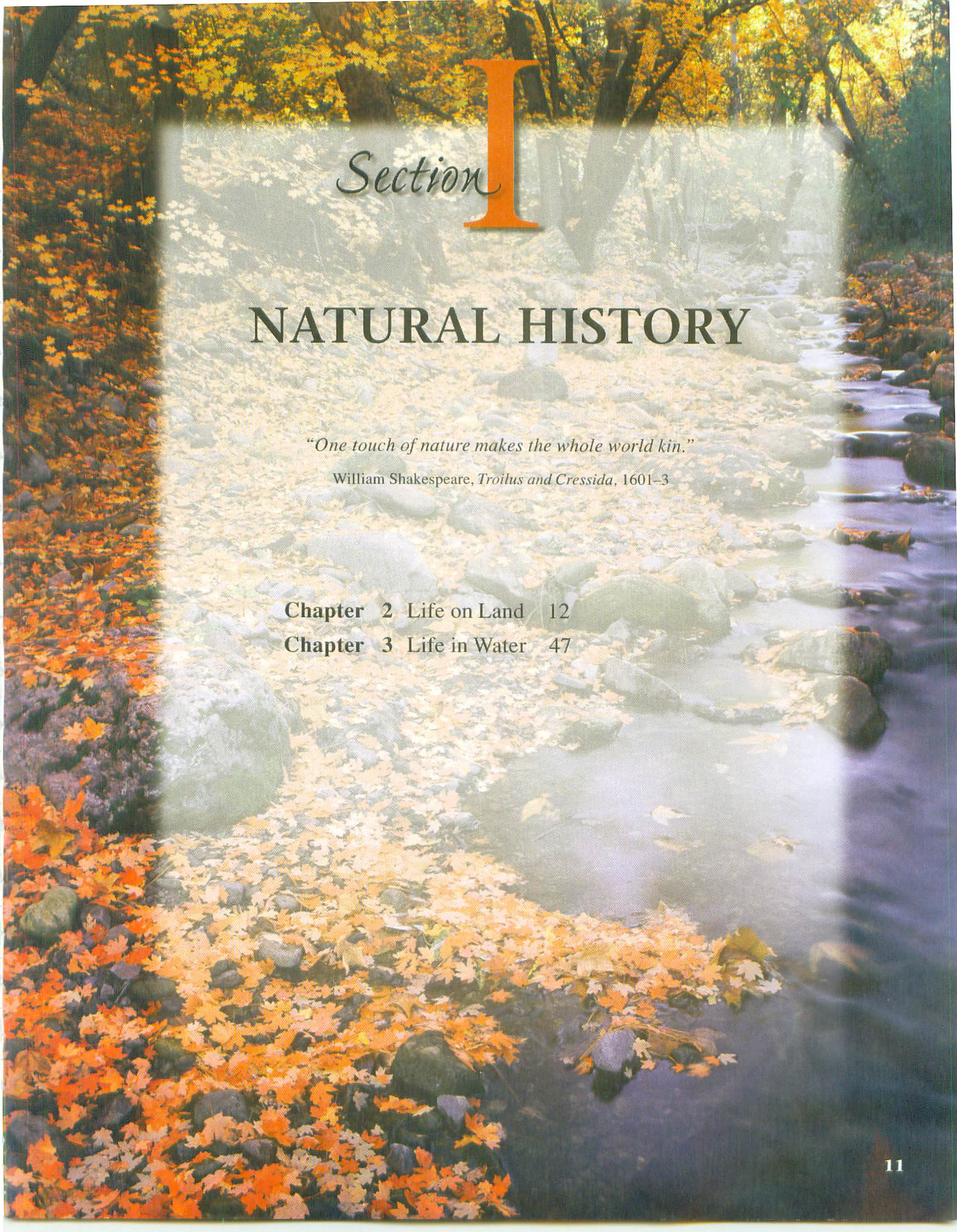
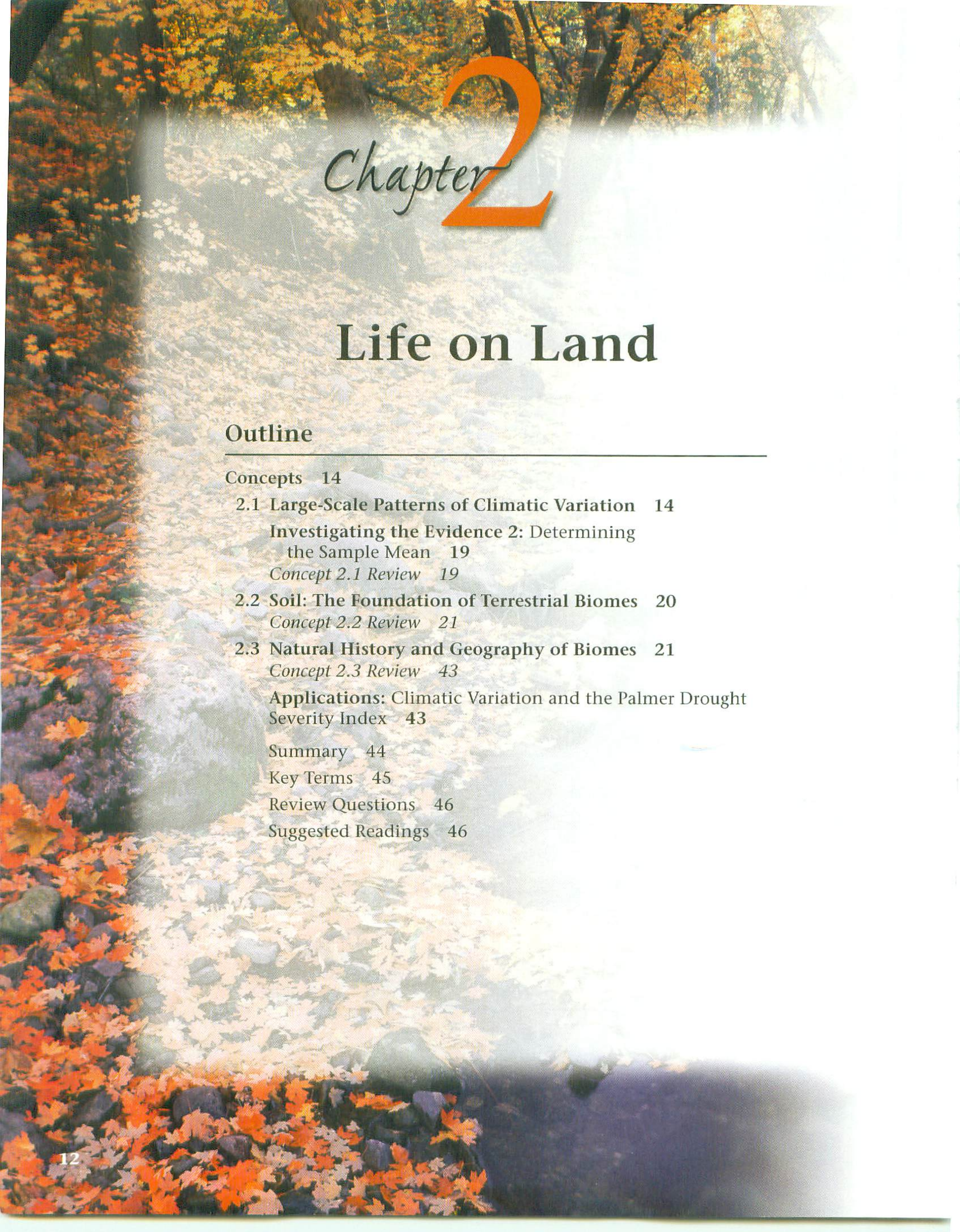


Section I

NATURAL HISTORY

"One touch of nature makes the whole world kin."

William Shakespeare, *Troilus and Cressida*, 1601–3



Chapter 2

Life on Land

Outline

Detailed knowledge of natural history is proving invaluable to restoration of natural ecosystems across the globe. One of the most dramatic restoration successes that incorporated natural history into its approach comes from Costa Rica. Daniel Janzen's goal was to restore tropical dry forest, a forest nearly as rich in species as tropical rain forest, to Guanacaste National Park, Costa Rica. As he studied the guanacaste tree, *Enterolobium cyclocarpum* (fig. 2.1), however, he realized that something was missing from the present-day forest. The guanacaste tree, a member of the pea family, produces disk-shaped fruit about 10 cm in diameter and 4 to 10 mm thick. Each year, a large tree produces up to 5,000 of these fruits, which fall to the ground when ripe. Janzen asked, Why does the guanacaste tree produce so much fruit? His answer to this question was that the fruit of the tree should promote seed dispersal by animals.

Janzen, however, knew of no living native animals of the size and behavior that would make them dependable dispersers of guanacaste seeds. Dependable dispersers would be necessary to speed restoration of tropical dry forest across Guanacaste National Park. True, some large herbivores fed on guanacaste fruits and dispersed the seeds with their feces. But most of these dispersers were cattle and horses, which were introduced during the Spanish colonial period. Had the guanacaste tree evolved an elaborate fruit and produced thousands of them each year in the absence of native dispersers? On the surface, it appeared so.

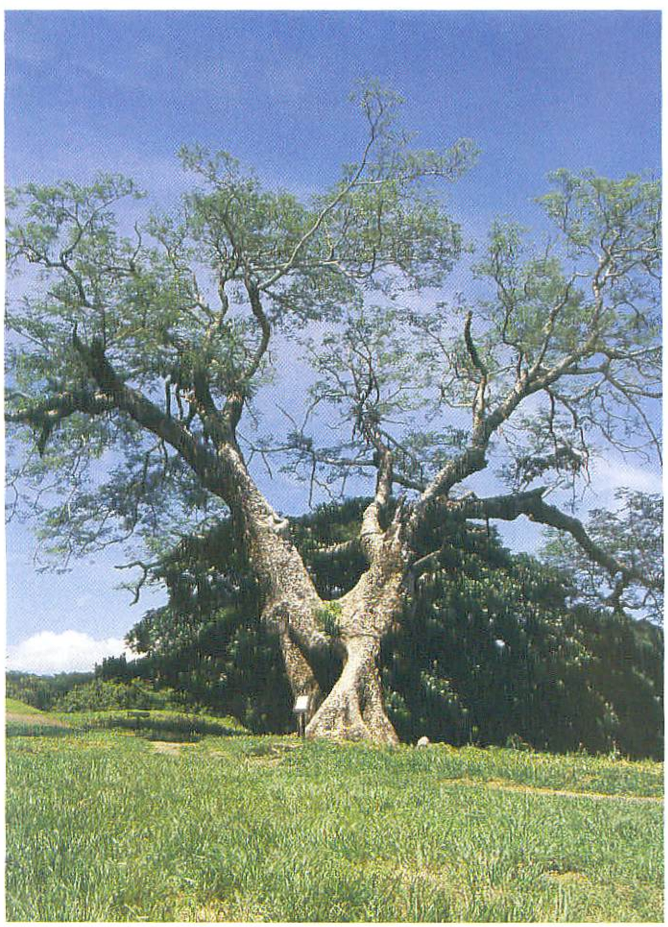


Figure 2.1 A guanacaste tree, *Enterolobium cyclocarpum*, growing in Costa Rica. Guanacaste trees, which produce large amounts of edible fruit, require large herbivores to disperse their seeds.

Janzen's restoration of tropical dry forest was guided by his knowledge of **natural history,** the study of how organisms in a particular area are influenced by factors such as climate, soils, predators, competitors, and evolutionary history. Natural history eventually led Janzen to an understanding of the fruiting biology of the guanacaste tree. As he considered the long-term natural history of Central American dry forest, he found what he was looking for: a whole host of large herbivorous animals, including ground sloths, camels, and horses. The dry forest had once supported plenty of potential dispersers of guanacaste seeds. However, all these large animals became extinct about 10,000 years ago; overhunting by humans may have been a contributory factor. For thousands of years following these extinctions the guanacaste tree prepared its annual feast of fruits, but there were few large animals to consume them. Then about 500 years ago, Europeans introduced horses and cattle, which ate the fruits of the guanacaste tree and dispersed its seeds around the landscape (fig. 2.2). Janzen recognized the practical value of livestock as seed dispersers and included them in his plan for tropical dry forest restoration.

Janzen first tested the hypothesis that contemporary horses can act as effective seed dispersers for the guanacaste tree. After this test, he applied his knowledge by incorporating horses into the management plan for Guanacaste National Park. The guanacaste tree and other trees in a similar predicament would have their dispersers, and restoration of tropical dry forest would be accelerated.

Janzen's natural history of tropical dry forest also includes people, unlike most natural histories. He worked closely with people from all parts of Costa Rican society, from the president of the country to local schoolchildren. He realized that long-term support for Guanacaste National Park depended upon its contribution to the economic and cultural well-being of local people. It's the people in Janzen's natural history that stand guard over the Guanacaste project. Janzen calls his approach "biocultural restoration," an approach that seeks to preserve tropical dry forest for its own sake and as a place that provides a host of human benefits, ranging from drinking water to intellectual stimulation. Using natural history as their guide, Janzen and the people of Costa Rica are restoring tropical dry forest in Guanacaste National Park.

Janzen's work (1981a, 1981b) shows how natural history can be used to address a practical problem. Natural history also formed the foundation upon which modern ecology developed. Because ecological studies continue to be built upon a solid foundation of natural history, we devote chapters 2 and 3 to the natural history of the biosphere. In chapter 2, we examine the natural history of life on land. Before we

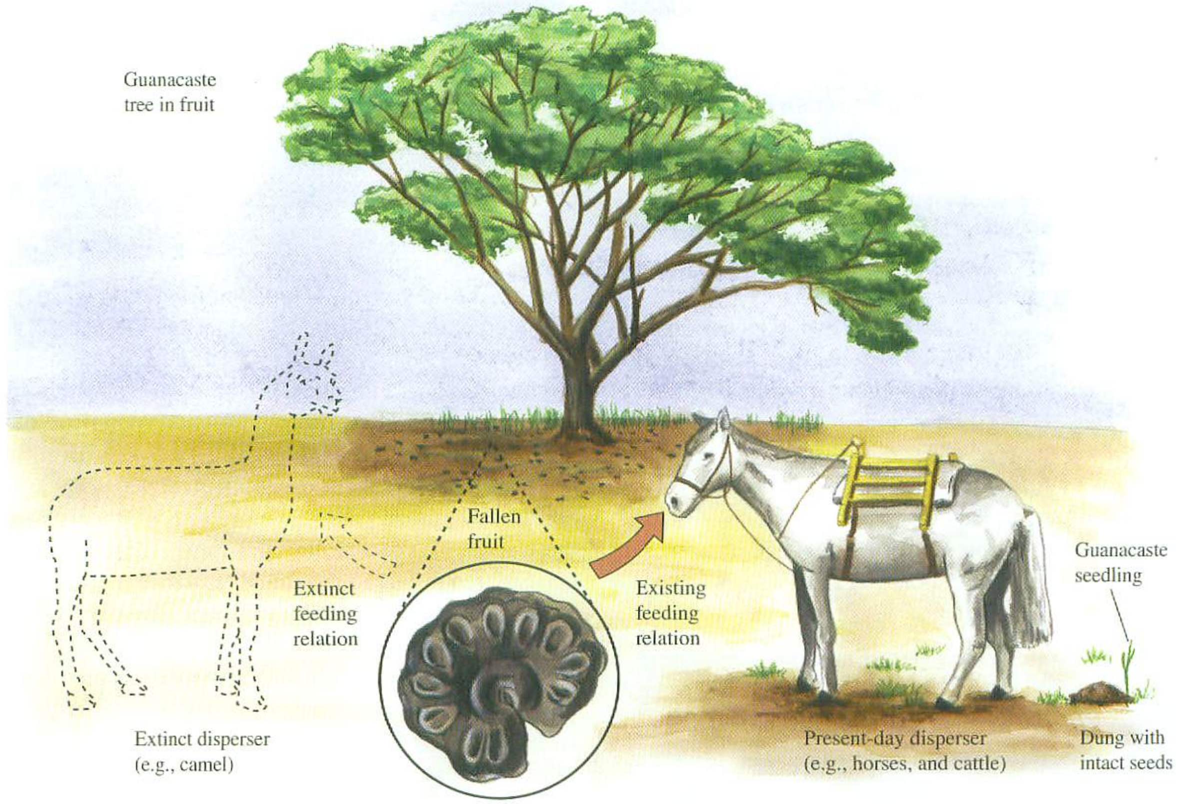


Figure 2.2 Dispersers of guanacaste seeds—past and present. Most of the original dispersers of quanacaste seeds went extinct over 10,000 years ago. Now the tree depends on introduced domestic livestock for its dispersal.

begin that discussion, we need to introduce terrestrial biomes, the concept around which this chapter is built. We also discuss the development and structure of soils, the foundation supporting terrestrial biomes.

Terrestrial Biomes

Chapter 2 focuses on major divisions of the terrestrial environment called **biomes.** Biomes are distinguished primarily by their predominant plants and are associated with particular climates. They consist of distinctive plant formations such as the tropical rain forest biome and the desert biome. Because tropical rain forest and desert are characterized by very different types of plants and animals and occur in regions with very different climates, the natural histories of these biomes differ a great deal. The student of ecology should be aware of the major features of those differences.

The main goal of chapter 2 is to take a large-scale perspective of nature before delving, in later chapters, into finer details of structure and process. We pay particular attention to the geographic distributions of the major biomes, the climate associated with each, their soils, their salient biological relationships, and the extent of human influences.

Concepts

2.1 Uneven heating of the earth's spherical surface by the sun and the tilt of the earth on its axis combine to produce predictable latitudinal variation in climate.

2.2 Soil structure results from the long-term interaction of climate, organisms, topography, and parent mineral material.

2.3 The geographic distribution of terrestrial biomes corresponds closely to variation in climate, especially prevailing temperature and precipitation.

2.1 Large-Scale Patterns of Climatic Variation

Uneven heating of the earth's spherical surface by the sun and the tilt of the earth on its axis combine to produce predictable latitudinal variation in climate. In chapter 1, ecology was defined as the study of the relationships between organisms and the environment. Consequently, geographic and seasonal variations in temperature and precipitation are fundamental aspects of terrestrial ecology and natural history. Several attributes of climate vary predictably over the earth. For instance, average temperatures are lower and more seasonal at middle and high latitudes. Temperature generally shows little seasonality near the equator, while rainfall may be markedly seasonal. Deserts, which are concentrated in a narrow band of latitudes around the globe, receive little precipitation, which generally falls unpredictably in time and space. What mechanisms produce these and other patterns of climatic variation?

Temperature, Atmospheric Circulation, and Precipitation

Much of earth's climatic variation is caused by uneven heating of its surface by the sun. This uneven heating results from the spherical shape of the earth and the angle at which the earth rotates on its axis as it orbits the sun. Because the earth is a sphere, the sun's rays are most concentrated where the sun is directly overhead. However, the latitude at which the sun is directly overhead changes with the seasons. This seasonal change occurs because the earth's axis of rotation is not perpendicular to its plane of orbit about the sun but is tilted approximately 23.5° away from the perpendicular (fig. 2.3).

Because this tilted angle of rotation is maintained throughout earth's orbit about the sun, the amount of solar energy received by the Northern and Southern Hemispheres changes seasonally. During the northern summer the Northern Hemisphere is tilted toward the sun and receives more solar energy than the Southern Hemisphere. During the northern summer solstice on approximately June 21, the sun is directly overhead at the tropic of Cancer, at 23.5° N latitude. During the northern winter solstice, on approximately December 21, the sun is directly overhead at the tropic of Capricorn, at 23.5° S latitude. During the northern winter, the Northern Hemisphere is tilted away from the sun and the Southern Hemisphere receives more solar energy. The sun is directly overhead at the equator during the spring and autumnal equinoxes, on approximately March 21 and September 22 or 23. On those dates, the Northern and Southern Hemispheres receive approximately equal amounts of solar radiation.

This seasonal shift in the latitude at which the sun is directly overhead drives the march of the seasons. At high latitudes, in both the Northern and Southern Hemispheres, seasonal shifts in input of solar energy produce winters with low average temperatures and shorter day lengths and summers with high average temperatures and longer day lengths. In many areas at middle to high latitudes there are also significant seasonal changes in precipitation. Meanwhile, between the tropics of Cancer and Capricorn, seasonal variations in temperature and day length are slight, while precipitation may vary a great deal. What produces spatial and temporal variation in precipitation?

Heating of the earth's surface and atmosphere drives circulation of the atmosphere and influences patterns of precipitation. As shown in figure 2.4*a*, the sun heats air at the equator, causing it to expand and rise. This warm, moist air cools as it rises. Since cool air holds less water vapor than warm air, the water vapor carried by this rising air mass

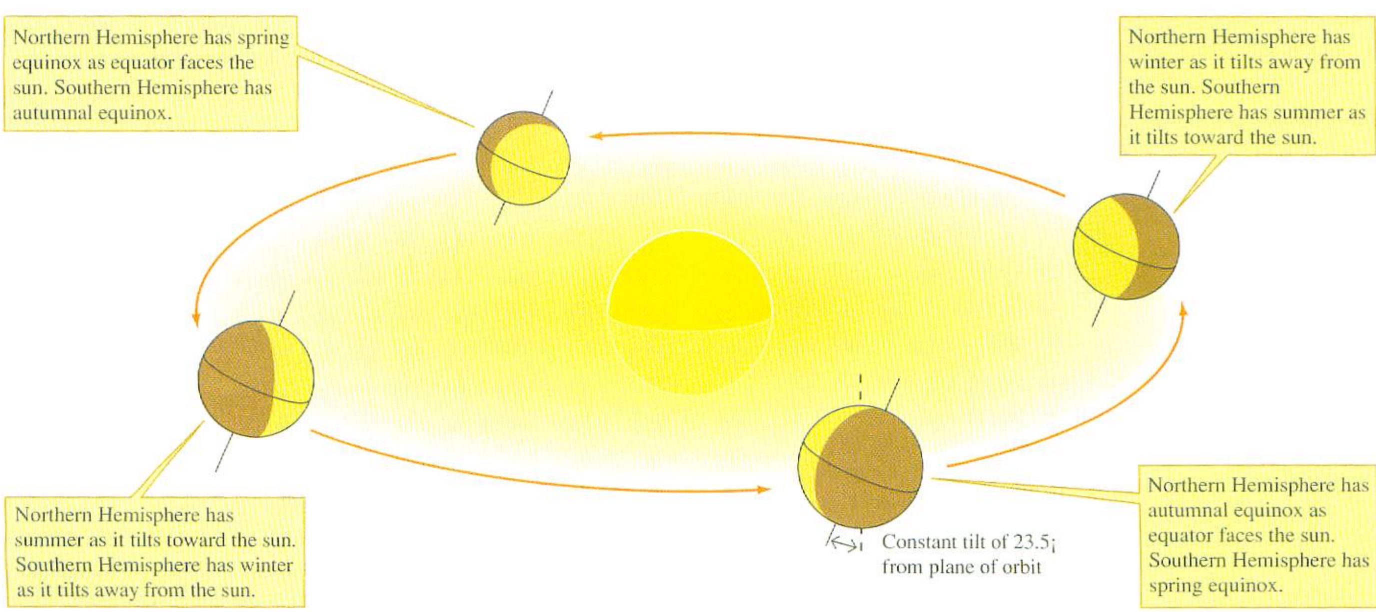
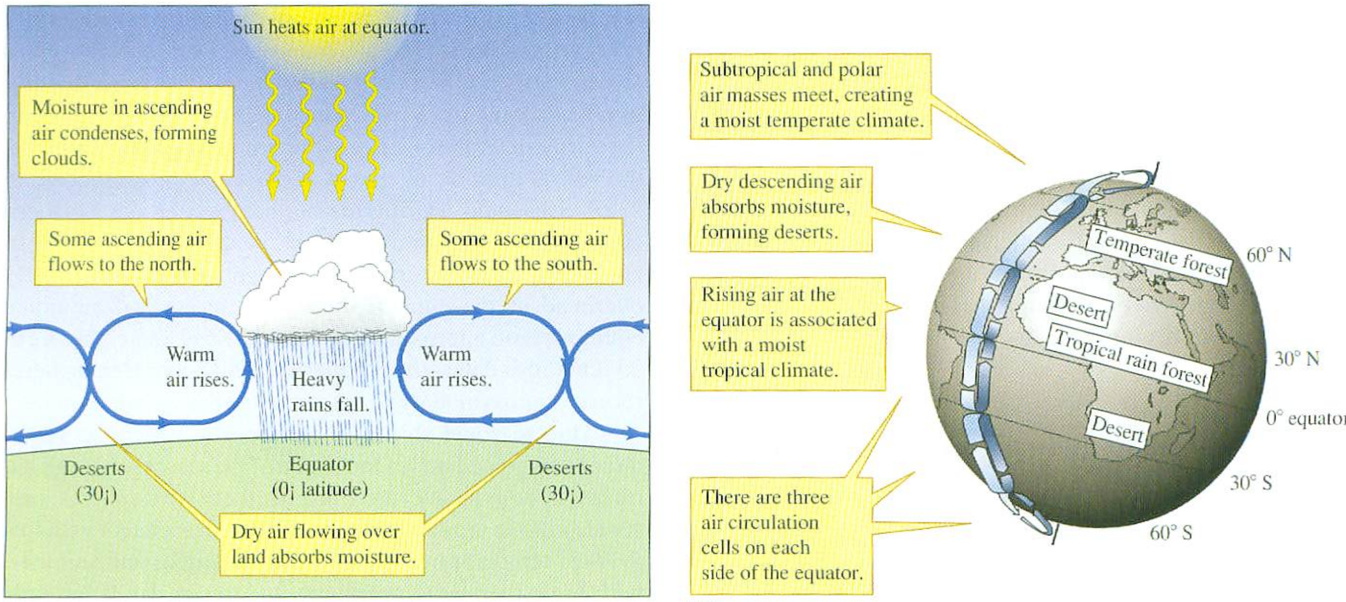


Figure 2.3 The seasons in the Northern and Southern Hemispheres.



(a) (b)

Figure 2.4 (*a*) Solar-driven air circulation. (*b*) Latitude and atmospheric circulation.

condenses and forms clouds, which produce the heavy rainfall associated with tropical environments.

Eventually, this equatorial air mass ceases to rise and spreads north and south. This high-altitude air is dry, since the moisture it once held fell as tropical rains. As this air mass flows north and south, it cools, which increases its density. Eventually it sinks back to the earth's surface at about 30° latitude and spreads north and south. This air draws moisture from the lands over which it flows and creates deserts in the process.

Air moving from 30° latitude toward the equator completes an atmospheric circulation cell at low latitudes. As figure 2.4*b* shows, there are three such cells on either side of the equator. Air moving from 30° latitude toward the poles is part of the atmospheric circulation cell at middle latitudes. This warm, moist air flowing from the south rises as it meets cold polar air flowing from the north. As this air mass rises, moisture picked up from desert regions at lower latitudes condenses to form the clouds that produce the abundant precipitation of temperate regions. The air rising over temperate regions spreads northward and southward at a high altitude, completing the middle- and high-latitude cells of general atmospheric circulation.

The patterns of atmospheric circulation shown in figure 2.4*b* suggest that air movement is directly north and south. However, this does not reflect what we observe from the earth's surface as the earth rotates from west to east. An observer at tropical latitudes observes winds that blow from the northeast in the Northern Hemisphere and from the southeast in the Southern Hemisphere (fig. 2.5). These are the *northeast* and *southeast trades*. Someone studying winds within the temperate belt between 30° and 60° latitude would observe that winds blow mainly from the west. These are the *westerlies* of temperate latitudes. At high latitudes, our observer would find that the predominant wind direction is from the east. These are the *polar easterlies*.

Why don't winds move directly north to south? The prevailing winds do not move in a straight north–south direction because of the **Coriolis effect.** In the Northern Hemisphere, the Coriolis effect causes an apparent deflection of winds to the right of their direction of travel and to the left in the Southern Hemisphere. We say "apparent" deflection because we see this deflection only if we make our observations from the surface of the earth. To an observer in space, it would appear that winds move in approximately a straight line, while the earth rotates beneath them. However, we need to keep in mind that the perspective from the earth's surface is the ecologically relevant perspective. The biomes that we discuss in chapter 2 are as earthbound as our hypothetical observer. Their distributions across the globe are substantially influenced by global climate, particularly geographic variations in temperature and precipitation.

Geographic variation in temperature and precipitation is very complex. How can we study and represent geographic variation in these climatic variables without being overwhelmed by a mass of numbers? This practical problem is addressed by a visual device called a climate diagram.

Climate Diagrams

Climate diagrams were developed by Heinrich Walter (1985) as a tool to explore the relationship between the distribution of terrestrial vegetation and climate. Climate diagrams summarize a great deal of useful climatic information, including seasonal variation in temperature and precipitation, the length and intensity of wet and dry seasons, and the

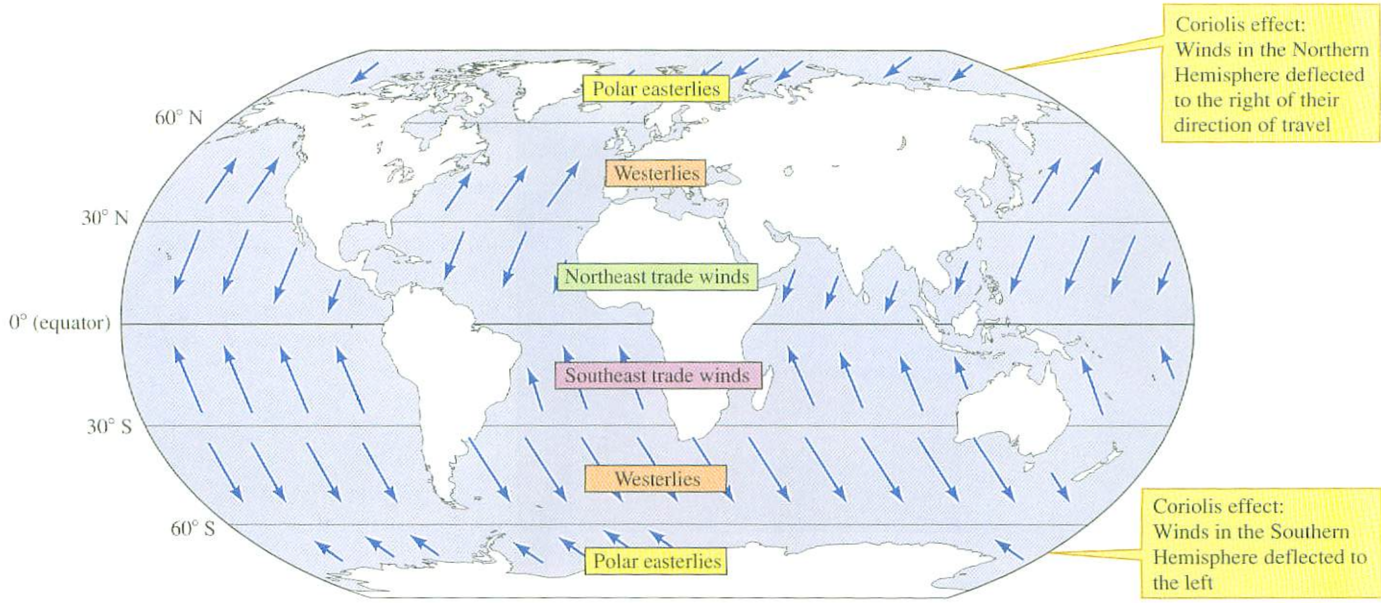


Figure 2.5 The Coriolis effect and wind direction.

portion of the year during which average minimum temperature is above and below 0°C.

As shown in figure 2.6, climate diagrams summarize climatic information using a standardized structure. The months of the year are plotted on the horizontal axis, beginning with January and ending with December for locations in the Northern Hemisphere and beginning with July and ending with June in the Southern Hemisphere. Temperature is plotted on the left vertical axis and precipitation on the right vertical axis. Temperature and precipitation are plotted on different scales so that 10°C is equivalent to 20 mm of precipitation. Climate diagrams for wet areas such as tropical rain forest compress the precipitation scale for precipitation above 100 mm so that 10°C is equivalent to 200 mm of precipitation. With this change in scale, rainfall data from very wet climates can be fit on a graph of convenient size. This change in scale is represented by darker shading in the climate diagram for Kuala Lumpur, Malaysia (fig. 2.7*a*). Notice that the precipitation at Kuala Lumpur exceeds 100 mm during all months of the year.

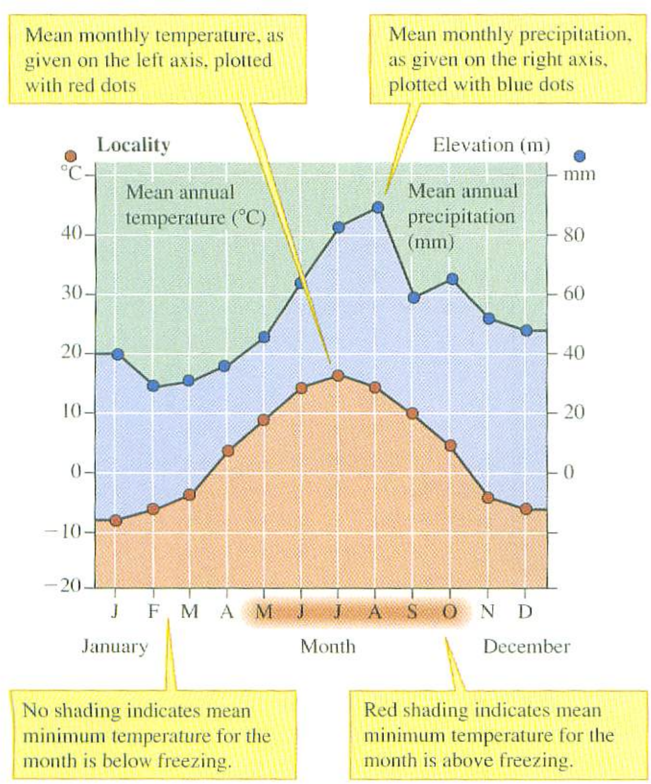


Figure 2.6 Structure of climate diagrams.

Because the temperature and precipitation scales are constructed so that 10°C equals 20 mm of precipitation, the relative positions of the temperature and precipitation lines reflect water availability. Theoretically, adequate moisture for plant growth exists when the precipitation line lies above the temperature line. These moist periods are indicated in the figure by blue shading. When the temperature line lies above the precipitation line, potential evaporation rate exceeds precipitation. These dry periods are indicated by gold shading in the climate diagram. Notice that gold shading of the climate diagram for Yuma, Arizona (fig. 2.7*b*), indicates year-round drought, while the blue shading of the climate diagram for Kuala Lumpur (fig. 2.7*a*) indicates moist conditions year-round.

The climate diagram for Dzamiin Uuded, Mongolia (fig. 2.7*c*), is much more complex than those of either the rain forest or hot desert. This complexity results from the much greater seasonal change in the cold desert climate. Dzamiin Uuded is moist from October to April. These moist periods

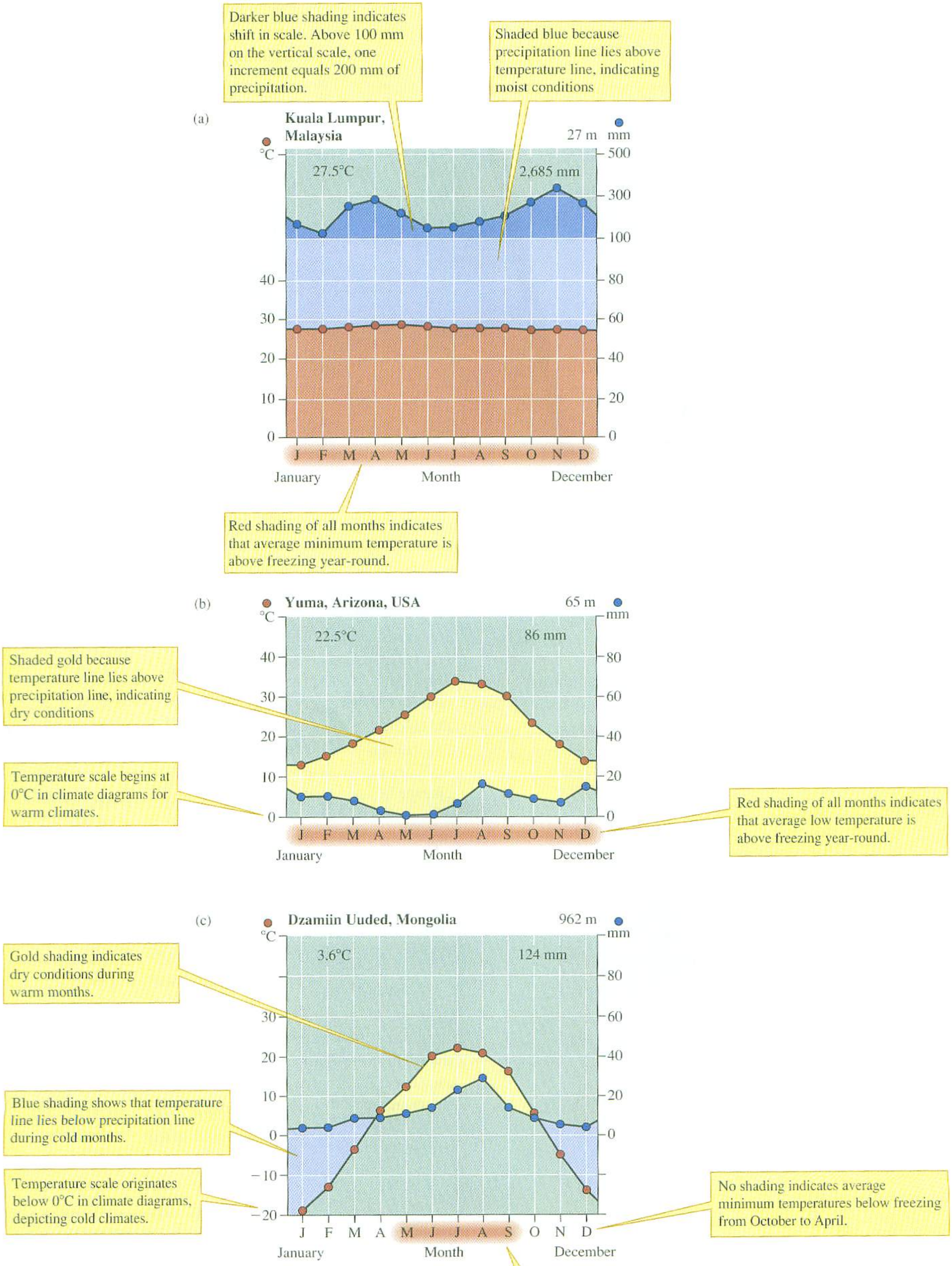


Figure 2.7 Climate diagrams for (*a*) a rain forest climate—Kuala Lumpur, Malaysia, (*b*) a hot desert climate—Yuma, Arizona, (*c*) a cold desert climate—Dzamiin Uuded, Mongolia.

Information
Hypothesis
Predictions
✓ *Testing*

Investigating the Evidence 2

Determining the Sample Mean

One of the most common and important steps in the processing of data is the production of summary statistics. First, what is a statistic? A statistic is a number that is used by scientists to estimate a measurable characteristic of an entire population. Population characteristics of interest to an ecologist might include features such as average mass, height, temperature, or growth rate. In order to determine the exact average value of such population characteristics, the ecologist would have to measure every individual in the population. Clearly, the opportunity to measure or test all the individuals in a population for any characteristic is extremely rare. For instance, an ecologist studying reproductive rate in a population of birds would be unlikely to locate and study all the nests in the population. As a consequence, ecologists generally estimate reproductive rates for birds, or other characteristics of any population, using samples drawn randomly from the population. An ecologist working with a population of rare plants, for example, might locate 11 seedlings and calculate the average height of these 11 individual plants. This average calculated from the sample of 11 seedlings would be the **sample mean.** The sample mean is a statistical estimate of the true population mean.

The sample mean is one of the most common and useful summary statistics. It is a statistic that we use extensively in this chapter as we discuss average temperature or average precipitation for biomes around the world. How is the sample mean calculated? Consider the following sample of seedling height.

Seedling number	1	2	3	4	5	6	7	8	9	10	11
Height in cm	3	6	8	7	2	4	9	4	5	7	8

What was the average height of seedlings in the population at the time of the study? Since we did not locate all the seedlings, we cannot know the true population mean, or parameter. However, our sample of 11 seedlings allows us to calculate a sample mean as follows:

Sum of measurements $= \Sigma X$

$$\Sigma X = 3 + 6 + 8 + 7 + 2 + 4 + 9 + 4 + 5 + 7 + 8$$

$$\Sigma X = 63$$

We calculate the sample mean by dividing the sum of measurements by the number of seedlings measured:

Sample mean $= \overline{X}$

$n =$ sample size, or 11

$$\overline{X} = \frac{\Sigma X}{n}$$

$$\overline{X} = \frac{63}{11}$$

$$\overline{X} = 5.7 \text{ cm}$$

Again, 5.7 cm, the sample mean, is the ecologist's estimate of the true mean height of seedlings in the entire population at the time of the study.

Critiquing the Evidence 2

1. If you measured the heights of 100 seedlings randomly drawn from the hypothetical population, instead of the 11 measured in the example, would the sample mean be likely to be exactly 5.7 cm?
2. Would the mean height of a sample of 100 seedlings likely be closer to the true population mean than the mean of a sample of 11?

are separated by the months of May to September, when the temperature line rises above the precipitation line, indicating drought. During October to April, the mean *minimum* temperature at Dzamiin Uuded is below freezing (0°C). The months when the mean minimum temperature is above freezing are May through September.

Climate diagrams also include the mean annual temperature, which is presented in the upper left corner (e.g., 27.5°C at Kuala Lumpur). The mean annual precipitation (e.g., 86 mm at Yuma, Arizona) is presented in the upper right corner of each climate diagram. The elevation of each site, in meters above sea level (e.g., 962 m at Dzamiin Uuded), is also presented in the upper right corner.

As you can see, climate diagrams efficiently summarize important environmental variables. In Concept section 2.3, we use climate diagrams to represent the climates associated with major terrestrial biomes.

Concept 2.1 Review

1. How would seasonality in temperature and precipitation be affected if earth's rotation on its axis were perpendicular to its plane of orbit about the sun?
2. Why does the annual rainy season in regions near 23° N latitude begin in June?

2.2 Soil: The Foundation of Terrestrial Biomes

Soil structure results from the long-term interaction of climate, organisms, topography, and parent mineral material. Soil is a complex mixture of living and nonliving material upon which most terrestrial life depends. Here we summarize the general features of soil structure and development. The biome discussions that follow include specific information about the soils associated with each.

Soil structure can be observed by digging a soil pit, a hole in the ground 1 to 3 m deep. In a soil pit you see one of the most significant aspects of soil structure, its vertical layering. Though soil structure usually changes gradually with depth, soil scientists generally divide soils into several discrete horizons. In the classification system used here the soil profile is divided into O, A, B, and C horizons (fig. 2.8). The **O, or organic, horizon** lies at the top of the profile. The most superficial layer of the O horizon is made up of freshly fallen organic matter, including whole leaves, twigs, and other plant parts. The deeper portions of the O horizon consist of highly fragmented and partially decomposed organic matter. Fragmentation and decomposition of the organic matter in this horizon are mainly due to the activities of soil organisms, including bacteria, fungi, and animals ranging from nematodes and mites to burrowing mammals. This horizon is usually absent in agricultural soils and deserts. At its deepest levels, the O horizon merges gradually with the A horizon.

The **A horizon** contains a mixture of mineral materials, such as clay, silt, and sand, and organic material derived from the O horizon. The A and O horizons both support high levels of biological activity. Burrowing animals, such as earthworms, mix organic matter from the O horizon into the A horizon. The A horizon is generally rich in mineral nutrients. It is gradually leached of clays, iron, aluminum, silicates, and humus, which is partially decomposed organic matter. These substances slowly move down through the soil profile until they are deposited in the B horizon.

The **B horizon** contains the clays, humus, and other materials that have been transported by water from the A horizon. The deposition of these materials often gives the B horizon a distinctive color and banding pattern. This horizon is also occupied by the roots of many plants. The B horizon gradually merges with the C horizon.

The **C horizon** is the deepest layer in our soil pit. It consists of weathered parent material, which has been worked by the actions of frost, water, and the deeper penetrating roots of plants. Weathering slowly breaks the parent material into smaller and smaller fragments to produce sand, silt, and clay-sized particles. Because weathering is incomplete and less intense than in the A and B horizons, the C horizon may contain many rock fragments. Under the C horizon we find unweathered parent material, which is often bedrock.

The soil profile gives us a snapshot of soil structure. However, soil structure is in a constant state of flux as a consequence of several influences. Those influences were summarized by Hans Jenny (1980) as climate, organisms, topography, parent material, and time. Climate affects the rate of weathering of parent materials, the rate of leaching of organic and inorganic substances, the rate of erosion and transport of mineral particles, and the rate of decomposition of organic matter. Climate also influences the kinds of vegetation and animals that occupy an area. These organisms, in turn, influence the quantity and quality of organic matter added to soil and the rate of soil mixing by burrowing animals. Topography affects the rates and direction of water flow and patterns of erosion. Meanwhile, parent materials, such as granite, volcanic rock, and wind- or water-transported sand,

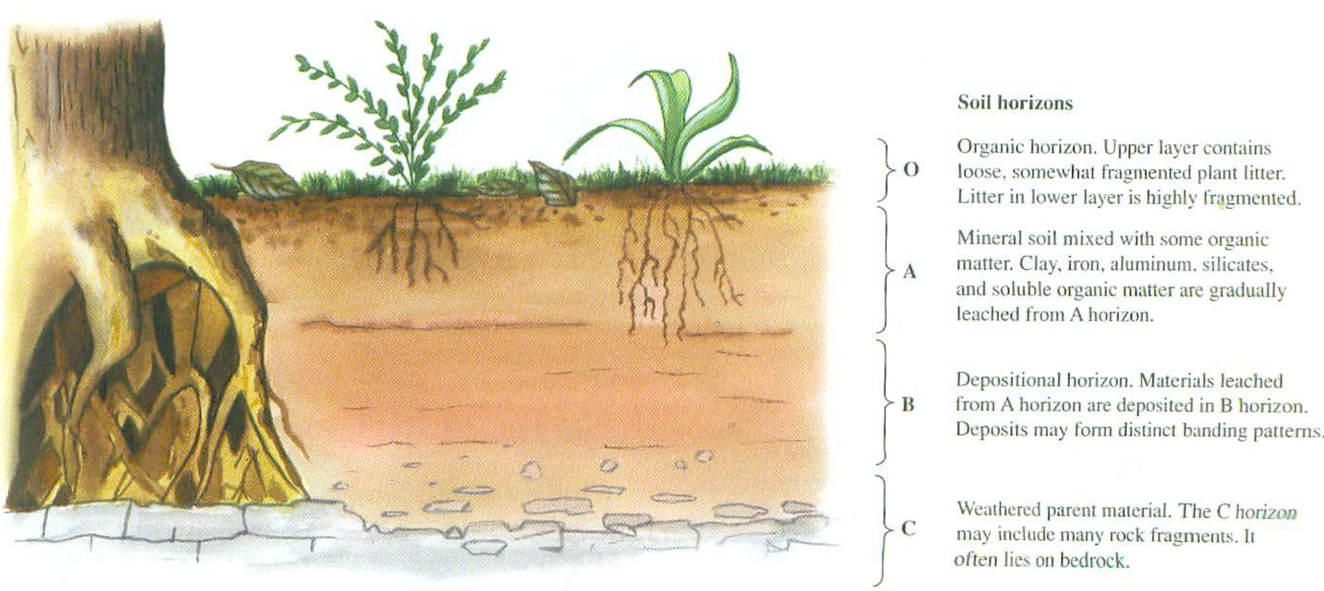


Figure 2.8 Generalized soil profile, showing O, A, B, and C horizons.

set the stage for all other influences. Last is the matter of time. Soil age influences soil structure.

In short, soil is a complex and dynamic entity. It forms the medium in which organisms grow, and the activities of those organisms, in turn, affect soil structure. As with many aspects of ecology, it is often difficult to separate organisms from their environment. The biome discussions that follow provide additional information on soils by including aspects of soil structure and chemistry characteristic of each biome.

Concept 2.2 Review

1. The organic horizon is generally absent from agricultural soils because tilling, e.g., plowing, buries organic matter. Why is an organic horizon generally absent from desert soils?

2.3 Natural History and Geography of Biomes

The geographic distribution of terrestrial biomes corresponds closely to variation in climate, especially prevailing temperature and precipitation. Early in the twentieth century, many plant ecologists studied how climate and soils influence the distribution of vegetation. Later ecologists concentrated on other aspects of plant ecology. Today, as we face the prospect of global warming (see chapter 23), ecologists are once again studying climatic influences on the distribution of vegetation. International teams of ecologists, geographers, and climatologists are exploring the influences of climate on vegetation with renewed interest and with much more powerful analytical tools.

In this section, we discuss the climate, soils, and organisms of the earth's major biomes and how they have been influenced by humans. However, don't be concerned if you know of some places that don't quite fit any of the biomes discussed. For instance, though our focus is on the biomes that occur in the absence of human disturbance, many of these regions now contain only remnants of their natural plant and animal associations. Though biomes are presented here as distinctive entities, they change gradually along environmental gradients. In addition, no two rain forests are exactly alike, nor are any two prairies or deserts. Discovery of the full extent of nature's diversity and of the mechanisms that produce and maintain that diversity remains an uncompleted task for future ecologists—perhaps for you. Now, let's have a look at natural history around the globe.

Tropical Rain Forest

Tropical rain forest is nature's most extravagant garden (fig. 2.9). Beyond its tangled edge, a rain forest opens into a surprisingly spacious interior, illuminated by dim greenish light shining through a ceiling of leaves. High above towers the forest canopy, home to many rain forest species and the aerial laboratory of a few intrepid rain forest ecologists (see fig. 1.4). The architecture of rain forests, with their vaulted ceilings and spires, has invited comparisons to cathedrals and mansions. However, this cathedral is alive from ceiling to floor, perhaps more alive than any other biome on the planet. In the rain forest, the sounds of evening and morning, the brilliant flashes of color, and rich scents carried on moist night air speak of abundant life, in seemingly endless variety.

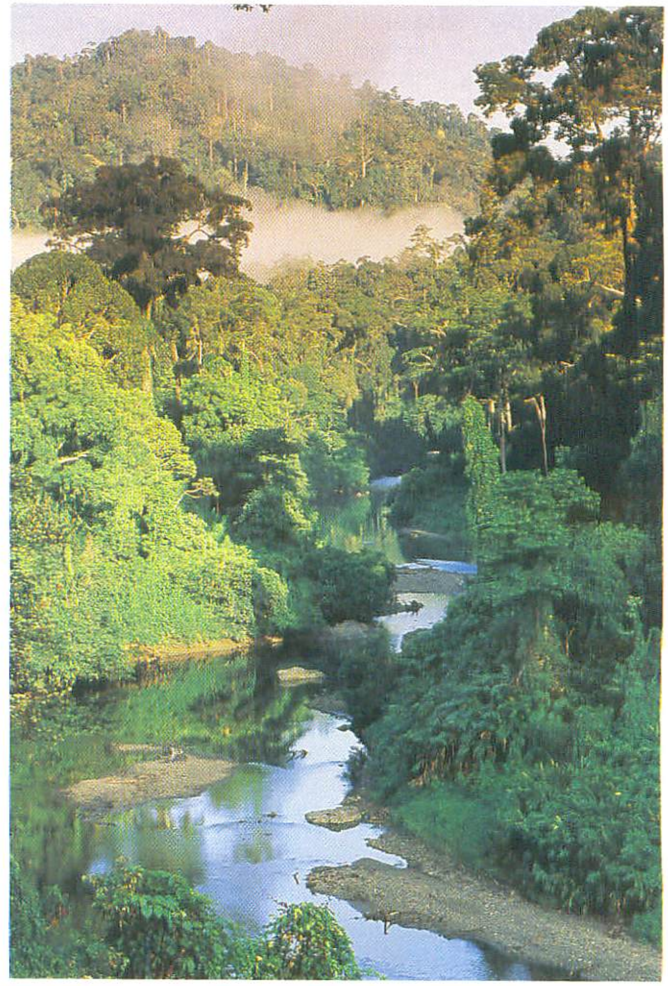


Figure 2.9 Tropical rain forest in Borneo. More species live within the three-dimensional framework of tropical rain forests than in any other terrestrial biome.

Geography

Tropical rain forests straddle the equator in three major regions: Southeast Asia, West Africa, and South and Central America (fig. 2.10). Most rain forest occurs within 10° of latitude north or south of the equator. Outside this equatorial band are the rain forests of Central America and Mexico, southeastern Brazil, eastern Madagascar, southern India, and northeastern Australia.

Climate

The global distribution of rain forests corresponds to areas where conditions are warm and wet year-round (fig. 2.10). Temperatures in tropical rain forests vary little from month

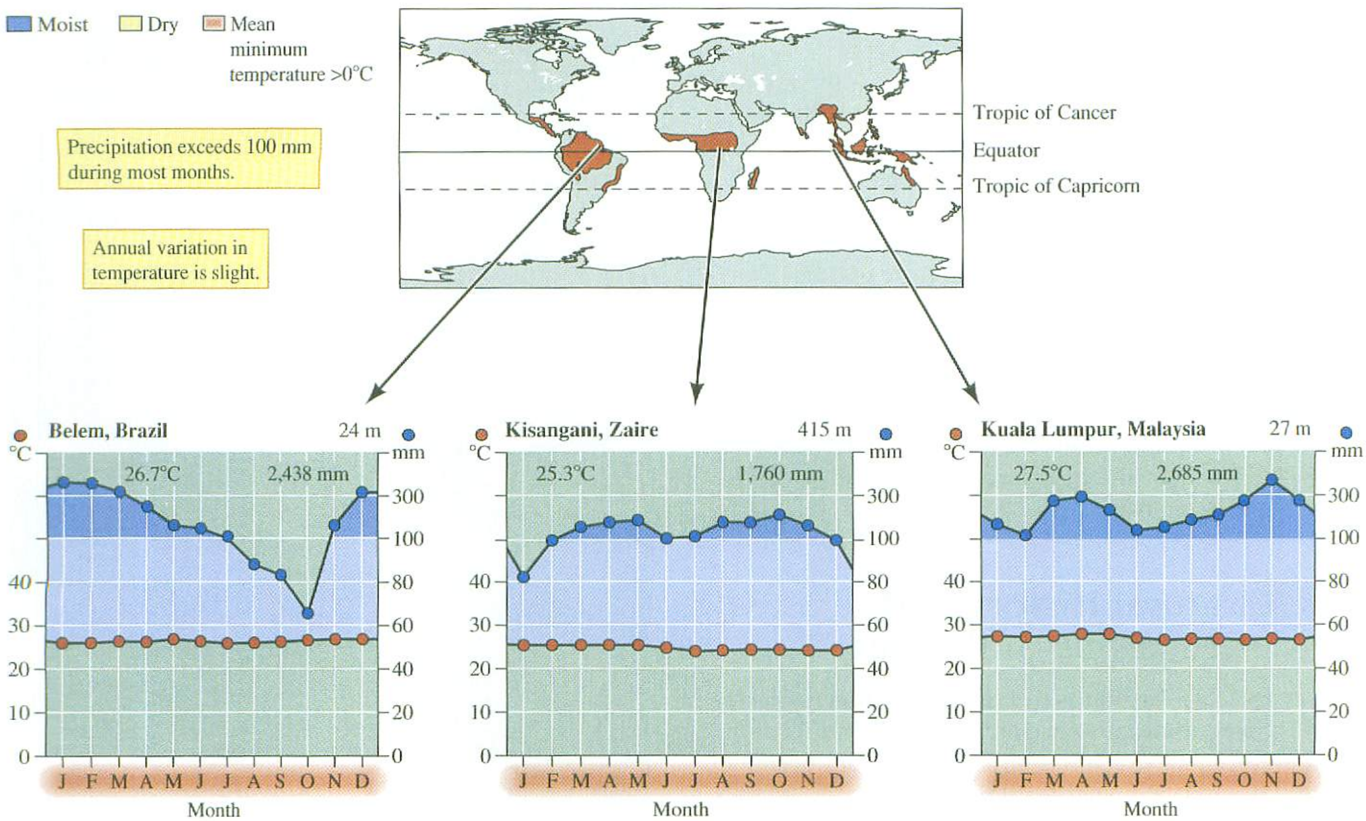


Figure 2.10 Tropical rain forest geography and climate.

to month and often change as much in a day as they do over the entire year. Average temperatures are about 25° to 27°C, lower than average maximum summer temperatures in many deserts and temperate regions. Annual rainfall ranges from about 2,000 to 4,000 mm, and some rain forests receive even more precipitation. In a rain forest, a month with less than 100 mm of rain is considered dry.

Soils

Heavy rains gradually leach nutrients from rain forest soils and rapid decomposition in the warm, moist rain forest climate keeps the quantity of soil organic matter low. Consequently, rain forest soils are often nutrient-poor, acidic, thin, and low in organic matter. In many rain forests, more nutrients are tied up in living tissue than in soil. Some rain forests, however, occur where soils are very fertile. For instance, rain forests grow on young volcanic soils that have not yet been leached of their nutrients by heavy tropical rains. Fertile rain forest soils also occur along rivers, where a fresh nutrient supply is delivered with each flood. Rain forest plants are adept at conserving nutrients. They get help in gathering nutrients from infertile soils from fungi associated with their roots, through mutually beneficial partnerships called **mycorrhizae.** Free-living fungi, bacteria, and soil animals, such as mites and springtails, rapidly scavenge nutrients from plant litter (leaves, flowers, etc.) and animal wastes, further tightening the nutrient economy of the rain forest.

Biology

Many organisms in the rain forest have evolved to use the vertical dimension provided by trees. Trees dominate the rain forest landscape and average about 40 m in height. However, some reach 50, 60, or even 80 m tall. The massive weight of these rain forest giants is often supported by well-developed buttresses. The diversity of rain forest trees is also impressive. One hectare (100 m × 100 m) of temperate forest may contain a few dozen tree species; 1 ha of tropical rain forest may contain up to 300 tree species.

The three-dimensional framework formed by rain forest trees is festooned with other plant growth forms. The trees are trellises for climbing vines and growing sites for epiphytes, plants that grow on other plants (fig. 2.11). The great diversity and sheer mass of epiphytes and vines give an impression of great biological richness, of a forest teeming with life. Look closely at rain forest animals and that impression is amplified. A single rain forest tree may support several thousand species of insects, many of which have not been described by scientists.

The rain forest is not, however, just a warehouse for a large number of dissociated species. Rain forest ecology is marked by intricate, complex relationships between species. In the tropical rain forest there are plants that cannot live without particular species of ants, mites that make their homes in the flowers of plants and depend on hummingbirds to get them from flower to flower, and there are trees and vines that compete continuously for light and space.

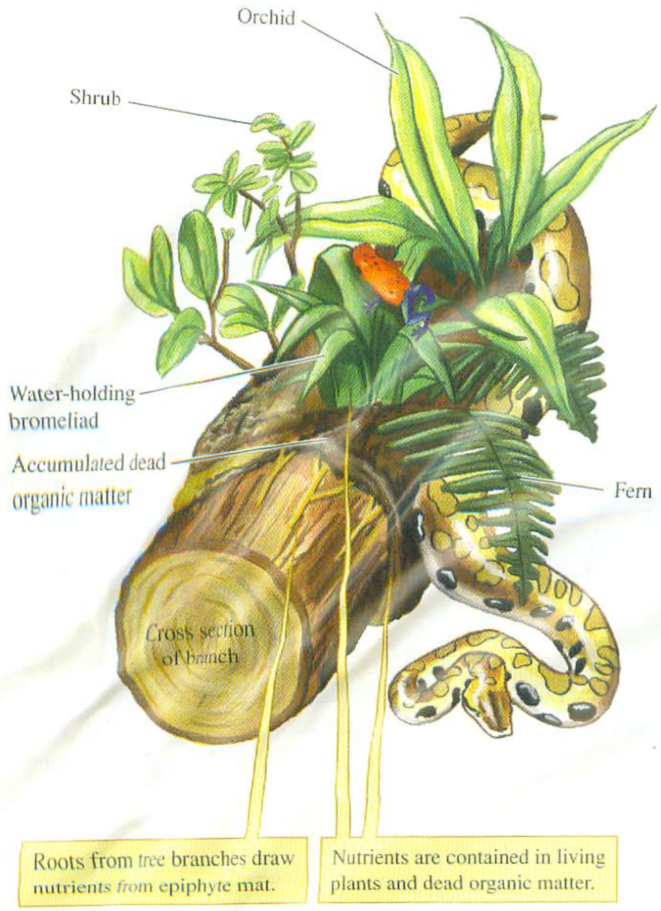


Figure 2.11 An epiphyte mat in the tropical rain forest canopy. Epiphyte mats store a substantial fraction of the nutrients in tropical rain forests and support a high diversity of plant and animal species.

Human Influences

People from all over the globe owe more to the tropics than is generally realized. Many of the world's staple foods, including maize (called corn in North America and Australia), rice, bananas, and sugarcane, and approximately 25% of all prescription drugs, were originally derived from tropical plants. Many more species, directly useful to humans, may await discovery. In addition, the tropics continue to harbor important genetic varieties of domesticated plant species. Unfortunately, tropical rain forests are fast disappearing. Without them, our understanding of the causes and maintenance of biological diversity will remain forever impoverished.

Tropical Dry Forest

During the dry season, the **tropical dry forest** is all earth tones; in the rainy season, it's an emerald tangle (fig. 2.12). Life in the tropical dry forest responds to the rhythms of the annual solar cycle, which drives the oscillation between wet and dry seasons. During the dry season, most trees in the tropical dry forest are dormant. Then, as the rains approach, trees flower and insects appear to pollinate them. The pace of life quickens. Eventually, as the first storms of the wet season arrive, the trees produce their leaves and transform the landscape.

Geography

Tropical dry forests occupy a substantial portion of the earth's surface between about 10° and 25° latitude (fig. 2.13). In Africa, tropical dry forests are found both north and south of the central African rain forests. In the Americas, tropical dry forests are the natural vegetation of extensive areas south and north of the Amazon rain forest. Tropical dry forests also extend up the west coast of Central America and into North America along the west coast of Mexico. In Asia, tropical dry

Figure 2.12 Tropical dry forest in the Galápagos Islands during the wet and dry seasons.

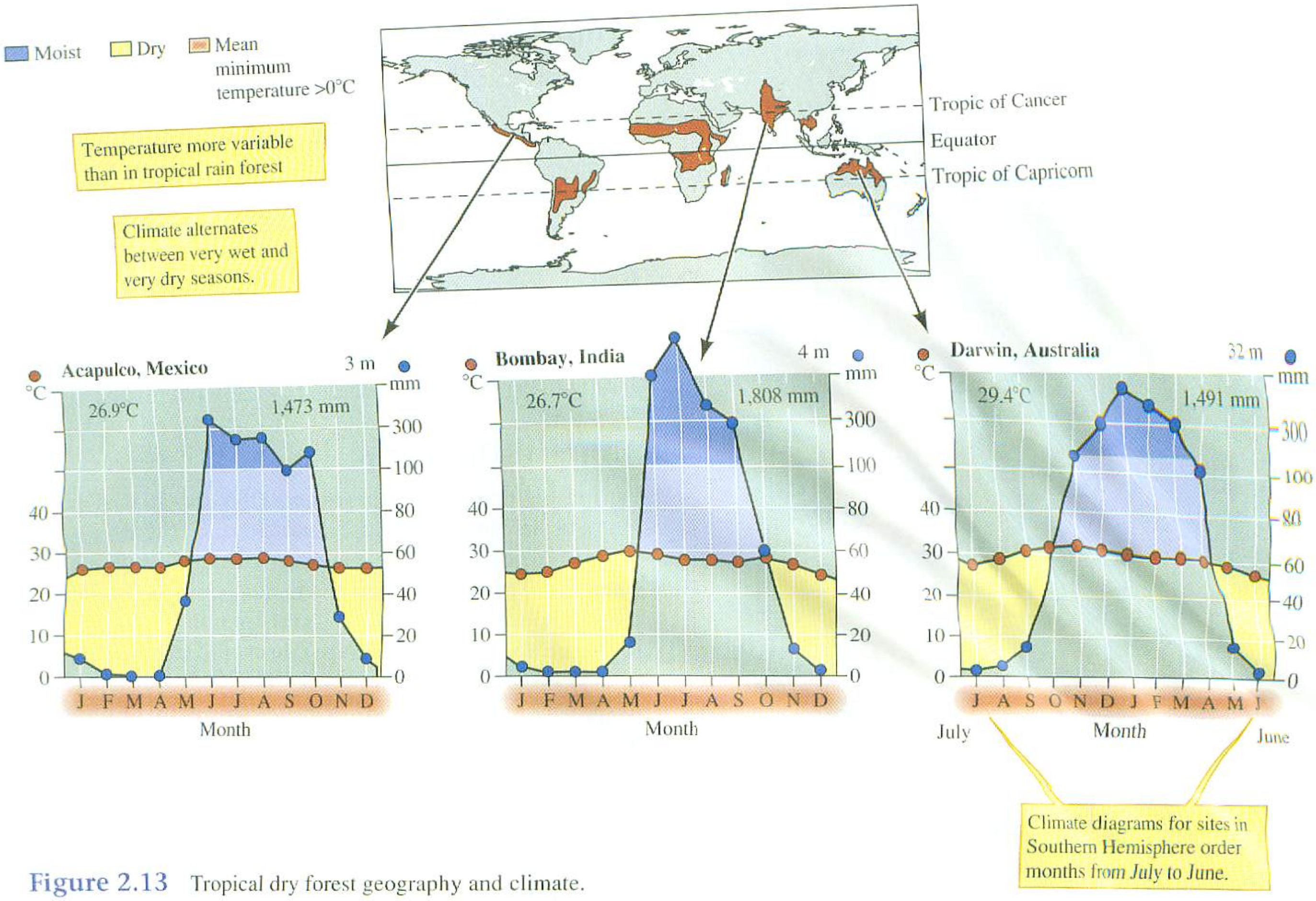


Figure 2.13 Tropical dry forest geography and climate.

forests are the natural vegetation of most of India and the Indochina peninsula. Australian tropical dry forests form a continuous band across the northern and northeastern portions of the continent.

Climate

The climate of tropical dry forests is more seasonal than that of tropical rain forests. The three climate diagrams shown in figure 2.13, for example, show a dry season lasting for 6 to 7 months, followed by a season of abundant rainfall, lasting 5 to 6 months. The climate diagrams also indicate more seasonal variation in temperature compared to tropical rain forest.

Soils

The soils of many tropical dry forests are of great age, particularly those in the parts of Africa, Australia, India, and Brazil that were once part of the ancient southern continent of Gondwana. The soils of tropical dry forests tend to be less acidic than those of rain forests and are generally richer in nutrients. However, the annual pulses of torrential rain make the soils of tropical dry forest highly vulnerable to erosion, particularly when deforested and converted to agriculture.

Biology

The plants of the tropical dry forest are strongly influenced by physical factors. For example, the height of the dry forest is highly correlated with average precipitation. Trees are tallest in the wettest areas. In the driest habitats, all trees drop their leaves during the dry season; in wetter areas over 50% may be evergreen. As in the tropical rain forest, many plants produce animal-dispersed seeds. However, wind-dispersed seeds are also common. Many dry forest birds, mammals, and even insects make seasonal migrations to wetter habitats along rivers or to the nearest rain forest.

Human Influences

Peter Murphy and Ariel Lugo (1986) studied the patterns of human settlement in the tropical forests of Central America, dividing the types of forests into rain forest, wet forest, moist forest, dry forest, and very dry forest. As figure 2.14 shows, the population density—the number of people per square kilometer—in tropical dry and moist forests is more than 10 times higher than in tropical wet and rain forests.

Heavy human settlement has devastated the tropical dry forest. While the world's attention has been focused on the plight of rain forests, intact tropical dry forests have nearly disappeared. The relatively fertile soil of tropical dry forests has attracted agricultural development. People have replaced tropical dry forests with cattle ranches, grain farms, and cotton fields. In addition, tropical dry forests are more vulnerable to human exploitation than tropical rain forests because the dry season makes them more accessible and easier to burn.

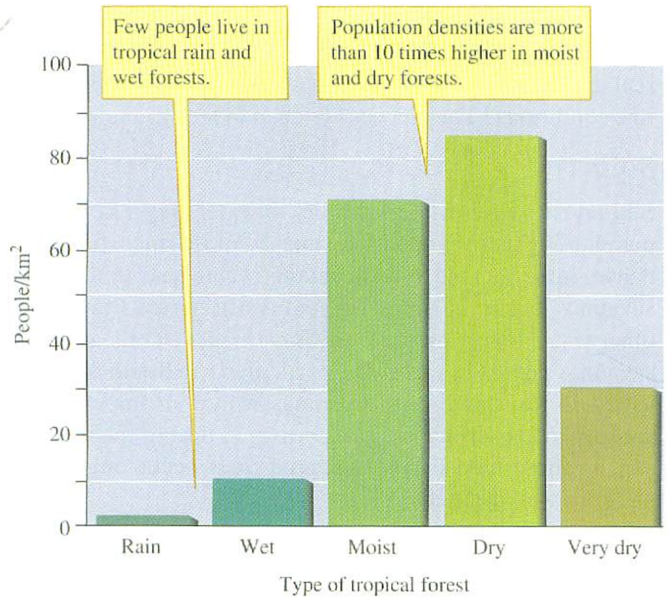


Figure 2.14 Human population density in the tropical forests of Central America (data from Murphy and Lugo 1986, after Tosi and Voertman 1964).

The loss of the dry forest is significant because, while rain forests may support a somewhat greater number of species, many dry forest species are found nowhere else. However, out of this devastation has come Guanacaste National Park in Costa Rica, a model attempt to restore a tropical dry forest in a way that also helps serve the cultural and economic needs of local people (see the introduction to chapter 2).

Tropical Savanna

Stand in the middle of a savanna, a tropical grassland dotted with scattered trees, and your eye will be drawn to the horizon for the approach of thunderstorms or wandering herds of wildlife (fig. 2.15). The **tropical savanna** is the kingdom of the farsighted, the stealthy, and the swift and is the birthplace of humankind. It was from here that humans eventually moved out into every biome on the face of the earth. Now, most humans live away from this first home. The first naturalists, our ancient ancestors, knew the tropical savanna biome best, and the fascination continues.

Geography

Most tropical savannas occur north and south of tropical dry forests within 10° to 20° of the equator. In Africa south of the

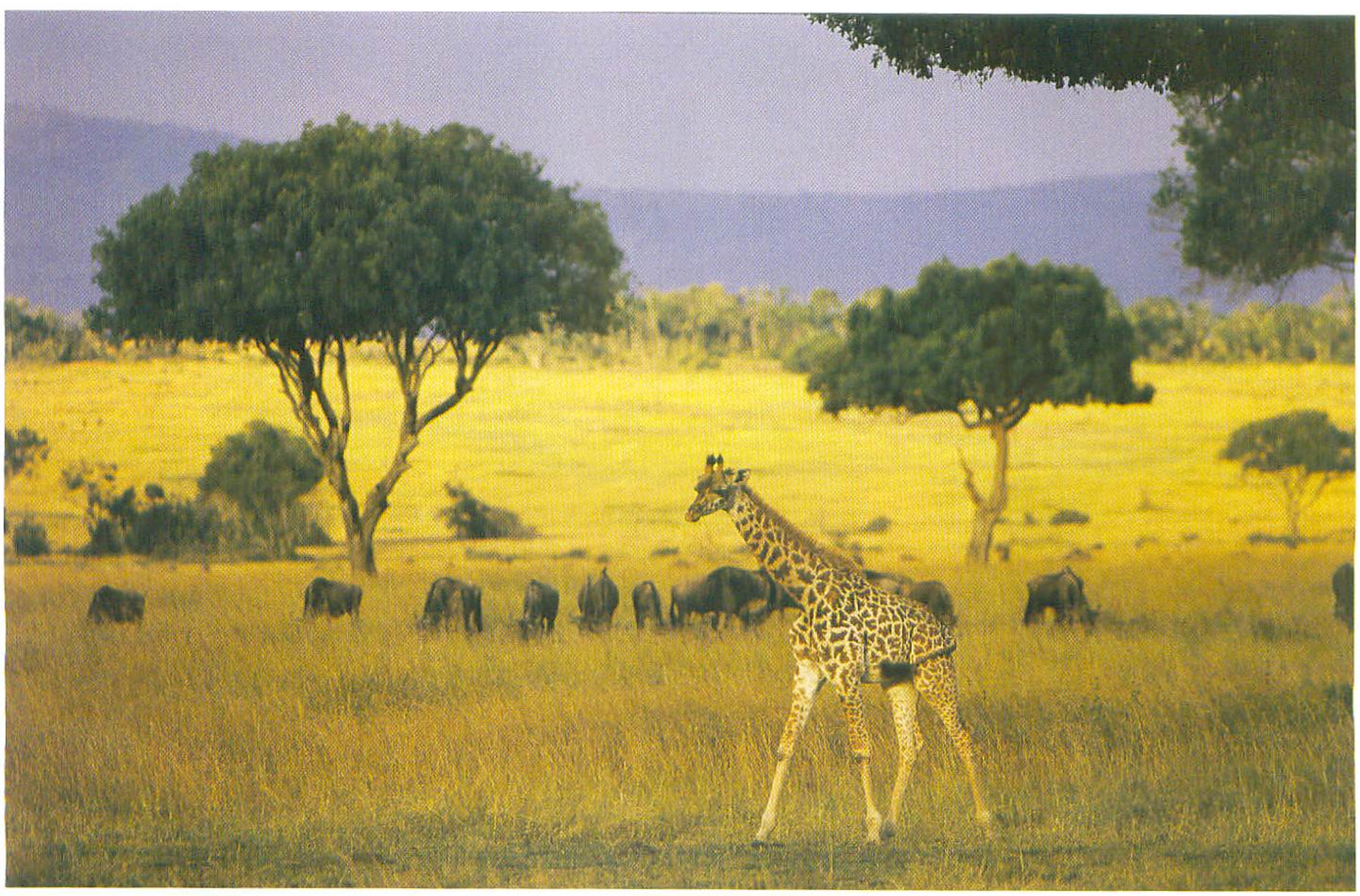


Figure 2.15 Tropical savanna and herbivores in Kenya. The tropical savanna landscape is partially maintained by periodic fires that help control the density of woody vegetation.

Sahara Desert, tropical savannas extend from the west to the east coasts, cut a north–south swath across the east African highlands, and reappear in south-central Africa (fig. 2.16). In South America, tropical savannas occur in south-central Brazil and cover a great deal of Venezuela and Columbia. Tropical savannas are also the natural vegetation of much of northern Australia in the region just south of the tropical dry forest. Savanna is also the natural vegetation of an area in southern Asia just east of the Indus River in eastern Pakistan and northwestern India.

Climate

As in the tropical dry forest, life on the savanna cycles to the rhythms of alternating dry and wet seasons (fig. 2.16). Here, however, seasonal drought combines with another important physical factor, fire. The rains come in summer and are accompanied by intense lightning. This lightning often starts fires, particularly at the beginning of the wet season when the savanna is tinder dry. These fires kill young trees while the grasses survive and quickly resprout. Consequently, fires help maintain the tropical savanna as a landscape of grassland and scattered trees.

The savanna climate is generally drier than that of tropical dry forest (fig. 2.16). However, San Fernando, Venezuela (fig. 2.16) receives as much rainfall as a tropical dry forest. Other savannas occur in areas that are as dry as deserts. What keeps the wet savannas near San Fernando from being replaced by forest and how can savannas persist under desert-like conditions? The answer lies deep in the savanna soils.

Soils

Soil layers with low permeability to water play a key role in maintaining many tropical savannas. For instance, because a dense, impermeable subsoil retains water near the surface, savannas occur in areas of southwest Africa that would otherwise support only desert. Impermeable soils also help savannas persist in wet areas, particularly in South America. Trees do not move onto savannas where an impermeable subsoil keeps surface soils waterlogged during the wet season. In these landscapes, scattered trees occur only where soils are well drained.

Biology

As you gaze out across the savanna landscape, think back to the tropical rain forest and dry forest. How is the savanna different? One difference is that trees don't completely dominate the landscape. Consequently, a greater proportion of the biological activity on the savanna takes place near ground level. Frequent fires have selected for fire resistance in the savanna flora. The few tree species on the savanna

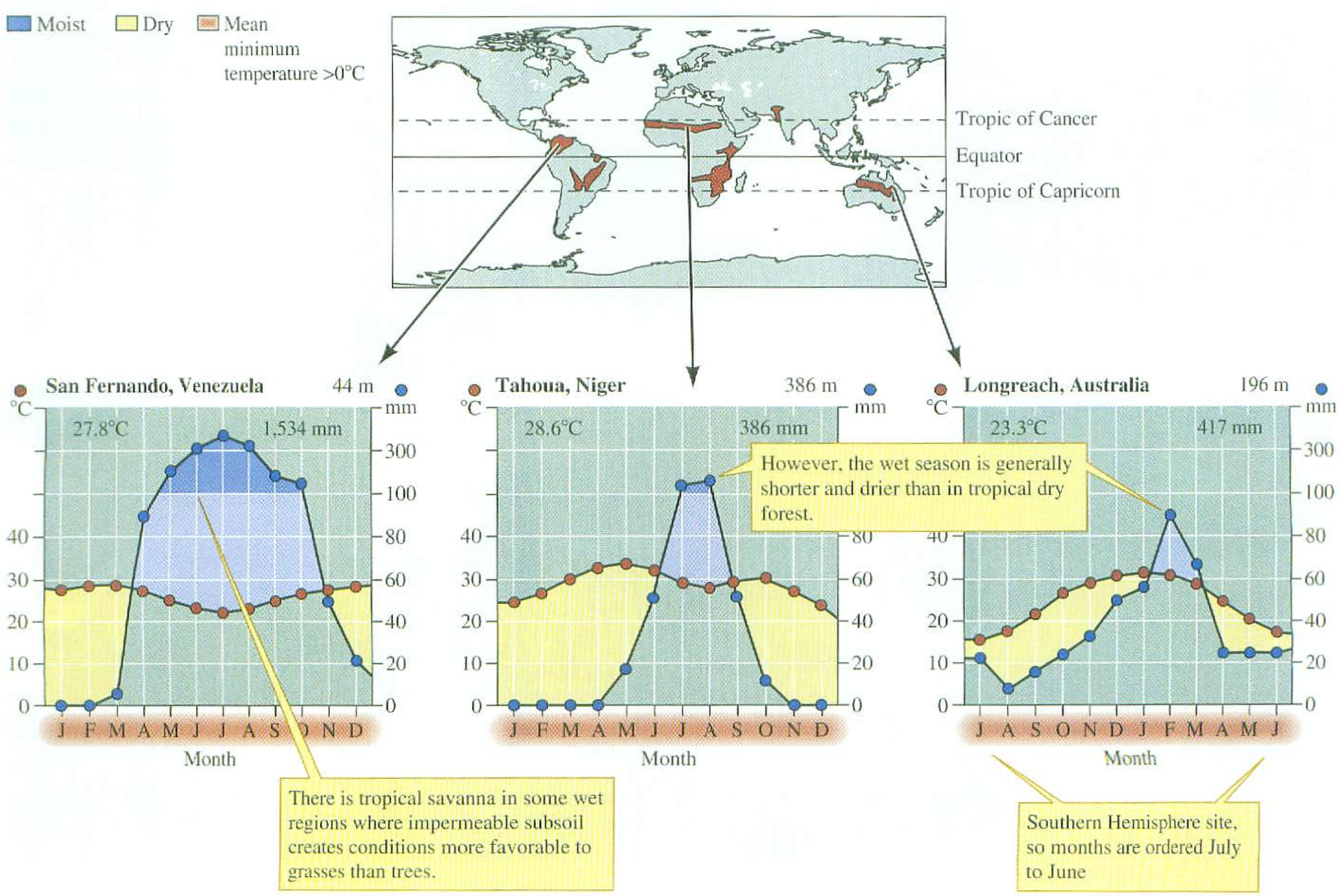


Figure 2.16 Tropical savanna geography and climate.

resist fire well enough to be unaffected by low-intensity fires.

The tropical savanna is populated by wandering animals that move in response to seasonal and year-to-year variations in rainfall and food availability. The wandering consumers of the Australian savannas include kangaroos, large flocks of birds, and, for at least 40,000 years, humans. During droughts, some of these Australian species travel thousands of kilometers in search of suitable conditions. The African savanna is home to a host of well-known mobile consumers, such as elephants, wildebeest, giraffes, zebras, lions, and, again, humans (see fig. 2.15).

Human Influences

Humans are, in some measure, a product of the savanna and the savanna, in turn, has been influenced by human activity. One of the factors that forged an indelible link between us and this biome is fire. Long before the appearance of hominids, fire played a role in the ecology of the tropical savanna. Later, the savanna was the classroom where early humans observed and learned to use, control, and make fire. Eventually, humans began to purposely set fire to the savanna, which, in turn, helped to maintain and spread the savanna itself. We had entered the business of large-scale manipulation of nature.

Originally, humans subsisted on the savanna by hunting and gathering. In time, they shifted from hunting to pastoralism, replacing wild game with domestic grazers and browsers. Today, livestock ranching is the main source of livelihood in all the savanna regions. In Africa, livestock raising has coexisted with wildlife for millennia. In modern-day subsaharan Africa, however, the combination of growing human populations, high density of livestock, and drought has devastated much of the region known as the Sahel (fig. 2.17).

Figure 2.17 Domestic livestock, such as these cattle on an African savanna, have had a major impact on tropical savannas around the world.

Desert

In the spare **desert** landscape, sculpted by wind and water, the ecologist grows to appreciate geology, hydrology, and climate as much as organisms (fig. 2.18). In the desert, drought and flash floods, and heat and bitter cold, often go hand in hand. Yet, the often repeated description of life in the desert as "life on the edge" betrays an outsider's view. Life in the desert is not luxuriant, but it does not follow that living

Figure 2.18 Life on the edge. Two dormant acacia trees living on the boundary between gravel plain and sand dunes in the Namib Desert of southwestern Africa.

conditions there are necessarily harsh. For many species, the desert is the center of their world, not the edge. In their own way, many desert organisms flourish on meager rations of water, high temperatures, and saline soils. To understand life in the desert, the ecologist must see it from the perspective of its natural inhabitants. The ecologist who can peer out at the desert environment from under the skin of a cactus or sand viper is on the threshold of understanding.

Geography

Deserts occupy about 20% of the land surface of the earth. Two bands of deserts ring the globe, one at about 30° N latitude and one at about 30° S (fig. 2.19). These bands correspond to latitudes where dry subtropical air descends (see fig. 2.4), drying the landscape as it spreads north and south. Other deserts are found either deep in the interior of continents, for example, the Gobi of central Asia, or in the rain shadow of mountains, for example, the Great Basin Desert of North America. Still others are found along the cool western coasts of continents, for example, the Atacama of South America and the Namib of southwestern Africa, where air circulating across a cool ocean delivers a great deal of fog to the coast but little rain.

Climate

Environmental conditions vary considerably from one desert to another. Some, such as the Atacama and central Sahara, receive very little rainfall and fit the stereotype of deserts as extremely dry places. Other deserts, such as some parts of the Sonoran Desert of North America, may receive nearly 300 mm of rainfall annually. Whatever their mean annual rainfall, however, water loss in deserts due to evaporation and transpiration by plants exceeds precipitation during most of the year.

Figure 2.19 includes the climate diagrams of two hot deserts. Notice that drought conditions prevail during all months and that during some months average temperatures exceed 30°C. The maximum shade temperatures in any biome, greater than 56°C, were recorded in the deserts of North Africa and western North America. However, some deserts can be bitterly cold. For example, average winter temperatures at Dzamiin Uuded, Mongolia, in the Gobi Desert of central Asia sometimes fall to −20°C (fig. 2.19).

Soils

Desert plants and animals can turn this landscape into a mosaic of diverse soils. Desert soils are generally so low in organic matter that they are sometimes classified as **lithosols,** which means stone or mineral soil. However, the soils under desert shrubs often contain large amounts of organic matter and form islands of fertility. Desert animals can also affect soil properties. For example, in North America, kangaroo rats change the texture and elevate the nutrient content of surface

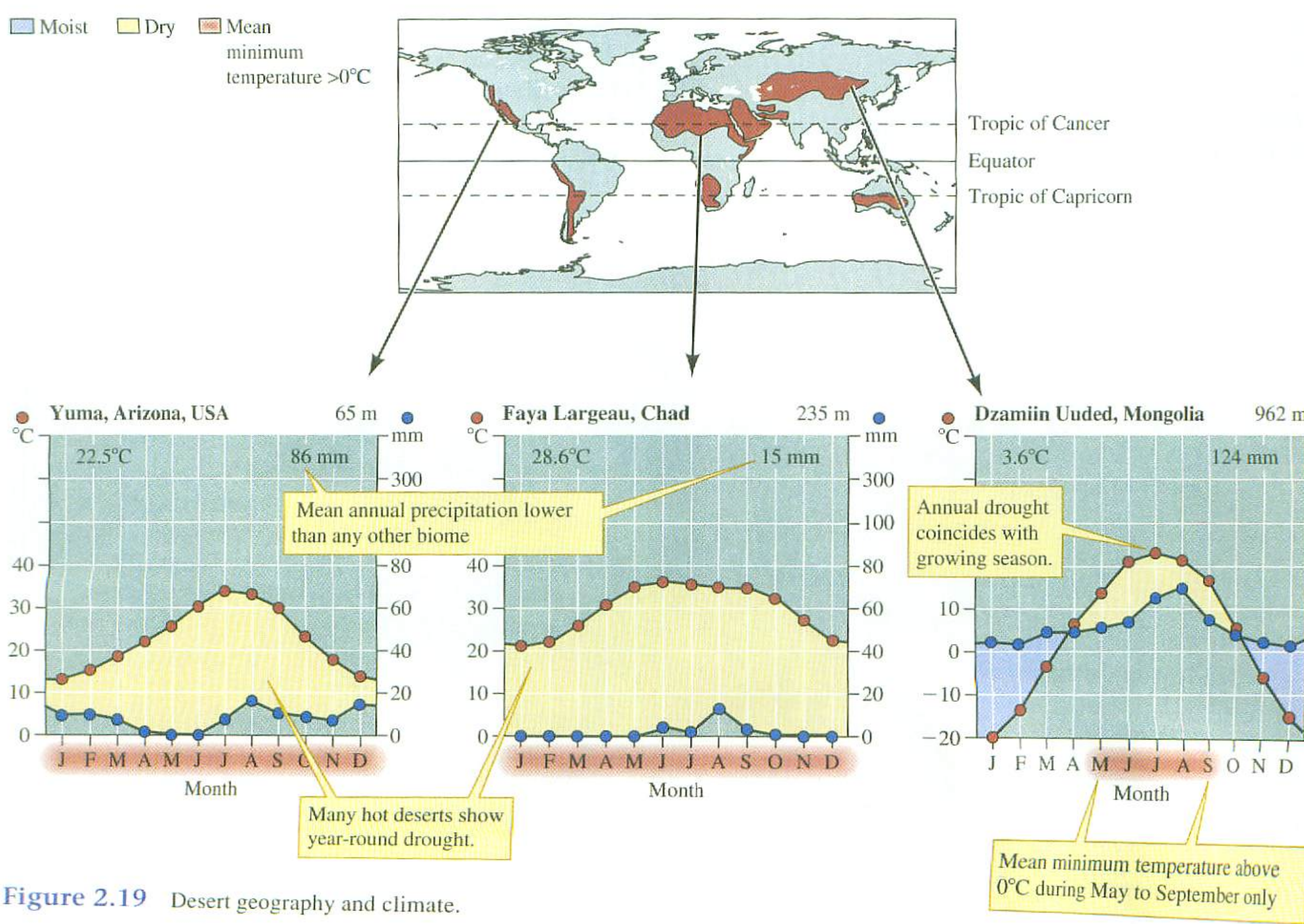
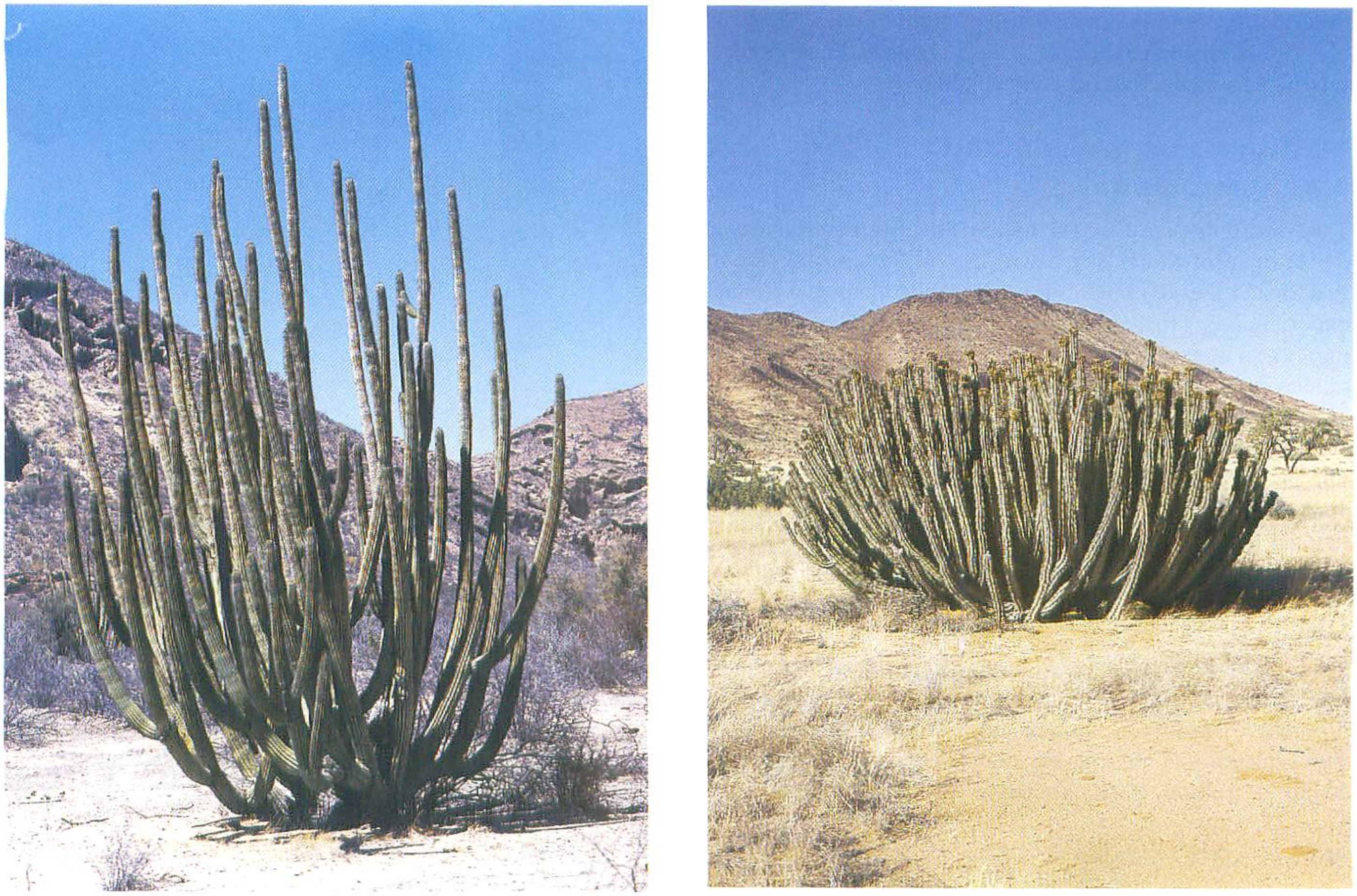


Figure 2.19 Desert geography and climate.



(a) (b)

Figure 2.20 Similarity among desert plants: (*a*) cactus in North America, (*b*) *Euphorbia* in Africa.

soils by burrowing and hoarding seeds. In Middle Eastern deserts, porcupines and isopods strongly influence a variety of soil properties.

Desert soils, particularly those in poorly drained valleys and lowlands, may contain high concentrations of salts. Salts accumulate in these soils as water evaporates from the soil surface, leaving behind any salts that were dissolved in the water. Salt accumulation increases the aridity of the desert environment by making it harder for plants to extract water from the soils. As desert soils age they tend to form a calcium carbonate–rich hardpan horizon called **caliche.** The extent of caliche formation has proved a useful tool for aging these soils.

Biology

The desert landscape presents an unfamiliar face to the visitor from moist climates. Plant cover is absent from many places, exposing soils and other geological features. Where there is plant cover, it is sparse. The plants themselves look unfamiliar. Desert vegetation often cloaks the landscape in a gray-green mantle. This is because many desert plants protect their photosynthetic surfaces from intense sunlight and reduce evaporative water losses with a dense covering of plant hairs. Other plant adaptations to drought include small leaves, producing leaves only in response to rainfall and then dropping them during intervening dry periods, or having no leaves at all (fig. 2.20). Some desert plants avoid drought almost entirely by remaining dormant in the soil as seeds, which germinate and grow only during infrequent wet periods.

In deserts, animal abundance tends to be low but diversity can be high. Most desert animals use behavior to avoid environmental extremes. In summer, many avoid the heat of the day by being active at dusk and dawn or at night. In winter, the same species may be active during the day. Animals (as well as plants) use body orientation to minimize heat gain in the summer.

Human Influences

Desert peoples have flourished where nature is stingiest. Compared to true desert species, however, humans are profligate water users. Consequently, human populations in desert regions are concentrated around oases and river valleys. Many desert landscapes that once supported irrigated agriculture now grow little as a result of salt accumulation in their soils.

The desert is the one biome that, because of human activity, is increasing in area. We must stop the spread of deserts that comes at the expense of other biomes. We must also establish a balanced use of deserts that safeguards their inhabitants, human and nonhuman alike.

Mediterranean Woodland and Shrubland

The **Mediterranean woodland and shrubland** climate was the climate of the classical Greeks and the coastal Native American tribes of Old California. The mild temperate climate experienced by these cultures was accompanied by high biological richness (fig. 2.21). The richness of the Mediterranean woodland flora is captured by a folk song from the Mediterranean region that begins: "Spring has already arrived. All the countryside will bloom; a feast of color!" To this visual feast, Mediterranean woodlands and shrublands around the Mediterranean Sea add a chorus of bird song and the smells of aromatic plants, including rosemary, thyme, and laurel.

Figure 2.21 A Mediterranean woodland in California shown during the cool moist season, when the herbaceous vegetation is green.

Geography

Mediterranean woodlands and shrublands occur on all the continents except Antarctica (fig. 2.22). They are most extensive around the Mediterranean Sea and in North America, where they extend from California into northern Mexico. They are also found in central Chile, southern Australia, and southern Africa. Under present climatic conditions Mediterranean woodlands and shrublands grow between about 30° and 40° latitude. This position places the majority of this biome north of

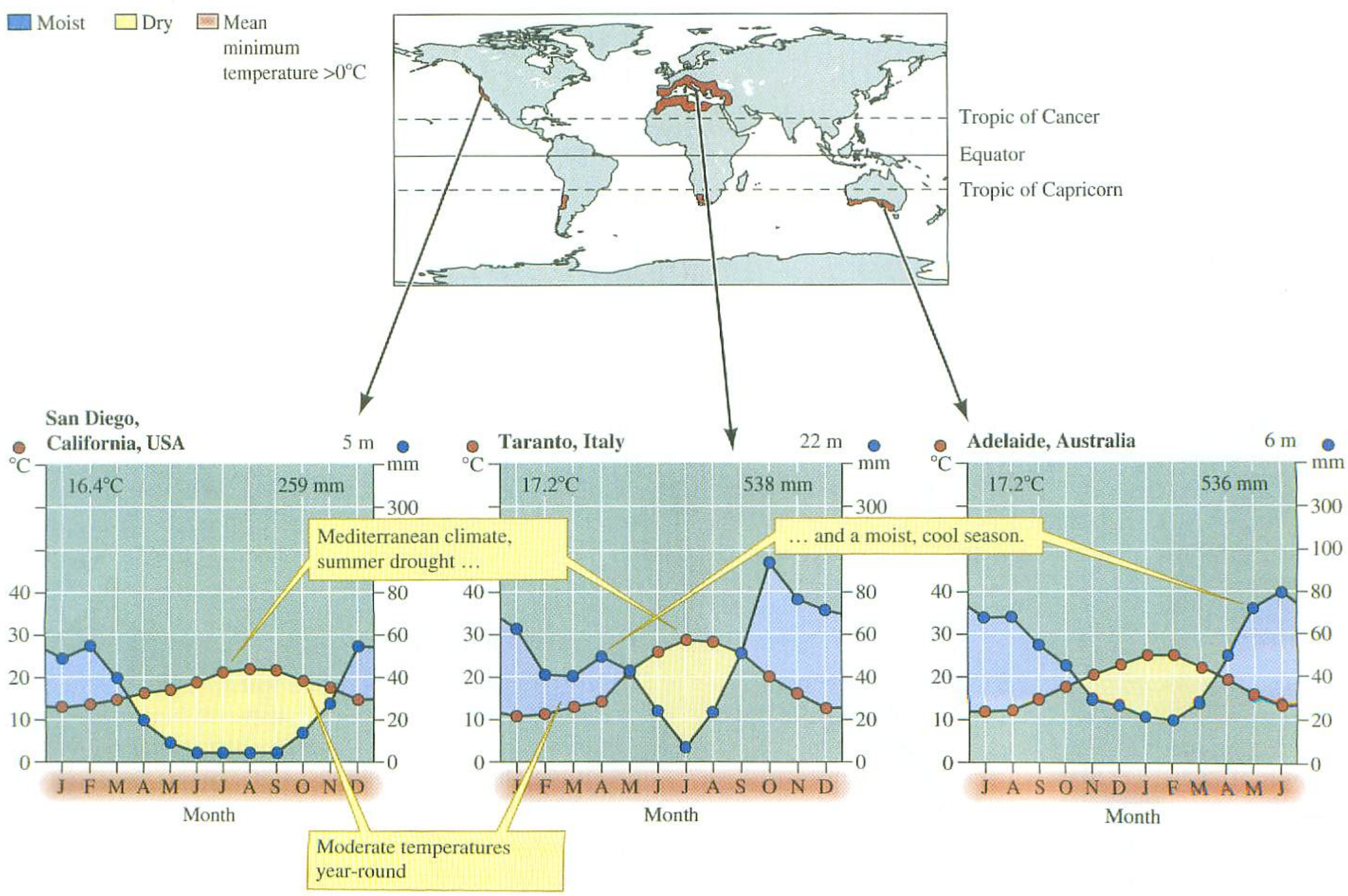


Figure 2.22 Mediterranean woodland and shrubland geography and climate.

the subtropical deserts in the Northern Hemisphere, and south of them in the Southern Hemisphere. The farflung geographic distribution of Mediterranean woodland and shrubland is reflected in the diversity of names for this biome. In western North America, it is called chaparral. In Spain, the most common name for Mediterranean woodland and shrubland is *matoral*. Farther east in the Mediterranean basin the biome is referred to as *garrigue*. Meanwhile in the Southern Hemisphere, South Africans call the biome *fynbos*, while Australians refer to at least one form of it as *mallee*. While the names for this biome vary widely, its climate does not.

Climate

The Mediterranean woodland and shrubland climate is cool and moist during fall, winter, and spring. In most regions the Mediterranean woodland and shrubland summers are hot and dry. The danger of frost varies considerably from one Mediterranean woodland and shrubland region to another. When they do occur, however, frosts are usually not severe. The combination of dry summers and dense vegetation, rich in essential oils, creates ideal conditions for frequent and intense fires.

Soils

The soils of Mediterranean woodlands and shrublands are generally of low to moderate fertility and have a reputation for being fragile. Some soils, such as those of the South African fynbos, have exceptionally low fertility. Soil erosion can be severe following fires. Fire coupled with overgrazing has stripped the soil from some Mediterranean woodland and shrubland landscapes. Elsewhere, these landscapes, under careful stewardship, have maintained their integrity for thousands of years.

Biology

The plants and animals of Mediterranean woodlands and shrublands are highly diverse, and like their desert neighbors, show several adaptations to drought. Trees and shrubs are typically evergreen and have small, tough leaves, which conserve both water and nutrients. Many plants of Mediterranean woodlands and shrublands have well-developed mutualistic relationships with microbes that fix atmospheric nitrogen.

The process of decomposition is greatly slowed during the dry summer and then started again with the coming of fall and winter rains. Curiously, this intermittent decomposition may speed the process sufficiently so that average rates of decomposition are comparable to those in temperate forests.

Fire, a common occurrence in Mediterranean woodlands and shrublands, has selected for fire-resistant plants. Many Mediterranean woodland trees have thick, tough bark that is resistant to fire (fig. 2.23). In contrast, many shrubs in Mediterranean woodlands are rich in oils and burn readily but resprout rapidly. Most herbaceous plants grow during the cool, moist season and then die back in summer, thus avoiding both drought and fire.

Figure 2.23 The thick bark of the Mediterranean cork oak protects the tree from fire.

Human Influences

Human activity has had a substantial influence on the structure of landscapes in Mediterranean woodlands and shrublands. For example, the open oak woodlands of southern Spain and Portugal are the product of an agricultural management system that is thousands of years old. In this system, cattle graze on grasses, pigs consume acorns produced by the oaks, and cork is harvested from cork oaks as a cash crop. Selected areas are planted in wheat once every 5 to 6 years and allowed to lie fallow the remainder of the time. This system of agriculture, which emphasizes low-intensity cultivation and long-term sustainability, may offer clues for sustainable agriculture in other regions.

High population densities coupled with a long history of human occupation have left an indelible mark on Mediterranean woodlands and shrublands. Early human impacts included clearing of forests for agriculture, setting fires to control woody species and encourage grass, harvesting brush for fuel, and grazing and browsing by domestic livestock. Today, Mediterranean woodlands and shrublands around the world are being covered by human habitations.

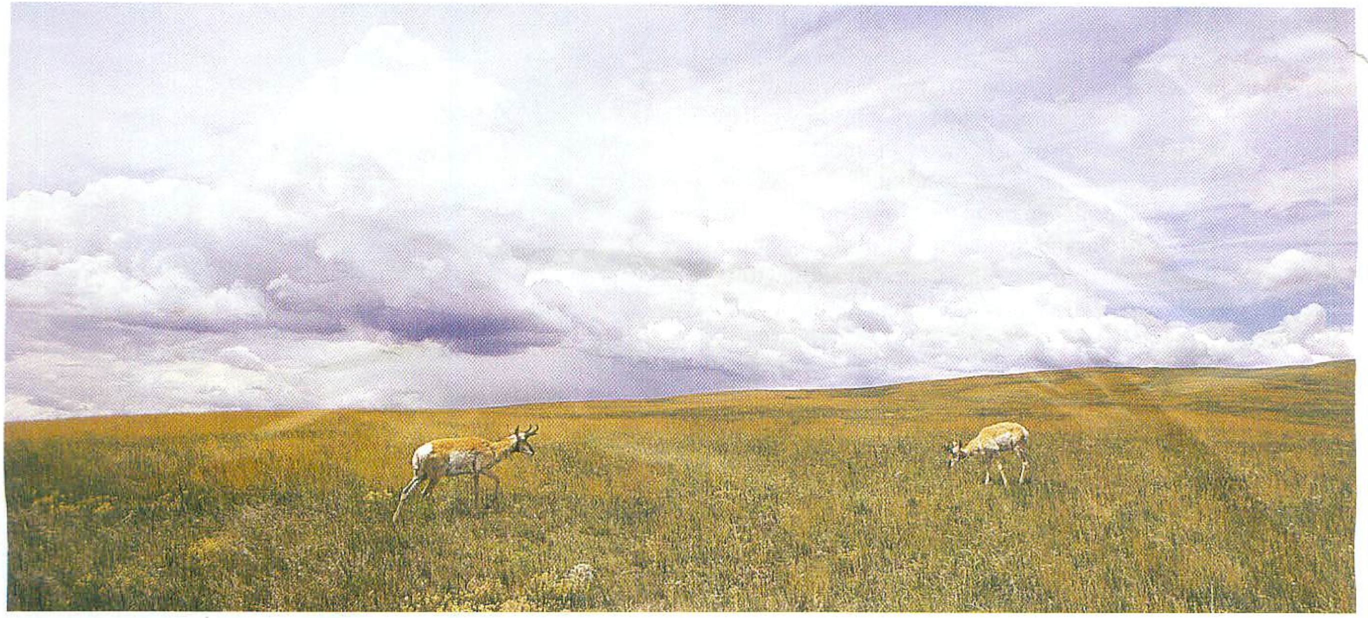


Figure 2.24 Pronghorn, native grazers of the temperate grasslands of North America.

Temperate Grassland

In their original state, **temperate grasslands** extended unbroken over vast areas (fig. 2.24). Standing in the middle of unobstructed prairie under a dome of blue sky evokes a feeling similar to that of being on a small boat in the open ocean. It is no accident that early visitors from forested Europe and eastern North America often referred to the prairie in the American Midwest as a "sea of grass" and to the wagons that crossed them as "prairie schooners." Prairies were the home of the bison and pronghorn and of the nomadic cultures of Eurasia and North America.

Geography

Temperate grassland, the largest biome in North America, is even more extensive in Eurasia (fig. 2.25). In North America, the prairies of the Great Plains extend from southern Canada to the Gulf of Mexico and from the Rocky Mountains to the deciduous forests of the east. Additional grasslands are found on the Palouse prairies of Idaho and Washington and in the central valley and surrounding foothills of California. In Eurasia, the temperate grassland biome forms a virtually unbroken band from eastern Europe all the way to eastern China. In the Southern Hemisphere, temperate grassland occurs in Argentina, Uruguay, southern Brazil, and New Zealand.

Climate

Temperate grasslands receive between 300 and 1,000 mm of precipitation annually. Though wetter than deserts, temperate grasslands do experience drought, and droughts may persist for several years. The maximum precipitation usually occurs in summer during the height of the growing season (fig. 2.25). Winters in temperate grasslands are generally cold and summers are hot.

Soils

Temperate grassland soils are derived from a wide variety of parent materials. The best temperate grassland soils are deep, basic or neutral, and fertile and contain large quantities of organic matter. The black prairie soils of North America and Eurasia, famous for their fertility, contain the greatest amount of organic matter. The brown soils of the more arid grasslands contain less organic matter.

Biology

Temperate grassland is thoroughly dominated by herbaceous vegetation. Drought and high summer temperatures encourage fire. As in tropical savannas, fire helps exclude woody vegetation from temperate grasslands, where trees and shrubs are often limited to the margins of streams and rivers. In addition to grasses, there can be a striking diversity of other herbaceous vegetation. Spring graces temperate grasslands with showy anemones, ranunculus, iris, and other wild flowers; up to 70 species can bloom simultaneously on the species-rich North American prairie. The height of grassland vegetation varies from about 5 cm in dry, short-grass prairies to over 200 cm in the wetter tall-grass prairies. The root systems of grasses and forbs form a dense network of sod that resists invasion by both trees and the plow.

Temperate grasslands once supported huge herds of roving herbivores: bison and pronghorns in North America (see fig. 2.24); wild horses and Saiga antelope in Eurasia. As in the open sea, the herbivores of the open grassland banded together in social groups; as did their attendant predators, the steppe and prairie wolves. The smaller animals, such as grasshoppers and mice, inconspicuous among the herbaceous vegetation, were even more numerous than the large herbivores.

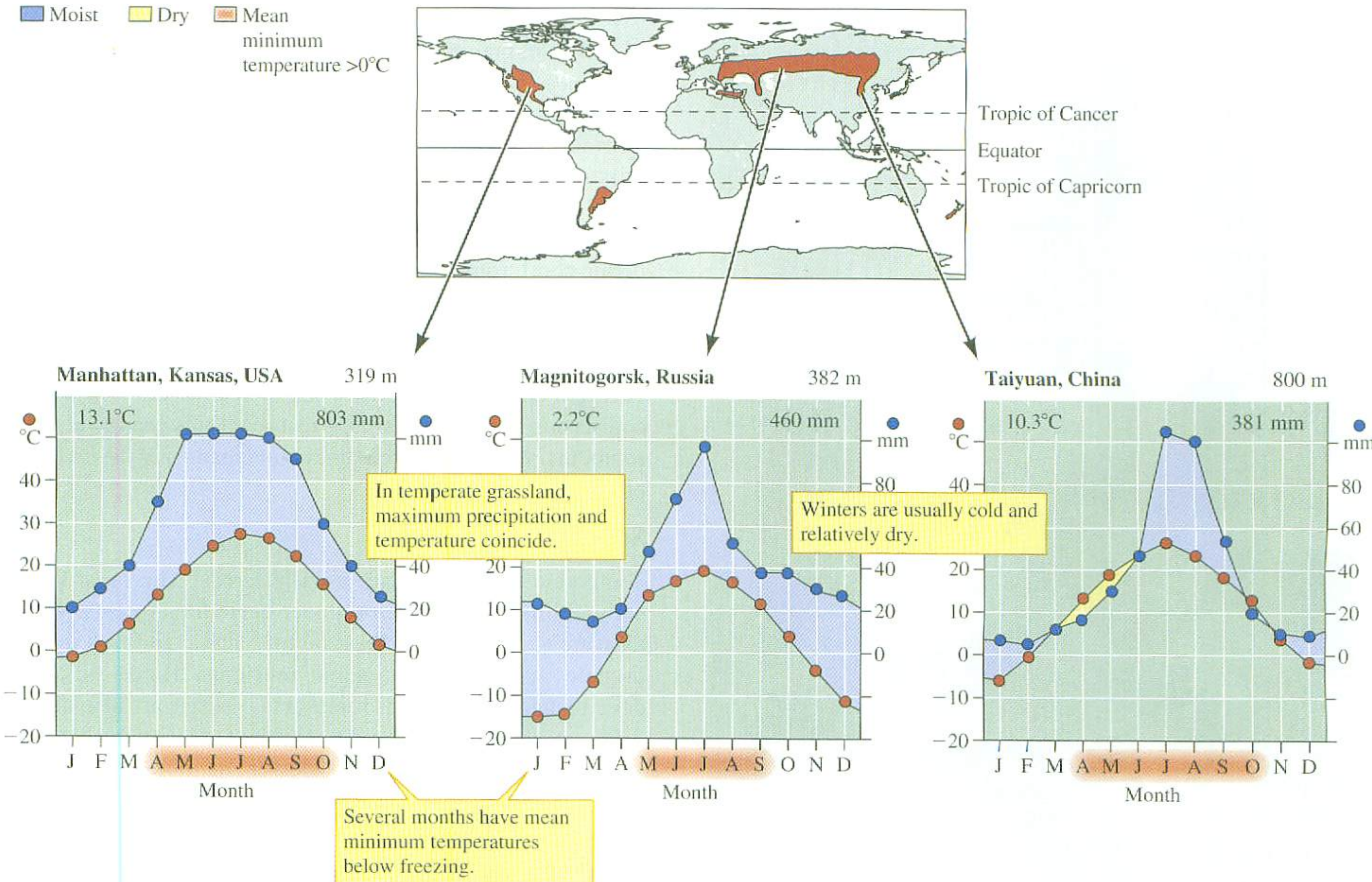


Figure 2.25 Temperate grassland geography and climate.

Figure 2.26 Once the most extensive biome in North America, temperate grasslands have been largely converted to agriculture.

Human Influences

The first human populations on temperate grasslands were nomadic hunters. Next came the nomadic herders. Later, with their plows, came the farmers, who broke the sod and tapped into fertile soils built up over thousands of years. Under the plow, temperate grasslands have produced some of the most fertile farm lands on earth and fed much of the world (fig. 2.26). However, much of this productivity depends on substantial additions of inorganic fertilizers, and we are "mining" the fertility of prairie soils. For example, prairie soils have lost as much as 35% to 40% of their organic matter in just 35 to 40 years of cultivation. In addition, the more arid grasslands, with their frequent droughts, do not appear capable of supporting sustainable farming.

Temperate Forest

Old-growth **temperate forest** offers *Homo sapiens* an alternative measure (fig. 2.27). The largest living organisms on earth, perhaps the largest that have ever lived, the sequoias of western North America and the giant *Eucalyptus* trees of southern Australia, live in temperate forests. The temperate forests of eastern North America, Europe, and Asia *still*

Figure 2.27 Old-growth redwood forest in western North America. Redwoods are the tallest trees in the world, with some individual trees growing over 100 m.

harbor ancient trees that are no less impressive. Enter the subdued light of this cool, moist realm, this world of mushrooms and decaying leaves, and feel yourself shrink before the giants of the biosphere.

Geography

Temperate forest can be found between 30° and 55° latitude. However, the majority of this biome lies between 40° and 50° (fig. 2.28). In Asia, temperate forest originally covered much of Japan, eastern China, Korea, and eastern Siberia. In western Europe, temperate forests extended from southern Scandinavia to northwestern Iberia and from the British Isles through eastern Europe. North American temperate forests are found from the Atlantic sea coast to the Great Plains and reappear on the West Coast as temperate coniferous forests that extend from northern California through southeastern Alaska. In the Southern Hemisphere, temperate forests are found in southern Chile, New Zealand, and southern Australia.

Climate

Temperate forests, which may be either coniferous or deciduous, occur where temperatures are not extreme and where annual precipitation averages anywhere from about 650 mm to over 3,000 mm (fig. 2.28). These forests generally receive more winter precipitation than temperate grasslands. Deciduous trees usually dominate temperate forests, where the growing season is moist and at least 4 months long. In deciduous forests, winters last from 3 to 4 months. Though snowfall may be heavy, winters in deciduous forests are relatively mild. Where winters are more severe or the summers drier, conifers are more abundant than deciduous trees. The temperate coniferous forests of the Pacific Coast of North America receive most of their precipitation during fall, winter, and spring and are subject to summer drought. Summer drought is shown clearly in the climate diagram for the H. J. Andrews Forest of Oregon (fig. 2.28). The few deciduous trees in these coniferous forests are largely restricted to streamside environments, where water remains abundant during the drought-prone growing season.

Soils

Temperate forest soils are usually fertile. The most fertile soils in this biome develop under deciduous forests, where they are generally neutral or slightly acidic and rich in both organic matter and inorganic nutrients. Rich soils may develop under coniferous forests but conifers are also able to grow on poorer, acidic soils. Nutrient movement between soil and vegetation tends to be slower and more conservative in coniferous forests; nutrient movement within deciduous forests is generally more dynamic.

Biology

While the diversity of trees found in temperate forests is lower than that of tropical forests, temperate forest biomass can be as great, or greater. Like tropical rain forests, temperate forests are vertically stratified. The lowest layer of vegetation, the herb layer, is followed by a layer of shrubs, then shade-tolerant understory trees, and finally the canopy, formed by the largest trees. The height of this canopy varies from approximately 40 m to over 100 m. Birds, mammals, and insects make use of all layers of the forest from beneath the forest floor through the canopy. Some of the most important consumers are the fungi and bacteria, which, along with a diversity of microscopic invertebrate animals, consume the large quantities of wood stored on the floor of old-growth temperate forest (fig. 2.29). The activities of these organisms recycle nutrients, a process upon which the health of the entire forest depends.

Human Influences

What, besides being large cities, do Tokyo, Beijing, Moscow, Warsaw, Berlin, Paris, London, New York, Washington, D.C., Boston, Toronto, Chicago, and Seattle have in common? They are all built on lands that once supported a temperate forest. The first human settlements in temperate forests were concentrated along forest margins, usually along streams and rivers. Eventually, agriculture was practiced in these forest clearings, and animals and plant products were harvested from the surrounding forest. This was the circumstance several thousand years ago, in Europe and

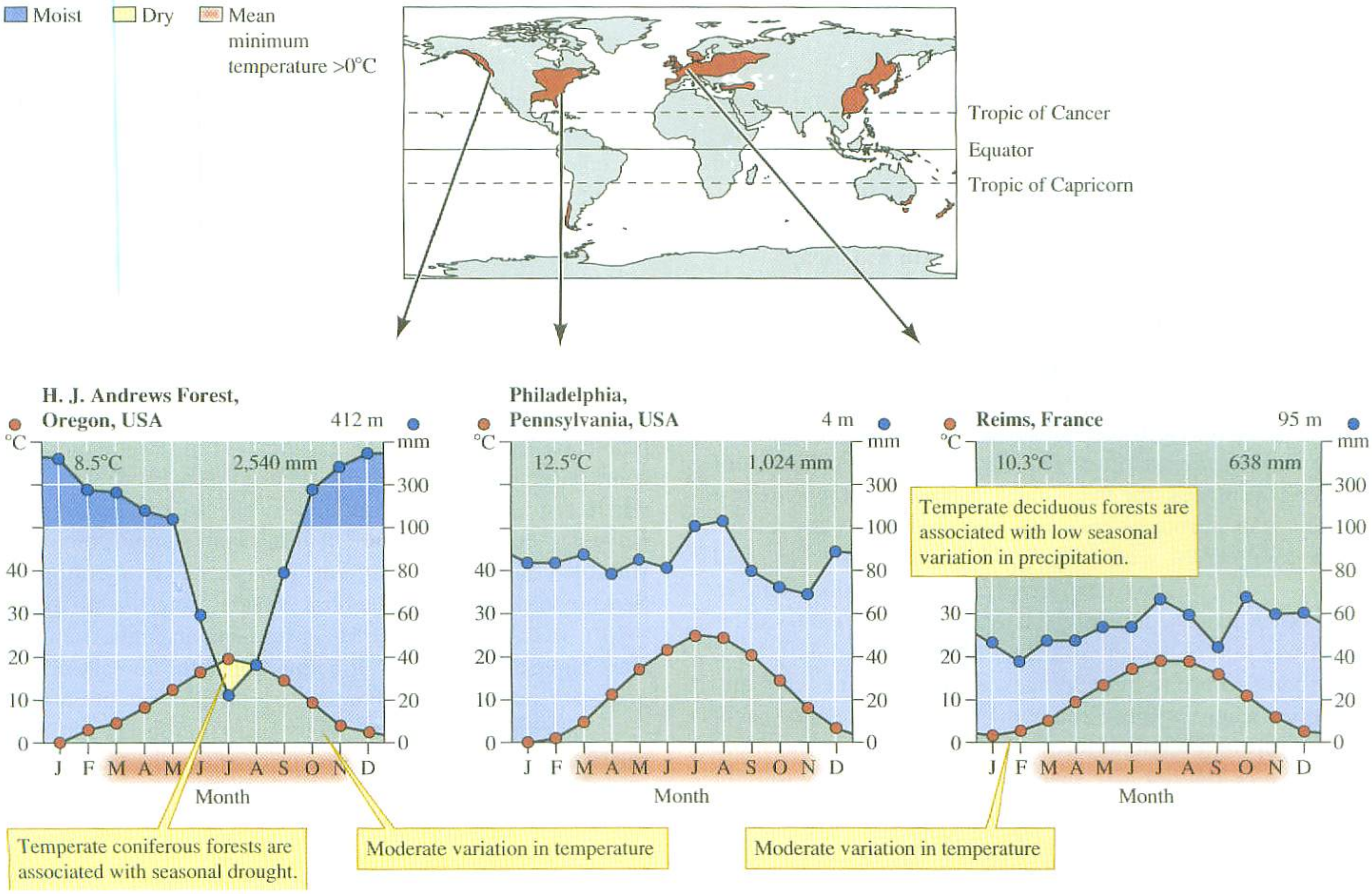


Figure 2.28 Temperate forest geography and climate.

Figure 2.29 Massive amounts of wood accumulate on the forest floor of temperate coniferous forests of the Pacific Northwest, such as this one in southeastern Alaska.

Asia, and five centuries ago, in North America. Since those times, most of the ancient forests have fallen to ax and saw. Few tracts of the virgin deciduous forest that once covered most of the eastern half of North America remain, and disparate interests struggle over the fate of the remaining 1% to 2% of old-growth forests in western North America.

Boreal Forest

The **boreal forest,** or **taiga,** is a world of wood and water that covers over 11% of the earth's land area (fig. 2.30). On the surface, the boreal forest is the essence of monotony. However, if you pay attention you are rewarded with plenty of variety. In places, the trees stand so close together you can barely walk through them. Elsewhere, so many trees have been toppled by wind that you can walk on their piled trunks, 1 to 2 m above the ground, for many kilometers. In still other places, the forest is open and you can wander wherever you like on its soft floor of needles and duff. Here and there, where light penetrates, are berry bushes of many varieties where wildlife and humans alike pause and snack. A trek through a boreal forest eventually leads to the shore of a lake or river, where shade and cover give way to light and space. Along the lake margins grow willows and other water- and light-loving plants. The summer forest is colored green, gray, and brown; the autumn adds brilliant splashes of yellow and red; and the long northern winter turns the boreal forest into a land of white solitude.

Geography

Boreal comes from the Greek word for north, reflecting the fact that boreal forests are confined to the Northern Hemisphere. Boreal forests extend from Scandinavia, through European Russia, across Siberia, to central Alaska, and across central Canada in a band between 50° and 65° N latitude (fig. 2.31). These forests are bounded in the south either by temperate forests or temperate grasslands and in the north by tundra. Fingers of boreal forest follow the Rocky Mountains south along the spine of North America, and patches of boreal forest reappear on the mountain slopes of south-central Europe and Asia.

Figure 2.30 Boreal forests, such as this one in Siberian Russia, are dominated by a few species of conifer trees.

Climate

The boreal forest is found where winters are too long, usually longer than 6 months, and the summers too short to support temperate forest (fig. 2.31). The boreal forest zone includes some fairly moderate climates, such as that at Umeå, Sweden, where the climate is moderated by the nearby Baltic Sea. However, boreal forests are also found in some of the most variable climates on earth. For instance, the temperature at Verkhoyansk, Russia, in central Siberia, ranges from about −70°C in winter to over 30°C in summer, an annual temperature range of over 100°C! Precipitation in the boreal forest is moderate, ranging from about 200 to 600 mm. Yet, because of low temperatures and long winters, evaporation rates are low, and drought is either infrequent or brief. When droughts do occur, however, forest fires can devastate vast areas of boreal forest.

Soils

Boreal forest soils tend to be of low fertility, thin, and acidic. Low temperatures and low pH impede decomposition of plant litter and slow the rate of soil building. As a consequence, nutrients are largely tied up in a thick layer of plant litter that carpets the forest floor. In turn, most trees in boreal forests have a dense network of shallow roots that, along with associated mycorrhizal fungi, tap directly into the nutrients bound up in this litter layer. The topsoil, which underlies the litter layer, is thin. In the more extreme boreal forest climates, the subsoil is permanently frozen in a layer of "permafrost" that may be several meters thick.

Biology

The boreal forest is generally dominated by evergreen conifers such as spruce, fir, and, in some places, pines. Larch, a deciduous conifer, dominates in the most extreme Siberian climates. Deciduous aspen and birch trees grow here and there in mature conifer forests and may dominate the boreal forest during the early stages of recovery following forest fires. Willows grow along the shores of rivers and lakes. There is little herbaceous vegetation under the thick forest canopy, but small shrubs such as blueberry and shrubby junipers are common.

The boreal forest is home to many animals. This is the winter home of migratory caribou and reindeer and the year-round home of moose and woodland bison. The wolf is the major predator of the boreal forest. This biome is also inhabited by black bears and grizzly bears in North America and the brown bear in Eurasia. A variety of smaller mammals such as lynx, wolverine, snowshoe hare, porcupines, and red squirrels also live in boreal forests. The boreal forest is the

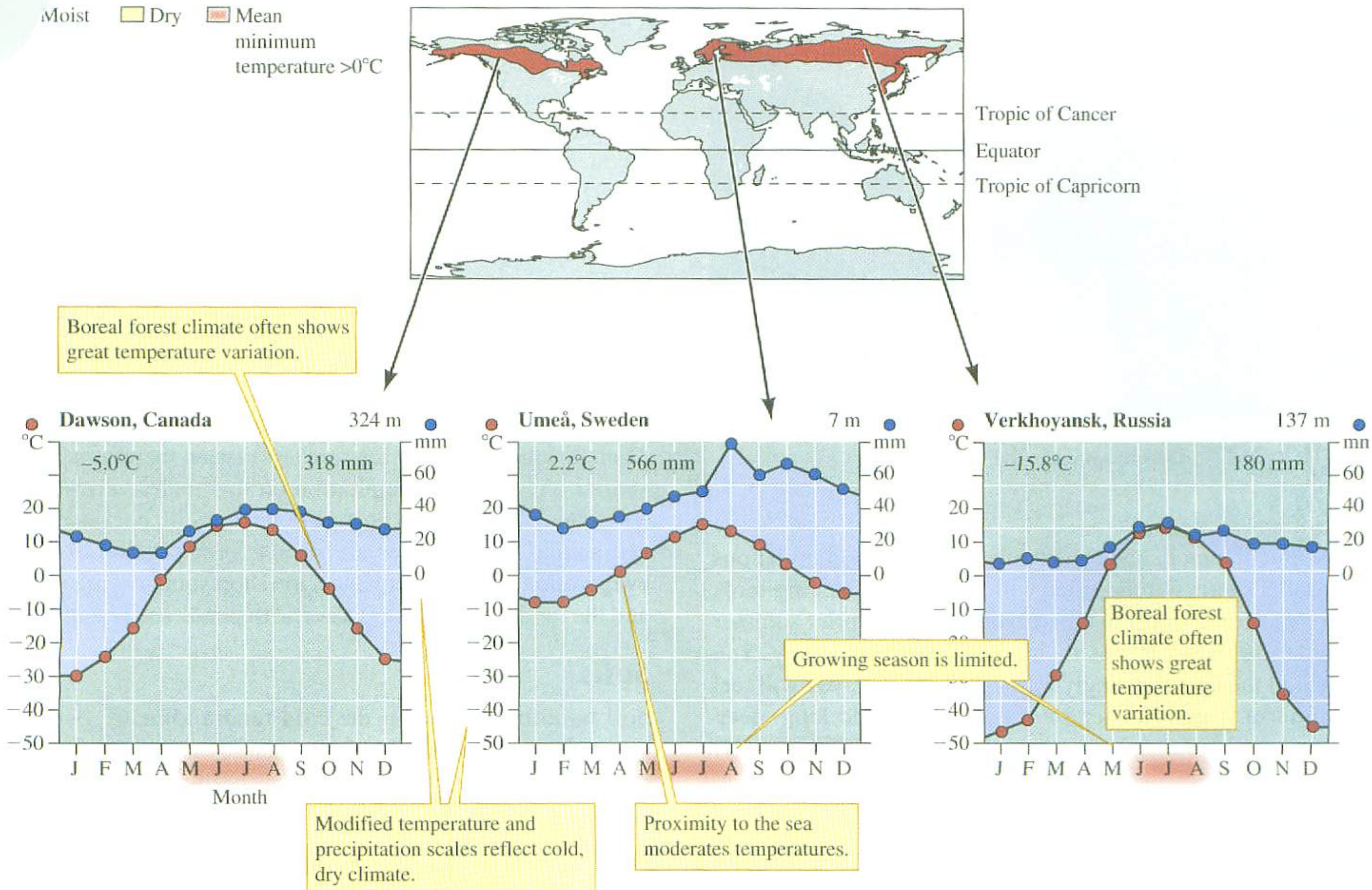


Figure 2.31 Boreal forest geography and climate.

nesting habitat for many birds that migrate from the tropics each spring and the year-round home of other birds such as crossbills and spruce grouse.

Our survey of the biosphere has taken us far from the rain forest, where we started. Let's reflect back on the tropical rain forest and where we've come. What has changed? Well, we're still in forest but a very different one. In the rain forest, a single hectare could contain over 300 species of trees; here, in the boreal forest, you can count the dominant trees on one hand. What about epiphytes and vines? The vines are gone and the epiphytes are limited to lichens and some mistletoe. In addition, most of the intricate relationships between species that we saw in the rain forest are absent. All the trees are wind pollinated, and none produce fleshy fruits like bananas or papayas. Now listen to the two forests at night. The rich tropical rain forest chorus is hushed. The silence of the boreal forest is broken by few animal voices—the howl of a wolf, the hoot of an owl, the cry of the loon, soloists of the northern forest—accompanied by incessant wind through the trees.

Human Influences

Ancient cave paintings in southern France and northern Spain, made during the last ice age when the climate was much colder, reveal that humans have lived off boreal forest animals, such as the migratory reindeer, for tens of thousands of years. In Eurasia, from Lapland in Scandinavia to Siberia, hunting of reindeer eventually gave way to domestication and herding. In northern Canada and Alaska, where some Native Americans still rely on wild caribou for much of their food, we find a reminder of the earliest human ways of making a living in these northern lands. Northern peoples have also long harvested the berries that grow in abundance in the boreal forest. The many berry dishes of Scandinavia are living testimony to this heritage.

For most of history, human intrusion in the boreal forest was relatively light. More recently, however, harvesting of both animals and plants has become intense. Hunting and trapping have devastated many wildlife species. Boreal forests are being rapidly cut for lumber and pulp (fig. 2.32). Human influences on the boreal forest are now substantial.

Tundra

Follow the caribou north as they leave their winter home in the boreal forest and you eventually reach an open landscape of mosses, lichens, and dwarf willows, dotted with small ponds and laced with clear streams (fig. 2.33). This is the **tundra.** If it is summer and surface soils have thawed, your progress will be cushioned by a spongy mat of lichens and

Figure 2.32 Deforestation in the boreal forest.

mosses and punctuated by sinking into soggy accumulations of peat. The air will be filled with the cries of nesting birds that have come north to take advantage of the brief summer population explosion of their plant and animal prey. You may find the air surprisingly warm. Just as often, you will feel the bite of a midsummer snowstorm. After the long, deep winter, the midnight sun signals an annual celebration of light and life.

Geography

Like the boreal forest, the arctic tundra rings the top of the globe, covering most of the lands north of the Arctic Circle (fig. 2.34). The tundra extends from northernmost Scandinavia, across northern European Russia, through northern Siberia, and right across northern Alaska and Canada. It reaches far south of the Arctic Circle in the Hudson Bay region of Canada and is also found in patches on the coast of Greenland and in northern Iceland.

Climate

The tundra climate is typically cold and dry. However, temperatures are not quite as extreme as in the boreal forest. Though winter temperatures are less severe, the summers are shorter (fig. 2.34). Precipitation on the tundra varies from less than 200 mm to a little over 600 mm. Still, because average annual temperatures are so low, precipitation exceeds evaporation. As a consequence, the short summers are soggy and the tundra landscape is alive with ponds and streams.

Soils

Soil building is slow in the cold tundra climate. Because rates of decomposition are low, organic matter accumulates in deposits of peat and humus. Surface soils thaw each sum-

Figure 2.33 The vegetation of the tundra is mostly low-growing mosses, lichens, perennial herbaceous plants, and dwarf willows and birches.

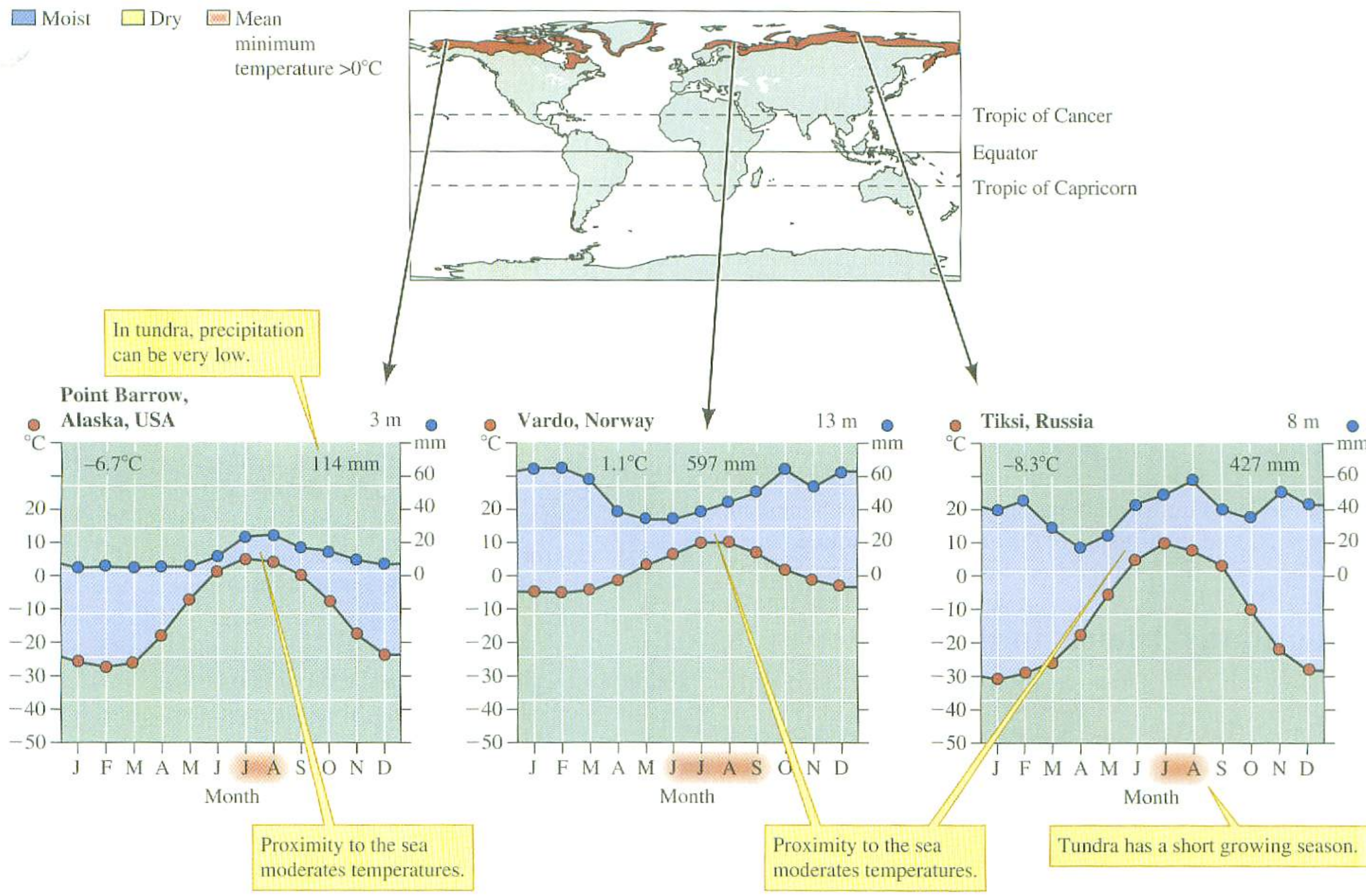


Figure 2.34 Tundra geography and climate.

mer but are generally underlain by a layer of permafrost that may be many meters thick. The annual freezing and thawing of surface soil combines with the actions of water and gravity to produce a variety of surface processes that are largely limited to the tundra. One of these processes, **solifluction,** slowly moves soils down slopes. In addition, freezing and thawing brings stones to the surface of the soil, forming a netlike, or polygonal, pattern on the surface of tundra soils (fig. 2.35).

Biology

The open tundra landscape is dominated by a richly textured patchwork of perennial herbaceous plants, especially grasses, sedges, mosses, and lichens. The lichens, associations of fungi and algae, are eagerly eaten by reindeer and caribou. The woody vegetation of the tundra consists of dwarf willows and birches along with a variety of low-growing shrubs.

The tundra is one of the last biomes on earth that still supports substantial numbers of large native mammals, including caribou, reindeer, musk ox, bear, and wolves. Small mammals such as arctic foxes, weasels, lemmings, and ground squirrels are also abundant. Resident birds such as the ptarmigan and snowy owl are joined each summer by a host of migratory bird species. Insects, though not as diverse as in biomes farther south, are very abundant. Each summer, swarms of mosquitoes and black flies emerge from the many tundra ponds and streams.

Figure 2.35 Freezing and thawing forms netlike polygons on the surface of the tundra as seen here in an aerial photo of Alaska.

Human Influences

Until recently, human presence in the tundra was largely limited to small populations of hunters and nomadic herders. As a consequence, the tundra has been viewed as one of the last pristine areas of the planet. Recently, however, human intrusion has increased markedly. This biome has been the focus of intense oil exploration and extraction. Airborne pesticides and radionuclides, which originate in distant human population centers, have been deposited on the tundra, sometimes with devastating results. For example, radioactive cesium-137 from the Chernobyl power plant disaster of 1986 was deposited with rainfall, more than 2,000 km away, on the tundra of Norway. In some areas, cesium-137 became so concentrated as it passed through the food chain from lichens to reindeer that both the milk and meat of reindeer were rendered unfit for human consumption. Such incidents have shattered the illusion of the tundra as an isolated biome and the last earthly refuge from human influence.

Mountains: Islands in the Sky

We now shift our attention to mountains. Because of the environmental changes that occur with altitude, several biomes may be found on a single mountainside. This environmental and biological diversity is something common to mountains. We include mountains here because they often introduce unique environmental conditions and organisms to regions around the globe.

Mountains capture the imagination as places of geological, biological, and climatic diversity (fig. 2.36). You can stand with eagles and gaze on the plains below, an experience that before air travel was unique to mountains. Mountains have long offered refuge for distinctive flora and fauna and humans alike. Like oceanic islands, they offer unique insights into evolutionary and ecological processes.

Geography

Mountains are built by geological processes, such as volcanism and movements of the earth's crust that elevate and fold the earth's surface. These processes operate with greater intensity in some places than others, and so mountains are concentrated in belts where these geological forces have been at work (fig. 2.37). In the Western Hemisphere, these forces have been particularly active on the western sides of both North and South America, where a chain of mountain ranges extends from northern Alaska across western North America to Tierra del Fuego at the tip of South America. Ancient low mountain ranges occupy the eastern sides of both continents. In Africa, the major mountain ranges are the Atlas Mountains of northwest Africa and the mountains of East Africa that run like beads on a string from the highlands of Ethiopia to southern Africa. In Australia, the flattest of the continents, mountains extend down the eastern side of the continent. Eurasian mountain ranges, which generally extend east to west, include the Pyrenees, the Alps, the Caucasus, and of course, the Himalayas, the highest of them all.

Figure 2.36 Mount Denali, Alaska. Environmental conditions and organisms vary greatly from low to high elevations on mountains.

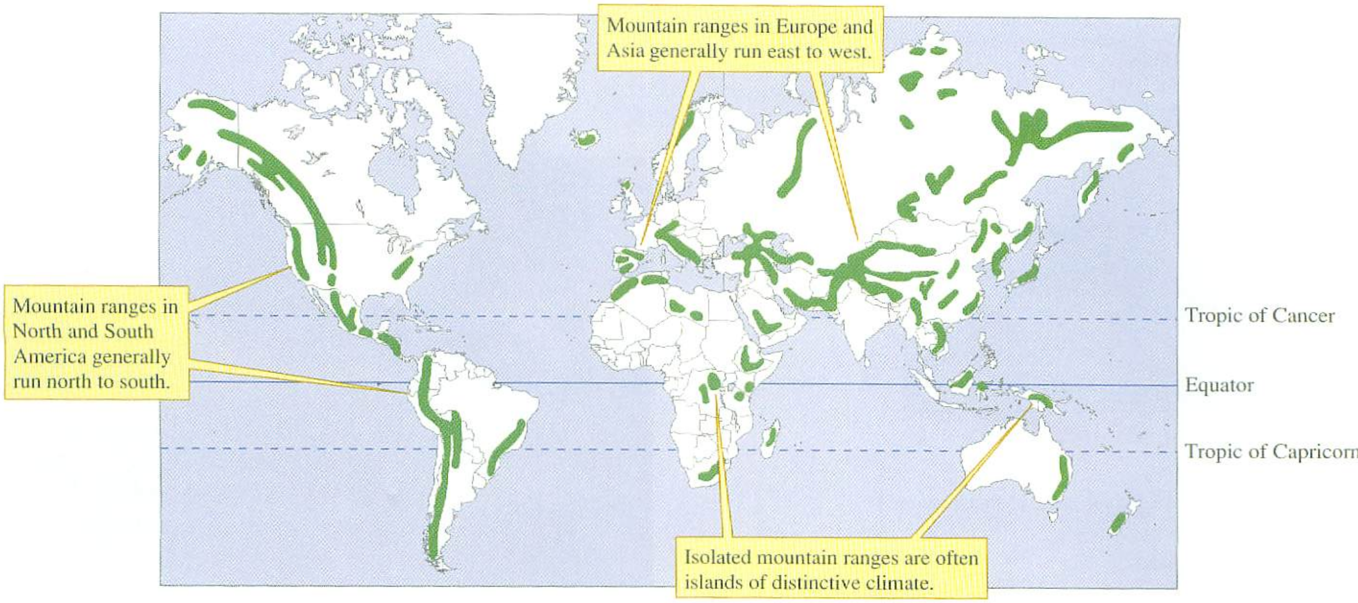


Figure 2.37 Mountain geography.

Climate

On mountains, climates change from low to high elevation, but the specific changes are different at different latitudes. On mountains at middle latitudes, the climate is generally cooler and wetter at higher altitudes (fig. 2.38). In contrast, there is less precipitation at the higher elevations of polar mountains and on some tropical mountains. In other tropical regions, precipitation increases up to some middle elevation and then decreases higher up the mountain. On high tropical mountains, warm days are followed by freezing nights. The organisms on these mountains experience summer temperatures every day and winter temperatures every night. The changes in climate that occur up the sides of mountains have profound influences on the distribution of mountain organisms.

Soils

Mountain soils change with elevation and have a great deal in common with the various soils we've already discussed. However, some special features are worth noting. First, because of the steeper topography, mountain soils are generally well drained and tend to be thin and vulnerable to erosion. Second, persistent winds blowing from the lowlands deposit soil particles and organic matter on mountains, materials that can make a significant contribution to local soil building. In some locations in the southern Rocky Mountains, coniferous trees draw the bulk of their nutrition from materials carried by winds from the valleys below, not from local bedrock.

Biology

Climb any mountain that is high enough and you will notice biological and climatic changes. Whatever the vegetation at the base of a mountain, that vegetation will change as you climb and the air becomes cooler. The sequence of vegetation up the side of a mountain may remind you of the biomes we encountered on our journey from the equator to the poles. In the cool highlands of desert mountains in the southwestern United States, you can hike through spruce and fir forests much like those we encountered far to the north. However, what you see on these desert mountains differs substantially from boreal forests. These mountain populations have been isolated from the main body of the boreal forest for over 10,000 years; in the interim, some populations have become extinct, some teeter on the verge of extinction, while others have evolved sufficiently to be recognized as separate species or subspecies. On these mountains, time and isolation have forged distinctive gene pools and mixes of species.

The species on high equatorial mountains are even more isolated. Think for a moment of the geography of high tropical mountains: some in Africa, some in the highlands of Asia, and the Andes of South America. The high-altitude communities of Africa, South America, and Asia share very few species. On the other hand, despite differences in species composition, there *are* structural similarities among the organisms on these mountains (fig. 2.39). These similarities suggest there may be general rules for associating organisms with environments.

Human Influences

Because mountains differ in climate, geology, and biota (plants and animals) from the surrounding lowlands, they have been useful as a source of raw materials such as wood, forage for animals, medicinal plants, and minerals. Some of these uses, such as livestock grazing, are highly seasonal. In temperate regions, livestock are taken to mountain pastures during the summer and back down to the lowlands in winter. Human exploitation of mountains has produced ecological degradation in many places and surprising balance

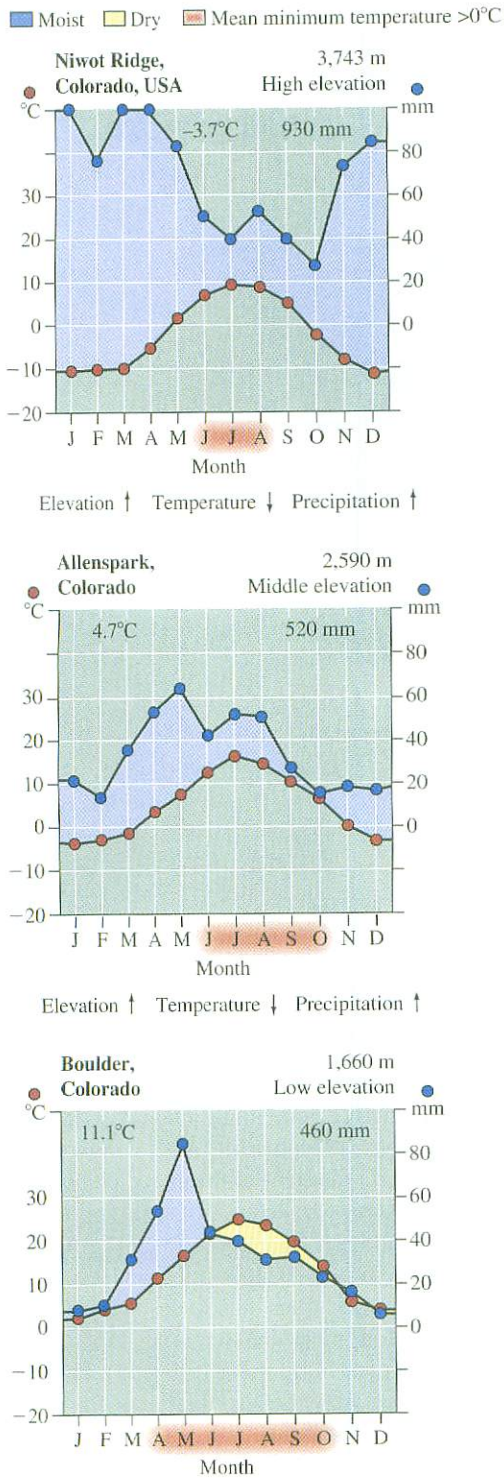


Figure 2.38 Mountain climates along an elevational gradient in the Colorado Rockies. Temperatures decrease and precipitation increases from low to high elevations in these midlatitude mountains.

(a)

(b)

Figure 2.39 Convergence among tropical alpine plants: (*a*) *Senecio* trees on Mount Kilimanjaro, Africa; (*b*) *Espeletia* in the Andes of South America.

in others. Increased human pressure on mountain environments has sometimes created conflict between competing economic interests, between recreation seekers and livestock ranchers, and even between groups of scientists. Because of their compressed climatic gradients and biological diversity, mountains offer living laboratories for the study of ecological and evolutionary responses to climatic variation.

Concept 2.3 Review

1. Why do those regions, whether tropical, desert, or temperate, which include high mountains, tend to be the most biologically diverse?
2. Why would the soils in tropical rain forests generally be depleted of their nutrients more rapidly compared to the nutrients in temperate forest soils?

Applications

Climatic Variation and the Palmer Drought Severity Index

In this chapter we've used climate diagrams to represent the climates of earth's biomes. Climate diagrams capture some of the climatically significant differences among the climates experienced by the various biomes. However since they focus on average climatic conditions, they emphasize only one aspect of climate. Recall that climate diagrams plot average (mean) monthly precipitation, which is plotted as a line graph (e.g., see fig. 2.38), and average monthly temperature, also plotted as a line graph but connecting red dots. Including mean annual temperature and mean annual precipitation in each climate diagram further reinforces the focus on average conditions. However as we all know, climates everywhere vary substantially from the average conditions presented in climate diagrams.

Here we explore a climatic index, the **Palmer Drought Severity Index,** which can be used to characterize climatic variation. While this index has been historically used to assess drought conditions, it indicates wet periods as well. First, what is a drought? A **drought** can be defined as an extended period of dry weather during which precipitation is reduced sufficiently to damage crops, impair the functioning of natural ecosystems, or cause water shortages for human populations. While such a definition may be sufficient for some needs, climatologists have tried to create quantitative indices of drought. The Palmer Drought Severity Index, or PDSI, is such an index. The PDSI uses temperature and precipitation to calculate moisture conditions relative to long-term averages for a particular region. Negative values of the PDSI reflect drought conditions, while positive values indicate relatively moist periods. What do zero values of the Palmer Drought Severity Index indicate? Values near zero indicate approximately average conditions in a particular region.

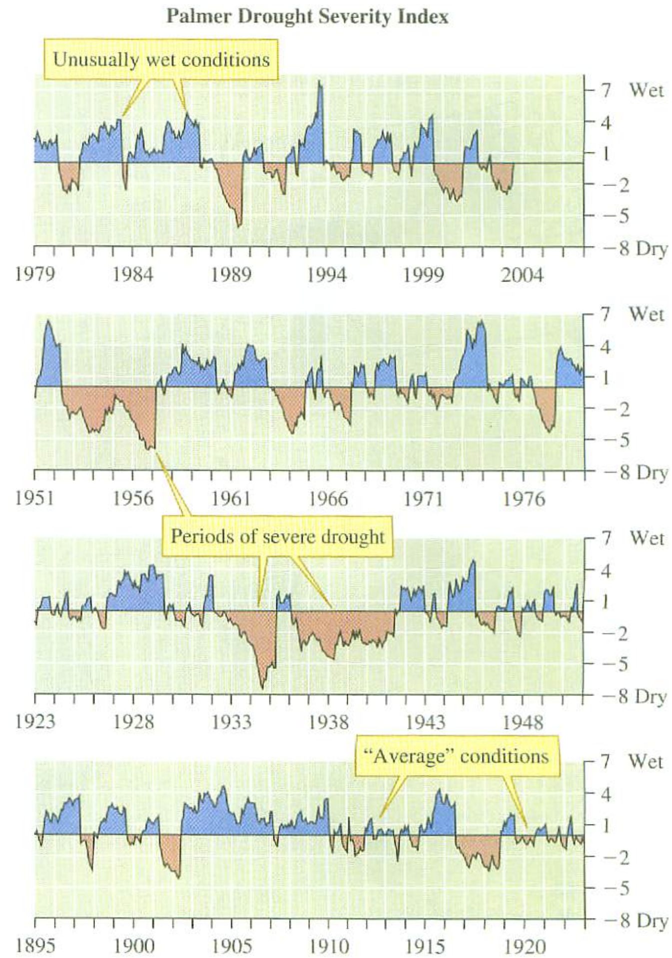


Figure 2.40 The Palmer Drought Severity Index for Kansas region 3 near Manhattan, Kansas, plotted for the years 1895 to 2004 indicates substantial climatic variation (data from www.drought.noaa.gov).

Figure 2.40 shows a plot of the Palmer Drought Severity Index for the region around Manhattan, Kansas, from 1895 through 2004. To ease interpretation, negative values of the Palmer Drought Severity Index are shaded red, indicating drought. Periods during which the index was positive are shaded blue, indicating moist conditions. The area of Kansas from which the climate data are plotted in figure 2.40 falls within the temperate grassland biome. What does figure 2.40 suggest about moisture availability in the region around Manhattan, Kansas? One of the most apparent characteristics of this plot is its great variability. Clearly the availability of water in the region is far from constant. Now compare figure 2.40 with the representation of climate for Manhattan, Kansas, shown in figure 2.25. How do the two figures compare? While the climate diagram and the PDSI represent climate from the same geographic location, the climate diagram, because it draws our attention to average climatic conditions, suggests climatic stability. Meanwhile the PDSI shows that the climate around Manhattan, Kansas is in fact highly variable.

Temporal climatic variability is matched or exceeded by climatic variation in space. Spatial variation in climatic

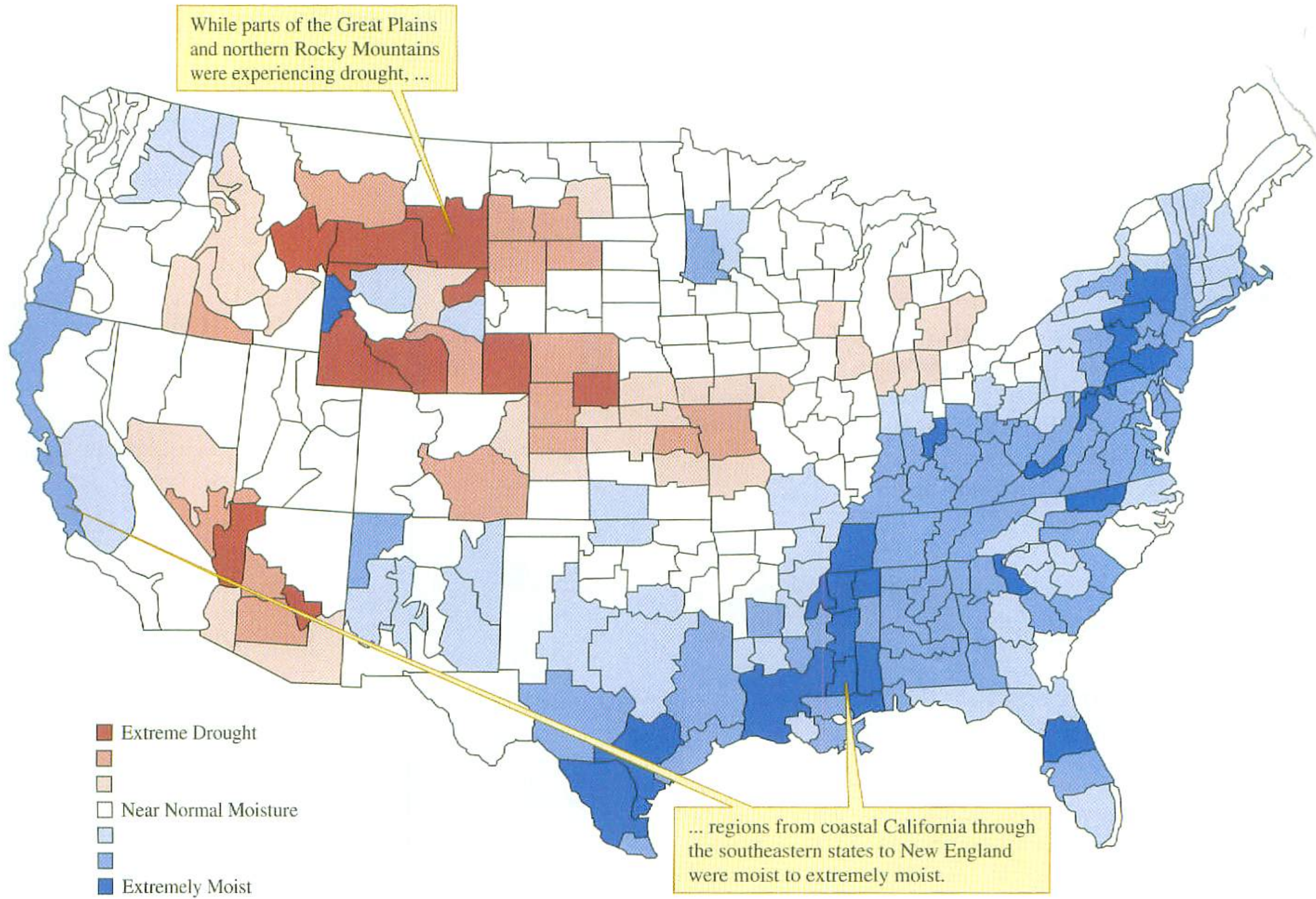


Figure 2.41 Regional variation in moisture conditions for the week of January 4, 2003, as indicated by the Palmer Drought Severity Index (data from www.cpc.drought.noaa.gov).

conditions can also be represented using the Palmer Drought Severity Index. For instance, figure 2.41 maps values of the Palmer Drought Severity Index across the United States for the week ending January 4, 2003. Notice that during this period, moisture conditions varied widely across this portion of the North American continent. While some parts of the desert Southwest and northern Rocky Mountain regions experienced severe to extreme drought conditions, other regions of the United States were very moist or extremely moist. In still other regions, the conditions were near normal.

The levels of regional and temporal variability shown on figures 2.40 and 2.41 are not exceptional. Similar levels of spatial variation occur on all continents. However, when considering temporal variation in climate, some regions are climatically more variable than others. For example, those regions under the influence of the El Niño Southern Oscillation (p. 533) are particularly variable. Ecologists study the relationships between organisms and environment. As these examples show, in the study of those relationships both averages and variation in environmental factors need to be considered.

Summary

Natural history is helping with the difficult task of restoring tropical dry forest in Costa Rica. Natural history also formed the foundation upon which modern ecology developed. Because ecological studies continue to be built upon a solid foundation of natural history, this chapter is devoted to the natural history of terrestrial biomes. Biomes are distinguished primarily by their predominant vegetation and are associated with particular climates.

Uneven heating of the earth's spherical surface by the sun and the tilt of the earth on its axis combine to produce predictable latitudinal variation in climate. Because the earth is a sphere, the sun's rays are most concentrated at the latitude where the sun is directly overhead. This latitude changes with the seasons because the earth's axis of rotation is not perpendicular to its plane of orbit about the sun but is tilted approximately 23.5° away from the perpendicular. The sun is directly overhead at the tropic of Cancer, at 23.5° N latitude during the northern summer solstice. During the northern winter solstice the sun is directly overhead at the tropic of Capricorn, at 23.5° S latitude. The sun is directly overhead at the equator during the spring and autumnal equinoxes. During the northern summer the Northern Hemisphere is tilted toward the sun and receives more solar energy than the Southern Hemisphere. During the northern winter, the Northern Hemisphere is tilted away from the sun and the Southern Hemisphere receives more solar energy.

Heating of the earth's surface and atmosphere drives atmospheric circulation and influences global patterns of precipitation. As the sun heats air at the equator, it expands and rises, spreading northward and southward at high altitudes. This high-altitude air cools as it spreads toward the poles, eventually sinking back to the earth's surface. Rotation of the earth on its axis breaks up atmospheric circulation into six major cells, three in the Northern Hemisphere and three in the Southern Hemisphere. These three circulation cells correspond to the trade winds north and south of the equator, the westerlies between 30° and 60° N or S latitude, and the polar easterlies above 60° latitude. These prevailing winds do not blow directly south because of the Coriolis effect.

As air rises at the tropics, it cools, and the water vapor it contains condenses and forms clouds. Precipitation from these clouds produces the abundant rains of the tropics. Dry air blowing across the lands at about 30° latitude produces the great deserts that ring the globe. When warm, moist air flowing toward the poles meets cold polar air, it rises and cools, forming clouds that produce the precipitation associated with temperate environments. Complicated differences in average climate can be summarized using a climate diagram.

Soil structure results from the long-term interaction of climate, organisms, topography, and parent mineral material. Terrestrial biomes are built upon a foundation of soil, a vertically stratified and complex mixture of living and nonliving material. Most terrestrial life depends on soil. Soil structure varies continuously in time and space. Soils are generally divided into O, A, B, and C horizons. The O horizon is made up of freshly fallen organic matter, including leaves, twigs, and other plant parts. The A horizon contains a mixture of mineral materials and organic matter derived from the O horizon. The B horizon contains clays, humus, and other materials that have been transported from the A horizon. The C horizon consists of weathered parent material.

The geographic distribution of terrestrial biomes corresponds closely to variation in climate, especially prevailing temperature and precipitation. The major terrestrial biomes and climatic regimes are: *Tropical rain forest:* Warm; moist; low seasonality; infertile soils; exceptional biological diversity and intricate biological interactions. *Tropical dry forest:* Warm and cool seasons; seasonally dry; biologically rich; as threatened as tropical rain forest. *Tropical savanna:* Warm and cool seasons; pronounced dry and wet seasons; impermeable soil layers; fire important to maintaining dominance by grasses; still supports high numbers and diversity of large animals. *Desert:* Hot or cold; dry; unpredictable precipitation; low productivity but often high diversity; organisms well-adapted to climatic extremes. *Mediterranean woodland and shrubland:* Cool, moist winters; hot, dry summers; low to moderate soil fertility; organisms adapted to seasonal drought and periodic fires. *Temperate grassland:* Hot and cold seasons; peak rainfall coincides with growing season; droughts sometimes lasting several years; fertile soils; fire important to maintaining dominance by grasses; historically inhabited by roving bands of herbivores and predators. *Temperate forest:* Moderate, moist winters; warm, moist growing season; fertile soils; high productivity and biomass; dominated by deciduous trees where growing seasons are moist, winters are mild, and soils fertile; otherwise dominated by conifers. *Boreal forest:* Long, severe winters; climatic extremes; moderate precipitation; infertile soils; permafrost; occasional fire; extensive forest biome, dominated by conifers. *Tundra:* Cold; low precipitation; short, soggy summers; poorly developed soils; permafrost; dominated by low vegetation and a variety of animals adapted to long, cold winters; migratory animals, especially birds, make seasonal use. *Mountains:* Temperature, precipitation, soils, and organisms shift with elevation; mountains are climatic and biological islands.

Key Terms

A horizon 20
B horizon 20
biome 14
boreal forest 36
caliche 29
C horizon 20
climate diagram 16
Coriolis effect 16
desert 27
drought 42
lithosol 28
Mediterranean woodland and shrubland 30
mycorrhizae 22
natural history 13
O (organic) horizon 20
Palmer Drought Severity Index 42
sample mean 19
solifluction 39
taiga 36
temperate forest 33
temperate grassland 32
tropical dry forest 23
tropical rain forest 21
tropical savanna 25
tundra 37

Review Questions

1. Daniel Janzen (1981a, 1981b) proposed that the seeds of the guanacaste tree were once dispersed by several species of large mammals that became extinct following the end of the Pleistocene about 10,000 years ago. There may have been other plant species with a similar relationship with large herbivorous mammals. How do you think the distributions of these plant species may have changed from the time of the extinctions of Pleistocene mammals until the introduction of other large herbivores such as horses? How might the introduction of horses about 500 years ago have affected the distribution of these species? How could you test your ideas?
2. Draw a typical soil profile, indicating the principal layers, or horizons. Describe the characteristics of each layer.
3. Describe global patterns of atmospheric heating and circulation. What mechanisms produce high precipitation in the tropics? What mechanisms produce high precipitation at temperate latitudes? What mechanisms produce low precipitation in the tropics?
4. Use what you know about atmospheric circulation and seasonal changes in the sun's orientation to earth to explain the highly seasonal rainfall in the tropical dry forest and tropical savanna biomes. (Hint: Why does the rainy season in these biomes come during the warmer months?)
5. We focused much of our discussion of biomes on their latitudinal distribution. The reasonably predictable relationship between latitude and temperature and precipitation provides a link between latitude and biomes. What other geographic variable might affect the distribution of temperature and precipitation and, therefore, of biomes?
6. You probably suggested altitude in response to question 5 because of its important influence on climate. Some of the earliest studies of the geographic distribution of vegetation suggested a direct correspondence between latitudinal and altitudinal variation in climate, and our discussion in this chapter stressed the similarities in climatic changes with altitude and latitude. Now, what are some major climatic differences between high altitude at midlatitudes and high altitude at high latitudes?
7. How is the physical environment on mountains at midlatitudes similar to that in tropical alpine zones? How do these environments differ?
8. English and other European languages have terms for four seasons: spring, summer, autumn, and winter. This vocabulary summarizes much of the annual climatic variation at midlatitudes in temperate regions. Are these four seasons useful for summarizing annual climatic changes across the rest of the globe? Look back at the climate diagrams presented in this chapter. How many seasons would you propose for each of these environments? What would you call these seasons?
9. Biologists have observed much more similarity in species composition among boreal forests and among areas of tundra in Eurasia and North America than among tropical rain forests or among Mediterranean woodlands around the globe. Can you offer an explanation of this contrast based on the global distributions of these biomes shown in figures 2.10, 2.22, 2.31, and 2.34?
10. To date, which biomes have been the most heavily affected by humans? Which seem to be the most lightly affected? How would you assess human impact? How might these patterns change during this century? (You may need to consult the discussion of human population growth in the Applications section of chapter 11).

Suggested Readings

Attenborough, D., P. Whitfield, P. D. Moore, and B. Cox. 1989. *The Atlas of the Living World*. Boston: Houghton Mifflin.

A survey of the biosphere written for the general reader. Richly illustrated and well written.

Breckle, S.-W. 2002. *Walter's Vegetation of the Earth*. 4th ed. New York: Springer-Verlag.

A review of global patterns of climate and their correspondence to major classes of vegetation. Climate diagrams are used throughout the presentation.

Coleman, D. C., D. A. Crossley, Jr., and P. F. Hendrik. 2004. *Fundamentals of Soil Ecology*. 2nd ed. Amsterdam, Boston: Elsevier Press.

Excellent modern introduction to the ecology of soils.

Kricher, J. C. 1997. *A Neotropical Companion: An Introduction to the Plants, Animals, and Ecosystems of the New World Tropics*. Princeton, N.J.: Princeton University Press.

Wilson, E. O. 1992. *The Diversity of Life*. New York: W. W. Norton.

A highly acclaimed synthesis on the patterns and threats to biological diversity—an engaging and provocative discussion.