Sixth Edition

Geosystems

An Introduction to Physical Geography

Annotated Instructor's Edition

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CHAPTER 19

Ecosystem Essentials

Key Learning Concepts

After reading the chapter, you should be able to:

- ***Define*** ecology, biogeography, and the ecosystem concept.
- ***Describe*** communities, habitats, and niches.
- ***Explain*** photosynthesis and respiration, and ***derive*** net photosynthesis and the world pattern of net primary productivity.
- ***List*** abiotic ecosystem components, and ***relate*** those components to ecosystem operations.
- ***Explain*** trophic relationships in ecosystems.
- ***Relate*** how biological evolution led to the biodiversity of life on Earth.
- ***Define*** succession, and ***outline*** the stages of general ecological succession in both terrestrial and aquatic ecosystems.

Diversity is an impressive feature of the living Earth. The diversity of organisms is a response to the interaction of the atmosphere, hydrosphere, and lithosphere, all powered by solar energy. The evolution of life on Earth, in all its forms, is intertwined with the evolution of Earth's physical and chemical systems. This interaction produces a variety of conditions within which the biosphere exists. The diversity of life also results from the intricate interplay and coevolution of living organisms themselves. We, as part of this vast natural complex, seek to find our place and understand the feelings nature stimulates within us.

The physical beauty of nature is certainly among its most powerful appeals to the human animal. The complexity of the aesthetic response is suggested by its wide-ranging expression from the contours of a mountain landscape to the ambient colors of a setting Sun to the fleeting vitality of a breaching whale. Each exerts a powerful aesthetic impact on most people, often accompanied by feelings of awe at the extraordinary physical appeal and beauty of the natural world.*

The biosphere, the sphere of life and organic activity, extends from the ocean floor to about 8 km (5 mi) altitude in the atmosphere. The biosphere includes myriad ecosystems from simple to complex, each operating within general spatial boundaries. An **ecosystem** is a self-sustaining association of living plants and animals and their nonliving physical environment. Earth's biosphere itself is a collection of ecosystems within the natural boundary of the atmosphere and Earth's crust.

Natural ecosystems are open systems for both solar energy and matter, with almost all ecosystem boundaries functioning as transition zones rather than as sharp demarcations. Distinct ecosystems—for example, forests, seas, mountaintops, deserts, beaches, islands, lakes, and ponds—make up the larger whole.

Ecology is the study of the relationships between organisms and their environment and among the various ecosystems in the biosphere. The word *ecology*, developed by German naturalist Ernst Haeckel in 1869, is derived from the Greek *oikos* ("household," or "place to live") and *logos* ("study of"). **Biogeography** is the study of the distribution of plants and animals, the diverse spatial patterns they create, and the physical and biological processes, past and present, that produce Earth's species richness.

The degree to which modern society understands Earth's biogeography and conserves Earth's living legacy will determine the extent of our success as a species and the long-term survival of a habitable Earth:

> The time is ripe to step up and expand current efforts to understand the great interlocking systems of air, water, and minerals nourishing the Earth. . . . Moreover, without vigorous action toward that goal, nations will be seriously handicapped in trying to cope with proven and suspected threats to ecosystems and to human health and welfare resulting from alterations in the cycles of carbon, nitrogen, phosphorus, sulfur, and related materials. . . . Society depends upon this life-support system of planet Earth.†

Earth's most influential biotic (living) agents are the humans. This is not arrogance; it is fact, because we powerfully influence every ecosystem on Earth. From the time humans first developed agriculture, the raising of animals, and the use of fire, we began a process that has led to our dominance over Earth's physical systems. The penguin colony in the chapter-opening photo has declined 24% in numbers since 1970 because of environmental changes we discuss in this chapter.

Since life arose on the planet, there have been six major extinctions. The fifth one was 65 million years ago, whereas the sixth is happening across the present decades. Of all these extinction episodes, this is the only one of biotic origin, caused for the most part by human activity. We are the greatest evolutionary force as we essentially dominate freshwater quantity and quality, croplands, ocean fishery production, nitrogen and other chemical budgets, the concentration of greenhouse gases, and the present extinction rate.

In this chapter: We explore ecosystems and the community, habitat, and niche concepts. Plants are the essential living component in the biosphere, translating solar energy into usable forms to energize life. The role of nonliving systems, including biogeochemical cycles, is examined. We cover the organization of living ecosystems along complex food chains and webs. The biodiversity of living organisms is seen as a product of biological evolution over the past 3.6 billion years. Ecosystem stability and resilience, and how living landscapes change over space and time through the process of succession, are important. Included is coverage of the effects of global change on ecosystems and rates of succession.

Ecosystem Components and Cycles

An ecosystem is a complex of many variables, all functioning independently yet in concert, with complicated flows of energy and matter (Figure 19.1). The key is to understand the linkages and interconnections within and between systems. As the quote in the caption says, ". . . The effects of what you do in the world will always spread out like ripples in a pond." The decrease in the Black-browed Albatross (*Diomedea melanophris*) colony evident from the empty nests in Figure 19.1b was the result of changes in regulations in the fishing industry around the Falkland Islands. An increase in quotas for the squid harvest, a primary food source for the albatross, led to the reduction in bird population.

An ecosystem includes both biotic (living) and abiotic (nonliving) components. Nearly all ecosystems depend on a direct input of solar energy; the few limited ones that exist in dark caves, in wells, or on the ocean floor depend on chemical reactions (chemosynthesis).

Ecosystems are divided into subsystems, with the biotic portion composed of producers (plants), consumers (animals), and detritus feeders (worms, mites, bacteria, fungi). The abiotic flows in an ecosystem include gaseous, hydrologic, and mineral cycles. Figure 19.2a illustrates these essential elements of an ecosystem. Figure 19.2b and c illustrates how biotic and abiotic ingredients operate together to form a delicate forest floor in the Northwest and the hearty lichens in the hostile environment of Antarctica.

*S. R. Kellert, "The biological basis for human values of nature," in S. R. Kellert and E. O. Wilson, eds., *The Biophilia Hypothesis* (Washington, DC: Island Press, 1993), p. 49.

†G. F. White and M. K. Tolba, *Global Life Support Systems*, United Nations Environment Programme Information, No. 47 (Nairobi, Kenya: United Nations, 1979), p. 1.

(a)

(b)

FIGURE 19.1 The web of life.
(a) Study the spider web as you read the following quotation:

Life devours itself: everything that eats is itself eaten; everything that can be eaten is eaten; every chemical that is made by life can be broken down by life; all the sunlight that can be used is used. . . . The web of life has so many threads that a few can be broken without making it all unravel, and if this were not so, life could not have survived the normal accidents of weather and time, but still the snapping of each thread makes the whole web shudder, and weakens it. . . . You can never do just one thing: the effects of what you do in the world will always spread out like ripples in a pond.

(b) Abandoned Black-browed Albatross nests indicate a change in government fishing regulations in the surrounding ocean—". . . snapping each thread makes the whole web shudder. . . ." [(a) Photo by author; quotation from Friends of the Earth and Amory Lovins, The United Nations Stockholm Conference, *Only One Earth* (London: Earth Island Limited, 1972), p. 20. (b) Photos by Bobbé Christopherson.]

Communities

A convenient biotic subdivision within an ecosystem is a community. A **community** is formed by interactions among populations of living animals and plants at a particular time. An ecosystem is the interaction of many communities with the abiotic physical components of its environment.

Some examples help to clarify these concepts. In a forest ecosystem, a specific community may exist on the forest floor, whereas another community functions in the canopy of leaves high above (Figure 19.3). Not all forests appear in familiar structure, as the dwarf willow forest in Greenland demonstrates (Figure 19.3c). Similarly, within a lake ecosystem, the plants and animals that flourish in the bottom sediments form one community, whereas those near the surface form another. A community is identified in several ways—by its physical appearance, the species present and the abundance of each, the complex patterns of their interdependence, and the trophic (feeding) structure of the community.

Within a community, two concepts are important: habitat and niche. **Habitat** is the type of environment where an organism resides or is biologically adapted to live. In terms of physical and natural factors, most species have specific habitat requirements with definite limits and a specific regimen of sustaining nutrients.

Niche (French *nicher*, "to nest") refers to the function, or occupation, of a life form within a given community. It is the way an organism obtains and sustains the physical, chemical, and biological factors it needs to survive. A niche

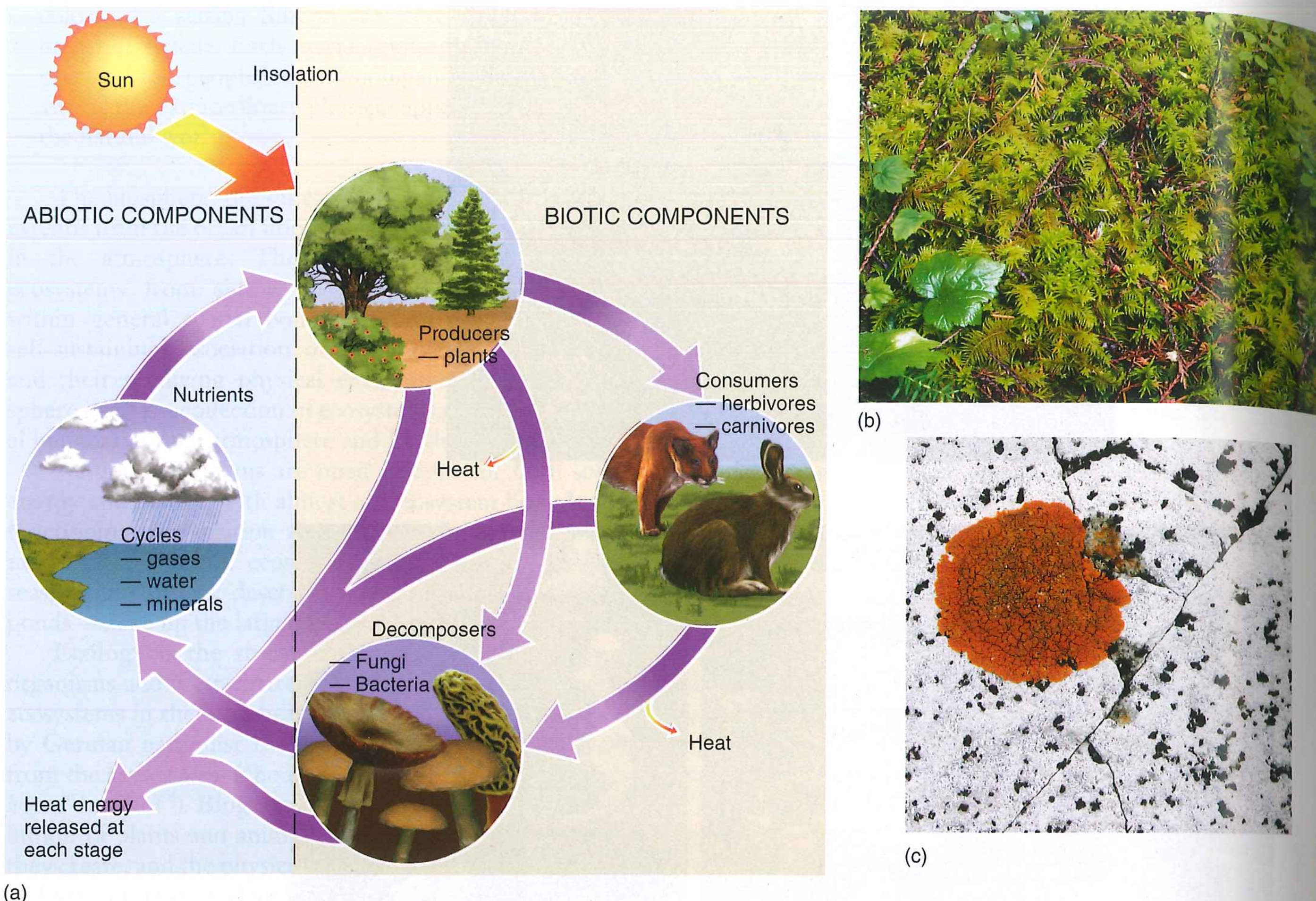


FIGURE 19.2 Biotic and abiotic components of ecosystems.
(a) Solar energy is the input that drives the biotic and abiotic components. Heat energy and biomass are the outputs from the biosphere. (b) Biotic and abiotic ingredients operate together to form this temperate forest-floor ecosystem in British Columbia, with mosses beginning the process of community development. (c) Two species of lichen in the photo, perhaps more, function under extremely hostile climate conditions in Antarctica. Each little indentation provides some advantage to the darker lichen. [Photos by Bobbé Christopherson.]

has several facets. Among these are a habitat niche, a trophic (food) niche, and a reproductive niche. For example, the Red-winged Blackbird (*Agelaius phoeniceus*) occurs throughout the United States and most of Canada in habitats of meadow, pastureland, and marsh. This species nests in blackberry tangles and thick vegetation in freshwater marshes, sloughs, and fields. Its trophic niche is weed seeds and cultivated seed crops throughout the year, and during the nesting season it adds insects to its diet—an aspect of its reproductive niche. These birds disperse seeds of many plants during their travels.

Other habitats produce comparable niches. In a stable community, no niche is left unfilled. The *competitive exclusion principle* states that no two species can occupy the same niche (food or space) successfully in a stable community. Thus, closely related species are spatially separated. In other words, each species operates to reduce competition and to maximize its own reproduction rate—literally, species survival depends on successful reproduction. This strategy in turn leads to greater diversity as species shift and adapt to fill each niche. Figure 19.4 shows eight different community environments and representative life forms.

Some species are *symbiotic*, an arrangement where two or more species exist together in an overlapping relationship. One type of symbiosis, *mutualism*, occurs when each organism benefits and is sustained over an extended period by the relation. For example, lichen (pronounced "liken") is made up of algae and fungi living together (Figure 19.2c). The alga is the producer and food source for the fungus, and the fungus provides structure and physical support. Their mutualism allows the two to occupy a niche in which neither could survive alone. Lichen developed from an earlier parasitic relationship in which the fungi broke into the alga cells. Today, the two organisms have evolved into a supportive harmony and symbiotic relationship. The partnership of corals and algae discussed in Chapter 16 is another example of mutualism in a symbiotic relationship.

By contrast, another form of symbiosis is a *parasitic* relationship, which may eventually kill the host, thus destroying the parasite's own niche and habitat. An example is parasitic mistletoe (*Phoradendron*), which lives on and may kill various kinds of trees. Some scientists are questioning whether our human society and the physical systems of Earth constitute a global-scale symbiotic

(a)

(b)

(c)

FIGURE 19.3 Different forest communities. (a) Pioneer Mothers' Memorial Forest near Paoli, Indiana, is 36 hectares (88 acres) of old-growth forest, virtually undisturbed since around 1816, featuring black walnut, white oak, yellow poplar, white ash, and beech trees, among others. (b) Turtles bask on a log in a subtropical swamp (low, waterlogged ground) at Juniper Springs Recreation Area, Florida. (c) Fall colors highlight this dwarf willow forest in Greenland. Musk Oxen are foraging for food and drinking meltwater. The inset photo shows a 13-year-old willow, dated by the small annual growth segments below the leaf. Some dwarf willows can range to over 300 years in age. [Photos by Bobbé Christopherson.]

relationship of mutualism, which is sustainable, or a parasitic one, which is unsustainable.

Plants: The Essential Biotic Component

Plants are the critical biotic link between solar energy and the biosphere. Ultimately, the fate of all members of the biosphere, including humans, rests on the success of plants and their ability to turn sunlight into food.

Land plants (and animals) became common about 430 million years ago, according to fossilized remains. **Vascular plants** developed conductive tissues and true roots for internal transport of fluid and nutrients. (*Vascular* is from a Latin word for "vessel-bearing," referring to the conducting cells.)

In the present day, about 270,000 species of plants are known to exist, and most are vascular. Many more species have yet to be identified. They represent a great untapped resource base. Only about 20 species of plants provide 90% of the world's food—just three, wheat, maize (corn), and rice, comprise half of the food supply. Plants are a major source of new medicines and chemical compounds that benefit humanity. Plants also are the core of healthy, functioning ecosystems that sustain all life.

Leaves are solar-powered chemical factories, wherein photochemical reactions take place. Veins in the leaf bring in water and nutrient supplies and carry off the sugars (food) produced by photosynthesis. The veins in each leaf connect to the stems and branches of the plant and to the main circulation system.

Flows of carbon dioxide, water, light, and oxygen enter and exit the surface of each leaf (see Figure 1.4). Gases flow into and out of a leaf through small pores called **stomata** (singular: *stoma*), which usually are most numerous on the lower side of the leaf. Each stoma is surrounded by guard cells that open and close the pore, depending on the plant's changing needs.

Water that moves through a plant exits the leaves through the stomata and evaporates from leaf surfaces, thereby assisting the plant's temperature regulation. As water evaporates from the leaves, a pressure deficit is created that allows atmospheric pressure to push water up through the plant all the way from the roots, in the same manner that a soda straw works. We can only imagine the complex operation of a 100-m (330-ft) tree!

Photosynthesis and Respiration

Powered by energy from certain wavelengths of visible light, **photosynthesis** unites carbon dioxide and hydrogen (hydrogen is derived from water in the plant). The term is descriptive: *photo-* refers to sunlight, and *-synthesis*

FIGURE 19.4 Plants and animals fit specific niches.
(a) Elephant heads (*Pedicularis groenlandica*), a wildflower that grows above 1800 m (6000 ft) in wet mountain meadows. (b) A western yellow-bellied racer (*Coluber constrictor*) lives in prairies and meadows and feeds on insects, lizards, and mice. (c) A female polar bear (*Ursus maritimus*) with two 8-month-old cubs on pack ice in the Arctic Ocean. (d) A Svalbard reindeer (*Rangifer tarandus platyrhynchus*) on Spitsbergen Island, Arctic Ocean, losing velvet from his antlers. (e) Killdeer chicks (*Charadrius vociferus*) begin life roughing it on an exposed rocky nest, with protective parents creating a noisy diversion nearby. (f) Coral mushroom (*Ramaria* sp.), a fungal decomposer at work on the organic matter accumulated on the forest floor. (g) A large barrel cactus flourishes in the rocky soils and harsh conditions of the desert. (h) A leopard seal (*Hydrurga leptonyx*) resting on a bergy bit (small iceberg) off the Antarctic Peninsula. Fur is stained with blood from a recent meal. [Photos (a, c, d, f, h) by Bobbé Christopherson; (b, e, g) by author.]

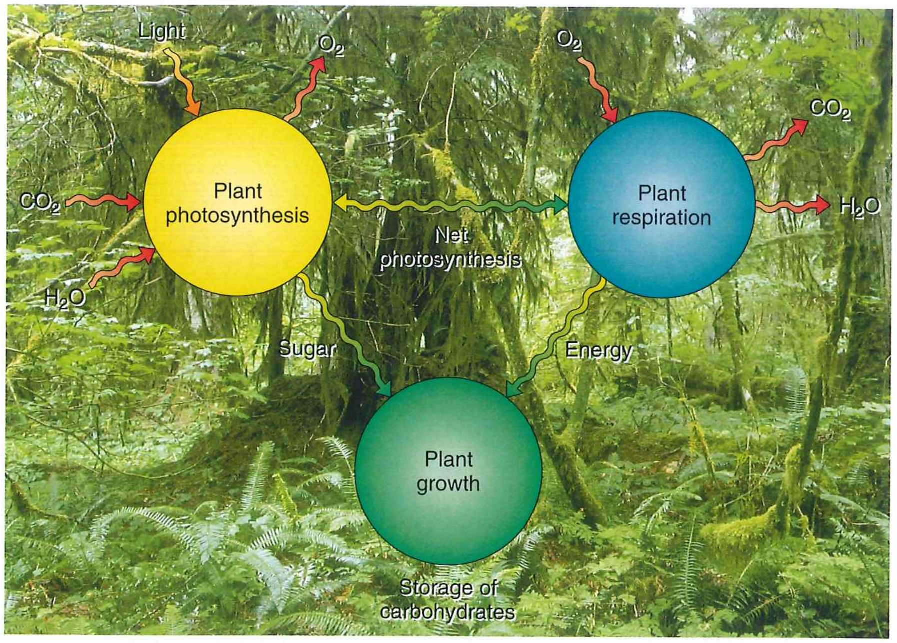


FIGURE 19.5 How plants live and grow.
The balance between photosynthesis and respiration determines net photosynthesis and plant growth. [Temperate rain forest photo by Bobbé Christopherson.]

describes the "manufacturing" of starches and sugars through reactions within plant leaves. The process releases oxygen and produces energy-rich food for the plant.

The largest concentration of light-responsive, photosynthetic structures (known as *organelles*) in a leaf rests below the leaf's upper layers. These organelle units within cells are called *chloroplasts*, and within each resides a green, light-sensitive pigment called **chlorophyll**. Within this pigment, light stimulates photochemistry. Consequently, competition for light is a dominant factor in the formation of plant communities. This competition is expressed in the height, orientation, distribution, and structure of plants.

Only about one-quarter of the light energy arriving at the surface of a leaf is useful to the light-sensitive chlorophyll. Chlorophyll absorbs only the orange-red and violet-blue wavelengths for photochemical operations, and it reflects predominantly green hues (and some yellow). That is why trees and other vegetation look green.

Photosynthesis essentially follows this equation:

$6CO_2$	+	$6H_2O$	+	Light	→	$C_6H_{12}O_6$	+	$6O_2$
(carbon dioxide)		(water)		(solar energy)		(glucose, carbohydrate)		(oxygen)

From the equation, you can see that photosynthesis removes carbon (in the form of CO_2) from Earth's atmosphere. The quantity is enormous: approximately 91 billion metric tonnes (100 billion tons) of carbon dioxide per year. Carbohydrates, the organic result of the photosynthetic process, are combinations of carbon, hydrogen, and oxygen. They can form simple sugars, such as *glucose* ($C_6H_{12}O_6$). Plants use glucose to build starches, which are more complex carbohydrates and the principal food stored in plants.

Plants store energy for later use. They consume this energy as needed through respiration by converting the carbohydrates to energy for their other operations. Thus, **respiration** is essentially a reverse of the photosynthetic process:

$C_6H_{12}O_6$	+	$6O_2$	→	$6CO_2$	+	$6H_2O$	+	energy
(glucose carbohydrate)		(oxygen)		(carbon dioxide)		(water)		(heat energy)

In respiration, plants oxidize carbohydrates (stored energy), releasing carbon dioxide, water, and energy as heat. The overall growth of a plant depends on a surplus of carbohydrates beyond what is lost through plant respiration. Figure 19.5 presents a simple schematic of this process, which produces plant growth.

The *compensation point* is the break-even point between the production and consumption of organic material. Each leaf must operate on the production side of the compensation point, or else the plant eliminates it—something each of us has no doubt experienced with a houseplant that received inadequate water or light. The difference between photosynthetic production and respiration loss is called *net photosynthesis*. The amount varies, depending on controlling environmental factors such as light, water, temperature, soil fertility, and the plant's site, elevation, and competition from other plants and animals.

The rapidly increasing carbon dioxide concentration in the atmosphere stimulates the photosynthetic processes. However, with higher temperatures of global warming occurring more at night than during the day in many regions, this results in higher respiration rates.

One of the key scientific findings is that this unnatural warming is emphasized during the night and during wintertime, whereas a natural warming cycle would be balanced day to night or summer to winter. Plants respire all the time but at night respiration processes are the

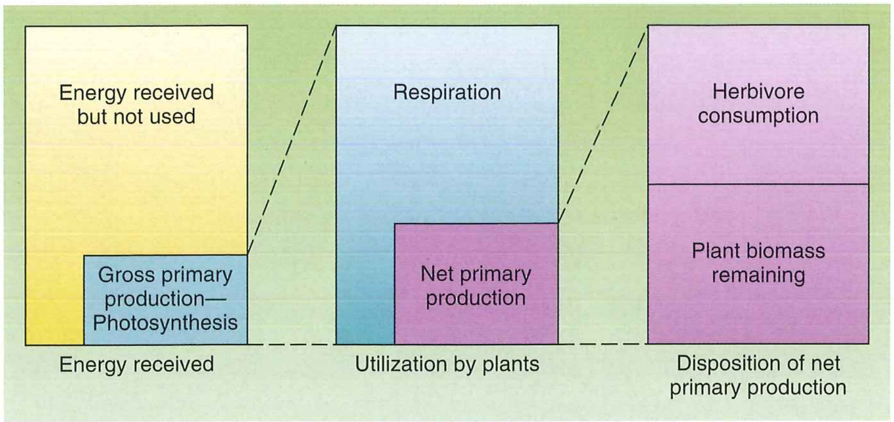


FIGURE 19.6 Energy budget of the biosphere.
Energy receipt, energy utilization, and energy disposition of net primary production by green plants.

plant's main operation. Studies of tropical rain forests in Costa Rica determined that increased respiration rates had made the forest a net carbon gain to the atmosphere.

Plant productivity increases as light availability increases—up to a point. When the light level is too high, *light saturation* occurs and most plants actually reduce their output in response. Some plants are adapted to shade, whereas others flourish in full sunlight. Crops such as rice, wheat, and sugarcane do well with high light intensity. Figure 19.6 portrays the general energy budget for green plants, showing energy receipt, energy utilization, and disposition of net primary production—how the energy is spent.

Net Primary Productivity The net photosynthesis for an entire plant community is its **net primary productivity**. This is the amount of stored chemical energy that the community generates for the ecosystem. **Biomass** is the net dry weight of all this organic material and its stored chemical energy.

Net primary productivity is measured as fixed carbon per square meter per year. ("Fixed" means chemically bound into plant tissues.) Study the map and satellite images in Figure 19.7 and you can see that on land, net primary production tends to be highest between the Tropics of Cancer and Capricorn at sea level and decreases toward higher latitudes and altitudes. Precipitation also affects productivity, as evidenced by the correlations of abundant precipitation with high productivity adjacent to the equator and reduced precipitation with low productivity in the subtropical deserts. Even though deserts receive high amounts of solar radiation, other controlling factors limit productivity, namely, water availability and soil conditions.

In the oceans, differing nutrient levels control and limit productivity. Regions with nutrient-rich upwelling currents off western coastlines generally are the most productive. The map in Figure 19.7 shows that the tropical ocean and areas of subtropical high pressure are quite low in productivity.

In temperate and high latitudes, the rate at which carbon is fixed by vegetation varies seasonally. It increases in spring and summer as plants flourish with increasing solar input and, in some areas, with more available (nonfrozen) water, and it decreases in late fall and winter. Productivity rates in the tropics are high throughout the year, and turnover in the photosynthesis–respiration cycle is faster, exceeding by many times the rates experienced in a desert environment or in the far northern limits of the tundra. A lush hectare (2.5 acres) of sugarcane in the tropics might fix 45 metric tonnes (50 tons) of carbon in a year, whereas desert plants in an equivalent area might achieve only 1% of that amount.

Table 19.1 lists various ecosystems, their net primary productivity, and an estimate of net total biomass worldwide—170 billion metric tons of dry organic matter per year. Compare the various ecosystems, especially cultivated land (in *italics*) with most of the natural communities. Net productivity is generally regarded as the most important aspect of any type of community, and the distribution of productivity over Earth's surface is an important subject of biogeography.

Abiotic Ecosystem Components

Critical in each ecosystem are the flow of energy and the cycling of nutrients and water in life-supporting systems. These abiotic (nonliving) components set the stage for ecosystem operations.

Light, Temperature, Water, and Climate Solar energy powers ecosystems, so the pattern of solar energy receipt is crucial. Solar energy enters an ecosystem by way of photosynthesis, and heat energy is dissipated from the system at many points. Of the total energy intercepted at Earth's surface and available for work, only about 1.0% is actually fixed by photosynthesis as chemical energy (energy stored as carbohydrates in plants).

The duration of Sun exposure is the *photoperiod*. Along the equator, days are essentially 12 hours long year-round; however, with increasing distance from the equator, seasonal effects become pronounced, as discussed in Chapter 2. Plants have adapted their flowering and seed germination to seasonal changes in insolation. Some seeds germinate only when daylength reaches a certain number of hours. A plant that responds in the opposite manner is the poinsettia (*Euphorbia pulcherrima*), which requires at least 2 months of 14-hour nights to start flowering.

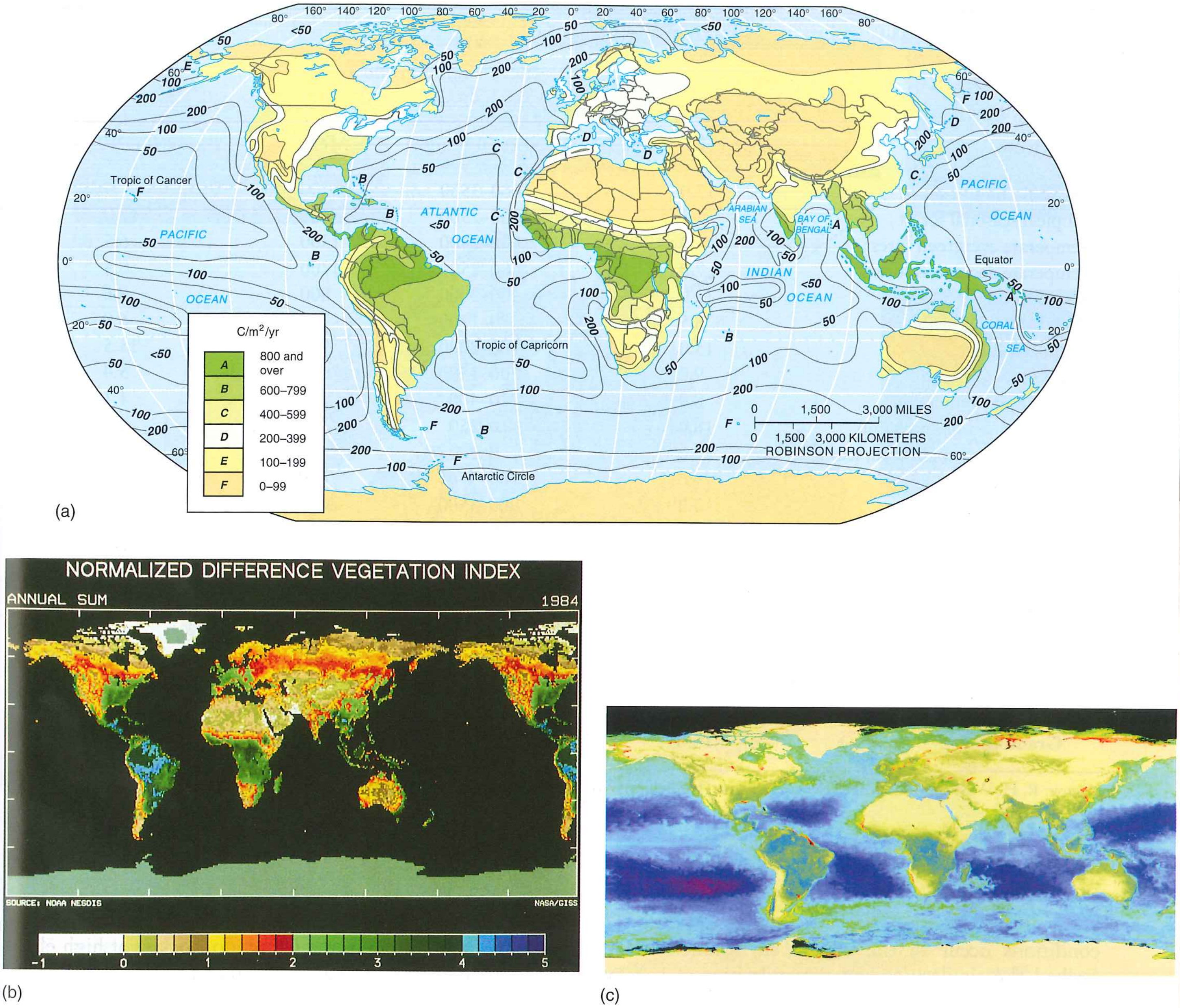


FIGURE 19.7 Net primary productivity.
(a) Worldwide net primary productivity in grams of carbon per square meter per year (approximate values). (b) Normalized difference vegetation index during 1984. False coloration indicates bare ground in browns, dense vegetation in blues. (c) *SeaWIFS* image of surface chlorophyll concentration for land and sea; intensity of green color represents higher levels of chlorophyll. This is the first continuous record over a 3-year period for the oceans. [(a) After D. E. Reichle, *Analysis of Temperate Forest Ecosystems* (Heidelberg: Springer, 1970). Adapted by permission. (b) NASA/GSFC. (c) *SeaWIFS* image by NASA/GSFC and ORBIMAGE, Dulles, VA. Used by permission.]

Other components are important to ecosystem processes. Air and soil temperatures determine the rates at which chemical reactions proceed (see Chapter 18). Significant temperature factors are seasonal variation and duration and the pattern of minimum and maximum temperatures (Chapter 5).

Operations of the hydrologic cycle and water availability depend on precipitation and evaporation rates and their seasonal distribution (see Chapters 7, 8, and 9). Water quality—its mineral content, salinity, and levels of pollution and toxicity—is important. Also, regional climates affect the pattern of vegetation and ultimately influence soil development. All of these factors work together to form the limits for ecosystems in a given location.

Figure 19.8 illustrates the general relationship among temperature, precipitation, and vegetation. Can you identify the characteristic vegetation type and related temperature and moisture regime that fits areas you know well, such as a place you have lived or an area around the school you now attend?

Life Zones Alexander von Humboldt (1769–1859), an explorer, geographer, and scientist, observed that plants and animals recur in related groupings wherever similar

Table 19.1 Net Primary Productivity and Plant Biomass on Earth

Ecosystem	Area (10^6 km^2)[a]	Net Primary Productivity per Unit Area (g/m^2/yr)[b]		World Net Biomass (10^9/tons/yr)[c]
		Normal Range	Mean	
Tropical rain forest	17.0	1000–3500	2200	37.4
Tropical seasonal forest	7.5	1000–2500	1600	12.0
Temperate evergreen forest	5.0	600–2500	1300	6.5
Temperate deciduous forest	7.0	600–2500	1200	8.4
Boreal forest	12.0	400–2000	800	9.6
Woodland and shrubland	8.5	250–1200	700	6.0
Savanna	15.0	200–2000	900	13.5
Temperate grassland	9.0	200–1500	600	5.4
Tundra and alpine region	8.0	10–400	140	1.1
Desert and semidesert scrub	18.0	10–250	90	1.6
Extreme desert, rock, sand, ice	24.0	0–10	3	0.07
Cultivated land	*14.0*	*100–3500*	*650*	*9.1*
Swamp and marsh	2.0	800–3500	2000	4.0
Lake and stream	2.0	100–1500	250	0.5
Total continental	**149**	—	**773**	**115.17**
Open ocean	332.0	2–400	125	41.5
Upwelling zones	0.4	400–1000	500	0.2
Continental shelf	26.6	200–600	360	9.6
Algal beds and reefs	0.6	500–4000	2500	1.6
Estuaries	1.4	200–3500	1500	2.1
Total marine	**361.0**	—	**152**	**55.0**
Grand total	**510.0**	—	**333**	**170.17**

Source: R. H. Whittaker, *Communities and Ecosystems* (Heidelberg: Springer, 1975), p. 224. Reprinted by permission.

[a]1 km^2 = 0.39 mi^2.

[b]1 g per m^2 = 8.92 lb per acre.

[c]1 metric ton (10^6 g) = 1.1023 tons.

conditions occur in the abiotic environment. He described the similarities and dissimilarities of vegetation and the associated uneven distribution of various organisms. After several years of study in the Andes Mountains of Peru, he described a distinct relation between altitude and plant communities as his *life zone concept.* As he climbed the mountains, he noticed that the experience was similar to that of traveling away from the equator toward higher latitudes (Figure 19.9a).

This zonation of plants with altitude is noticeable on any trip from lower valleys to higher elevations. Each **life zone** possesses its own temperature, precipitation, and insolation relations and therefore its own biotic communities.

The Grand Canyon in Arizona provides a good example. Plants and animals of the inner gorge at the bottom of the canyon (600 m, or 2000 ft, in elevation) are characteristic of the lower Sonoran Desert of northern Mexico. However, communities similar to those of southern Canadian forests dominate the north rim of the canyon (2100 m, or 7000 ft, in elevation). On the summits of the nearby San Francisco Mountains (3600 m, or 12,000 ft, in elevation), the vegetation is similar to that of the arctic tundra of northern Canada. Needleleaf forest and alpine tundra in the Colorado Rockies at high elevation are pictured in Figure 19.9b and c.

Other Factors Beyond these general conditions, each ecosystem further produces its own *microclimate*, which is specific to individual sites. For example, in a forest the insolation reaching the ground is reduced and shade from its own trees blankets the forest floor. A pine forest cuts light by 20%–40%, whereas a birch–beech forest reduces it by as much as 50%–75%. Forests also are about 5% more humid than nonforested landscapes, have moderated temperatures (warmer winters and cooler summers), and experience reduced winds.

Slope orientation and Sun exposure are important, too, for they translate into differences in temperature and moisture efficiency, especially in middle and higher latitudes. With all other factors equal, slopes facing away from the Sun's rays tend to be moister and more vegetated than slopes facing toward the Sun. (In the Northern Hemisphere, these moister slopes face north, as evidenced by the apparent tendency of moss, a plant that needs high moisture and shade, to grow on the north side of tree trunks.) Such highly localized *microecosystems* are evident

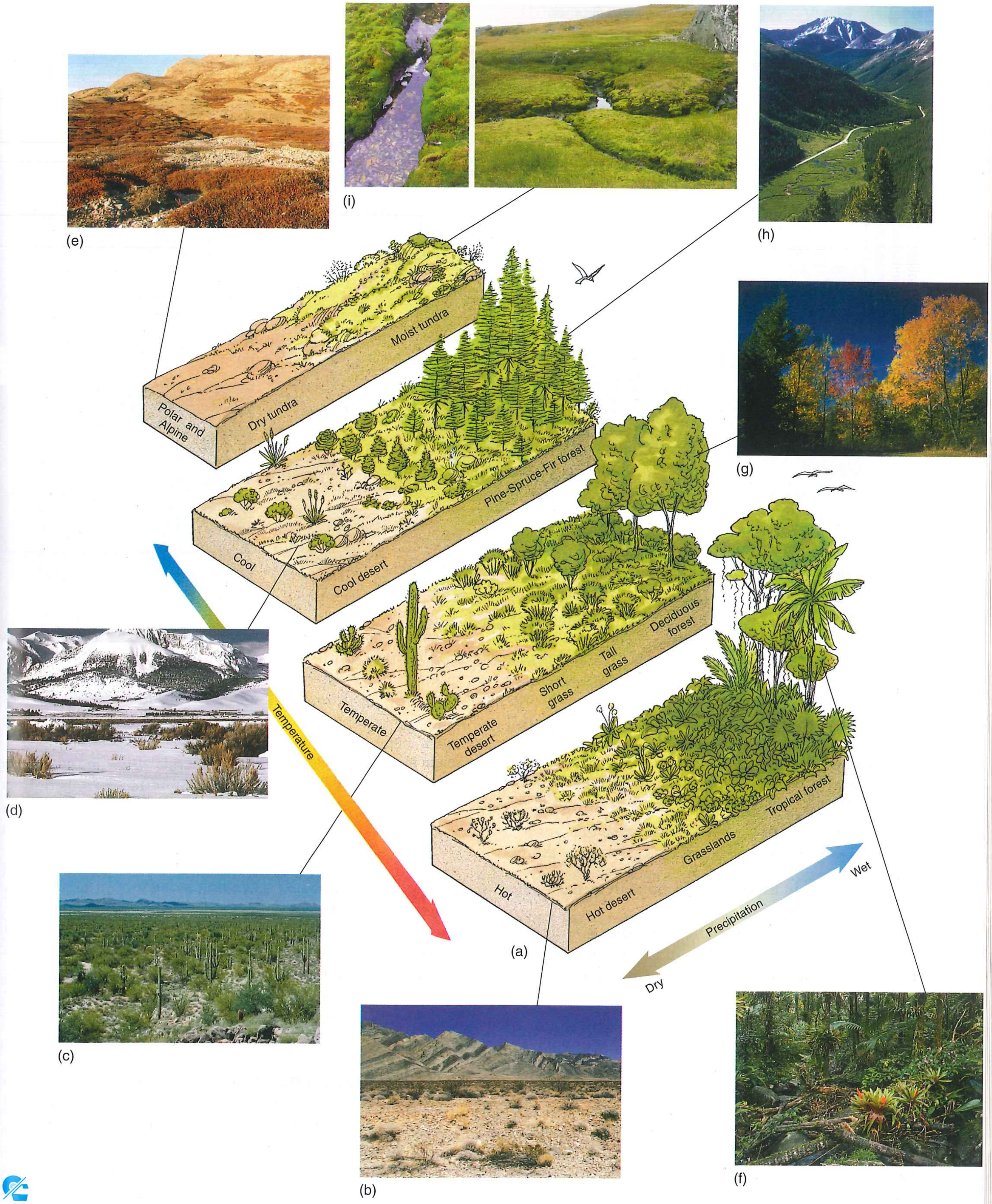


FIGURE 19.8 How temperature and precipitation affect ecosystems.
(a) Climate controls (wetness, dryness, warmth, cold) and ecosystem types; (b) subtropical desert near Death Valley, California; (c) Sonoran desert of Arizona; (d) cold desert of north-central Nevada; (e) dry tundra of East Greenland; (f) El Yunque tropical rain forest of Puerto Rico; (g) deciduous trees in fall colors in Ohio; (h) needleleaf forest near Independence Pass, Colorado; and (i) moist tundra of Spitsbergen, Arctic Ocean. [Photos (c, d) by author; (f) photo by Tom Bean; (b, e, g, h, i) by Bobbé Christopherson.]

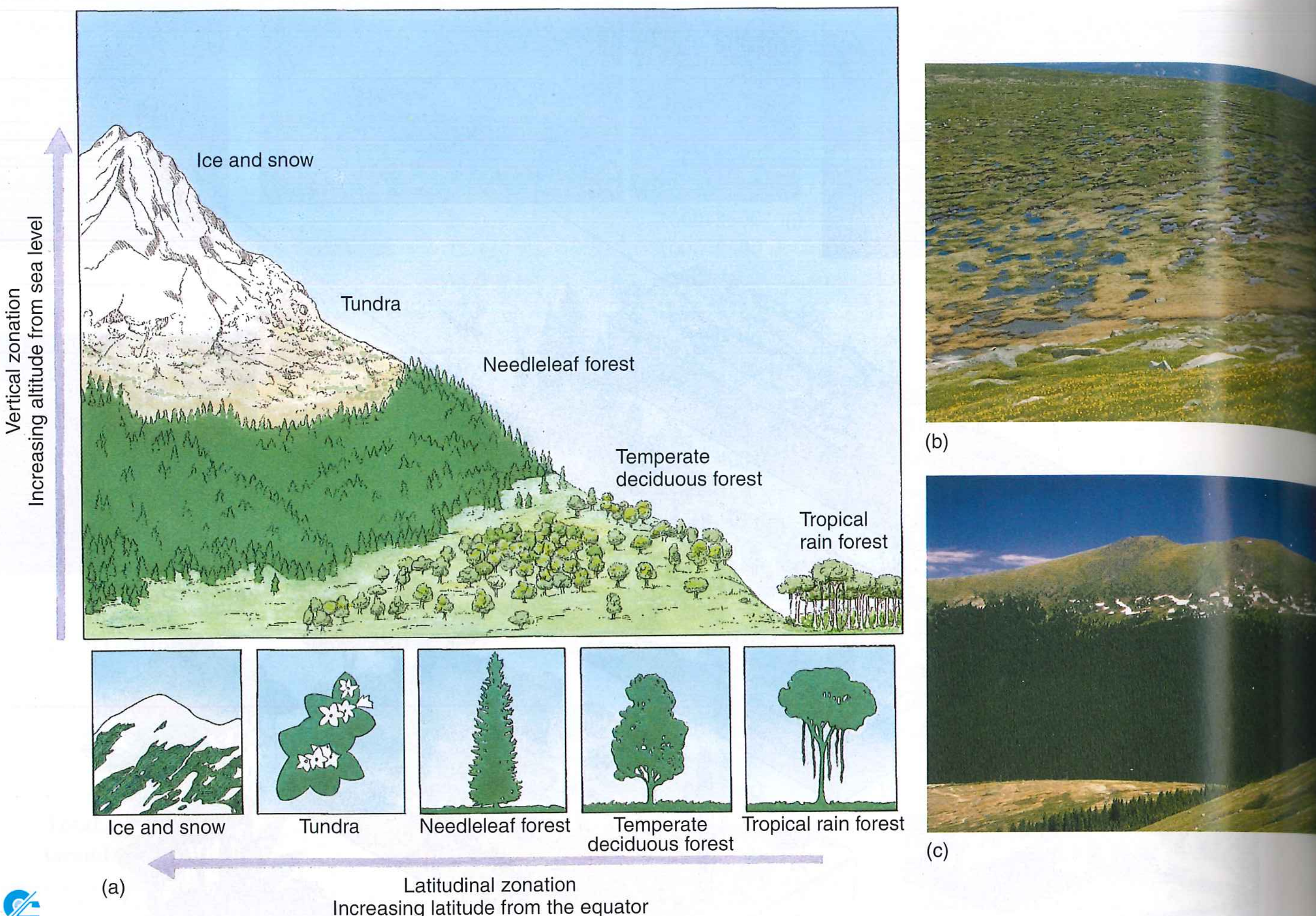


FIGURE 19.9 Vertical and latitudinal zonation of plant communities.
(a) Progression of plant community life zones with changing altitude or latitude. (b) Alpine tundra ecosystem in the Colorado Rockies. (c) The timberline for a needleleaf forest in the Rockies. The line of trees marks the limit of highest continuous forest, whereas the area above it marks the zone above which no trees grow. [Photos by Bobbé Christopherson.]

where changes in exposure and moisture occur related to geographic orientation.

Even Earth's magnetic field, another abiotic component, plays an interesting role in ecosystems. Read about turtle and animal navigation in News Report 19.1.

Elemental Cycles

The most abundant natural elements in living matter are hydrogen (H), oxygen (O), and carbon (C). Together, these elements make up more than 99% of Earth's biomass; in fact, all life (organic molecules) contains hydrogen and carbon. In addition, nitrogen (N), calcium (Ca), potassium (K), magnesium (Mg), sulfur (S), and phosphorus (P) are significant nutrients, elements necessary for the growth of a living organism.

Several key chemical cycles function in nature. Oxygen, carbon, and nitrogen each have *gaseous cycles*, part of which are in the atmosphere. Other elements have *sedimentary cycles*, which principally involve mineral and solid phases; major elements that have these cycles include phosphorus, calcium, potassium, and sulfur. Some elements combine gaseous and sedimentary cycles. The recycling of gases and sedimentary (nutrient) materials forms Earth's **biogeochemical cycles**, so called because they involve chemical reactions necessary for growth and development of living systems. The chemical elements themselves recycle over and over again in life processes.

Oxygen and Carbon Cycles We consider these two cycles together because they are so closely intertwined through photosynthesis and respiration (Figure 19.10). The atmosphere is the principal reserve of available oxygen. Larger reserves of oxygen exist in Earth's crust, but they are unavailable, being chemically bound with other elements, especially the silicate (SiO_2) and carbonate (CO_3) mineral families. Unoxidized reserves of fossil fuels and sediments also contain oxygen.

The oceans are enormous pools of carbon—about 42,900 billion metric tonnes. (Metric tonnes times 1.10

News Report 19.1

Earth's Magnetic Field—An Abiotic Factor

The fact that birds and bees can detect Earth's magnetic field and use it for finding direction is well established. Small amounts of magnetically sensitive particles in the skull of the bird and the abdomen of the bee provide compass directions for bird migration and for alerting the hive to the location of the latest nectar find. For migrating birds, the timing and accuracy of an exact flight path is important, for the birds know the nutritional places they need to visit to build their fat storage for long journeys and where each "pit stop" is located along the way.

A team of biologists from the University of North Carolina, Catherine and Kenneth Lohmann, have found that sea turtles can detect magnetic fields of different strengths and the inclination (angle) of these magnetic fields. This means that the turtles have a built-in navigation system that helps them know where they are on Earth (like our global positioning system, which requires multimillion-dollar satellites). Using magnetic field strengths and inclination, the turtles evidently are aware of their global position—similar to knowing their latitude and longitude. This magnetic map is evidently imprinted in their brain.

Loggerhead sea turtles hatch in Florida, crawl into the water, and spend the next 70 years traveling thousands of miles between North America and Africa around the subtropical high-pressure gyre in the Atlantic Ocean (see Figure 6.14). The females return to near where they were hatched to lay their eggs! The researchers think that the hatchlings are imprinted with magnetic data unique to the beach where they hatched and then develop a more global sense as they live a life swimming across the ocean.

equals short tons, or, here, 47,190 billion tons.) However, all of this carbon is bound chemically in carbon dioxide, calcium carbonate, and other compounds. The ocean initially absorbs carbon dioxide by means of the photosynthesis carried on by phytoplankton; it becomes part of the living organisms and is fixed in certain carbonate minerals, such as limestone ($CaCO_3$).

The atmosphere, which is the integrating link in the cycle, contains only about 700 billion tonnes of carbon (as carbon dioxide) at any moment. This is far less carbon than is stored in fossil fuels and oil shales (13,200 billion metric tonnes, as hydrocarbon molecules) or in living and dead organic matter (2500 billion metric tonnes, as carbohydrate molecules). Carbon dioxide is released into the atmosphere by the respiration of plants and animals, volcanic activity, and fossil fuel combustion by industry and transportation.

The carbon dumped into the atmosphere by human activity constitutes a vast geochemical experiment, using the real-time atmosphere as a laboratory. Since 1970, we have added to the atmospheric pool an amount of carbon equivalent to more than 25% of the total amount added since 1880; fourfold since 1950.

Global emissions of carbon from fossil fuels declined slightly from a 1997 high of 6.395 down to 6.299 billion metric tonnes (combined with oxygen in 18.9 billion metric tonnes of carbon dioxide) in 2000—400% more than the 1.6 billion metric tonnes of carbon in 1950. Emissions rose to more than 6.500 billion metric tonnes in 2003. About 50% of the carbon dioxide emitted since the beginning of the Industrial Revolution and not absorbed by oceans and organisms remains in the atmosphere, enhancing Earth's natural greenhouse effect. The greenhouse effect was covered more fully in Chapters 3, 5, and 10.

Nitrogen Cycle Nitrogen, which accounts for 78.084% of each breath we take, is the major constituent of the atmosphere. Nitrogen also is important in the makeup of organic molecules, especially proteins, and therefore is essential to living processes. A simplified view of the nitrogen cycle is portrayed in Figure 19.11.

This vast atmospheric reservoir of nitrogen is not directly accessible to most organisms. *Nitrogen-fixing bacteria* provide the key link to life, live principally in the soil, and are associated with the roots of certain plants—for example, the *legumes* such as clover, alfalfa, soybeans, peas, beans, and peanuts. Colonies of these bacteria reside in nodules on the legume roots and chemically combine the nitrogen from the air in the form of nitrates (NO_3) and ammonia (NH_3).

Plants use these chemically bound forms of nitrogen to produce their own organic matter. Anyone or anything feeding on the plants thus ingests the nitrogen. Finally, the nitrogen in the organic wastes (sewage, manure) of these consuming organisms is freed by denitrifying bacteria, which recycle nitrogen back to the atmosphere.

To improve agricultural yields, many farmers use synthetic inorganic fertilizers, as opposed to soil-building organic fertilizers (manure and compost). Inorganic fertilizers are chemically produced through artificial nitrogen fixation at factories using the Haber–Bosch process developed in 1913, a process that takes inert nitrogen gas and hydrogen to form ammonia (NH_3, or as the ammonium ion NH_4^+), a reactive form of nitrogen that plants can use. The annual production of inorganic fertilizers far exceeds the ability of natural denitrification systems—and the present production of synthetic fertilizers now is doubling every 8 years; some 1.82 million tonnes (2 million tons) are produced per week, worldwide. Humans presently

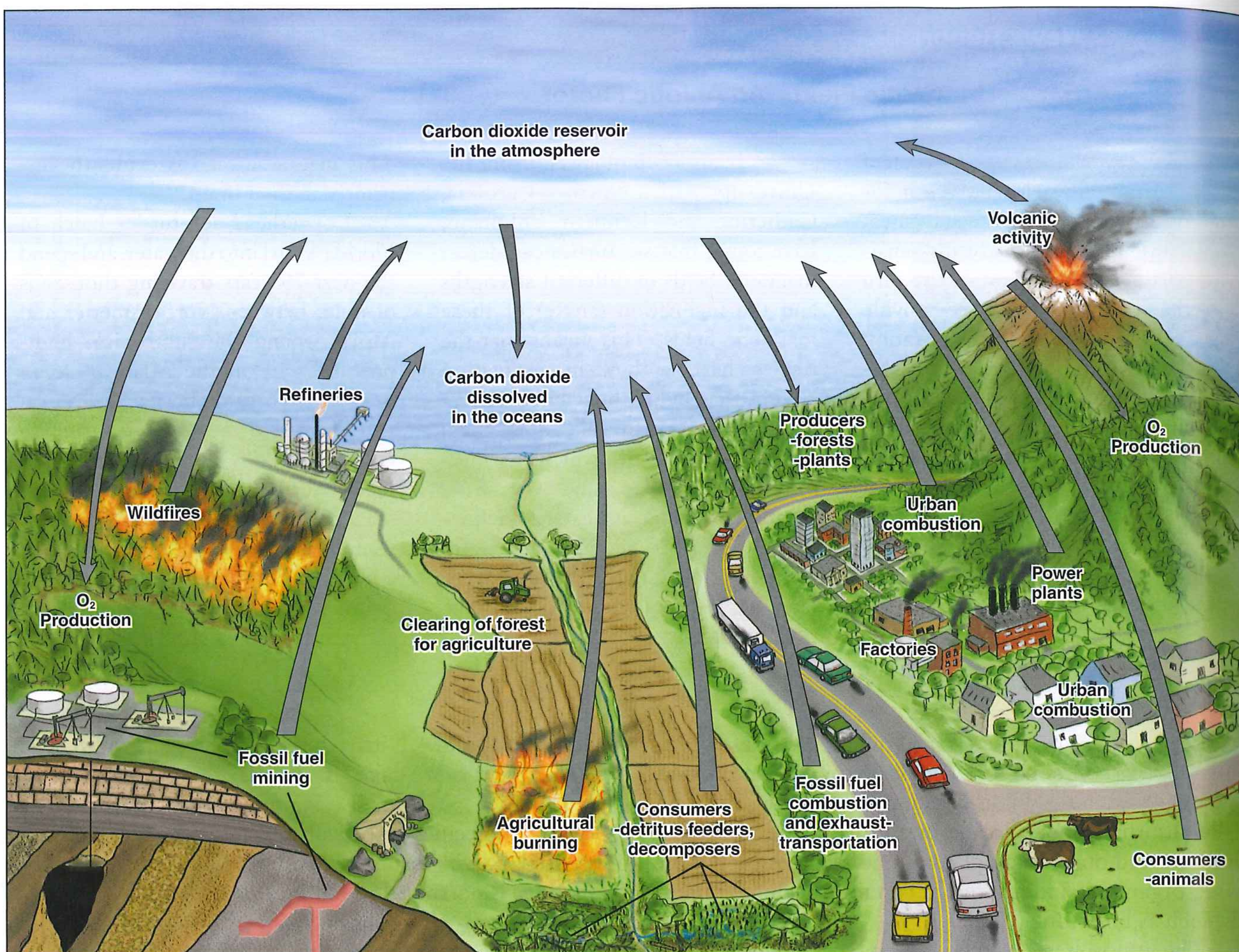


FIGURE 19.10 The carbon and oxygen cycles.
Carbon is fixed through photosynthesis and begins its passage through ecosystem operations. Respiration by living organisms, burning of forests and grasslands, and the combustion of fossil fuels releases carbon to the atmosphere. These cycles are greatly influenced by human activities.

ANIMATION The Global Carbon Cycle

fix more nitrogen per year than all terrestrial sources combined. The cross-over point when anthropogenic sources of fixed nitrogen exceeded the normal range of natural fixed nitrogen was 1970.

A recent scientific study compared nitrogen content of woodland streams in more industrialized North America and Europe with more pristine streams in South America. The type of dissolved nitrogen exported by the streams from each ecosystem demonstrates the human dominance of the nitrogen cycle. Some 98% of the North American river export was in an inorganic nitrogen form. Yet, from the relatively pristine forests of Argentina and Chile, sampled streams contained 70% dissolved organic nitrogen. The conclusion points to the presence of inorganic nitrogen from industrial pollution and fossil fuel burning, rather than the previous assumptions that forests naturally produced inorganic nitrogen in runoff, since the pristine streams were naturally dominated by organic nitrogen.

This surplus of usable nitrogen accumulates in Earth's ecosystems. Some is present as excess nutrients, washed from soil into waterways and eventually to the ocean. This excess nitrogen load begins a water pollution process that feeds an excessive growth of algae and phytoplankton, increases biochemical oxygen demand, diminishes dissolved oxygen reserves, and eventually disrupts the aquatic ecosystem. In addition, excess nitrogen compounds in air pollution are a component in acid deposition, further altering the nitrogen cycle in soils and waterways (see Chapter 3). For more on this problem, specific to North America, read News Report 19.2.

Limiting Factors

The term **limiting factor** identifies the one physical or chemical abiotic component that most inhibits biotic operations, through either its lack or its excess. Here are a few examples:

- Low temperatures limit plant growth at high elevations.
- Lack of water limits growth in a desert.

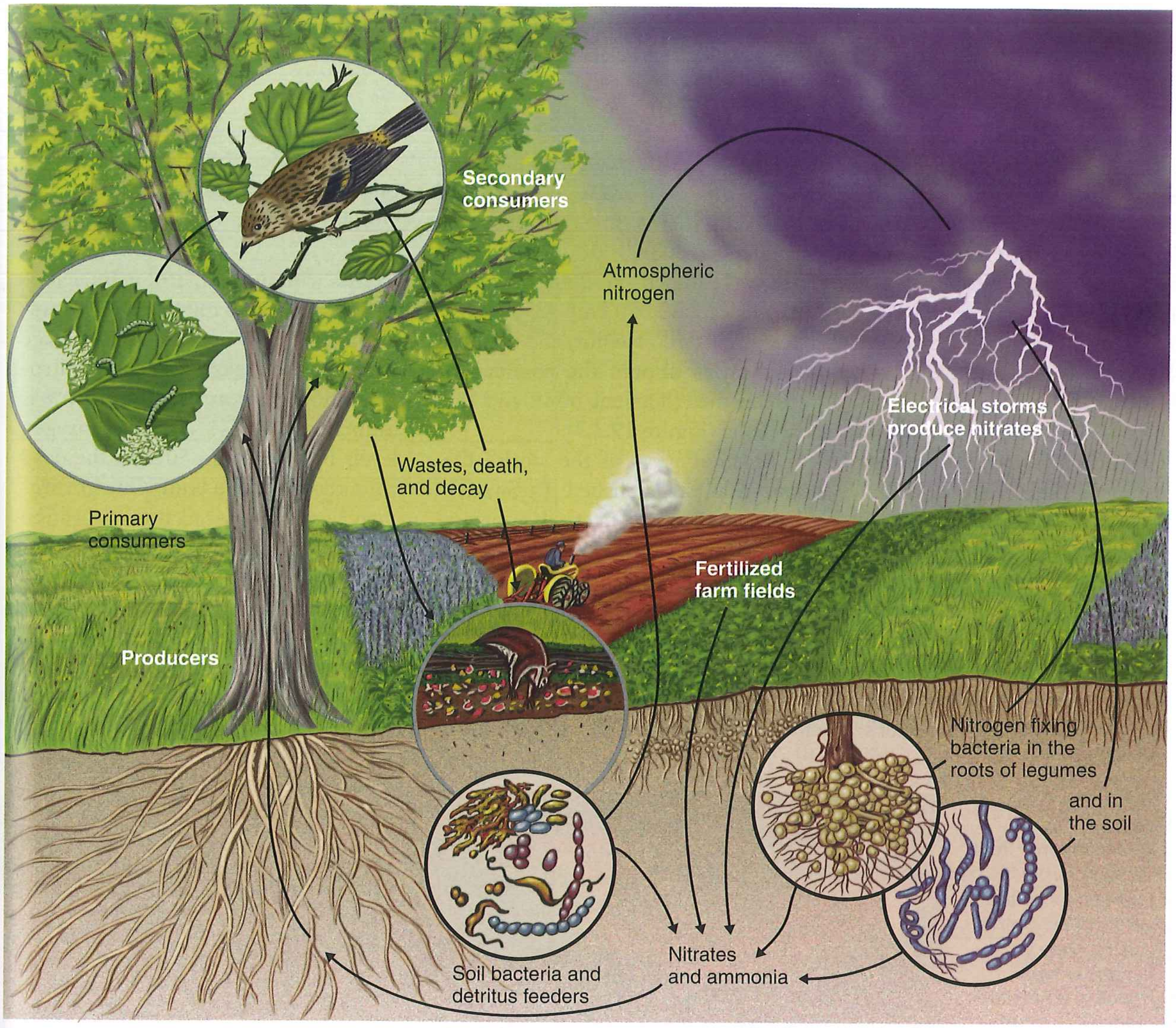


FIGURE 19.11 The nitrogen cycle.
The atmosphere is the essential reservoir of gaseous nitrogen. Atmospheric nitrogen gas is chemically fixed by bacteria to produce ammonia. Lightning and forest fires produce nitrates, and fossil fuel combustion forms nitrogen compounds that are washed from the atmosphere by precipitation. Plants absorb nitrogen compounds and produce organic material. [From T. Audesirk and G. Audesirk, *Biology: Life on Earth,* 4th ed., Figure 45-10, p. 903. © 1996 Prentice Hall Inc. Used by permission.]

- Excess water limits growth in a bog.
- Changes in salinity levels affect aquatic ecosystems.
- Lack of iron in ocean surface environments limits photosynthetic production.
- Low phosphorus content of soils limits plant growth.
- General lack of active chlorophyll above 6100 m (20,000 ft) limits primary productivity.

In most ecosystems, precipitation is the limiting factor. However, temperature, light levels, and soil nutrients certainly affect vegetation patterns.

Each organism possesses a range of tolerance for each limiting factor in its environment. This fact is illustrated vividly in Figure 19.12, which shows the geographic range for two tree species and two bird species. The coast redwood (*Sequoia sempervirens*) is limited to a narrow section of the Coast Ranges in California, covering barely 9500 km^2 (less than 4000 mi^2), concentrated in areas that receive necessary summer advection fog. On the other hand, the red maple (*Acer rubrum*) thrives over a large area under varying conditions of moisture and temperature, thus demonstrating a broader tolerance to environmental variations.

The Mallard Duck (*Anas platyrhynchos*) and the Snail Kite (*Rostrhamus sociabilis*) also demonstrate a variation in tolerance and range (Figure 19.12b). The Mallard, a generalist, feeds from widely diverse sources, is easily domesticated, and is found throughout most of North America in at least one season of the year. By contrast, the Snail Kite is a specialist that feeds only on one specific type of snail. This single food source, then, is its limiting factor. Note its small habitat area near Lake Okeechobee in Florida.

News Report 19.2

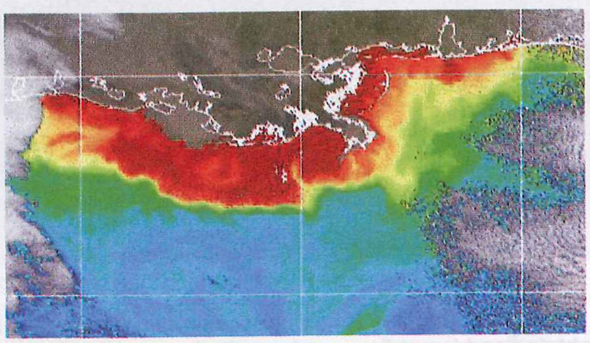
The Dead Zone

The flush of agricultural runoff and fertilizers, animal manure, sewage, and other wastes is carried by the Mississippi River to the Gulf, causing huge spring blooms of phytoplankton. By summer, the biological oxygen demand of bacteria feeding on the decay exceeds the dissolved oxygen, and hypoxia develops, killing any fish that ventures into the area. These low-oxygen conditions act as a limiting factor on marine life. Figure 19.2.1 shows the dead zone, a region of oxygen-depleted (hypoxic) water off the coast of Louisiana in the Gulf of Mexico.

The Mississippi drainage system handles the runoff for 41% of the continental United States. When the 1993 Midwest floods hit, the river's nutrient discharge was such that the size of the dead zone doubled to 17,500 km^2 (6755 mi^2). In 1999, it expanded to 20,000 km^2 (7720 mi^2). This was topped in 2002 when it expanded to 22,000 km^2 (8500 mi^2). The agricultural, feedlot, and fertilizer industries dispute the connection between their nutrient input and the dead zone (Figure 19.2.2).

In other parts of the world, the connection is established. In Sweden and Denmark, a concerted effort to reduce nutrient flows into their rivers reversed hypoxic conditions in the Kattegat Strait (between the Baltic and North Seas). And, with the fall of the U.S.S.R. and state agriculture in 1990, fertilizer use is down more than 50%, and for the first time in recent decades the Black Sea is getting several months' break from year-around hypoxia off river discharge inlets.

As with most environmental situations, the cost of mitigation is cheaper than the cost of continued damage to marine ecosystems. A cut in nitrogen inflow upstream of 20% to 30% is estimated to raise dissolved oxygen levels by more than 50% in the dead zone region of the Gulf. One government estimate placed the application of excess nitrogen fertilizer at 20% more than needed in Iowa, Illinois, and Indiana. The initial step to resolving this issue might be to mandate applying only the levels of fertilizer needed—a savings in overhead costs for agricultural interests.


(a)

(b)

FIGURE 19.2.1 The Gulf Coast dead zone. (a) The flush of nutrients from the Mississippi River drainage basin enriches the offshore waters in the Gulf of Mexico, causing huge phytoplankton blooms in early spring (red areas). (b) By late summer, oxygen-depleted waters (hypoxic) dominate what is known as the *dead zone*. [SeaWiFS image from the NASA/GSFC, courtesy of ORBIMAGE, Dulles, VA.]

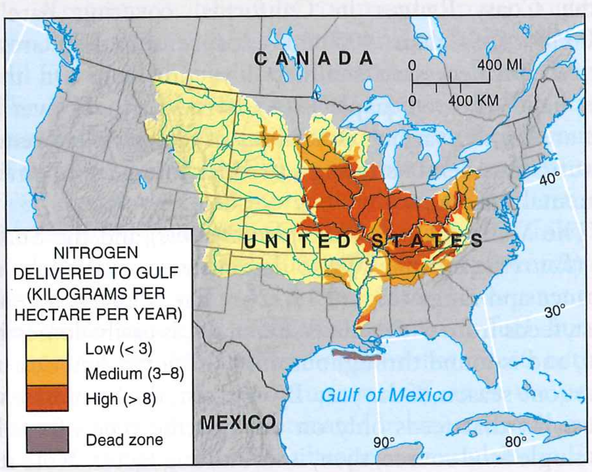


FIGURE 19.2.2 Nitrogen sources for the dead zone. Mapped total nitrogen originating in the upstream watershed that feeds the Mississippi River system. [Adapted from R. B. Alexander, R. A. Smith, and G. E. Schwarz, "Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico," *Nature* (February 17, 2000); 761, as presented in *Environment*, Jan/Feb 2001, 16.]

ANIMATION Midlatitude Productivity