The physical environments of biological communities vary tremendously. For instance, rainfall in terrestrial habitats varies from the hot, dry desert to the hot, wet tropical rain forest (shown here).

16

The Biosphere and the Physical Environment

Organisms are victims of their environments. If it rains or gets very hot, they must find shelter. When it is cold, they must protect themselves from freezing. The physical environment is a major determinant of life and death.

For this reason, the physical environment is important ecologically and evolutionarily. Some environments, like the desert, may simply be too hot and dry for many plants and animals to survive there. Therefore those species will never be found in a desert climate. Many organisms that can survive in the harsh desert climate have adaptations that conserve water, permitting them to flourish in the extreme dryness of the desert.

Extreme environments are not randomly distributed across the Earth. Global patterns of air movement and ocean currents contribute to their creation. In the discussion of "Global Climates", which begins with Module 16.1, we will see how climates are a natural product of such global patterns.

Global forces are not the only determinants of climates. Local geography may also influence climate. Even living organisms may influence the temperature, moisture, or light intensity experienced by other plants and animals, as we will see in the topic "Local Climates," beginning with Module 16.6.

The biological communities that are found in different physical environments vary dramatically in their species composition and biological characteristics. In "The Ecology and Evolution of Biomes," which begins with Module 16.9, we review some of the major biomes on Earth.

Of course, the single species that has had the greatest recent impact on the environment is our own, *Homo sapiens*. Humans often have adverse effects on the survival of plants and animals. Many environmental changes caused by humans happen so fast that the affected populations may not be able to adapt to these changes before they go extinct. We will review some of the more disastrous environmental changes caused by humans in a discussion of "Global Change," beginning with Module 16.13. ❖

Global Climates

16.1 Global climates are not static, but show major cycles every 100,000 years

Anyone who is considering two job offers—one in San Diego, California, and the other in Fairbanks, Alaska—will think about the great climate differences between the two locations. Fairbanks has a seasonal climate with very cold, long winters; San Diego has very little seasonal variation in temperature, with increased rainfall in the winter being the major seasonal distinction.

Weather and Climates The climates of Fairbanks and San Diego reflect the weather that has been experienced in these locations over long periods of time. **Climate** is defined as the long-term average weather of a particular locality. On any given day, the **weather** may deviate from long-term averages, sometimes by a lot. We typically cannot predict weather accurately more than 3–5 days in advance.

Does Climate Change? The question whether climate can change is very relevant to evolution and ecology, given the pressure that natural selection exerts on organisms to adapt to their environment. Because climate is the long-term average weather of a particular locality, departures from the average that last just a few years are not considered a change in climate. However, there is evidence of long-term changes in temperature that are associated with climate changes. Figures 16.1A through 16.1E document cycles in global temperature changes, each cycle lasting about 100,000 years. Although the average temperature changes by no more than 6°C, these cycles mark major global changes. During the coolest periods, there were large-scale advances of glaciers southward. **Glaciers** are ice sheets that may have been more than 1 km deep. During these glaciation events, the average surface temperature of the Earth was 10°C. Between glaciation events, the average temperature rises to 15°C. Glaciation events have occurred about every 100,000 years over the last 700,000 years.

We see that over the last 90 years (Figure 16.1D), there has been a gradual warming trend. Because this change is well within the limits of Earth's historical variation in temperature, it is unclear if this marks a natural cycle or is perhaps due to human influence. We will consider this issue in more detail later, in Module 16.5.

Factors That Affect Climate Many factors influence climate. Some factors are global in nature and lead to predictable patterns. We know that the *distance from the equator* is one way to predict climate. Because the equator gets the

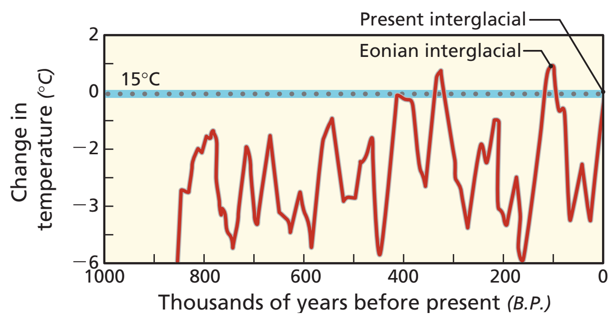


FIGURE 16.1A Long-Term Global Temperature Change over the Past Million Years

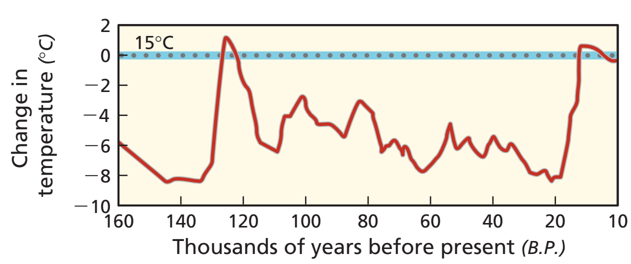


FIGURE 16.1B Long-Term Global Temperature Change over the Past 160,000 Years

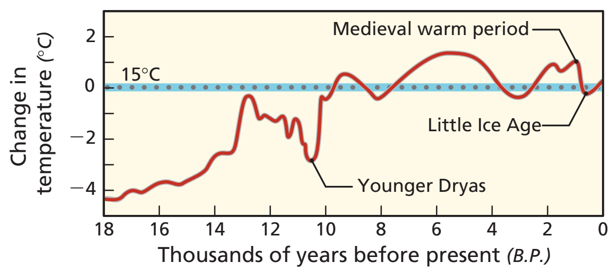


FIGURE 16.1C Long-Term Global Temperature Change over the Past 18,000 Years

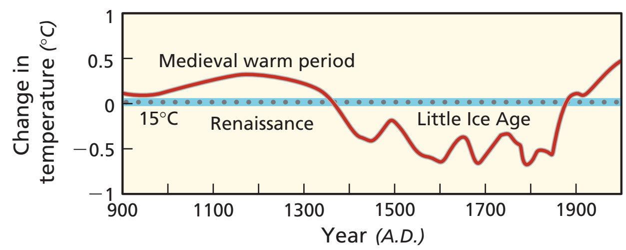


FIGURE 16.1D Long-Term Global Temperature Change over the Past 1000 Years

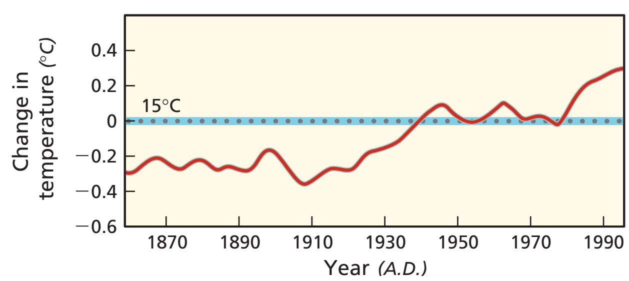


FIGURE 16.1E Long-Term Global Temperature Change over the Past 120 years

most direct energy from the sun, the *temperature* there is typically very warm. As we move to localities north and south of the equator, the average weather should be cooler. However, as we will see in Module 16.2, other global patterns appear as one moves north and south of the equator, such as the air currents that produce desert and rain-forest ecosystems.

Besides temperature, another factor that varies predictably with latitude is **seasonality**, or variation in weather according to the seasons. Seasonality is related to the tilt of the Earth's axis relative to the sun. Thus, as we move north and south of the equator, we also expect to encounter habitats that vary over a yearly cycle. Organisms must not only be able to tolerate the average environment, but they must be able to cope with the extremes. We discuss the basis of seasonality in Module 16.3. Local climate may also depend on conditions other than those that vary with the distance from the equator. For instance, Seattle, Washington, is farther north than Bangor, Maine. Yet Seattle has fairly mild winters in which snowfall is unusual, while in Bangor snowfall is quite common. Clearly, factors other than latitude affect climate (Figure 16.1F). Some of these other factors include proximity to large bodies of water and the prevailing air and ocean currents. We consider these factors in Module 16.4.

Global Climates Affect Ecosystem Composition

By understanding the forces that give rise to these global climate patterns, we start to understand the factors that affect the biological communities that are found in different regions of the world. In Module 16.2, for example, we review global patterns of air flow that are responsible for the hot, moist conditions near the equator and the dry climates found just north and south of the equator. As we will see, many of the great deserts of the Earth are created by the same airflow patterns responsible for the rain forests. These climates largely determine the types of biological communities that are found there.

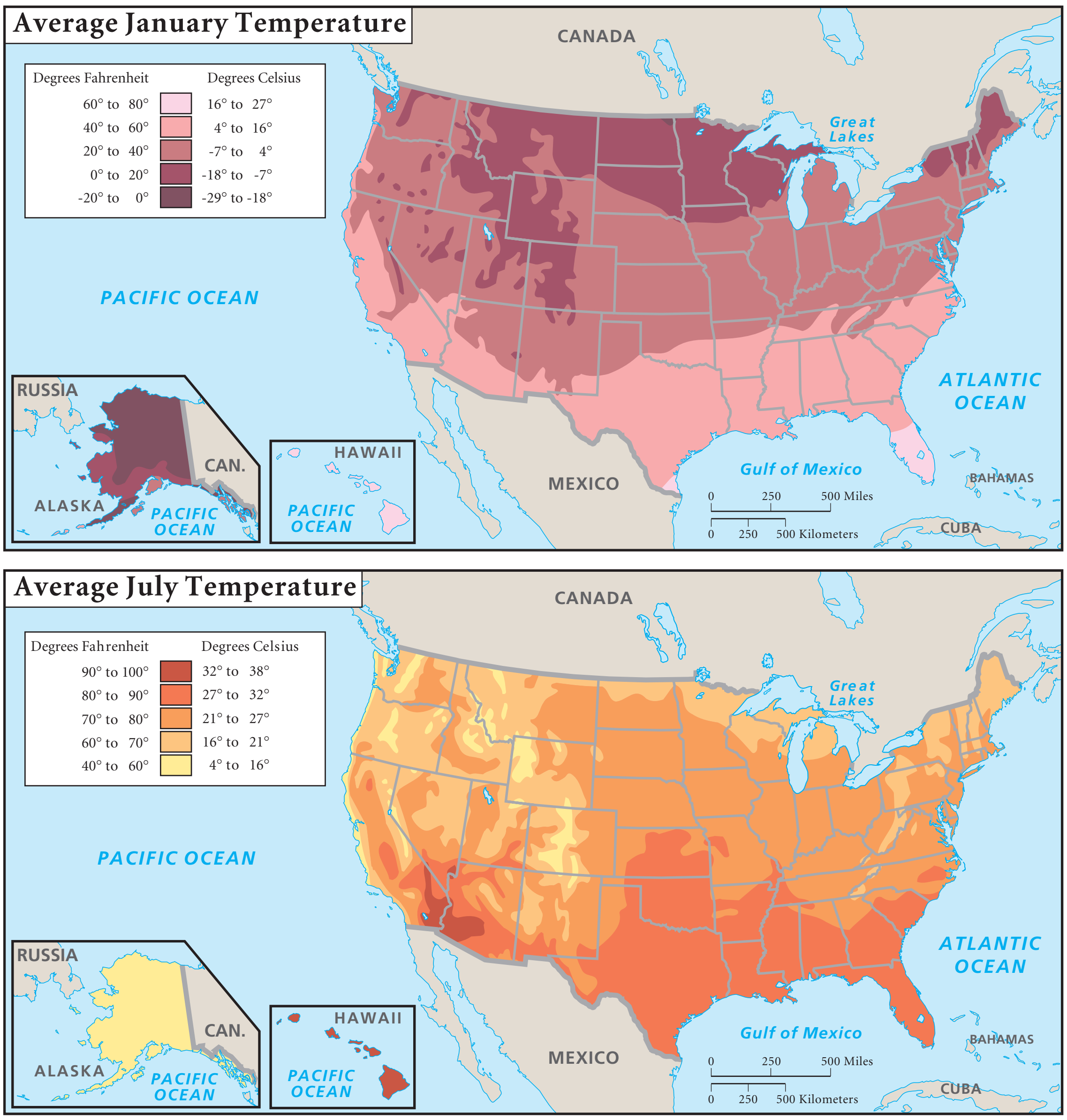


FIGURE 16.1F Average Temperature Profile of the United States

16.2 The sun's energy and air currents are responsible for rain forests and deserts

Life on Earth depends on the sun's energy. The most important biological use of the sun's energy is photosynthesis. But the Earth's climates are also dependent on the sun's energy. As Figure 16.2A shows, about 50 percent of the incoming energy from the sun actually hits the surface of the Earth. Much of the sun's energy is reflected back into space. Some is reflected from the surface, but most of it is reflected higher in the atmosphere of Earth. About 70 percent of the incoming solar energy is radiated out to space as longwave (infrared) radiation. Although a lot of energy is radiated from the surface of the Earth, most of that energy is not lost due to the greenhouse effect, which we discuss later in this chapter.

The Sun's heating of the surface of the Earth causes air to flow in predictable directions that have important consequences for climates near the equator.

The sun's heating of the surface of the Earth causes air to flow in predictable directions that have important consequences for climates near the equator. A cycle of airflow called a **Hadley cell** is responsible for both rain forests and deserts in certain areas. Figure 16.2B diagrams the air circulation in a Hadley cell. As a starting point, note that because it receives the most direct sun rays, the equator gets more energy from the sun than does any other place on Earth. This energy heats up the air near the Earth's surface, and the air then starts rising. Air near the equator is also quite moist: and as the air rises, it cools. Eventually the air becomes sufficiently cool that water condenses and is released as rain. This rainfall keeps the Earth's surface moist near the equator. In fact, the major rain forests of the world are mostly found 10° north and 10° south of the equator. The largest of these rain forests is in the Amazon basin of Brazil. The other major rain forests are in Indonesia, Malaysia, and New Guinea and in the central African region of the Congo.

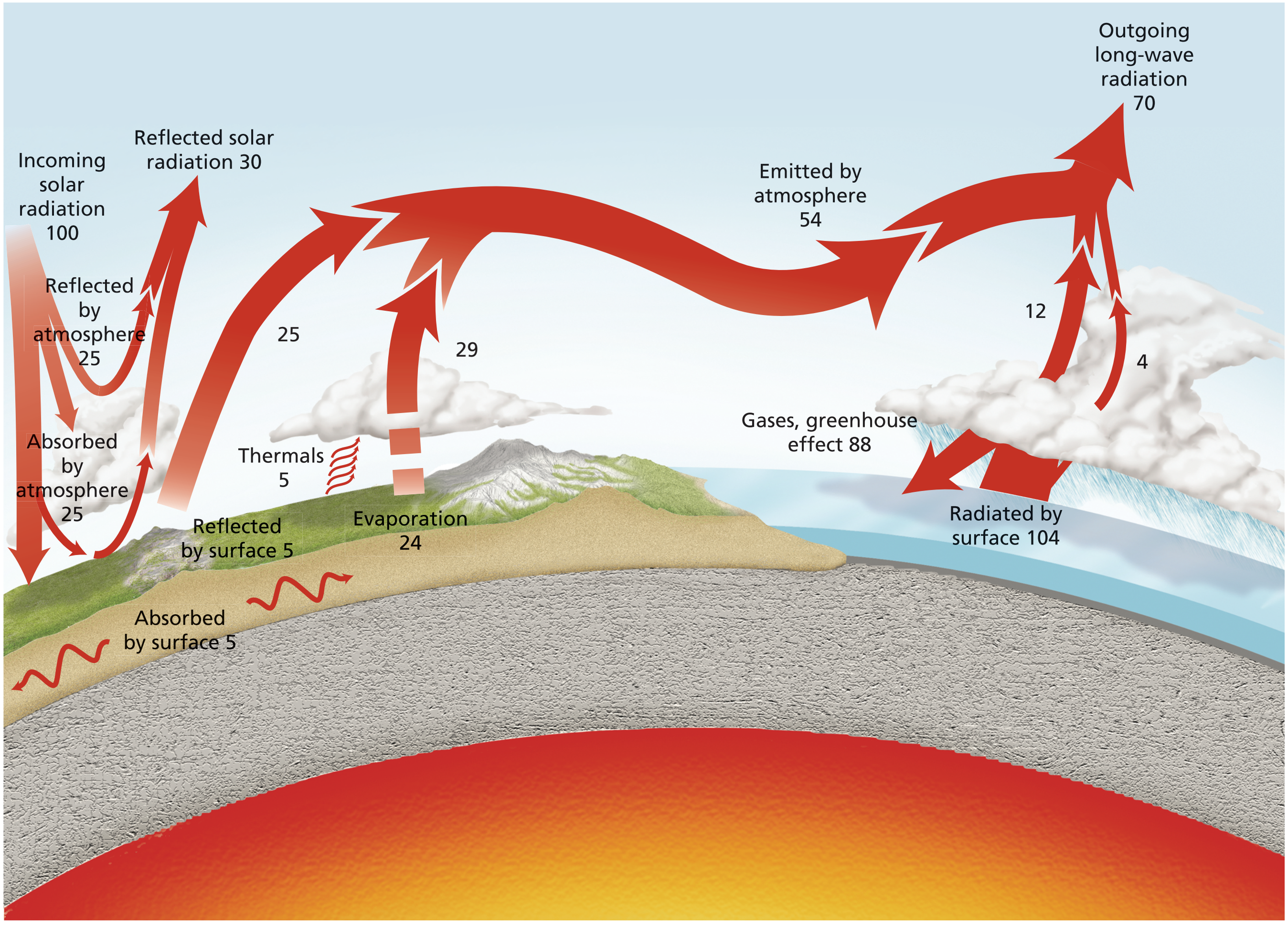


FIGURE 16.2A **Distribution of Incoming and Outgoing Radiation as a Percentage of the Total Incoming Solar Radiation**

After releasing water, the air above the equator continues to rise and cool; but it is now dry. This dry air eventually stops rising and flows north and south from the equator. This air from the equator then starts pushing back toward the Earth's surface. As this air descends, it is compressed and becomes hot, although it is still quite dry. When this hot, dry air hits the Earth's surface, it absorbs water, creating deserts roughly 20–30° north and south of the equator. This pattern of airflow accounts for some of the great deserts of the world, including the Sahara in North Africa, the Kalahari and Namib in South Africa, the Great Victoria desert in Australia, the Great Indian desert in India, and the Atacama desert in South America. Plants and animals with very specialized adaptations to extreme aridity make up these desert communities.

These airflows tend to result in high air pressure near 20–30° north and south of the equator, and low pressure at the equator. Air moves from high-pressure areas to low-pressure areas. Thus the hot, dry air at the desert moves back toward the equator, picking up moisture along the way and completing the cycle of airflow in a Hadley cell.

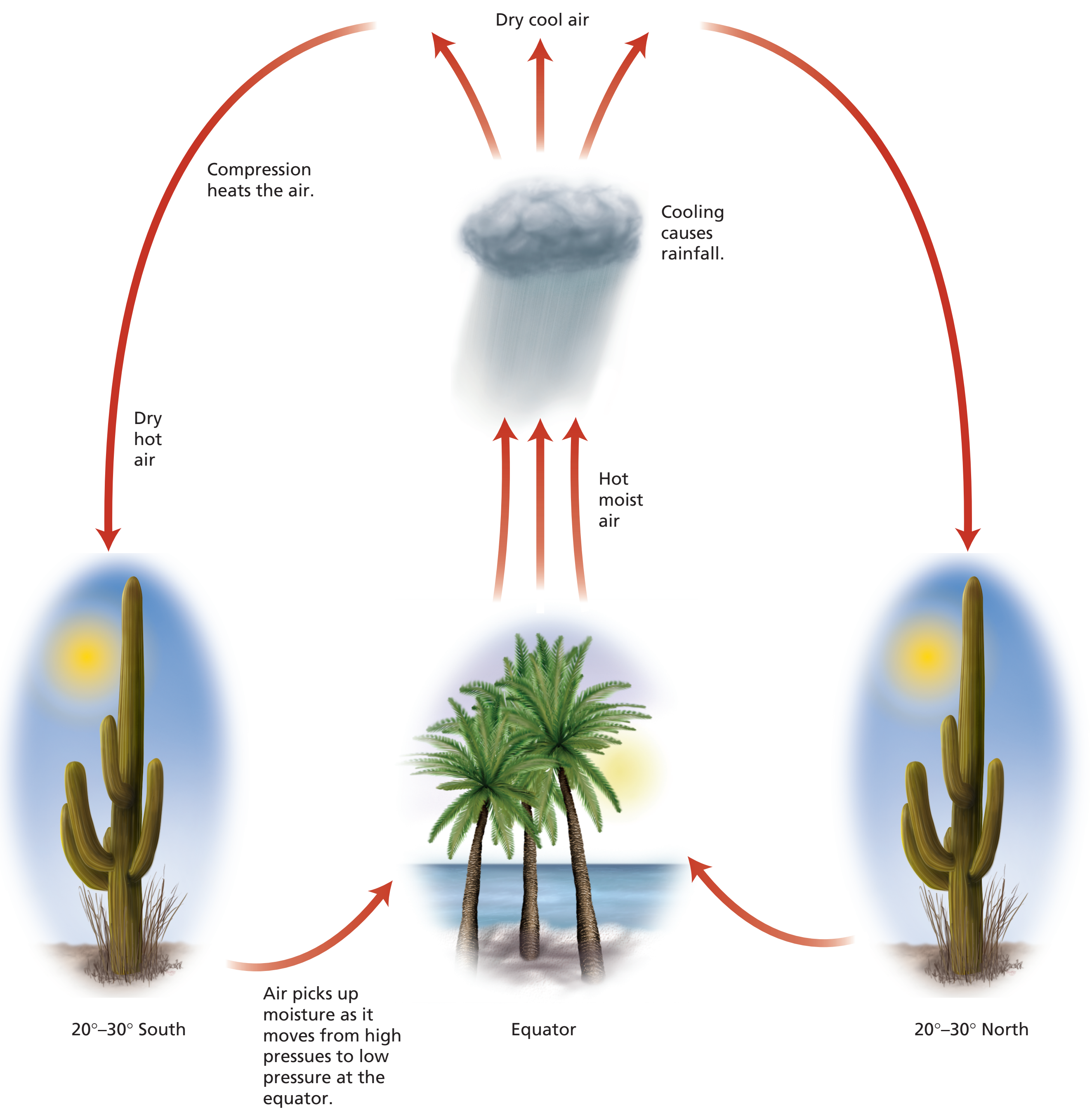


FIGURE 16.2B Air Circulation in a Hadley Cell

16.3 The tilt of the Earth on its axis results in seasonal cycles in temperature and daylight

The air currents produced in Hadley cells create global climate patterns that persist all year long. Other global patterns are not only persistent and dramatic, but seasonal. The degree of seasonality is related roughly to how far from the equator you are. The seasons experienced by any locality also depend on whether it is north or south of the equator. In Figure 16.3A we show how the Earth's tilt affects the seasons in the Northern Hemisphere. Places south of the equator will experience the opposite set of seasons shown in this figure. For example, while it is winter in the Northern Hemisphere, it will be summer in the Southern Hemisphere.

The energy delivered by the sun to the surface of the Earth can be attenuated, for two reasons. First, because the Earth's atmosphere absorbs energy, light passing through more atmosphere will have less energy when it strikes the Earth's surface than will light passing through less atmosphere. In the spring and fall, for instance, sunlight passes through more of the Earth's atmosphere on its way to the poles than when it hits the equator (see Figure 16.3A).

Second, the energy per unit of area will be greater when light hits the Earth's surface directly, compared with when light hits the Earth's surface at an angle. To demonstrate this point to yourself, take a flashlight and shine it directly on a wall about six inches from the flashlight. Then tilt the flashlight up toward the ceiling, so the light hits the wall at a severe angle. Although the light covers a greater area, it is not as bright as it was when you pointed it directly at the wall.

Because the Earth tilts on its axis, the portion of the Earth that receives the direct rays of the sun varies over a yearly cycle. In the fall and spring, the equator receives the direct rays. These direct rays also pass through less atmosphere, and thus deliver more energy to the Earth's surface (see Figure 16.3A). During the summer months, the point on the Earth that receives the direct rays moves north of the equator, resulting in increased temperatures in the Northern Hemisphere along with longer days. During the winter months, the Northern Hemisphere receives the indirect rays of the sun, like the top part of your wall in the flashlight experiment. Consequently, the Northern Hemisphere cools off and has shorter days.

The Earth's tilt on its axis also affects the length of days. Figure 16.3B shows the distribution of light during the summer in the Northern Hemisphere. Each of the views shown in Figure 16.3B is looking down on either the North or South Pole. As the Earth goes through its daily east-to-west rotation, land in the Northern Hemisphere (top illustration in Figure 16.3B) is shielded from the sun for a much shorter time than land in the Southern Hemisphere (bottom illustration in Figure 16.3B). In fact, areas near the North and South Poles experience 24 hours of light during the summer and 24 hours of darkness during the winter months. These areas are designated as the Arctic and Antarctic circles at 66°30′ for the North and South poles respectively. ❖

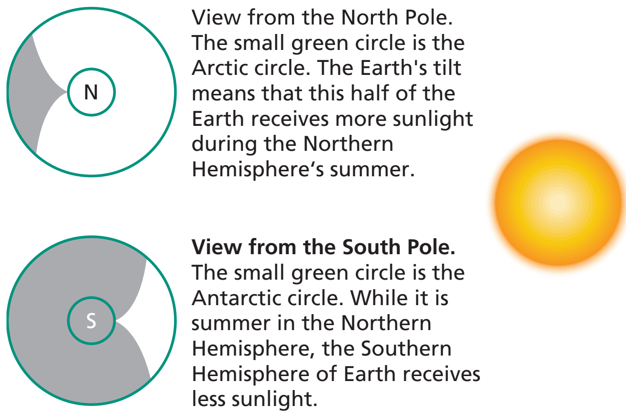


FIGURE 16.3B During summer, days are longer.

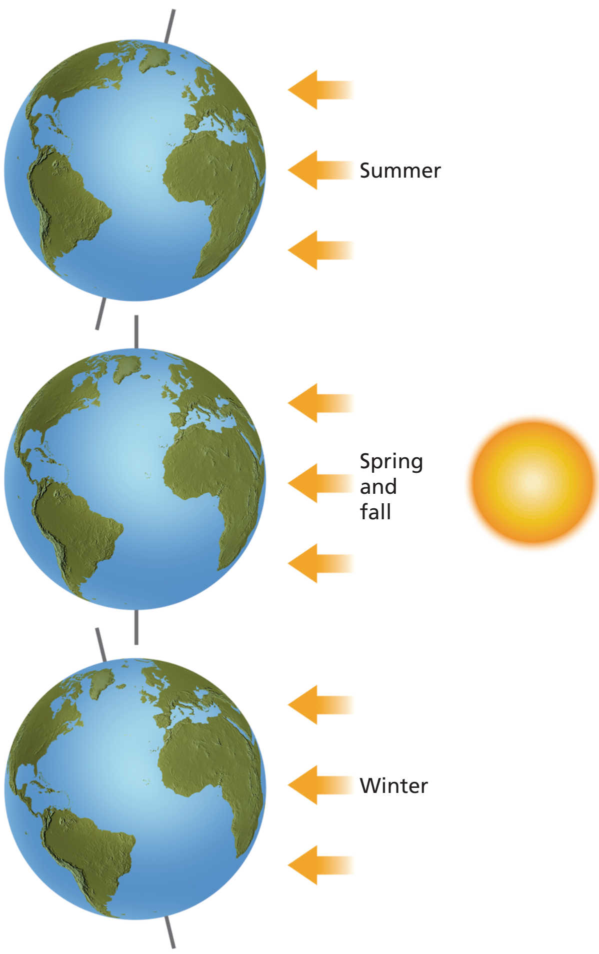


FIGURE 16.3A The Earth's tilt on its axis results in seasons. This figure shows the seasons in the Northern Hemisphere.

16.4 The ocean currents modify land climates

Local climates are affected not only by air temperature, but by the temperature of nearby bodies of water. The critical difference between air and water is the very large heat capacity of water compared with air. It takes 1 calorie of energy to raise 1 mL of water 1°C; it takes only 10^{-4} calories to heat a similar volume of air. As a result, air temperatures fluctuate more than water temperatures. In addition, when the land and air near an ocean are at a different temperature, the ocean can exchange heat with them, causing the air and nearby land either to warm up or cool down, depending on the temperature differences.

Directed flows of water in the oceans are called **currents** or **gyres**. These currents are caused by several factors, including winds that move the surface waters and the Coriolis forces that result from the Earth's rotation on its axis (see Module 11.4). An important source of cold-water currents is the Antarctic gyre (Figure 16.4A) that flows in a clockwise fashion around the South Pole. This current gives rise to the cold Peru current in the Pacific Ocean and the Westwind Drift in the Indian Ocean (Figure 16.4B).

Two important warm currents are the Gulf Stream in the North Atlantic and the Japan current in the North Pacific. Both of these currents are warmed in the southwest portion of their cycles, and they are responsible for warming landmasses in the northeast portion of their cycle. The Japan current warms the west coast of Canada and the United States, while the Gulf Stream provides significant warmth to Northern Europe and Iceland. It is estimated that in the depth of winter, Iceland may receive half of its heat energy from the Gulf Stream.

Another type of current is created by a process called **upwelling** (Figure 16.4C). Offshore winds cause warm surface waters to move away from the land. The water is then replaced by cold, nutrient-rich water that rises from the depths. This process not only cools off the surface waters near the land but also leads to increased productivity of plankton and fish populations. Upwelling is found, for example, off the west coast of Mexico and the coast of Peru. ❖

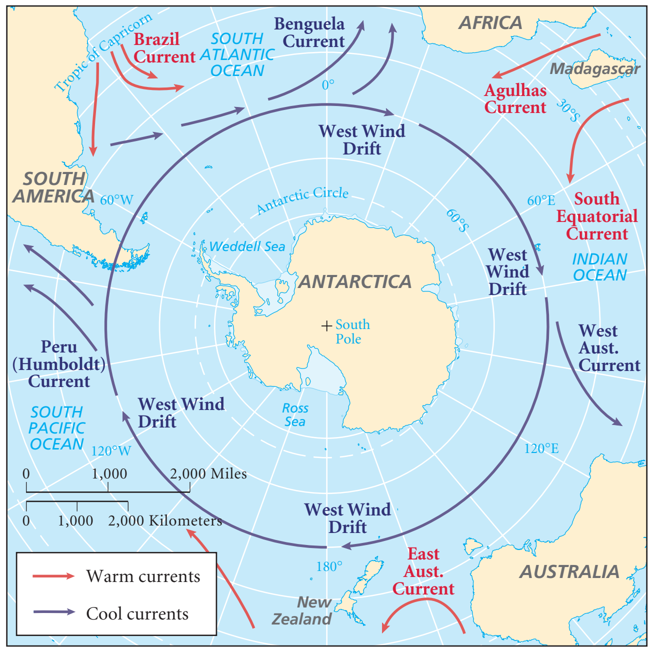


FIGURE 16.4A The Antarctic Gyre

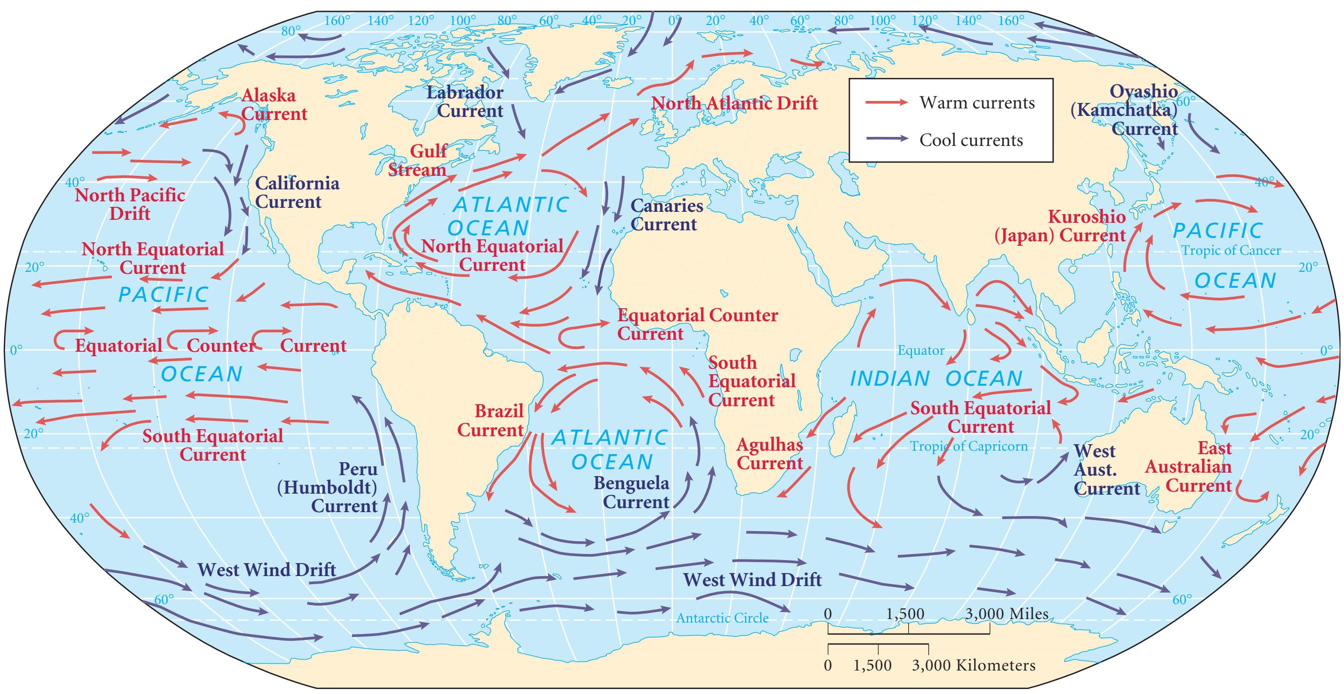


FIGURE 16.4B Ocean Currents

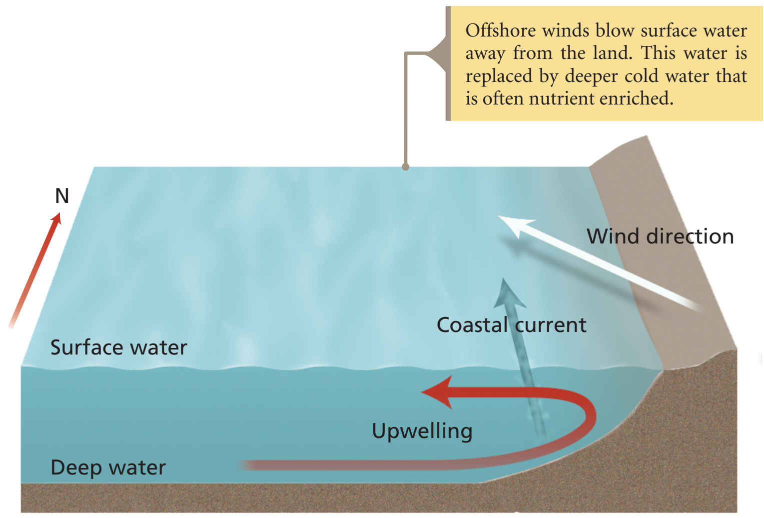


FIGURE 16.4C Upwelling in the Southern Hemisphere

16.5 Atmospheric CO_2 and water vapor trap much of the sun's energy by a process called the greenhouse effect

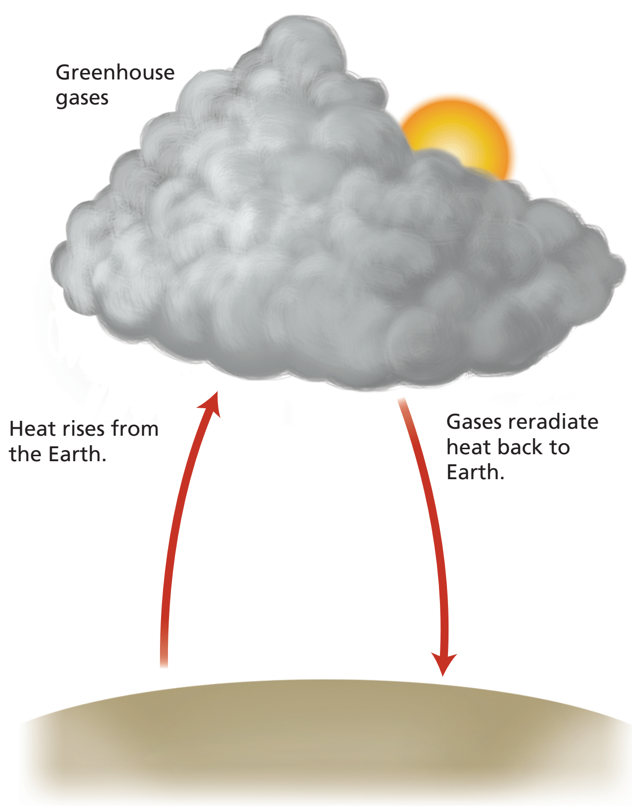
We saw in Module 16.2 that only some of the sun's energy strikes the surface of the Earth, and that the Earth also radiates infrared radiation (heat) back to the atmosphere. This energy may then be absorbed by atmospheric gases (Figure 16.5A) and radiated back to the Earth's surface, conserving heat. Collectively these conserving atmospheric gases are called **greenhouse gases**. If the Earth had no atmosphere, its average temperature would be −18°C. So the effect of the atmosphere is critical to maintaining the temperatures necessary for life.

So the effect of the atmosphere is critical to maintaining the temperatures necessary for life.

Not all gases play a role in heat capture. The most important greenhouse gas is water vapor. Gases other than water vapor play a fairly small role in capturing heat energy. One of the most important of these gases is carbon dioxide (CO_2). Human activities such as burning fossil fuels and using refrigerants add to the pool of greenhouse gases.

Some of the greenhouse gases contributed by human sources are listed in Figure 16.5A. Chlorofluorocarbons (CFCs) have been used as propellants in spray cans and as refrigerants. Nitrous oxide (N_2O) is produced by the combustion of fossil fuels and the application of fertilizers. Carbon dioxide, produced by burning fossil fuels, has been steadily increasing in the atmosphere for the last 50 years or more. Methane (CH_4) is produced from human activities like raising cattle and burning fuels.

Will the human introduction of greenhouse gases inevitably cause an increase in world temperatures? Many scientists think so global temperatures have already begun to rise and the only uncertainty is how much more they will increase. It is clear that there is a close correlation in historical data between atmospheric CO_2 concentrations and global temperatures (Figure 16.5B). The concern is sufficiently great that the world's industrialized countries have attempted to reach agreements on the reduction of greenhouse gases. International agreements are essential, because no country can keep its emissions of greenhouse gases within its own political borders. ❖



Fraction of all heat captured by different greenhouse gases	
Water vapor	85%
Small particles of water	12%
All other gases	3%

Relative contribution to other gases by human sources	
CFC	15-25%
CH_4	12-20%
O_3	8%
N_20	5%
CO_2	50-60%

FIGURE 16.5A The Greenhouse Effect

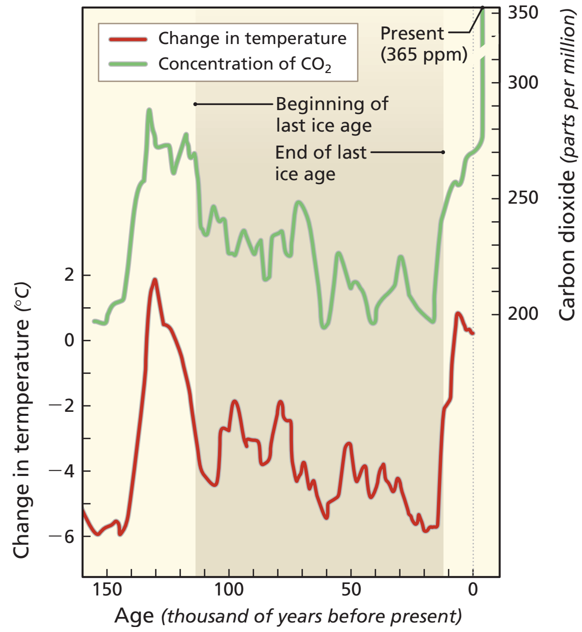


FIGURE 16.5B Historical Values of CO_2 Concentration and Global Temperatures

Local Climates

16.6 Many factors may affect local climates

We have seen that local climate may depend not only on latitude and global patterns of airflow but also on local conditions. These local factors include proximity to large bodies of water, such as an ocean, and the prevailing air and ocean currents. Another important factor influencing local climates is local topography, or the position of local geographic features, such as the location of mountain ranges. In Module 16.7 we will see how mountain ranges can create deserts.

Local Climates Affect Biological Communities

Why should we be interested in local climates? One reason is that they can have a substantial impact on biological communities. For example, there are similar local climates along the West Coast of the United States and the coast of Chile that are called **Mediterranean** because of their similarity to the climates of regions bordering the Mediterranean Sea (Figure 16.6A). Mediterranean climates have mild, wet winters and summer droughts that may be one or two months long. Living in this type of climate requires the ability to withstand these long, dry periods. Consequently, many of the plants found in Mediterranean climates have similar adaptations that prevent water loss, such as small leaves, thickened cuticles (waxy outer coverings), glandular hairs, and sunken stomata (pores). The biological communities found along the coasts of California and Chile are called **chaparral** (Figure 16.6B).

Many of these chaparral plants are evergreens. This is advantageous, because it permits the plants to grow in the winter, when most of the rainfall occurs. The exact timing of the winter rains is variable. By having green leaves all year long, the plants can start growing as soon as the rains begin. These plants also have deep, extensive root systems that extract water during dry periods. The root system of one chaparral plant may extend over a fairly large area, and it can prevent competing plants from becoming established—an important influence on ecological competition within these communities.

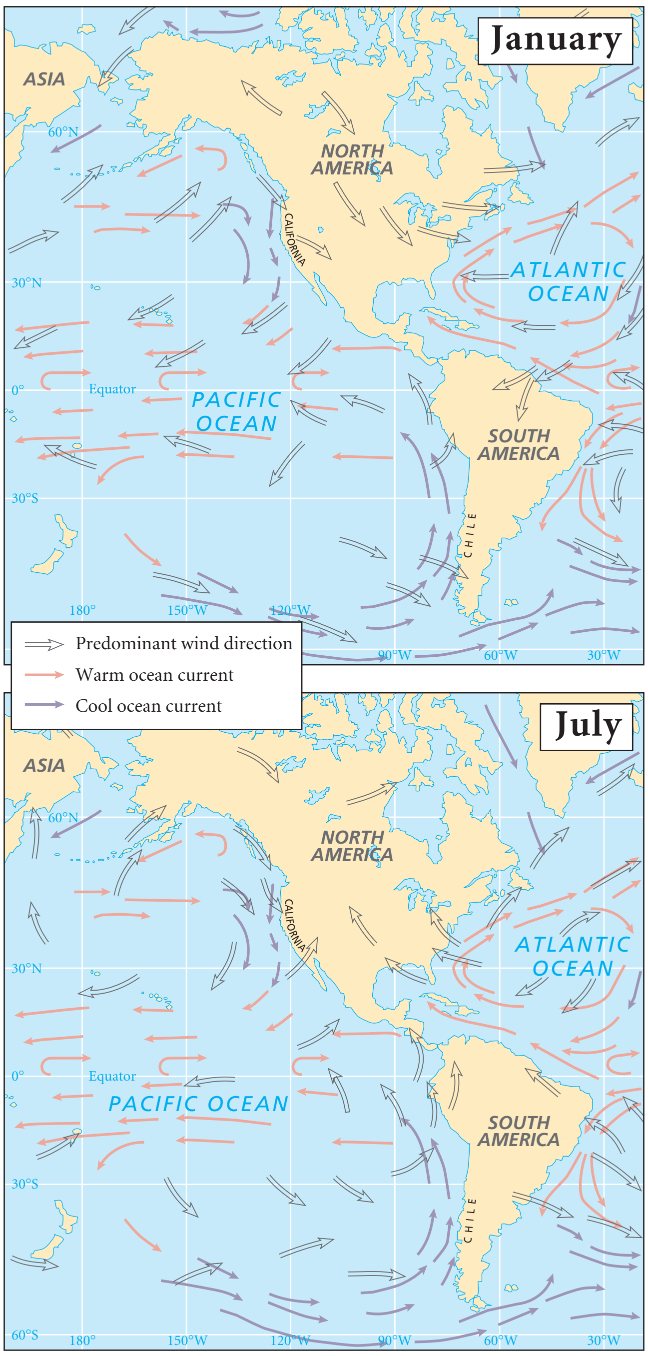


FIGURE 16.6A Ocean currents off the coasts of California and Chile have a substantial moderating effect on local climates and are responsible for the Mediterranean climate in these areas.

These effects on competition can result in a patchy distribution of plants, with some areas bare of plants.

Plants Affect Local Climate For plants, sunlight is an important aspect of climate. It affects photosynthesis, which is fueled by sunlight. But sunlight also affects the plant temperature, and thus all aspects of metabolism, including growth. In many communities, large trees affect the penetration of light to the lower levels of the forest. Thus these trees modify the local climate of lower-level vegetation, with secondary impacts on the animals living in the understory. In Module 16.8, we review these effects of plants on the light and heat profile of a community. ❖

FIGURE 16.6B Plants adapted to the climates of California (top) and Chile (bottom) show many similar morphologies.

16.7 Local topography may affect climate: Rain-shadow deserts

Local topographies can result in predictable effects on climate. One example is found along coastal areas of the world, where there is a predictable flow of moist air from the ocean (Figure 16.7A). If there is also a sizable mountain range near the coast, then this moist air will be forced to climb up the side of the mountains. Air cools as it moves up the side of a mountain, until it reaches the **dew point**, which is the temperature at which the air is saturated with water and condensation begins. Water is less soluble in cold air, just as solutes like sugar and salt are less soluble in cold water than in hot water. The cooling of the air thus results in rainfall and a reduction of the air's water content.

As the now-dry air mass passes over the mountain and begins to go down the other side, it warms and absorbs moisture from the land. For this reason, the side of the mountain that faces away from the prevailing onshore airflow is often dry. The deserts created in this fashion are often referred to as **rain-shadow deserts**, due to close proximity of a mountain range in whose "shadow" they form.

This pattern of climate is observed along the West Coast of the United States in several places. Air flows reliably in a west-to-east direction along the West Coast of the United States. In Oregon, the coastal Cascade mountain range comes into contact with this airflow, and the Great Sandy Desert is found just east of this mountain range (Figure 16.7B). In a similar fashion, in California the Sierra Nevada mountains run north to south and are responsible for several deserts interior to the range, including the Mojave Desert.

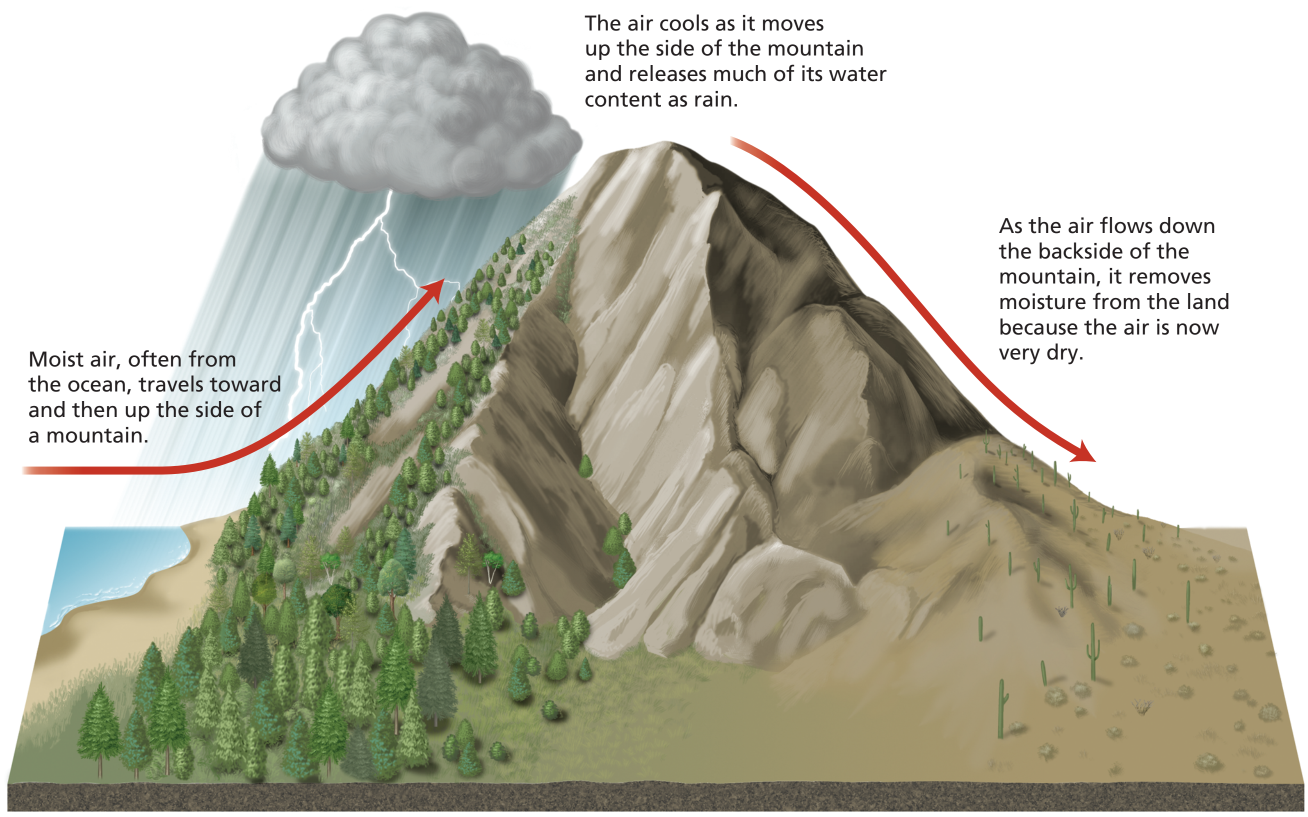


FIGURE 16.7A **Creation of a Rain-Shadow Desert**

FIGURE 16.7B **Rain-Shadow Deserts in the Western United States**

16.8 The biological community may affect the climate

Climatic conditions can vary on a local level over distances as small as a few meters. These small or **microclimatic** effects may be very important for the affected organisms. This is especially true of organisms that are not mobile, such as plants.

Often plants themselves may determine the local microclimates. Figure 16.8A illustrates the changes in light intensity in a yellow-poplar stand over a year. There is a predictable seasonal change in light intensity, thanks to the tilt of the Earth. For instance, light intensities of 400–450 lumens occur only during the summer months. Also in the summer, the leaves on the poplar trees filter out much of the light, so that the light intensity drops to 50 lumens at 10 meters above the ground. The shading effects of the poplar trees mean that small shrubs growing on the forest floor have to be adapted to low light levels. During the winter and spring there are fewer leaves on the trees to filter out light, so that the light intensity at the forest floor is greater during the spring than at any other time.

In addition to the size of the trees, other factors such as leaf shape and tree density affect the local microclimate.

Plants also intercept and dissipate heat in a complicated fashion. In a study of meadow vegetation, roughly 45 percent of the incoming radiation and heat were absorbed by the upper layers of plants, as Figure 16.8B shows. Smaller amounts were absorbed by the understory and finally by the ground (Figure 16.8B).

Heat is lost during the day by two routes, evaporation (V) and convection (L). Evaporation is the major source of heat loss during the day. Heat is lost from the plants or ground when water changes state from liquid to gas. Convection depends on the movement of air over the plants and the ground surface. At night the flow of heat energy is in the opposite direction, with radiant energy (Q) accounting for all losses from plants and the soil (Figure 16.8C).

The profile in Figure 16.8C is over a distance less than 1 meter. These types of gradients in energy absorption will be even greater in forests with large trees. In addition to the size of the trees, other factors such as leaf shape and tree density affect the local microclimate.

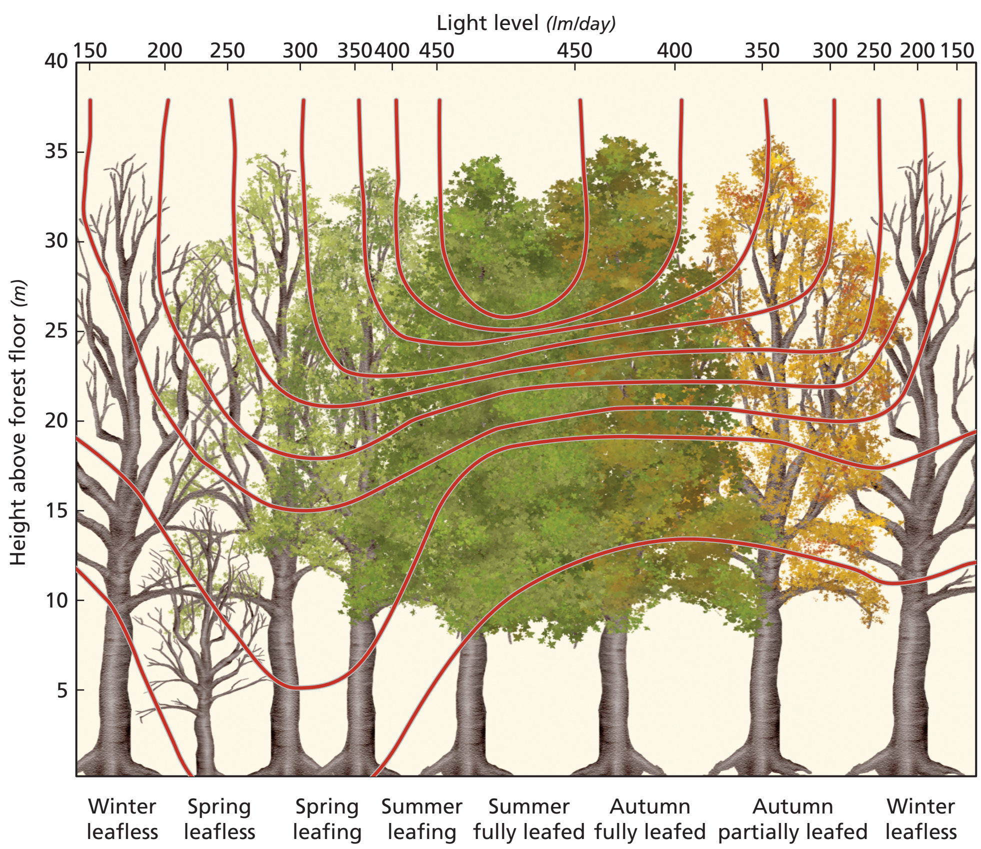


FIGURE 16.8A Light Levels at Different Places and Times in a Forest

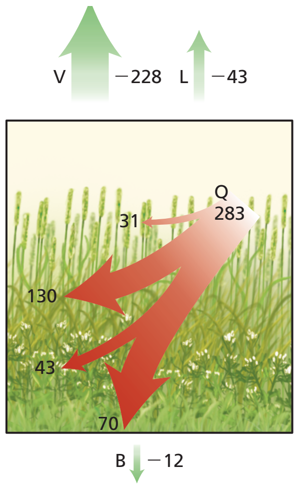


FIGURE 16.8B Energy Transfer in a Meadow (Day) The numbers indicate relative amounts of energy coming into or leaving the meadow. The arrow at the bottom of the figure represents energy transfer to the soil and the arrows leaving the top of the figure represent energy exchange with the atmosphere.

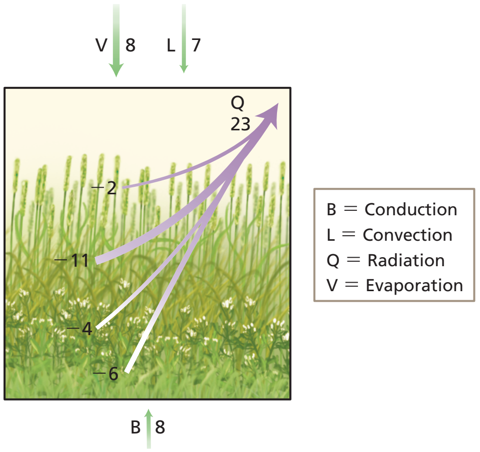


FIGURE 16.8C Energy Transfer in a Meadow (Night) The symbols have the same meaning as in Figure 16.8B.

THE ECOLOGY AND EVOLUTION OF BIOMES

16.9 The ocean biomes cover 70 percent of the Earth's surface

Plant and animal communities change almost continuously across environmental gradients. Some obvious exceptions are where very different environments meet, such as the land and sea. Ecologists have nevertheless sought to simplify the description of communities by noting some very general categories into which most communities can fit. These categories, called **biomes**, are characterized by their plant and animal communities as well as their geographic location. The plants and animals that are typical residents of a biome are expected to have physiological and behavioral adaptations that make them well suited to the physical properties of the biome. In the next three modules, we consider some of the most important biomes and their distinguishing features.

The oceans are the most conspicuous biome on Earth. They cover 70 percent of the Earth's surface. Life originated in the oceans, and today there are many entire phyla (like Echinoderms) whose members are found only in the oceans. Many of the physical properties of oceans have profound effects on the types of communities of plants and animals that can be supported. We review some of these properties now.

Oceans are characterized by saline water, which has a fairly constant concentration of salts—equal to 35 parts per thousand. Of these salts, 86 percent is composed of sodium and chlorine. While the salinity of the oceans is usually very constant, it can vary—especially near the surface. Rainfall causes local reductions in salinity near the surface. Rivers that flow out to the oceans will create local gradients of salinity where the river mouth meets the ocean. These brackish waters are characterized by very different communities than are found in either the ocean or river.

Despite the many dissolved salts in ocean water, it has typically very little nitrogen and phosphorus. As a result, the levels of primary productivity in oceans are quite low. The primary reason for the low levels of nitrogen and phosphorus is that when plants and animals die in the ocean, they fall to the ocean floor to decompose. There is usually very little mixing of the water near the surface of the ocean and the ocean floor, thus plants that must live near the surface are deprived of these nutrients. In temperate regions, currents occasionally bring nutrients to the surface; these are called upwelling currents (Module 16.4). Temperate regions are relatively more productive than, say, tropical oceanic areas. In the tropics, there are layers of water that differ in their temperatures. These layers, called thermoclines, almost never mix in the tropics. Consequently, tropical waters are some of the least productive ocean regions.

Different regions of the ocean are given names to help in discussing them. The surface areas of the oceans are referred to as **pelagic**, while the bottom is called the **benthic** region (Figure 16.9A). The pelagic region is further subdivided into the **neritic**, referring to the regions over the continental shelf, and the **oceanic** for the remaining area. Other regions of the ocean are characterized by their depths. The **photic** zone refers to the region where light can penetrate, which includes about the top 200 meters. However, the region that can support plant growth is much more limited—from the surface to perhaps 30 meters or so, depending on local conditions.

In the open ocean, plants and animals may be found in the surface water in a community referred to as the **plankton**. The plants, called **phytoplankton**, are mostly unicellular plants. Many invertebrates have larval stages that are part of the animal plankton community; they are called **zooplankton**, and they may feed on the phytoplankton. Many other animals then feed on these small animals. In some especially productive areas, large populations of small crustaceans may live in the zooplankton and then serve as food for large animals like whales.

The region where the ocean meets land is referred to as the **intertidal zone**. Intertidal areas are often capable of supporting very productive communities of plants and animals. The unique feature of the intertidal is that areas within it are exposed to the air for varying periods of time (Figure 16.9B). Consequently, the organisms that occupy the intertidal show varying adaptations to desiccation resistance. Those in the highest reaches of the intertidal may be exposed to air and high temperatures for hours at a time, those in the lowest regions are rarely exposed, and then only briefly. ❖

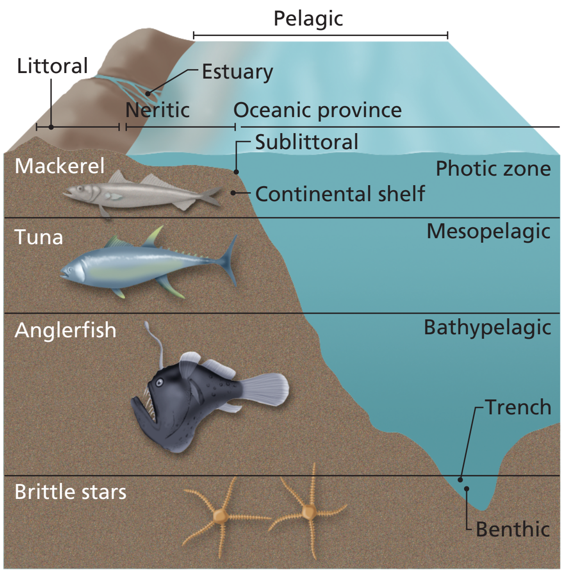
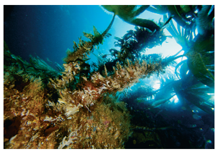


FIGURE 16.9A **Major Regions of the Ocean**

ZONE 1
Uppermost Horizon. Mainly a region of bare rocks, sometimes with green algae (*Enteromorpha* or *Cladophora*). Characteristic rock-shore animals: the pill bug *Ligia*, the barnacle *Balanus glandula*, the snail *Littorina planaxis*, and the limpet *Acmaea digitalis*. On sand the beach hoppers *Orchestia* and *Orchestoidea*.

ZONE 2
High intertidal. Typically with rockweeds (*Pelvetia*), but bare toward upper limits. Rocky shores: *Balanus glandula, Littorina scutulata, Tegula funebralis,* and several species of limpets. *Pachygrapsus* very common under rocks. *Aletes* in the south. The chiton *Nuttallino* and the red barnacle *Tetraclita* in high surf. *Hemigrapsus* on mud flats.

ZONE 3
Middle Intertidal. Many algae. Animals predominant here are rarely taken subtidally. Rocky shores: *Hemigrapsus nudus,* the seastar *Leptasterias,* the hermit *Pagurus hemphilli,* many others. *Ischnochiton* under rocks. In high surf: the snail *Thais emarginata,* the common seastar *Pisaster ochraceus,* the goose or leaf barnacle *Pollicipes,* the California mussel (*Mytilus*), and the black abalone. The chiton *Katharina. Balanus cariosus* in Puget Sound.



ZONE 4
Low intertidal. Laminarians and corallines. Predominant animals also occur subtidally. Rocky shores have a great variety of animals, but not the hosts of individuals per species that charaterize the upper zones. Probably these are animals that have only recently learned to tolerate a slight exposure.

Characteristics of zones

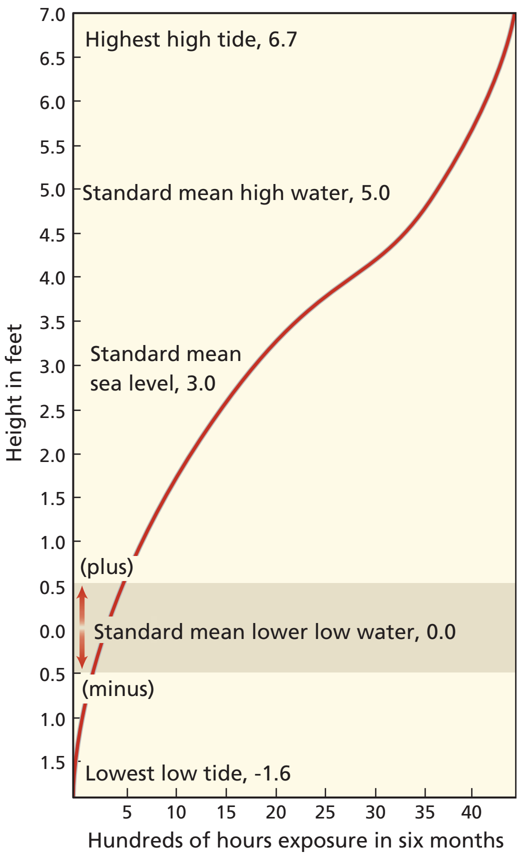


FIGURE 16.9B Intertidal zone experience varying levels of exposure to air.

16.10 The physical properties of water have important consequences for life in freshwater lakes and ponds

Lakes and ponds are inland bodies of freshwater that can vary tremendously in size and biological composition (Figure 16.10A). Their depths may vary from 1 meter to over 2000. Lakes and ponds receive runoff from rainfall that drains off the surrounding land. The characteristics of the local area can then affect the quality of inorganic ions and organic matter that the lakes and ponds receive.

However, three properties of water still determine many of the important physical properties of lakes and ponds: (1) The high specific heat of water means that its temperature will change much more slowly than does air temperature. Diurnal cycles in air temperature will typically have no appreciable effect on the temperature of lakes and ponds. (2) Water is most dense at a temperature of 4°C. (3) Ice floats on water.

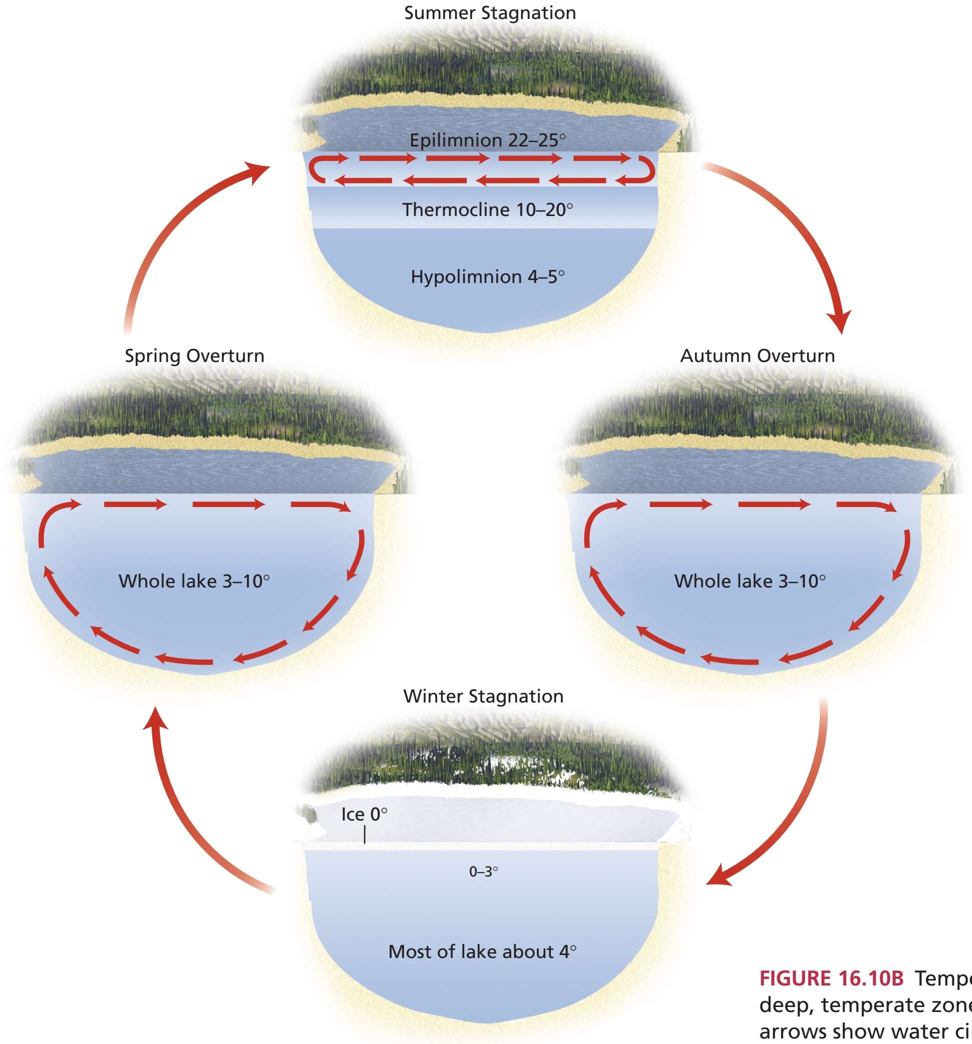
During the summer, the top layer of a lake warms and forms a layer of water, called the **epilimnion**, that mixes very little with the lower layers, or **hypolimnion** (Figure 16.10B). This creates a gradient of temperatures, or **thermocline**, that can be quite dramatic depending on the size of the lake. Phytoplankton and plants that live near the surface will keep the epilimnion well oxygenated. However, because organic matter falls to the bottom of lakes, its decomposition depletes oxygen at the bottom of lakes. These conditions lead to what is called the summer stagnation. By the fall, air temperatures have dropped and solar insolation decreases, causing the surface waters to cool. The cooler, denser water then falls to the lake bottom, and warmer water from below rises to the surface (Figure 16.10B). This creates mixing within the lake, called fall overturn. In climates with freezing weather, water may cool to 4°C, at which point it will fall to the bottom of the lake; as the water gets colder, it will stay above this dense layer. Thus the first water to freeze will be water near the surface of the lake. Once frozen, the ice continues to float on the surface and in fact provides insulation from the very cold air, thus forestalling further freezing. At this point, most of the lake will stay at about 4°C, and there will be little movement of water, leading to the condition called the winter stagnation. If ice were denser than water, it would sink to the bottom and then lakes would continue to freeze from the bottom up. Eventually the entire lake would be frozen and all animal life killed. The fact that ice floats prevents the mass mortality of many animals that overwinter in lakes and ponds.

Many factors may affect the levels of nutrients reaching lakes and ponds. However, human activities like logging, mining, agriculture, and construction can add significant amounts of nitrogen, phosphorus, and organic matter to lakes. This can lead to a process of eutrophication. Lakes and ponds without these extra sources of nutrients are called oligotrophic or low-nutrient lakes.

The presence of high levels of nitrogen and phosphorus will stimulate the growth of plants and algae near the surface of the lakes. As the large biomass of plants dies and falls to the bottom of the lake, the oxygen is depleted by aerobic decomposition to the point where aerobic organisms can no longer live [Figure 16.10C, part (ii)]. Although the biomass of a eutrophic lake is greater due to the high primary productivity, the species diversity typically falls. The accumulation of organic matter on the bottom of the lake makes it shallower and may eventually change it to a bog or swamp.

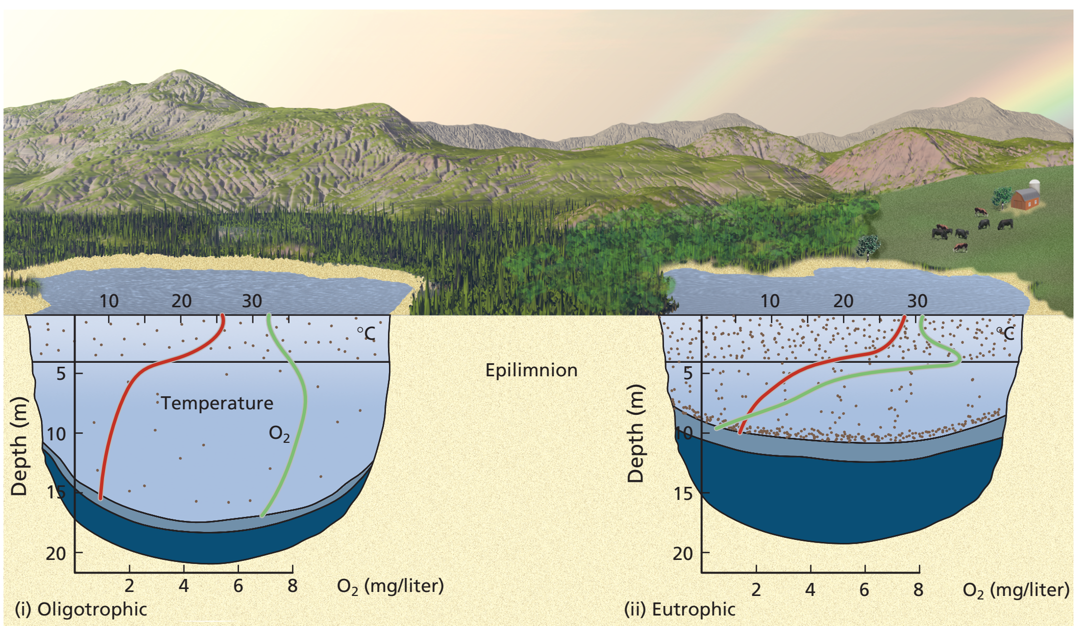
An oligotrophic lake will be deep and have much higher levels of oxygen near the bottom [Figure 16.10C, part (i)]. While the biomass of plants is much lower, the overall species diversity—especially of animals—is much higher in oligotrophic lakes.

FIGURE 16.10A Lakes and ponds come in a variety of sizes and shapes.



(B)

FIGURE 16.10B Temperatures (°C) with depth for a fairly deep, temperate zone lake for four seasons. The small arrows show water circulation caused by wind blowing across the lake.



(C)

FIGURE 16.10C Comparison of Oligotrophic and Eutrophic Lakes

16.11 Adaptations to reduce water loss characterize the plant and animal life found in deserts

Deserts are environmentally stressful biomes that challenge their inhabitants to survive on a daily basis (Figure 16.11A). The hallmark of deserts is low rainfall, or more specifically where potential evapotranspiration is greater than precipitation per year. There is no precise value of rainfall that defines a desert, but rather a continuum, so areas that receive 150–400 mm of rainfall per year are called semideserts. Much of the land area of California would fall in this range. True deserts receive less than 120 mm of rainfall, and extreme deserts less than 70 mm of rain. As we have seen in Module 16.2, global patterns of air circulation in Hadley cells create many of the world's deserts at 20—30° latitude north and south of the equator.

The plants and animals that make deserts their home are almost without exception characterized by unusual adaptations to the dry conditions of the desert. Examining how evolution has adapted these organisms is fascinating. We consider only a few examples here.

Plants lose much of their water through their leaves while their stomates are open. Desert plants have altered designs and physiology to reduce this water loss as much as possible. Many desert plants, like cacti, have no leaves and consist of thick, stalk-like branches. This effectively reduces the surface-area-to-volume ratio of the plant, greatly reducing water loss. Some plants, like the ocotillo (*Fouquieria splendens*, Figure 16.11B), reduce water loss through their leaves by shedding their leaves

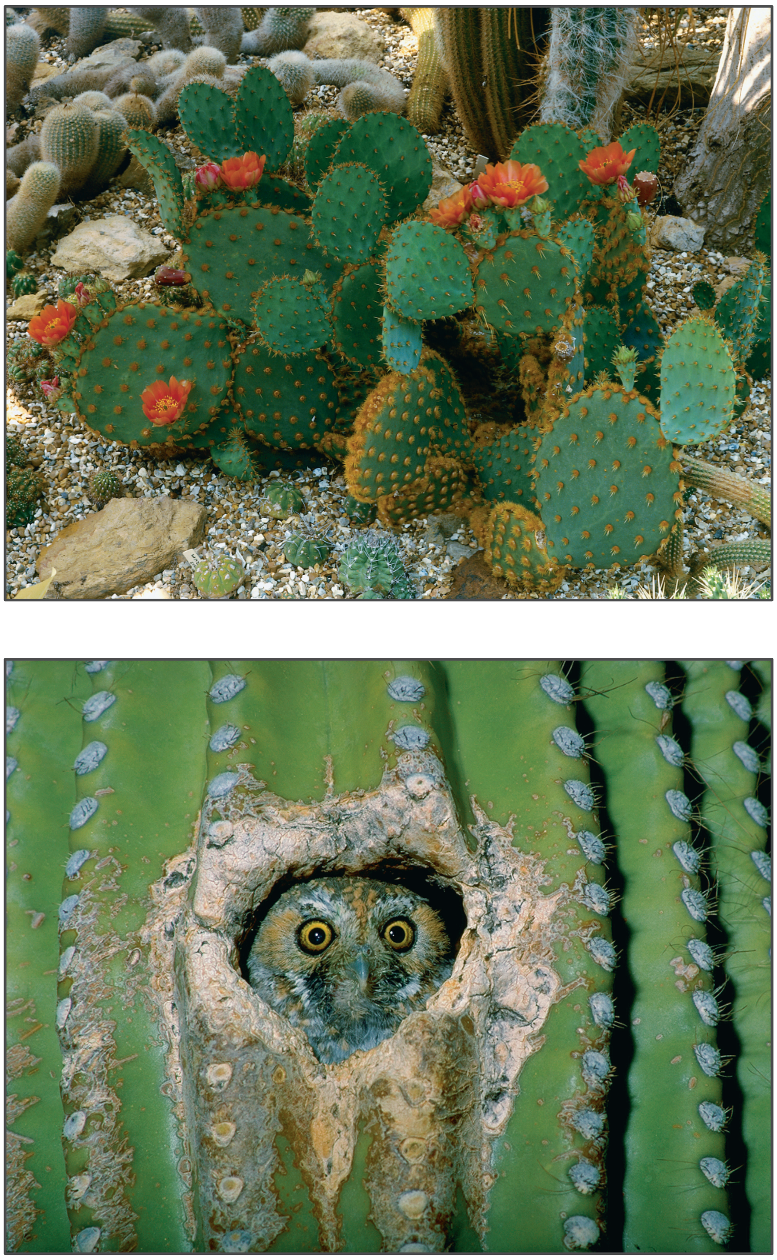


FIGURE 16.11A Deserts are typically sparsely covered with plants. To reduce water loss, these plants are often small with thick branches and few if any leaves.

FIGURE 16.11B Ocotillo Cactus, Anza-Borrego Desert State Park, California.

during periods of drought. After a rainfall, the ocotillo regrows its leaves; this may happen four or five times a year. Many succulents separate the chemical reactions for fixing CO_2 from those that capture light energy. As a result, the plant does not need to open its stomates during the day, when light energy is captured; rather, this is done during the night to reduce water loss.

Animals also show a variety of adaptations to dry conditions. Some of these adaptations are relatively simple, like being active only during the night. Other adaptations are more elaborate. The spadefoot toad, which lives in the desert Southwest of the United States, will bury itself underground and go into a state of reduced metabolic activity called estivation (Figure 16.11C). When rain returns, the toads become active again. Some animals are able to withstand large losses of body water. Desert rabbits can withstand water losses of up to 50 percent of their body weight (Figure 16.11D).

FIGURE 16.11C **Plains Spadefoot, Spea bombifrons, Kansas**

The kangaroo rat is probably the most accomplished water-conserving mammal (Figure 16.11E). These animals never drink water, but gain all their required moisture by metabolizing carbohydrates. During the day, the kangaroo rat remains in underground tunnels to reduce water loss. To reduce the loss of water through respired air, the kangaroo rat has a countercurrent system that cools the air and then reabsorbs much of the moisture. Another major source of water loss for mammals is excretion of urine. Kangaroo rats have extremely efficient kidneys that reabsorb much of the water in urine. As a result, the urine of kangaroo rats is 30 times more concentrated in dissolved solutes than their blood is. No other animal produces such concentrated urine. ❖

FIGURE 16.11D **Black-Tailed Jack Rabbit**

FIGURE 16.11E **Kangaroo Rat**

16.12 Forests are important terrestrial biomes often characterized by their dominant tree species

On land, forest biomes constitute a heterogeneous but important group of biological communities (Figure 16.12A). Forests are typically characterized by their physical location and their dominant plant species, which are often large trees. The worldwide distribution of some of these biomes is shown in Figure 16.12B. The importance of these biomes is evident from just the extent of the area covered by forests. In this module we review the characteristics of a few of these forest biomes to give you some flavor of their diversity.

Northern Coniferous Forest Northern coniferous forests are found across North America and northern Eurasia. The climate of northern coniferous forests typically consists of cold winters and short, mild summers. Although the rainfall is low (40–100 cm per year), the cool temperatures keep evaporation low; thus, the climates are often humid. These biomes often receive very heavy snowfall.

The forest is usually dominated by one or two tree species. Some typical species are white spruce, balsam fir, black spruce, and white cedar. Coniferous trees are especially well adapted to the environments of northern forests. Their needles shed snow effectively and thus prevent damage that can occur from large accumulations of snowfall. Because the trees do not shed their needles, they can begin photosynthesis as soon as it is warm enough in the spring. This adaptation is especially advantageous in climates with short growing seasons.

Temperate Deciduous Forest Temperate deciduous forests are found in eastern North America, western Europe, Japan, eastern China, and Chile. The climate of these forests typically includes a warm summer and a cool to cold winter. There is also fairly high precipitation. The types of trees that dominate these forests are quite variable. However, some typical species are oaks and maples.

Tropical Rain Forests Tropical rain forests receive more than 200 cm of rainfall per year; in some cases, it can approach 1000 cm. Many rain forests are found in equatorial regions of the world. These areas are prone to becoming rain forests due to the weather patterns of Hadley cells (Module 16.2). One month out of the year may be relatively dry, during the cooler months. However, temperature in the rain forests changes little over a year; it averages about 27°C.

The very high rainfall leaches the rain-forest soils of most inorganic nutrients. The moisture and warm temperatures also mean that organic matter decays quickly. Rain-forest soils do not do well under traditional agriculture either. The low cation exchange capacity prevents these soils from holding nutrients when added as fertilizer, since fertilizer binds to cations. In some locations, when the land is cleared the soil turns to a hard red substance called laterite. The laterite can be used to make bricks, but it supports only scrubby growth.

Tropical rain forests are notable for their very high diversity of plants and animals. Many species in the rain forests remain to be discovered and described. However, there has been increasing pressure to harvest wood from rain forests and convert land to agriculture. As a result, the amount of land surface covered by rain forests is dwindling. It is almost certain that this activity is also leading to the extinction of species, many of which have never been described.

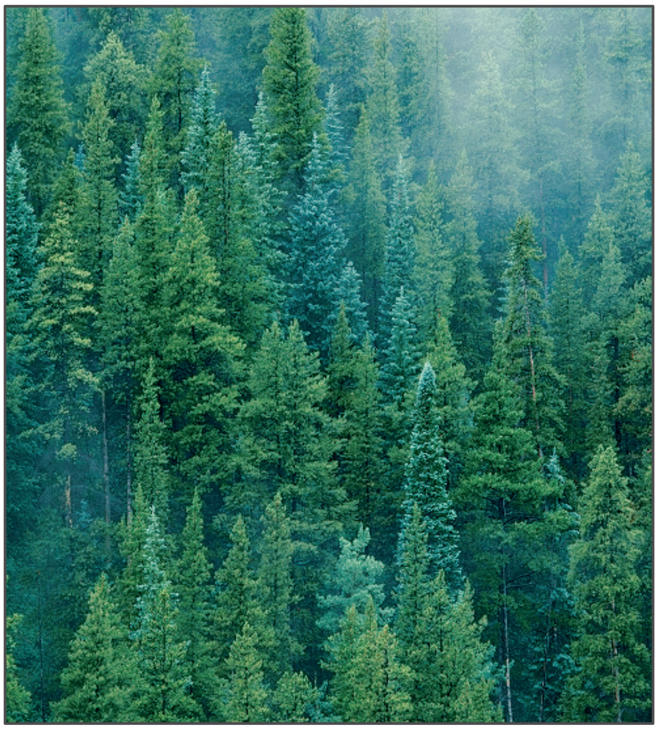


FIGURE 16.12A The top figure shows a pine forest. A deciduous forest in New England is shown below.

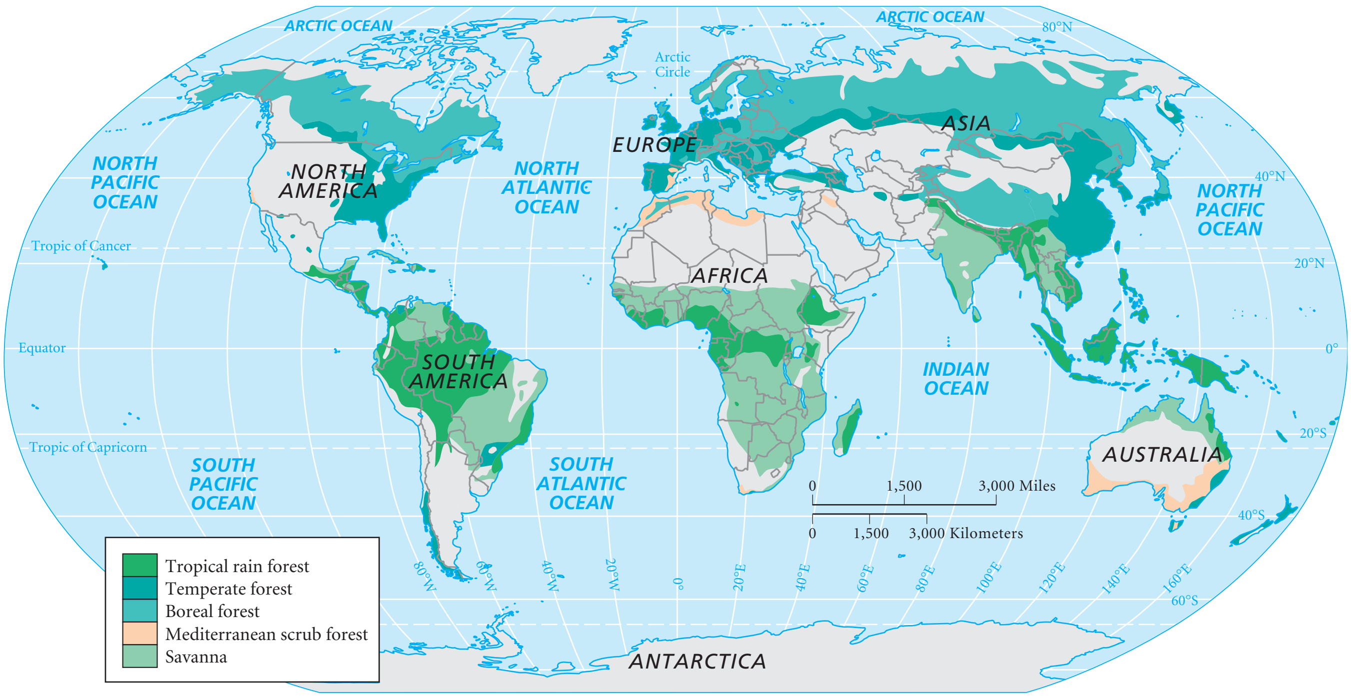


FIGURE 16.12B **Worldwide Distribution of Forest Biomes and Savannas.**

Global Change

16.13 Human activities can quickly cause global environmental change

Humans have been aware for some time that their activities can have effects on the environment. Indeed, the industrial pollution of England deposited soot on trees and was partly responsible for the change in frequency of color morphs of the moth *Biston betularia,* as we saw in Chapter 4. These changes had been documented by collections of moths in the late nineteenth century, although natural selection was not implicated as the cause of these changes until the 1950s.

Atmospheric Pollution The real danger of air pollution was dramatically illustrated in London in 1952. In December of that year, a temperature inversion caused the air to stagnate, and cloud cover blocked the sunlight. Temperatures dipped to below freezing, and the people of London turned up their furnaces. At that time many homes were heated by coal, and the increased coal burning caused the air to become even thicker with pollution. In a seven-day period, nearly 4000 people died of pollution-related complications.

Smog in London and Los Angeles (Figure 16.13A) has effects primarily at a local level, but we are now learning that human pollution can have a truly global effect. That is, pollution in the United States affects everyone on the planet. Burning fossil fuels continues to cause problems. Many of the by-products of coal and gas combustion undergo chemical changes in the atmosphere and can become strong acids, giving rise to acid rain (Figure 16.13B). The acid rain will not necessarily be localized to the area where the pollution was first created. Pollution at the global level means that pollution control will require cooperation from many countries to be effective.

Another form of air pollution is produced by chemicals used as propellants and refrigerants. While the total amount of these gases is not that large, their impacts on levels of atmospheric *ozone* (O_3), an unstable and highly reactive form of oxygen, can be significant. But isn't ozone a type of pollution? In fact, ozone levels can increase close to the Earth's surface due to car emissions; but ozone in the upper part of the atmosphere plays a crucial role in filtering out damaging radiation. Without this filter, humans will experience much higher levels of skin cancer. We discuss the dangers of acid rain and ozone depletion in more detail in Module 16.14.

Agricultural Practices Civilization would not be what it is today without the development of modern agriculture. The ability of a small number of people to produce food for many has allowed modern civilizations to create a workforce that is not tied to the land and does not need to hunt and gather food. Ecology and evolutionary biology have much to offer agricultural science. Some agricultural pests can be controlled by natural predators and parasites. Other agricultural pests have been controlled by chemical agents. We have seen repeatedly, however, that insects evolve and can become resistant to these chemicals.

Modern agriculture has potential downsides as well. Many plant crops remove nitrogen from the soil. Because crops are often planted in large expanses of *monocultures* (one-species crops), there are no natural means of replenishing the soil's nitrogen supply. However, soil nitrogen can be replenished through *crop rotation* rather than by adding

FIGURE 16.13A Los Angeles Smog Can you find the clear day?

synthetic fertilizer. In crop rotation, a nitrogen-using crop like corn is followed by a crop like soybeans, which fixes nitrogen in the soil. Crop rotation is a means of trying to restore the balance of soil nutrients that becomes disrupted in highly artificial agricultural ecosystems.

In many of the less developed parts of the world, more severe problems face populations that use marginal land for agriculture and grazing. Overuse of these areas can cause land to convert to desert (Figure 16.13C). In Module 16.15 we review this problem and the many factors contributing to it.

FIGURE 16.13B A statue in Chicago damaged by acid rain, before (left) and after (right) restoration.

FIGURE 16.13C Poor agricultural practices in the United States led to soil erosion and the Dust Bowl in parts of Oklahoma during the 1930s.

16.14 Human activities add gases to our atmosphere, leading to acid rain and ozone depletion

In this chapter we have already reviewed the impact of fossil fuel combustion on atmospheric CO_2 and the resulting greenhouse effect (see Module 16.5). But the combustion of fossil fuels has consequences beyond the greenhouse effect. For instance, coal is still a common fuel in industry, especially in power plants. Coal contains sulfur compounds that, when burned, produce sulfur dioxide (SO_2), which is released into the atmosphere. Burning coal and natural gas also produces nitrogen dioxide (NO_2) and nitrous oxide (NO) during their combustion (Figure 16.14A). These compounds may then undergo additional chemical reactions in the atmosphere to give rise to the derivative compounds sulfuric acid (H_2SO_4) and nitric acid (HNO_3). These acids are very soluble in water. They dissolve in rain and snow, returning to Earth in a solution called **acid rain**.

Natural rainfall is slightly acidic (pH = 5.6) because the carbon dioxide normally present in air produces a mild acid called carbonic acid. However, nitric and sulfuric acid are strong acids that can lower the pH of rainwater substantially. Rainfall with a pH as low as 1.5 has been recorded in Wheeling, West Virginia. Acid rain may be responsible for killing forest trees directly and substantially lowering the pH of lakes. A substantial drop in pH has been documented in the Adirondack Lakes region of New York over the past 45 years (Figure 16.14B). These effects of acid rain then cause additional cascading effects on the organisms that live, or depend on life, in these lakes or forests. The effects of acid rain can be seen in the faces of public marble statues that have been eroded by atmospheric acids over time (see Figure 16.13B).

Ozone is an unstable and highly reactive form of oxygen. Unlike the stable diatomic oxygen molecule (O_2) that makes up 21 percent of our atmosphere, ozone (O_3) has three atoms of oxygen and is relatively rare. However, in the portion of our atmosphere called the stratosphere (Figure 16.14C), ozone concentrations reach high values. They also serve their most important function there. Sunlight reaching the outer atmosphere of the Earth contains high-energy radiation, including three types of ultraviolet light (UV). The lowest-energy ultraviolet light is called **UVA**. It can cause some damage to biological cells and typically is not filtered by the atmosphere. **UVB**

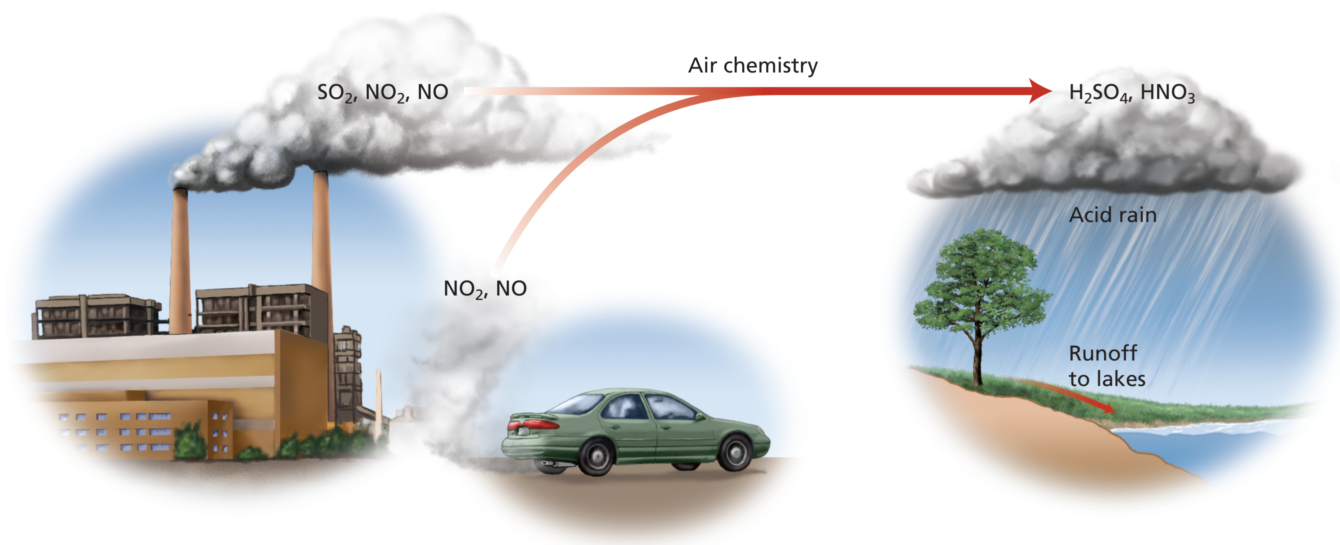


FIGURE 16.14A **Acid Rain Production**

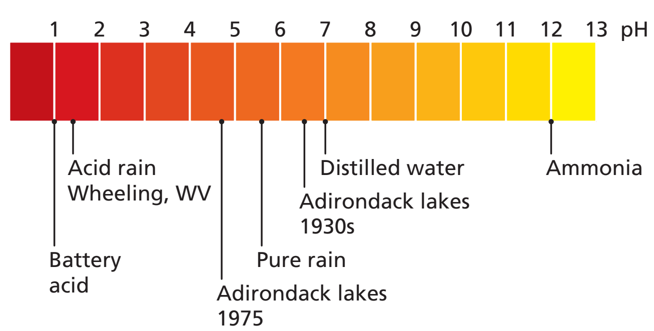


FIGURE 16.14B Acid rain lowers pH in natural lakes.

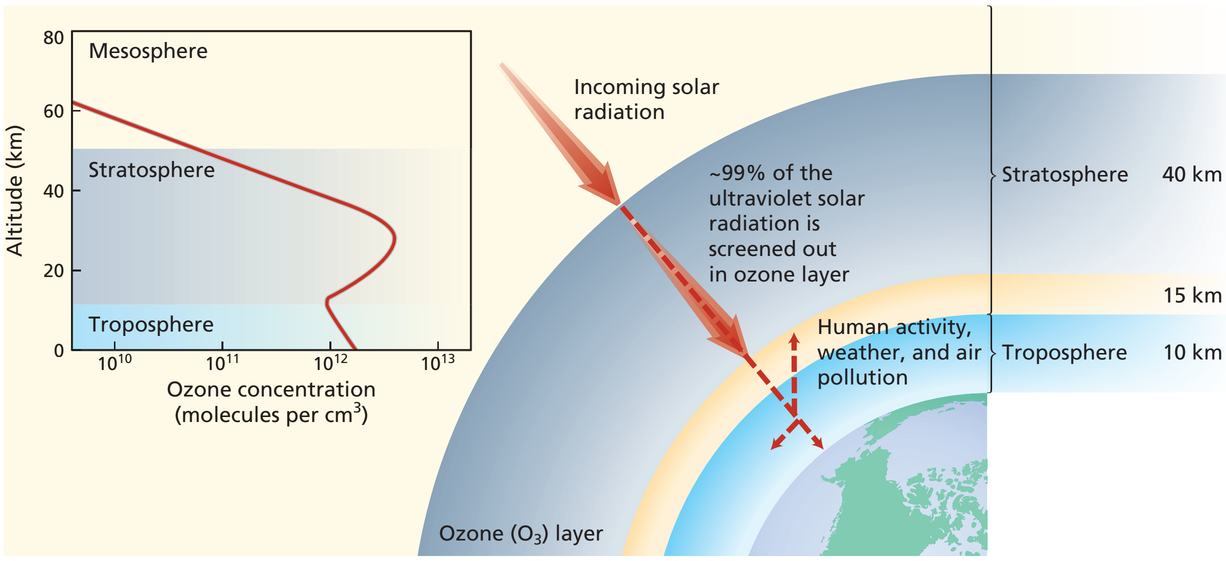


FIGURE 16.14C Ozone absorbs UV light in the stratosphere.

Average % change 1969-86	–2.3%	–3.0%	–1.7%
Winter change	–6.2%	–4.7%	–2.3%
Summer change	+0.4%	–2.1%	–1.9%

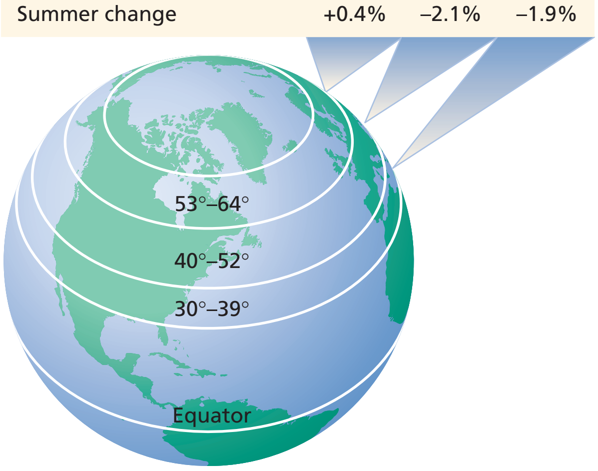


FIGURE 16.14D Global Changes in Ozone Levels

has more energy than UVA, and can cause substantial damage to living cells. Ozone plays a crucial role by absorbing UVB radiation, which splits the ozone into one molecule of diatomic oxygen and one molecule of atomic oxygen. This reaction prevents much of the UVB from reaching the Earth's surface. The highest-energy UV is **UVC**. It is strongly absorbed by the atmosphere, so almost none of it reaches the Earth's surface.

In the absence of human activities, the atmospheric ozone reached an equilibrium between its destruction by UV energy and its creation by a variety of other chemical processes. Humans, however, have been adding chemicals to the atmosphere that can dramatically destroy ozone. In so doing, we are increasing our exposure to damaging UVB energy. The chemicals that destroy ozone include chlorofluorocarbons (CFCs), used in aerosols and refrigerators; carbon tetrachloride and methyl chloroform, both used as solvents; and halons, used as refrigerants and in fire extinguishers. These compounds produce reactive chlorine molecules that can destroy ozone. Just one of these chlorine molecules may destroy up to 100,000 ozone molecules before it is removed from the atmosphere. Reduced ozone levels in our atmosphere are now well documented (Figure 16.14D).

16.15 Human agricultural practices have increased the spread of deserts

Deserts are characterized by very low rainfall and sandy soil with little organic matter. Desert soils are also unable to hold much water. There is typically little organic matter in deserts because so few plants can grow in dry sandy soils. Human activity can be a major contributor to **desertification,** the process of becoming a desert. When marginal lands are converted to agriculture or grazing, a number of changes occur that may accelerate the conversion of land to desert. Conversion of land to human use involves removing native plants that may be important in maintaining soil integrity. Often large trees in these areas are the first to go, being harvested for firewood. With the loss of native plants and the planting of commercial crops, there can be a loss of organic matter from the soil, erosion, and loss of soil productivity (Figure 16.15A). Some grazing animals, such as goats, at high densities can be so efficient at feeding that they destroy all plant life and prevent any new growth from becoming established. Larger animals, such as cows, physically trample new growth and break up the soil, fostering erosion. As the land becomes less useful for agriculture or grazing, humans move to new areas and the process is repeated.

In northern Africa, for example, the Masai people have adopted a nomadic lifestyle to make a living on marginal lands. The Masai travel over great distances to find new food for their herds of cattle. The Masai have increasingly faced famine in recent years as a result of desertification and crop failures. These problems have been caused by many factors. Political problems have restricted the movement of the Masai, leading to overgrazing by their cattle. In addition, this region of Africa has been subject to historically severe drought for the last 30 years.

Northern Africa is not the only region of the world facing problems of desertification (Figure 16.15B). Solutions to these problems are hard to come by. Maintaining agriculture in marginal habitats is prone to failure due to the unpredictable nature of these habitats. There may also be cultural practices that are hard to reverse. For instance, the status of a Masai is related to the number of cattle owned. This practice fosters overgrazing in marginal lands. Although world governments often provide aid to prevent mass starvation, these measures in no way necessarily lead to lasting improvements in such underlying ecological problems as desertification.

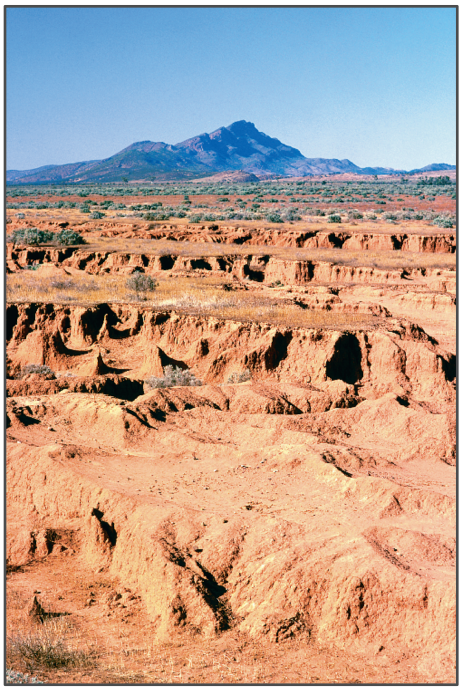


FIGURE 16.15A Soil erosion can lead to the loss of organic matter and soil productivity.

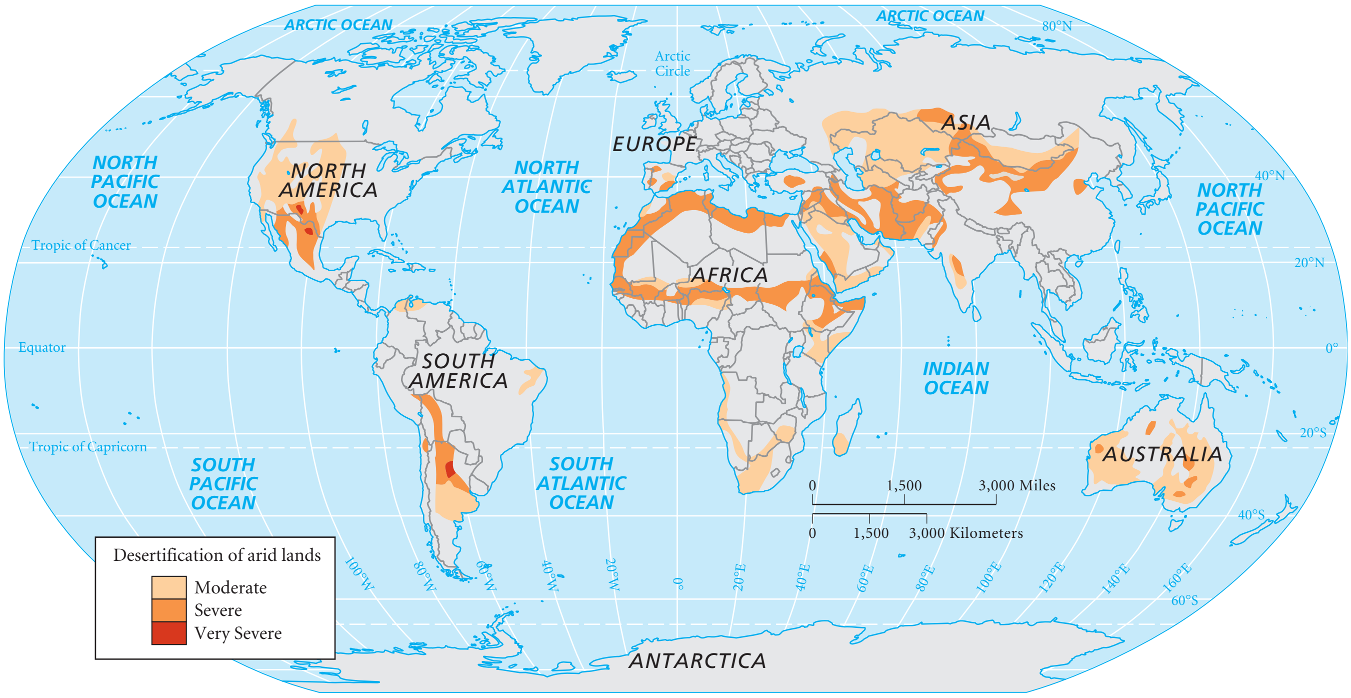


FIGURE 16.15B **Areas of the World Currently Threatened with Desertification**

SUMMARY

1. The Earth's environments vary tremendously. Many patterns of climatic variation are due to physical properties of the Earth and its movement about the sun.
2. Seasonal and daily variation in duration of daylight and average temperature are strongly affected by the rotation of the Earth on its axis and its orbit around the sun.
3. The intense energy of the sun that strikes the equator sets up a predictable flow of air called Hadley cells, which contribute to the existence of rain forests on the equator and deserts just north and south of the equator.
4. Climate is affected by local conditions.
   - **a.** Deserts can form on one side of a mountain as a consequence of the rain-shadow effect.
   - **b.** These types of deserts form only when the right combinations of topography and airflow exist.
   - **c.** Plants can also alter the microclimatic effects. Large trees can substantially reduce the penetration of light and heat to the forest floor.
5. Communities are classified into biomes that have characteristic vegetation and occupy specific geographic and climatic regions.
   - **a.** Oceans cover 70 percent of the Earth's surface and are characterized by low primary productivity.
   - **b.** Deserts form as a consequence of local climates or global conditions like Hadley cells. The plants and animals that characterize the desert community show unusual adaptations to the low water and high temperatures of deserts.
   - **c.** Lakes and ponds often show seasonal cycles of temperature and dissolved oxygen content that have important consequences for their animal communities.
   - **d.** Forests are a heterogeneous terrestrial biome occurring in the tropics and the cold northern latitudes. Forest communities are often identified by their dominant tree species.
6. The global environment is not immune to human activity.
   - **a.** Burning fossil fuels has contributed to elevated levels of carbon dioxide. This in turn may be warming the Earth.
   - **b.** Other by-products of fossil fuel oxidation, like SO_2 and NO_2, contribute to acid rain production.
   - **c.** The protective layer of ozone in our atmosphere is also under attack from certain chlorinated compounds. The potential harm from the loss of ozone is not as immediate and obvious as that from acid rainfall, but in the long run it could be much more dangerous.

REVIEW QUESTIONS

1. Explain how the airflow within a Hadley cell contributes to rain forests at the equator and deserts 20–30° north and south of the equator.
2. Describe two specific ocean currents and their general effects on the climates of landmasses they pass by.
3. What is the greenhouse effect? How do human activities influence this process?
4. How are rain-shadow deserts formed?
5. Why don't most lakes in temperate climates become a solid block of ice in the winter?
6. Describe two adaptations used by plants to cope with the dry conditions of the desert.
7. Describe how acid rain is formed.

KEY TERMS

acid rain
benthic
biome
chaparral
climate
currents
desertification
dew point
epilimnion
glacier
greenhouse gases
gyres
Hadley cell
hypolimnion
intertidal zone
Mediterranean climate
microclimate
neritic
oceanic
ozone
pelagic
photic
phytoplankton
plankton
rain-shadow deserts
seasonality
thermocline
upwelling
UVA
UVB
UVC
weather
zooplankton

FURTHER READINGS

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