dicot wood contains tracheids, vessels, and supportive fibers, whereas wood from softwood trees is more homogeneous, consisting mainly of tracheids.



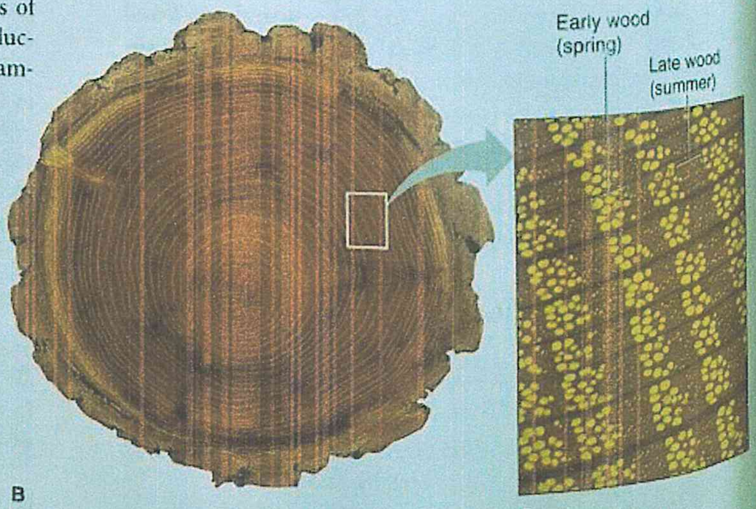


FIGURE 26.20 Anatomy of a Secondary Stem. **(A)** Wood is secondary xylem, and bark is all the tissue outside the vascular cambium. **(B)** Differences in available soil moisture when wood forms in spring and summer result in different-sized cells **(C)**, which are visible as growth rings.

Investigating Life

26.1

Tree Rings Reveal the Past

Studying tree ring patterns—a technique called dendrochronology—is helping to fill gaps in our knowledge of ancient civilizations and providing information on past climatic events. Rings arise in trees that grow in temperate climates, where wood cells that form in the spring are larger than those that form in summer, creating a distinctive pattern in the wood grain.

Tree rings also provide information on climate, fire and herbivory. The thicker the ring, the more plentiful the rainfall that year. A fire leaves behind a charred "burn scar." Two rings fall very close together when voracious caterpillars or locusts eat the season's early leaves. With fewer leaves, the tree cannot obtain sufficient nutrition from photosynthesis, so the plant does not produce much secondary xylem. The tree rings appear narrower than in a better year. Tree ring structures and patterns also provide clues about light availability, altitude, temperature, and length of the growing season in times past.

Researchers at Cornell University combined dendrochronology with other types of evidence to "anchor" a nearly 1,500-year sequence in the history of a little-understood society—that of ancient Turkey—into an absolute time frame. They used wood and charcoal samples from the Midas burial mound that were once juniper trees. The evidence may actually rewrite some ancient history.

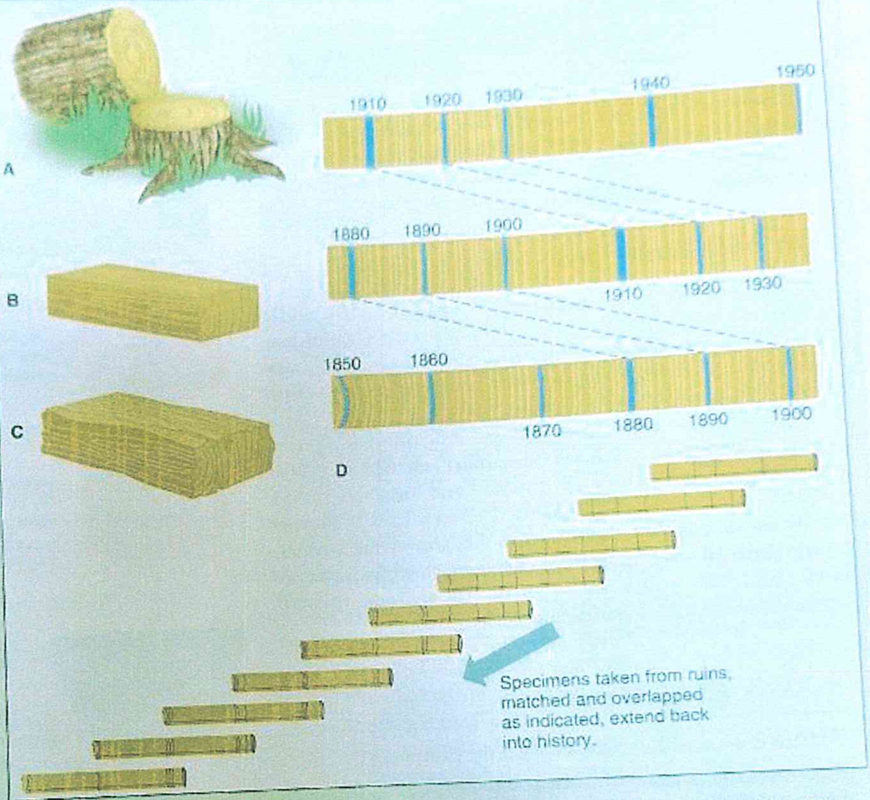


FIGURE 26.A Researchers Infer the Age of Wooden Structures by Studying Tree Ring Patterns. To establish a chronology, dendrochronologists overlap tree ring patterns. In the study depicted here, a tree cut down in 1950 establishes a starting date (**A**). This tree's rings are compared to those of a tree cut down and used as a wooden beam in a newer house (**B**) and then to those of a tree used as a beam in an older house (**C**). The tree ring data pictured begin shortly after 1840 and extend until 1950. When a starting date can be established, scientists can use historical tree ring data to infer the age of centuries-old wood (**D**).

When researchers can align overlaps in the patterns among several trees, tree ring data can span many years. As long as one of the trees has a ring next to the vascular cambium, so that the dendrochronologist can determine the most recent year, such comparisons can yield a very accurate "master chronology" (figure 26.A). For example, the oldest known living tree is a bristlecone pine (*Pinus longaeva*) growing in the White Mountains of California. It is more than 4,760 years old. Combining its tree ring information with information from older, dead trees in the area has provided rainfall data going back 8,200 years!

The juniper remains from the Midas Mound in ancient Turkey, however, had no link to the present, and so the Cornell researchers had a "floating" dendrochronology, a sequence of events with no anchoring end. But the researchers used two clever approaches to assign absolute dates.

First, in a technique called wiggle-matching, the researchers correlated irregularities in the tree ring data to irregularities in radioactive carbon dating and established an approximate date. Then they aligned an unusual wideness in the tree rings to similar anomalies in patterns from trees in the United States and Europe, which had been linked to a volcanic eruption on the island of Thera, near Crete, in 1628 B.C. With the new tree ring data, anthropologists now have a time frame in which to place objects found with the wooden remains in ancient Turkey. Tree rings may have much to tell us about early history.

As a result, dicot wood is usually stronger and denser than wood from gymnosperms (the soft, light wood from the balsa tree, a dicot, is a notable exception). The terms "hardwood" and "softwood" are not scientific terms. They are used mainly in industry to reflect the observation that dicot wood is usually harder than wood from gymnosperms.

The tissues to the outside of the vascular cambium are collectively called **bark** (see figure 26.19). Secondary phloem forms the live, innermost layer of bark and transports phloem sap within the tree (the primary phloem is crushed as the stem or root continues to grow outward). The outer layer of bark includes the **periderm**, a protective layer of tissue that replaces the epidermis as the girth of a stem or root increases. The outer bark also includes dead tissues outside the periderm.

Cork Cambium

The **cork cambium** is the second type of lateral meristem, and it gives rise to cork to the outside and phelloderm to the inside (see figure 26.19). Together, the phelloderm, cork cambium, and cork make up the periderm. Older trees may have multiple periderms, arising at successively greater depths.

Cork cells are waxy, densely packed cells covering the surfaces of mature stems and roots. Their inner cell walls are coated with suberin. They are dead at maturity and form waterproof, insulating layers that protect plants. The cork used to stopper wine bottles comes from cork oak trees that grow in the Mediterranean. Every 10 years, harvesters remove much of the cork cambium and cork, which grows back. In contrast to cork, phelloderm cells are live parenchyma cells.

26.3 Mastering Concepts

1. How does secondary growth affect the plant body?
2. What is the function of vascular cambium?
3. What are the components of bark?

This chapter has described many structural features of flowering plants and noted some of the differences between the two main groups of angiosperms—monocots and dicots. **Figure 26.21** illustrates some of these differences (including some mentioned earlier, in chapter 22). In chapters 27 through 29, the functions, growth, and development of these structures are described in greater detail.

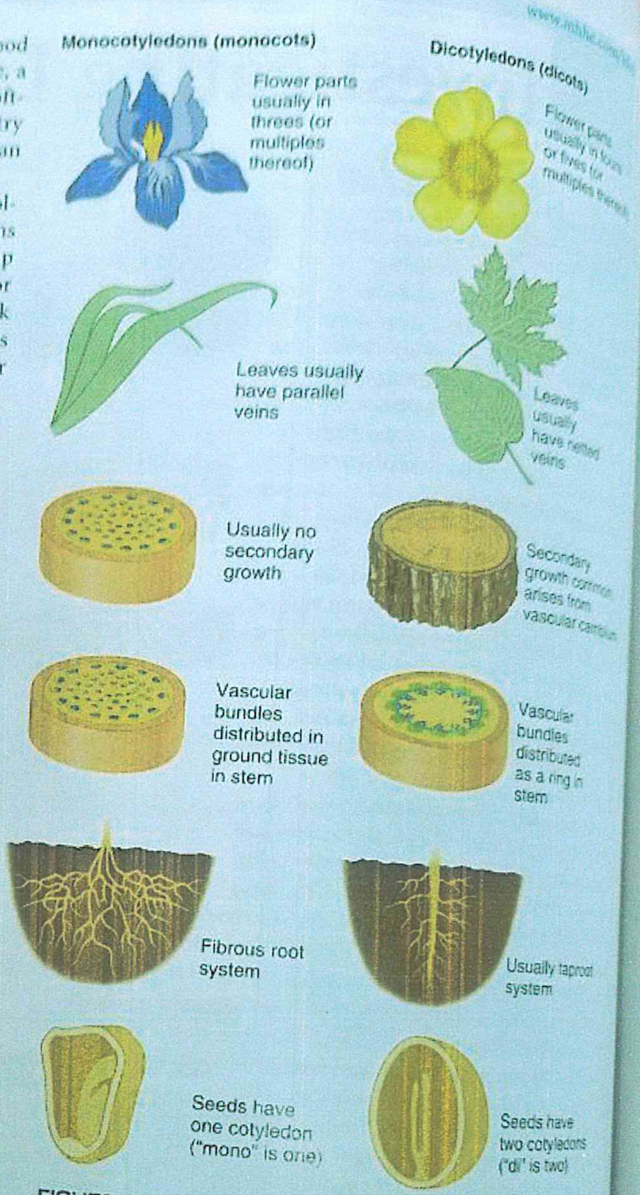


FIGURE 26.21 **Monocots and Dicots Compared.** Although many variations occur, most monocots and dicots differ from each other in flower and leaf morphology, stem anatomy, root system architecture, and seed structure.

8. Cite a stem specialization and a leaf specialization that provide protection.
9. Corn is a monocot and sunflower is a dicot. How do these plants differ in the following?
   a) stem structure
   b) leaf venation
   c) root organization
10. Moving from the outermost bark layer to the center of a tree's trunk, which tissues are encountered, and what type of meristem produced each?

Thinking Scientifically

1. If an overzealous tomato picker tears off some tomato plant stems and leaves, the plant regrows these parts in a few weeks. Which tissue type is responsible for this regrowth?
2. What plant structures are adaptations to conserve and transport water?
3. Paper "fibers" actually include fibers, tracheids, and vessel elements. Describe each of these.
4. Which plant tissues have cells that are dead at maturity? Why is it advantageous to the plant for these cells to die?
5. How are plants' primary and secondary tissues protective?

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FUNDAMENTALS OF ECOLOGY AND ENVIRONMENT

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2 authors:

Pranav Kumar
Pathfinder Research and Training Foundation, India and Pathfinder Academy, India

Usha Mina
Jawaharlal Nehru University

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Pranav Kumar | Usha Mina

Fundamentals of

Ecology and Environment

Pranav Kumar
Former faculty,
Department of Biotechnology,
Jamia Millia Islamia,
New Delhi, India

Usha Mina
Associate Professor,
School of Environmental Sciences,
Jawaharlal Nehru University (JNU),
New Delhi, India

Pathfinder Publication
New Delhi, India

Preface

Fundamentals of Ecology and Environment covers the basic concepts, ideas, major findings and current challenges. As knowledge and best practice in the ecology are constantly changing, the fundamentals are written in a sharply focused manner without overwhelming or excessive details. This book provides a balanced introduction to all major areas of the subject. It is designed to promote understanding of the basic principles and concepts of a subject rather than memorization of details.

We feel that understanding ecology and environment as a whole is far more important than merely identifying separate components of a natural community. With this in mind, the readers will come to understand some basic and underlying concepts, and we trust that, through an understanding and appreciation of these concepts, the overall environmental picture of the Earth will be more fully realized and admired for what it is.

Although the chapters of this book can be read independently of one another, they are arranged in a logical sequence. Our intention is to highlight only the essentials that are most relevant to understanding ecology and environment. The most significant feature of this book is its clear, up-to-date, accurate explanations of mechanisms, rather than the mere description of facts and events. This book has been conceived, designed and written in a manner to meet the aspirations of graduate and postgraduate students. We have tried to maintain a balance between describing the classic works and recent advances in ecology.

Each page is carefully laid out to place related text, figures and tables near one another, minimizing the need for page turning while reading a topic. Sincere efforts have been made to support textual clarifications and explanations with the help of figures and tables to make learning easy and convincing.

This book is intended to go beyond the traditional helping books. This book is divided into four parts– Basic ecology (The Environment, Ecosystem Ecology, Population Ecology and Community Ecology), Biodiversity, Pollution and Climate change. It is organized to provide an even, logical flow of concepts and to provide clear illustrations of the major ecological and environmental issues. It is our hope that this book will be utilized intensively by students and ecologists to gain a basic understanding of ecology.

This book is the result of the combined efforts of several persons. Several diligent and hardworking minds have come together to bring out this book in this complete form. During the prolonged period of writing this book, several of our students, took the time to read most of the chapters and make careful comments on them. For that I thank them. Special thanks to Aditya Arya who read and gave us feedback on all of the chapters as they were being written. This book is a team effort, and producing it would be impossible without the outstanding people of Pathfinder Publication. We acknowledge all the individuals whose special efforts went into this book. We wish to thanks especially to our students for their numerous comments and suggestions.

Pranav Kumar

Usha Mina

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Ecology as a science

Ecology is the scientific study of the relationships between organisms and their environment. These relationships are complex, varied and hierarchical. The word 'ecology' was first used by German biologist Ernst Haeckel in 1869. The word is derived from the Greek words, *oikos* (meaning 'house' or 'dwelling place') and *logos* (meaning the study of). Haeckel defined ecology as '*the study of the natural environment including the relations of organisms to one another and to their surroundings*'.

Ecology describes the relationships between living organisms and their environments, the interaction of organisms with each other and the pattern and cause of the abundance and distribution of organisms in nature. The *environment* includes everything (biotic as well as abiotic) that surrounds an organism. Thus, it is the science that attempts to answer questions about how the nature works. According to one of the most widely accepted definition,

'Ecology is the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance.'

Ecology is an interdisciplinary science

Ecology, as a unifying science, is integrating the knowledge of life on our planet. It has changed from a basic science to applied science. It has become an essential science in learning how life survive and grow. Several questions such as why do animals live in groups, what determines the distribution of a species, how does organism interact with biotic and abiotic components, behavioural aspects of animals often drive us to look into this subject. Ecology is not just biology but an interdisciplinary science that deals with the totality of living organisms and their relationship with the environment. Different kinds of physical, chemical and biological processes occurring within ecological systems involve complex interactions among different components of the system. To study these interactions, ecologists must involve other sciences like physiology, biochemistry, genetics, geology, hydrology and meteorology. Ecology has turned into more experimental rather than philosophical subject. With increasing scientific informations, this science also involves complex mathematical modeling and algorithms – a true interdisciplinary sciences.

Chapter 1

The Environment

Organisms and their environments are dynamic and interdependent. The term 'environment' etymologically means *surroundings*. Thus, the *environment* includes everything (biotic as well as abiotic) that surrounds an organism. Any factor, abiotic or biotic, that influences living organisms is called **environmental factor** (or *ecological factor* or *ecofactor*). Abiotic factors include ambient temperature, amount of sunlight, pH of the water, soil in which an organism lives and many other factors. Biotic factors include the availability of prey, competitors, predators and parasites.

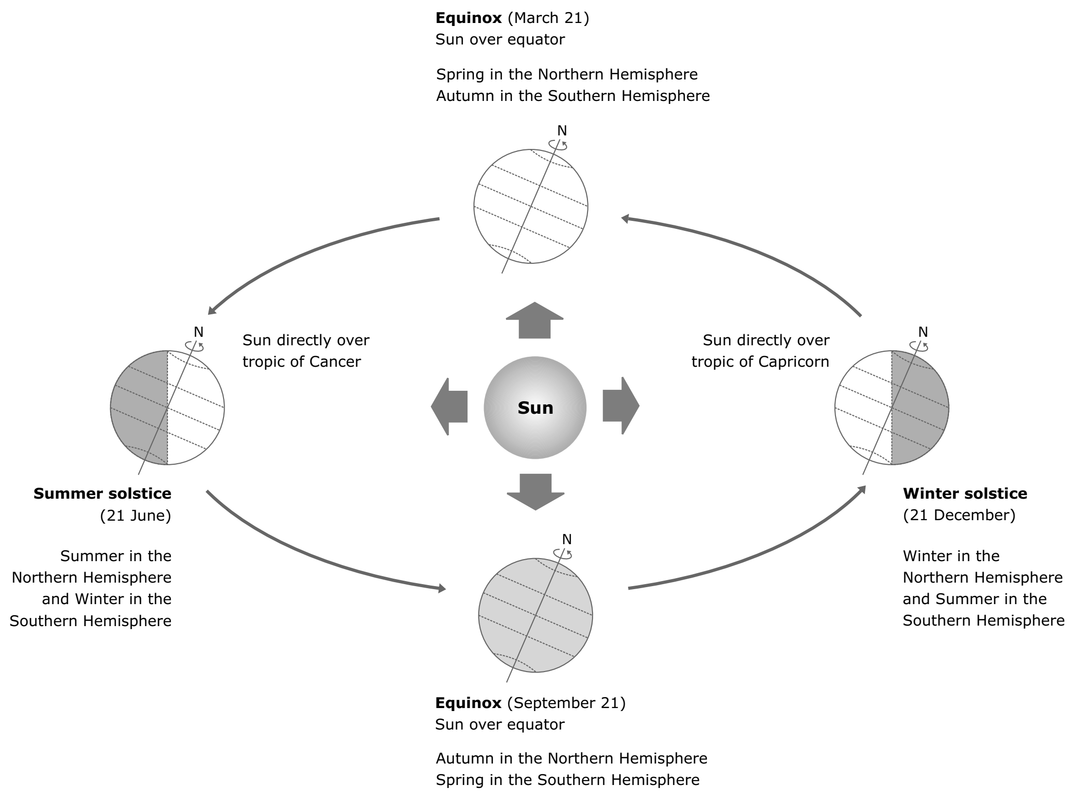
1.1 Physical environment

Soil

Soil is the uppermost weathered layer of the earth's crust. It is a mixture of weathered mineral rock particles, organic matter (i.e. both living and dead), water and air. Soil is a biologically active matrix and home of diverse organisms. The study of soil is called **pedology**.

Weathering and soil formation

The process of soil formation includes the formation of unconsolidated materials by the weathering process and the soil profile development. Weathering refers to the *physical disintegration* and *chemical decomposition* of the rocks and minerals contained in them. Physical disintegration breaks down rock into smaller fragments and eventually into sand and silt particles that are commonly made up of individual minerals. Simultaneously, the minerals decompose chemically, releasing soluble materials and synthesizing new minerals. New minerals form either by minor chemical alterations or by a complete chemical breakdown of the original mineral and resynthesis of new minerals. Based on the location of soil mineral particles formation and deposition, the soils are classified as *residual soil* and *transported soil*. If the soil mineral particles have been formed in place from the bedrock below, it is called **residual soil**. If the soil mineral particles have been carried from some other location by wind, water, gravity or ice then it is termed as **transported soil**. The transported soil can be classified into **colluvium** (transported by gravity), **alluvium** (transported by the movement of water), **glacial soil** (transported by the movement of glaciers) and **eolian soil** (transported by wind).



Since a large portion of the Northern Hemisphere is getting light from the sun, it is *summer* in the regions north of the equator. The longest day and the shortest night at these places occur on 21st June. At this time in the Southern Hemisphere, all these conditions are reversed. It is winter season there. The nights are longer than the days. This position of the earth is called the **Summer Solstice**. The combination of more direct rays of sunlight and more hours of daylight causes the hemisphere tilted toward the sun to receive more solar radiation and to have warmer temperatures.

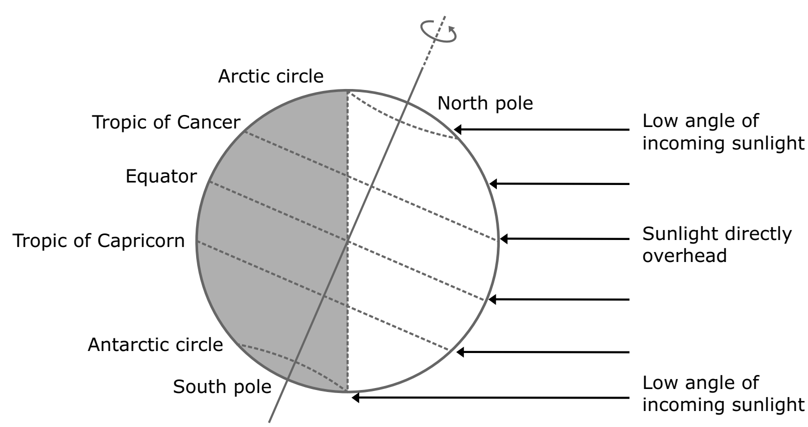


Figure 1.5 Inclination of the sun at Summer Solstice. The Sun is directly (90°) over the Tropic of Cancer and is at 66.5° over the equator. At this time, the area above the Arctic Circle is in light 24 hours a day, while the area below the Antarctic Circle is in darkness 24 hours a day.

When the incoming solar radiation is nearly perpendicular, the solar radiation is concentrated over a smaller surface area, causing high temperatures. At higher latitudes, the angle of solar radiation is smaller, causing solar radiation to spread over a larger surface area, causing lower

Poikilothermic (Greek *poikilos* – various, and *therme* – heat) animals like reptiles, fishes and amphibians are not able to maintain their body temperature at a constant level. In these organisms, the body temperature fluctuates with changes in the environmental temperature.

Poikilotherms have low metabolic rates and high thermal conductance. Environmental temperatures control their rates of metabolism. Poikilotherms have an upper and lower thermal limit that they can tolerate. The range of body temperatures at which poikilotherms carry out their daily activities is the *operative temperature range.* Upper and lower limits of tolerance to temperature vary among the poikilotherm species. To maintain a tolerable and fairly constant body temperature during active periods, terrestrial and amphibious poikilotherms rely on behavioral thermoregulation such as changing position or location.

To escape the long, cold winters, many terrestrial poikilotherms go into a long, seasonal torpor called **hibernation**. Torpor is a state of decreased physiological activity in an animal. Hibernation is characterized by physiological changes such as slow breathing and heart rate and low metabolic rate.

We also distinguish between **endothermic** (in Greek *endo* means 'within' and *therme* means 'heat') animals that produce sufficient metabolic heat to maintain a high body temperature and **ectothermic** (in Greek *ecto* means 'outside' and *therme* means 'heat') animals, which obtain much of their heat from the environment. *Endotherms* regulate their temperature by the production of heat within their own bodies, and *ectotherms* rely on external sources of heat.

Although it is true that many homeotherms are endotherms and many poikilotherms are ectotherms, we should not use the terms *endothermy* and *homeothermy* (or *ectothermy* and *poikilothermy*) synonymously. *Ectotherm* and *endotherm* emphasize the mechanisms that determine body temperature. The other two terms, *homeotherm* and *poikilotherm,* represent the nature of body temperature (either constant or variable).

The influence of temperature is size dependent. Small animals have relatively more surface area and relatively less metabolically active tissue to generate heat. Therefore, a small animal, when challenged with cold, lose heat more rapidly than a larger animal. If such an animal attempted to generate heat to offset the heat loss and maintain *body temperature*, it would require a relatively higher rate of energy generation. On the other hand, large animals have relatively small surface areas and cool slowly if placed in a cold environment.

A number of *rules* generalize the adaptive response of organisms to temperature. As with many other generalizations, exceptions to these rules exist. Among the best known is **Bergmann's rule**, which relates body size in endothermic vertebrates to average environmental temperature. Bergmann's rule states that individuals of species in cooler climates tend to be larger than those in warmer climates. This relationship derives primarily because bodies with larger volumes have small surface area-to-volume ratio. Because heat loss relates to surface area, larger bodies can retain heat more efficiently in cooler climates, whereas smaller bodies (large surface area-to-volume ratio) can eliminate heat more efficiently in warmer climates. An extension of Bergmann's rule is **Allen's rule** which states that endothermic animals from colder climates tend to have shorter extremities or appendages (e.g. ears and tail) than closely related species from warmer climates (*shorter extremities dissipate less heat*).

Another extension of Bergmann's rule is **Hesse's rule** (also known as the *heart–weight rule*) which states that species inhabiting colder climates have a larger heart in relation to body weight than closely related species inhabiting warmer climates.

1.3 Ecotype and Ecads

Many populations show a series of phenotypic variations as a result of environmental variations. These phenotypic variations usually remain even if the organisms are put in a different environment, and are inherited by their offspring, indicating that the characters are genetically rather than environmentally determined. A Swedish ecologist Turesson (1925) studied a plant species which showed some genetically fixed phenotypic variations between populations of the *Campanula rotundifolia*. He found that mountain populations were shorter and flowered earlier than the lowland forms. This suited their growth in short mountain turf and their adaptation for rapid flowering and seed production in the shorter growing season in high altitude mountain habitats. Turesson called these phenotypically different forms **ecotypes**.

An *ecotype* describes a genetically different population (subspecies) within a species which is adapted to specific environmental conditions. In ecotypes, adaptations become irreversible or genetically fixed. The different ecotypes of a particular species may differ in their edaphic, biotic or microclimatic requirements. Thus, ecotypes are genetically adapted local population. However, they are able to reproduce with other ecotypes of the same species and produce fertile offspring. Ecotypes can be classified and grouped together. A unit of classification which contains one or more ecotypes of a species is termed **ecospecies**. The term ecospecies has been proposed by Turesson. It is a unit of classification which contains one or more ecotypes, which although interfertile but do not cross or at least do not produce viable offsprings if crossed with ecotypes of other ecospecies.

A species with a continuous distribution cannot be divided at any one point into two ecotypes. For this pattern of distribution, the term **ecocline** has been applied. Ecocline represents the continuous variation or gradual change in plant phenotype, and associated genotype along an environmental gradient.

An **ecad** (also known as *ecophene)* is a plant species is a population of individuals which although belong to the same genetic stock, but differ markedly in phenotypes such as size, shape and number of leaves, etc. These variations are environmentally induced, and thus are temporary or reversible, i.e. one type of ecad may change into another with a change in its habitat. So, if different ecads are transplanted in the same habitat, all would become similar in appearance. Thus, ecads show **phenotypic plasticity** i.e. environmentally induced phenotypic variation. The phenotypic plasticity is the capacity of a single genotype to exhibit variable phenotypes in different environments. It is considered one of the major means by which plants can cope with environmental factor variability.

1.4 Metabolic rate and size of individuals

The *metabolic rate* of an organism is the amount of energy it needs per unit time. It is often estimated by measuring the rate at which oxygen is consumed. The most important factor affecting the metabolic rate of an individual is its size (mass). The study of the relationship of body size to shape, anatomy and physiology is called **allometry**. It can be defined broadly as 'the study of size and its consequences'.

An *allometric* relationship is one in which a physical or physiological property of an organism alters relative to the size of the organism.

Metabolic rate varies with body mass. However, rates are not directly proportional to body mass. The metabolic rate per unit of body mass in very small organisms is immensely higher than

Chapter 2

Ecosystem Ecology

An **ecosystem** (or *ecological system*) is a functional unit comprising all the organisms in a particular place interacting with one another and with their physical environment and interconnected by an ongoing flow of energy and a cycling of materials.

The concept of an ecosystem was first formally proposed by the English botanist Arthur Tansley in 1935. The term **biogeocoenosis** (proposed in the 1940s by the Soviet ecologist V. N. Sukachev) frequently used in Russian literature is roughly equivalent to the ecosystem. Its literal meaning is '*life and earth functioning together*'.

A key advance in the adoption of the ecosystem concept occurred after the appearance of a popular textbook by Eugene Odum. Odum's textbook was organized around the ecosystem concept. After Odum's textbook, a famous article in Science by Francis Evans (1956) mentioned the ecosystem as '*the basic unit in ecology*'. In the broadest sense, *an ecosystem is the interacting system made up of all the living and non-living objects in a physically defined space.*

Ecosystems ecology deals with the flow of energy and cycling of nutrients among organisms within a community and between organisms and the environment.

According to this simple definition, the size, location and timescale at which ecosystems are defined can therefore precisely match the question that the scientist is trying to answer. An ecosystem could be of any size depending on the communities to be studied and its boundaries can be either real or arbitrary. An ecosystem may be as small as a single tree or as large as the entire Earth and can be studied for time periods as long as millions of years.

An ecosystem can be visualized as a functional unit of nature. It has all components: biological and physical, necessary for survival. Accordingly, it is the basic unit around which theories and experiments of ecology are organized.

A *thermodynamic system* (or simply 'system') is a definite macroscopic region or space in the universe, in which one or more thermodynamic processes take place. Everything external to a thermodynamic system is called *surroundings*. System and surroundings are separated by a definite border called *boundary*.

All ecosystems are *open systems* in the sense that energy and matter are exchanged with their surroundings. It might be theoretically possible to define particular examples of ecosystems that are *closed systems*, not exchanging matters with their surroundings, but nearly all ecosystems do exchanges of energy and matters with their surroundings.

Ecosystems change through time. These changes may be gradual and subtle (losses of minerals from a weathering soil) or fast and dramatic (a fire sweeping through a forest). Both external forces (changes in climate or nutrient inputs) and internal dynamics (accumulation or depletion of materials in a soil or a lake) are important in driving temporal changes in ecosystems. In some cases, changes are directional and predictable (e.g. soil weathering, the filling of a lake basin), while in other cases changes may be specific and difficult to predict (e.g. the arrival of an invasive species).

Box 2.1 Levels of organization

To study how organisms interact with each other and with their physical environments, several hierarchical levels of the organization have been recognized. Ecological patterns and processes vary as a function of the level of organization at which they operate.

Ecologists have identified four fundamental levels of the organization to study the interactions between organisms and their environment. These levels of organization include *individual organism, population, community* and *ecosystem*. Therefore, ecology ranges in scale from the study of an individual organism through the study of populations to the study of communities and ecosystems.

The most basic level of the ecological organization starts with the **individual** (a single plant, insect or bird). At the level of the organism, ecology deals with how individual organisms are affected by (and how they affect) their environment. *Organismal ecology* gives focus on the individual organisms' behaviour, physiology, morphology, etc. in response to the environment.

The next level of organization is the **population**. The term *population* has many uses and meanings in other fields of study. In ecology, a population is a group of individuals of the same species that occupy a given area. The *population ecology* deals with population growth and how and why a population changes over time.

Populations of different species in an area do not function independently of each other. They interact with each other. Hence, the next, more complex level of organization of the interacting population of different species form is the **community**. *Ecological communities* are made up of interacting populations of different species within some defined geographical area. *Community ecology* deals with the composition and organization of ecological communities and community development. Communities occur on a wide variety of scales from small pond communities to huge tropical rainforests. At the largest scales, these communities are known as 'biomes'. A **biome** is a distinct ecological community of plants and animals living together in a particular climate (for example, tropical rainforests, coniferous forests, savannas). It is characterized by distinctive vegetation distributed over a wide geographical area and defined largely by regional climatic conditions.

An **ecosystem** (or *ecological system*) is the interacting system made up of all the living and non-living components in a physically defined space. Because an ecosystem is a system, it has boundaries. All systems that encompass interacting biotic and abiotic components may be considered as an ecosystem. Ecosystems are complex, open, hierarchically organized, self-organizing and self-regulated systems. Ecosystems ecology deals with the flow of energy and cycling of nutrients among organisms within a community and between organisms and the environment. The highest level of organization for the ecological study is the **biosphere**. It is an ultimate ecosystem. It includes all ecosystems present on the Earth. In a strict sense, the biosphere represents all the living organisms of the Earth. But in ecology, the biosphere (also known as the **ecosphere**) is a functional concept which emphasizes the interrelationship between all living organisms and their environment on a planetary scale.

Although many ecologists have recognized 'ecosystem' as the fourth level of organization for an understanding of ecological phenomena. Some ecologists are considering the use of 'ecosystem' as the fourth level of organization is inappropriate because it does not include any new biological organization. Some have argued that the term 'landscape' would be a suitable term for a level of organization defined as an ecological system containing more than one community type.

Autecology is the study of the interaction between organisms and their environments at the level of an individual, a population or an entire species.

Synecology is the study of an ecological community. It is also called *community ecology*. It is the synecology which describes the ecological community as a whole, especially the links between organisms.

Food chains

A classic paper by Lindeman (1942) laid the foundations of ecological energetics. He attempted to quantify the concept of food chains by considering the efficiency of energy transfer between trophic levels. The first trophic level belongs to the primary producers, the second level to the herbivores (primary consumers), and the higher levels of the carnivores (secondary consumers). Some consumers occupy a single trophic level, but many others, such as omnivores, occupy more than one trophic level. The relationship between one trophic level and adjacent trophic levels may be described by a food chain.

'The transfer of food energy from producers (plants) through a series of organisms that consume and are consumed is termed as a ***food chain****.'* A food chain shows the movement of energy through a system by indicating the path of food from a producer to a final consumer.

In general, food chains have 3 to 5 trophic links with 15 to 20 species. The length of food chain also may reflect the physical characteristics of a particular ecosystem. A harsh arctic landscape has a much shorter food chain than a temperate or tropical one.

Why are food chains relatively short? There are two main hypotheses. One, the **energetic hypothesis**, suggests that the length of a food chain is limited by the inefficiency of energy transfer along the chain. As we know, only about 10% of the energy stored in the organic matter of each trophic level is converted to organic matter at the next trophic level. At each transfer, a proportion (often as high as 80% to 90%) of the potential energy is lost as heat. Therefore, the shorter the food chain — or the nearer the organism to the first trophic level — the greater the energy available to that population. The second hypothesis, the **dynamic stability hypothesis**, proposes that long food chains are less stable than short chains. Population fluctuations at lower trophic levels are magnified at higher levels, potentially causing the local extinction of top predators. This hypothesis predicts that food chains should be shorter in unpredictable environments. Most of the data available support the energetic hypothesis.

Types of food chains

Within any ecosystem, there are two major food chains: the **grazing food chain** and the **detritus food chain**. The distinction between these two food chains is the source of energy for primary consumers. In the grazing food chain, the source of energy is living plant biomass (or net primary production). In the detrital food chain, the source of energy is dead organic matter or detritus.

Grazing food chains begin with photosynthetic plants (primary producers). Primary consumers (or herbivores) form the second link in the grazing food chain. They gain their energy by consuming primary producers. Secondary consumers (or primary carnivores), the third link in the chain, gain their energy by consuming herbivores. Tertiary consumers (or secondary carnivores) are animals that receive their energy by consuming primary carnivores.

Producer	→	Herbivore	→	Primary carnivore	→	Secondary carnivore
e.g. Grass		*e.g. Insect*		*e.g. Frog*		*e.g. Snake*

More often than not, such simple food chains are oversimplified versions of the reality of feeding relationships. Instead, there are often multiple and interconnecting pathways, as well as numbers of different species involved at each trophic level. These complex pathways

Autotroph and detritus-based ecosystem

The *autotroph based ecosystems* depend directly on the influx of solar radiation. They are characterized by a dependence on energy capture by photosynthetic autotrophs and secondarily by the movement of that captured energy through the system via herbivory and carnivory. A large number of ecosystems function in this way and numerous herbivores, carnivores and omnivores are dependent on such autotrophic ecosystems.

Some ecosystems depend less on direct solar energy incorporation and more on the influx of dead organic material, or detritus, produced in another ecosystem. Ecosystems, such as caves, are independent of direct solar energy and are dependent on the influx of detritus for energy. These ecosystems are regarded as *detritus-based ecosystems*.

Ecological efficiencies

In ecosystems, living organisms are linked together by feeding relationships. Producers (or autotrophs) have the ability to fix carbon through photosynthesis *via* chlorophylls in their leaves. Herbivores are the primary consumers of organic molecules fixed by the producers. Carnivores are secondary consumers, living on the organic molecules of the herbivores. There may be several levels of carnivores in any one ecosystem; in such cases, the ultimate level will be occupied by the top carnivore. The final groups of organisms in an ecosystem are decomposers, bacteria and fungi which can break down the complex organic chemicals of dead materials and waste products. *The amount of energy reaching each trophic level is determined by the NPP and the efficiencies with which food energy is converted to biomass energy within each trophic level.*

Percentage of energy in the biomass produced by one trophic level that is incorporated into the biomass produced by the next higher trophic level is called **ecological efficiency** (also called as *transfer efficiency* or *Lindeman's efficiency*)**.**

The proportions of net primary production that flow along each of the possible energy pathways depend on transfer efficiencies in the way energy is used and passed from one step to the next. A knowledge of three categories of transfer efficiency is required to predict the pattern of energy flow. These are *consumption efficiency* (CE), *assimilation efficiency* (AE) and *production efficiency* (PE).

Consumption efficiency (or *exploitation efficiency*) is the percentage of total productivity available at one trophic level (P_{n-1}) that is actually consumed (i.e. ingested) by a trophic compartment one level up (I_n).

Ingestion
Ingestion is the process by which food is taken into the alimentary canal.

Assimilation
Assimilation is the process by which digested foods are taken into the cells of the alimentary canal.

$$\text{Consumption efficiency (CE)} = \frac{I_n}{P_{n-1}} \times 100$$

In the case of secondary consumers, it is the percentage of herbivore productivity eaten by carnivores. Consumption efficiencies of herbivores are typically low in most ecosystems dominated by vascular plants, which are in many cases well defended against herbivores. For example, herbivores consume less than 10% of primary production in most terrestrial ecosystems. Herbivory in aquatic ecosystems is generally greater than in terrestrial ecosystems especially for algal-based ecosystems where herbivores often consume more than 50% of primary production. Similarly, in terrestrial forests, consumption efficiencies of herbivores are less as compared to grasslands where most plants are nonwoody.

Nutrient cycling

The Earth is essentially a *closed system* with respect to matter and *all matter on the Earth cycles*. Every matter that is used by living organisms passes between the biotic and abiotic components of the Earth. By 'matter' we mean *elements* (such as carbon, nitrogen, oxygen) or *molecules* (water). *Nutrient cycling* (or more precisely *element cycling*) is the movement of elements through both the biotic and abiotic components of the Earth. It is the transport and transformation of elements within and among ecosystems. It involves the incorporation of elements by living organisms and their subsequent release back into the environment via decomposition. It links biotic and abiotic parts of ecosystems. The movement of elements through atmosphere, hydrosphere, lithosphere and biosphere is generally termed as a **biogeochemical cycle**. An element's specific route through a biogeochemical cycle depends on the nature of element. All elements occurring in organisms are part of biogeochemical cycles. In addition to being a part of living organisms, these elements also cycle through abiotic components of ecosystems.

There are two basic types of biogeochemical cycles: *gaseous* and *sedimentary*. This classification is based on the primary source of element input to the ecosystem. In **gaseous cycles**, the *atmosphere* acts as a major reservoir of the element. Such cycles show little or no permanent change in the distribution and abundance of the element. Carbon and nitrogen are prime representatives of biogeochemical cycles with a prominent gaseous phase. In **sedimentary cycle**, the major reservoir is the lithosphere from which the elements are released largely by weathering. The sedimentary cycles, exemplified by phosphorus, sulfur and most of the other biologically important elements, have a tendency to stagnate. In such cycles, a portion of the supply may accumulate in large quantities, as in the deep ocean sediment, and thereby become inaccessible to organisms and to continual cycling. Some of the elements that are characterized by sedimentary cycles do have a gaseous phase, sulfur and iodine being among them, but these phases are insignificant in that there is no large gaseous reservoir.

An element's specific route through a biogeochemical cycle varies with the particular element. Based on spatial scale, there are, however, two general categories of biogeochemical cycles: *global* and *local cycle.* In **local cycles** such as the phosphorus cycle, there are no mechanisms for long distance transfer of elements; whereas **global cycles** such as nitrogen cycle, involve atmosphere for long distance transfer of elements. Global cycles unite the Earth into one giant interconnected ecosystem. Gaseous forms of carbon, oxygen, sulfur and nitrogen occur in the atmosphere, and cycles of these elements are essentially global. Other, less mobile elements, including phosphorus, potassium and calcium, generally cycle on a more localized scale, at least over the short term. Lithosphere is the main abiotic reservoir of elements performing local cycle.

Lithosphere
The lithosphere is composed of all the solid land mass comprising Earth's crust and upper mantle.

Biosphere
All the living things in the planet are categorized under the biosphere. In this view, the biosphere includes all the biotic components of the Earth.

Atmosphere
The atmosphere is the body of gases that surrounds our planet. Most of our atmosphere is located close to the Earth's surface.

Hydrosphere
The hydrosphere includes all the gaseous, liquid and solid forms of water of the Earth.

General model of nutrient cycling

Although the nutrient cycling of the various elements differ in detail, from the perspective of the ecosystem all nutrient cycles have a common pattern. A general model of nutrient cycling includes the main reservoirs of elements and the processes that transfer elements between reservoirs. Each reservoir is defined by two characteristics: whether it contains organic or inorganic materials and whether or not the materials are directly available for use by organisms. The nutrients in living organisms and in detritus are available to other organisms when

Nitrogen fixation

Natural processes of nitrogen fixation are of two types – *Biological nitrogen fixation* and *Nonbiological nitrogen fixation* (including nitrogen fixation by lightning and photochemical reactions). Approximately 90% of nitrogen fixation is biological nitrogen fixation, in which prokaryotic organisms fix molecular nitrogen into ammonia. It is a reductive biosynthetic process. Few prokaryotic organisms (termed as nitrogen-fixing organisms or **diazotroph**) are capable of biological nitrogen fixation only. Eukaryotic organisms are unable to fix nitrogen. The biological reaction of nitrogen fixation generates at least one mole of H_2 in addition to two moles of NH_3 for each mole of nitrogen molecule. Hence, total eight electrons are required in the reduction of one mole of nitrogen to two moles of NH_3.

$$N_2 \xrightleftharpoons{8e^- + 8H^+} 2NH_3 + H_2$$

Ammonification

Most of the nitrogen in the soil exists in organic forms. When organic nitrogen is converted into ammonium ions by bacteria and fungi, it is called *ammonification* or *mineralization.* Mineralization is a general term used for a process in which organically bound nutrient is released in an inorganic form.

Nitrification

The oxidation of ammonium ions to nitrite and subsequent oxidation of nitrite to nitrate is called *nitrification*. It is carried out exclusively by bacteria. There are two distinct steps of nitrification that are carried out by distinct types of bacteria. The first step in nitrification is the oxidation of ammonium ions to nitrite. This step is carried out by nitrifying bacteria (known as *ammonia-oxidizers*) of genera *Nitrosomonas*, *Nitrosospira* and *Nitrosococcus*.

The second step in nitrification is the oxidation of nitrite to nitrate. This step is carried out by nitrifying bacteria (known as *nitrite - oxidizers*) of genera *Nitrospira*, *Nitrobacter* and *Nitrococcus*.

$$2NH_4^+ + 3O_2 \longrightarrow 2NO_2^- + 4H^+ + 2H_2O$$

$$2NO_2^- + O_2 \longrightarrow 2NO_3^-$$

Denitrification

The process of conversion of NO_3^- into N_2 by anaerobic denitrifying bacteria is called *denitrification*. These bacteria use nitrate rather than oxygen as an electron acceptor during respiration. This causes nitrate to be reduced, producing in turn NO_2^-, NO, N_2O and finally N_2. Denitrification can only be performed under anaerobic conditions.

The process is performed primarily by heterotrophic denitrifying bacteria (such as *Paracoccus denitrificans* and various pseudomonads), although autotrophic denitrifiers have also been identified (e.g. *Thiobacillus denitrificans*).

$$2NO_3^- \longrightarrow 2NO_2^- \longrightarrow 2NO \longrightarrow N_2O \longrightarrow N_2$$

Anammox

Anammox (an abbreviation for ANaerobic AMMonium OXidation) is a recently discovered bacterial process which involves the anaerobic oxidation of ammonium to molecular nitrogen using nitrite as electron acceptor. Therefore, this process couples the oxidation of ammonium concentrations of some nutrients in the soil of tropical rainforests result from a faster nutrient cycling rate. In temperate forests, where decomposition is much slower, the soil may contain a large amount of the dead organic matter in the forest. Decomposition on land is also slower when conditions are either too dry for decomposers to thrive or too wet to supply them with enough oxygen.

2.2 Ecosystem services

Ecosystem services are '*the benefits which people obtain from ecosystems*'. According to IPCC (Intergovernmental Panel on Climate Change), ecosystem services are ecological processes or functions which have value to individuals or society. For example, forest ecosystems purify air and water, mitigate droughts and floods, cycle nutrients, generate fertile soils, provide wildlife habitat, maintain biodiversity, pollinate crops, provide storage site for carbon and also provide aesthetic, cultural and spiritual values.

Ecosystem services are grouped into four broad categories. All of these services are provided by complex chemical, physical, and biological processes, powered by the Sun, and operate at different temporal and spatial scales.

Provisioning, such as the production of food and water;

Regulating, such as the control of climate and disease;

Supporting, such as nutrient cycles and crop pollination; and

Cultural, such as spiritual and recreational benefits.

Provisioning services Products obtained from ecosystem.	**Regulating services** Benefits obtained from regulation of ecosystem processes.	**Cultural services** Non-material benefits obtained from ecosystem.	**Supporting services** Services necessary for the production of all other from ecosystem.
• Food • Fresh-water • Fuelwood • Fiber • Biochemicals • Genetic resources	• Climate regulation • Disease regulation • Water regulation • Water purification • Pollination	• Spiritual and religious • Recreation and ecotourism • Aesthetic • Inspirational • Educational • Sense of place • Cultural heritage	• Soil formation • Nutrient cycling • Primary production

2.2.1 Control of trophic structure: top–down versus bottom–up control

We have learned about how materials and energy flow through ecosystems. Now, we can address the question of 'what controls the trophic structure'? The control of tropic structure i.e. the partitioning of biomass between trophic levels is broadly divided into two categories. The first of these categories, **bottom-up control**, emphasizes the energy inputs into the primary producers and the subsequent efficiency of energy transfer between trophic levels in determining the biomass accumulation at each trophic level. The second category, **top-down control**, emphasizes the importance of predation in influencing patterns of biomass accumulation at different trophic levels.

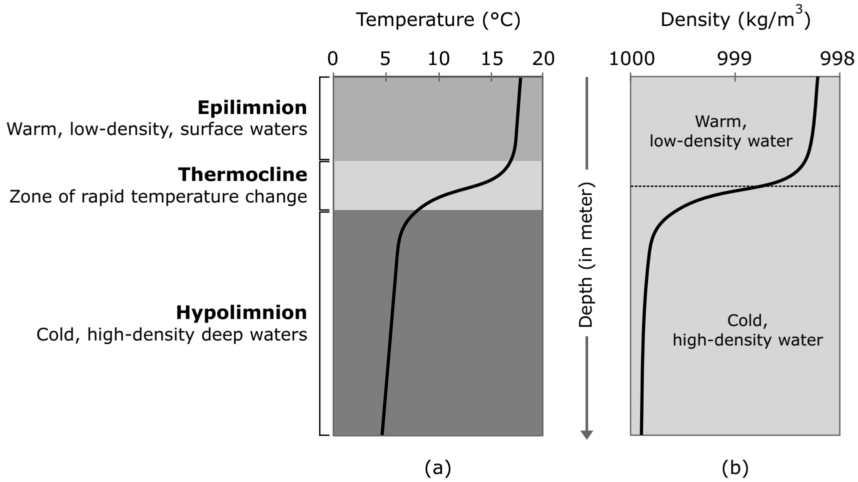


Figure 2.17 Temperature and density profiles with water depth for a temperate lake during summer. (a) The region of the vertical depth profile where the temperature declines most rapidly is called the thermocline. The thermocline is located between an upper layer of warm, less dense water called the epilimnion and a deeper layer of cold, denser water called the hypolimnion. (b) The rapid decline in temperature in the thermocline results in a distinct difference in water density in the warmer epilimnion as compared to the cooler waters of the hypolimnion, leading to a two-layer density profile—warm, low-density surface water and cold, high-density deep water.

Seasonal changes in water temperature

The temperature profile of a deep-water lake of *temperate region* changes from one season to the next and creates a cyclic pattern. Due to seasonal variation in the input of solar radiation to the water surface give rise to seasonal changes in the vertical profile of temperature.

Let us begin with spring season. After the ice melts on a lake, the lake water is generally has the same temperature from the surface to the bottom. It allows circulation and mixing of the lake water. Surface water can be pushed to the lake bottom and bottom water can rise to the surface. This circulation pattern allows large amounts of oxygen to reach the bottom of the lake. The mixing of the lake water at this time of year is called **spring overturn**.

As air temperature rises in summer, heat from the Sun begins to warm the lake. The layer of warm water at the surface of the lake is called the *epilimnion*. The cold layer below the epilimnion is called the *hypolimnion*. These two layers are separated by a layer of water which rapidly changes temperature with depth. This is called the *thermocline* (or *metalimnion*). Stratification during the summer acts as a deterrent to complete lake mixing. Wind circulates the surface water, but the warm water of the epilimnion is unable to move through the cold, dense water of the hypolimnion. As a result, the water is only mixed in the epilimnion.

As autumn (fall) approaches and temperature decreases, the epilimnion begins to decrease in depth. Eventually, the epilimnion gets so shallow that it can no longer be maintained as a separate layer and the lake loses its stratification. Thus, as in the spring, the lake water in the autumn has generally uniform temperatures and wind can once again thoroughly mix the lake water. In addition, surface water, which is in direct contact with the cold air, gets cooled faster than the water below. This cold, dense water sinks and further helps to mix the lake, and again more oxygen and nutrients are replenished throughout the lake. This process is called **autumn overturn**.

Box 2.4	Ramsar Convention

The Ramsar Convention (also known as the Convention on Wetlands) is an intergovernmental treaty that provides the framework for national action and international cooperation for the conservation and wise use of wetlands and their resources. It is named after the city of Ramsar in Iran, where the Convention was signed in 1971. The 2nd of February each year is **World Wetlands Day**, marking the date of the adoption of the Convention on Wetlands on 2 February 1971.

There are presently 169 Contracting Parties to the Convention. India is also a signatory to the Ramsar Convention on Wetlands. The 'Ramsar List' (list of wetlands of international importance) has 2,282 Ramsar Sites (wetlands of international importance) in March 2016. The country with the highest number of Ramsar Sites is the United Kingdom with 170; India currently has 26 Ramsar Sites.

Terrestrial ecosystem

Terrestrial ecosystems are those that are found only on land. The key to the meaning of terrestrial ecosystems lies in the word 'terrestrial', which generally means anything occurring on land. Therefore, terrestrial ecosystem refers to the interacting system made up of living organisms and non-living objects occurring on land. Only 28 percent of the Earth's surface belongs to terrestrial ecosystems.

Forest ecosystem

A **forest** is a complex ecosystem which is predominantly composed of trees and shrubs. It is defined as 'a land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 percent' (UN FAO). It does not include land that is predominantly under agricultural or urban land use. Forests are the dominant terrestrial ecosystem of Earth and are distributed across the globe. Forests account for 75% of the gross primary productivity of the Earth's biosphere and contain 80% of the Earth's plant biomass. Based on canopy cover, forest can be *very dense forest* (all lands with tree cover of canopy density of 70% and above), *moderately-dense forest* (all lands with tree cover of canopy density between 40% and 70% above) and *open forest* (all lands with tree cover of canopy density between 10% and 40%). Forest types differ widely, determined by factors including latitude, altitude, temperature, rainfall patterns and soil composition. Climate (temperature and rainfall), soil types and topography are the main factors that determine the type of forest. There are three major types of forest – taiga forest, temperate forests and tropical forests

Taiga forest (*coniferous forest* or *boreal forest*) is located at higher latitudes, close to the polar region and is dominated by needle-leaved, drought tolerant, evergreen trees. The taiga or boreal forest has a subarctic climate. Winter is long and very cold and summer is short and cool. Precipitation occurs primarily in the form of snow, 40–100 cm annually.

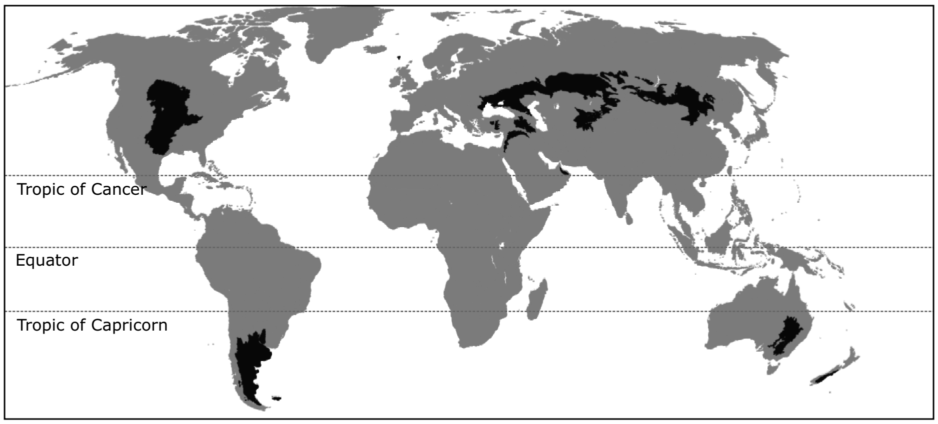
The UNFCCC defines 'a *forest* as an area of land 0.05–1 hectare in size, of which more than 10–30% is covered by tree canopy. Trees must also have the potential to reach a minimum height of 2-5 metres'.

Temperate forests are found in the temperate climatic zone (between the tropics and boreal regions) in both the Northern and Southern Hemisphere. They may also be called 'four-season forests' because these forests experience four distinct seasons. In the temperate region, winters are mild and rainfall is moderate. Temperate forests are a mix of deciduous, broad-leaved and coniferous evergreen trees. They are simpler in structure than tropical forests and support a lesser number of tree species. Temperate forests can be further distinguished by weather

Temperate grasslands are known as the *veldts* of South Africa, the *puszta* of Hungary, the *pampas* of Argentina and Uruguay, the *steppes* of the former Soviet Union and the *plains* and *prairies* of central North America.

Temperate grasslands

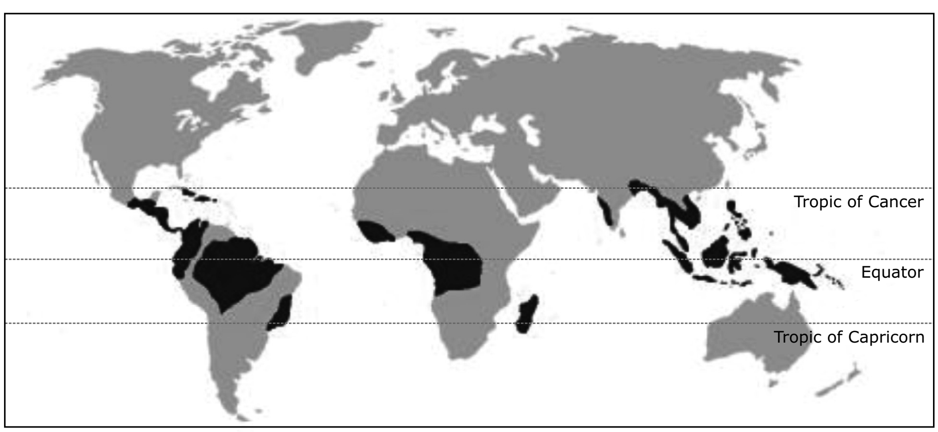
Temperate grasslands are characterized as having grasses as the dominant vegetation. Trees and large shrubs are absent. Temperate grasslands have hot summers and cold winters and the amount of rainfall (25 to 75 cm) is less than in savannas. As in the savanna, seasonal drought and occasional fires are very important to maintain biodiversity. However, their effects aren't as dramatic in temperate grasslands as they are in savannas. The type of grassland community that develops, and the productivity of grasslands, depends strongly upon precipitation. Higher precipitation leads to tall grasses with a high biodiversity of grasses. Temperate grasslands can be further subdivided. *Prairies* are grasslands with tall grasses while *steppes* are grasslands with short grasses.



Temperate grassland biome

Tropical rainforests

Tropical rainforests occur at low altitude zones near the equator (found within 23.5° latitude of the equator) and are characterized by a high temperature, high rainfall and greatest diversity of species. The average temperature is between 20–25°C and varies little throughout the year. Winter is absent. Annual rainfall exceeds 200 cm. Although, the climate of tropical rainforest regions varies geographically but is typically characterized by a mean temperature of all months exceeding 18°C and minimum monthly precipitation above 6 cm. Warm and moist conditions promote strong chemical weathering and rapid leaching of soluble materials.



Tropical Rainforests

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Chapter 3

Population Ecology

Each species in an ecosystem exist as a population. A **population** is a group of individuals of the same species that live together in a region. Members of a population rely on the same resources, are influenced by similar environmental factors and are bred with one another. In other words, a population (synonymous with *biological population*) consists of a group of interbreeding or potentially interbreeding organisms found in the same space or area at the same time. The study of populations (especially population abundance) and how they change over time is called **population ecology**. It studies the spatial and temporal patterns in the abundance and distribution of organisms and of the mechanisms that produce those patterns. The study of population ecology includes understanding, explanation and prediction of population growth, regulation and dynamics or demography.

Multicellular organisms are of two kinds, unitary organisms and modular organisms. Most animal populations are made up of **unitary organisms**. In unitary organisms, the form is highly determinate consisting usually of a strictly defined number of parts (such as legs or wings) established only during embryogenesis. Their pattern of development and final form are predictable. For example, all dogs have four legs, all squid have two eyes, etc. In **modular organisms**, on the other hand, neither timing nor form is predictable. These organisms grow by the repeated iteration of modules, usually to yield a branching pattern. Examples of modular organisms include plants and many sessile benthic invertebrates. In modular organisms, a single genetic individual (or *genet*) can consist of many modules (or *ramets*) capable of existence as individuals. In plants, a **genet** is an individual that has arisen from a seed. A **ramet** is a new plant which has arisen through vegetative propagation and is now a completely independent plant with its own roots and shoots. For example, a population of grasses may consist of several genets, each of which has several ramets.

3.1 Population characteristics

A population has several characteristics or attributes which are a function of the whole group and not of the individual. Different populations can be compared by measuring these attributes. These attributes are population density, natality, mortality, distributions, etc. The study of the group characteristics of a population, their changes over time and prediction of future changes is known as **demography**.

Population density

The size of the population is represented by its fundamental property called *density*. It is generally expressed as the number of individuals or the population biomass per unit area or volume. Two types of densities are described – *crude density* and *specific* (or ecological) *density.* **Crude density** is the density per unit of total space. Generally, populations do not occupy all the space as whole because all area may not be habitable. Hence, density per unit of habitable space is called **specific density**. It includes only that portion of total space that can actually be colonized by the population.

Determining population size

Population size (or abundance) is a function of population density and the area that is occupied (geographic distribution). Usually, population size is estimated by counting all the individuals from a smaller sample area, then extrapolated over a larger area. When the individuals are not mobile - their population size may be estimated by counting individuals within a specified area. When individuals are very mobile and frequently move from one area to another then we can count the number by applying a common method called a **mark-recapture method**. Using this method, a small random sample of the population is captured, marked, then released to disperse within the general population. The marked individuals mix freely with unmarked individuals and within a short time are randomly mixed within the population. The population is resampled and the numbers of marked and unmarked individuals are recorded. We then assume that the ratio of marked to unmarked individuals in the second sample taken is the same as the ratio of marked to unmarked individuals in the first sample. We can use a simple formula for estimating total population size (N):

$$N = \frac{\text{Total individuals marked in first sample} \times \text{Size of second sample}}{\text{Number of marked individuals recaptured in second sample}}$$

This expression is known as the **Lincoln-Peterson index** to population size.

Let's take an example to understand mark-recapture method. Suppose, we catch 50 fish (*Labeo rohita*) in a lake and mark (color) them. After that, we release all marked fishes immediately as close as possible to the collection site. A week later (after giving sufficient time to mix randomly with the whole population) we catch 40 fish (a second sample) and 5 of them are previously marked fish. If we assume no immigration or emigration has occurred, which is quite likely in a closed system like a lake, and we assume there have been no births or deaths of fish, then the total population size of fish is 400 (50×40/5).

Natality

Natality refers to the birth of individuals in a population. The natality rate (or birth rate) is expressed as the number of individuals produced per female per unit time. To describe 'rate', we must specify time interval (such as one year or one month) and a base population. Two bases are commonly used – *Per capita or per individual* (it is equivalent to the number of births per individual per unit of time) or *Per 1000 individuals*.

Natality may be *maximum natality* or *ecological* natality*.* **Maximum natality** (sometimes called *absolute* or *physiological natality*) is the theoretical maximum number of individuals produced under ideal environmental conditions (i.e. no ecological limiting factors) and is a constant for a given population. **Ecological** or **realized natality** refers to the number of individuals produced

Exponential growth

A population shows *exponential growth* if there is no limitation on growth i.e. in an idealized unlimited environment. Under an ideal unlimited environment, the per capita rate of increase (the number of offspring born per individual) is maximum. During exponential growth, the number increases in the geometric progression 2^0, 2^1, 2^2, 2^3,.... In *geometric growth*, the rate of increase is expressed as a constant fraction or an exponent by which a particular population is multiplied (like 2, 4, 8, 16...). By contrast, a pattern of growth that increases at a constant amount per unit of time (i.e. 1, 2, 3, 4 or 1, 3, 5, 7...) is called *arithmetic growth*. The *exponential* form of growth may be represented by the simple model based on the exponential equation:

$$\frac{dN}{dt} = rN \quad \text{or,} \quad \frac{dN}{dt} \times \frac{1}{N} = r$$

Where, *N* is the *population size* and *r* is the *intrinsic rate of increase*.

During exponential population growth under an ideal unlimited environment, per capita rate of increase is maximum and is called the **intrinsic rate of increase**. The maximum value of *r* is often referred by the less specific but widely used expression **biotic potential** (or *reproductive potential*). It is the maximum per capita growth rate in the absence of *environmental resistance.* The sum total of all environmental factors that together act to limit the biotic potential of an organism from being realized is called *environmental resistance*. It includes both biotic factors such as predation, competition, parasitism and abiotic factors such as drought, fire, flood etc. Biotic potential differs from one species to another e.g. deer populations can grow faster than a population of elephants.

In a *closed* population, *r* is defined as the *per capita birth rate* (b) minus the *per capita death rate* (d).

$$\frac{dN}{dt} = (b - d)N \qquad \text{where, } r = b - d$$

When per capita birth rate exceeds per capita death rate (b > d), the population is increasing and *r* is *positive*; when death rate exceeds birth rate (d > b), then *r* is *negative* and the population is decreasing.

The integral form of the exponential growth equation is:

$$N_t = N_0 e^{rt}$$

Where, N_t = Population size after time t,

N_0 = Population size at time zero,

r = Intrinsic rate of increase and

e = Exponent, a mathematical constant

$$\frac{N_t}{N_0} = e^{rt}$$

By taking the natural log of both sides,

$$\ln N_t - \ln N_0 = rt$$

When resources (food and space) in a habitat are unlimited, all members of a species have the ability to grow exponentially. The population size that increases exponentially at a constant rate, results in a *J-shaped growth curve* when population size (N) is plotted over time (t).

3.4 Population regulation

Are populations regulated? If so, how? What does population regulation really mean? Population ecologists have identified a number of mechanisms by which populations could be regulated. Broadly speaking, factors regulating population growth are either density-dependent or density-independent.

Density-dependent factors affect population growth as a *function of the population density*. These factors include disease, competition for resources and predation. For example, a population of rabbits may increase exponentially until competitive intraspecific interactions cause either the birth rate to decrease or the death rate to increase, leading to a net decline in reproductive rate and subsequent decrease in population density. Density-dependent factors often include resources that are in limited supply such as space, water and nutrients.

Density-dependent factors can have either a positive or a negative correlation to population size. As population size increases, either birth rate declines or mortality rate increases or both. It is a *negative feedback*. However, not always density-dependent factors are negatively related to population size. In some cases, growth rate increases with population size. This phenomenon is referred to as the **Allee effect** (after W. Allee, who first described it) and is an example of *positive feedback.* A positive relationship between fitness and population size can be caused by a variety of mechanisms that affect reproduction and survival. A well-established reason of Allee effect is the *mate limitation*. Because sexual reproduction requires contact between male and female gametes, mate limitation reduces reproduction in small population. Second reason is the increased vulnerability to predators. The per capita risk of predation is less in large prey populations than small prey populations. Finally, genetic mechanisms may give rise to Allee effects. For many organisms, when population size is small, inbreeding depression can cause an Allee effect by reducing average fitness as population size declines.

Density-independent factors affect population growth, irrespective of the density of the population. These factors are usually associated with abiotic events – changes in the physical environment – that either promote or repress population growth, but their effects are *independent of population density*. Density-independent factors may include natural catastrophes such as hurricanes, floods, and seasonal variation in weather patterns.

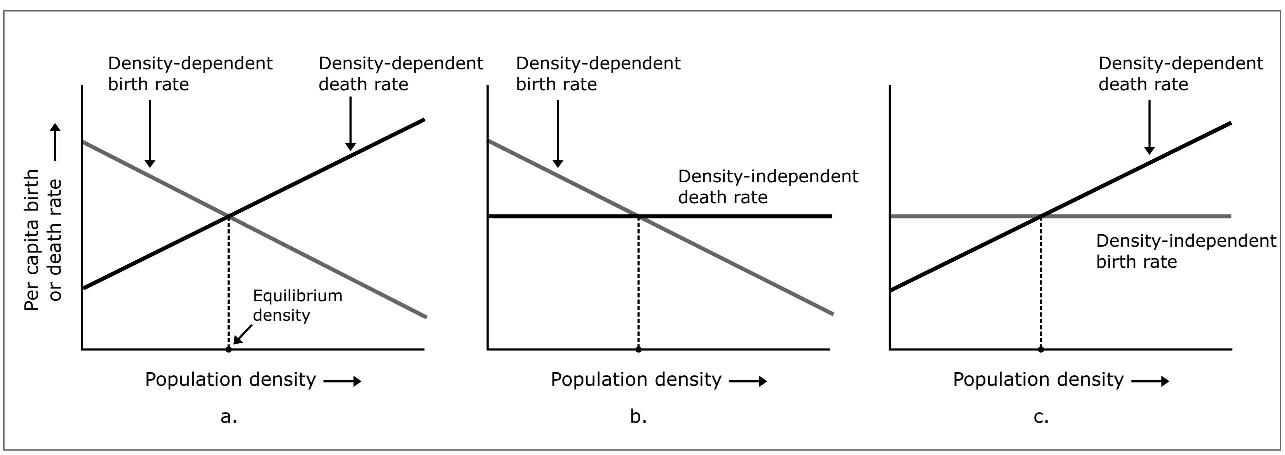

Figure 3.7 Determining equilibrium for population density. This simple model considers only birth and death rates. a. Both birth rate and death rate change with population density. b. Birth rate changes with population density while death rate is constant. c. Death rate changes with population density while birth rate is constant

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Chapter 4

Community Ecology

An **ecological community** is a group of species that coexist in a space and time and interact with one another directly or indirectly. The term 'community' means different things to different ecologists. Most definitions of ecological communities include the idea of a collection of species found in a particular place. For instance, Robert Whittaker (1975) defined ecological community as,

'...an assemblage of populations of plants, animals, bacteria and fungi that live in an environment and interact with one another, forming together a distinctive living system with its own composition, structure, environmental relations, development and function.'

Simply, an ecological community is a group of interacting species that inhabit a particular location at a particular time. Most communities are extraordinarily complex. However, main features of ecological communities include:

Firstly, a community represents the biotic or a living component of the ecosystem. Organisms within a community include primary producers, consumers and decomposers. In terrestrial communities, the community structure is largely defined by the vegetation.

Secondly, considering the functional aspect, communities are made up of organisms with interlocking food chains and each species depends on many other species in a community which are taxonomically unrelated.

Thirdly, a community may be of any size. It can range from small pond communities to huge tropical rain forests.

Community ecology is a field that examines the effects of abiotic and biotic features on community or assemblage structure. Community ecologists study the number of species and their relative abundance in a particular location and ask why the number of species and their abundance changes over time. They also do study communities in different locations and differences in the species diversity with location. In a broad sense, the goal of community ecology is to understand the origin, maintenance and consequences of biological diversity within communities.

Community is a group of interacting populations of different species occurring together in space whereas *assemblage* is a taxonomically related group of species populations that occur together in space.

There are two contrasting concepts of the community – *organismal* and *individualistic concepts*. The **organismal concept** of communities (put forward by Clements, 1916) views the community as a unit, an association of species, in which each species is representing an interacting, integrated component of the whole and development of the community through

4.1.2 Species diversity

Species diversity is one of the most important and basic characteristic of a community. The number of species and their relative abundance define *species diversity* of a community. It includes the number of species in a community (i.e. **richness**) and the relative abundance of each species (i.e. **evenness**). Species richness is simply the number of species in a community. But, among the array of species that make up the community, not all are equally abundant. We can find the *relative abundance* by counting all the individuals of each species within a community and determining what percentage each species contributes to the total number of individuals of all species. Communities in which the species are all more or less equal in abundance exhibit *evenness,* whereas communities with one or a few abundant species (i.e. present in large numbers) show *dominance*. Species evenness is highest when all species in a sample have the same abundance. Abundance patterns in communities can be examined by numbers of individuals per species, biomass per species, or percent cover per species.

Species diversity

Species Richness
The number of different species present.

Community 1	*Community 2*
Dog	Dog
Frog	Squirrel
Elephant	Elephant
Lion	Tiger
Horse	Bear
	Leopard
	Gorilla
Number of species: Five	Number of species: Seven
Species richness: Low	Species richness: High

Species Evenness
The abundance of each species in a community.

Community 1		*Community 2*	
Dog	30	Dog	20
Frog	48	Squirrel	15
Elephant	03	Elephant	20
Lion	09	Tiger	25
Horse	20	Bear	18
Number of species: Five		Number of species: Five	
Species evenness: Low		Species evenness: High	

Both number of species (*species richness*) and their relative abundance (*species evenness*)define species diversity. In table 4.1, two hypothetical communities– 1 and 2 – both have 5 species and 50 individuals. Species richness is the same in both communities. But the community–2

Table 4.1 Comparison of species richness and species evenness

Species	*Individuals per species*	
	Community 1	*Community 2*
Dog	10	05
Frog	10	05
Elephant	10	05
Lion	10	05
Horse	10	30
Total individuals	50	50
Total number of species	05	05

the x-axis. Thus, the most abundant species is plotted first along the x-axis, with the corresponding value on the y-axis being the value of relative abundance. This process is continued until all species are plotted. The resulting graph is called a **rank-abundance diagram**. It is a graphical plot of numbers of individuals per species against the rank of species commonness in the community. A rank abundance diagram can be drawn for the number of individuals in a community, biomass of individuals, ground area covered by plants and other variables all plotted against rank abundance.

4.1.3 Diversity index

A *diversity index* is a mathematical measure of species diversity in a community. It is a measure of the number of species in an area and the relative abundance of individuals among those species. That is, it takes into account the number of species present (*species richness*) as well as the abundance of each species (*species evenness*). A variety of indices have been used to estimate species diversity. We can divide them into two broad categories: *dominance indices* and *information statistic indices*. Dominance indices are more influenced by the abundance of common or dominant species. A widely used dominance index is *Simpson's diversity index*. Information statistic indices are more influenced by the numbers of rare species. Most commonly used information statistic index is the *Shannon diversity index*.

Simpson's diversity index

Simpson's diversity index is a simple mathematical measure that characterizes species diversity in a community. The term *Simpson's diversity index* can actually refer to any one of two closely related indices – *Simpson's index* and *Simpson's index of diversity*.

Simpson's index (D) is a measure of the species diversity of an ecosystem based on the concept of dominance. It measures the probability that two individuals randomly selected from a sample will belong to the same species. It is actually a measurement of dominance. There are two versions of the formula for calculating D.

$$D = \sum P_i^2 = \sum \left(\frac{n}{N}\right)^2$$

where, P_i = the relative abundance of each species (n/N).

n = total number of individuals of a particular species in the sample.

N = total number of individuals of all species present in the sample.

For a finite community, this is

$$D = \frac{\sum n\,(n-1)}{N\,(N-1)}$$

D is a measure of dominance, so as D increases, diversity (in the sense of evenness) decreases. The value of D ranges between 0 and 1. With this index, 0 represents an infinite diversity and 1, no diversity. That is, the bigger the value of D, the lower the diversity.

Simpson's index is usually reported as its complement 1-D called **Simpson's index of diversity**. The value of this index also ranges between 0 and 1, but now, the greater the value, the greater the sample diversity. In this case, the index represents the probability that two individuals randomly selected from a sample will belong to different species.

Positive interaction

Mutualism

Mutualism is a symbiotic relationship between members of two different species in which both members of the association benefited. On the basis of this relationship, individuals of both species enhance their survival, growth, or reproduction. Mutualistic relationships involve diverse interactions. Mutualisms can be characterized by the degree of dependency, the kinds of benefits received, the degree of specificity and duration of the interactions.

Mutualisms can vary in the degree of dependency between mutualists. Based on this, mutualisms can be *obligate* or *facultative*. In **obligate mutualism**, both organisms benefit by living in close association, and the relationship is obligatory (i.e. neither can survive without each other). Obligate mutualists cannot survive or reproduce without the mutualistic interaction. In **facultative mutualism** (also called **protocooperation**), mutualists benefit by living in close association, but the relationship is not obligatory. The cooperating species do not depend on each other for survival. One good example is the mutualistic association between a coelenterate, sea anemone — *Adamsia palliata* and a hermit crab – *Pagurus prideaux*. The sea anemone is carried by the crab to fresh feeding sites and crab in turn is said to be protected from its enemies by sea anemone.

The term **symbiosis** is sometimes used in the same sense as mutualism. 'Symbiosis' (termed used by de Barry in 1879) simply means *living together*. In narrowest sense, it is used to describe an association in which two species are deriving mutual benefit. However, now this term is used in a broad sense to describe all types of interactions (positive, negative or neutral). So, symbiosis is a close ecological relationship between the individuals of two (or more) different species.

The duration of intimacy among mutualistic interactions and also the degree of specificity of mutualistic interactions varies from one interaction to another. The mutualistic interactions can range from one-to-one, species-specific associations (termed *specialists*) to association with a wide diversity of mutualistic partners (*generalists*). Mutualisms can also be subdivided according to the services provided, regardless of whether the participants are obligate or facultative mutualists. Based on the nature of service involved, mutualisms can be *dispersive*, *defensive* and *resource-based mutualism.* **Dispersive mutualism** involves mutualistic association in which one partner species distributing pollens or seeds of another species and in return receives resources for growth. **Defensive mutualism** involves mutualistic association in which one partner provides protection to other partner against herbivores or parasites in exchange for a place to live or for nutrients needed for growth. **Resource-based mutualism** involves interactions where resources (such as nutrients) obtained by one mutualist is made available to another.

There are many classic examples of mutualistic associations in nature. Reef-forming corals of the tropical waters provide an excellent example of *resource-based mutualism*. **Coral reefs** are a special subtype of ocean floor ecosystem. One fascinating feature of shallow water, reef-building corals is their mutualistic relationship with photosynthetic algae called **zooxanthellae**, which live in their tissues. The coral provides the algae with a protected environment and the compounds they need for photosynthesis. In return, the algae produce oxygen and help the coral to remove wastes.

Box 4.2 Host-parasite coevolution

Coevolution is the process by which ecologically interacting species, evolve in tandem by exerting selection pressures on each other. It involves an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals in a second population, followed by an evolutionary response by the second population to the change in the first. Examples of coevolutionary systems include host and parasites, predators and prey, and mutualistic or symbiotic interactions. Coevolution in parasites and hosts is antagonistic, unlike the mutualistic coevolution of ants and caterpillars or of flowering plants and pollinators.

Coevolution that is driven by antagonistic interactions, so-called 'antagonistic coevolution' can be defined as 'reciprocal adaptation and counter-adaptation of two interacting species for which fitness is negatively correlated'. In other words, an adaptation that increases fitness in one species will decrease the fitness of the other species. Theoretical and empirical studies of antagonistic coevolution have generally focused on two distinct mechanisms, one driven by negative frequency-dependent selection and the other by positive directional selection. These two mechanisms are expected to have fundamentally different influences on important evolutionary phenomena (e.g. the maintenance of genetic variation and sex).

Negative frequency–dependent selection: Red Queen coevolution

Frequency-dependent selection is defined as a situation where fitness is dependent upon the frequency of a phenotype or genotype in a population. In case of *negative frequency-dependent selection*, the fitness of a phenotype or genotype increases as its frequency in a population decreases. On the other hand, in case of *positive frequency-dependent selection*, the fitness of a phenotype or genotype increases as its frequency in a population increases.

Negative frequency-dependent selection is believed to be a primary driver of coevolution between biological antagonists. According to this selection, the parasite should adapt to the most common host genotype, because it can then infect a large number of hosts. In turn, a rare host genotype may then be favoured by selection, its frequency will increase and eventually it becomes common. Subsequently, the parasite should adapt to the former infrequent genotype. Coevolution determined by negative frequency-dependent selection is rapid. It maintains high genetic diversity by favouring uncommon alleles. Negative frequency-dependent selection is considered by many evolutionary biologists to be a particularly important and interesting form of natural selection because, unlike directional and stabilizing selection, negative frequency-dependent selection favours rare genotypes and can thus maintain high levels of genetic diversity.

Positive directional selection: Arms race coevolution

If an allele provides a fitness benefit, its frequency will increase within a population – the selection is a *positive directional selection*. Under positive directional selection, relative fitness increases as the value of a trait increases. Dawkins and Krebs (1970) suggested that reciprocal positive directional selection exerted by coevolving hosts and parasites could lead to a situation where hosts continually become more resistant to parasitism while parasites respond by becoming more virulent or evolving new mechanisms of evading host immunity (i.e. *Arms race coevolution*). 'Arms race' is a specific form of coevolution that is characterized by increased levels of defense and counterdefense in antagonistic interactions. The process is considered to be slower in comparison to negative frequency-dependent selection. In contrast to Arms race coevolution, Red Queen coevolution, synonymous with *negative frequency-dependent selection*, occur when rare host genotypes have a selective advantage over common ones.

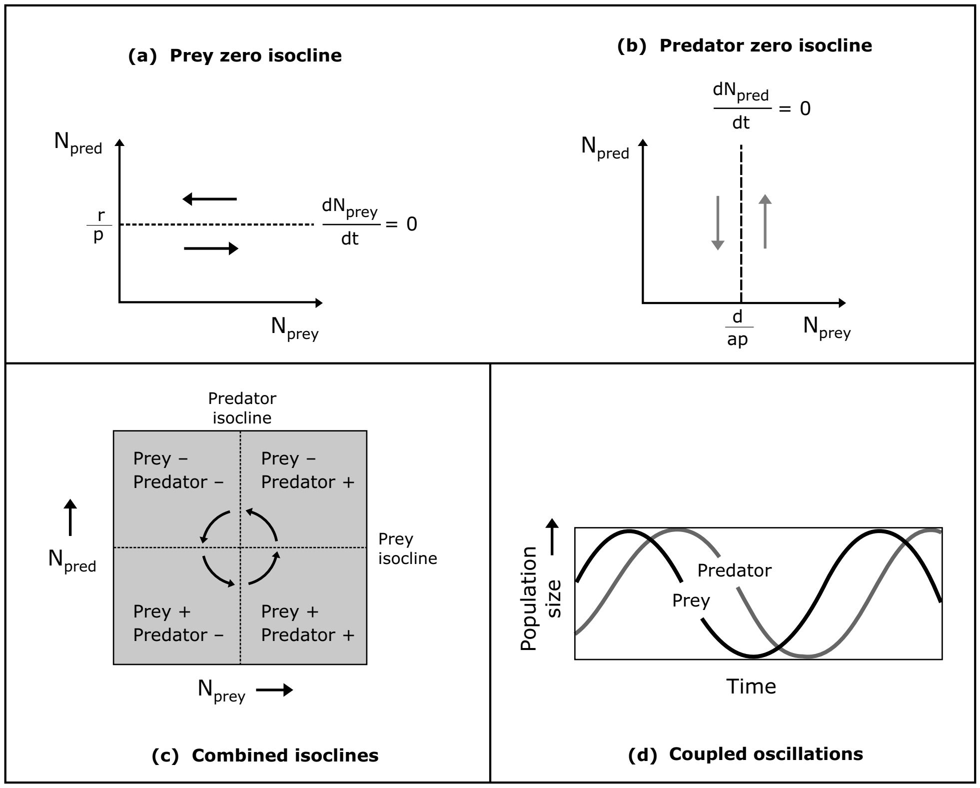

Figure 4.7 The basic Lotka-Volterra predator-prey model. (a and b) Zero isoclines (dN/dt = 0) for the prey and predator populations. Note that the zero isocline for the prey population is defined by a fixed number of predators, and the zero isocline for the predator population is defined by a fixed number of prey. Arrows show the direction of change in population size relative to the isoclines. The prey zero isocline: The number of prey increases at low predator densities and decrease at high predator densities. The predator zero isocline: The number of predators increases when prey numbers are high and decreases when prey numbers are low. (c) When prey and predator isoclines are combined, coupled oscillations result. When the zero isoclines are combined, the arrows can also be combined, and these joint arrows progress in anticlockwise circles. A minus sign indicates population decline, and a plus sign indicates population increase. This trajectory shows the cyclic nature of the predator–prey interaction. (d) By plotting the changes in size for both the predator and prey populations through time, we can see that the two populations continuously cycle out of phase with each other, and the density of predators lags behind that of prey. Adapted from Begon, et al., 1996.

Odum (1959) defined the ecological niche as 'the position or status of an organism within its community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behavior (inherited and/or learned).' He emphasized that 'the ecological niche of an organism depends not only on where it lives but also on what it does.' The place an organism lives, or where one would go to find it, is its habitat. For Odum the habitat is the organism's 'address,' whereas the niche is its 'profession.'

4.8 Ecological niche

Organisms do not live in isolation. They interact with other organisms, inhabit particular environment and coevolve with other organisms and with changing environment. *Niche* represents the place where members of a species live, the ways in which the environmental resources are used and interactions with other individuals of their own or of other species. Thus, the niche concept expresses the relationship of the individuals to all aspect of its environment.

The term 'niche' was used for the first time by Grinnell is frequently misunderstood and misused. It is often used loosely to describe the sort of place in which an organism lives. Strictly, however, the place in which a particular organism lives is its **habitat**. Niche is different from habitat. It is not simply a place where organism lives. *It is the sum total of all the ecological requisites and activities of a species.* It includes not only the physical space occupied by an

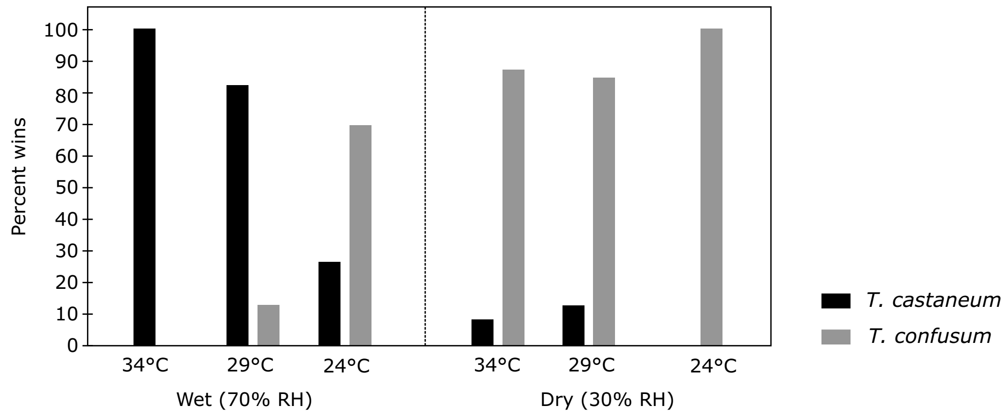

Figure 4.11 Competitive ability can be influenced by the abiotic environment. Biologist Thomas Park cultured two different species of flour beetles, *Tribolium castaneum* and *Tribolium confusum*, together at varied temperature and moisture. Results of competition between two flour beetles show that each species usually performs better in a given habitat; for example, *T. confusum* does better in dry conditions.

Competitive exclusion and coexistence

The species coexistence is rooted in the competitive exclusion principle, which states that two species competing for the same resource cannot coexist. The species that is better at gaining the limiting resource will eventually eliminate the inferior competitor. If a superior and an inferior competitor are placed into a habitat at initially equal abundance, the former will inevitably eliminate the latter. Differences between species in their competitive ability drive the superior to dominance and the inferior to exclusion. If complete competitors drive one another to local extinction, then how two very related species will coexist?

One answer to reduce interspecific competition between species and thus competitive exclusion of inferior species is the *niche differentiation*. For example, the niche differences of the two rodent species may include differences in the size of seeds consumed – one rodent tends to consume larger seeds and other smaller seeds. By niche differentiation two rodent species can reduce competition for food and coexist.

Resource partitioning

Niche differentiation may take a variety of forms, of which *resource partitioning* is most common. Because the degree of competition is assumed to depend upon the degree of niche overlap, hence, some species evolve to reduce niche overlap through resource partitioning. The term 'resource partitioning' describes the niche differentiation, both in space and time that enables similar species to coexist in a community. It refers to the state of reduced overlap in resource use between coexisting species. By consuming slightly different forms of a limiting resource or using the same limiting resource at a different place, individuals of different species compete less with one another (interspecific competition). Through resource partitioning in temporal scale, species also able to manage to coexist by using the same limiting resources at different times. The assumption is that competition among species that are active at different times would be less intense than if the same set of species all attempted to use the same resource at the same time. Resource partitioning is often viewed as a product of the coevolution of characteristics that function to reduce competition.

Chapter 5

Biodiversity

Biodiversity, short for **biological diversity**, refers to the sum total of all the variety and variability of life in a defined area. In contrast to the more specific term *species diversity*, the term *biodiversity* was coined to emphasize the many complex kinds of variations that exist within and among organisms at different levels of organization. It refers to the totality of genes, species and ecosystems of a region. United Nations Earth Summit defined biological diversity as:

'*Biological diversity means the variability among living organisms from all sources including, inter alia (among other things), terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems*.'

Convention on Biological Diversity, 1992

5.1 Levels of biodiversity

Biodiversity includes three hierarchical levels: Genetic, species and ecosystem diversity

Genetic diversity

Genetic diversity refers to the variation in the genetic composition of individuals within or among species. The genetic diversity enables the population to adapt to its environment and respond to natural selection. The amount of genetic variation is the basis of speciation. Genetic diversity occurs at several levels of organization such as among higher taxonomic categories such as kingdoms phyla and families, among species and among populations. Most genetic diversity one can see between organisms of two kingdoms (such as plants versus animals), between phyla (such as arthropods versus chordates), between classes (such as birds versus reptiles) and so on.

Species diversity

According to *biological species concept*, species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. Simply, species diversity refers to the variety of species within a region i.e. species richness. However, in the broad sense, species diversity includes species richness, species evenness as well as taxonomic (or phylogenetic) diversity. Taxonomic or phylogenetic diversity describes the genetic relationship between different groups of species. A more taxonomically diverse community is therefore considered richer compared to the less taxonomically diverse community.

Species richness and evenness

The simplest measure of species diversity is species richness, i.e. the number of species present in per unit area. Species richness is only one aspect of diversity. Not all species exist in equal numbers: some are rare, some are common but not numerous, and others are very abundant. Imagine two forests, both of which contain a total of 100 individuals belonging to 5 different species. In one forest, there are 20 individuals of each species. In the other, one species has 60 individuals, while each of the other four species has 10 individuals. These two samples differ in a property called *evenness*. The first, in which the species are represented by the same number of individuals, is more even, and thus, has high overall species diversity. Thus, the species diversity of a community depends on both its richness as well as evenness: higher species numbers, with the individuals more evenly distributed among them, contribute to higher community diversity.

Ecosystem diversity

Ecosystems include all the species, plus all the abiotic factors characteristic of a region. For example, a desert ecosystem has soil, temperature, rainfall patterns, and solar radiation that affect not only what species occur there, but also the morphology, behaviour and the interactions among those species. Ecosystem diversity describes the number of niches, trophic levels and various ecological processes that sustain energy flow, food webs and the recycling of nutrients.

5.2 Gradients and Magnitude of biodiversity

Gradients of biodiversity

Biodiversity varies with changes in latitude or altitude. As we move from the poles to the equator, the biodiversity increases, and vice versa. The increase in species richness or biodiversity that occurs from the poles to the tropics often referred to as the *latitudinal gradient* in species diversity, is one of the most widely recognized patterns in ecology.

In general, species diversity decreases as we move away from the equator towards the poles. With very few exceptions, tropics (latitudinal range of 23.5° N to 23.5° S) harbour more species than temperate or polar areas. For example, Colombia located near the equator has nearly 1,400 species of birds while New York at 41° N has about 105 species and Greenland at 71° N only about 56 species. India, with much of its land area in the tropical latitudes, has more than 1,200 species of birds. The tropical Amazon rain forest in South America has the greatest biodiversity on the Earth – it is home to more than 40,000 species of plants.

The two key factors in latitudinal gradients of species richness are probably *evolutionary history* and *climate*. Over the course of evolutionary time, species diversity may increase in a community as more speciation events occur. Tropical communities are generally older than temperate or polar communities. In effect, speciation events occur about five times as fast in the tropics as near the poles. Climate is another important reason of the latitudinal gradient in biodiversity. In terrestrial communities, the two main climatic factors correlated with biodiversity are solar energy input and water availability, both of which are relatively high in the tropics.

Just like latitudinal variation, *altitudinal variation* also causes changes in the biodiversity. A decrease in species diversity occurs from lower to higher altitudes on a mountain. A 1000 m increase in altitude results in a temperature drop of about 6.5°C. The drop in temperature and greater seasonal variability at higher altitudes are major factors that reduce biodiversity.

Critically endangered

A species is critically endangered when it is facing an extremely high risk of extinction in the wild in the immediate future. To be defined as critically endangered, a species must meet any of the following criteria.

- Population reduction: ≥80-90% population decline
- Geographic range
  Extent of occurrence: <100 km^2
  Area of occupancy: <10 km^2
- Population size: <250 mature individuals
- Extinction probability (in the wild): at least 50% within 10 years or 3 generations.

Example: Gharial, Great Indian bustard, Ganges shark, Pygmy hog.

Reduction of population size causes loss of genetic diversity due to loss of some alleles from the species. It also increases the chance of inbreeding and homozygosity. Increased homozygosity increases mortality of young, and inbreeding depression leads to reduced offspring fitness.

Endangered

A species, whose numbers are so small that the species is at risk of extinction. To be defined as endangered, a species must meet any of the following criteria.

- Population reduction: 50-70% population decline
- Geographic range
  Extent of occurrence: <5,000 km^2
  Area of occupancy: <500 km^2
- Population size: <2,500 mature individuals
- Extinction probability (in the wild): at least 20% within 20 years or 5 generations.

Example: Red panda, Snow leopard, Bengal Tiger and One horned rhinoceros and Black buck.

Vulnerable

A species is vulnerable when it is not critically endangered or endangered, but is facing a high risk of becoming endangered in the near future.

- Population reduction: ≥30-50% population decline
- Geographic range
  Extent of occurrence: <20,000 km^2
  Area of occupancy: <2,000 km^2
- Population size: <10,000 mature individuals
- Extinction probability (in the wild): at least 10% within 100 years.

Near threatened

A category on the IUCN Red List of threatened species which indicates that a taxon has been evaluated against the Red List criteria does not qualify for critically endangered, endangered and vulnerable status now but it is close to qualify or likely to qualify for a threatened category in the near future. Polar bears, giraffes, and white rhinos are listed as Near Threatened species because their survival depends on conservation programs.

Of the 47,677 species in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species of 2009, 17,291 are deemed to be at serious risk. The list reveals that 21 percent of all known mammals, 30 percent of all known amphibians, 12 percent of all known birds, 28 percent of reptiles, 37 percent of freshwater fishes, 70 percent of plants and 35 percent of invertebrates assessed so far, are under threat.

Experts on Biological Diversity in November 1988. The Convention was opened for signature at the Earth Summit in Rio de Janeiro on 5 June 1992 and entered into force on 29 December 1993. It has three main objectives:

- The conservation of biological diversity.
- The sustainable use of the components of biological diversity.
- The fair and equitable sharing of the benefits arising out of the utilization of genetic resources.

CITES

CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora), also known as the **Washington Convention**, is an international agreement to protect endangered plants and animals. It was drafted as a result of a resolution adopted in 1963 at a meeting of members of the International Union for Conservation of Nature (IUCN). The convention was opened for signature in 1973 and CITES entered into force on 1 July 1975. Its aim is to ensure that international trade in specimens of wild animals and plants does not threaten the survival of the species in the wild, and it accords varying degrees of protection to more than 35,000 species of animals and plants. India become party to CITES in 1976.

World Heritage Convention (WHC)

The convention concerning the protection of the world cultural and natural heritage commonly known as the 'World Heritage Convention', is an international treaty, adopted in 1972. The convention recognizes the way in which people interact with nature, and the fundamental need to preserve the balance between the two. The convention sets out the duties of states parties in identifying potential sites and their role in protecting and preserving them. By signing the convention, each country pledges to conserve not only the World Heritage sites situated on its territory, but also to protect its national heritage.

World Heritage sites are places on Earth that are of Outstanding Universal Value (OUV) to humanity and therefore, have been inscribed on the World Heritage List to be protected for future generations. Places as diverse and unique as the Great Barrier Reef in Australia, Galapagos Islands in Ecuador and the Grand Canyon in the USA are examples of places inscribed on the World Heritage List. The World Heritage Convention 1, which has been ratified by 191 countries, was adopted by United Nations Educational, Scientific and Cultural Organization's (UNESCO) General Conference in 1972, and came into force in 1975, for the identification, protection, conservation, presentation and transmission to future generations of the world cultural and natural heritage. The secretariat to the World Heritage Convention is the UNESCO World Heritage Centre, whilst three organisations: International Council on Monuments and Sites (ICOMOS), International Centre for the Study of the Preservation and Restoration of Cultural Property (ICCROM) and the International Union for Conservation of Nature (IUCN) act as its Advisory Bodies. The Advisory Body on natural heritage is IUCN.

Convention on the Conservation of Migratory Species of Wild Animals

The CMS, or the *Bonn Convention* aims to conserve terrestrial, marine and avian migratory species throughout their range. Parties to the CMS work together to conserve migratory species and their habitats by providing strict protection for the most endangered migratory species, by concluding regional multilateral agreements for the conservation and management

Chapter 6

Pollution

Pollution is any undesirable change in the physical, chemical, or biological characteristics of the air, water and land that can harmfully affect the living organisms and the ecosystem as a whole. Any substance introduced into the environment that adversely affects the physical, chemical or biological properties of the environment that have a harmful effect on the ecosystem as a whole is termed as **pollutant**. There are three major types of environmental pollution: air pollution, water pollution and soil pollution.

6.1 Air pollution

Air pollution may be defined as any atmospheric condition in which *substances* are present at concentrations above their normal permissible levels to produce a *measurable effect* on man, animals, vegetation or materials. Substances mean any natural or anthropogenic (man-made) chemical compounds capable of being airborne. They may exist in the atmosphere as gases, liquid drops or solid particles.

According to Air (prevention and control) act, 1981, an *air pollutant* is any solid, liquid or gaseous substance (including noise) present in the atmosphere in such concentration as may be or tend to be injurious to human being or other living creatures or plants or property or environment.

6.1.1 Composition of air

Air is a heterogenous mixture of different gases that makes the atmosphere. *Atmosphere* is the gaseous mass or envelope surrounding the Earth and retained by the Earth's gravitational field. The troposphere is the lowest portion of Earth's atmosphere. It contains approximately 80% of the atmosphere's mass. By volume, dry air contains 78.08% nitrogen, 20.9% oxygen, 0.9% argon, 0.033% carbon dioxide, and small amounts of other gases. There are two common ways by which one can represent the composition of air – *percentage of gas by volume* or *percentage of the gas by mass.* It is important to note that, the composition of different gases (in dry air) by mass is a fixed one whereas the percentage composition of the gases by volume or mass in wet air (i.e. air containing moisture) is dependent on humidity or the moisture in the air.

Table 6.1 Composition of clean, dry air (expressed in volume)

Constituent	*Percent by volume*	*In ppm*
Nitrogen	78.084%	780840
Oxygen	20.9%	209440
Argon	0.93%	9340
Carbon dioxide	0.0355%	355 (Year 1990)
Others	0.065%	650

6.1.2 Sources of air pollution

There are two main sources of air pollution:

Natural sources – such as wind-blown dust, wildfires and volcanoes

Man-made (or anthropogenic) **sources**

Man-made sources can be mobile or stationary in nature.

Mobile sources: These sources account for most of the air pollution and the primary mobile source of air pollution is the automobile.

Stationary sources: Air pollution sources that do not move from location to location. It can be either point source or area source.

Point sources include pollution from power plants, oil refineries, emit large amounts of pollution from a single location.

Area sources include emissions from many smaller stationary sources present in an industrial, commercial and residential area.

6.1.3 Types of air pollutants

Air pollutant can be of natural origin or man-made. It can be classified on the following basis:

- the physical state of the pollutant
- the basis of origin
- the occurrence and nature of the threat

Classification based on the physical state of the pollutant

According to the physical state of pollutant, pollutants may be gaseous and particulate in nature.

Aerosol
An aerosol is a colloid of fine solid particles or liquid droplets, in gas. A *colloid* is a broad category of mixtures, and is defined as one phase suspended in another. Aerosol can be *liquid aerosol* (*liquid* suspended in gas) and *solid aerosol* (*solid* suspended in gas).

Gaseous pollutants include carbon dioxide, sulfur oxides, oxides of nitrogen, carbon monoxide, volatile organic compounds, chlorofluorocarbons, ammonia and other gases.

Particulate matters are tiny solid or liquid particles suspended in air.

Classification based on origin

Air pollutants can also be classified as either *primary* or *secondary,* based on origin.

Primary air pollutants are substances which are directly emitted into the atmosphere from natural and anthropogenic sources, such as SO_2 from a volcanic eruption and the carbon monoxide gas from motor vehicles.

6.5 Bioremediation

Bioremediation is a biological process whereby organic wastes are biologically degraded under controlled conditions. The process involves the use of living organisms, primarily microorganisms, to degrade the environmental contaminants. In this process, contaminant compounds are transformed by living organisms through reactions that take place as a part of their metabolic processes. For bioremediation to be effective, microorganisms must enzymatically attack the contaminants and convert them to harmless products. Hence it is effective only where environmental conditions permit microbial growth and activity. Thus, its application involves the manipulation of environmental parameters to allow microbial growth and degradation to proceed at a faster rate. The control and optimization of bioremediation processes is a complex phenomenon. Various factors influence this process. These factors include: the existence of a microbial population capable of degrading the pollutants; the availability of contaminants to the microbial population; the environment factors (type of soil, temperature, pH, the presence of oxygen or other electron acceptors and nutrients).

Bioremediation strategies

Bioremediation strategies can be *in-situ* or *ex-situ*. *In situ bioremediation* involves treating the contaminated material at the site while *ex-situ bioremediation* involves the removal of the contaminated material to be treated elsewhere. *In-situ* bioremediation techniques are generally the most desirable option due to lower cost and less disturbance since they provide the treatment at a site avoiding excavation and transport of contaminants. *Ex-situ* bioremediation requires transport of the contaminated water or excavation of contaminated soil prior to remediation treatments.

In-situ and *ex-situ* strategies involve different technologies such as bioventing, biosparging, bioreactor, composting, landfarming, bioaugmentation and biostimulation.

Bioventing is an *in-situ* bioremediation technology that uses microorganisms to biodegrade organic constituents adsorbed on soils in the *unsaturated zone* (extends from the top of the ground surface to the water table). Bioventing enhances the activity of indigenous bacteria and stimulates the natural *in-situ* biodegradation of contaminated materials in soil by inducing air or oxygen flow into the unsaturated zone and, if necessary, by adding nutrients.

Biosparging is also an *in-situ* bioremediation technology that uses indigenous microorganisms to biodegrade organic constituents in the *saturated zone*. In biosparging, air (or oxygen) and nutrients (if needed) are injected into the saturated zone to increase the biological activity of the indigenous microorganisms.

Biostimulation involves the modification of the environment to stimulate the existing bacteria capable of bioremediation. This can be done by the addition of various forms of rate limiting nutrients and electron acceptors, such as phosphorus, nitrogen, oxygen, or carbon (e.g. in the form of molasses).

Bioaugmentation is a process where selected, standardized bacteria (microbes) are added to an area that has been contaminated with an unwanted substance. These bacteria cause breakdown of contaminants.

Composting is a controlled decomposition of organic matters. It involves mixing of contaminated soil with non-hazardous organic materials such as manure or agricultural wastes. The presence of these organic materials supports the development of a rich microbial population, which causes decomposition of organic contaminants.

Chapter 7

Climate Change

Climate is the long-term pattern of weather in a locality, region or even over the entire globe. It is the statistics of weather, usually over a 30-year interval. It is measured by assessing the patterns of variation in temperature, humidity, atmospheric pressure, wind, precipitation and other meteorological variables in a given region over long periods of time.

'*Climate in a narrow sense is usually defined as the average weather, or more rigorously, as the statistical description in terms of the mean and variability of relevant quantities over a period of time ranging from months to thousands or millions of years. The classical period for averaging these variables is 30 years, as defined by the World Meteorological Organization. The relevant quantities are most often surface variables such as temperature, precipitation and wind. Climate in a wider sense is the state, including a statistical description, of the climate system*.'

Intergovernmental Panel on Climate Change (IPCC), 2001

The terms climate and weather have different meanings. **Weather** is the short-term properties (such as temperature, pressure, moisture) of atmospheric conditions for a specific place and time. Weather differs both spatially and temporally. Two of the most important factors determining an area's climate are air temperature and precipitation. The climate of a region will determine which plants will grow there and which animals will inhabit it.

7.1 Climate change

Climate science is a process of collective learning that relies on the careful gathering and analyses of data, the formulation of hypotheses, the development of models to study key processes and make predictions, and the combined use of observations and models to test scientific understanding.

Climate change is a large-scale, long-term shift in the planet's weather patterns. According to Intergovernmental Panel on Climate Change (IPCC),

'*Climate change refers to a change in the state of the climate that can be identified* (*e.g. by using statistical tests*) *by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forcings such as modulations of the solar cycles, volcanic eruptions and persistent anthropogenic changes in the composition of the atmosphere or in land use*'.

The United Nations Framework Convention on Climate Change (UNFCCC) defines climate change as, 'a change of climate that is attributed directly or indirectly to human activity that alters

IPCC
The Intergovernmental Panel on Climate Change (IPCC) is the international body for assessing the science related to climate change. The IPCC was set up in 1988 by the World Meteorological Organization (WMO) and United Nations Environment Programme (UNEP) to provide policymakers with regular assessments of the scientific basis of climate change, its impacts and future risks, and options for adaptation and mitigation. The IPCC produces reports that support the United Nations Framework Convention on Climate Change (UNFCCC), which is the main international treaty on climate change.

Box 7.1 ***Scientific consensus***

'Climate change is real. There will always be uncertainty in understanding a system as complex as the world's climate. However, there is now strong evidence that significant global warming is occurring. The evidence comes from direct measurements of rising surface air temperatures and subsurface ocean temperatures and from phenomena such as increases in average global sea levels, retreating glaciers, and changes to many physical and biological systems. It is likely that most of the warming in recent decades can be attributed to human activities'.

Joint science academies' statement: Global response to climate change (2005)

7.2 Greenhouse effect

The Earth receives energy from the Sun in the form of solar radiation. Various gases in the atmosphere absorb incoming solar radiation. The ability of atmospheric gases to absorb radiation varies with the wavelength. All of the incoming solar radiation with wavelengths less than 0.3 µm is absorbed by oxygen and ozone. This absorption occurs mainly in the stratosphere. Most of the solar radiation passes through the atmosphere without being absorbed. A large fraction of this radiation is absorbed by land and oceans. This absorbed energy is then re-radiated upward from the Earth's surface in the form of longwave infrared radiation.

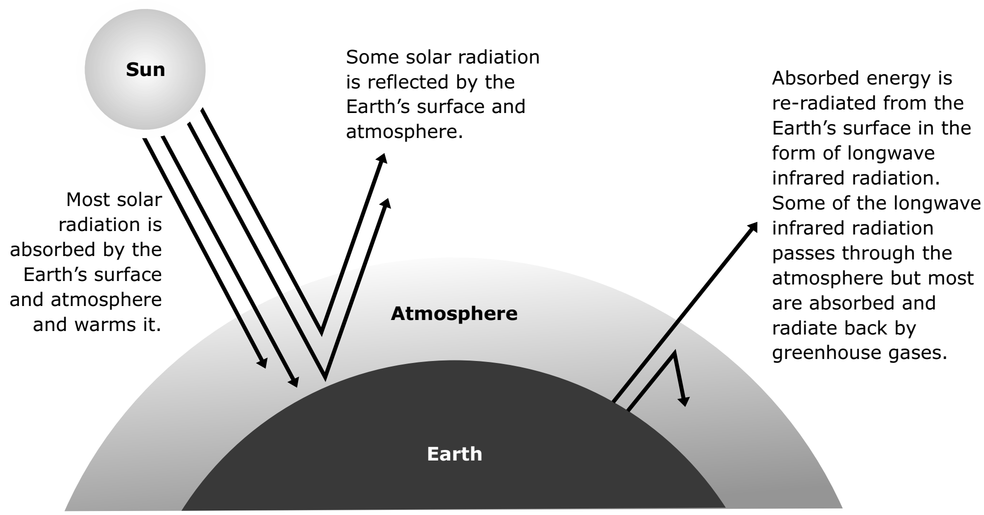

Figure 7.1 Incoming shortwave solar radiations (ultraviolet, visible and a limited portion of infrared energy) from the Sun drive the Earth's climate system. Some of this incoming radiation is reflected by the atmosphere and the Earth's surface whereas some is absorbed by the atmosphere and the Earth's surface. The heat generated by this absorption is emitted as longwave infrared radiation. Some of which radiates out into space but most of the Earth's emitted longwave infrared radiation is absorbed by greenhouse gases present in the atmosphere, which heats the lower atmosphere.

Most of these longwave infrared radiation (greater than 4 µm) re-radiated by the Earth's surface is absorbed by atmospheric gases, most importantly water vapor (H_2O), carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4). Radiatively active gases that absorb wavelengths longer than 4 µm are called **greenhouse gases**. This absorption heats the atmosphere, which in turn, radiates energy back to the Earth. Thus, the greenhouse gases act as a thermal blanket around the Earth, raising the Earth's temperature. This effect is known as **greenhouse effect**.

$$O_2 \xrightarrow{<242 \text{ nm}} O + O$$

The atomic oxygen, in turn, reacts with molecular oxygen to form ozone,

$$O + O_2 \xrightarrow{M} O_3 + M$$

Where M represents a third body (N_2 or O_2) necessary to carry away the energy released in the reaction. The ozone that is formed in this process is also dissociated by solar radiation to form an oxygen atom and an oxygen molecule. Ozone absorbs UV radiation in the 200 to 320 nm wavelength region and generates molecular oxygen as a result of photodissociation.

$$O_3 \longrightarrow O_2 + O$$

This cyclic process leads to a natural steady-state concentration of stratospheric ozone. These three reactions are called the **Chapman cycle**, after the person who discovered them.

Levels of ozone in the stratosphere are measured in **Dobson Units** (D.U.). The average amount of stratospheric ozone throughout the world is about 300 D.U (equivalent to a layer 3 millimeters thick if it is compressed into a single layer). Ozone concentrations over Antarctica during the period of greatest depletion usually fall well below 200 D.U.

Box 7.3 Dobson Unit

The Dobson Unit (D.U.) is the most common unit for measuring ozone concentration. Instead of measuring the amount of ozone at a particular height, the Dobson Unit measures the total amount of ozone in a column extending vertically from Earth's surface to the top of the atmosphere. A column of air with an ozone concentration of 1 Dobson Unit would contain about 2.69×10^{16} ozone molecules for every square centimeter of area at the base of the column. The number of molecules of ozone present in one Dobson Unit would form a layer of 0.01 millimeters thick layer at the base of the column if it were compressed into a single layer at a temperature of 0°C and a pressure of 1 atmosphere. 100 Dobson Unit of ozone would form a layer only 1 millimeter thick if it were compressed into a single layer.

Ozone layer thickness is expressed in terms of Dobson units, which measure what its physical thickness would be if compressed in the Earth's atmosphere. Over the Earth's surface, the ozone layer's average thickness is about 300 Dobson Units or a layer that is 3 millimeters thick.

Stratospheric ozone depletion

Ozone is continuously being synthesized from molecular oxygen in the stratosphere by the absorption of short-wavelength ultraviolet (UV) radiation, while at the same time it is continuously being removed by various chemical reactions that convert it back to molecular oxygen. The rates of synthesis and destruction at any given time determine the concentration of ozone in the stratosphere. This balance is being affected by increasing stratospheric concentrations of chlorine and bromine, which increase the destruction process. One chlorine atom can destroy over 100,000 ozone molecules before it is removed from the stratosphere. *Bromine atom is believed to be 40 times more destructive than chlorine molecules.*

Some compounds release chlorine or bromine when they are exposed to intense UV light in the stratosphere. The chlorine and bromine containing compounds that cause significant depletion of the ozone layer are chlorofluorocarbons, carbon tetrachloride, methyl chloroform, hydrochlorofluorocarbons, hydrobromoflurocarbons and halons. These compounds contribute to

Biological Diversity Act, 2002

An act to provide for the conservation of biological diversity, sustainable use of its components and fair and equitable sharing of the benefits arising out of the use of biological resources and knowledge associated with it.

Scheduled Tribes & other Traditional forest Dwellers (Recognition of Forest Rights) Act, 2006

To address the adverse living conditions of many tribal families living in forests was on account of non-recognition and vesting of pre-existing rights, a landmark legislation viz. Scheduled Tribes and Other Traditional Forest Dwellers (Recognition of Forest Rights) Act, 2006, has been enacted to recognize and vest the forest rights and occupation of forest land in forest dwelling Scheduled Tribes and other traditional forest dwellers, who have been residing in such forests for generations, but whose rights could not be recorded.

Environment and Pollution

Water (Prevention and Control of Pollution) Act, 1974

Establishes an institutional structure for preventing and abating water pollution. It establishes standards for water quality and effluent. Polluting industries must seek permission to discharge waste into water bodies. The CPCB was constituted under this act. This act has been last amended in 1988.

Water (Prevention and Control of Pollution) Cess Act, 1977

An act to provide for the levy and collection of cess or fees on water consuming industries and local authorities. This act has been last amended in 2003.

Air (Prevention and Control of Pollution) Act, 1981

An act to provide for the prevention, control and abatement of air pollution. It entrusts the power of enforcing this act to the central board or state board. This act has been last amended in 1987.

Environment (Protection) Act, 1986

Authorizes the central government to protect and improve environmental quality, control and reduce pollution from all sources and prohibit or restrict the setting and/or operation of any industrial facility on environmental grounds. The EPA (Environment Protection Act), 1986 came into force soon after the Bhopal gas tragedy. This act has been last amended in 1991.

Manufacture, Storage and Import of Hazardous Chemical Rules, 1989

Define the terms used in this context, and sets up an authority to inspect, once a year, the industrial activity connected with hazardous chemicals and isolated storage facilities. These rules have been last amended in 2000. These rules were notified under the Environment (Protection) Act, 1986.

Public Liability Insurance Act, 1991

An Act to provide for public liability- insurance for the purpose of providing immediate relief to the persons affected by accident occurring while handling any hazardous substance and for matters connected therewith or incidental thereto. This act has been last amended in 1992.

The Economics of Ecosystems and Biodiversity (TEEB) for National and International Policy Makers 2009, noted different types of carbon emissions as colors of carbon:

Brown carbon
Industrial emissions of greenhouse gases that affect the climate.

Green carbon
Carbon incorporated into plant biomass and the soils below.

Blue carbon
Blue carbon is the term for carbon captured by the world's ocean and coastal ecosystems.

Black carbon
Formed through incomplete combustion of fuels.

all greenhouse gases in one standard unit. The 'equivalent' means that the footprint is made up of a number of different greenhouse gases, which have been converted into the equivalent quantity of carbon dioxide in order to show all emissions in a single number.

A carbon footprint is made up of the sum of two parts, the primary footprint and the secondary footprint. The primary footprint is a measure of our direct emissions of carbon dioxide from the burning of fossil fuels including domestic energy consumption and transportation (e.g. car and plane). The secondary footprint is a measure of the indirect carbon dioxide emissions from the whole lifecycle of products we use – those associated with their manufacture and eventual breakdown.

Why carry out a carbon footprint?

Carbon footprints are useful for a number of purposes:

1. For publicly reporting greenhouse gas emissions.
2. For setting a target for reducing emissions (in order to set a reduction target it is necessary to know what current emissions are).
3. To identify which activities contribute the most to a footprint (in order to identify the important areas for reduction efforts).
4. In order to measure changes in emissions over time and to monitor the effectiveness of reduction activities.
5. To offset emissions (in order to offset emissions it is necessary to know how many reductions credits to purchase).

Nitrogen footprint

Nitrogen is an important component in air, land and water. While necessary to life, reactive nitrogen (all forms of the nitrogen except N_2) can be detrimental to both ecosystem and human health when present in excessive amounts. Different forms of reactive nitrogen contribute to smog and reduced air quality, acid deposition, eutrophication, reduced drinking water quality, biodiversity loss, global warming and more.

The nitrogen footprint is a measurement of the amount of reactive nitrogen released into the environment as a result of human activities. It mainly includes NOx, N_2O, NO_3^-, and NH_3 emission. The two main pathways through which we release reactive nitrogen to the environment are fossil fuel combustion and food production. When a fossil fuel is burned, reactive nitrogen is emitted to the atmosphere as a waste product. The use of nitrogen in food production, on the other hand, is intentional. Nitrogen is a key nutrient for food production and is contained in fertilizers. The nitrogen footprint includes nitrogen contained in consumed food, plus nitrogen released during the whole chain of production, distribution and preparation of the food. The other component of the nitrogen footprint determines the amount of nitrogen (as NOx emissions) released from the burning of fossil fuels related to energy use in housing (e.g. cooking, heating, cooling); transport (e.g. use of private or public transport) and the energy used to produce goods and provide services.

Water footprint

The 'water footprint' concept was introduced by Hoekstra in 2002. It is defined as the total volume of freshwater used to produce the goods and services consumed by the individual or producer. It accounts for both the direct (domestic water use) and indirect (water required

Fundamentals of

Ecology and Environment

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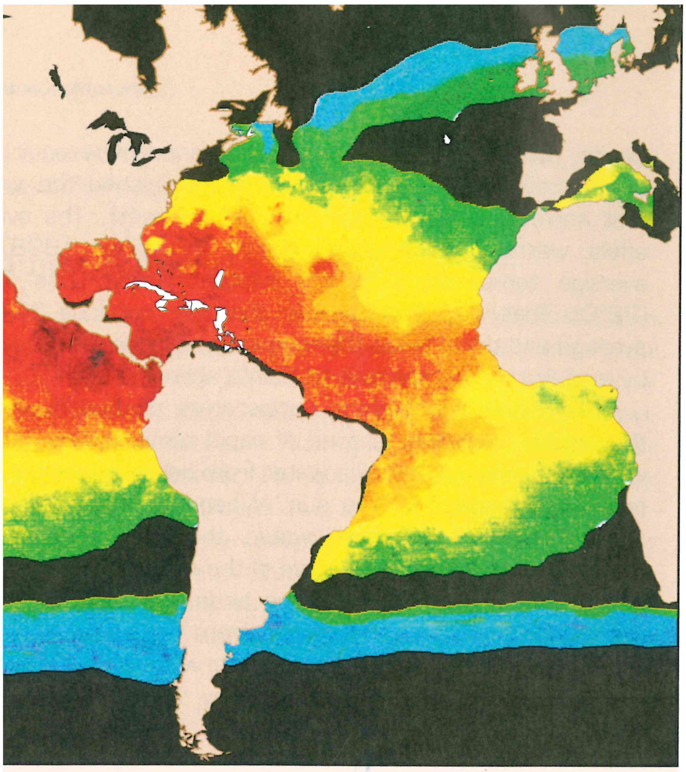


΄Ι Niño brings warm water to the Peruvian and Ecuadoran
ıts. In this map, red areas represent warm water.

ɔsystems in Flux At the Epicenter ΞΙ Niño

the people who fish along the coasts of Peru and ador, El Niños are part of life. An El Niño is a periodic al climate shift in which a slack in the trade winds sends sually warm water from the western Pacific eastward, ng into motion an unstoppable ecological chain reaction. espread changes in wind patterns, rainfall, and tempera- drastically alter food webs. Some populations swell, e others starve. Along the Peruvian coast, scallop and np populations explode, yet many types of fishes become carce that for a time, the fishing industry collapses. With ishes gone, birds, seals, and sea lions starve.

"El Niño" is Spanish for "the child," and refers to the Yule- beginnings of the phenomenon. The event usually occurs y 2 to 7 years, and typically lasts a year or two. Ten have ırred since about 1960. An El Niño is often followed by a rsal of conditions called a La Niña.

The 1982–83 event was supposed to be the "El Niño of century." In some places, the wind shifted direction, sing powerful storms and raising sea surface tempera- s along a 5,000-mile (8,050-kilometer) belt in the Pacific nd the equator. Fishes that were adapted to tropical and ropical waters followed the warmth toward the poles. y shore populations starved as changing sea levels and peratures drastically disrupted ecosystems.

–continued

Biomes and Aquatic Ecosystems

Severe weather patterns also affected the distribution of life. Monsoons in the central Pacific, typhoons in Hawaii, and forest fires raging through Indonesia and Australia decimated many local populations. In northern Peru and Ecuador, torrential rains, caused by the unusually warm Pacific waters, turned deserts into muddy grasslands. Here, insects flourished, providing food for burgeoning toad and bird populations. Fish populations suffered, however, as the animals migrated from the swollen ocean to pockets of salinity in the transient lakes that appeared in what was usually desert. When conditions began to reverse, fishes became trapped and died as the pools dried up.

In the United States, the 1982–83 El Niño caused flooding in southern California, blizzards in the Rockies, a warm winter in the Northeast, and rising chicken prices, as the fishes used in chicken feed migrated south from their usual habitats in Peru and Ecuador and escaped fishing nets. Yet at the same time, areas of Mexico, India, the Philippines, Australia, and southern Africa lost countless plants and animals to severe droughts.

The El Niño that began in December 1996 eclipsed the 1982 event. After a year-long period of starvation, the beaches of Peru became littered with sea lion pups, born prematurely because their mothers were starving. Adult carcasses washed ashore weeks later. Dead Peruvian boobies, a guano-producing bird, appeared too, as seabird nests went empty. Humboldt penguins were especially hard hit, an entire generation of nestlings wiped out by a 52-hour rainstorm in an area that hardly ever sees rain. Ecologists canvassed the area to assess the damage to populations.

Ecologists reconstructed the chain reaction of climatic and biological events comprising this recent El Niño. An atmospheric event called the Madden-Julian oscillation (MJO) boosted the Pacific warming that was already beginning in December 1996, and again in March 1997. An MJO is a 1- to 2-month-long wind burst near the equator that forms a patch of clouds that moves quickly over the Pacific from west to east. The MJO also increased evaporation in the western Pacific, which cooled conditions there. When the western Pacific cooled, the temperature difference between it and the eastern Pacific lessened, which diminished the winds that normally keep warmer water in the west. The overall effect: warming of the eastern Pacific. By January 1998, the average temperature of the eastern Pacific was 72°F (22°C). That was 13°F greater than the previous 30-year average and three times the temperature increase predicted by models that did not take MJO into account.

The rising sea surface temperature pushed down the thermocline, which is a zone of rapid temperature change where the cold nutrient-rich water from below meets the surface water heated by the sun. When the thermocline fell under the influx of warm water, the huge numbers of anchovies and sardines that live in the colder waters moved down. When this happened, the birds and seals that normally scoop these smaller fishes from the water could no longer reach them. The predators starved.

El Niño began to subside by May 1998. A year later, many of the areas in the Americas overwhelmed by El Niño–induced floods began to experience droughts caused by La Niña. This event begins in the eastern tropical Pacific Ocean, as low barometric pressure combines with a pool of westward-moving warm surface water. Despite these changes, the fishing families off the coast of Peru know that it is just a matter of time until the oceans warm again.

El Niño-induced Changes in Selected Animal Populations

	Number of Living Animals	
Population	**January 1997**	**May 1998**
Humboldt penguins	5,000	50
Fur seals	40,000	2,800
Sea lions	150,000	28,000

44.1 Biomes

We can view the planet as a patchwork of large geographic areas characterized by specific temperature and precipitation ranges, soils, and plant communities, which determine communities of other organisms. Biomes include several types of forests, savannas, grasslands, deserts, and tundra.

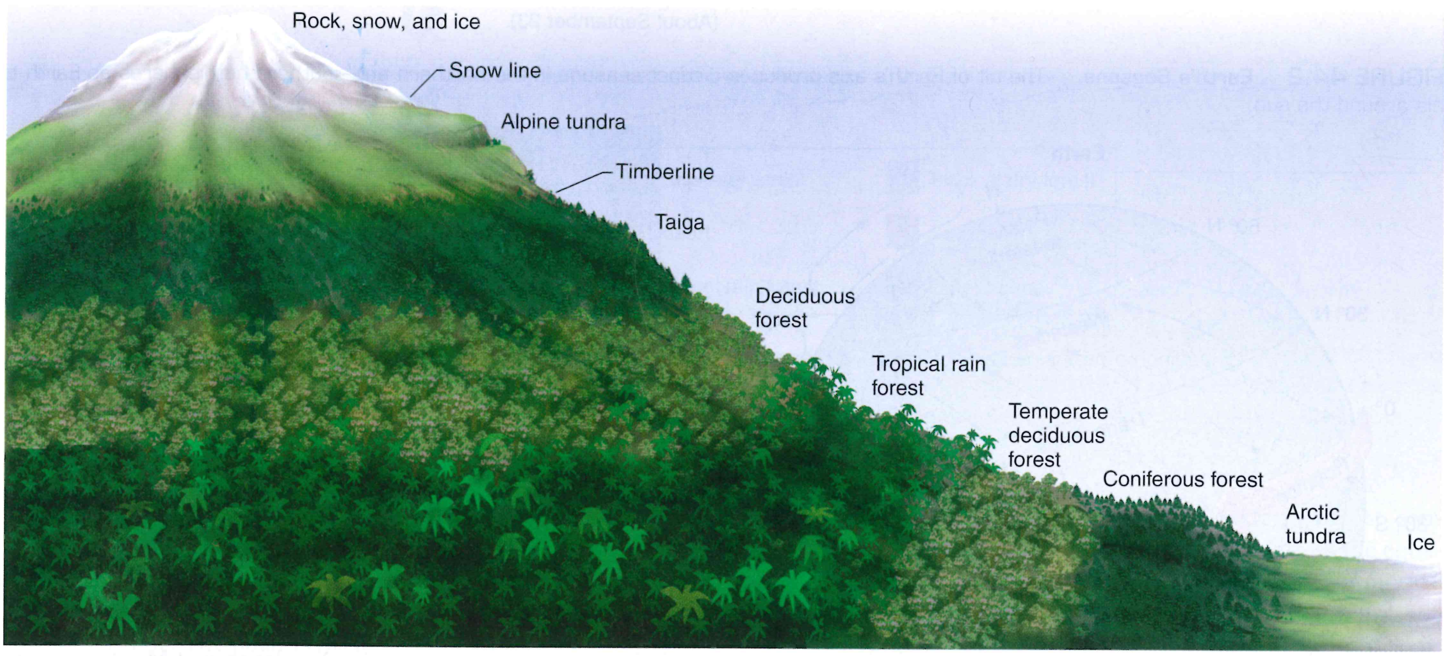
Ecology can be studied at several levels, from populations, to communities, to ecosystems. Several distinctive major types of terrestrial ecosystems, called **biomes,** occupy large geographic areas. Forests, deserts, and grasslands are examples of biomes, each of which supports characteristic communities. The water-based equivalents of biomes are called aquatic ecosystems. They occur in fresh water, in the oceans, and in the regions where salt and fresh water meet.

Plants define biomes because as primary producers, they form the bases of food webs. An overall pattern of vegetation influences which microorganisms, fungi, and animals can exist in the biome. The types of plants reflect long-term interactions with regional climate and soils, although the taxa in a given biome may differ on different continents. Animals also contribute to the structure of a biome. Humans have drastically altered many natural biomes, replacing forests, for example, with farmland, suburban housing, ıd cities. Finally, regional disturbances such as periodic fires and eezes influence the communities in some biomes.

limate Influences Biomes

he planet can be divided into major climatic regions based on mperature, within which biomes can be distinguished by the ailability of moisture, which determines the spectrum of ecies present. The major climatic regions, in order of decreasg average temperature, are the tropics, the temperate zone, the barctic, and the arctic. For example, tropical biomes range om the wettest, the tropical rain forest, to the tropical dry fort, to the still drier savanna, to semidesert and the hot, dry sert. Major changes in temperature also occur with elevation ithin biomes. **Figure 44.1** depicts these temperature-defined gions in terms of latitude and altitude. Conditions generally become drier and colder at higher latitudes and increasing altitudes, and biodiversity tends to decrease (**table 44.1**). Resident populations must be adapted to specific ranges of temperature, moisture, and wind conditions, and also to how these aspects of climate fluctuate during the year.

The great variety of physical environments on Earth is a consequence of the fact that the planet is a sphere that rotates at an angle as it orbits the sun (**figure 44.2**). Solar energy is most intense at the equator, where the sun is directly overhead. In other areas, the sun's rays hit the surface at oblique angles. Due to Earth's curvature, the same amount of solar energy is distributed over a larger area, so the average temperature falls with distance from the equator. Different latitudes receive the strongest solar rays at different times of the year because of the tilt to the axis of rotation. The northern and southern hemispheres alternate in receiving maximal sunlight, getting equal amounts on about March 21 and



GURE 44.1 Latitude and Altitude Influence Plant Communities. With increasing elevation on a mountain, the dominant types of plants rallel many of the types that appear as distance from the equator (latitude) increases.

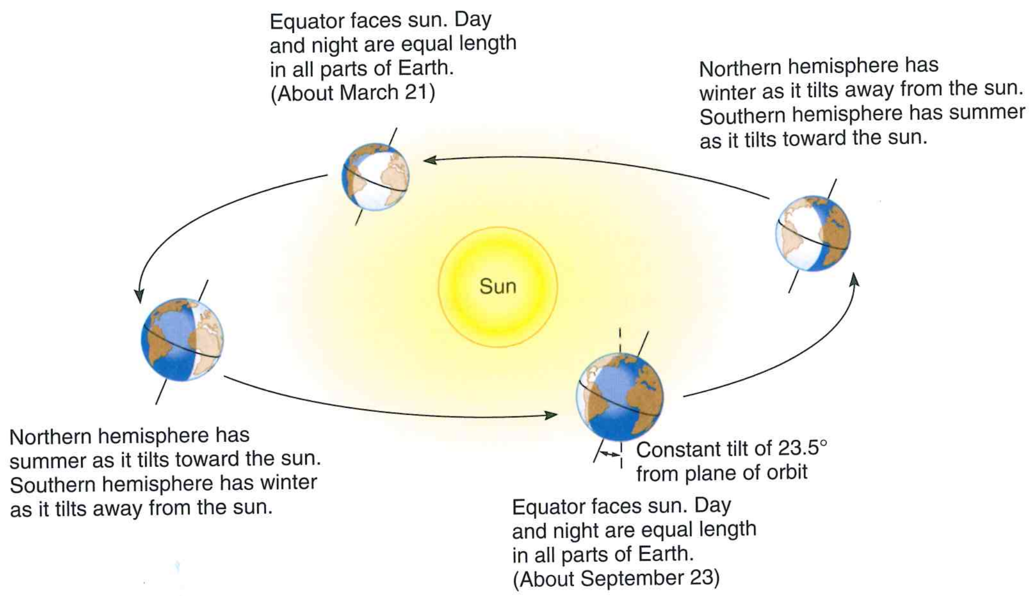
TABLE 44.1

Butterfly Species Diversity

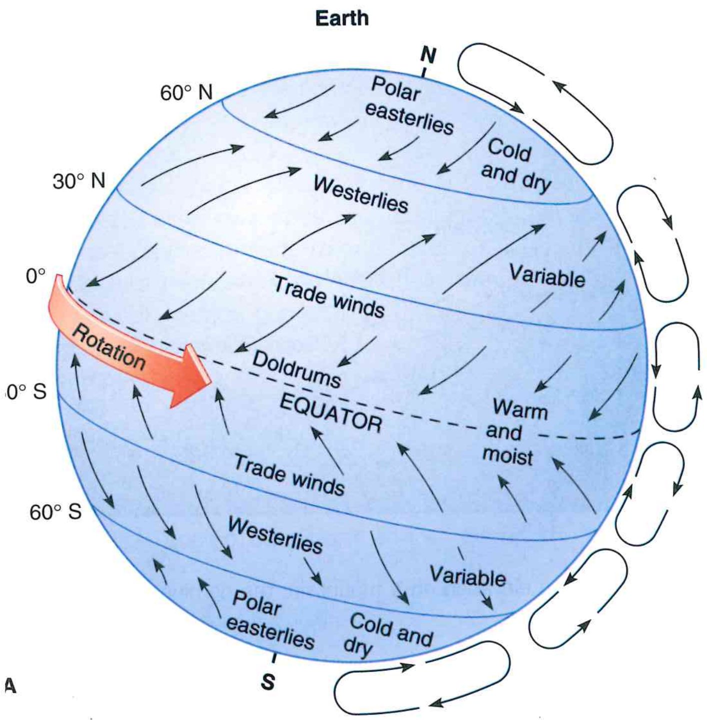
ocation	Latitude	Area (hectares)	Total species	Number of Species/Hectare
iarza Cocha, Ecuador	0° 29′	500	676	1.35
a Selva, Costa Rica	10° 26′	1,000	442	0.44
stacion Los Tuxlas, Mexico	18° 35′	700	212	0.30
I. J. Andrews Forest, Oregon	44° 14′	6,400	62	0.01

ource: P. J. DeVries, "Diversity of Butterflies" in S. Levin (ed.), *Encyclopaedia of Biodiversity*, 2000, Academic Press.

44.3



ɜURE 44.2 Earth's Seasons. The tilt of Earth's axis produces distinct seasons in the northern and southern hemispheres as Earth trav- around the sun.



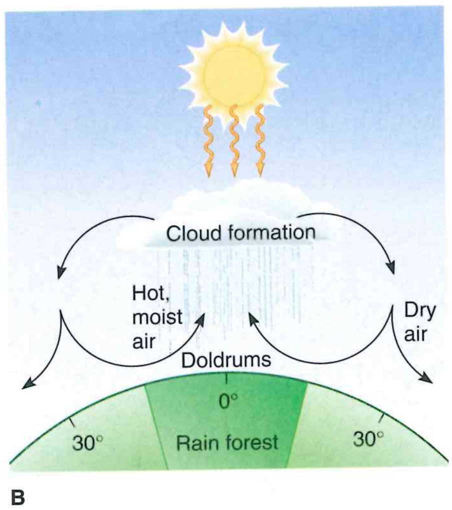


FIGURE 44.3 Patterns of Air Circulation and Moisture. **(A)** Air heated over the equator rises, cools, and drops its moisture. The air falls at about 30° north and south latitude, absorbs moisture from the land, then some spreads farther north and south. Six patterns of air circulation (cells) form. The winds are deflected to the right in the northern hemisphere and to the left in the southern hemisphere because of Earth's rotation. **(B)** Clouds form over the tropics as equatorial air cools and releases moisture. Light winds here are called doldrums.

ɔout September 23. Therefore, from the middle to high latitudes, mperature and day length change throughout the year.

Unequal heating of Earth's surface causes the air movements ıat distribute moisture. When intense sunlight heats the air over ıe equator, the air rises and expands. As the air rises, it cools. ecause cool air cannot hold as much moisture as warm air, the ҳcess water vapor condenses, forming the thick cloud cover that ours near-constant rain over the tropics. Equatorial air also ·avels north and south, rising and drying. As it cools at higher .titudes and elevations, the air's density increases, and it sinks ack down, at about 30° north and south latitude. Here it absorbs moisture from the land, creating the vast deserts of Asia, Africa, the Americas, and Australia. Some of the air continues poleward, rising and cooling at about 60° north and south latitude, causing the rain that supports temperate forests in these areas. The air rises, and some continues toward the poles, where precipitation is quite low, and some returns to the equator. Near the equator, the air is heated again, and the cycle begins anew. A cycle of heating and cooling, rising and falling air is called a cell. Rising, moist air loses water as it cools; falling dry air heats up and retains moisture. The planet has three such cells above the equator and three below (**figure 44.3**).

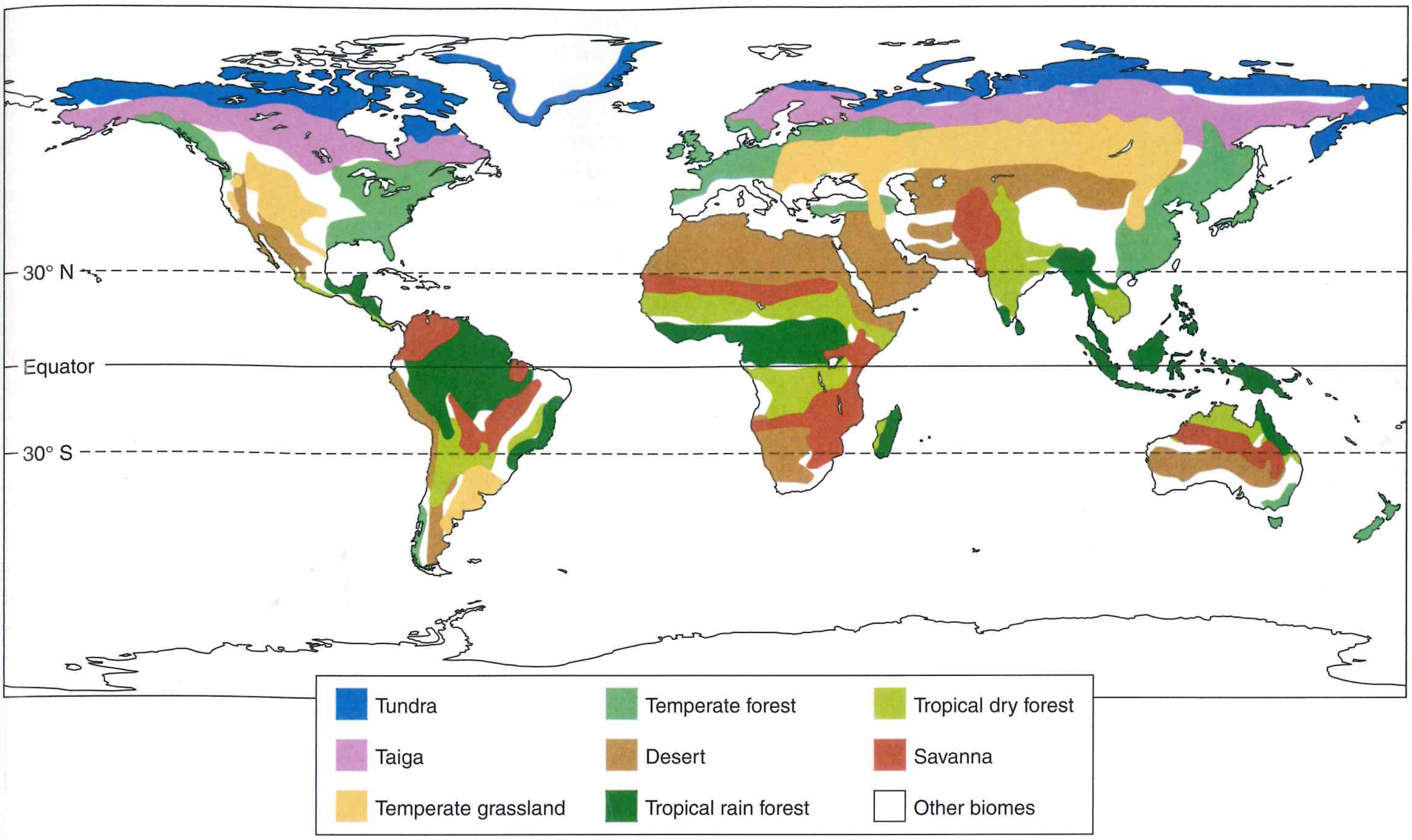


FIGURE 44.4 **Earth's Major Biomes.** Biomes are large terrestrial areas that have characteristic plant communities.

Overall, Earth's tilt results in uneven solar energy distribution, which causes major winds. The slight winds over the equator are called the doldrums. Trade winds lie above and below the doldrums, blowing from the east–northeast in the northern hemisphere and from the east–southeast in the southern hemisphere. Westerlies blow from west to east from 30° to 60° south and north latitude. The polar areas have weak winds called easterlies. The trades, westerlies, and easterlies blow from the east or west because of Earth's rotation. Together, these winds power the major ocean currents, which also contribute to climatic patterns.

Soils form the framework of biomes, for they directly support the defining plant life. Recall from figure 27.4 that soil is a complex mixture of nonliving and living matter, rich with fragmented and pulverized rocks and microbial life.

Climate influences soil development in many ways. Heavy precipitation may leach soluble materials from surface layers and deposit them in deeper layers, or it may remove them entirely from the soil system. Temperature and moisture conditions may also determine the fate of organic matter from living organisms. Under a warm, moist climate, rapid decomposition may leave little humus (organic material) in the soil. In cold, damp climates, undecomposed peat may accumulate in the soil.

The following discussion considers some of the world's major biomes, as shown in **figure 44.4.** There are others, and they tend to be more continuous than the lines on the map imply.

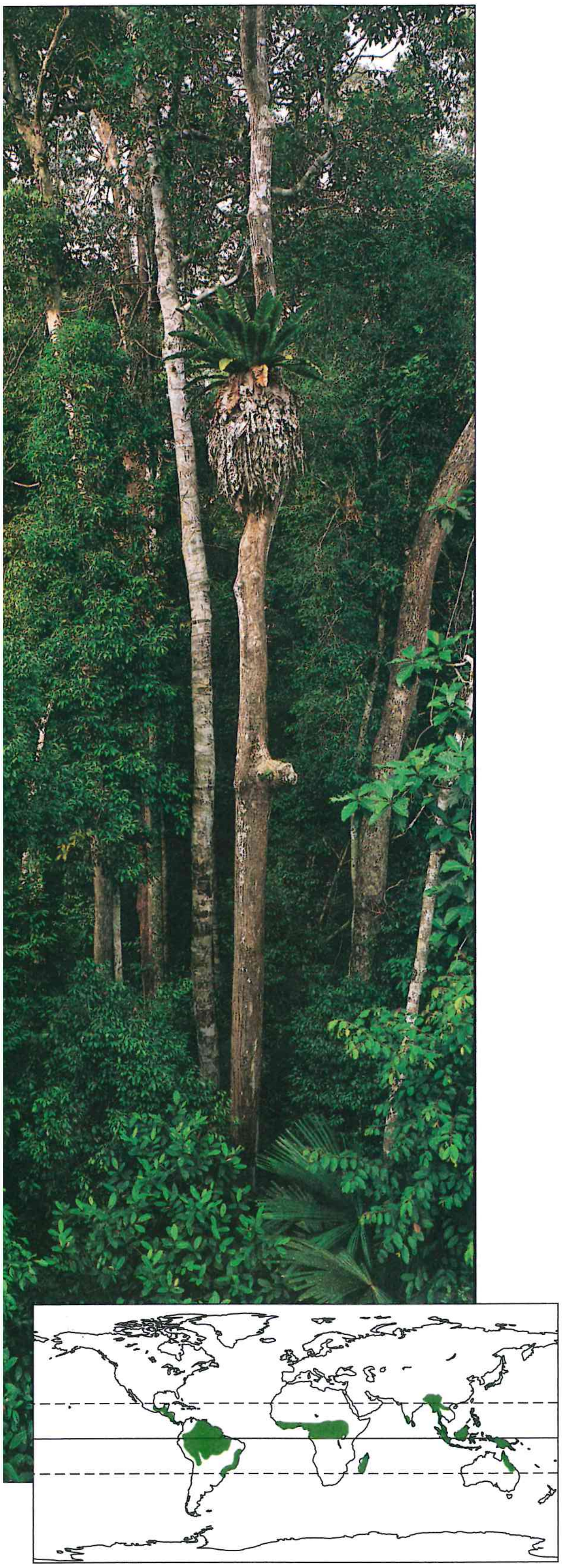
44.5

Tropical Rain Forest

Tropical rain forests occur where the climate is almost constantly warm and moist, within 10° north and south of the equator in Africa, Southeast Asia, and Central and South America. Rainfall is typically between 79 and 157 inches (200 and 400 centimeters) per year, and the soils are often poor in nutrients because water leaches them away. The tropical rain forest of the Amazon Basin in South America is incredibly vast; its meandering rivers and dense foliage cover an area 90% the size of the continental United States. Within the lush maze of intertwined branches and moss-covered vines live a staggering diversity of species. An area of tropical rain forest 4 miles square (10.4 kilometers square) is likely to house, among its 750 tree species, 60 species of amphibians, 100 of reptiles, 125 of mammals, and 400 of birds. One tree alone may support thousands of insect species.

From the air, a tropical rain forest appears as a solid, endless canopy of green, consisting of treetops 50 to 200 feet (15 to 66 meters) above the forest floor. Plants beneath the canopy compete for sunlight and form layers of different types of organisms. This layering of different plant species from the forest floor to the canopy is called **vertical stratification** (**figure 44.5**).

Plants in the tropical rain forest are adapted in different ways to capture sunlight. Very tall trees poke through the canopy. Other trees have broad, flattened crowns that maximize their sun



IGURE 44.5 **The Tropical Rain Forest.** Plants in the tropical ain forest form distinct layers, from the tallest trees emerging from e canopy to the tiniest residents of the shady forest floor.

exposure in this equatorial region where the sun's rays are almost perpendicular to Earth's surface. Vines and epiphytes (small plants that grow on the branches, bark, or leaves of another plant) grow on tall trees. Epiphytes may have aerial roots that penetrate masses of decaying plant matter on branches. The ground of the tropical rain forest looks rather bare beneath the overwhelming canopy, but it is a habitat for countless shade-adapted species. Many tree saplings grow slowly in the deep shade, but growth surges when a gap opens in the canopy.

The lush vegetation feeds a variety of herbivores. Insects, sloths, and tapirs devour leaves. Small deer and peccaries, monkeys, rodents, bats, and birds primarily eat fruit. Many carnivores, such as large cats, birds of prey, and snakes, consume the herbivores. Most animals are small or medium in size, but a few are enormous. The pirarucu fish of the Amazon River is more than 7 feet (2.1 meters) long, and the wingspans of many insects are several inches.

Nutrients cycle rapidly in the tropical rain forest. Frequent torrential rains wash away nutrients that bacteria and fungi release as they decay dead organisms. The heat and humidity speed decomposition. Termites recycle nutrients with the help of protista in their guts, which break down cellulose and release its atoms back to the environment. Roots of giant trees absorb nutrients so efficiently that most decaying plant material is saved. Essential in a tree's recycling program are fine roots that permeate the upper 3 inches (7.6 centimeters) of ground and attach to dead leaves. These roots absorb nutrients from falling dust and rain. Mycorrhizal fungi on rootlets quickly absorb nutrients released from dead leaves. Animals recycle nutrients too. Certain leaf-cutting ants, for example, farm gardens of fungi that hasten decomposition. • **ants, bacteria, and fungi, p. 458**

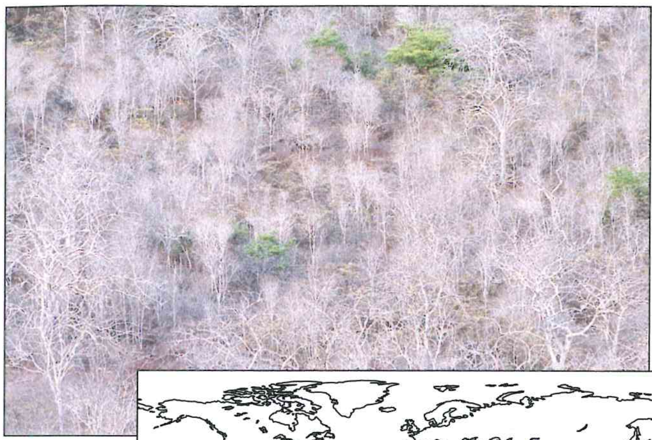
Tropical Dry Forest

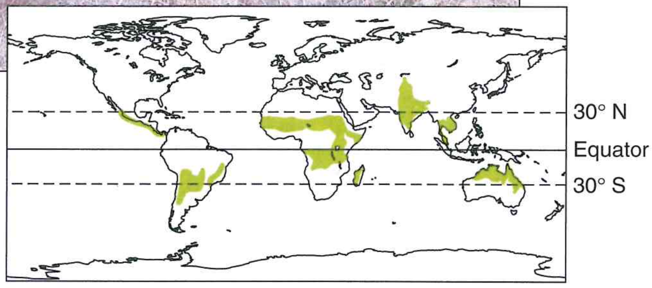
From 10° to 25° latitude lie **tropical dry forests,** which correspond to the diminishing moisture level with distance from the equator. These biomes border the rain forests of central Africa and the Amazon. They cross Australia, and they run along Mexico's west coast. In these forests, life is adapted to yearly dry and rainy seasons and fluctuating temperatures. The soil is richer in nutrients than rain forest soils, although the torrential rains of the wet season may quickly erode them away.

The residents of a tropical dry forest are adapted to the seasons. Trees enter states of dormancy during the 6-month dry season, as **figure 44.6** vividly illustrates by comparing the same forest in different seasons. Animals depart when conditions become too dry, migrating to wetter habitats such as the nearby rain forests or river ecosystems. In the wet season, the plants produce abundant flowers and fruits that attract pollinators and herbivores. The rich soil makes these areas prime agricultural land, and many of these forests have been lost to cultivation. In Central America and Mexico, most of the tropical dry forests have become cotton fields, cattle ranches, and grain farms. Because of the dry season, these forests are easier to burn and clear than are tropical rain forests.

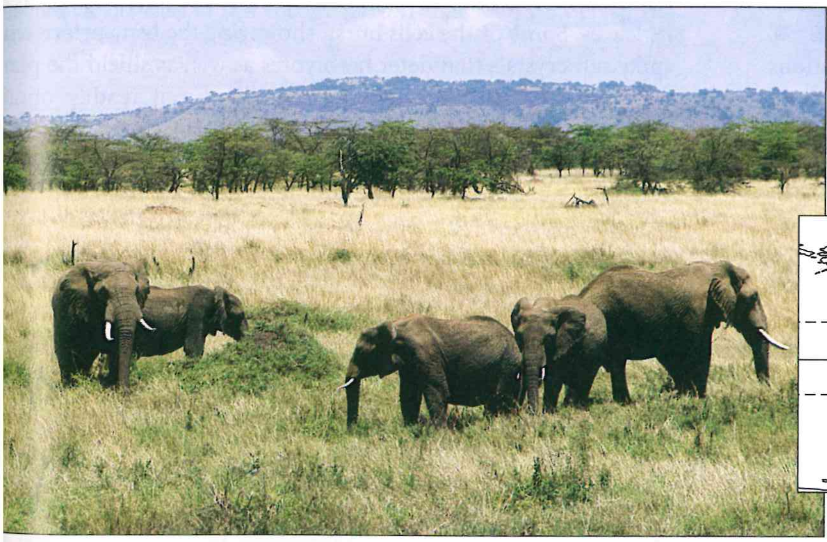
Costa Rica's Guanacaste National Park is a tropical dry forest that is being preserved. It is named for the guanacaste tree, which

44.6





IGURE 44.6 **Tropical Dry Forest.** It's easy to distinguish the wet from ie dry season in a tropical dry forest. With the rains, trees spring back to ctivity, turning the landscape a lush green (**A**). This forest in the Galápagos lands appears dead during the dry season (**B**).



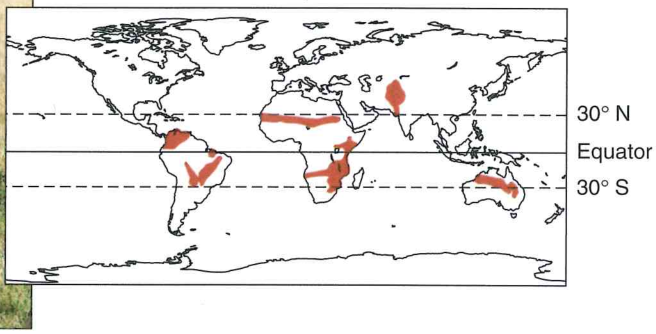


FIGURE 44.7 **Tropical Savanna.** The savanna is home to grasses, scattered trees, and large herbivores such as these elephants.

roduces abundant disc-shaped fruits. Today, domesticated aniials such as cattle and horses eat the fruits and disperse the ndigested seeds in their feces, but these animals are non-natives. ı times past, large populations of wild horses, camels, ground oths, and other herbivores did the job, and the trees flourished. hese animals became extinct about 10,000 years ago. Introducig more horses into the park is helping to restore this biome.

ropical Savanna

t 10° to 20° latitude, neighboring tropical dry forests are the drier opical **savannas.** Rainfall is about 12 to 20 inches (30 to 50 centieters) annually, but certain tropical savannas may exceed this. A stinct dry season lasts at least 5 months and alternates with a wet season. Savannas are grasslands with scattered trees or shrubs and bands of woody vegetation along stream courses (**figure 44.7**). Tropical savannas are in Africa south of the Sahara; in South America in south-central Brazil, Venezuela, and Colombia; in northern Australia; and in northwest India and eastern Pakistan.

The animal communities of the tropical savanna differ in different parts of the world. They include many migrating populations, an adaptation to the seasonality of this biome. The Australian savanna, for example, is home to many birds and kangaroos, whereas the grassland in Africa is covered with herds of zebra, giraffes, wildebeests, gazelles, and elephants, with lions, cheetahs, wild dogs, and hyenas preying on them and vultures and other scavengers eating the leftovers. In many tropical savannas, termites are major detritivores, and their huge nests dot the

44.7

landscape. It was from the African savanna that hominids and hominoids—our ancestors—evolved, emerged, and spread. • **hominoids and hominids, p. 363**

A complex interaction of soils, rainfall, grazing, and fire determines the particular vegetation pattern of a tropical savanna. Fires start at the very end of the dry season, when lightning easily ignites dried plants. Grasses, however, can resprout following fire, but often trees cannot. The frequent fires help maintain the grasses.

Desert

Deserts receive less than 8 inches (20 centimeters) of rainfall per year. The days can be searingly hot because few clouds block or filter the sun's strongest rays. Nights are cool, sometimes 86°F (30°C) below the daytime temperature, because heat radiates rapidly to the clear night sky. Deserts ring the globe at 30° north and south latitude, corresponding to where the circulating atmosphere soaks up moisture.

Deserts vary in biodiversity. Many desert habitats support only a few species; others, such as the upland desert of southern Arizona, are species-rich (**figure 44.8**). In the driest and largest desert in the world, Africa's great Sahara, rainfall is less than 1 inch (2 centimeters) per year. Many areas are almost devoid of life.

Desert plants and animals show many striking adaptations to heat and drought. Some shrubs, such as mesquite, have extremely long taproots that exploit groundwater far below the surface. Annual plants grow quickly, squeezing their entire life cycles into wet periods between droughts. Most of their seeds germinate only after a soaking rain, which rinses growth inhibitors from their coats. The thick-skinned, fleshy leaves of succulent perennials help hold precious water. In rainy times, annual and perennial flowers bloom magnificently.

The reduced leaves of cacti minimize water loss. After a rainfall, the stems of barrel and saguaro cacti expand as they take up and store water. Spines guard their succulent tissues, although some desert animals still eat them. The root system of a cactus is shallow but widespread—that of a large cactus extends up to 55 to 65 yards (50 to 60 meters). Some desert plants produce chemicals that inhibit the growth of other plants nearby, decreasing competition for water.

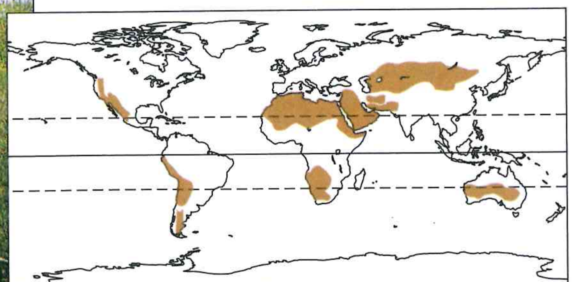
Desert animals also cope with water scarcity. Body coverings, such as a scorpion's exoskeleton or a reptile's leathery skin, minimize water loss. Some small mammals, such as the kangaroo rat, have very concentrated urine, which saves water. Few animals face the midday sun. Most burrow or seek shelter during the day and become active when the sun goes down and the risk of water loss lessens.

Particularly harsh areas in the deserts of North and South America, Africa, and Australia are salt flats, where runoff collects in basins and evaporates, leaving behind extremely salty soil. Most plants cannot tap into the water table beneath the flats, even though it is shallow, because the high salinity would actually draw water by osmosis from their cells. However, the members of one family of plants, the Chenopodiaceae, are adapted to these salty surroundings (**figure 44.9**). They can sequester salt within their cells at higher concentrations than are found in the salt flats, enabling them to extract water from these areas. These plants are called "halophytes," which means salt-loving. They thrive where others cannot grow. • **osmosis, p. 63**

The saltbush plant *Atriplex* is one such salt-loving desert resident. It concentrates environmental salt in the outermost cells of its leaves. Some of the cells burst, showering the leaf surface with spiky salt crystals that deter herbivores as well as shield the plant from sunlight. Because the saltbush plant can readily obtain water from beneath the salt flats, its leaves remain green year-round. The high salt content of the saltbush plant deters herbivores too—because any fluid animals obtained from the plant would be saltier than their cells. The animals would actually lose water by eating them, much as a person dying of thirst on the ocean cannot survive by drinking seawater.

In a striking example of convergent evolution, three distantly related types of rodents can eat *Atriplex*. The chisel-toothed kangaroo rat lives in the Great Basin Desert in North America; the red vizcacha rat is from the Monte Desert in Argentina; and the fat sand rat is from the Sahara Desert. All three rodent species have unusually shaped teeth that enable them to peel off the outer leaf cells, exposing the less salty tissues within.

FIGURE 44.8 Desert. Saguaro cacti and many other plants that have water-conserving adaptations live in the Sonoran Desert in the Southwestern United States.

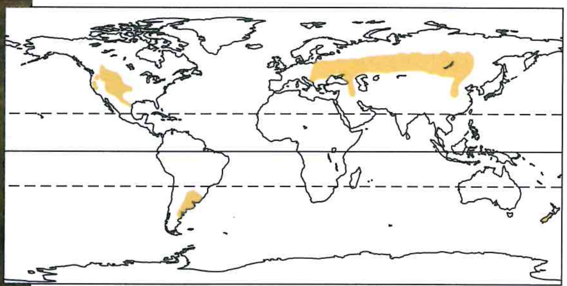


44.8

B

ɜURE 44.9 **Adaptations in the Desert.** (**A**) The saltbush ɪnt *Atriplex* stores salt in the outer cells of its leaves, enabling it to ːract water from beneath salt flats. When some of the cells burst, ɜy coat the leaves with salt crystals. Three species of rodents, from ·ee continents, have teeth and bristles that enable them to strip the ty layer from *Atriplex* so they can eat the less-salty interior. The red ɔacha rat (**B**) has the characteristic leaf-shredding incisors but also ɜ bristle bundles in the mouth (*arrow*) that aid in stripping the nts of their salty coverings.

FIGURE 44.10 Temperate Grassland. Bison once dominated the North American prairie, a temperate grassland.



ːmperate Grasslands

ɪnperate grasslands have 10 to 40 inches (25 to 100 centi-·ters) of rainfall annually, which is often not sufficient to sup-ɪrt trees. These biomes usually have one or two severe dry ɜsons, when the vegetation becomes dry and flammable, so fire ːn important ecological factor.

The North American prairie is a temperate grassland (**fig-ɜ 44.10**). The height of the grasses reflects local moisture. ɑsses reach 4 to 8 feet (1.2 to 2.4 meters) around the Missis-pi Valley, where moisture from the Great Lakes and Gulf of ːxico contributes to an annual rainfall of about 39 inches (100 centimeters). In this tallgrass prairie, grazing and fire suppress the growth of trees. Westward, toward the Rocky Mountains, annual rainfall decreases, and shorter grass species dominate the landscape. Unlike many trees, grasses can do quite well with little water. Varied blade texture, surface, and shape are adaptations that enable grasses to conserve water. Root systems are extensive, with some species sending roots 6 feet (1.8 meters) underground, where they reach water. The mat of roots holds soil together and prevents it from blowing away during drought. Growth response to rain is rapid.

Unlike trees, perennial grasses easily survive damage from fire and herbivores. The perennial buds of grasses lie below the il surface and are protected from flames. Because these plants ›w from below, removal of the blade does not hinder growth. ›en chunks of grass kicked up by a grazing animal can reroot. In ntrast, the growing regions of trees—the tips of branches—are e first structures that fire or herbivores destroy.

Grasslands are rich in plant and animal species. In North nerica, bison, elk, and pronghorn antelope were originally the ıportant grazing herbivores. Their predators were the gray wolf d coyote. Antelope used speed to escape these predators. The :e and power of elk and bison were sufficient protection against tural predators, but they were no match for humans with guns. :her herbivores include rodents, prairie chickens, and insects. any rodents, such as prairie dogs, retreat into burrows to escape edators. Mouse and grasshopper populations can grow partic- ırly large in a temperate grassland.

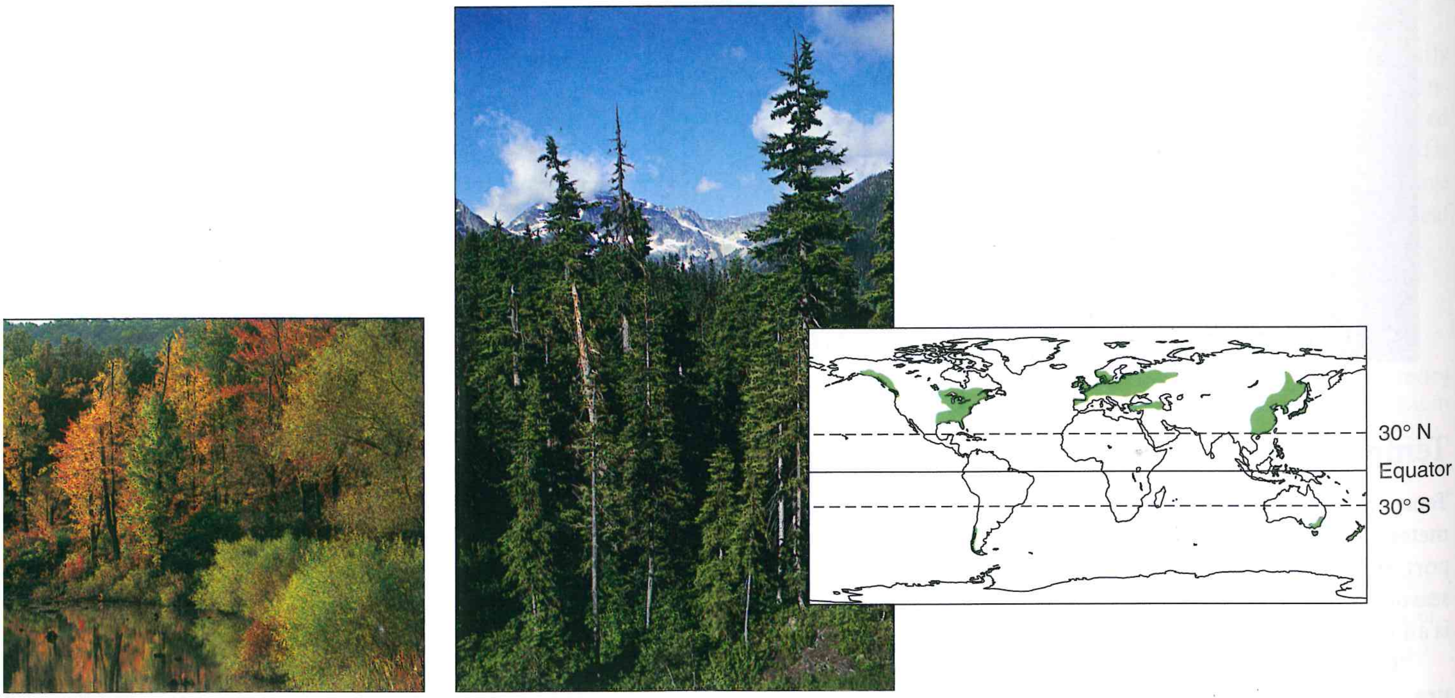
Today, the once expansive North American prairie has been attered into thousands of pieces called, appropriately, "rem- nts." Farmland has replaced the prairie, wheat and corn taking e place of diverse grasses. The plant survivors in the remnants ek out at the edges of housing developments and graveyards, ›ng railroad tracks and roadsides, and at the borders of culti- ted fields. Some remnants are so small that they partition off ıall groups from populations, leading to genetic drift and pop- ation bottlenecks that decrease genetic diversity and locally danger the species. Prairie remnants are usually too small to stain the herds of large herbivores that once roamed the plains.

In Prairie City, Iowa, the U.S. Fish and Wildlife Service is tempting to resurrect a larger, more self-sustaining prairie. A ndful of researchers and volunteers combed the state, collecting seeds from different places and planting them on a 5,000-acre site that was slated to become a nuclear power plant. The project began in the early 1990s, and the area now boasts native grasses exceeding 12 feet (3.6 meters) in height and a few dozen other plant species—not close to the 150 to 200 plant species native to the prairie, but a start. Buffalo, elk, birds, bats, and of course many insects have been reintroduced or have returned on their own.

Temperate Forests

Covering much of Earth between 30° and 55° latitude, temperate forests are either deciduous (composed of trees that shed their leaves seasonally) or coniferous, although a walk in the woods reveals that many such forests contain both types of trees. Deciduous trees are predominant in temperate forests that have mild winters and a moist growing season lasting at least 4 months, rainfall ranging from 26 to 118 inches (65 to 300 centimeters), and soil rich in nutrients. In contrast, dry summers and long, harsh winters favor the conifers. Vertical stratification occurs in temperate forests, although species diversity is lower than in tropical forests.

Usually one or two species of trees predominate in the **temperate deciduous forest,** as in oak-hickory or beech-maple forests (**figure 44.11A**). The dominant trees, victors in the competition for light, are also best suited for the average rainfall. Trees in the deciduous forest often have ball-shaped tops that maximize light absorption for the angle of the sun's rays at these latitudes. Shrubs grow beneath the towering trees. Below them,



B

GURE 44.11 Temperate Forests. Trees that lose their leaves each fall dominate temperate deciduous forests (**A**). Temperate coniferous ›ests (**B**) have evergreen trees such as these western hemlocks in Washington State.

44.10

rbaceous flowering plants grow mostly in early spring, when ;ht penetrates the leafless tree canopy. Mosses and liverworts at damp spots on the forest floor. • **bryophyte diversity, p. 431**

Decomposers in temperate forests—nematodes, earth-orms, bacteria, and fungi—break down leaf litter and create a :h soil. In the North American deciduous forest, herbivores clude whitetail deer, ruffed grouse, and gray squirrels. Red fox d raccoon are common carnivores. All inhabitants of the ciduous forest must cope with seasonal changes. In winter, me insects enter an inactive state called diapause, and mam-als may hibernate. Some birds migrate to warmer climates. any mammals survive winter by fattening up, growing thicker ats, and recovering hidden stores of food.

The remains of the once-great temperate deciduous forest at stretched from the Great Lakes to the Atlantic and from ınada to the southern states is currently changing, becoming ikingly redder. The red maple is taking over the niche of oaks d hickories, thriving because it can live under a variety of nditions. In the past, fires—natural events in this biome—eferentially killed the thin-barked red maples, while at the me time clearing the land in a way that enabled oak seedlings to ke root. With the coming of humans, fires became less frequent. ie red maples flourished on land that people had cleared for rming and then abandoned as they moved westward.

Red maples are well adapted to take over because they are neralists. They grow under a wide range of shade and moisture nditions and can tolerate the acid deposition that kills other es. The red maples drop their fruit in the spring, giving their fspring a head start on those of oaks and hickories, which dis-rse their seeds in the fall. Plus, red maples produce alkaloid mpounds that render their leaves unpalatable to gypsy moths d deer, which instead devour the leaves of other tree species. As e red maple thrives, many other types of trees become diseased, cluding sycamore, sugar maple, dogwood, elms, chestnut, wal-it, hemlock, white ash, and balsam fir. In parallel to the shifting ant species will be changes in the communities of animal ecies that are adapted to living with mostly oaks. Affected pop-ations include beetles and other insects that live in and on bark, d the many types of birds and small mammals that eat acorns. **acid deposition, p. 901**

In contrast to the deciduous forest, most trees in the **temper-e coniferous forest** are evergreen (figure 44.11B). They lose ıves a few at a time, so most conifers are green all year. Many niferous forest soils are thin, acidic, and poor in nutrients. ruce, pine, fir, and hemlock are the dominant trees. The short-e of nutrients favors evergreen plants over deciduous species, ıich require these resources to replace all their leaves in a short ne.

The coniferous forest also has a dense understory of shrubs ch as alder and hazelnut. In North America, herbivores include e whitetail deer, red squirrel, spruce grouse, and moose. The bcat and black bear are typical carnivores. Legions of tiny vertebrates, fungi, and bacteria recycle nutrients.

Conifers are adapted to more severe winters and drier sum-ers than are deciduous trees. They are also adapted to recurring es. Fire recycles nutrients and selects against some species, opening new niches. The thick bark on certain pine trees resists flames, and some pine cones liberate their seeds only after expo-sure to the extreme temperature of a forest fire.

Parts of New Jersey's Pine Barrens near Atlantic City burn about every 30 years. The sandy soil, the pine needles and branches that litter the ground, and the "pitch" that seals pine cones all create conditions just right for fire. In the last big fire in the Pine Barrens, in 1994, squirrels, deer, reptiles, and rabbits fled the affected area. The fire cleared the forest floor of three decades of accumulated plant debris, leaving space for future growth. The seeds that the fire liberated soon yielded abundant seedlings against the backdrop of blackened trees. The forest is beginning to look as if a fire had never happened.

Taiga

North of the temperate zone in the northern hemisphere lies the cold, snowy **taiga,** also called the boreal forest for the Greek word for "north" (**figure 44.12**). From above, the taiga appears as alter-nately heavily treed areas, regions of sparser trees where shrubs and bushes such as juniper and blueberry grow, and lakes and rivers. The taiga extends across central Canada, central Alaska, Siberia and Russia, to Scandinavia, between 50° and 65° north latitude, and also through parts of the Rocky Mountains and on mountains in Asia and south-central Europe. Because of the harsh conditions, biodiversity is lower than it is in the temperate zone.

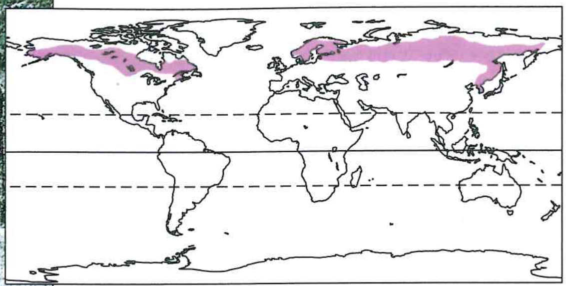
The species that inhabit the taiga are adapted to the biome's long winters and large annual temperature fluctuations. In cen-tral Siberia, for example, summer temperatures may reach 86°F (30°C), but can plunge to –94°F (–70°C) in winter. Annual pre-cipitation is 8 to 24 inches (20 to 60 centimeters), most of it snow and ice.

Soils in the taiga are cold, damp, acidic, and nutrient-poor. The topsoil is thin, and the subsoil may be frozen. The low tem-perature and pH slow decomposition of dead organisms, and nutrients tend to stay in the leaf litter above the soil, rather than entering the topsoil. Mycorrhizal fungi on the shallow and abun-dant roots of trees help the plants maximize nutrient uptake from the leaf litter (see figure 23.14).

Spruce, fir, pine, and tamarack (larch) are the dominant trees in the taiga, but aspen and birch grow after fires, and wil-lows ring lakeshores. Conifers are well adapted to an environ-ment so cold that water is usually frozen throughout the winter. With a scant amount of sap, a conifer has little liquid to freeze. The needle shape, waxy coat, and minimal stomata set in deep pits are adaptations of conifer leaves to conserve water. The coni-cal tree shape helps capture the oblique rays of light in northern latitudes and prevents damaging snow and ice buildup.

The taiga forest floor is often boggy, with scattered shrubs and mats of mosses and lichens. Fungi are common decomposers in the taiga. Typical herbivores include the woodland caribou, porcupines, red squirrels, snowshoe hares, moose, and spruce grouse. Carnivores include lynx, gray wolves, and wolverines. As is true nearly everywhere else on the planet, insect populations can at times grow very dense.

FIGURE 44.12 **Taiga.** Woodland caribou forage for food in the Canadian taiga.

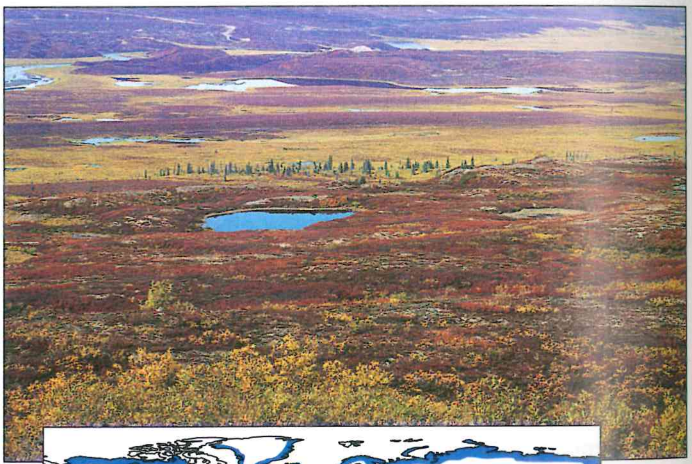


'undra

. band of **tundra** runs across the northern parts of Asia, Europe, nd North America. Winter is bitterly cold, with typical tempera- ıres about –26°F (–3°C). Precipitation is 8 to 24 inches (20 to 60 entimeters) per year. The ground remains frozen, in a zone alled **permafrost,** even during summer, when temperatures ange from 40°F to 70°F (4.5°C to 21°C). Permafrost begins at 18 ıches (46 centimeters) below the surface and extends 300 feet)1.5 meters) down. Because the permafrost blocks water infil- ·ation, spring runoff from ice and snow drains rapidly into vers or accumulates, forming bogs and small, stagnant ponds. ermafrost also limits rooting depth, which prevents large plants ·om becoming established.

The shallow tundra soil supports dwarf shrubs, low- rowing perennial plants such as sedges and broad-leafed erbs, and reindeer lichens (**figure 44.13**). It is difficult for nnual plants to germinate, grow, and flower in the short grow- ıg season, which may be less than 60 days, so most plants are erennials. Tundra plants are low and flat, a shape that lets the 'ind blow over them and protects them under snow. The lants often clump, which helps to conserve moisture, and they re often buried amid rocks, which block the wind. Some lants have protective hairs that insulate them and help break ıe wind. The dark green color of many plants allows them to bsorb more light for photosynthesis.

Animal inhabitants of the tundra include caribou, musk xen, reindeer, lemmings, snowy owls, foxes, and wolverines. Polar ears sometimes visit coastal areas of the tundra to den. In the ımmer, migratory birds stop to raise their young and feed on the ısects that flourish in the tundra and its ponds.



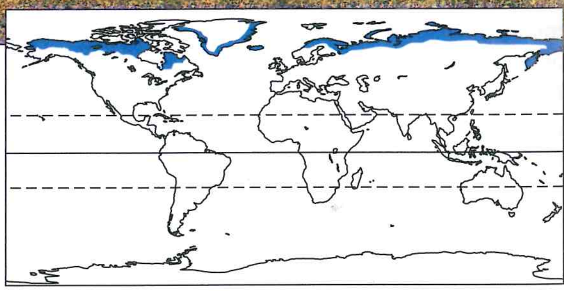


FIGURE 44.13 **Tundra.** In the tundra, permafrost limits plant life to shallow-rooted shrubs and abundant lichens.

Like plants, the animals of the tundra have adapted to the h climate. Both the hunters and the hunted benefit from ouflage. White winter colors make the arctic fox, ptarmigan, ine, and arctic hare as inconspicuous against snow as their vn summer colors make them against the snow-free land- e. These animals often have short extremities, a form that s to conserve heat. The snowshoe hare's big feet are natural vshoes. The shallow soil, short growing season, and slow mposition of the tundra make it a very fragile environment.

.1 Mastering Concepts

. What are the major climatic regions of the world?
. How do climate and soil composition determine characteristics of biomes?
. Describe the rainfall and temperature patterns, nutrient cycling, and inhabitants of each of the major terrestrial biomes.

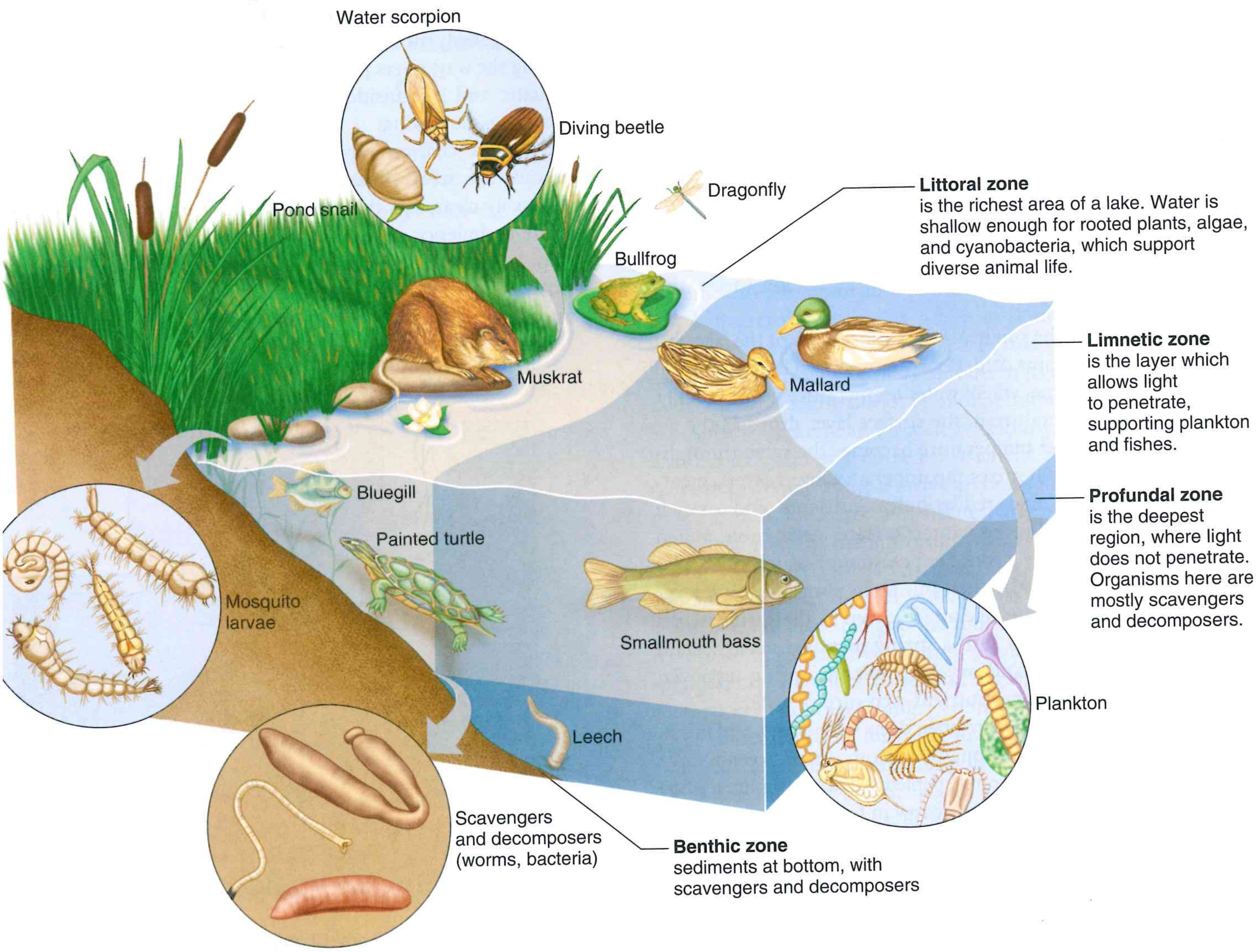
44.2 Freshwater Ecosystems

Life in lakes, rivers, and streams must be adapted to water velocities, changing nutrient and oxygen concentrations, and drought and flooding conditions.

Earth's waters house diverse species adapted to the temperature, light, current, and nutrient availability of their surroundings. Aquatic ecosystems are distinguished by physical and chemical factors such as current pattern and degree of salinity. Two types of freshwater ecosystems are standing water, such as lakes, swamps, and ponds, and running water, such as rivers and streams.

Lakes and Ponds

Light penetrates the regions of a lake to differing degrees. These differences determine the types of organisms that live in particular areas (**figure 44.14**).



GURE 44.14 **Zones of a Lake.** The littoral, limnetic, profundal, and benthic zones of a lake describe where different types of organisms live.

44.13

The **littoral zone** is the shallow region along the shore where reaches the bottom sufficiently for photosynthesis to occur. e photosynthetic organisms in this region are free-floating; oth- e rooted to the bottom and have submerged, floating, or emer- leaves. The littoral zone is the richest area of a lake or pond. ucers here include free-floating and attached cyanobacteria, algae, and diatoms. Floating plants such as water lilies and gent plants such as cattails, reeds, and rushes are also part of the Animal life is diverse and includes damselfly and dragonfly hs, crayfish, rotifers, flatworms, *Hydra,* snails, snakes, turtles, , and the young of some species of deep-water fishes.

The **limnetic zone** is the layer of open water where light pen- es. Plankton (mostly protista, such as diatoms, ciliates, and) and fishes inhabit this area. The **profundal zone** is the region beneath the limnetic zone where light does not pen- e. Organisms here, which rely on falling organic material above, include mostly scavengers and decomposers such as t larvae and bacteria. The sediment at the lake bottom com- s the **benthic zone.**

Oxygen and mineral nutrients in a lake are distributed enly. The concentration of oxygen is usually greater in the r layers, where it comes from the atmosphere and from osynthesis. As dead organic matter sinks to the bottom, nposers consume oxygen and release phosphates and es into the lower layers of the lake. In a shallow lake, wind ing across the surface mixes the water, redistributes nutri- and restores oxygen to bottom waters.

Deeper lakes in temperate regions often develop layers with different water temperatures and densities. This thermal fication prevents the free circulation of nutrients and oxy- n the lake. The degree of thermal stratification varies with ason.

n the summer, the sun heats the surface layer of the lake, but eepest layer remains cold. Between these two layers is a third n, the thermocline, where water temperature drops quickly. e fall, the temperature in the surface layer drops as the air Gradually, water temperature becomes the same through- ne lake. Wind then mixes the upper and lower layers, creat- **fall turnover** that redistributes nutrients and oxygen ghout the lake. During winter, surface water cools. When cools to 39°F (4°C), the temperature at which it is most , it sinks. Water colder than this floats above the 39°F layer nay freeze, giving the lake an ice cover. In the spring, when rface layer warms to 39°F, a **spring turnover** occurs, again ributing nutrients and oxygen. After the spring turnover, thrive in the warming, nutrient-rich surface water.

akes age. Younger lakes are often deep, steep-sided, and low in nt content. The deep zone of bottom water stores a large ity of oxygen, which is rarely depleted. These lakes are termed **rophic,** which means they are low in fertility and productiv- ey are clear and sparkling blue, because phytoplankton aren't lant enough to cloud the water. Lake trout and other organ- hat thrive in cold, oxygen-rich deep water are numerous.

s a lake ages, organic material from decaying organisms and ent begins to fill it in, and nutrients accumulate. These lakes rmed **eutrophic,** which means they are nutrient-rich and high in productivity. The rich algal growth turns the water green and murky. Decomposing organisms in the deeper waters deplete oxygen during the summer. Fish and plankton communities change, and fishes that can tolerate low oxygen conditions replace species such as lake trout. In time, the lake becomes a bog or marsh and, eventually, dry land. Discharge of nutrient-rich urban waste-water and runoff carrying phosphate-rich fertilizers from cultivated lands can speed conversion of oligotrophic lakes to eutrophic lakes. This transformation is termed eutrophication. In extreme cases, the nutrients promote excessive algal growth. When the algae die, they sink to the lake bottom, where decomposers deplete the water of oxygen. Fish kills and unpleasant odors often result.

Rivers and Streams

The rivers and streams that flow across the terrestrial landscape carry rainwater, groundwater, snowmelt, and sediment from all portions of the land toward the ocean or an interior basin (such as the Great Salt Lake). The flow is not constant, however. Where the landscape flattens, the water may slow to a virtual standstill, forming pools. Elsewhere, the water flows in shallow runs or bends called riffles. Rapids are fast-moving, turbulent parts. Along the way, rivers provide moisture and habitat to a variety of aquatic and streamside organisms, which are adapted to both flooding and drying.

Rivers change, physically and biologically, as they move toward the ocean (**figure 44.15**). At the headwaters, the water is relatively clear, and the channel is narrow. Where the current is swift, turbulence mixes air with water, so the water is rich in oxygen. In fast-moving streams, some organisms cling to any available stationary surface, such as rocks or logs. Algae, diatoms, mosses, and snails that graze on them, live here. Larval and adult

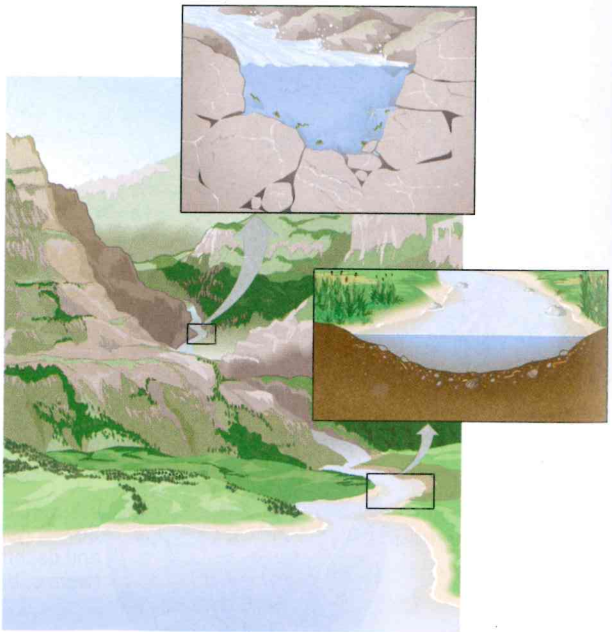


FIGURE 44.15 **Rivers Change Along Their Course.** A narrow, swift stream in the mountains becomes a slow-moving river as it accumulates water and sediments and approaches the ocean.

cts burrow into sediments or adhere to the undersides of :s with hooks or suckers. Many of these invertebrates eat ıying plant material that drops in from streamside vegetation, :h often provides the bulk of the energy that fuels the head- :r stream food chain.

As the river flows toward the ocean, it continues to pick up ment and nutrients from the channel. Tributaries contribute to :r flow, so the river widens, and as the land flattens, the current s. The river is murky, restricting photosynthesis to the banks water surface. As a result, the oxygen content is low relative to river upstream. Such slower-moving rivers and streams sup- : more diverse life, including crayfish, snails, bass, and catfish. ms burrow in the muddy bottom, and plants line the banks.

Rivers and streams depend heavily on the land for water and :ients. Dead leaves and other organic material that fall into a r add to the nutrients that resident organisms recycle. Rivers return nutrients to the land. Many rivers flood each year, lling with meltwater and spring runoff and spreading nutrient- silt onto their floodplains. When a river approaches the ocean, urrent diminishes, which deposits fine, rich soil that forms new a lands. The opener to chapter 45 describes the incredible dis- tion to ecosystems that occurred when people altered a river's rse in southern Florida.

4.2 Mastering Concepts

. Describe the types of organisms that live in each zone of a lake or pond.
. How are oxygen and nutrients distributed (and redistributed) in lakes?
. What is eutrophication?
. What adaptations enable organisms to survive in moving water?
. Describe the ways a river changes from its headwaters to its mouth.

4.3 Marine Ecosystems

areas where salt water meets fresh water, organisms are adapted to ıctuating salinity. In the intertidal zone, the ebb and flow of the tide allenges organisms. Life in the oceans is abundant and diverse, but we ıow little about it because oceans are vast and mostly inaccessible.

: ocean, covering 70% of Earth's surface and running 7 miles .2 kilometers) deep in places, is the largest and most stable ıatic ecosystem. Specific regions are based on proximity to land.

ɔasts

eral types of aquatic ecosystems border shorelines. **Figure 16** illustrates these coastal areas.

Estuaries At the margin of the land, where the fresh water of a river meets the salty ocean, is an **estuary.** Life in an estuary must be adapted to a range of chemical and physical conditions. The water is brackish, which means that it is a mixture of fresh water and salt water; however, the salinity fluctuates. When the tide is out, the water may not be much saltier than water in the river. The returning tide, however, may make the water nearly as salty as the sea. As the tide ebbs and flows, nearshore areas of the estuary are alternately exposed to drying air and then flood.

Organisms able to withstand these environmental extremes enjoy daily deliveries of nutrients from the slowing river as well as from the tides. Photosynthesis occurs in shallow water. An estuary houses a very productive ecosystem, its rocks slippery with algae, its shores lush with salt marsh vegetation, and its water teeming with plankton. Almost half of an estuary's photosynthetic products go out with the tide and nourish coastal communities.

Estuaries are nurseries for many sea animals. More than half the commercially important fish and shellfish species spend some part of their life cycle in an estuary. Migratory waterfowl feed and nest here as well. Human activities can threaten these important ecosystems. • **endangered estuaries, p. 909**

Mangrove Swamps Another type of aquatic ecosystem where salinity varies is a **mangrove swamp,** which is distinguished by characteristic salt-tolerant plants. The general term "mangrove" refers to plants that are adapted to survive in shallow, salty water, typically with aerial roots. About 40 species of trees are considered to be mangrove. Mangrove swamps mark the transitional zone between forest and ocean and are located in many areas of the tropics. Within them, salinity varies from the salty ocean, to the brackish estuary region, to the fresh water of the forest.

A mangrove swamp is home to a diverse assemblage of species because it provides a variety of microenvironments, from its treetops to deeply submerged roots in its own version of vertical stratification. Life is least abundant in the treetops, where sun exposure is greatest and water availability the lowest. Snakes, lizards, birds, and many insects live here. A hollow elevated mangrove branch may house a thriving community of scorpions, termites, spiders, mites, roaches, beetles, moths, and ants.

Aerial roots of mangroves provide the middle region of the swamp's vertical stratification. Here, roots are alternately exposed and submerged as the tide goes in and out. Barnacles, oysters, crabs, and red algae cling to the roots. Lower down lies the root region of the mangrove swamp, populated by sea anemones, sponges, crabs, oysters, algae, and bacteria. The algal slime that coats roots discourages hungry animals.

Submerged roots form the lowest region of the mangrove swamp. Here live sea grasses, polychaete worms, crustaceans, jellyfishes, the ever-present algae, and an occasional manatee. Ecologists estimate that up to 30% of the resident species here are unknown.

Unfortunately, many mangrove swamps are in prime vacation spots for humans—which means habitat destruction. When people cut down mangrove trees, small shrubs that can tolerate salt grow in the area, and trees cannot grow back. The diverse mangrove ecosystem shrinks and may vanish.

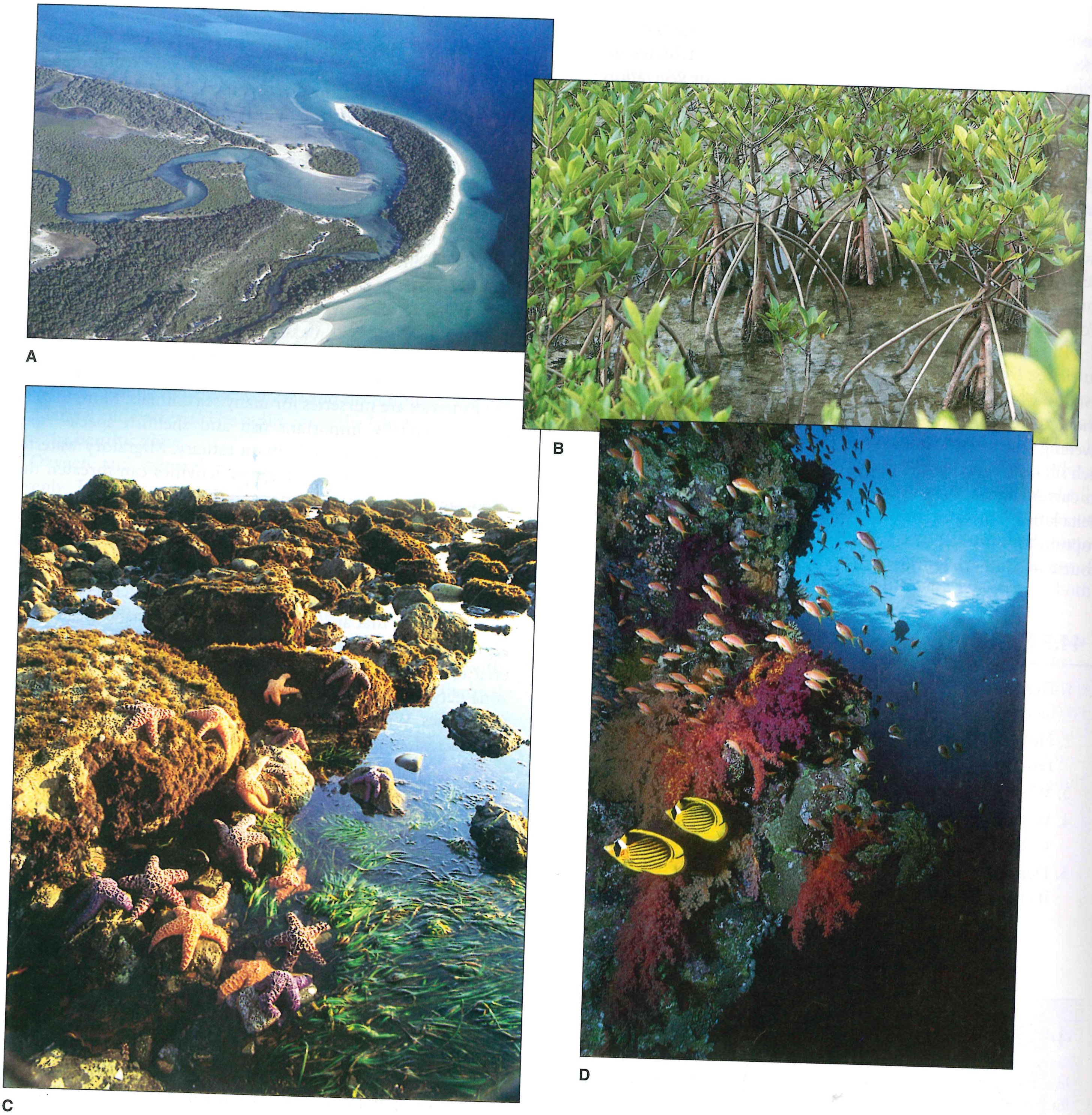


FIGURE 44.16 **Coastal Ecosystems.** Coastal ecosystems include estuaries (**A**), where salt water and fresh water meet. Some coastal areas have mangrove swamps (**B**), rocky intertidal zones (**C**), or coral reefs (**D**).

44.16

Intertidal Zone Along coastlines, in the littoral zone, lie ·ocky or sandy areas of the **intertidal zone.** This region is alter-ly exposed and covered with water as the tide ebbs and flows.

The organisms in a rocky intertidal zone often attach to s, which prevents wave action from carrying them away. dfasts attach large marine algae (seaweeds) to rocks. Threads suction fasten mussels to rocks. Sea anemones, sea urchins, ls, and sea stars live in pools of water that form between rocks ie tide ebbs. The organisms of the sandy beach, such as mole s, burrow to escape the pounding waves that would wash ı away. Sandy beaches have very little primary production.

al Reefs Colorful and highly productive **coral reef** ecosys-; border some tropical coastlines. Coral reefs are vast, under-r structures of calcium carbonate whose nooks and crannies ctively provide habitats for a million species of plants and ıals and an unknown variety of microorganisms. The Great ier Reef of Australia, for example, is composed of some 400 ies of coral and supports more than 1,500 species of fishes, of sponges, and 4,000 of mollusks. Other residents include ·, snails, sea stars, sea urchins, and octopuses. Food is abun- because the sun penetrates the shallow water, allowing osynthesis to occur, and constant wave action brings in addi-ıl nutrients.

Coral animals have colorful popular names based on their ·d forms—brain, staghorn, lace, vase, bead, button, and npipe corals are just a few. Recall from chapter 24 that indi-al animals, called polyps, build the reefs and house symbiotic · that are essential for the coral's, and the ecosystem's, survival figure 24.12). The living coral is a thin layer atop the remains of stors. A coral reef, then, is at the · time an immense graveyard and ·iving ecosystem. It is rich in bio-·sity, yet fragile. Chapter 45 con-·s threats to coral reefs.

·eans

oceans cover 70% of Earth's sur-but we know less about biodiver-there than we do about iversity in a single tree in a tropi-·ain forest. The reason for our t knowledge of life in the oceans be simply the vastness of this tic ecosystem. Populations are ·times small, usually very dis-·d, and nearly always difficult for to observe. Biologists have ·red only 5% of the ocean floor 1% of the huge volume of water e. Yet by the year 2010, 65% of world's human population will e within 10 miles (16.1 kilome- of an ocean.

We can, however, describe the ocean's physical characteristics, which determine the nature of its biological communities. The planet's five oceans and many seas, plus the bridging waters that interconnect them, hold about 95 trillion gallons (360 cubic kilometers) of water. The temperature ranges from 35°F (1.7°C) in the Antarctic Ocean to 81°F (27°C) near the equator. Sunlight quickly dissipates with depth. Within the first 10 meters, the water absorbs 80% of incoming sunlight, reflecting the blue wavelengths. The blue deepens with depth, and from about 600 meters and lower, everything is black, except for the occasional glow from bioluminescent organisms.

The sun heats the surface water, causing its molecules to move faster than molecules below. This warm upper layer is separated from denser, colder water below by a thin thermocline layer where the temperature changes rapidly. Tropical oceans and seas have a thermocline year round, but it appears only in the summer in temperate waters.

Very productive ocean environments arise where cooler, nutrient-rich bottom layers move upward in a process called **upwelling.** The resulting sudden influx of nutrients causes phytoplankton to "bloom," and with this widening of the food web base, many ocean populations grow. Upwelling generally occurs on the western side of continents, where wind pushes surface waters offshore, such as along the coasts of southern California, South America, parts of Africa, and the Antarctic.

Like other aquatic ecosystems, the ocean is considered in zones (**figure 44.17**). These designations are horizontal and vertical (depth). The horizontal zones describe the relationship between the ocean and the land. The intertidal zone, discussed in

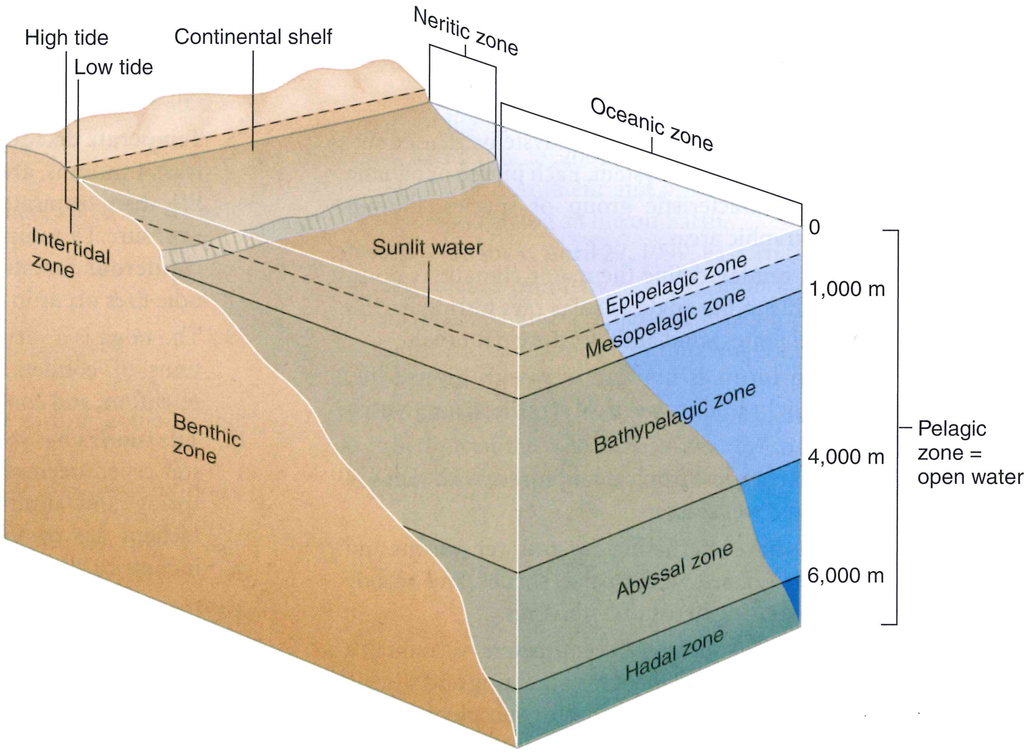


FIGURE 44.17 **Zones of the Ocean.** Zones in the ocean describe the relationship between regions of water and the land.

44.17

the previous section, is the shoreline. The **neritic zone** is the area from the coast to the edge of the continental shelf, and its waters reach a depth of 200 meters. The remainder of the ocean is the **oceanic zone,** which is, in turn, subdivided according to depth.

Two general divisions of the oceanic zone that refer to habitats are the benthic, or bottom zone, and the waters above, collectively called the **pelagic zone.** The pelagic zone is, in turn, subdivided according to depth. From about 200 meters to the surface lies the epipelagic zone, the only area where photosynthesis can occur. Beneath that is the mesopelagic zone (200 to 1,000 meters), and then the bathypelagic zone (1,000 to 4,000 meters). Beneath these zones lies the abyssal zone, from 4,000 to 6,000 meters. The hadal zone describes the areas of the ocean that dip down even more, as far as 10 kilometers below sea level.

Chapter 43 considered life at the very top of the ocean—the surface microlayer—as well as life in deep-sea hydrothermal vents. The very top of the epipelagic zone is rich in microscopic species that photosynthesize and form the bases of the great oceanic food webs. Other microorganisms and small animals feed on them. These top-dwelling organisms die and provide a continual rain of nutrients to the species below. The diverse living communities of the hydrothermal vents are fueled by chemosynthetic bacteria that harness the chemical energy inside Earth. In between lies a universe of diverse species, including great numbers and varieties of fishes, mollusks, echinoderms, crustaceans, and organisms yet to be discovered and described. One estimate of biodiversity in the benthic zone is 10 million species; it may be even higher in the vast pelagic zone.

We have much to learn about the oceans and seas, which are the environmental descendants of the aquatic setting where life probably arose. But we may never do so unless the current state of the oceans changes, and soon. Already the oceans include 50 "dead zones," areas devoid of life. In some cases, the cause of the dead zone is obviously human intervention, or population shifts such as algal blooms or the effects of dinoflagellate toxins. But in some dead zones, the trigger for the unraveling of food webs and ecosystems is a mystery. Chapter 45 explores some of the ways that the oceans, and other biomes and aquatic ecosystems, are struggling.

44.3 Mastering Concepts

1. Describe and distinguish among types of coastal aquatic ecosystems.
2. What are some adaptations of organisms to life where water meets land or salt water meets fresh water?
3. What are the major zones of the ocean?

Chapter Summary

44.1 Biomes

1. **Biomes** are major types of terrestrial ecosystems. The equivalent in water is an aquatic ecosystem. Each biome or aquatic ecosystem has a characteristic group of species. Biomes occupy large geographic areas.
2. Temperature and rainfall define the major climatic regions. Uneven heating due to the angle of solar rays hitting Earth's curved surface generates wind and moisture patterns.
3. The **tropical rain forest** is hot and wet, with diverse life. Competition for light leads to **vertical stratification.** Nutrients cycle rapidly.
4. **Tropical dry forest** borders tropical rain forest, with rich soil and distinct dry and wet seasons.
5. Tropical **savannas** have alternating dry and wet seasons and are dominated by grasses, with sparse shrubs and woody vegetation and migrating herds of herbivores.
6. **Deserts** have less than 8 inches (20 centimeters) of rainfall a year. Desert plants are well adapted for obtaining and storing water, with rapid life cycles, deep roots, or succulent tissues. Animals minimize water loss with tough integuments, and they are active at night. Some desert organisms are adapted to living in high salt conditions.
7. **Temperate grasslands** receive less water than deciduous forests and more water than deserts. The more moisture, the taller the grasses.
8. **Temperate deciduous forests** require a growing season of at least 4 months, are vertically stratified, and have less diverse life than tropical rain forests. Tree shapes maximize sun exposure. Decomposers form soil from leaf litter. **Temperate coniferous forests** have poor soil and a cold climate. Periodic fires occur in these areas.
9. The **taiga** is a very cold northern coniferous forest. Adaptations of conifers include needle shapes, year-round leaf retention, and conical tree shape.
10. The **tundra** has very cold and long winters. A layer of frozen soil called **permafrost** lies beneath the surface. During the spring and summer, meltwater forms rivers and pools. Lichens are common in the treeless tundra, and animals include caribou, reindeer, lemmings, and snowy owls.

44.2 Freshwater Ecosystems

11. Freshwater ecosystems include standing water (lakes and ponds) and running water (rivers and streams).

The **littoral zone** of a lake is the shallow area where light reaches the bottom; the **limnetic zone** is the lit upper layer of open water; the **profundal zone** is the dark deeper layer. The lake bottom is the **benthic zone.** In the littoral zone, most producers are rooted plants. In the limnetic zone, phytoplankton predominate. Nutrients fall from the upper layers and support life in the profundal and benthic zones.

Deep lakes in the temperate zone rely on **fall turnover** and **spring turnover** to mix oxygen and nutrients. Young, deep, **oligotrophic** lakes are clear blue, with few nutrients to support algae. Nutrients gradually accumulate, and algae tint the water green. The lake becomes a productive, or **eutrophic,** lake.

In rivers, organisms are adapted to local current conditions. Near the headwaters, the channel is narrow, and the current is swift. As the river accumulates water and sediments, the current slows, and the channel widens.

3 Marine Ecosystems

In **estuaries,** rivers empty into oceans. Life here is adapted to fluctuating salinity.

Mangrove swamps have changing salinity and are defined by characteristic salt-tolerant plant species.

Residents of the **intertidal zone** are adapted to stay in place as the tide ebbs and flows.

Coral reefs support many thousands of species in and around 400 or so types of coral.

The region of ocean near the shore is the **neritic zone.** Open water is the **oceanic zone** and includes the benthic zone (the bottom), and the **pelagic zone** (open water above the ocean floor). The most productive areas are in the neritic zones where **upwelling** occurs.

sting Your Knowledge

How does the fact that Earth is a sphere tilted on its axis influence the distribution of life?

Describe the zones of a(n):

a) lake.
b) ocean.
c) mangrove swamp.

What are the sources of energy in the various zones of the ocean?

List adaptations that enable organisms to survive conditions in the following biomes:

a) tropical rain forest
b) tropical dry forest
c) savanna
d) temperate grassland
e) tundra
f) desert
g) taiga

5. How can the tropical rain forest support diverse and abundant life with such poor soil?
6. What is permafrost?
7. How does photosynthetic activity differ in the zones of a lake?

Thinking Scientifically

1. Excess nutrients in a lake or in the ocean can greatly disrupt biological communities. Organisms die. How can this happen if life depends upon a supply of nutrients?
2. Researchers and citizens in Prairie City, Iowa, are reconstructing the prairie by collecting seeds from remnants and reintroducing animals. Which other biomes and aquatic ecosystems discussed in the chapter might be possible to reconstruct, and which not?
3. Cite two biomes or aquatic ecosystems where population bottlenecks might occur, and describe how this might happen.
4. How can a devastating fire be a natural part of a biome's dynamics? Give an example of a biome in which fires occur regularly.
5. Some scientists are currently attempting to catalog all of the world's biodiversity. What are some of the technical problems they may encounter?

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EPITHELIAL TISSUE: INTRODUCTION

Despite its complexity, the human body is composed of only **four basic types of tissue:** epithelial, connective, muscular, and nervous. These tissues, which are formed by cells and molecules of the **extracellular matrix,** exist not as isolated units but rather in association with one another and in variable proportions, forming different organs and systems of the body. The main characteristics of these basic types of tissue are shown in Table 4–1. Also of great functional importance are the free cells found in body fluids such as blood and lymph.

Table 4–1. Main characteristics of the four basic types of tissues.

Tissue	Cells	Extracellular Matrix	Main Functions
Nervous	Intertwining elongated processes	None	Transmission of nervous impulses
Epithelial	Aggregated polyhedral cells	Small amount	Lining of surface or body cavities, glandular secretion
Muscle	Elongated contractile cells	Moderate amount	Movement
Connective	Several types of fixed and wandering cells	Abundant amount	Support and protection

Connective tissue is characterized by the abundance of extracellular material produced by its cells; muscle tissue is composed of elongated cells specialized for contraction and movement; and nerve tissue is composed of cells with elongated processes extending from the cell body that have the specialized functions of receiving, generating, and transmitting nerve impulses. Organs can be divided into **parenchyma,** which is composed of the cells responsible for the main functions typical of the organ, and **stroma,** which is the supporting tissue. Except in the brain and spinal cord, the stroma is made of connective tissue.

Epithelial tissues are composed of closely aggregated polyhedral cells with very little extracellular substance. These cells have strong adhesion and form cellular sheets that cover the surface of the body and line its cavities.

The principal functions of epithelial (Gr. *epi,* upon, + *thele,* nipple) tissues are:

- Covering, lining, and protecting surfaces (eg, skin)
- Absorption (eg, the intestines)
- Secretion (eg, the epithelial cells of glands)
- Contractility (eg, myoepithelial cells).

Specific cells of certain epithelia are also highly specialized sensory cells, such as those of taste buds or the olfactory epithelium. Because epithelial cells line all external and internal surfaces of the body, everything that enters or leaves the body must cross an epithelial sheet.

CHARACTERISTIC FEATURES OF EPITHELIAL CELLS

The forms and dimensions of epithelial cells range from high **columnar** to **cuboidal** to low **squamous** cells. Their common polyhedral form results from their close juxtaposition in cellular layers or masses and is similar to what would be observed if a large number of inflated balloons were compressed into a limited space. Epithelial cell nuclei have a distinctive shape, varying from spherical to elongated or elliptic. The nuclear form often corresponds roughly to the cell shape; thus, cuboidal cells have spherical nuclei, and squamous cells have flattened nuclei. The long axis of the nucleus is always parallel to the main axis of the cell.

Because the lipid-rich membranes between cells are frequently indistinguishable with the light microscope, the stained cell nucleus is a clue to the shape and number of cells. Nuclear form is also useful to determine whether the cells are arranged in layers, a primary morphologic criterion for classifying epithelia.

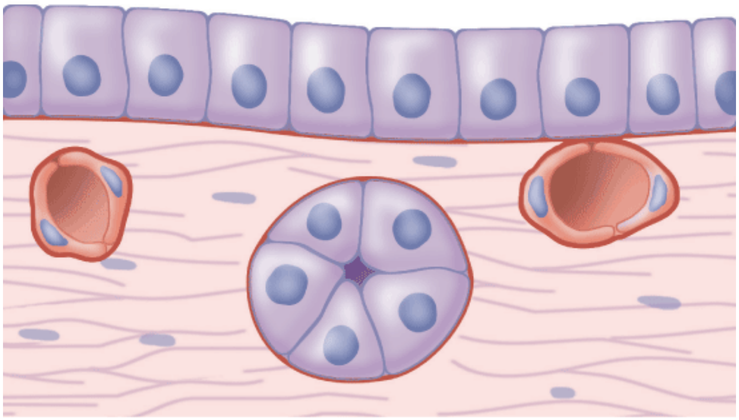
Most epithelia rest on connective tissue. In the case of epithelia lining the cavity of internal organs (especially in the digestive, respiratory, and urinary systems) this layer of connective tissue is often called the **lamina propria**. The lamina propria not only serves to support the epithelium but also provides nutrition and binds it to underlying structures. The area of contact between epithelium and lamina propria is increased by irregularities in the connective tissue surface in the form of small evaginations called **papillae** (L. diminutive of *papula*, nipple; singular **papilla**). Papillae occur most frequently in epithelial tissues subject to friction, such as the covering of the skin or tongue.

Epithelial cells generally show **polarity**, with organelles and membrane proteins distributed unevenly in different parts of the cell. The region of the cell that faces the connective tissue is called the **basal pole**, whereas the opposite pole, usually facing a space, is the **apical pole** and the intervening sides apposed in neighboring cells are the **lateral surfaces**. The membranes on the lateral surfaces of adjoining cells often have numerous infoldings to increase the area of that surface, increasing its functional capacity. The different regions of polarized cells may have different functions.

Basal Laminae & Basement Membranes

All epithelial cells in contact with subjacent connective tissue have at their basal surfaces a felt-like sheet of extracellular material called the **basal lamina** (Figure 4–1). This structure is visible only with the electron microscope, where it appears as an electron-dense layer, 20–100 nm thick, consisting of a network of fine fibrils, the **dense layer** or **lamina densa** (Figure 4–2). In addition, basal laminae may have electron-lucent layers on one or both sides of the dense layer, called **clear layers** or **laminae lucida.** Between epithelia with no intervening connective tissue, such as in lung alveoli and renal glomeruli, the basal lamina is often thicker due to the fusion of the basal laminae from each epithelial layer.

Figure 4–1.



Basal laminae.

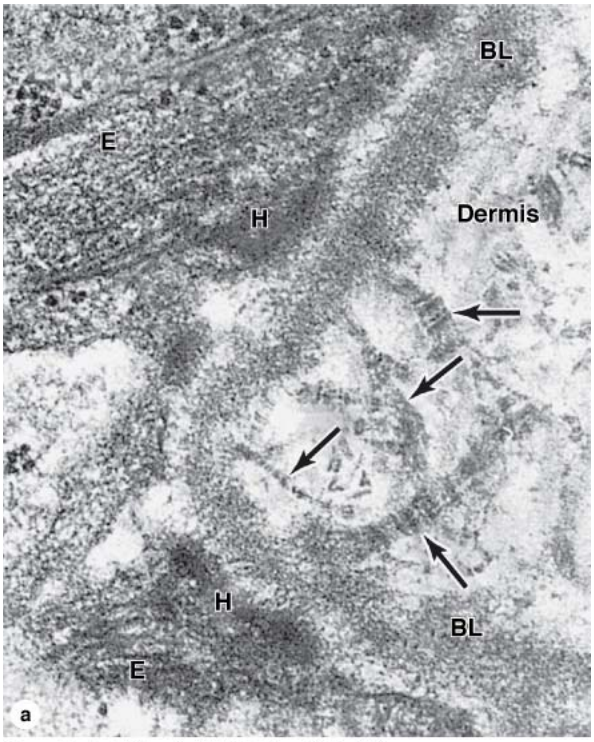
An extracellular **basal lamina** always lies at the interface of epithelial cells and connective tissue. The basal laminae to two neighboring epithelia can fuse or appear to fuse in places where there is no intervening connective tissue. Nutrients for epithelial cells must diffuse across the basal lamina. Nerve fibers normally penetrate this structure, but small blood capillaries (being epithelial themselves) never enter an epithelium across a basal lamina. When components of a basal lamina are resolved with the light microscope, the structure is often called a **basement membrane**.

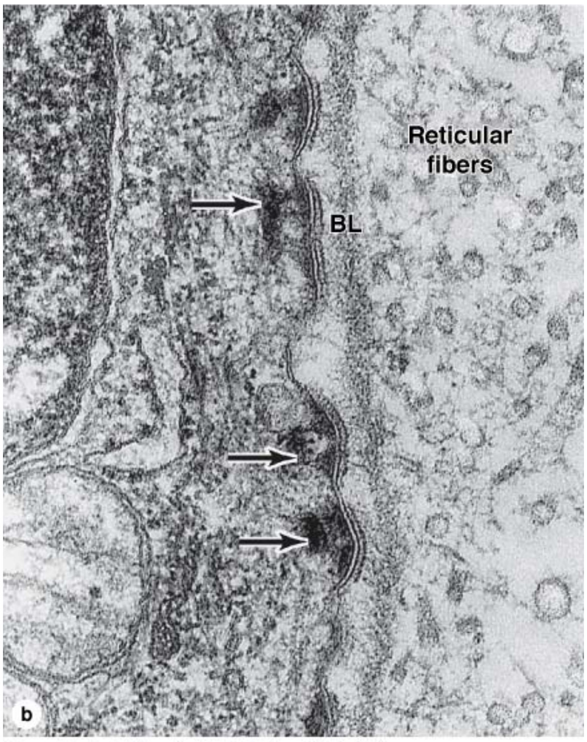
The macromolecular components of basal laminae form precise three-dimensional arrays and are described individually in the next chapter. The best known of these include:

- **Laminin**: These are large glycoprotein molecules that self-assemble to form a lace-like sheet immediately below the cells' basal poles where they are held in place by the transmembrane integrins.
- **Type IV collagen**: Monomers of type IV collagen contain three polypeptide chains and self-assemble further to form a felt-like sheet associated with the laminin layer.
- **Entactin (nidogen)**, a glycoprotein, and **perlecan**, a proteoglycan with heparan sulfate side chains: these glycosylated proteins and others serve to link together the laminin and type IV collagen sheets.

All these components are secreted at the basal poles of the epithelial cells. Their precise proportions in basal laminae vary between and within tissues. Basal laminae are attached to **reticular fibers** made of **type III collagen** in the underlying connective tissues by **anchoring fibrils** of **type VII collagen**. These proteins are produced by cells of the connective tissue and form a layer below the basal lamina called the **reticular lamina** that is also visible by TEM (Figure 4–2).

Figure 4–2.





Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition*: http://www.accessmedicine.com

Ultrastructural components of the basal lamina.

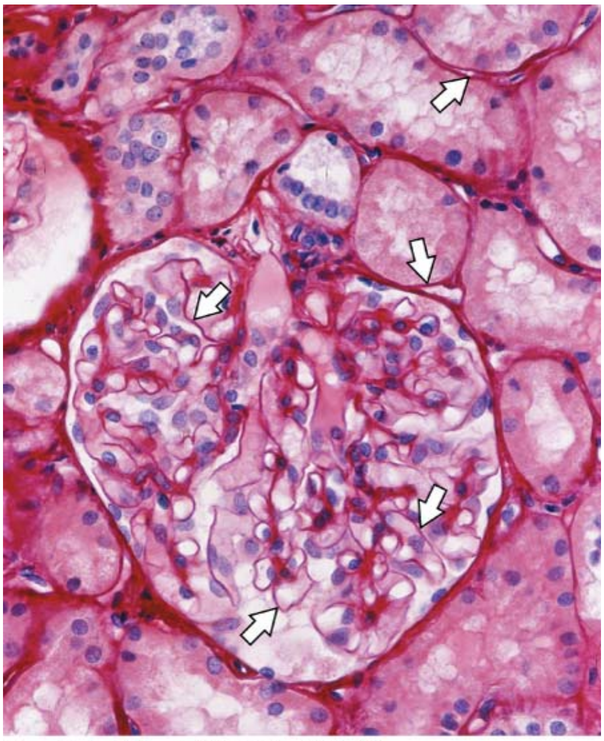
Details of the basal lamina are revealed by two TEM of sectioned human skin. **(a):** The basal lamina (BL) is shown to have a dense layer with a clear layer on each side. The underlying dermis contains **anchoring fibrils** (arrows) of collagen which help anchor the epithelium to the underlying connective tissue. Hemidesmosomes (H) occur at the epithelial–connective tissue junction. X54,000. **(b):** The basal lamina, hemidesmosomes (arrows), and underlying **reticular fibers** of the reticular lamina typically comprise a basement membrane sometimes visible with the light microscope. X80,000.

Basal laminae are found not only in epithelial tissues but also where other cell types come into contact with connective tissue. Muscle cells, adipocytes, and Schwann cells secrete laminin, type IV collagen, and other components that provide a barrier limiting or regulating exchanges of macromolecules between these cells and connective tissue.

Basal laminae have many functions. In addition to simple structural and filtering functions, they are also able to influence cell polarity; regulate cell proliferation and differentiation by binding and concentrating growth factors; influence cell metabolism and survival; organize the proteins in the adjacent plasma membrane (affecting signal transduction); and serve as pathways for cell migration. The basal lamina seems to contain the information necessary for many cell-to-cell interactions, such as the reinnervation of denervated muscle cells. The presence of the basal lamina around a muscle cell is necessary for the establishment of new neuromuscular junctions.

The term **basement membrane** is used to specify a periodic acid–Schiff (PAS)-positive layer, visible with the light microscope beneath epithelia (Figure 4–3). The basement membrane is formed by the combination of a basal lamina and a reticular lamina and is therefore thicker. The terms basement membrane and basal lamina are often used indiscriminately, causing confusion. In this book, "basal lamina" is used to denote the lamina densa and its adjacent layers and structures seen with the TEM. "Basement membrane" is used to denote the structures seen with the light microscope.

Figure 4–3.



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Basement membranes.

This section of kidney shows the typical basement membranes (arrows) of several tubules and of structures within the single glomerulus included here. In renal glomeruli the basement membrane, besides having a supporting function, has an important role as a filter. X100. Picrosirius-hematoxylin (PSH).

Intercellular Adhesion & Other Junctions

Several membrane-associated structures contribute to adhesion and communication between cells. They are present in most tissues but are particularly numerous and prominent in epithelia and will be described here. Epithelial cells are extremely cohesive and relatively strong mechanical forces are necessary to separate them. Intercellular adhesion is especially marked in epithelial tissues that are subjected to traction and pressure (eg, in the skin).

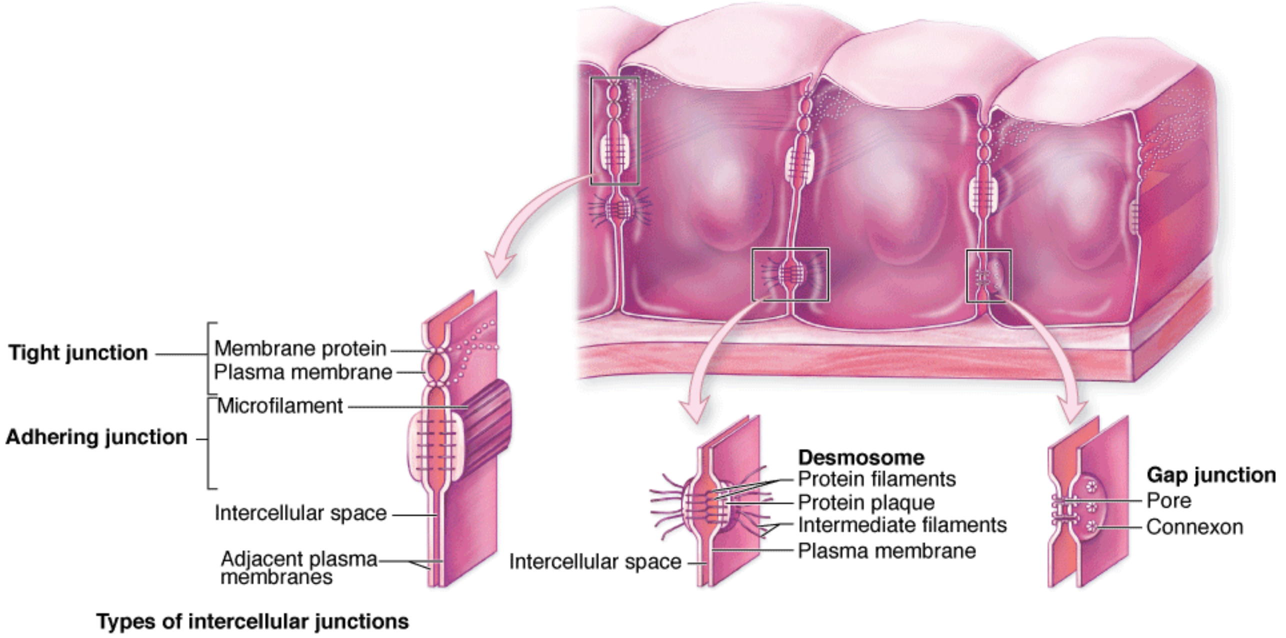
The lateral membranes of epithelial cells exhibit several specialized **intercellular junctions.** Various junctions serve to function as:

- Seals to prevent the flow of materials between the cells (**occluding junctions**)
- Sites of adhesion (**adhesive** or **anchoring junctions**)
- Channels for communication between adjacent cells (**gap junctions**).

In several epithelia such junctions are present in a definite order from the apical to the basal ends of the cells.

Tight junctions, or **zonulae occludens** (singular, **zonula occludens**), are the most apical of the junctions. The Latin terminology gives important information about the geometry of the junction. "Zonula" indicates that the junctions form bands completely encircling each cell, and "occludens" refers to the membrane fusions that close off the space between the cells. In properly stained thin sections viewed in the TEM, the adjacent membranes appear tightly apposed or fused (Figures 4–4 and 4–5). The seal between the membranes is due primarily to direct interactions between the transmembrane protein **claudin** on each cell. After cryofracture (Figure 4–6), the replicas show these fusion sites as a band of branching strands around each cell. The number of these sealing strands or fusion sites is inversely correlated with the leakiness of the epithelium. Epithelia with one or very few fusion sites (eg, proximal renal tubule) are more permeable to water and solutes than are epithelia with numerous fusion sites (eg, the lining of the urinary bladder). Thus, the principal function of the tight junction is to form a seal that prevents the flow of materials between epithelial cells (the paracellular pathway) in either direction. In this way, zonulae occludens in sheets of epithelial cells help form two functional compartments: an apical compartment that is composed of an organ cavity (such as the lumen of a secretory unit or the gut) and a basal compartment that begins at the junctions and encompasses the underlying tissue.

Figure 4–4.

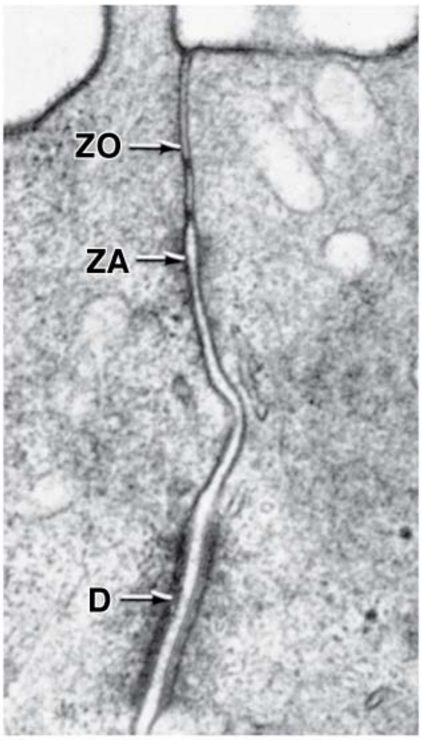


Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition:* http://www.accessmedicine.com

Junctional complexes of epithelial cells.

Three cuboidal epithelial cells, emptied of their contents, show the four major types of junctional complexes between cells. The **tight junction** (zonula occludens) and **adherent junction** (zonula adherens) are typically close together and each forms a continuous ribbon around the cell's apical end. Multiple ridges of the tight, occluding junctions prevent passive flow of material between the cells, but are not very strong; the adhering junctions immediately below them serve to stabilize and strengthen these circular bands around the cells and help hold the layer of cells together. Both desmosomes and gap junctions make spotlike plaques between two cells. Bound to intermediate filaments inside the cells, **desmosomes** form very strong attachment points which supplement the role of the zonulae adherens and play a major role to maintain the integrity of an epithelium. **Gap junctions**, each a patch of many **connexons** in the adjacent cell membranes, have little strength but serve as intercellular channels for flow of molecules. All of these junctional types are also found in certain other cell types besides epithelia.

Figure 4–5.

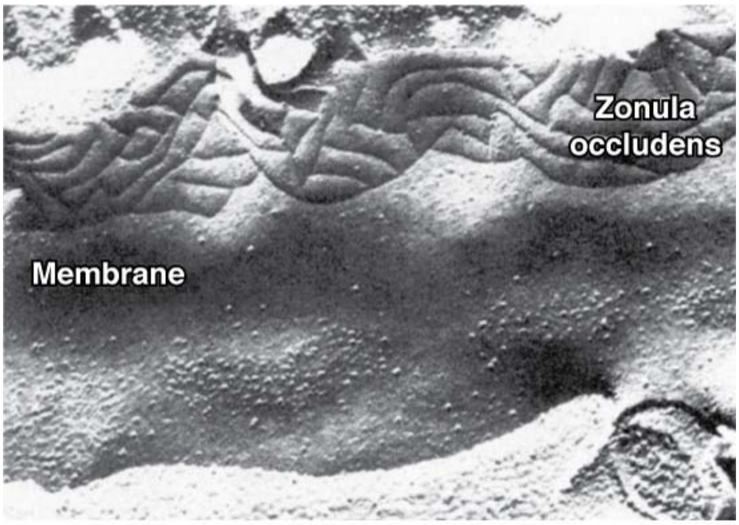


Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition:* http://www.accessmedicine.com

Junctional complex as seen in the TEM.

A section showing the apical regions of two epithelial cells reveals a junctional complex with its zonula occludens (ZO), zonula adherens (ZA), and a desmosome (D). The major components of zonula occludens are each cell's transmembrane proteins called claudins which make tight contact across the intercellular space, creating a seal. The cytoplasmic electron-dense material at the zonula adherens includes cadherins, catenin, actin-binding proteins and actin filaments, but that of the desmosomes consists of a plaque of "anchoring proteins," such as plakophilin, plakoglobin, and desmoplakin, which are bound by intermediate filaments primarily those composed of keratins. X80,000.

Figure 4–6.



Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition:* http://www.accessmedicine.com

View of zonula occludens after cryofracture.

In this electron micrograph of an epithelial cell after cryofracture, the fracture crosses through the cytoplasm in the lower portion, then shows a region of relatively smooth cell membrane, above which are the ridges and grooves of the zonula occludens. The membranes of adjoining cells basically fuse in the zonula occludens caused by tight interaction between claudins. X100,000.

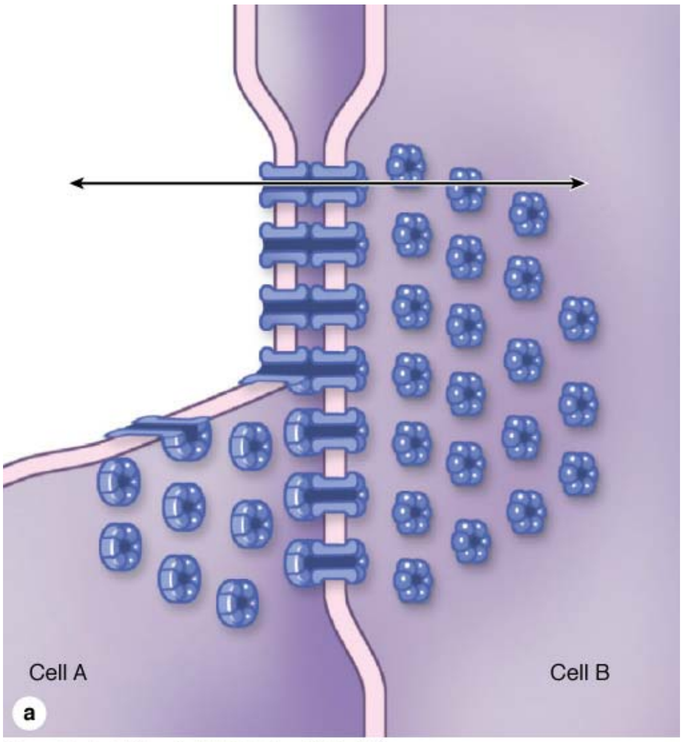
Besides forming a seal between compartments on either side of an epithelium, the zonulae occludens of epithelial cells help prevent the integral membrane proteins of the apical surface from being transferred to the basolateral surface and vice versa. This allows the two sides of the epithelium to maintain different receptors and function differently.

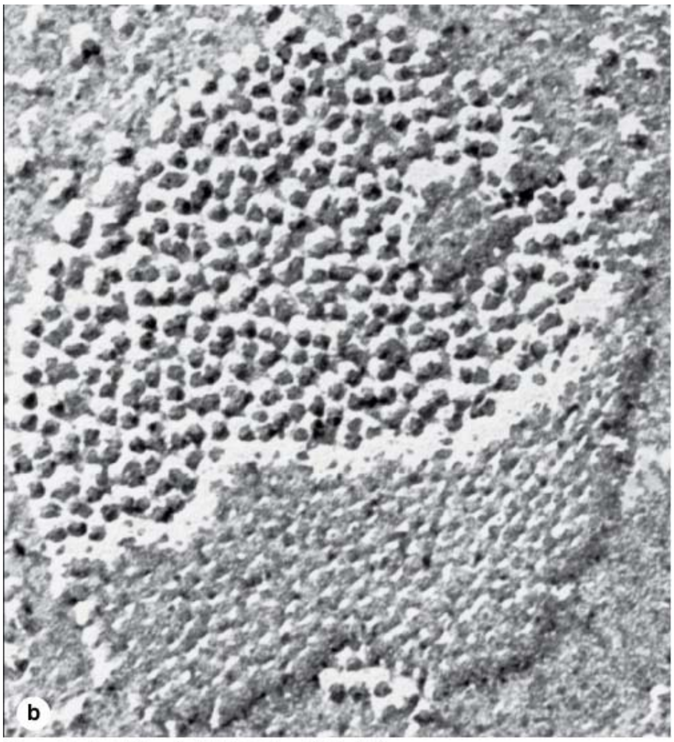
The next type of junction is the **adherent junction** or **zonula adherens** (Figures 4–4 and 4–5). This junction also encircles the cell, usually immediately below the zonula occludens, and provides for the firm adhesion of one cell to its neighbors. Adhesion is mediated by transmembrane glycoproteins of each cell, the **cadherins**, which lose their adhesive properties in the absence of Ca^{2+}. Inside the cell, cadherins bind the protein catenin which is linked by means of actin-binding proteins to actin filaments, all of which produce electron-dense plaques of material on the cytoplasmic surfaces of adherent junctions. The numerous actin filaments form part of the **terminal web,** a cytoskeletal feature at the apical pole in many epithelial cells with a role in cytoplasmic motility and other functions.

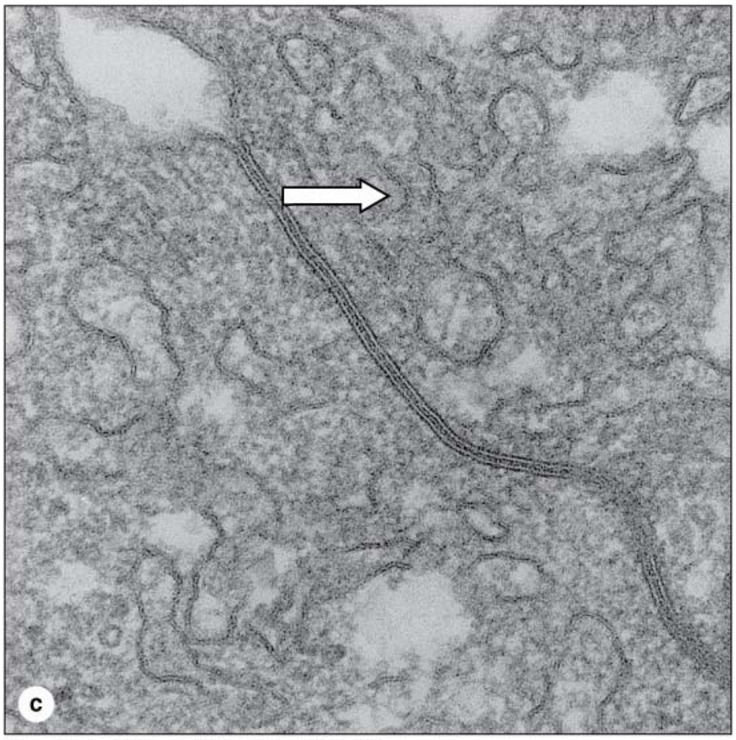
Another junction specialized for adhesion is the **desmosome** or **macula adherens** (L. *macula,* spot). As the names imply, this junctional type resembles a single "spot-weld" and does not form a belt around the cell. The desmosome is a disk-shaped structure at the surface of one cell that is matched with an identical structure at the surface of an adjacent cell (Figures 4–4 and 4–5). Between cell membranes at a desmosome are variable amounts of electron-dense material, principally larger members of the cadherin family. On the cytoplasmic side of each cell membrane these cadherin-type proteins inset into a dense **attachment plaque** of anchoring proteins (**plakophilin, plakoglobin,** and **desmoplakin**) which bind intermediate filaments rather than actin filaments. Cable-like filaments of **cytokeratin** are most common in desmosomes of epithelia. Because intermediate filaments of the cytoskeleton are very strong, desmosomes provide firm adhesion among the cells. In nonepithelial cells, the intermediate filaments attached to desmosomes are composed of other proteins, such as desmin or vimentin.

Gap or **communicating junctions** can occur almost anywhere along the lateral membranes of epithelial cells, but are also found between cells in nearly all mammalian tissues. With conventional TEM, gap junctions appear as regions where adjacent cell membranes are closely apposed (Figure 4–7a). After cryofracture, these junctions are seen as aggregated transmembrane protein complexes that form circular patches in the plasma membrane (Figure 4–7b).

Figure 4–7.


Cell A
Cell B
a


b



Gap junctions.

(a): The diagram of a gap junction (oblique view) depicts the structural elements that allow the exchange of nutrients and signal molecules between cells without loss of material into the intercellular space. The communicating channels are formed by pairs of abutting particles (**connexons**), which are in turn composed of six dumbbell-shaped protein subunits (connexins) that span the lipid bilayer of each cell membrane. The channel passing through the cylindrical bridges (arrow) is about 1.5 nm in diameter, limiting the size of the molecules that can pass through it. **(b):** A cryofracture preparation shows a gap junction between epithelial cells. The junction appears as a plaquelike agglomeration of intramembrane protein particles, the connexons. X45,000. **(c):** A section through a gap junction between two cells shows that the two cell membranes are very closely apposed, separated only by a 2-nm-wide electron-dense space. Individual connexons are not resolved in cell sections. X193,000. (Figure 4–7c, with permission, from Mary C. Williams, Pulmonary Center, Boston University School of Medicine.)

The proteins of gap junctions, called **connexins**, form hexameric complexes called **connexons**, each of which has a central hydrophilic pore about 1.5 nm in diameter. When two cells attach, connexins in the adjacent cell membranes move laterally and align to form connexons between the two cells (Figure 4–4), with each gap junction having dozens or hundreds of aligned pairs of connexons. Gap junctions permit the rapid exchange between cells of molecules with small (<1.5 nm) diameters. Some molecules mediating signal transduction, such as cyclic AMP, cyclic GMP, and ions, move readily through gap junctions, allowing cells in many tissues to act in a coordinated manner rather than as independent units. A good example is heart muscle, where abundant gap junctions are greatly responsible for the heart's coordinated beat.

In the contact area between epithelial cells and the subjacent basal lamina, **hemidesmosomes** (Gr. *hemi,* half, + *desmos* + *soma*) can often be observed ultrastructurally. These adhesive structures resemble a half-desmosome and bind the cell to the basal lamina (Figure 4–2). However, while in desmosomes the attachment plaques contain cadherins, in hemidesmosomes the plaques contain abundant **integrins,** transmembrane proteins that are receptor sites for the extracellular macromolecules laminin and collagen type IV.

Blood vessels do not normally penetrate an epithelium and nutrients for the epithelial cells must pass out of the capillaries in the underlying lamina propria. These nutrients then diffuse across the basal lamina and are taken up through the basolateral surfaces of the epithelial cell, usually by an energy-dependent process. Receptors for chemical messengers (eg, hormones, neurotransmitters) that influence the activity of epithelial cells are localized in the basolateral membranes. In absorptive epithelial cells, the apical cell membrane contains, as integral membrane proteins, enzymes such as disaccharidases and peptidases, which complete the digestion of molecules to be absorbed.

SPECIALIZATIONS OF THE APICALCELL SURFACE

The free or apical surface of many types of epithelial cells has specialized structures to increase the cell surface area or to move substances or particles bound to the epithelium.

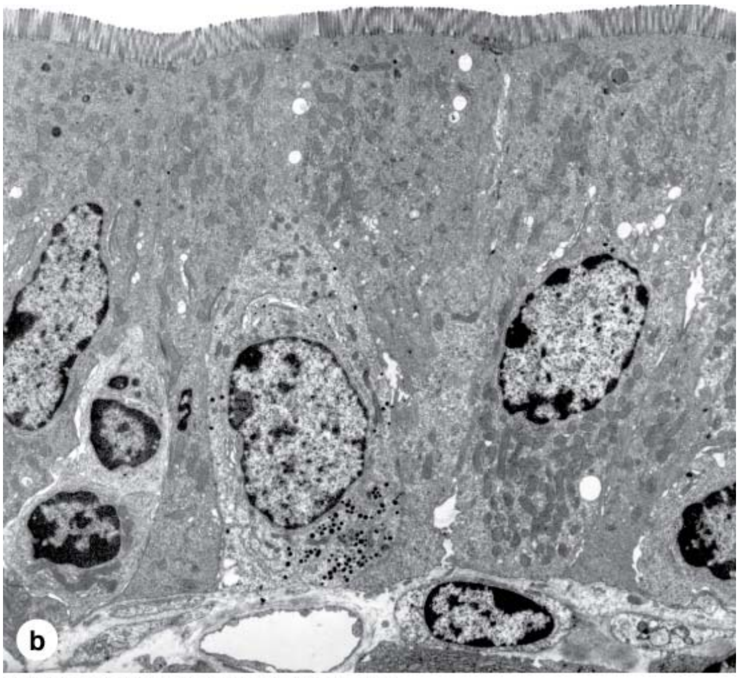
Microvilli

When viewed in the electron microscope, many cells are seen to have cytoplasmic projections. These projections may be short or long fingerlike extensions or folds that pursue a sinuous course, and they range in number from a few to many. Most are temporary, reflecting cytoplasmic movements and the activity of actin filaments.

In absorptive cells, such as the lining epithelium of the small intestine, the apical surface presents orderly arrays of many hundreds of more permanent **microvilli** (L. *villus,* tuft) (Figure 4–8). The average microvillus is only about 1 µm high and 0.08 µm wide, but with hundreds or thousands present on the end of each absorptive cell, the total surface area can be increased as much as 20- or 30-fold. In these absorptive cells the glycocalyx is thicker than that of most cells and includes enzymes for the final stages of certain macromolecules' breakdown. The complex of microvilli and glycocalyx is easily seen in the light microscope and is called the **brush** or **striated border.**

Figure 4–8.

Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition:* http://www.accessmedicine.com



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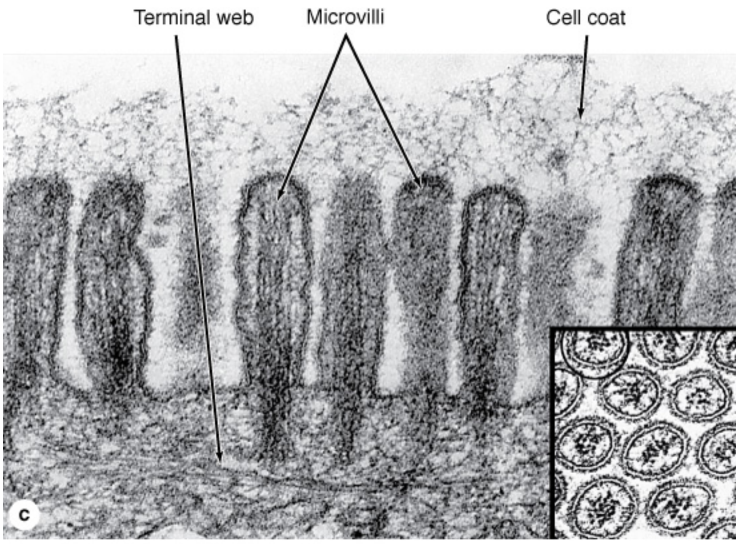

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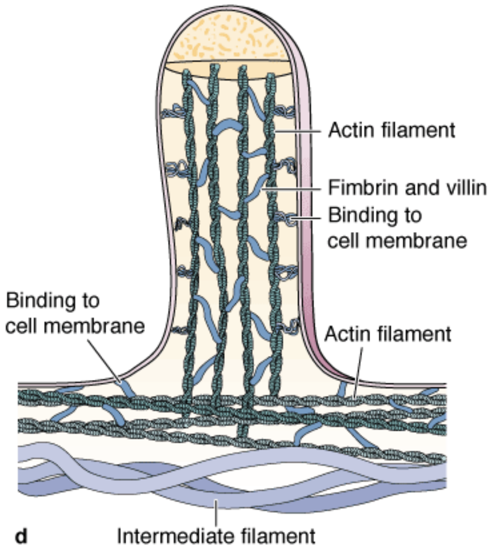


Microvilli.

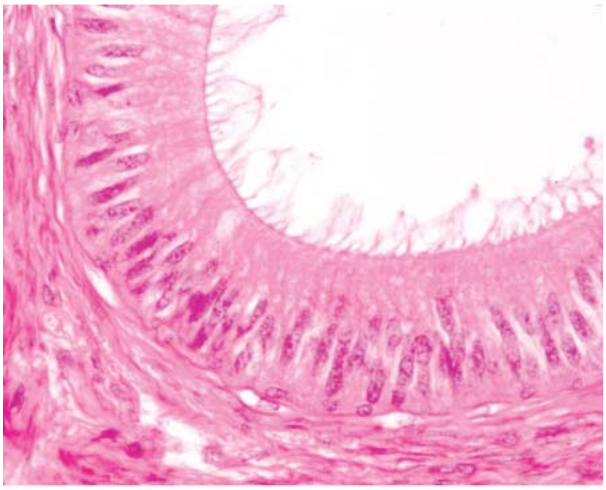
Absorptive cells lining the small intestine demonstrate microvilli particularly well. **(a):** With the light microscope microvilli at the apical side of the epithelium are usually faintly visible and make up the so-called **striated border** of the cells. **(b):** Individual microvilli are better seen by the TEM with a slightly higher magnification. Scattered endocrine cells (E) in this epithelium do not extend to the apical surface and lack microvilli. **(c):** At higher magnification the bundles of vertical microfilaments constituting the core of each microvillus are clearly seen. Below the microvilli is the terminal web, a horizontal network of actin microfilaments and associated proteins including myosins. On the plasmalemma of the microvilli is a thick extracellular cell coat (glycocalyx) containing glycoproteins and enzymes that allow the final stages of digestion to be linked to the uptake of digestion products across the cell membrane. The inset of cross-sectioned microvilli shows the internal disposition of the bundled actin filaments, the surrounding cell membrane, and the glycocalyx. X45,000. **(d):** The diagram indicates important proteins in a microvillus: the **actin filaments** cross-linked to one another by proteins such as **fimbrin** and **villin** and bound to the plasma membrane by proteins such as myosin I. The actin filaments are oriented in the same direction, with their plus ends associated with amorphous material at the tip of the microvillus.

Within each microvillus are bundles of actin filaments (Figure 4–8c,d) cross-linked to each other and to the surrounding plasma membrane by other proteins. These filaments insert into the actin filaments of the terminal web. The array of microfilaments stabilizes the microvillus and allows it to contract slightly and intermittently which helps maintain optimal conditions for absorption across its plasmalemma.

Stereocilia

Stereocilia are long apical processes of cells in other absorptive epithelia such as that lining the epididymis (Figure 4–9) and ductus deferens. These structures are much longer and less motile than microvilli, are branched, and should not be confused with true cilia. Like microvilli, stereocilia also increase the cells' surface area, facilitating the movement of molecules into and out of the cell.

Figure 4–9.



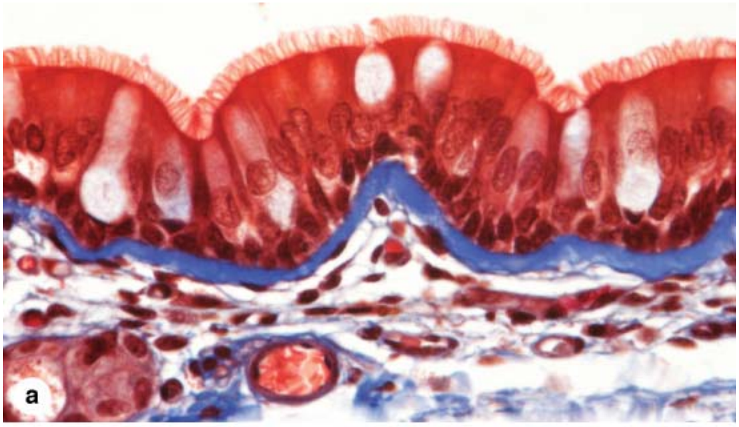
Stereocilia.

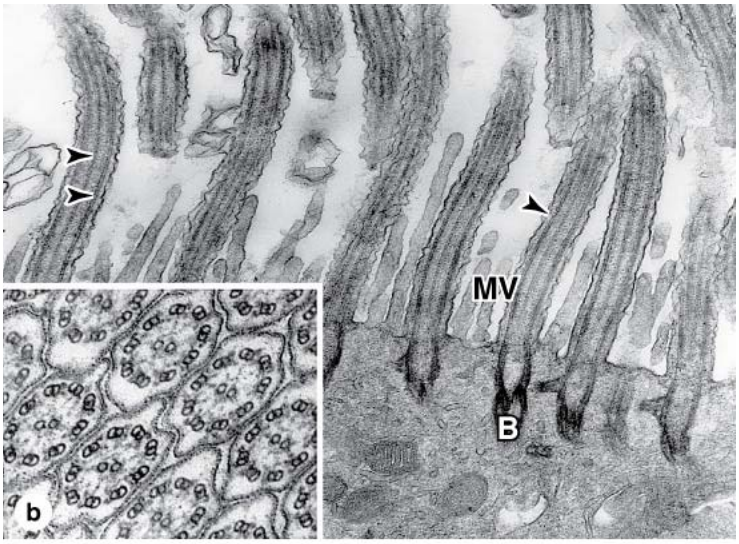
At the apical ends of the tall epithelial cells lining organs such as the epididymis (shown here) are numerous very long stereocilia, which increase the surface area available for cellular absorption. Each stereocilium is typically much longer than a microvillus and may show a branching structure. Stereocilia have cytoplasmic actin filament bundles and external cell coats similar to those of microvilli. X400. H&E.

Cilia

Cilia are elongated, highly motile structures on the surface of some epithelial cells, 5–10 μm long and 0.2 μm in diameter, which is much longer and two times wider than a typical microvillus. As discussed in Chapter 2, each cilium is bounded by the cell membrane and contains an axoneme with a central pair of microtubules surrounded by nine peripheral microtubular pairs (Figure 4–10). Cilia are inserted into **basal bodies,** which are electron-dense structures at the apical pole just below the cell membrane (Figure 4–10). Basal bodies have a structure similar to that of centrioles. In living organisms, cilia exhibit rapid back-and-forth movements coordinated to propel a current of fluid and suspended matter in one direction over the ciliated epithelium. The motion occurs due to activity of **ciliary dynein** present on the peripheral microtubular doublets of the axoneme, with adenosine triphosphate (ATP) as the energy source. A ciliated cell of the trachea lining is estimated to have about 250 cilia. Flagella, present in the human body only in spermatozoa (Chapter 21), are similar in structure to cilia but are much longer and are normally limited to one flagellum per cell.

Figure 4–10.





Cilia.

TEMs of the apical portions of cells lining the respiratory tract show very well-developed cilia. **(a):** By light microscopy cilia usually appear as long, somewhat tangled projections. X400. Mallory trichrome. **(b):** TEM of cilia sectioned longitudinally reveals the axoneme of each, with arrowheads on the left side showing the central and peripheral microtubules. The arrowhead at right indicates the plasma membrane surrounding a cilium. At the base of each cilium is a basal body (B) from which it grows. Much shorter microvilli (MV) can be seen between the cilia. X59,000. **Inset:** Cilia seen in cross section clearly show the 9 + 2 array of the axoneme microtubules in each cilium. X80,000.

TYPES OF EPITHELIA

Epithelia can be divided into two main groups according to their structure and function: **covering (or lining) epithelia** and **glandular epithelia.** This is an arbitrary division, for there are lining epithelia in which all the cells secrete (eg, the lining of the stomach) or in which glandular cells are distributed among the lining cells (eg, mucous cells in the small intestine or trachea).

Covering or Lining Epithelia

Covering epithelia are tissues in which the cells are organized in layers that cover the external surface or line the cavities of the body. They are classified according to the number of cell layers and the morphologic features of the cells in the surface layer (Table 4–2). **Simple epithelia** contain only one layer of cells and **stratified epithelia** contain more than one layer.

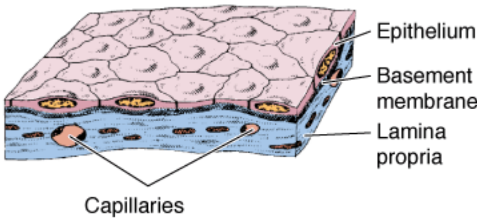
Table 4–2. Common types of covering epithelia in the human body.

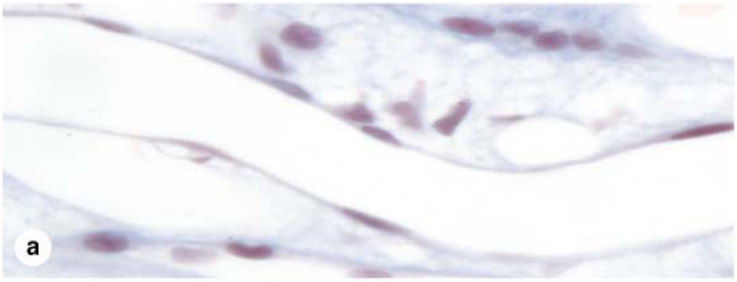
Number of Cell Layers	Cell Form	Examples of Distribution	Main Function
Simple (one layer)	Squamous	Lining of vessels (endothelium). Serous lining of cavities; pericardium, pleura, peritoneum (mesothelium).	Facilitates the movement of the viscera (mesothelium), active transport by pinocytosis (mesothelium and endothelium), secretion of biologically active molecules (mesothelium).
	Cuboidal	Covering the ovary, thyroid.	Covering, secretion.
	Columnar	Lining of intestine, gallbladder.	Protection, lubrication, absorption, secretion.
Pseudostratified (layers of cells with nuclei at different levels; not all cells reach surface but all adhere to basal lamina)		Lining of trachea, bronchi, nasal cavity.	Protection, secretion; cilia-mediated transport of particles trapped in mucus out of the air passages.
Stratified (two or more layers)	Squamous keratinized (dry)	Epidermis.	Protection; prevents water loss.

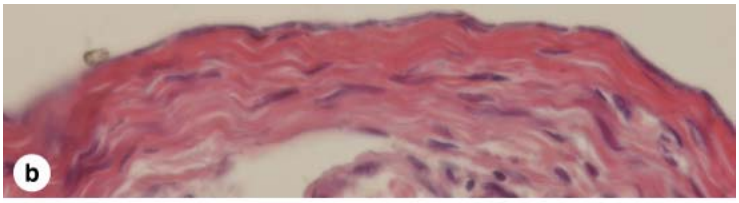
Number of Cell Layers	Cell Form	Examples of Distribution	Main Function
	Squamous nonkeratinized (moist)	Mouth, esophagus, larynx, vagina, anal canal.	Protection, secretion; prevents water loss.
	Cuboidal	Sweat glands, developing ovarian follicles.	Protection, secretion.
	Transitional	Bladder, ureters, renal calyces.	Protection, distensibility.
	Columnar	Conjunctiva.	Protection.

Based on cell shape, simple epithelia are classified as **squamous** (thin cells)**, cuboidal** (cells roughly as thick as they are wide) or **columnar** (cells taller than they are wide) Examples of simple epithelia are shown in Figures 4–11, 4–12, and 4–13.

Figure 4–11



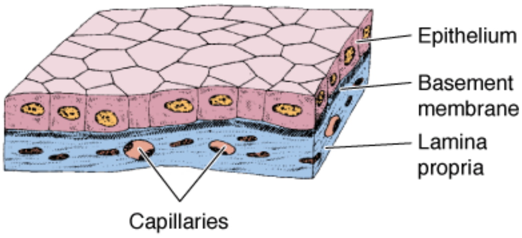


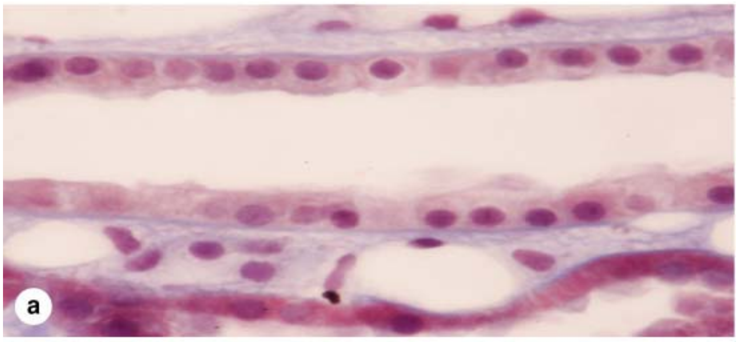


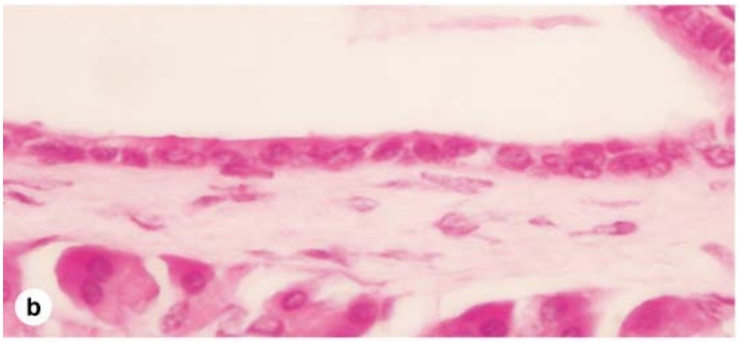
Simple squamous epithelia.

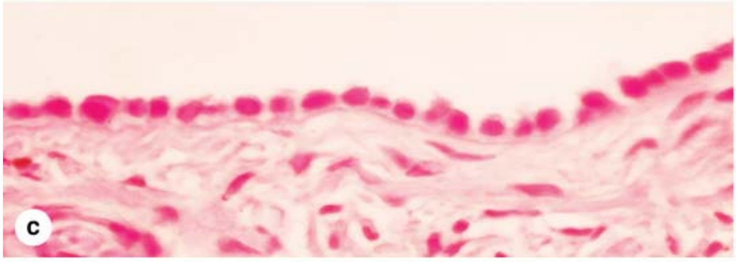
In simple squamous epithelium, cells of the single layer are flat and usually very thin, with only the thicker cell nucleus appearing as a bulge to denote the cell. Simple epithelia are typically specialized as lining of vessels and cavities and regulate substances which can enter underlying tissue from the vessel or cavity. The thin cells often exhibit transcytosis. Examples shown here are those lining the renal loops of Henle **(a),** the mesothelium lining a mesentery **(b),** and the endothelium lining the inner surface of the cornea **(c).** Endothelium and mesothelium are nearly always simple squamous. All X400. H&E.

Figure 4–12.





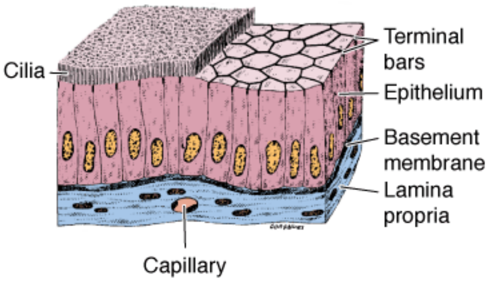


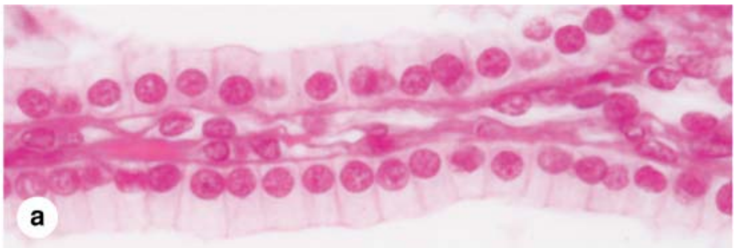


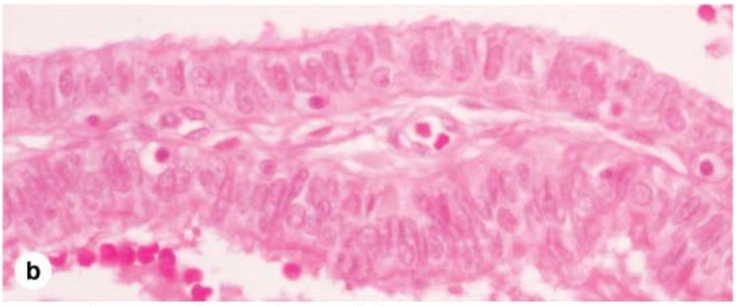
Simple cuboidal epithelium.

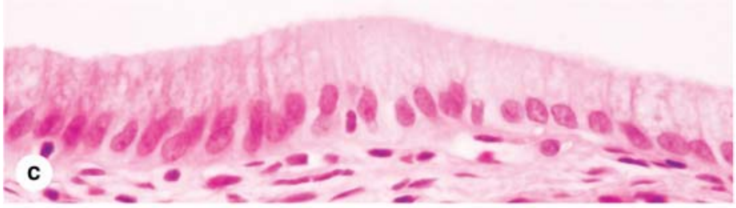
Cells of simple cuboidal epithelia vary in their height but are roughly as tall as they are wide. Their greater thickness often includes cytoplasm rich in mitochondria providing energy for a high level of active transport of substances across the epithelium. Examples of simple cuboidal epithelia shown here are from a renal collecting tubule **(a),** a pancreatic duct **(b),** and the mesothelium covering an ovary **(c).** All X400. H&E.

Figure 4–13.









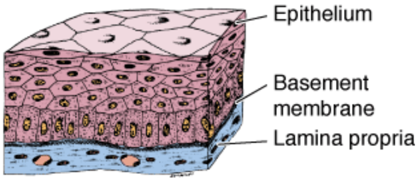
Simple columnar epithelium.

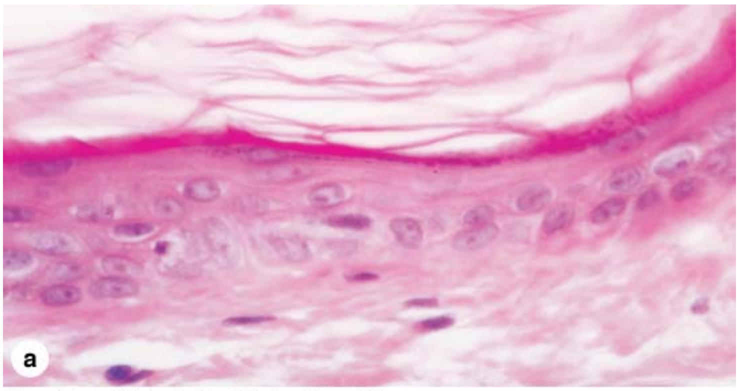
Cells of simple columnar epithelia are taller than they are wide. Such cells are usually highly specialized for absorption, with microvilli, and often have interspersed secretory cells or ciliated cells. Such epithelial cells always have tight and adherent junctional complexes at their apical ends, but are often loosely associated in more basolateral areas. This allows for rapid transfer of absorbed material to the space between the cells rather than transport the full length of the cells. The additional cytoplasm in columnar cells allows additional mitochondria and other organelles needed for absorption and processing. The examples shown here are from a renal collecting duct **(a),** the oviduct lining, with both secretory and ciliated cells **(b),** and the lining of the gall bladder **(c).** All X400. H&E.

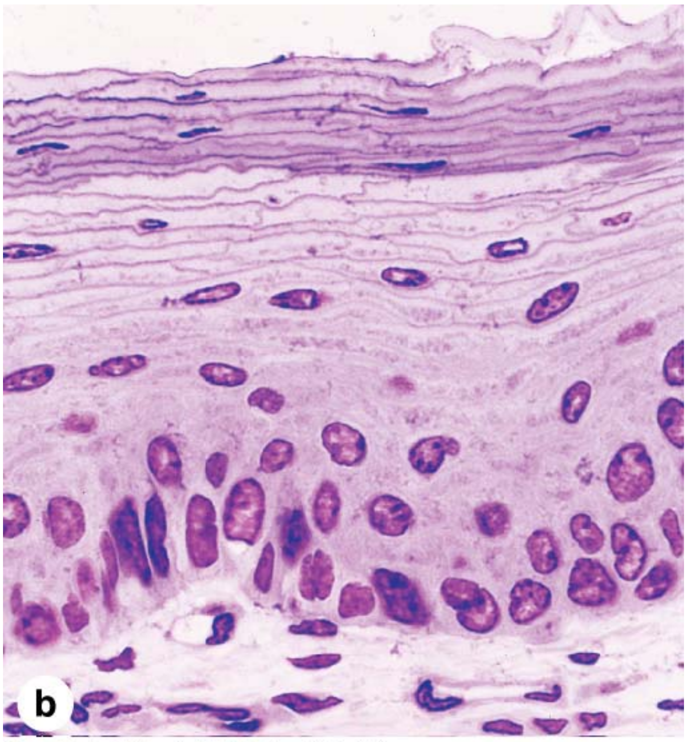
Stratified epithelia are classified according to the cell shape of the *superficial* layer(s): **squamous, cuboidal, columnar,** and **transitional.**

The very thin surface cells of stratified squamous epithelia can be "keratinized" (rich in keratin intermediate filaments) or "nonkeratinized" (with relatively sparse amounts of keratin). **Stratified squamous keratinized epithelium** is found mainly in the epidermis of skin. Its cells form many layers, and the cells closer to the underlying connective tissue are usually cuboidal or low columnar. The cells become irregular in shape and flatten as they accumulate keratin in the process of **keratinization** and are moved progressively closer to the surface, where they become thin, metabolically inactive packets (**squames**) of keratin lacking nuclei. This surface layer of cells helps protect against water loss across this epithelium. (See Chapter 18 for more detailed information on skin.) **Stratified squamous nonkeratinized epithelium** (Figure 4–14) lines wet cavities (eg, mouth, esophagus, and vagina). In such areas where water loss is not a problem, the flattened cells of the epithelial surface layer are living cells containing much less keratin and retaining their nuclei.

Figure 4–14.







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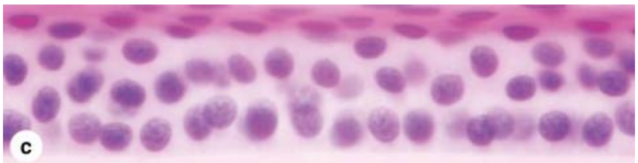

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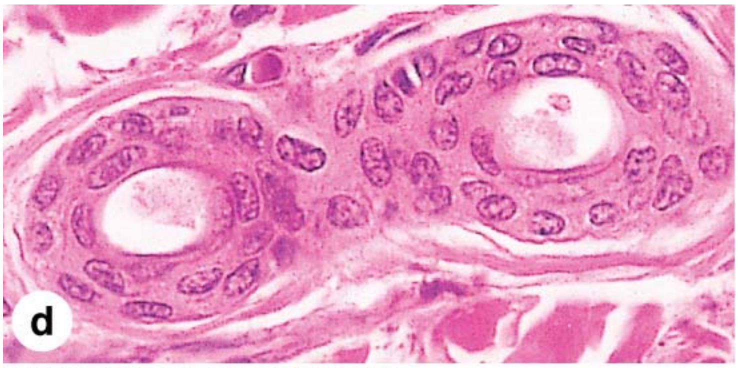

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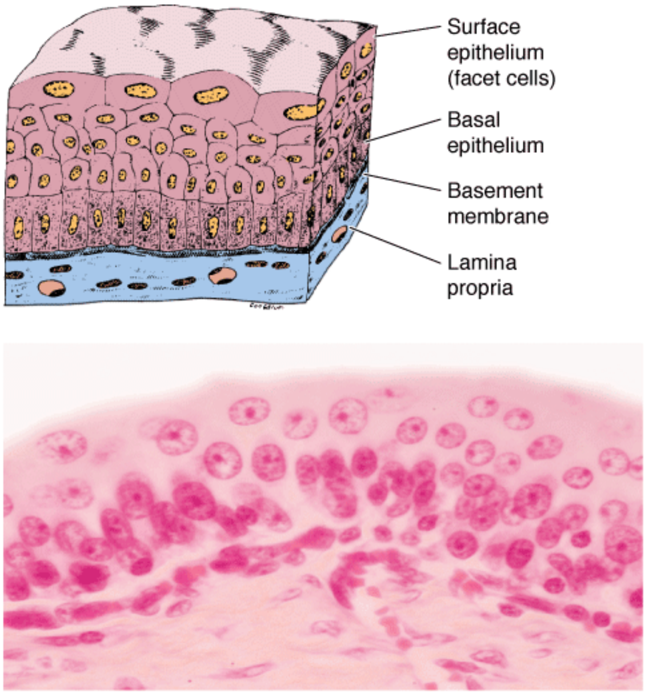
Stratified epithelia.

Stratified squamous epithelia have protective functions: protection against easy invasion of underlying tissue by microorganisms and protection against water loss. In the skin, protection against water loss and desiccation is particularly important and the epithelium is **keratinized**. As epidermal cells of the skin **(a)** differentiate they become filled with keratin and other substances and eventually lose their nuclei and other organelles. The superficial flattened squames form a layer which impedes water loss and eventually slough off and are replaced from below. Keratinization will be discussed fully in Chapter 18. Epithelia lining many internal surfaces such as the esophagus **(b),** or covering the cornea **(c)** are considered **nonkeratinized** because the differentiating cells accumulate much less keratin and retain their nuclei. Such epithelia still provide protection against microorganisms, but do not fill with keratin because water loss is less of an issue. Stratified cuboidal or columnar epithelia are fairly rare, but are found in excretory ducts of some glands (**d**) where the double layer of cells apparently provides a more robust lining than a simple epithelium would. All X400; (b) PT, (a, c, and d) H&E.

Stratified cuboidal and **stratified columnar epithelia** are rare. Stratified columnar epithelium can be found in the conjunctiva lining the eyelids, where it is both protective and mucus secreting. Stratified cuboidal epithelium is restricted to large excretory ducts of sweat and salivary glands, where it apparently provides a lining more robust than that of a simple epithelium.

Transitional epithelium or **urothelium**, which lines only the urinary bladder, the ureter, and the upper part of the urethra, is characterized by a superficial layer of domelike cells that are neither squamous nor columnar (Figure 4–15). These cells, sometimes called umbrella cells, are essentially protective against the hypertonic and potentially cytotoxic effects of urine. Importantly, the form of the surface cells changes according to the degree of distention of the bladder wall. This type of epithelium is discussed in detail in Chapter 19.

Figure 4–15.

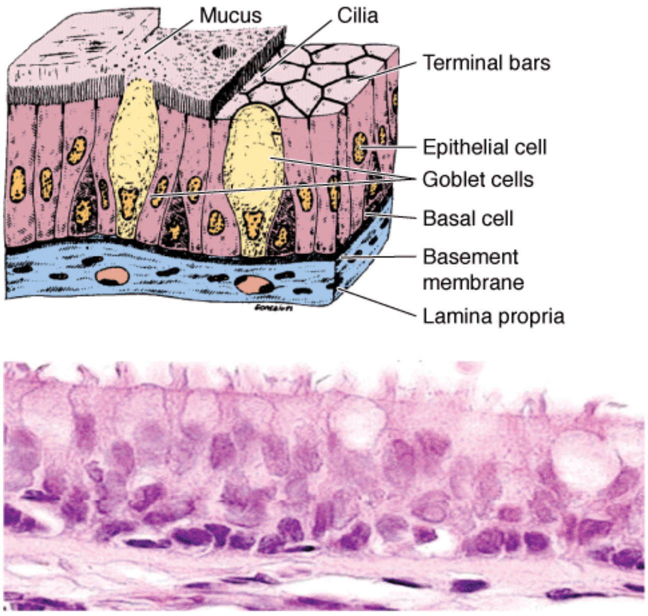


Transitional epithelium or urothelium.

Stratified transitional epithelium lining the urinary bladder has rounded or dome-shaped superficial cells with two unusual features. The surface cells have specialized membranes and are able to withstand the hypertonic effects of urine and protect underlying cells from this toxic solution. Cells of transitional epithelium are also able to adjust their relationships with one another as the bladder fills and the wall is stretched, so that the transitional epithelium of a full, distended bladder seems to have fewer cell layers than that of an empty bladder. These unique features of urothelium will be discussed more fully in Chapter 19. X400. H&E.

In addition to these various stratified epithelia, there is another type classified as **pseudostratified columnar epithelium**, so called because all cells are attached to the basal lamina even though their nuclei lie at different levels in the epithelium and the height of some cells does not extend to the surface. The best-known example of pseudostratified columnar epithelium is that lining the passages of the upper respiratory tract (Figure 4–16). The columnar cells of this epithelium are also heavily ciliated.

Figure 4–16.



Pseudostratified epithelium.

Cells of pseudo-stratified epithelia appear to be in layers, but the basal ends of the cells are all in contact with the basement membrane, which is often very thick in these epithelia. The best example of this epithelial type is the pseudostratified ciliated columnar epithelium of the upper respiratory tract, which contains cell types with their nuclei at different levels that give the false appearance of cellular stratification. This epithelium is discussed in detail in Chapter 17. X400. H&E.

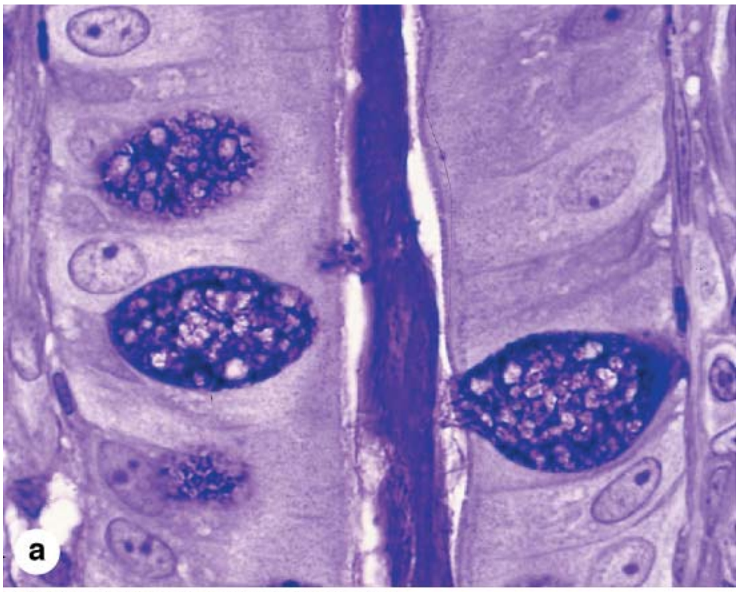
Glandular Epithelia

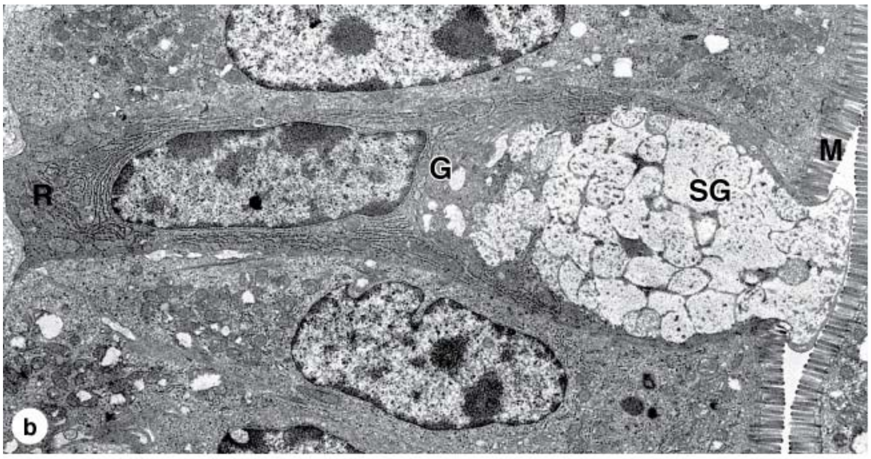
Glandular epithelia are formed by cells specialized to secrete. The molecules to be secreted are generally stored in the cells in small membrane-bound vesicles called **secretory granules.**

Glandular epithelial cells may synthesize, store, and secrete proteins (eg, in the pancreas), lipids (eg, adrenal, sebaceous glands), or complexes of carbohydrates and proteins (eg, salivary glands). Mammary glands secrete all three substances. The cells of some glands have low synthetic activity (eg, sweat glands) and secrete mostly water and electrolytes transferred into the gland from the blood.

The epithelia that form glands can be classified according to various criteria. Unicellular glands consist of large isolated secretory cells and multicellular glands have clusters of cells. The classic unicellular gland is the **goblet cell** in the lining of the small intestine (Figure 4–17) or respiratory tract. The term "gland," however, is usually used to designate large aggregates of secretory epithelial cells, such as in the salivary glands and the pancreas.

Figure 4–17.



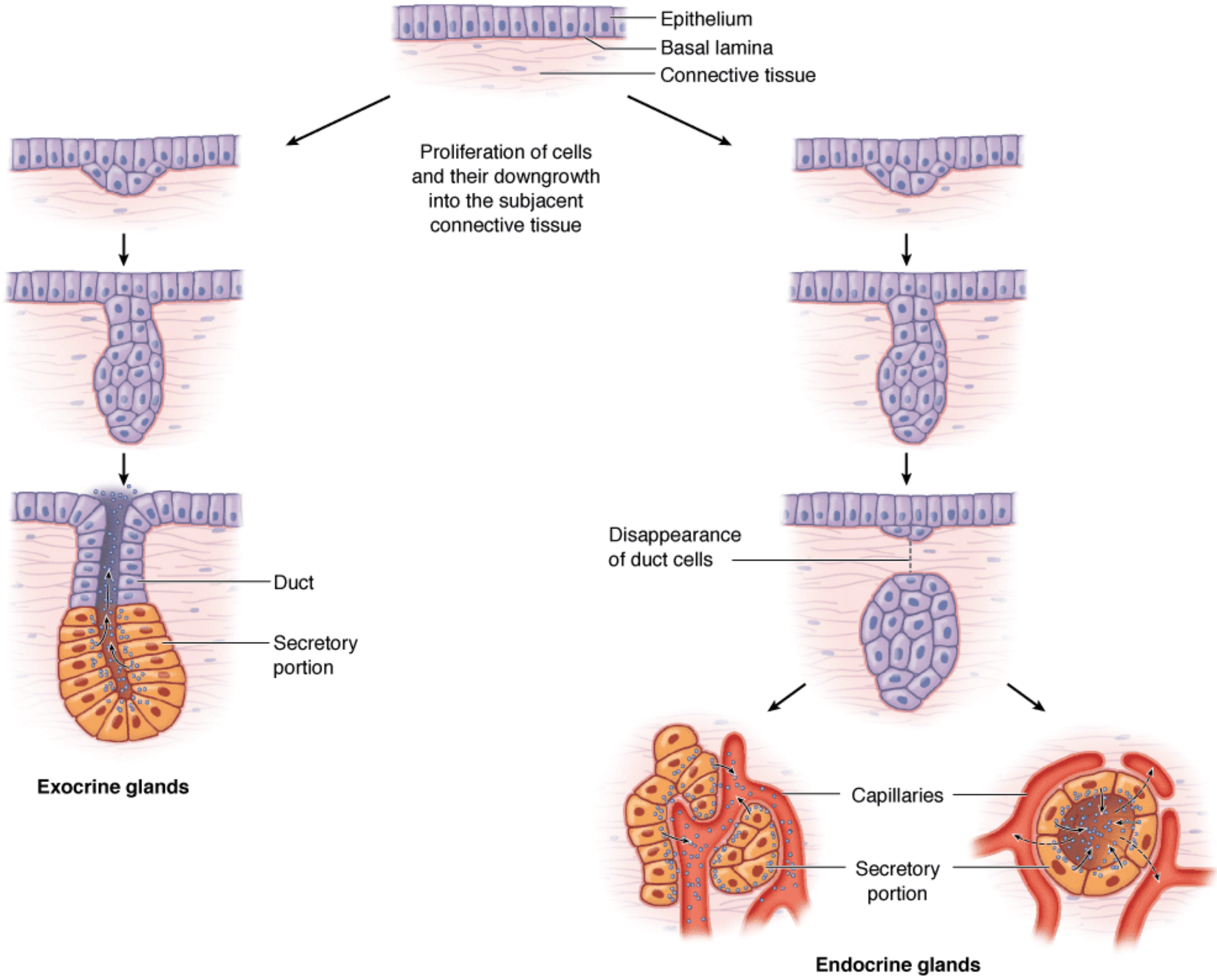


Goblet cells: unicellular glands.

A section of epithelial lining of the large intestine shows scattered goblet cells secreting mucus to the extracellular space **(a):** With the stain for glycoproteins used here, both the mucus precursor stored in cytoplasmic graules of the goblet cells as well as the secreted mucus are stained dark blue. X400. PAS-PT. **(b):** Ultrastructurally a goblet cell shows a basal nucleus surrounded by RER (R), a large Golgi complex (G) just above the nucleus, and an apical end filed with large secretory granules (SG) containing mucins. This highly viscous material is secreted by exocytosis and is then hydrated to form mucus in the lumen lined by microvilli (M). X17,000.

Glands develop during fetal life from covering epithelia by means of cell proliferation and invasion of the subjacent connective tissue, followed by further differentiation (Figure 4–18). **Exocrine glands** retain their connection with the surface epithelium, the connection taking the form of tubular ducts lined with epithelial cells through which the secretions pass to the surface. **Endocrine glands** have lost their connection to the surface from which they originated during development. These glands are therefore ductless and their secretions are picked up and transported to their sites of action by the bloodstream rather than by a duct system. Multicellular glands, whether exocrine or endocrine, also have connective tissue in a surrounding capsule and in septa that divide the gland into lobules. These lobules then subdivide, and in this way the connective tissue separates and binds the glandular components together (Figure 4–19).

Figure 4–18.

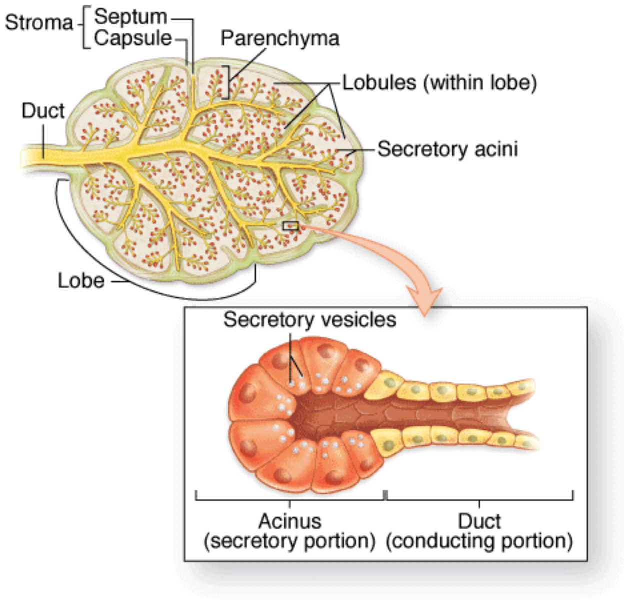


Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition*: http://www.accessmedicine.com

Formation of glands from covering epithelia.

During fetal development epithelial cells proliferate and penetrate the underlying connective tissue. They may—or may not—maintain a connection with the surface epithelium. When the connection is maintained, exocrine glands are formed; with the connection lost, endocrine glands are formed. Exocrine glands secrete to the body surface or gut via duct systems formed from the epithelial connection. The cells of endocrine glands, which secrete hormones (see Chapter 20) can be arranged in cords or in follicles with lumens for storing the secretory product. From either the cords (left) or follicles (right) of endocrine cells, the secretory product is released outside the cells and picked up by the blood vessels for distribution throughout the body.

Figure 4–19.



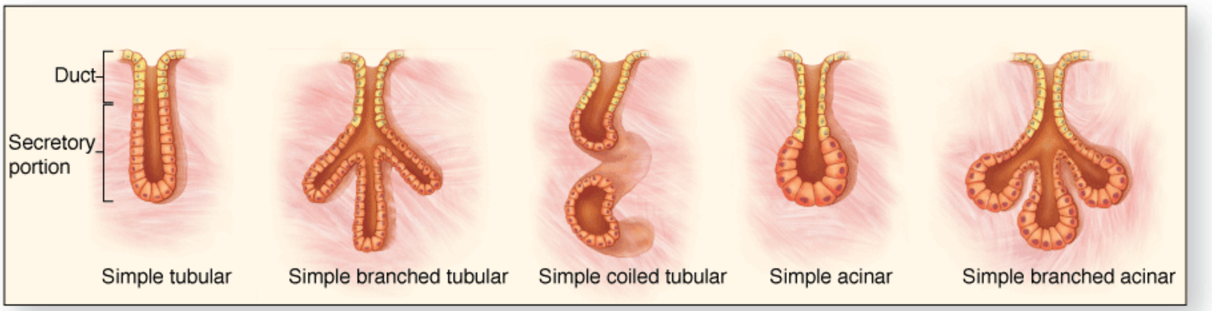
General structure of exocrine glands.

Exocrine glands by definition have ducts that lead to an organ or body surface. Inside the gland the duct runs through connecting septa and branches repeatedly, until its smallest branches end in the secretory portions of the gland.

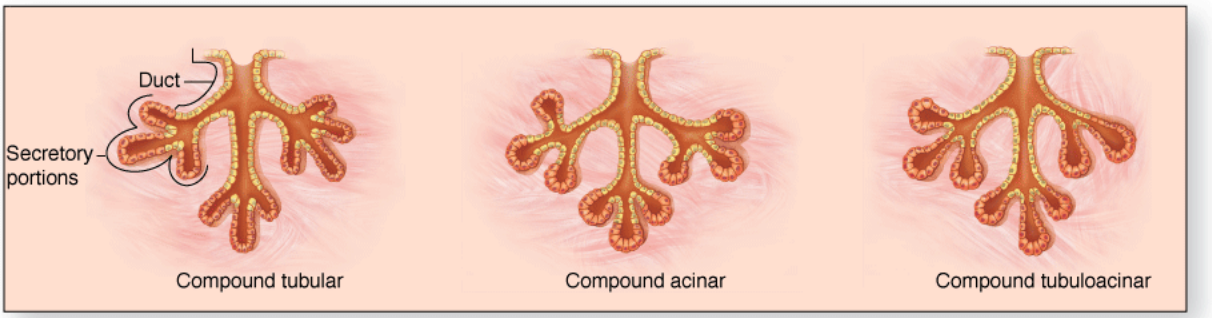
Exocrine glands have a **secretory portion,** which contains the cells specialized for secretion, and **ducts,** which transport the secretion out of the gland. The morphology of these components allows the glands to be classified according to the scheme shown in Figure 4–20 and summarized as follows:

- Ducts can be **simple** (unbranched) or **compound** (with two or more branches).
- Secretory portions can be **tubular** (either short or long and **coiled**) or **acinar** (round or globular).
- Either type of secretory portion may be **branched**.
- Compound glands can have tubular, acinar, or tubuloacinar secretory portions.

Figure 4–20.



a Simple glands



b Compound glands

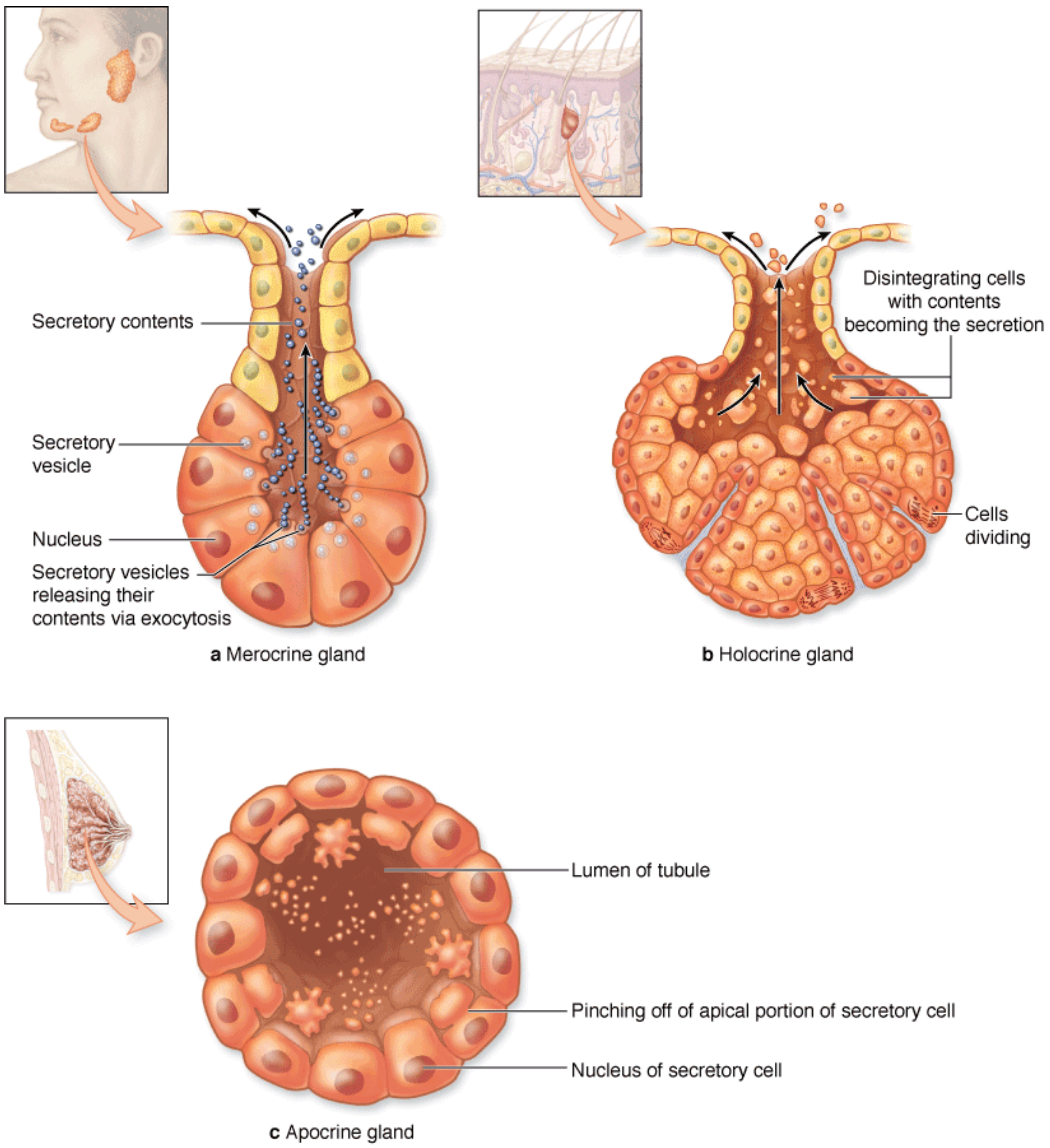
Structural classes of exocrine glands.

(a): Simple glands have unbranched ducts, although the ducts may be short or long and coiled. The secretory portions attached to these ducts may themselves be branched. The secretory portions are either **tubular**, if more or less cylindrical in shape, or **acinar**, if bulbous or saclike. **(b):** If the ducts branch to serve multiple secretory units, the gland is **compound**. On compound glands, the secretory units may be all tubular, all acinar, or a combination of the two shapes.

Exocrine glands are also classified functionally according to the way the secretory products leave the cell (Figure 4–21):

- **Merocrine secretion** (sometimes called eccrine) involves typical exocytosis of proteins or glycoproteins. This is the most common mode of secretion.
- **Holocrinesecretion** involves the cell filling with secretory product and then the whole cell being disrupted and shed. This is best seen in the sebaceous glands of skin (Figure 4–22).
- In an intermediate type, **apocrinesecretion**, the secretory product is typically a large lipid droplet and is discharged together with some of the apical cytoplasm and plasmalemma (Figure 4–23).

Figure 4–21.

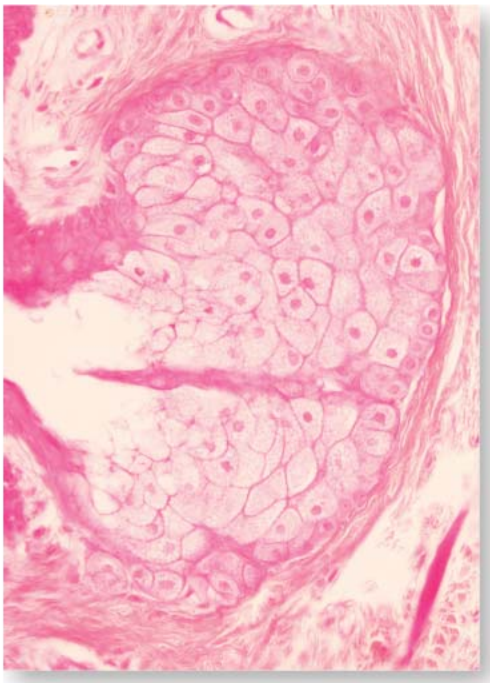


Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition*: http://www.accessmedicine.com

Functional classification of exocrine glands.

Different cellular secretion processes are used in exocrine glands, depending on what substance is being secreted. **(a):** Merocrine glands secrete products, usually containing proteins, by means of exocytosis at the apical end of the secretory cells. Most exocrine glands are merocrine. **(b):** Holocrine gland secretion is produced by the disintegration of the secretory cells themselves as they complete differentiation which involves becoming filled with product. Sebaceous glands of hair follicles are the best examples of holocrine glands. **(c):** Apocrine gland secretion involves loss of a large membrane-enclosed portion of apical cytoplasm, usually containing one or more lipid droplets. This apical portion of the cell may subsequently break down to release its contents during passage into the duct. Apocrine secretion, along with merocrine secretion, is seen in mammary glands.

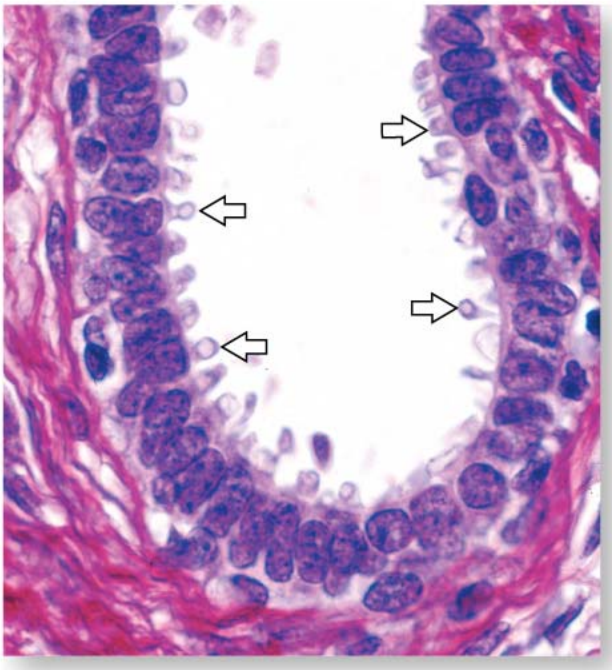
Figure 4–22.



Holocrine secretion in a sebaceous gland.

In holocrine secretion, best seen in the sebaceous gland adjacent to hair follicles, entire cells fill with a product and are released during secretion. Undifferentiated cells deep and peripheral in the gland fill with lipid-rich granules and become metabolically inactive as they mature and move upward and toward the gland's center. When terminally differentiated, the cells separate and quickly disintegrate to form the secretion which serves to protect and lubricate adjacent skin and hair. Sebaceous glands lack myoepithelial cells; cell proliferation inside a dense, inelastic connective tissue capsule continuously forces product into the duct. X200. H&E.

Figure 4–23.

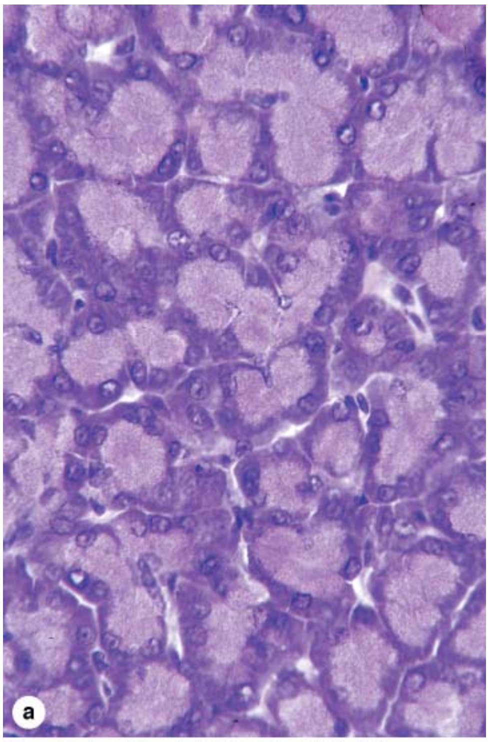


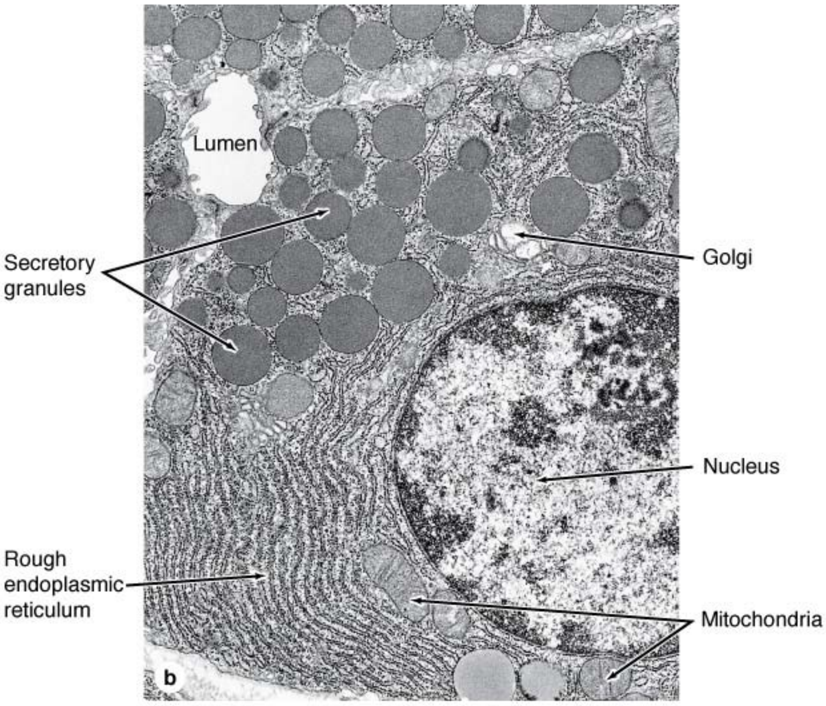
Apocrine secretion in the mammary gland.

The secreting portions of a mammary gland demonstrate apocrine secretion and are characterized by the discharge of the secretion product with a pinched off portion of the apical cytoplasm (arrows). The released portion of cell contains lipid droplet(s). Merocrine secretion also occurs from the same and other cells of the secretory units. X400. PSH.

Exocrine glands with merocrine secretion can be further categorized as either **serous** or **mucous** according to the nature of the proteins or glycoproteins secreted and the resulting staining properties of the secretory cells. The acinar cells of the pancreas and parotid salivary glands are examples of the serous type which secrete **digestive enzymes**. The basal ends of serous cells have well-developed RER and Golgi complexes and the cells are filled apically with secretory granules in different stages of maturation (Figure 4–24). Serous cells therefore stain intensely with any basophilic or acidophilic stain.

Figure 4–24.



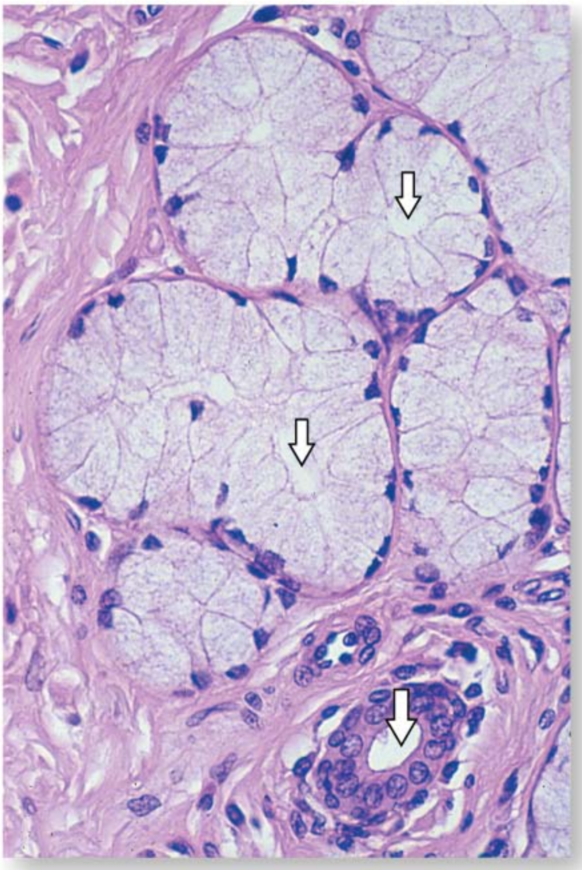


Serous cells.

Serous acinar cells of the exocrine pancreas are arranged in small acini of 5-10 cells with a very small central lumen. Each acinar cell is roughly pyramid-shaped, with its apex at the lumen. **(a):** As seen by light microscopy, the apical ends are eosinophilic due to the abundant immature and mature secretory granules present there. The cells' basal ends contain the large rounded nuclei and an abundance of rough ER, making the cells highly basophilic basally. X200. PT. **(b):** A portion of one acinar cell is shown ultrastructurally, indicating the abundant RER, Golgi complexes, and secretory granules and the very small size of the acinus lumen. X13,000. Secretion here is merocrine and typically the mature zymogen granules, filled with digestive enzymes, remain in the apical cell region until the cell is stimulated to secrete. Other cells secrete constitutively, with small granules undergoing exocytosis as soon as they emerge fully formed from the Golgi apparatus.

Mucous cells, such as goblet cells, while also rich in RER and Golgi complexes are filled apically with secretory granules containing strongly hydrophilic glycoproteins called **mucins.** When mucins are released from the cell, they become hydrated and form **mucus**, a viscous, elastic, protective lubricant material. Mucin-containing granules stain well with the periodic acid-Schiff (PAS) method for glycoproteins (Figure 4–17a), but are not intensely acidophilic like zymogen granules of serous cells (Figure 4–25). Mucous cells of large glands are organized as secretory tubules and in mixed seromucous salivary glands crescent-shaped clumps of serous cells frequently share the ends of the tubules as serous demilunes (Figure 4–26).

Figure 4–25.

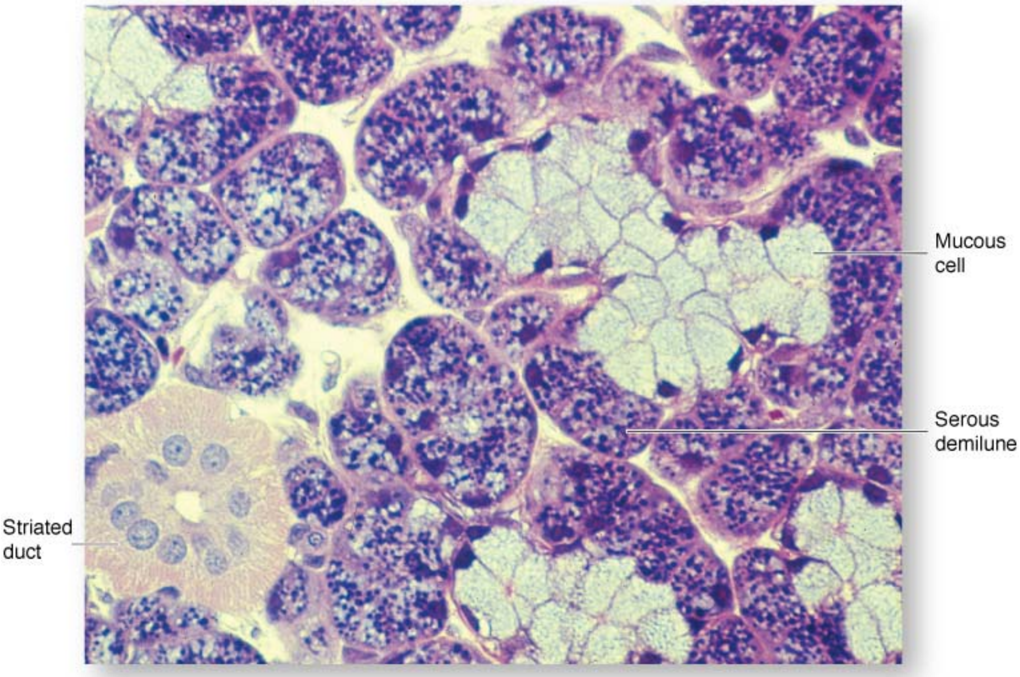


Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition:* http://www.accessmedicine.com

Mucous cells.

Mucous cells are typically larger than serous cells, with more flattened basal nuclei. The apical region and most of the other cytoplasm of each mucous cell is filled with secretory granules containing mucin like that of goblet cells. The basal region contains the RER, nucleus, and a well-developed Golgi apparatus. The RER and Golgi are very rich in enzymes called glycosyltransferases, which attach sugars to polypeptide chains to make glycoproteins. Mucus contains many glycoproteins with important water-binding properties. The lumens (small arrows) of mucous tubules are larger than those of serous acini. The large arrow indicates a secretory duct. X200. PT. Other types of mucous cells are found in the stomach, the various salivary glands, the respiratory tract, and the genital tract. These cells show great variability in both their morphologic features and in the chemical nature of their secretions.

Figure 4–26.



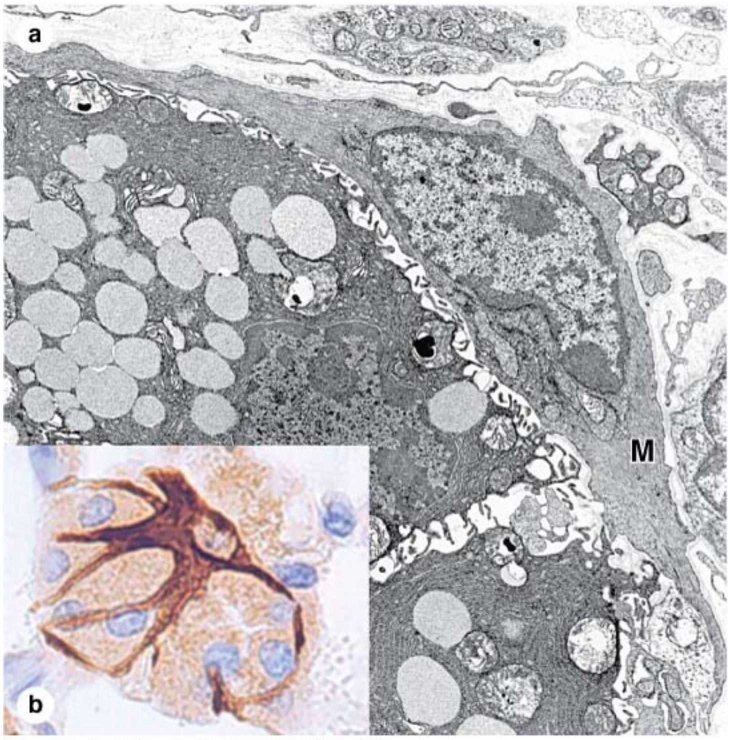
Source: Mescher AL: *Junqueira's Basic Histology: Text and Atlas, 12th Edition:* http://www.accessmedicine.com

Seromucous, compound tubuloacinar gland.

The submandibular salivary glands have both mucous and serous secretory units, typically shaped as acini and tubules respectively. Clumps of serous cells at the ends of some mucous tubules appear as crescent-shaped structures called **serous demilunes.** At the left is seen a **striated duct** whose cells' basal membranes are folded into long folds with many mitochondria, an arrangement specialized for ion transport across the epithelium. X400. PT.

Several exocrine glands (eg, sweat, lachrymal, salivary, and mammary glands) contain stellate or spindle-shaped **myoepithelial cells** located between the basal lamina and the basal pole of secretory or duct cells (Figure 4–27). Long processes of these cells embrace an acinus as an octopus might embrace a rounded boulder. Along ducts they are more longitudinally arranged. Myoepithelial cells are connected to each other and to the epithelial cells by both gap junctions and desmosomes. These cells are specialized for contraction, containing myosin and a large number of actin filaments. Their major function is to contract around the secretory or conducting portion of the gland and thus help propel secretory products into the duct.

Figure 4–27.



Myoepithelial cells.

(a): Portion of a salivary gland acinus shows two secretory cells with secretory granules. A myoepithelial cell (M) embraces the acinus with contractile processes. X20,000. **(b):** A myoepithelial cell immunostained against smooth muscle actin shows its association with an entire acinus. Contraction of the myoepithelial cell compresses the acinus and aids in the expulsion of secretory products into the duct. X200. H&E counterstain.

Endocrine glands are the producers of **hormones**, which are generally polypeptide or lipid-derived factors that are released into the interstitial fluid. Hormones diffuse into the blood for circulation and bind specific receptors on target cells elsewhere in the body, often within other endocrine glands. The receptors may also be on cells very close to the hormone-secreting cells or on the secreting cell itself; in these cases the cellular signaling is termed **paracrine** or **autocrine,** respectively. Hormones can be secreted from single cells that are sparsely distributed or from cells with other major functions, such as certain cardiac muscle cells. In the large endocrine glands the parenchymal cells form strands or cords interspersed between dilated capillaries (eg, the adrenal cortex; see Figure 4–18) or can line a follicle filled with stored secretory product (eg, the thyroid gland; Figure 4–18). Some endocrine glands have cells releasing more than one hormone.

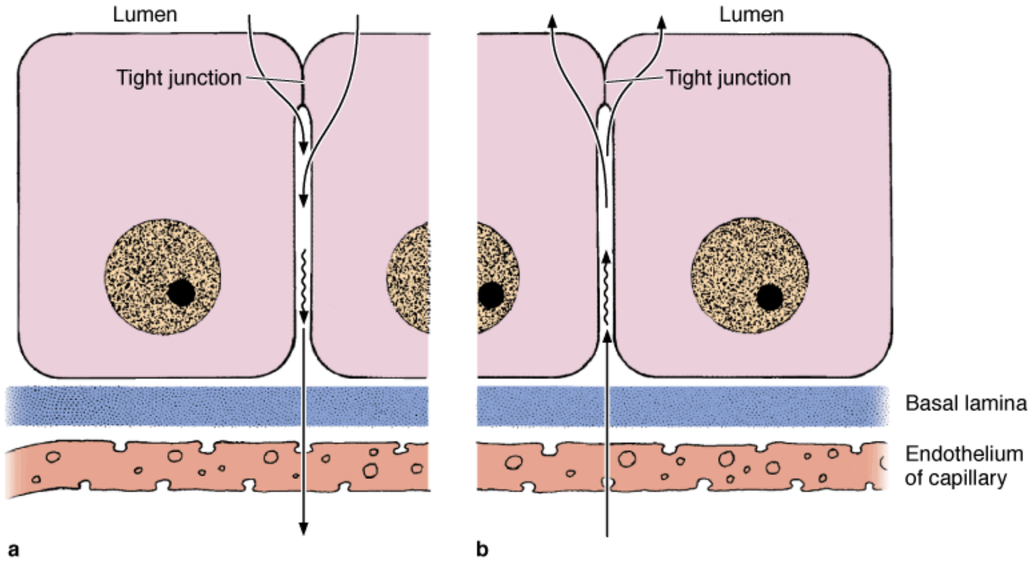
Some organs such as the pancreas have both endocrine and exocrine functions, and in the liver one cell type may function both ways, secreting bile components into a duct system, as well as releasing other products into the bloodstream.

TRANSPORT ACROSS EPITHELIA

As discussed in Chapter 2, all cells have the ability to actively transport certain ions against a concentration and electrical-potential gradient. An important example is the active extrusion of Na^+ by means of Mg^{2+}-activated Na^+/K^+-ATPase (**sodium pump**), by which cells maintain the required low intracellular sodium concentration (5-15 mmol/L vs. ~140 mmol/L in extracellular fluid).

Some epithelial cells actively transfer ions and fluid across the epithelium, from its apex to its base or vice-versa; this is known as **transcellular transport** (Figure 4–28). For transport in either direction, the tight junctions play an important role in the transport process, sealing the apical portions of the epithelium and preventing back-diffusion of materials already transported across the epithelium. A well-studied site of epithelial transport is the proximal renal tubule cell, where the apical surface is freely permeable to Na^+ in the lumen. To maintain electrical and osmotic balance, equimolar amounts of chloride and water follow the Na^+ ion into the cell. The basal surfaces of these cells are elaborately folded and many long invaginations of the basolateral membrane are seen in electron micrographs (Figure 4–29). In addition, there is interdigitation of membrane folds between adjacent cells, all of which increase the surface area for transport. Sodium pumps are localized in both the basal and the lateral plasma membranes and located between the folds are vertically oriented mitochondria that supply the ATP for the active extrusion of Na^+ from the cell basally. Chloride and water again follow passively. In this way, sodium is returned to the circulation and is not lost in massive amounts in the urine.

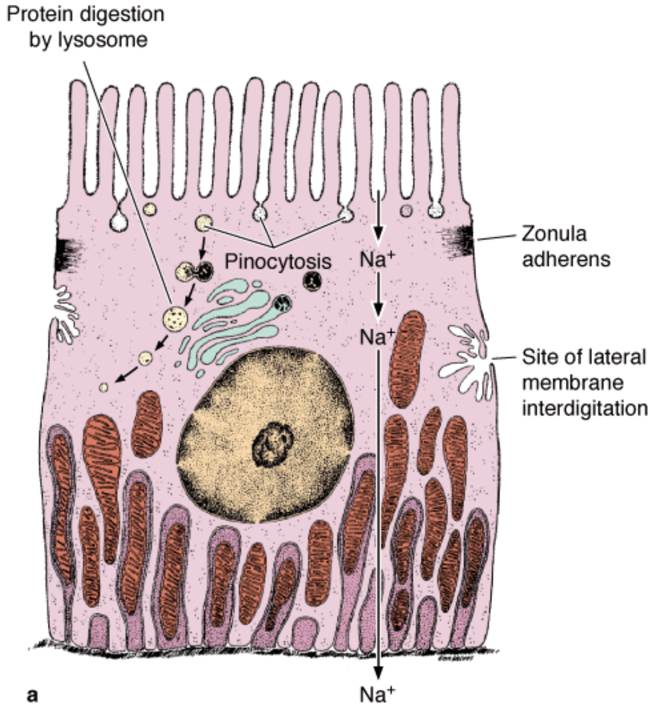
Figure 4–28.

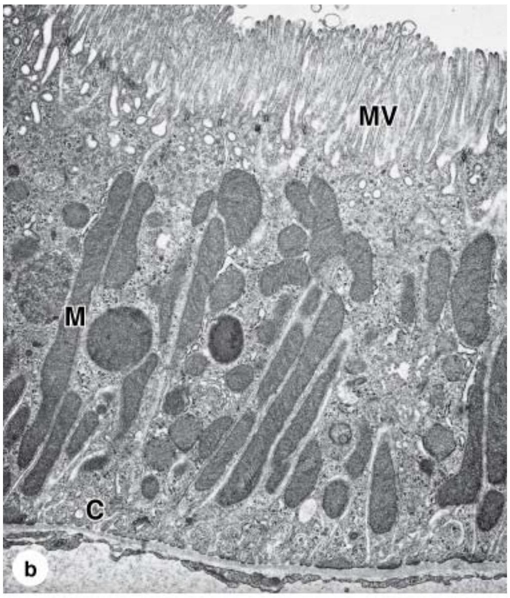


Ion and water absorption and secretion.

Ion and water transport across epithelia can occur in different directions, depending on which tissue is involved. **(a):** The direction of transport is from the lumen to the blood vessel, as in the gallbladder and intestine. This process is called **absorption**, and serves to concentrate bile and obtain water and ions in these organs**.** **(b):** Transport in the opposite direction, as in the choroid plexus, ciliary body, and sweat glands, is called **secretion** and serves to expel water from the interstitial fluid into specialized aqueous fluids in these tissues**.** Whether the epithelia are absorbing or secreting water, the presence of apical occluding junctions is necessary to maintain tight compartmentalization and consequent control over ion distribution.

Figure 4–29.





Absorptive cells.

An ultrastructural diagram and TEM of epithelial cells highly specialized for absorption: cells of proximal convoluted tubule of the kidney. Long invaginations of the basal cell membrane outline regions filled with vertically oriented mitochondria, a typical disposition present in ion-transporting cells. Interdigitations from neighboring cells interlock with those of this cell. Immediately below the microvilli are junctional complexes between individual cells. The basolateral membranes can be discerned in continuity with the junctional complexes. Apically are vesicles that have undergone pinocytosis, soon to fuse with lysosomes, as shown in the upper left portion of the diagram. Sodium ions diffuse passively through the apical membranes of renal epithelial cells and are then actively transported out of the cells by Na^+/K^+ -ATPase located in the basolateral membranes of the cells. Energy for this sodium pump is supplied by the nearby mitochondria. Immediately below the basal lamina is a capillary for removal of the water absorbed across this part of the epithelium. X9600.

Extracellular molecules and fluid are also internalized in the cytoplasm of most cells by pinocytotic vesicles that form abundantly at the plasmalemma. This activity is clearly observed in the simple squamous epithelia that line the blood and lymphatic capillaries (endothelia) or the body cavities (mesothelia). These cells have few organelles other than the abundant pinocytotic vesicles, which cross the thin cells in both directions and secrete their contents on the opposite side by exocytosis. This process, termed **transcytosis**, is not restricted to simple squamous epithelia. Uptake of material at the apical epithelial pole followed by exocytosis at the basolateral surface occurs actively in many simple cuboidal and columnar epithelia and is important in various physiological processes.

RENEWAL OF EPITHELIAL CELLS

Epithelial tissues are relatively labile structures whose cells are renewed continuously by mitotic activity. The renewal rate is variable; it can be fast in tissues such as the intestinal epithelium, which is replaced every week, or slow, as in the large glands. In stratified epithelial tissues, mitosis only occurs within the basal layer in contact with the basal lamina. In some functionally complex epithelia, stem cells have been identified only in restricted niches some distance from the transit amplifying cells and differentiating cells. For example, the epithelium lining the small intestine is derived completely from stem cells found in the simple glands between the intestinal villi. In the epidermis, stem cells are located at a characteristic position along the wall of hair follicles.

MEDICAL APPLICATION

Both benign and malignant tumors can arise from most types of epithelial cells. A **carcinoma** (Gr. *karkinos,* cancer, + *oma,* tumor) is a malignant tumor of epithelial cell origin. Malignant tumors derived from glandular epithelial tissue are usually called **adenocarcinomas** (Gr. *adenos,* gland, + *karkinos*); these are by far the most common tumors in adults. In children up to age 10 years, most tumors develop (in decreasing order) from hematopoietic organs, nerve tissues, connective tissues, and epithelial tissues. This proportion gradually changes, and after age 45 years, more than 90% of all tumors are of epithelial origin.

Carcinomas composed of differentiated cells reflect cell-specific morphologic features and behaviors (eg, the production of keratins, mucins, and hormones). Undifferentiated carcinomas are often difficult to diagnose by morphologic analysis alone. Since these carcinomas usually contain keratins, the detection of keratins by immunocytochemistry often helps to determine the diagnosis and treatment of these tumors.

Epithelia are normally capable of rapid repair and replacement of apoptotic or damaged cells. In some large glands, most notably the liver, mitotic activity is normally rare but is actively renewed following major damage to the organ. When a portion of liver tissue is removed surgically or lost by the acute effects of toxic substances, cells of undamaged regions quickly begin active proliferation and normal functional mass of liver tissue is soon regenerated.

MEDICAL APPLICATION

Some epithelial cells are prone to abnormal growth called neoplasia that may lead to cancers. Neoplastic growth is reversible and does not always result in cancer.

Under certain abnormal conditions, one type of epithelial tissue may undergo transformation into another type in another reversible process called **metaplasia**, which is illustrated by the following examples.

In heavy cigarette smokers, the ciliated pseudo-stratified epithelium lining the bronchi can be transformed into stratified squamous epithelium.

In individuals with chronic vitamin A deficiency, epithelial tissues of the type found in the bronchi and urinary bladder are gradually replaced by stratified squamous epithelium.

Metaplasia is not restricted to epithelial tissue; it may also occur in connective tissue.