The Biome Concept in Ecology

I magine that you are on safari on an East African savanna and one of your group shouts, "Look over there, a cactus tree!" With your training in botany, you know immediately that this can't be so, because the cactus family (Cactaceae) is restricted to the Western Hemisphere. Yet the plant looks just like cacti you have seen in similar environments in Mexico (Figure 5.1). Closer inspection of the flowers shows that the African plant is a cactus look-alike, a member of the spurge family (Euphorbiaceae).

Your friend was fooled by a common phenomenon in biology, that of convergence. **Convergence** is the process by which unrelated organisms evolve a resemblance to each other in response to similar environmental conditions. The leafless, thick, fleshy branches of both the cactus and the cactuslike euphorb evolved as adaptations to reduce water loss in semiarid environments. The two plants look alike because they evolved under the same conditions, although they descended from unrelated, different-looking ancestors. Natural selection and evolution are oblivious to the ancestry of a particular organism as long as it is capable of an adaptive response to a particular condition of the environment.

Convergence explains why we can recognize an association between the forms of organisms and their particular environments anywhere in the world. Tropical rain forest trees have the same general appearance no matter where they are found or to which evolutionary lineage they belong. The same can be said of shrubs inhabiting seasonally dry environments, which produce small, deciduous leaves and often arm their stems with spines to dissuade herbivores. The podocarp trees (Podocarpaceae) that grow in temperate forests of New Zealand resemble the broad-leaved trees of the Northern Hemisphere even though they are gymnosperms, more closely related to pines and firs than to oaks and maples.

FIGURE 5.1 Unrelated organisms can evolve similar forms in response to common environmental conditions. (a) A tree-forming cactus near Oaxaca, Mexico, and (b) an East African euphorb tree have converged in response to arid conditions. Photos by R. E. Ricklefs.

(a)

(b)
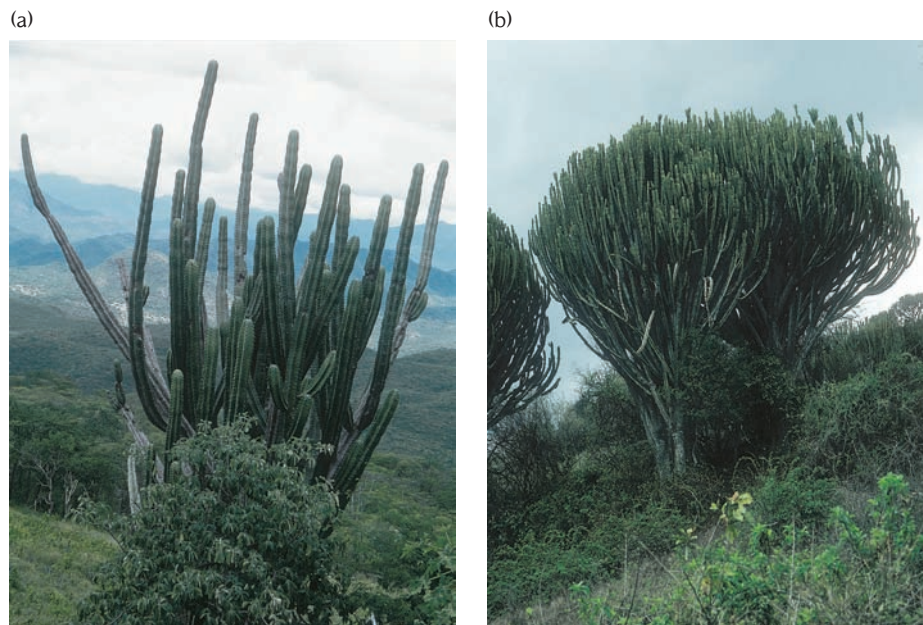
CHAPTER CONCEPTS

- Climate is the major determinant of plant growth form and distribution

- Climate defines the boundaries of terrestrial biomes

- Walter climate diagrams distinguish the major terrestrial biomes

- Temperate climate zones have average annual temperatures between 5°C and 20°C

- Boreal and polar climate zones have average temperatures below 5°C

- Climate zones within tropical latitudes have average temperatures exceeding 20°C

- The biome concept must be modified for freshwater aquatic systems

- Marine aquatic systems are classified principally by water depth

Climate, topography, and soil—and parallel influences in aquatic environments—determine the changing character of plant and animal life, as well as ecosystem functioning, over the surface of the earth. Although no two locations harbor exactly the same assemblage of species, we can group biological communities and ecosystems into categories based on climate and dominant plant form, which give them their overall character. These categories are referred to as **biomes.** Ecosystems belonging to the same biome type in different parts of the world develop a similar vegetation structure and similar ecosystem functioning, including productivity and rates of nutrient cycling, under similar environmental conditions. Thus, biomes provide convenient reference points for comparing ecological processes on a global scale. Ecosystems of the woodland/shrubland biome characteristic of Mediterranean climates (cool, wet winters and hot, dry summers),

for example, look similar and function similarly whether in southern California, southern France, Chile, South Africa, or Australia.

The important terrestrial biomes of the United States and Canada are tundra, boreal forest, temperate seasonal forest, temperate rain forest, shrubland, grassland, and subtropical desert. As one would expect, the geographic distributions of these biomes correspond closely to the major climate zones of North America. To the south in Mexico and Central America, tropical rain forest, tropical deciduous forest, and tropical savanna are important biomes. Although each biome is immediately recognizable by its distinctive vegetation, it is important to realize that different systems of classification make coarser or finer distinctions, and that the characteristics of one biome usually intergrade with those of the next. The biome concept is nonetheless a useful tool that enables ecologists throughout the world

to work together toward understanding the structure and functioning of large ecological systems.

That biomes can be distinguished at all reflects the simple fact that no single type of plant can endure the whole range of conditions at the surface of the earth. If plants had such broad tolerance of physical conditions, the earth would be covered by a single biome. To the contrary, trees, for example, cannot grow under the dry conditions that shrubs and grasses can tolerate, simply because the physical structure, or **growth form,** of trees creates a high demand for water. The grassland biome exists because grasses and other herbs (called forbs) can survive the cold winters typical of the Great Plains of the United States, the steppes of Russia, and the pampas of Argentina.

This matching of growth form and environment allows us to understand the global distributions of vegetation types and the extents of biomes. If that were the whole of it, however, the study of ecology could simply focus on the relationships of individual organisms to their physical environments, and everything else in ecology would emanate from that point. However, we must remind ourselves that life is not so simple. In addition to physical conditions, two other kinds of factors influence the distributions of species and growth forms. The first of these is the myriad interactions between species—such as competition, predation, and mutualism—that determine whether a species or growth form can persist in a particular place. For example, grasses can grow perfectly well in eastern North America, as we see along roadsides and on abandoned agricultural lands, but trees predominate in that environment, and in the absence of disturbance, they exclude grasses, which cannot grow and reproduce under their deep shade.

The second kind of factor is that of chance and history. The present biomes have developed over long periods, during which the distributions of landmasses, ocean basins, and climate zones have changed continuously. Most species fail to occupy many suitable environments simply because they have not been able to disperse to all ends of the earth. This fact is amply illustrated by the successful introduction by humans of such species as European starlings (*Sturnus vulgaris*) and Monterey pines (*Pinus radiata*) to parts of the world that have suitable environmental conditions but which were far outside the restricted natural distributions of these species.

In addition, evolution has proceeded along independent lines in different parts of the world, leading in some cases to unique biomes. Australia has been isolated from other continents for the past 40 million to 50 million years, which accounts both for its unusual flora and fauna and for the absence of many of the kinds of plants and animals familiar to outsiders. Because of its unique history, areas of Australia with a climate that would support scrubland or oak savanna in California are clothed instead with tall eucalyptus woodland. Similarities between chaparral—as scrublands are called in California—and eucalyptus woodland include drought and fire resistance, but the predominant plant growth forms differ, primarily because of historical accident. We shall consider these biological and historical factors later in this book. As we shall see in the present chapter, the physical environment ultimately defines the character and distribution of the major biomes.

Climate is the major determinant of plant growth form and distribution

We can classify ecosystems into biomes because climate, along with other influences, determines the plant growth form best suited to an area, and because plants with particular growth forms are restricted to particular climates. These principles establish the close relationship between climate and vegetation. Keep in mind, however, that there are other, less conspicuous similarities among areas of the same biome type, including biological productivity, nutrient regeneration in soils, and the structure of animal communities.

One cannot understand the adaptations of an organism independently of the environment in which it lives. Different physical conditions characterize each biome, and its inhabitants are adapted to live under those conditions. The leaves of deciduous forest trees growing in the temperate seasonal forest biome are typically broad and thin, providing a large surface area for light absorption but little protection from desiccation or frost. In contrast, the leaves of many desert species are small and finely divided to dissipate heat (see Figure 3.8), and some desert species have no leaves at all.

Because of these adaptations, the vegetation of the temperate seasonal forest and subtropical desert biomes differs dramatically. These differences extend to the spacing of plants as well as their form. In temperate forests, trees form closed canopies, and the entire surface of the ground is shaded. In drier environments, including deserts, woodlands, and savannas, trees and shrubs are more widely spaced owing to competition among their root systems for limited water, and this spacing allows drought-resistant grasses to grow in the gaps between trees. In the most extreme deserts, much of the soil surface is bare because the scarce water cannot support an uninterrupted expanse of vegetation.

Given that organisms are adapted to the physical conditions of their biome, it is not surprising that the ranges of many species are limited by those same physical conditions. In terrestrial environments, temperature and moisture are the most important variables, particularly for plants. The distributions of several species of maples in eastern North America show how these factors operate. The sugar maple (*Acer saccharum*), a common forest tree in the northeastern United States and southern Canada, is limited by cold winter temperatures to the north, by hot summer temperatures to the south, and by summer drought to the west. Thus, the sugar maple is confined to roughly the northern portion of the temperate seasonal forest biome in North America (Figure 5.2). Attempts to grow sugar maples outside their normal range fail because these trees cannot tolerate average monthly summer temperatures above about 24°C or winter temperatures below about −18°C. The western limit of the sugar maple, determined by dryness, coincides with the western limit of forest in eastern North America. Because temperature and rainfall interact to control the availability of moisture, sugar maples require less annual precipitation at the northern edge of their range (about 50 cm) than at the southern edge (about 100 cm). To the east, the range of the sugar maple stops abruptly at the Atlantic Ocean.

The distributions of the sugar maple and other tree-sized maple species—black, red, and silver—reflect differences in the range of conditions within which each species can survive (Figure 5.3). Where their geographic ranges overlap, the maples exhibit distinct preferences for certain local environmental conditions created by differences in
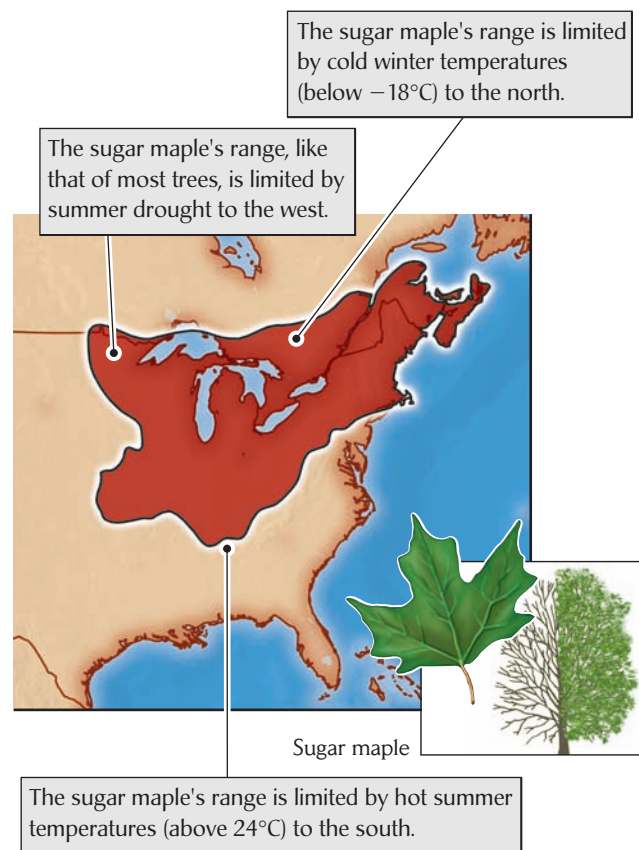

The sugar maple's range is limited by cold winter temperatures (below −18°C) to the north.

The sugar maple's range, like that of most trees, is limited by summer drought to the west.

Sugar maple

The sugar maple's range is limited by hot summer temperatures (above 24°C) to the south.

FIGURE 5.2 The distributions of species are limited by physical conditions of the environment. The red area shows the range of sugar maple in eastern North America. After H. A. Fowells, *Silvics of Forest Trees of the United States,* U.S. Department of Agriculture, Washington, D.C. (1965).
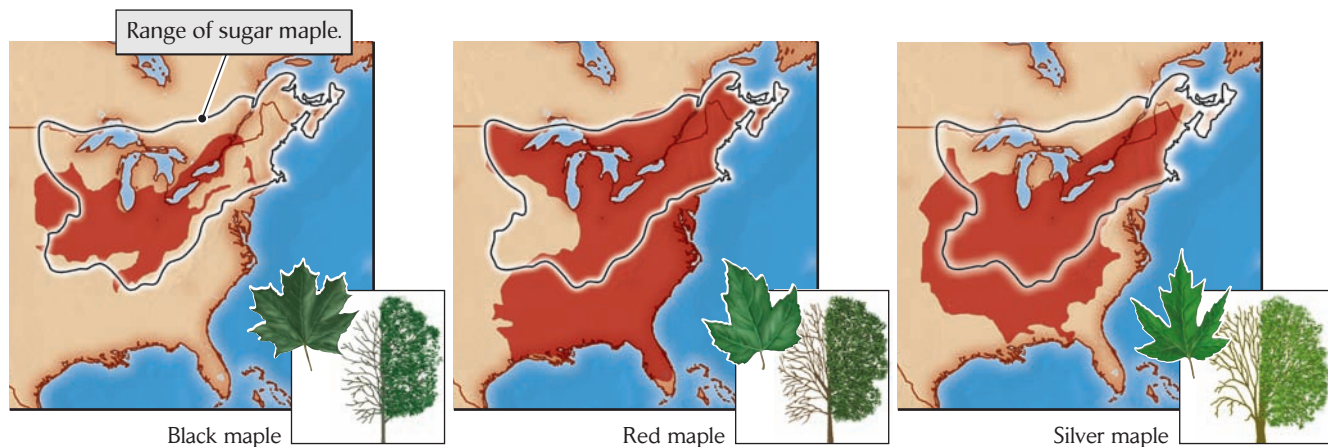

Range of sugar maple.

Black maple

Red maple

Silver maple

FIGURE 5.3 Related species may differ in their ecological tolerances. The red areas show the ranges of black, red, and silver maples in eastern North America. The range of the sugar maple is outlined on each map to show the area of overlap. After H. A. Fowells, *Silvics of Forest Trees of the United States,* U.S. Department of Agriculture, Washington, D.C. (1965).

soil and topography. Black maple (*A. nigrum*) frequently occurs in the same areas as the closely related sugar maple, but usually on drier, better-drained soils higher in calcium content (and therefore less acidic). Silver maple (*A. saccharinum*) occurs widely in the eastern United States, but especially on the moist, well-drained soils of the Ohio and Mississippi river basins. Red maple (*A. rubrum*) grows best either under wet, swampy conditions or on dry, poorly developed soils—that is, under extreme conditions that limit the growth of the other species. Nonetheless, these trees all have a similar growth form and naturally occur within—and partially define—the temperate seasonal forest biome.

Climate defines the boundaries of terrestrial biomes

One of the most widely adopted climate classification schemes is the **climate zone** system developed by the German ecologist Heinrich Walter. This system, which has nine major divisions, is based on the annual cycle of temperature and precipitation. The important attributes of climate and characteristics of vegetation in each of these zones are set out in Figure 5.4. The values of temperature and precipitation used to define climate zones correspond to the conditions of moisture and cold stress that are particularly important determinants of plant form. For example, within tropical latitudes, the tropical climate zone is distinguished from the equatorial climate zone by the occurrence of water stress during a pronounced dry season. The subtropical climate zone, which occurs at somewhat higher latitudes, is perpetually water-stressed. The typical vegetation types in these three climate zones are evergreen rain forest (equatorial), seasonal forest or savanna (tropical), and desert scrub (subtropical), respectively. We will look at Walter's climate zones in more detail below.

Many classification schemes for biomes exist. Walter's is based first on climate, with boundaries between climate zones drawn to match changes between major vegetation types. Cornell University ecologist Robert H. Whittaker defined biomes first by their vegetation type, and then devised a simple climate diagram on which he plotted

Biome name	Climate zone		Vegetation
Tropical rain forest	I	Equatorial: Always moist and lacking temperature seasonality	Evergreen tropical rain forest
Tropical seasonal forest/savanna	II	Tropical: Summer rainy season and "winter" dry season	Seasonal forest, scrub, or savanna
Subtropical desert	III	Subtropical (hot deserts): Highly seasonal, arid climate	Desert vegetation with considerable exposed surface
Woodland/shrubland	IV	Mediterranean: Winter rainy season and summer drought	Sclerophyllous (drought-adapted), frost-sensitive shrublands and woodlands
Temperate rain forest	V	Warm temperate: Occasional frost, often with summer rainfall maximum	Temperate evergreen forest, somewhat frost-sensitive
Temperate seasonal forest	VI	Nemoral: Moderate climate with winter freezing	Frost-resistant, decidous, temperate forest
Temperate grassland/desert	VII	Continental (cold deserts): Arid, with warm or hot summers and cold winters	Grasslands and temperate deserts
Boreal forest	VIII	Boreal: Cold temperate with cool summers and long winters	Evergreen, frost-hardy needle-leaved forest (taiga)
Tundra	IX	Polar: Very short, cool summers and long, very cold winters	Low, evergreen vegetation, without trees, growing over permanently frozen soils

FIGURE 5.4 Heinrich Walter classified the climate zones of the world according to the annual cycle of temperature and precipitation. The biome names given to these zones under Whittaker's classification scheme are shown in the left-hand column.

FIGURE 5.5 Whittaker's biomes are delineated according to average temperature and precipitation. Whittaker plotted the boundaries of observed vegetation types with respect to average temperature and precipitation. In climates intermediate between those of forest and desert biomes, climatic seasonality, fire, and soils determine whether woodland, grassland, or shrubland develops. *Inset:* Average annual temperature and precipitation for a sample of localities more or less evenly distributed over the land area of the earth. Most of the points fall within a triangular region that includes almost the full range of climates. Only the climates of high mountains do not fall within the triangle. From R. H. Whittaker, *Communities and Ecosystems,* 2nd ed., Macmillan, New York (1975).
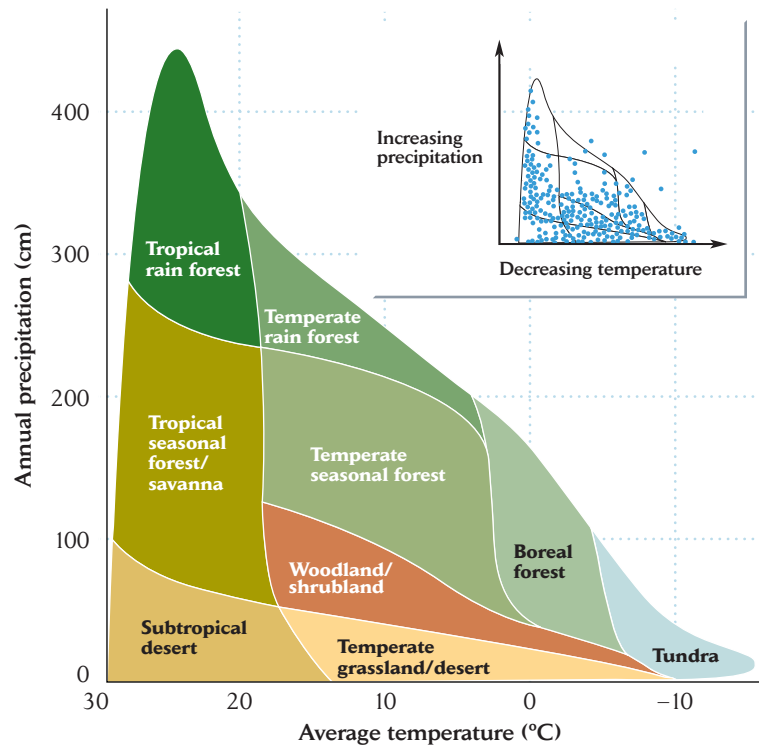
the approximate boundaries of his biomes with respect to average temperature and precipitation (Figure 5.5). The result is similar to Walter's scheme, as one would expect, and their nine biome types correspond directly. When plotted on Whittaker's diagram, most locations on earth fall within a triangular area whose three corners represent warm moist, warm dry, and cool dry climates. (Cold regions with high rainfall are rare because water does not evaporate rapidly at low temperatures and because the atmosphere in cold regions holds little water vapor.)

At tropical and subtropical latitudes, where average temperatures range between 20°C and 30°C, vegetation ranges from rain forest, which is wet throughout the year and generally receives more than 250 cm (about 100 inches) of rain annually (Walter's equatorial climate zone), to desert, which generally receives less than 50 cm of rain (Walter's subtropical climate zone). Intermediate climates support seasonal forests (150–250 cm rainfall), in which some or all trees lose their leaves during the dry season, or scrub and savannas (50–150 cm rainfall).

Plant communities at temperate latitudes follow the pattern of tropical communities with respect to rainfall, falling conveniently into four vegetation types: temperate rain forest (as in the Pacific Northwest of North America), temperate seasonal forest, woodland/shrubland, and temperate grassland/desert. At higher latitudes, precipitation varies so little from one locality to another that vegetation

types are poorly differentiated by climate. Where average temperature falls between 0°C and −5°C, boreal forest predominates. Where average annual temperatures are below −5°C, all plant communities may be lumped into one type: tundra.

Toward the drier end of the precipitation spectrum within each temperature range, fire plays a distinct role in shaping plant communities. The influence of fire is greatest where moisture availability is intermediate and highly seasonal. Deserts and moist forests burn infrequently because deserts rarely accumulate enough plant debris to fuel a fire and moist forests rarely dry out enough to become highly flammable. Grassland and shrubland have the combination of abundant fuel and seasonal drought that make fire a frequent visitor. In these biomes, fire is a dominating factor to which all community members must be adapted and, indeed, for which many are specialized. Some species require fire for germination of their seeds and growth of their seedlings. Toward the moister edges of African savannas and North American prairies, frequent fires kill the seedlings of trees and prevent the encroachment of forests, which could be sustained by the local precipitation if it were not for fire. Burning favors perennial grasses and forbs with extensive root systems and meristems (growth centers) that can survive underground. (Grasses tolerate grazing for the same reason.) After an area has burned, grass and forb roots sprout fresh shoots

and quickly establish new vegetation above the surface of the soil. In the absence of frequent fires, tree seedlings become established and eventually shade out savanna and prairie vegetation.

As in all classification systems, exceptions appear, and boundaries between biomes are fuzzy. Moreover, not all plant growth forms correspond to climate in the same way; as mentioned earlier, Australian eucalyptus trees form forests under climatic conditions that support only scrubland or grassland on other continents. Finally, plant communities reflect factors other than temperature and rainfall. Topography, soils, fire, seasonal variations in climate, and herbivory all leave their mark. The overview of the major terrestrial biomes in this chapter emphasizes the distinguishing features of the physical environment and how these features are reflected in the form of the dominant plants.

MORE ON THE WEB *Biomes and Animal Forms.* Why are biome definitions based on the predominant life forms of plants, rather than referring to their animal inhabitants?
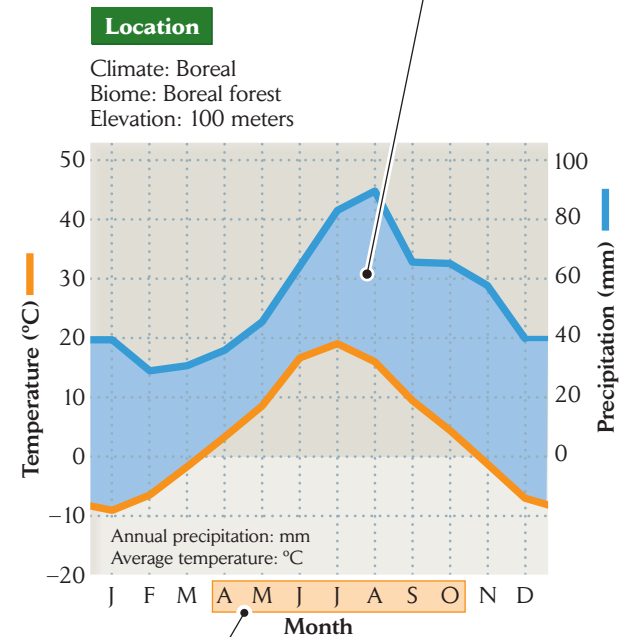
MORE ON THE WEB *Characterizing Climate.* Integrated descriptions of climate emphasize the interaction of temperature and availability of water.

Walter climate diagrams distinguish the major terrestrial biomes

Temperature and precipitation interact to determine the conditions and resources available for plant growth. It is not surprising, then, that the distributions of the major biomes of the earth follow patterns of temperature and precipitation. Because of this close relationship, it is important to describe climate in a manner that reflects the availability of water, taking into consideration changes in temperature and precipitation through the year.

Heinrich Walter developed a climate diagram that illustrates seasonal periods of water deficit and abundance and therefore permits ecologically meaningful comparisons of climates between localities (Figure 5.6). The Walter climate diagram portrays average monthly temperature and precipitation throughout the course of a year. The vertical scales of temperature and precipitation are adjusted so that when precipitation is higher than temperature on the diagram, water is plentiful and plant production is limited primarily by temperature. Conversely, when temperature is higher than precipitation, plant production is limited by availability of water. Walter's scales equate 20 mm of

As a rule of thumb, about 20 mm of monthly precipitation for each 10°C in temperature provides sufficient moisture for plant growth. This occurs wherever the precipitation line (blue) is above the temperature line (orange) on this graph.

Location

Climate: Boreal
Biome: Boreal forest
Elevation: 100 meters

Annual precipitation: mm
Average temperature: °C

These months of above–freezing temperatures are the effective growing season for plants.

FIGURE 5.6 Walter climate diagrams allow ecologically meaningful comparisons between localities. These diagrams, such as the one illustrated here for a hypothetical locality in the boreal forest biome, portray the annual progression of monthly average temperature (left-hand scale) and precipitation (right-hand scale).

monthly precipitation with 10°C in temperature. Thus, as a rule of thumb, at an average temperature of 20°C, 40 mm of monthly precipitation provides sufficient moisture for plant growth. We'll use Walter climate diagrams to compare the biomes characterized below.

Climate diagrams for locations in each of Walter's climate zones are shown in Figure 5.7. The seasonal distributions of wet and dry periods differ among the climate zones at lower latitudes. Equatorial climates (climate zone I) like that at Andagoya, Colombia, are aseasonal; that is, they are warm and wet throughout the year. Subtropical climates (III), such as that of Chiclayo, Peru, are warm and dry throughout the year. Summer rains and winter drought characterize tropical climates (II, Brasília, Brazil). Mediterranean climates (IV, Lisbon, Portugal) experience winter rains and summer drought. The climate of Sitka,
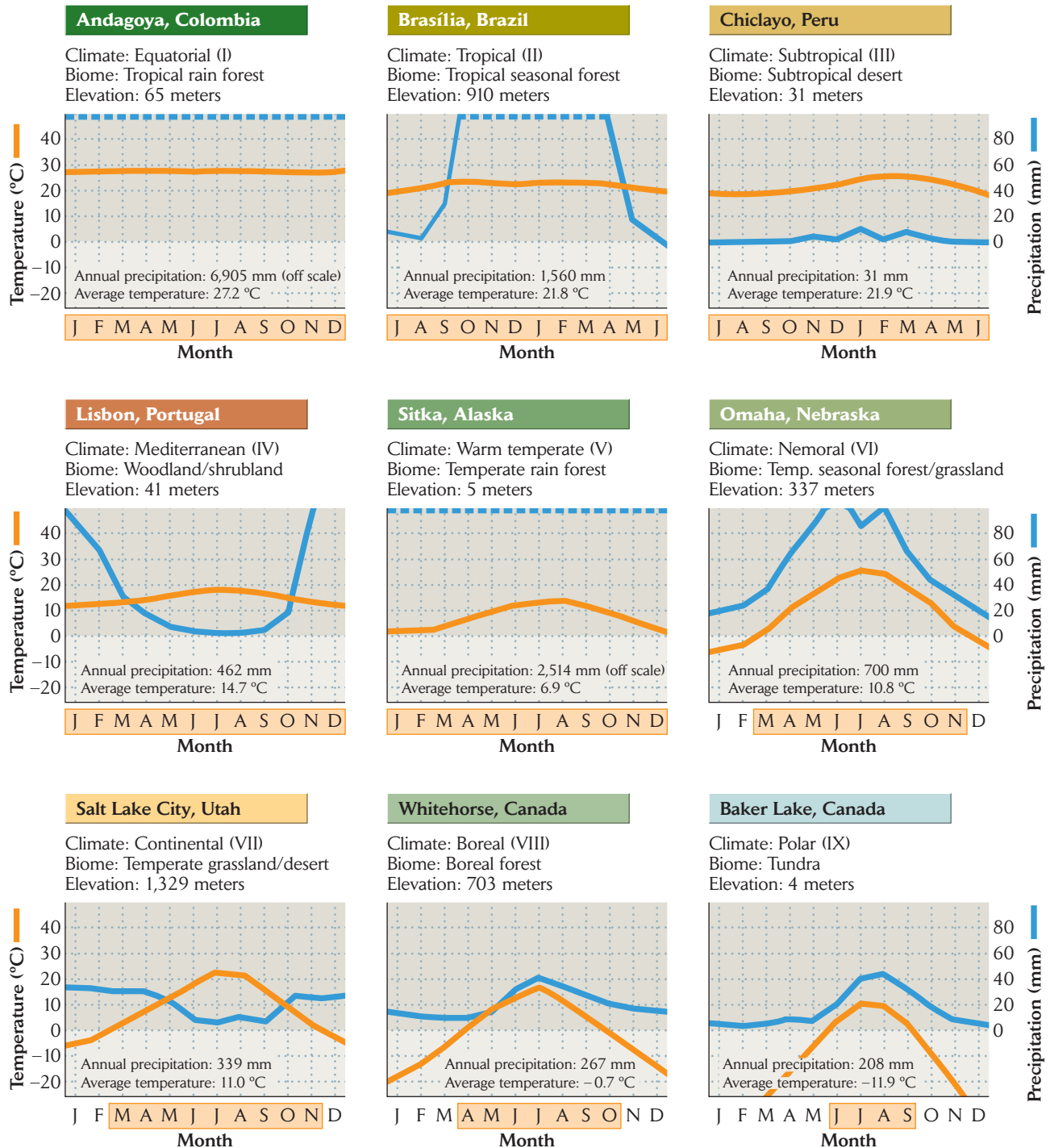
Andagoya, Colombia

Climate: Equatorial (I)
Biome: Tropical rain forest
Elevation: 65 meters

Annual precipitation: 6,905 mm (off scale)
Average temperature: 27.2 °C

J F M A M J J A S O N D
Month

Brasília, Brazil

Climate: Tropical (II)
Biome: Tropical seasonal forest
Elevation: 910 meters

Annual precipitation: 1,560 mm
Average temperature: 21.8 °C

J A S O N D J F M A M J
Month

Chiclayo, Peru

Climate: Subtropical (III)
Biome: Subtropical desert
Elevation: 31 meters

Annual precipitation: 31 mm
Average temperature: 21.9 °C

J A S O N D J F M A M J
Month

Lisbon, Portugal

Climate: Mediterranean (IV)
Biome: Woodland/shrubland
Elevation: 41 meters

Annual precipitation: 462 mm
Average temperature: 14.7 °C

J F M A M J J A S O N D
Month

Sitka, Alaska

Climate: Warm temperate (V)
Biome: Temperate rain forest
Elevation: 5 meters

Annual precipitation: 2,514 mm (off scale)
Average temperature: 6.9 °C

J F M A M J J A S O N D
Month

Omaha, Nebraska

Climate: Nemoral (VI)
Biome: Temp. seasonal forest/grassland
Elevation: 337 meters

Annual precipitation: 700 mm
Average temperature: 10.8 °C

J F M A M J J A S O N D
Month

Salt Lake City, Utah

Climate: Continental (VII)
Biome: Temperate grassland/desert
Elevation: 1,329 meters

Annual precipitation: 339 mm
Average temperature: 11.0 °C

J F M A M J J A S O N D
Month

Whitehorse, Canada

Climate: Boreal (VIII)
Biome: Boreal forest
Elevation: 703 meters

Annual precipitation: 267 mm
Average temperature: −0.7 °C

J F M A M J J A S O N D
Month

Baker Lake, Canada

Climate: Polar (IX)
Biome: Tundra
Elevation: 4 meters

Annual precipitation: 208 mm
Average temperature: −11.9 °C

J F M A M J J A S O N D
Month

FIGURE 5.7 Each climate zone has a typical seasonal pattern of temperature and precipitation. Walter climate diagrams for representative locations in each of the nine major terrestrial climate zones are shown. The dashed blue line at the top of the graphs for climate zones I, II, and V indicates monthly precipitation exceeding 100 mm all year long. From H. Walter and S.-W. Breckle, *Ecological Systems of the Geobiosphere, I, Ecological Principles in Global Perspective*, Springer-Verlag, Berlin (1985).

Alaska (warm temperate, V), is wet and mild throughout the year and supports evergreen forest vegetation.

Seasonality of temperature is a major factor in climate zones VI–IX, which occur at middle and high latitudes.

Precipitation is typically low, but because of the low temperatures, moisture is generally not limiting during the short summer growing season. Continental climates (VII, Salt Lake City, Utah) are typically dry throughout the year
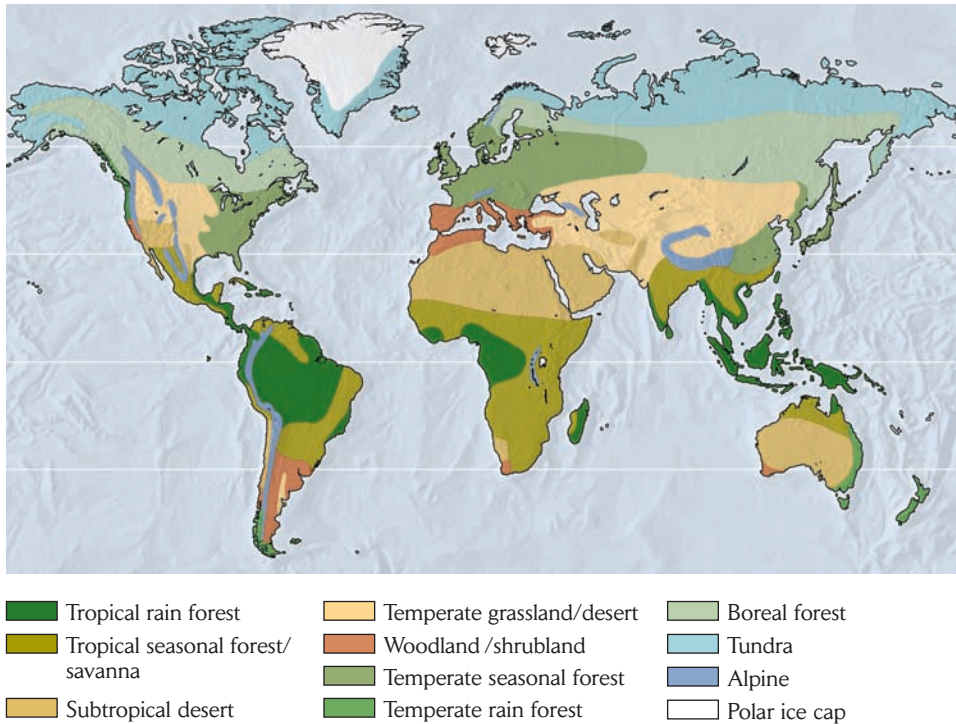
FIGURE 5.8 Global distribution of the major biomes.

Legend:
- Tropical rain forest
- Tropical seasonal forest/savanna
- Subtropical desert
- Temperate grassland/desert
- Woodland/shrubland
- Temperate seasonal forest
- Temperate rain forest
- Boreal forest
- Tundra
- Alpine
- Polar ice cap

and become warm enough in summer to develop significant water stress. Such areas, which include much of the Great Basin of the western United States, support shrubby desert vegetation.

The same climate zones can be recognized where they occur around the world. For example, the tropical climates of Brasília (Brazil), Harare (Zimbabwe), and Darwin (Australia) all share the even year-round warm temperatures and summer rainfall typical of climate zone II. And each of these areas supports deciduous forest vegetation grading into savanna where precipitation is particularly low. Indeed, each climate zone supports characteristic vegetation that defines the biome type and makes it easy for us to recognize the general attributes of these ecosystems in any region.

Walter's climate zones are one of several systems of biome classification. While these systems differ in the number of biomes recognized, and some emphasize biological characteristics more than the physical environment, they all present essentially the same picture of ecosystem variation over the surface of the earth. For example, the World Wildlife Fund recognizes fourteen biomes, rather than Walter's nine, adding (i) temperate and (ii) tropical coniferous forests, both characterized by seasonal climates but tending to be drier and existing on poorer soils than biomes with broad-leaved trees; (iii) montane grasslands and shrublands, including the puna and páramo zones of the high Andes; (iv) seasonally flooded grasslands and savannas in both tropical and temperate regions, and

(v) mangrove wetlands, which comprise a specialized vegetation type within the marine intertidal zone. Its system is designed to identify the major ecological regions of the earth whose conservation would preserve the largest part of the diversity of the earth's ecosystems.
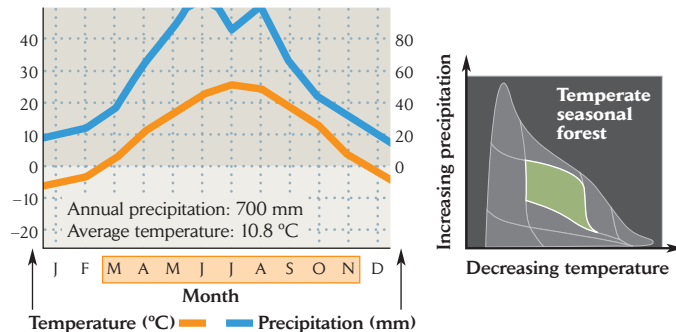
The worldwide distribution of biome types arranged by any system follows the same general patterns of temperature and precipitation over the earth (Figure 5.8). We shall consider the biomes and general ecological characteristics of each of the major Walter climate zones in the series of vignettes that follow. Because most readers of this book live within temperate latitudes, this is a good place to start.

Temperate climate zones have average annual temperatures between 5°C and 20°C

The climates within temperate latitudes are characterized by average annual temperatures in the range of 5°–20°C at low elevations. Such climates are distributed approximately between 30°N and 45°N in North America and Asia and between 40°N and 60°N in Europe, which is warmed by the Gulf Stream and by westerly winds. Frost is an important factor throughout the temperate latitudes, perhaps even defining their general character. Within those latitudes, biomes are distinguished primarily

Biome: Temperate seasonal forest

(a) Beech–maple forest in fall, New York.

Omaha, Nebraska

Climate: Nemoral (VI)
Elevation: 337 meters

Annual precipitation: 700 mm
Average temperature: 10.8 °C

Month

Temperature (°C) ━━ Precipitation (mm) ━━

Increasing precipitation

**Temperate
seasonal
forest**

Decreasing temperature

(b) Young deciduous forest in winter, Massachusetts.

FIGURE 5.9 Major features of the temperate seasonal forest biome. Photos by R. E. Ricklefs.

by total amounts and seasonal patterns of precipitation. The length of the frost-free season, which is referred to as the **growing season,** and the severity of frost are also important.

Temperate seasonal forest biome (climate zone VI)

Often referred to as deciduous forest, the temperate seasonal forest biome occurs under moderate conditions with winter freezing. In North America, this biome is found principally in the eastern United States and southeastern Canada; it is also widely distributed in Europe and eastern Asia (Figure 5.9). This biome is poorly developed in the Southern Hemisphere because the larger ratio of ocean surface to land moderates winter temperatures and prevents frost. In the Northern Hemisphere, the length of the growing season in this biome varies from 130 days at higher latitudes to 180 days at lower latitudes. Precipitation usually exceeds evaporation and transpiration; conse-

quently, water tends to move downward through soils and to drain from the landscape as groundwater and as surface streams and rivers. Soils are often podsolized, tend to be slightly acidic and moderately leached, and are brown in color owing to abundant organic matter. Deciduous trees are the dominant plant growth form. The vegetation often includes a layer of smaller trees and shrubs beneath the dominant trees as well as herbaceous plants on the forest floor. Many of these herbaceous plants complete their growth and flower early in spring, before the trees have fully leafed out.
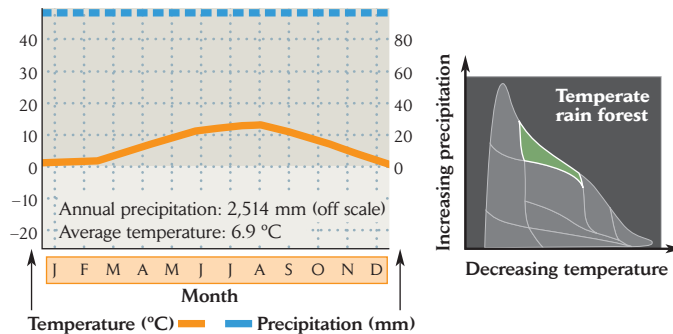
Warmer and drier parts of the temperate seasonal forest biome, especially where soils are sandy and nutrient poor, tend to develop needle-leaved forests dominated by pines. The most important of these ecosystems in North America are the pine forests of the coastal plains of the Atlantic and Gulf states of the United States; pine forests also exist at higher elevations in the western United States. Because of the warm climate in the southeastern United States, soils there are usually lateritic and nutrient poor.

Biome: Temperate rain forest

(a) California redwoods.

Sitka, Alaska

Climate: Warm temperate (V)
Elevation: 5 meters

Annual precipitation: 2,514 mm (off scale)
Average temperature: 6.9 °C

J F M A M J J A S O N D
Month

Temperature (°C) ▬▬ **Precipitation (mm)** ▬▬

Increasing precipitation

**Temperate
rain forest**

Decreasing temperature

(b) Old-growth Douglas fir forest, Pacific Northwest.

FIGURE 5.10 **Major features of the temperate rain forest biome.** Photo (a) by PhotoSphere Images/PictureQuest; photo (b) by Tom and Pat Leeson/Photo Researchers.

The low availability of nutrients and water favors evergreen, needle-leaved trees, which resist desiccation and give up nutrients slowly because they retain their needles for several years. Because soils tend to be dry, fires are frequent, and most species are able to resist fire damage.

Temperate rain forest biome (climate zone V)

In warm temperate climates near the Pacific coast in northwestern North America, and in southern Chile, New Zealand, and Tasmania, mild winters, heavy winter rains, and summer fog create conditions that support extremely tall evergreen forests (Figure 5.10). In North America, these forests are dominated toward the south by coast redwood (*Sequoia sempervirens*) and toward the north by Douglas-fir (*Pseudotsuga* spp.). These trees are typically 60–70 m tall and may grow to over 100 m. Ecologists do not understand why these sites are dominated by needle-leaved trees, but the fossil record shows that these plant
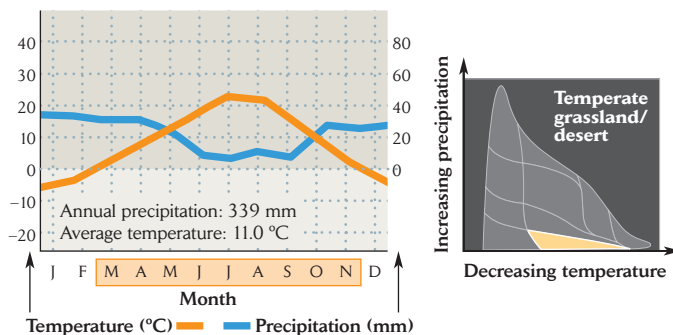
communities are very old and that they are remnants of forests that were vastly more extensive during the Mesozoic era, as recently as 70 million years ago. In contrast to rain forests in the tropics, temperate rain forests typically support few species.

Temperate grassland/desert biome (climate zone VII)

In North America, grasslands develop within continental climate zones where rainfall ranges between 30 and 85 cm per year and winters are cold (Figure 5.11). The growing season increases from north to south from about 120 to 300 days. These grasslands are often called **prairies.** Extensive grasslands are also found in central Asia, where they are called **steppes.** Precipitation is infrequent, so organic detritus does not decompose rapidly, and the soils are rich in organic matter. Because of their low acidity, prairie soils, which belong to the mollisol group, are not heavily leached and tend to be rich in nutrients. The

Biome: Temperate grassland/desert

(a) Great Basin grassland, western Colorado.

Salt Lake City, Utah

Climate: Continental (cold deserts) (VII)
Elevation: 1,329 meters

Annual precipitation: 339 mm
Average temperature: 11.0 °C

Temperature (°C)   Precipitation (mm)

(b) Sagebrush, eastern Washington.

FIGURE 5.11 Major features of the temperate grassland/desert biome. Photos by R. E. Ricklefs.

vegetation is dominated by grasses, which grow to heights over 2 m in the moister parts of these grasslands and to less than 0.2 m in more arid regions. Forbs are also abundant. Fire is a dominant influence in these grasslands, particularly where the habitat dries out during the late summer. Most grassland species have fire-resistant underground stems, or **rhizomes,** from which shoots resprout, or they have fire-resistant seeds.

Where precipitation ranges between 25 and 50 cm per year, and winters are cold and summers are hot, grasslands grade into deserts. The temperate desert biome covers most of the Great Basin of the western United States. In the northern part of the region, sagebrush (*Artemisia*) is the dominant plant, whereas toward the south and on somewhat moister soils, widely spaced juniper and piñon trees predominate, forming open woodlands less than 10 m in stature with sparse coverings of grass. In these temperate deserts, evaporation and transpiration exceed precipitation during most of the year, so soils are dry and little water percolates through them to form streams and
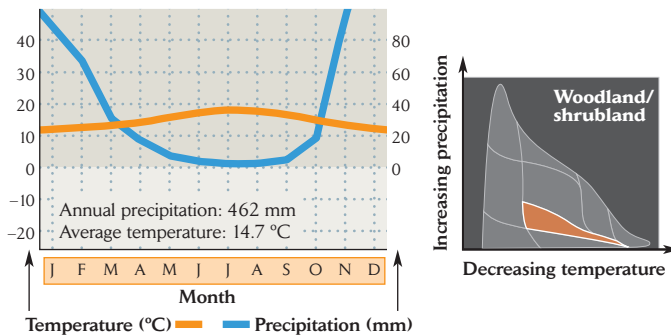
rivers. Calcium carbonate leached from the surface layers of the soil tends to accumulate at the depths to which water usually penetrates. Fires are infrequent in temperate deserts because the habitat produces little fuel. However, because of the low productivity of the plant community, grazing can exert strong pressure on the vegetation and may even favor the persistence of shrubs, which are not good forage. Indeed, many dry grasslands in the western United States and elsewhere in the world have been converted into deserts by overgrazing.

Woodland/shrubland biome (climate zone IV)

The Mediterranean climate zone is found at 30°–40° north and south of the equator—and at somewhat higher latitudes in Europe—on the western sides of continental landmasses, where cold ocean currents and winds blowing from the continents dominate the climate. Mediterranean climates are found in southern Europe and

Biome: Woodland/shrubland

(a) Chaparral at wet site at low elevation with infrequent fire, southern California.

Lisbon, Portugal

Climate: Mediterranean (IV)
Elevation: 41 meters

Annual precipitation: 462 mm
Average temperature: 14.7 ºC

Temperature (ºC)   Precipitation (mm)
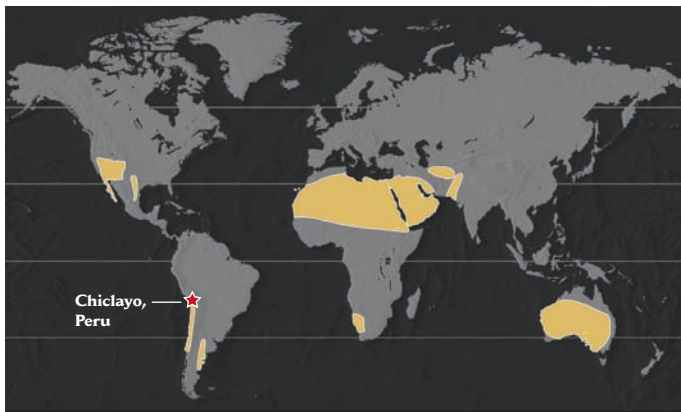

(b) Fynbos vegetation in the Cape region of South Africa.

FIGURE 5.12 Major features of the woodland/shrubland biome. Photo (a) by Earl Scott/Photo Researchers; photo (b) by Fletcher & Baylis/Photo Researchers

southern California in the Northern Hemisphere and in central Chile, the Cape region of South Africa, and southwestern Australia in the Southern Hemisphere. Mediterranean climates are characterized by mild winter temperatures, winter rain, and summer drought. These climates support thick, evergreen, shrubby vegetation 1–3 m in height, with deep roots and drought-resistant foliage (Figure 5.12). The small, durable leaves of typical Mediterranean-climate plants have earned them the label of **sclerophyllous** ("hard-leaved") vegetation. Fires are frequent in the woodland/shrubland biome, and most plants have either fire-resistant seeds or root crowns that resprout soon after a fire.
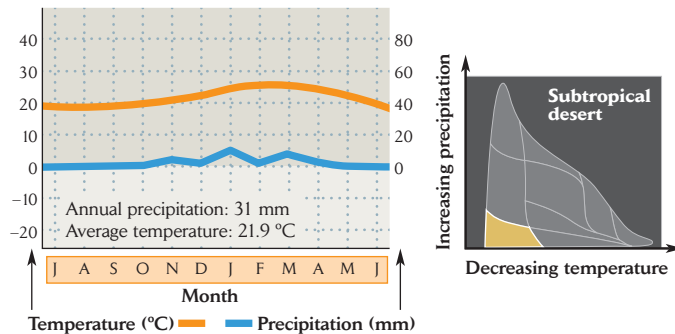
Subtropical desert biome (climate zone III)

What people call "desert" varies tremendously. Many people refer to the dry areas of the Great Basin and of central Asia as deserts—the Gobi Desert is a name famil-

iar to most of us. But the climates of those "deserts" fall within Walter's continental climate zone, characterized by low precipitation and cold winters. These areas are referred to as cold deserts. In contrast, subtropical deserts (Figure 5.13), often called hot deserts, develop at latitudes 20°–30° north and south of the equator, in areas with high atmospheric pressure associated with the descending air of the Hadley cells (Chapter 4). Subtropical deserts have very sparse rainfall (less than 25 cm), high temperatures, and generally long growing seasons. Because of the low rainfall, the soils of subtropical deserts (aridosols) are shallow, virtually devoid of organic matter, and neutral in pH. Impermeable hardpans of calcium carbonate often develop at the limits of water penetration—at depths of a meter or less. Whereas sagebrush dominates the cold deserts of the Great Basin, creosote bush (*Larrea tridentata*) takes its place in the subtropical deserts of the Americas. Moister sites within this biome support a profusion of succulent cacti, shrubs, and small trees, such as mesquite (*Prosopis*) and paloverde (*Cercidium microphyllum*). Most

Biome: Subtropical desert

(a) Cholla cactus in northern Sonora, Mexico.

Chiclayo, Peru

Climate: Subtropical (hot deserts) (III)
Elevation: 31 meters

Annual precipitation: 31 mm
Average temperature: 21.9 °C

Temperature (°C) ━━ Precipitation (mm) ━━

Increasing precipitation

Subtropical desert

Decreasing temperature

(b) Saguaro cactus in southern Arizona.

FIGURE 5.13 Major features of the subtropical desert biome. Photos by R. E. Ricklefs.

subtropical deserts receive summer rainfall. After summer rains, many herbaceous plants sprout from dormant seeds, grow quickly, and reproduce before the soils dry out again. Many of the plants in subtropical deserts are not frost-tolerant. Species diversity is usually much higher than it is in temperate arid lands.
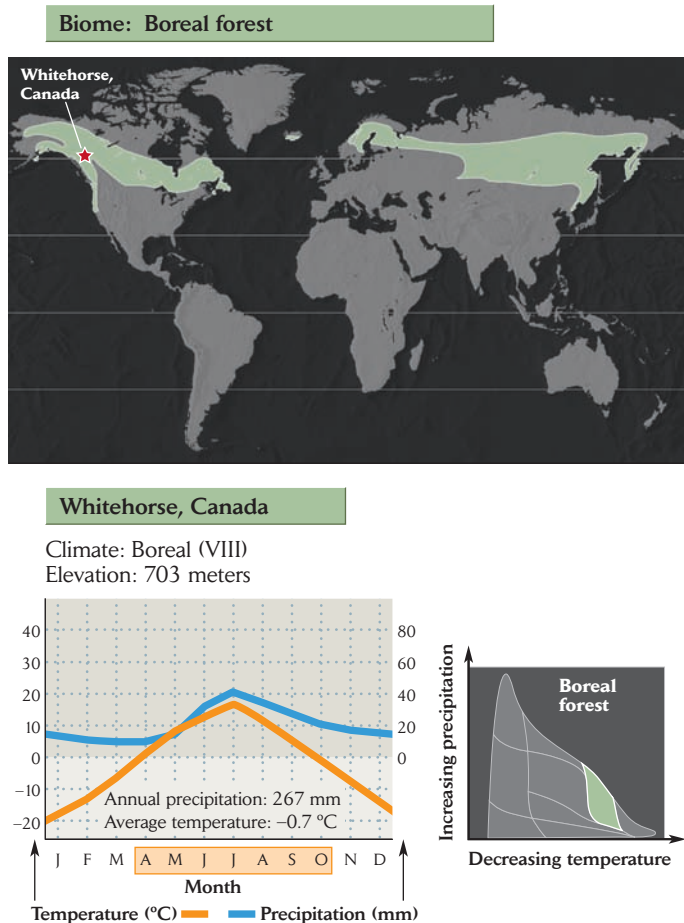
Boreal and polar climate zones have average temperatures below 5°C

At high latitudes, cold temperatures predominate. Precipitation is often very sparse because water evaporates slowly into the atmosphere at low temperatures, but soils are often saturated, and water availability is not an important limitation in high-latitude climate zones. Biological productivity during the short summer growing seasons is generally low, and cold temperatures slow the decomposition of organic matter and the release of nutrients in

the soil. As a result, plants retain their foliage for many years, and the vegetation tends to be evergreen and highly adapted to cold winter temperatures.

Boreal forest biome (climate zone VIII)

Stretching in a broad belt centered at about 50°N in North America and about 60°N in Europe and Asia lies the boreal forest biome, often called **taiga** (Figure 5.14). The average annual temperature is below 5°C, and winters are severe. Annual precipitation generally ranges between 40 and 100 cm, and because evaporation is low, soils are moist throughout most of the growing season. The vegetation consists of dense, seemingly endless stands of 10–20 m tall evergreen needle-leaved trees, mostly spruces and firs. Because of the low temperatures, plant litter decomposes very slowly and accumulates at the soil surface, forming one of the largest reservoirs of organic carbon on earth. The needle litter produces high levels of

Biome: Boreal forest

Whitehorse, Canada

(a) Boreal forest, near Fairbanks, Alaska.

Whitehorse, Canada

Climate: Boreal (VIII)
Elevation: 703 meters

Annual precipitation: 267 mm
Average temperature: −0.7 °C

Temperature (°C)   Precipitation (mm)

Increasing precipitation

Boreal
forest

Decreasing temperature

(b) Boreal forest with willow scrub in fall, Denali National Park, Alaska.

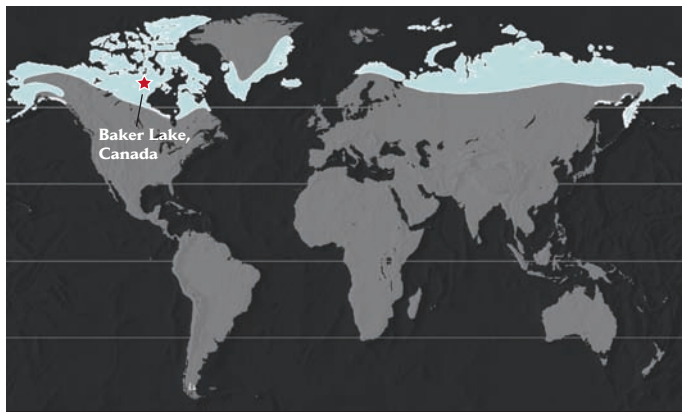**FIGURE 5.14 Major features of the boreal forest biome.** Photos by R. E. Ricklefs.

organic acids, so the soils are acidic, strongly podsolized, and generally of low fertility. Growing seasons are rarely as much as 100 days, and often half that. The vegetation is extremely frost-tolerant, as temperatures may reach −60°C during the winter. Species diversity is very low.
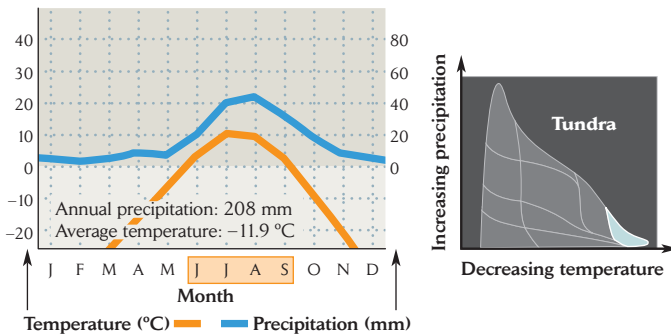
Tundra biome (climate zone IX)

To the north of the boreal forest, in the polar climate zone, lies the Arctic tundra, a treeless expanse underlain by permanently frozen soil, or **permafrost** (Figure 5.15). The soils thaw to a depth of 0.5–1 m during the brief summer growing season. Precipitation is generally less, and often much less, than 60 cm, but in low-lying areas where drainage is prevented by permafrost, soils may remain saturated with water throughout most of the growing season. Soils tend to be acidic because of their high organic matter content, and they contain few nutrients. In this nutrient-poor environment, plants hold their foliage for years. Most

plants are dwarf, prostrate woody shrubs, which grow low to the ground to gain protection under the winter blanket of snow and ice. Anything protruding above the surface of the snow is sheared off by blowing ice crystals. For most of the year, the tundra is an exceedingly harsh environment, but during the 24-hour-long summer days, the rush of biological activity in the tundra testifies to the remarkable adaptability of life.

At high elevations within temperate latitudes, and even within the tropics, one finds vegetation resembling that of the Arctic tundra and even including some of the same species, or their close relatives. These areas of *alpine tundra* above the tree line occur most broadly in the Rocky Mountains of North America, the Alps of Europe, and especially on the Plateau of Tibet in central Asia. In spite of their similarities, alpine and Arctic tundra have important points of dissimilarity as well. Areas of alpine tundra generally have warmer and longer growing seasons, higher precipitation, less severe winters, greater

Biome: Tundra

(a) Wet tundra near Churchill, Manitoba, Canada.

Baker Lake, Canada

Climate: Polar (IX)
Elevation: 4 meters

Annual precipitation: 208 mm
Average temperature: −11.9 °C

Month

Temperature (°C)   Precipitation (mm)

Increasing precipitation

Tundra

Decreasing temperature

(b) Close-up of tundra vegetation with lichens and dwarf rhododendrons.

FIGURE 5.15 Major features of the tundra biome. Photos by R. E. Ricklefs.

productivity, better-drained soils, and higher species diversity than Arctic tundra. Still, harsh winter conditions ultimately limit the growth of trees.

Climate zones within tropical latitudes have average temperatures exceeding 20°C

Within 20° of latitude from the equator, the temperature varies more throughout the day than average monthly temperatures vary throughout the year. Average temperatures at sea level generally exceed 20°C. Climates within tropical latitudes are distinguished by differences in the seasonal pattern of rainfall. These differences create a continuous gradient of vegetation from wet, aseasonal rain forest through seasonal forest, scrub, savanna, and desert. Frost is not a factor in tropical biomes, even at high
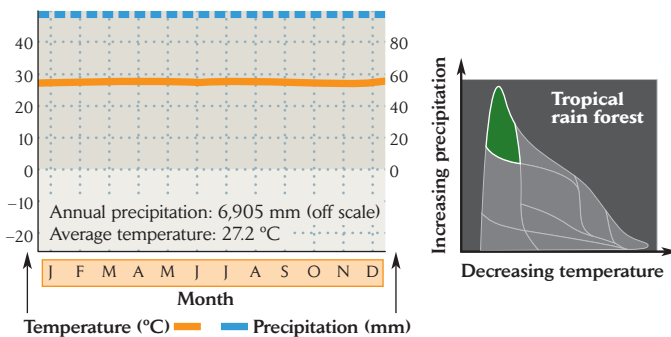
elevations, and tropical plants and animals generally cannot tolerate freezing.

Tropical rain forest biome (climate zone I)

Climates where tropical rain forests develop (in Walter's equatorial climate zone) are always warm and receive at least 200 cm of precipitation throughout the year, with no less than 10 cm during any single month. These conditions prevail in three important regions within the tropics (Figure 5.16). First, the Amazon and Orinoco basins of South America, along with additional areas in Central America and along the Atlantic coast of Brazil, constitute the Neotropical rain forest. Second, the area from southernmost West Africa and extending eastward through the Congo River basin makes up the African rain forest (with an added area on the eastern side of the island of Madagascar). Third, the Indo-Malayan rain forest covers parts of Southeast Asia (Vietnam, Thailand, and the Malay

Biome: Tropical rain forest

(a) Cloud forest during dry season, central Panama.

Andagoya, Colombia

Climate: Equatorial (I)
Elevation: 65 meters

Annual precipitation: 6,905 mm (off scale)
Average temperature: 27.2 °C

Temperature (°C) ▬▬   Precipitation (mm) ▬▬

Tropical rain forest

Increasing precipitation

Decreasing temperature

(b) Mid-elevation cloud forest, Jamaica, West Indies.

FIGURE 5.16 Major features of the tropical rain forest biome. Photos by R. E. Ricklefs.

Peninsula); the islands between Asia and Australia, including the Philippines, Borneo, and New Guinea; and the Queensland coast of Australia.
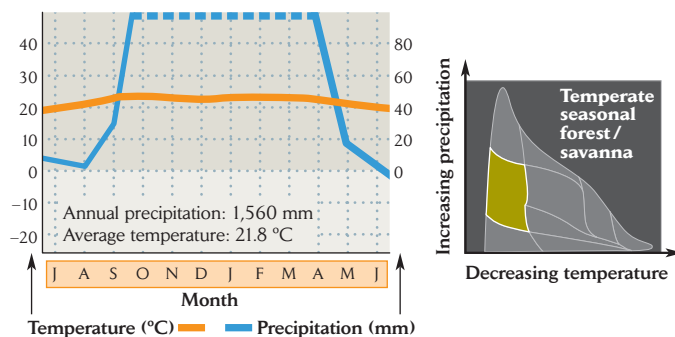
The tropical rain forest climate often exhibits two peaks of rainfall centered on the equinoxes, corresponding to the periods when the intertropical convergence lies over the equator (see Chapter 4). Rain forest soils are typically old and deeply weathered oxisols. Because they are relatively devoid of humus and clay, they take on the reddish color of aluminum and iron oxides and retain nutrients poorly. In spite of the low nutrient status of the soils, rain forest vegetation is dominated by a continuous **canopy** of tall evergreen trees rising to 30–40 m. Occasional **emergent** trees rise above the canopy to heights of 55 m or so. Because water stress on emergent trees is great due to their height and exposure, they are often deciduous, even in a mostly evergreen rain forest. Tropical rain forests typically have several **understory** layers beneath the canopy, containing smaller trees, shrubs, and herbs, but these are usually quite sparse because so little light penetrates the canopy. Climbing **lianas,** or woody vines, and **epiphytes,** plants that grow on the branches of other plants and are not rooted in soil (also called air plants; see Figure 1.5), are prominent in the forest canopy itself. Species diversity is higher than anywhere else on earth.

Per unit of area, the biological productivity of tropical rain forests exceeds that of any other terrestrial biome, and their standing biomass exceeds that of all other biomes except temperate rain forests. Because of the continuously high temperatures and abundant moisture, plant litter decomposes quickly, and the vegetation immediately takes up the released nutrients. This rapid nutrient cycling supports the high productivity of the rain forest, but it also makes the rain forest ecosystem extremely vulnerable to disturbance. When tropical rain forests are cut and burned, many of the nutrients are carted off in logs or go up in smoke. The vulnerable soils erode rapidly and fill the streams with silt. In many cases, the environment degrades rapidly and the landscape becomes unproductive.

Biome: Tropical seasonal forest/savanna

(a) Acacia trees with weaverbird nests, Kenya, East Africa.

Brasília, Brazil

Climate: Tropical (II)
Elevation: 910 meters

Annual precipitation: 1,560 mm
Average temperature: 21.8 ºC

Temperature (ºC)   Precipitation (mm)

(b) Tropical savanna in Orinoco Basin of eastern Colombia.

FIGURE 5.17 Major features of the tropical seasonal forest/savanna biome. Photos by R. E. Ricklefs.

Tropical seasonal forest/savanna biome (climate zone II)

Within the tropics, but beyond 10° from the equator (in Walter's tropical climate zone), there is typically a pronounced dry season, corresponding to winter at higher latitudes. Seasonal forests in this climate zone have a preponderance of deciduous trees that shed their leaves during the season of water stress (Figure 5.17). Where the dry season is longer and more severe, the vegetation becomes shorter, and thorns develop to protect leaves from grazing. With progressive aridity, the vegetation grades from dry forest into thorn forest and finally into true desert in the rain shadows of mountain ranges or along coasts with cold ocean currents running alongside. As in more humid tropical environments, the soils tend to be strongly lateritic and nutrient poor.

Savannas are grasslands with scattered trees. They are spread over large areas of the dry tropics, especially at moderate elevations in East Africa. Rainfall is typically 90–150 cm per year, but the driest three or four months bring less than 5 cm each. Fire and grazing undoubtedly play important roles in maintaining the character of the savanna biome, particularly in wetter regions, as grasses can persist better than other forms of vegetation under both influences. When grazing and fire are controlled within a savanna habitat, dry forest often begins to develop. Vast areas of African savanna owe their character to the influence of human activities, including burning, over many millennia.

The biome concept must be modified for freshwater aquatic systems

Terrestrial and aquatic ecologists have generated concepts and descriptive terms for ecological systems independently. The biome concept was developed for terrestrial ecosystems, where the growth form of the dominant vegetation

reflects climatic conditions. In aquatic systems, however, depth, water temperature, flow rate, and oxygen and nutrient concentrations are the dominant physical factors, and the structural attributes of aquatic organisms do not differ much in relation to these factors. As a consequence, aquatic "biomes" do not exist in the sense in which the term is applied to terrestrial ecosystems. Indeed, defining aquatic biomes according to vegetation would be impossible, because the producers in many aquatic systems are single-celled algae, which do not form "vegetation" with a characteristic structure. As a result, aquatic systems have been classified primarily by such physical characteristics as salinity, water movement, and depth. The major kinds of aquatic environments are streams and rivers, lakes, wetlands, estuaries, and oceans, and each of these can be subdivided further with respect to many factors.

Flowing water: Streams and rivers

Streams form wherever precipitation exceeds evaporation and excess water drains from the land. Streams grow with distance as they join together to form rivers. Stream and river systems are often referred to as **lotic** systems, a term generally applied to flowing fresh waters. The continuous change in environments and ecosystems from the small streams at the headwaters of a river system to the mouth of the river is the basis for the **river continuum** concept. As one moves downstream, water flows more slowly and becomes warmer and richer in nutrients; ecosystems become more complex and generally more productive.

Within small streams, ecologists distinguish areas of **riffles,** where water runs rapidly over a rocky substratum, and **pools,** which are deeper stretches of more slowly moving water (Figure 5.18). Water is well oxygenated in riffles, whereas pools tend to accumulate silt and organic matter. Both areas tend to be unproductive because the nutrients needed for life are washed away in riffles, whereas the oxygen and sunlight needed for life are lacking in pools.

In general, streams lack the richness and diversity of life seen in other aquatic systems. Toward the headwaters of rivers, where small streams are often shaded and nutrient poor, the productivity of algae and other photosynthetic organisms tends to be low. Streams are usually bordered by a **riparian zone** of terrestrial vegetation that is influenced by seasonal flooding and elevated water tables. Much of the food web of headwater ecosystems depends on leaves and other organic matter that falls or washes into streams from this surrounding vegetation.

FIGURE 5.18 Within a stream, conditions differ between pools and riffles. Photo by Ed Reschke/Peter Arnold.

Such organic material that enters the aquatic system from the outside is termed **allochthonous.**

The larger a river, the more of its organic material is homegrown, or **autochthonous.** As one moves down the river continuum, rivers become wider, slower moving, more heavily nutrient laden, and more exposed to direct sunlight (Figure 5.19). The nutrients and sunlight support the growth of algae and plants within the river itself. However, rivers also become more heavily laden with sediments washed into them from the land and carried downstream. The high turbidity caused by suspended sediments in the lower reaches of silt-laden rivers can block light and reduce production. **Fluvial** systems, as rivers are sometimes called, are also distinguished by the fact that currents continuously move material, including animals, plants, and nutrients, downstream. To maintain a fluvial system in a steady state, this downstream drift must be balanced by the upstream movement of animals, production in the upstream portions of the system, and input of allochthonous materials.

All aquatic ecosystems interact with the terrestrial biomes that surround them. We have seen that streams receive runoff, groundwater, and organic matter from the surrounding land. A variety of organisms live their lives in both aquatic and terrestrial environments. Many frogs and salamanders, for example, have aquatic larval stages and terrestrial adult stages. Some terrestrial animals feed on organisms that grow in streams and lakes, effectively moving nutrients from aquatic to nearby terrestrial systems.

FIGURE 5.19 Nutrient-laden large rivers are highly productive. This river is a tributary in the vast wetland area of the lower Amazon River floodplain in Pará State, Brazil. Photo by Jacques Jangoux/Peter Arnold.

Conversely, many organisms with aquatic larval stages, such as mosquitoes, feed on terrestrial organisms. Thus, while aquatic and terrestrial biomes have recognizable borders, organisms readily cross these borders, and the borders themselves move, extending onto and retreating from floodplains as rivers rise and fall.

Lotic systems are extremely sensitive to any modification of their water flow. Tens of thousands of dams of all sizes interrupt stream flow in the United States alone. These dams are built for flood control, to provide water for irrigation, or to generate electricity. Dams alter rates of flow, water temperature, and sedimentation patterns. Typically, water behind dams becomes warmer, and bottom habitats become choked with silt, destroying habitat for fish and other aquatic organisms. Large dams used for hydroelectric power often release water downstream that has low concentrations of dissolved oxygen. Using dams for flood control changes the seasonal cycles of flooding necessary for maintaining many kinds of riparian habitats on floodplains. Dams also disrupt the natural movement of aquatic organisms upstream and downstream, fragmenting river systems and isolating populations. Thus, lotic systems are among the most vulnerable of all biomes to habitat modification.

Standing water: Lakes and ponds

Lakes and **ponds,** referred to as **lentic** systems, are distinguished by nonflowing water. Lakes and ponds can form in any kind of depression. They range in size from small, temporary rainwater pools a few centimeters deep to Lake Baikal, in Russia, which has a maximum depth of 1,740 m (about a mile) and contains about one-fifth of all the fresh water at the surface of the earth. Many lakes and ponds are formed by the retreat of glaciers, which leave behind gouged-out basins and blocks of ice buried in glacial deposits, which eventually melt. The Great Lakes of North America formed in glacial basins, overlain until 10,000 years ago by thick ice. Lakes are also formed in geologically active regions, such as the Great Rift Valley of Africa, where vertical shifting of blocks of the earth's crust creates basins within which water accumulates. Broad river valleys, such as those of the Mississippi and Amazon rivers, have oxbow lakes, which are broad bends of the former river cut off by shifts in the main channel.

An entire lake could be considered a biome, but it is usually subdivided into several ecological zones, each of which has distinct physical conditions (Figure 5.20). The **littoral zone** is the shallow zone around the edge of a lake or pond within which one finds rooted vegetation, such as water lilies and pickerelweed. The open water beyond the littoral zone is the **limnetic** (or **pelagic) zone,** where the producers are floating single-celled algae, or *phytoplankton*. Lakes may also be subdivided vertically on the basis of light penetration and the formation of thermally stratified layers of water (the epilimnion toward the surface and the hypolimnion at depth; see Figure 4.12). The sediments at the bottoms of lakes and ponds constitute the **benthic zone,** which provides habitat for burrowing animals and microorganisms.

Lakes and ponds are not permanent. Small temporary ponds can dry out each year, often multiple times during a season. Most small temperate lakes that formed when glaciers retreated will gradually fill in with sediment until
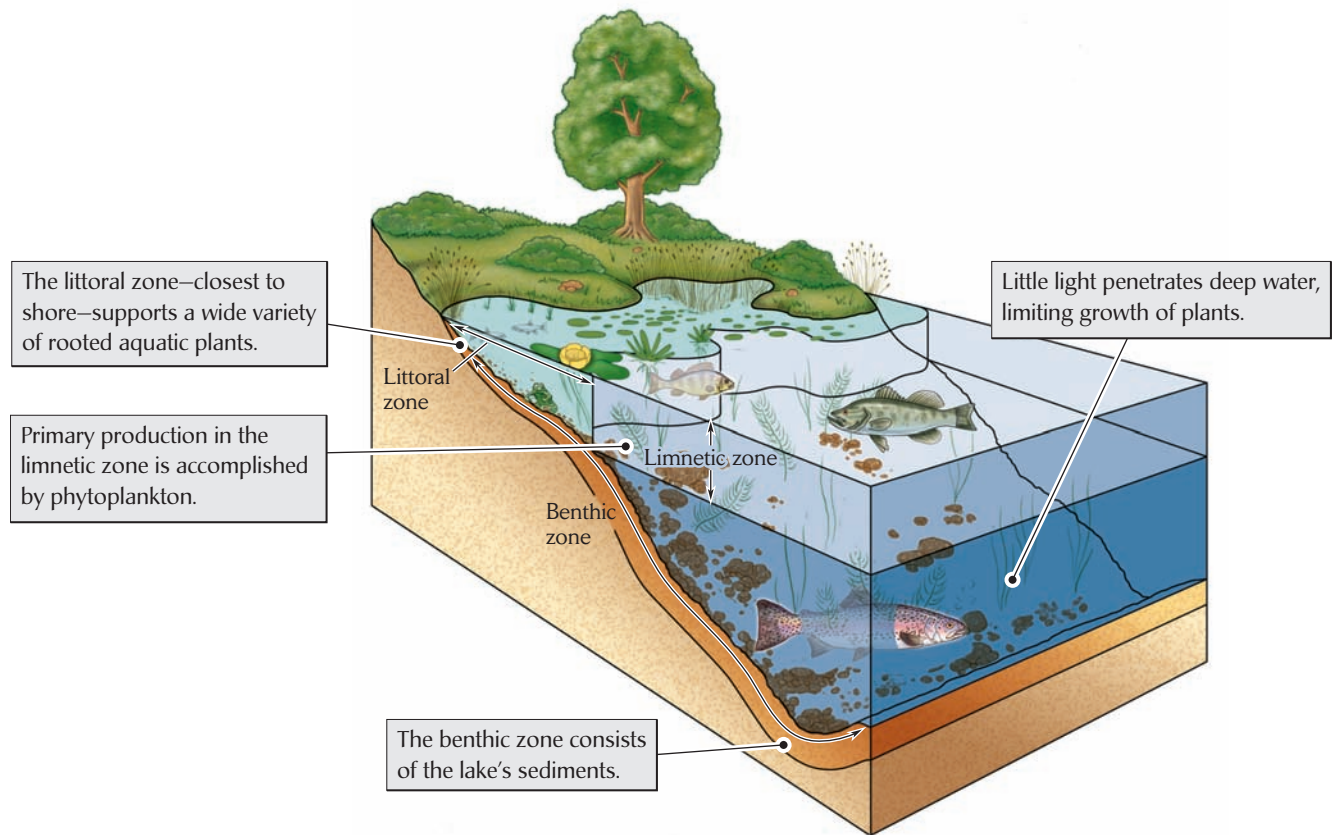
The littoral zone–closest to shore–supports a wide variety of rooted aquatic plants.

Primary production in the limnetic zone is accomplished by phytoplankton.

Little light penetrates deep water, limiting growth of plants.

Littoral zone

Limnetic zone

Benthic zone

The benthic zone consists of the lake's sediments.

FIGURE 5.20 A lake can be divided horizontally or vertically into ecological zones.

there is no open water. The formerly aquatic ecosystem will gradually change into a terrestrial ecosystem, first a wet meadow and later the natural terrestrial biome of the region.

Wetlands

Aquatic and terrestrial communities often come together in **wetlands,** which are areas of land consisting of soil that is saturated with water and supports vegetation specifically adapted to such conditions. Wetlands include swamps, marshes, and bogs when they derive from freshwater, and salt marshes and mangrove wetlands when they are associated with marine environments. Wetlands range in size from vernal pools formed in the aftermath of spring rains to vast areas of river deltas, such as the Okavango Swamp of Botswana, the Everglades of southern Florida, and the Pantanal of Brazil, Bolivia, and Paraguay—at 195,000 km², the world's largest wetland. Most of the plants that grow in wetlands can tolerate low oxygen concentrations in the soil; indeed, many are specialized for these anoxic conditions and grow nowhere else. Wetlands also provide important habitat for a wide variety of animals, notably waterfowl and the larval stages of many species of fish

and invertebrates characteristic of open waters. Wetlands protect coastal areas from the ravages of hurricanes and other storms. Wetland sediments immobilize potentially toxic or polluting substances dissolved in water and are thus natural water purifying plants.

Unfortunately, wetlands also occupy space, and they have been cut, drained, and filled to obtain wood products, to develop new agricultural lands, and for ever-increasing urban and suburban sprawl. Since the 1970s, increasing awareness of the natural values of wetland habitats, and legislation, such as the U.S. Clean Water Act (1977), have helped to conserve large areas of wetlands and restore them as closely as possible to their natural state.

Estuaries

Estuaries are found at the mouths of rivers, especially where the outflow is partially enclosed by landforms or barrier islands (Figure 5.21). Estuaries are unique because of their mix of fresh and salt water. In addition, they are abundantly supplied with nutrients and sediments carried downstream by rivers. The rapid exchange of nutrients between the sediments and the surface in the shallow waters of the estuary supports extremely high biological

FIGURE 5.21 Estuaries are extremely productive ecosystems. Estuaries develop at the mouths of rivers and are often bordered by extensive salt marshes, as in this view along the Georgia coast. Photo by S. J. Krasemann/Peter Arnold.

productivity. Because estuaries tend to be areas of sediment deposition, they are often edged by extensive tidal marshes at temperate latitudes and by mangrove wetlands in the tropics. Tidal marshes are among the most productive habitats on earth, owing to a combination of high nutrient levels and freedom from water stress. They contribute organic matter to estuarine ecosystems, which in turn support abundant populations of oysters, crabs, fish, and the animals that feed on them.

Human inputs into freshwater biomes

Freshwater biomes of all kinds are subject to a variety of inputs produced by human activities that can dramatically change their quality and ecological functioning. The most important of these are acid rain and eutrophication, which we shall discuss in more detail in later chapters. These inputs and their effects further demonstrate the intimate connections between terrestrial and aquatic biomes.

Acid rain forms when various gases produced by the combustion of fossil fuels, particularly sulfur dioxide and nitrogen oxides, dissolve in atmospheric moisture to form sulfuric and nitric acids. This acidified precipitation enters lakes and streams, where it can reduce the pH to as low as 4, well beyond the tolerance limits of many organisms. Acidified waters lose plant life and algae, and the low pH

disrupts the normal reproduction of fish and other aquatic animals. In the most extreme case, the entire ecosystem can collapse.

Eutrophication is the addition of limiting nutrients, such as phosphorus, to aquatic ecosystems. These nutrients may come from runoff carrying sewage, industrial wastes, or fertilizers or animal wastes from agricultural lands. A sudden abundance of nutrients may not only increase production dramatically, but may also disrupt normal ecosystem functioning by favoring certain organisms over others. The abundant organic material stimulates the growth of exploding populations of decomposing bacteria, but the process of decomposition depletes waters of oxygen that other organisms need.

Marine aquatic systems are classified principally by water depth

Oceans cover the largest portion of the surface of the earth. Beneath the surface of the ocean lies an immensely complex realm harboring a great variety of physical conditions and ecological systems (Figure 5.22). Variation in marine environments comes from differences in temperature, salinity, depth (which influences light and pressure), currents, substrata, and at the edge of the oceans, tides.

Many marine ecologists categorize marine ecological zones according to depth. The **littoral zone** (also called the *intertidal zone*) extends between the highest and lowest tidal water levels, and thus is exposed periodically to air (Figure 5.23). Ecological conditions within the littoral zone change rapidly as the tide flows in or out. A frequent consequence is the sharp **zonation** of organisms according to their ability to tolerate the stresses of terrestrial conditions, to which they are exposed to a varying extent depending on their position within the intertidal range. Beyond the range of the lowest tidal level, the **neritic zone** extends to depths of about 200 m, which correspond to the edge of the continental shelf. The neritic zone is generally a region of high productivity because the sunlit surface layers of water are close enough to the nutrients in the sediments below that strong waves can move them to the surface. Beyond the neritic zone, the seafloor drops rapidly to the great depths of the **oceanic zone.** Here, nutrients are sparse, and production is strictly limited. The seafloor beneath the oceanic zone constitutes the **benthic zone.** Both the neritic and the oceanic zones may be subdivided vertically into a superficial **photic zone,** in which there is sufficient light for photosynthesis, and an **aphotic zone** without light. Organisms in the
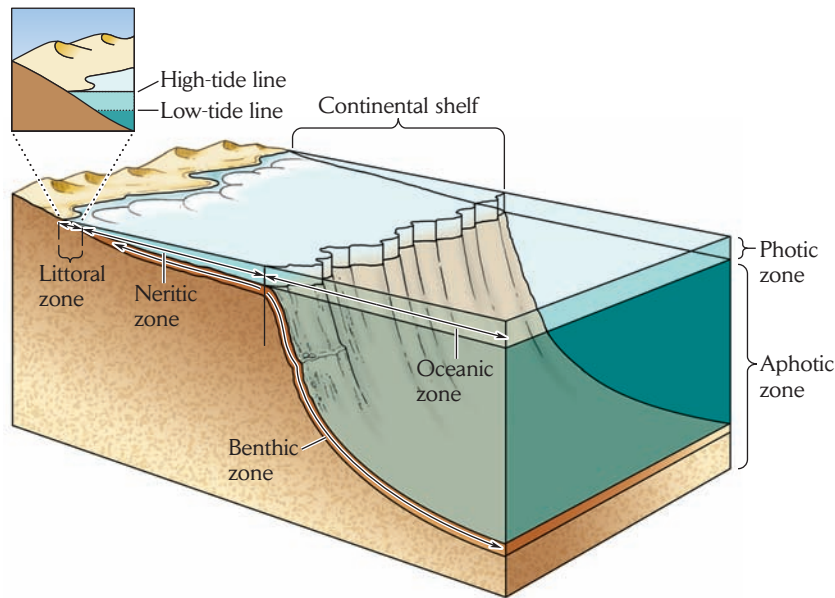
aphotic zone depend mostly on organic material raining down from above.

Other systems of marine biome classification divide the oceans into biomes in different ways. One example is provided by the World Wildlife Fund's global list of 200 habitat types that are priorities for conservation. The World Wildlife Fund has singled out the following marine biomes as among the most productive and diverse on earth: polar, temperate shelves and seas, temperate upwelling, tropical upwelling, and tropical coral reefs. These biomes have traditionally provided most of the marine resources exploited by humans. Polar regions, which contain large areas of shallow seas, and continental shelves at temperate latitudes are highly productive because nutrients in seafloor sediments are not far below the surface waters, as indicated above. Upwelling zones are also highly productive because upwelling currents carry nutrients from the ocean depths to the sunlit surface waters.

Whereas the open ocean has been compared to a desert because of its low productivity, **coral reefs** are like tropical rain forests, both in the richness of their biological production and the diversity of their inhabitants (Figure 5.24). Reef-building corals are found in shallow waters of warm oceans, usually where water temperatures remain above 20°C year-round. Coral reefs often surround volcanic islands, where they are fed by nutrients eroding from the rich volcanic soil and by deep-water currents forced upward by the profile of the island. Corals are doubly productive because photosynthetic algae within their tissues generate the carbohydrate energy that fuels the corals' phenomenal rates of growth. Moreover, the complexity of the structure built by the corals over

time provides a wide variety of substrata and hiding places for algae and animals, making coral reefs among the most diverse biomes on earth. Unfortunately, rising sea surface temperatures in the tropics are killing the algal symbionts
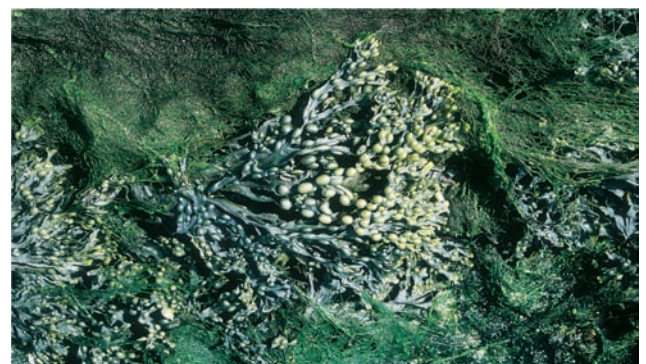

FIGURE 5.23 **The littoral zone is exposed to terrestrial conditions twice each day.** Nonetheless, it may support prolific growth of algae and a variety of marine animals, as in this area of the New Brunswick coast in Canada. Photos by R. E. Ricklefs.

FIGURE 5.24 Coral reefs are productive and diverse ecosystems. In contrast to the open ocean, where productivity is low, coral reef ecosystems provide abundant food for a diverse biological community. This photo was taken in the Red Sea, near Egypt. Photo by Eric Hanauer.

of corals over large areas—a phenomenon known as coral bleaching. The stability of these biomes is now at risk.

Other marine biomes have physical conditions that foster unique forms of life and distinctive ecosystem properties. For example, the kelp forests that develop in shallow, fertile waters along continental coasts provide habitat for a rich variety of marine life (see Figure 1.16). Large areas of shallow polar seas are covered with pack ice that seals the air–water interface and increases the salinity of water as salts are excluded from ice. The result is a dim, salty environment without any wave disturbance. Hydrothermal vents are deep-sea environments dominated by the input of hot water laden with hydrogen sulfide, which provides the reducing power used by chemosynthetic bacteria to fuel high productivity in the otherwise sterile abyssal environment.

The physical qualities that characterize each terrestrial and aquatic biome constitute the environments to which their inhabitants are adapted in form and function. The close association between organisms and their environments over evolutionary time is the basis for ecological specialization and the resulting limits of the distributions of organisms and populations. Adaptations, however, reflect not only these physical factors in the environment, but also the many interactions of organisms with individuals of their own and other species. In the next part of this book, we shall examine the process of evolutionary adaptation and see how it has created the tremendous diversity of life on earth.

SUMMARY

1. The geographic distributions of plants are determined primarily by climate. Each climatic region has characteristic types of vegetation that differ in growth form.

2. Because plant growth form is directly related to climate, the major types of vegetation match temperature and precipitation closely. Major vegetation types can be used to classify ecosystems into categories called biomes.

3. Two ways of classifying biomes are represented by the climate zone approach of Walter and the vegetation approach exemplified by Whittaker. The first classifies regions on the basis of climate, within which a characteristic type of vegetation normally develops. The second classifies regions according to vegetation type, which generally reflects the local climate.

4. Climate zones and biomes are grouped within tropical, temperate, boreal, and polar latitudes. The adaptations of plants to different temperature ranges distinguish the

vegetation types of each of these latitudinal bands. Within each of these latitudinal bands, annual precipitation, the seasonality of precipitation, and additional factors such as fire further differentiate terrestrial biomes.

5. Within temperate latitudes, the major biomes are temperate seasonal forest, temperate rain forest, and temperate grassland/desert. The woodland/shrubland biome is found at lower temperate latitudes in areas with a Mediterranean climate. Subtropical deserts lie between temperate and tropical latitudes.

6. At high latitudes, one encounters boreal forest, usually consisting of needle-leaved trees with evergreen foliage on nutrient-poor, acidic soils, and tundra, a treeless biome that develops on permanently frozen soils, or permafrost.

7. Tropical latitudes are dominated by tropical rain forest and tropical seasonal forest, which grades from deciduous forest to thorn forest as aridity increases, and some-

times to savanna, which is grassland with scattered trees maintained by fire and grazing pressure.

8. Aquatic systems are not usually classified as biomes because they lack the equivalent of terrestrial vegetation with a characteristic structure. One may, however, distinguish streams (lotic systems), lakes (lentic systems), wetlands, estuaries, and oceans, and each of these systems can be further subdivided on the basis of other factors, such as depth of water.

9. The river continuum concept describes changes in the character of lotic systems from their headwaters to their mouths. Headwater streams tend to be shaded by surrounding vegetation, have low nutrient levels, and receive most of their organic material from outside (allochthonous) sources.

10. The lower reaches of rivers are wide and slow moving, carry heavy nutrient and sediment loads, receive plentiful sunlight, and grade into surrounding terrestrial habitats on floodplains.

11. Lakes and ponds vary tremendously in size, but are all distinguished by containing nonflowing water. Large lakes can be differentiated into ecological zones that differ in water depth, temperature, nutrients, oxygen, and light.

12. Wetlands are areas in which the soil is saturated with water, including marshes, swamps, bogs, and mangrove wetlands. Wetlands support unique plants and animals and also serve important ecosystem functions, such as removing pollutants from water.

13. Estuaries, which occur at the mouths of rivers where fresh water mixes with seawater, support high levels of productivity. Because they are areas of sediment deposition, many estuaries are edged by extensive tidal marshes at temperate latitudes and by mangrove wetlands in the tropics.

14. Marine ecosystems are categorized mainly by depth. They include the littoral zone, on the shoreline between high and low tide levels; the neritic zone, made up of open waters to a depth of about 200 m; and the deep waters of the oceanic zone. Light penetration divides the oceans into a superficial photic zone and a deep aphotic zone, lacking all light. Many specialized types of marine ecosystems are found in connection with upwelling currents and tropical coral reefs.

REVIEW QUESTIONS

1. Why do unrelated plants often assume the same growth form in different parts of the world?

2. Which types of environmental conditions limit the distributions of plants?

3. What climatic conditions are used to define biomes?

4. What types of plants are found in each of the four biomes at temperate latitudes, and what environmental condition differs among these biomes?

5. Why is the boreal forest biome found on several different continents, including North America, Europe, and Asia?

6. Explain why tropical rain forests experience two peaks of rainfall.

7. How can fire shift an area from one biome type to another?

8. Compare and contrast the factors used to categorize terrestrial biomes with those used to categorize aquatic biomes.

9. How do headwater streams and larger rivers differ in their major source of organic material?

10. How do the littoral zone and the limnetic zone of a lake differ in their source of production?

11. What conditions allow coral reefs to be highly productive?

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