

Silver Springs, Florida. This small river was the site of one of the earliest comprehensive studies of ecosystem structure and function.

© Mark J. Barrett 2005 www.markjbarrett.com



STUDY PLAN

51.1 Energy Flow and Ecosystem Energetics

Sunlight provides the energy input for practically all ecosystems

Primary productivity varies greatly on global and local scales

Some stored energy is always lost before it is transferred from one trophic level to the next

Ecological pyramids illustrate the effects of energy losses

Consumers sometimes regulate ecosystem processes

51.2 Nutrient Cycling in Ecosystems

Ecologists describe nutrient cycling with a generalized compartment model

The hydrologic cycle recirculates all the water on Earth

The carbon cycle includes a large atmospheric reservoir

The nitrogen cycle depends upon the activity of diverse microorganisms

The phosphorus cycle includes a large sedimentary reservoir

51.3 Ecosystem Modeling

Ecologists use conceptual models and simulation models to understand ecosystem dynamics

51 Ecosystems

WHY IT MATTERS

Poor Lake Erie, the shallowest of the Great Lakes. Several major industrial cities, including Toledo, Cleveland, Erie, and Buffalo, sprawl along its shoreline. Most of its water comes from the Detroit River, which flows past Detroit; the other rivers that flow into Lake Erie carry runoff from agricultural fields in Canada and the United States.

When Europeans first settled along its shores roughly 300 years ago, Lake Erie was a wetland paradise. Fishes and waterfowl reproduced in marshes and bays. Even after steel mills and oil refineries were built nearby in the 1860s and 1870s, the lake supported a busy fishing industry and was famous as a recreation area.

By 1970, wetlands had been filled for building; bays had been dredged for shipping lanes; and the shoreline had been converted to beaches. Worst of all, household sewage, industrial effluent, and agricultural runoff had so polluted the lake that it no longer supported the activities that had made it famous (**Figure 51.1**). The water was murky with algae and cyanobacteria; dead fishes washed up on the shore; local health departments closed beaches; and the fishing industry collapsed.



Laurence Lowry/Photo Researchers, Inc.

Figure 51.1
Pollution of Lake Erie. A steel mill in Lackawanna, New York, discharged industrial wastes into Lake Erie until 1983, when the mill was closed.

How can a vibrant natural resource become a foul smelling dump? The answer lies in the human activities that disrupt an **ecosystem**, a biological community and the physical environment with which it interacts. Between the 1930s and the 1970s, Lake Erie's concentration of phosphorus, which had been a limiting nutrient, tripled, largely from household detergents and agricultural fertilizers. High phosphorus concentrations encouraged the growth of photosynthetic algae, changing the phytoplankton community. The density of coliform bacteria, which originate in the human gut and serve as indicators of organic pollution, also skyrocketed as a result of the surge in sewage and nutrients entering the lake.

Increased phytoplankton and bacterial populations depleted oxygen in the lake's waters, contributing to changes elsewhere in the lake. Mayflies (*Hexagenia* species), whose larvae live in well-oxygenated bottom sediments, had once been so abundant that their aerial breeding swarms were a public nuisance. But they became nearly extinct in the polluted lake, replaced by oligochaete worms, snails, and other invertebrates. Along with overfishing, changes in the bottom fauna shifted the composition of the fish community; the catch of desirable food fishes declined to almost zero by the mid-1960s.

In 1972, Canada and the United States began efforts to restore the lake. They spent billions of dollars to reduce the influx of phosphates and limited fishing of the most vulnerable native species. Nonnative salmon (*Onchorhynchus* species) and other predatory fishes were introduced in the hope that they could bring the lake back to its original condition. Even the accidental introduction of zebra mussels (*Dreissina polymorpha*), an aquatic pest, inadvertently helped the effort because they feed on phytoplankton.

But, although somewhat improved, Lake Erie will never return to its former glory. Some native species

are now extinct there, and the introduced species that replaced them function differently within the ecosystem. The lake still suffers periods of uncontrolled algal growth, fish kills, and high levels of harmful bacteria.

This story of an ecological disaster and partial recovery introduces ecosystem ecology, the branch of ecology that analyzes the flow of energy and the cycling of materials between an ecosystem's living and nonliving components. These processes make the resident organisms highly dependent on each other and on their physical surroundings. Ultimately, the Lake Erie ecosystem unraveled because human activities disrupted the flow of energy and the cycling of materials upon which the organisms depended.

51.1 Energy Flow and Ecosystem Energetics

Ecosystems receive a steady input of energy from an external source, which in virtually all cases is the sun. Energy flows through an ecosystem, but, as dictated by the laws of thermodynamics (see Section 4.1), much of it is lost without being used by organisms.

Food webs define the pathways by which energy moves through an ecosystem's biotic components (see Section 50.3). In most ecosystems, energy moves simultaneously through a *grazing food web* and a *detrital food web* (**Figure 51.2**). The grazing food web includes the producer, herbivore, and carnivore trophic levels. The detrital food web includes detritivores and decomposers. Because detritivores and decomposers subsist on the remains and waste products of organisms at every trophic level, the two food webs are closely interconnected. Detritivores also contribute to the grazing food web when carnivores eat them.

All of the organisms in a trophic level are the same number of energy transfers from the ecosystem's ultimate energy source. Plants are one energy transfer removed from sunlight; herbivores are two transfers away; carnivores feeding on herbivores are three transfers away; and carnivores feeding on other carnivores are four transfers away. In this section, we consider the details of energy flow and the efficiency of energy transfer from one trophic level to another.

Sunlight Provides the Energy Input for Practically All Ecosystems

Virtually all life on Earth depends on the input of solar energy. Every minute of every day, the atmosphere intercepts roughly 19 kcal of energy per square meter. (Recall from Chapter 2 that 1 kcal = 1000 calories.) About half that energy is absorbed, scattered, or reflected by gases, dust, water vapor, and clouds without ever reaching the planet's surface (see Chapter 52). Most energy that reaches the surface falls on bodies of water or bare ground, where it is absorbed as heat or

reflected back into the atmosphere; reflected energy warms the atmosphere, as we discuss later in this chapter. Only a small percentage contacts primary producers, and most of that energy evaporates water, driving transpiration in plants (see Section 32.3).

Ultimately, photosynthesis converts less than 1% of the solar energy that arrives at Earth's surface into chemical energy. But primary producers capture enough energy to create an average of several kilograms of dry plant material per square meter per year. On a global scale, they produce more than 150 billion metric tons of new biological material annually. Some of the solar energy that producers convert into chemical energy is transferred to consumers at higher trophic levels.

The rate at which producers convert solar energy into chemical energy is an ecosystem's **gross primary productivity**. But like all other organisms, producers also use energy for their own maintenance. After deducting the energy used for these functions, which are collectively called *cellular respiration* (see Section 8.1), whatever chemical energy remains is the ecosystem's **net primary productivity**. In most ecosystems, net pri-

mary productivity is between 50% and 90% of gross primary productivity. In other words, producers use between 10% and 50% of the energy they capture for their own respiration.

Ecologists generally measure primary productivity in units of energy captured ($\text{kcal}/\text{m}^2/\text{yr}$) or in units of biomass created ($\text{g}/\text{m}^2/\text{yr}$). *Biomass* is the dry weight of biological material per unit area or volume of habitat. (We measure biomass as the *dry* weight of organisms because their water content, which fluctuates with water uptake or loss, has no energetic or nutritional value.) You should not confuse an ecosystem's productivity with its **standing crop biomass**, the total dry weight of plants present at a given time. Net primary productivity is the *rate* at which the standing crop produces *new* biomass.

The energy captured by plants is stored in biological molecules—mostly carbohydrates, lipids, and proteins. Ecologists can convert units of biomass into

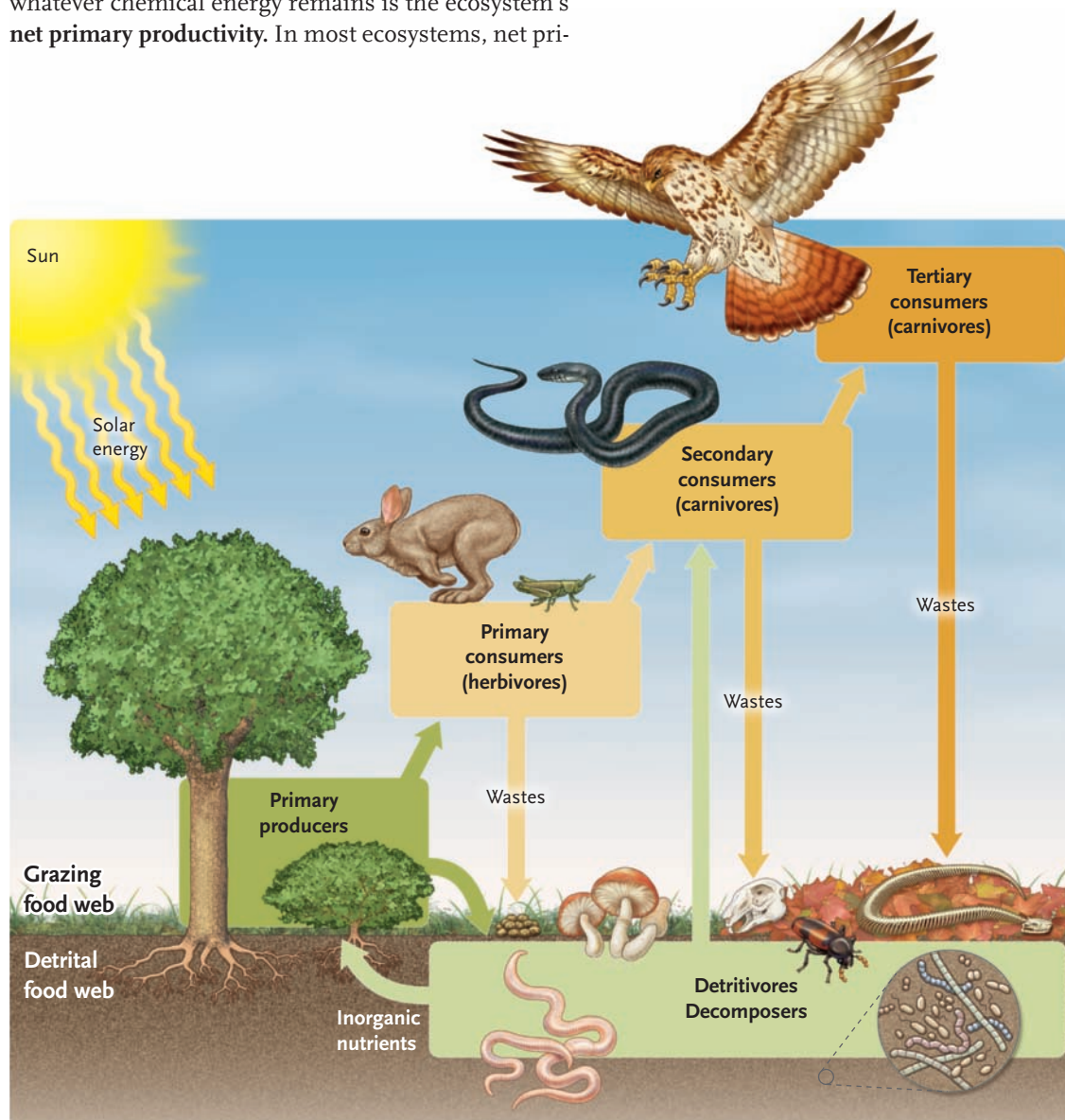
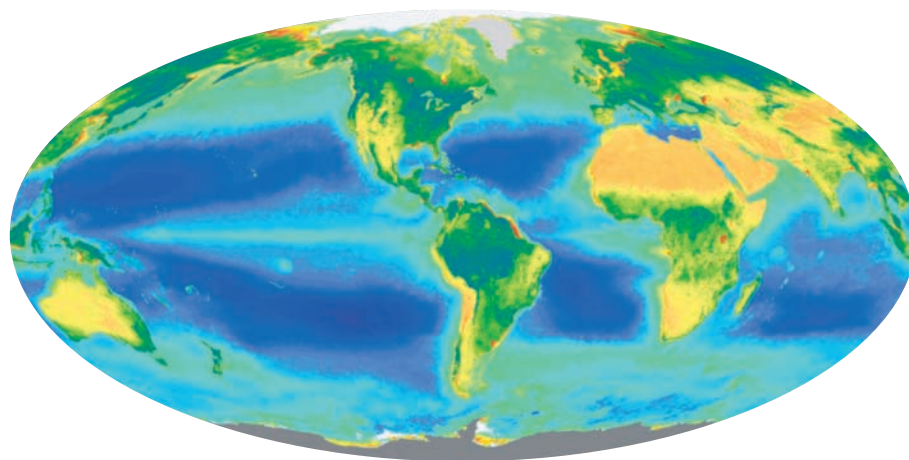


Figure 51.2

Grazing and detrital food webs. Energy and nutrients move through two parallel food webs in most ecosystems. The grazing food web includes producers, herbivores, and carnivores. The detrital food web includes detritivores and decomposers. Each box in this diagram represents many species, and each arrow represents many arrows.

Figure 51.3

Global variation in primary productivity. Satellite data for 1997–2000 provide a visual portrait of net primary productivity across Earth's surface. High-productivity regions on land are dark green; low-productivity regions are yellow. For the oceans, the highest productivity is red, down through orange, yellow, and green, with blue the lowest.



SeeWIFS Project, NASA/Goddard Space Flight Center and ORBIMAGE

units of energy or vice versa as long as they know how much carbohydrate, protein, and lipid a sample of biological material contains (4.2 kcal/g of carbohydrate; nearly 4.1 kcal/g of protein; and 9.5 kcal/g of lipid). Thus, net primary productivity is a measure of the rate at which producers accumulate energy as well as the rate at which new biomass is added to an ecosystem. Because it is far easier to measure biomass than energy content, ecologists usually measure changes in biomass to estimate productivity. New biomass takes several forms: the growth of existing producers; the creation of new producers by reproduction; and the storage of energy as carbohydrates. Because herbivores eat all three forms of new biomass, net primary productivity also measures how much new energy is available for primary consumers.

Primary Productivity Varies Greatly on Global and Local Scales

The potential rate of photosynthesis in any ecosystem is proportional to the intensity and the duration of sunlight, which vary geographically and seasonally (see

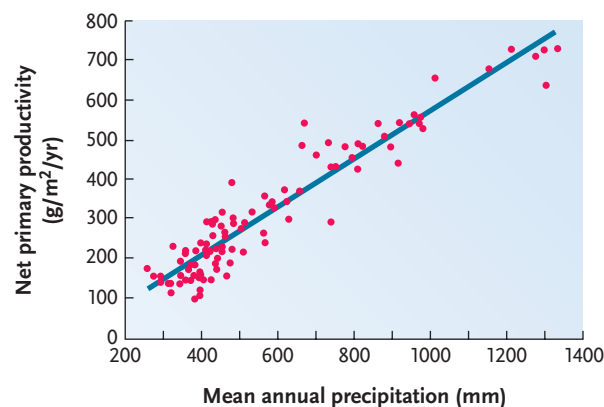


Figure 51.4

Water and net primary productivity. Mean annual net primary productivity increases with mean annual precipitation among 100 sites in the Great Plains of North America. These data include only aboveground productivity.

Chapter 52). Sunlight is most intense and day length least variable near the equator. By contrast, light intensity is weakest and day length most variable near the poles. Thus, producers at the equator can photosynthesize nearly 12 hours a day, every day of the year. Near the poles, photosynthesis is virtually impossible during the long, dark winter; in summer, however, plants can photosynthesize around the clock.

Sunlight is not the only factor that influences the rate of primary productivity, however; temperature as well as the availability of water and nutrients also have big effects. For example, many of the world's deserts receive plenty of sunshine but have low rates of productivity because water is in short supply and the soil is nutrient-poor. Thus, mean annual net primary productivity varies greatly on a global scale (**Figure 51.3**), reflecting variations in these environmental factors (see Chapter 52).

On a finer geographical scale, within a particular terrestrial ecosystem, mean annual net productivity often increases with the availability of water (**Figure 51.4**). In systems with sufficient water, a shortage of mineral nutrients may be limiting. All plants need specific ratios of macronutrients and micronutrients for maintenance and photosynthesis (see Section 33.1). But plants withdraw nutrients from soil, and if nutrient concentration drops below a critical level, photosynthesis may decrease or stop altogether. In every ecosystem, one nutrient inevitably runs out before the supplies of other nutrients are exhausted. The element in short supply is called a **limiting nutrient** because its absence limits productivity. Productivity in agricultural fields is subject to the same constraints as productivity in natural ecosystems. Farmers increase productivity by irrigating (adding water to) and fertilizing (adding nutrients to) their crops.

In freshwater and marine ecosystems, where water is always readily available, the depth of the water and the combined availability of sunlight *and* nutrients govern the rate of primary productivity. Productivity is high in near-shore ecosystems where sunlight pene-

trates shallow, nutrient-rich waters. Kelp beds and coral reefs, for example, which occur along temperate and tropical coastlines respectively, are among the most productive ecosystems on Earth (Table 51.1). By contrast, productivity is low in the open waters of a large lake or ocean: sunlight penetrates only the upper layers, and nutrients sink to the bottom. Thus, the two requirements for photosynthesis, sunlight and nutrients, are available in different places.

Although ecosystems vary in their net primary productivity, the differences are not always proportional to variations in their standing crop biomass (see Table 51.1). For example, biomass in temperate deciduous forests and temperate grasslands differs by a factor of 20, but the difference in their rates of net primary productivity is only twofold. Most biomass in trees is present in non-photosynthetic tissues such as wood. As a result, their ratio of productivity to biomass is low ($1200 \text{ g/m}^2 \div 30,000 \text{ g/m}^2 = 0.040$). By contrast, grasslands don't accumulate much biomass because annual mortality, herbivores, and fires remove plant material as it is produced; and their productivity to biomass ratio is much higher ($600 \text{ g/m}^2 \div 1600 \text{ g/m}^2 = 0.375$).

Some ecosystems contribute more than others to overall net primary productivity (Figure 51.5). Ecosystems that cover large areas make substantial contributions, even if their productivity is low. Conversely, geographically restricted ecosystems make large contributions if their productivity is high. For example, the open ocean and tropical rain forests contribute about equally to total global productivity, but for different reasons. Open oceans have low productivity, but they cover nearly two-thirds of Earth's surface. Tropical rain forests cover only a small area, but they are highly productive.

Some Stored Energy Is Always Lost before It Is Transferred from One Trophic Level to the Next

Net primary productivity ultimately supports all the consumers in grazing and detrital food webs. Consumers in the grazing food web eat some of the biomass at every trophic level except the highest; uneaten biomass eventually dies and passes into detrital food webs. However, consumers assimilate only a portion of the material they ingest, and unassimilated material is passed as feces, which also supports detritivores and decomposers.

As energy is transferred from producers to consumers, some is stored in new consumer biomass, called **secondary productivity**. Nevertheless, two factors cause energy to be lost from the ecosystem every time it flows from one trophic level to another. First, animals use much of the energy they assimilate for maintenance or locomotion rather than the production of new biomass. Second, as dictated by the second law of thermodynamics, no biochemical reaction is 100% effi-

Table 51.1 Standing Crop Biomass and Net Primary Productivity of Different Ecosystems

Ecosystem	Mean Standing Crop Biomass (g/m ²)	Mean Net Primary Productivity (g/m ² /yr)
Terrestrial Ecosystems		
Tropical rain forest	45,000	2,200
Tropical deciduous forest	35,000	1,600
Temperate rain forest	35,000	1,300
Temperate deciduous forest	30,000	1,200
Savanna	4,000	900
Boreal forest (taiga)	20,000	800
Woodland and shrubland	6,000	700
Agricultural land	1,000	650
Temperate grassland	1,600	600
Tundra and alpine tundra	600	140
Desert and thornwoods	700	90
Extreme desert, rock, sand, ice	20	3
Freshwater Ecosystems		
Swamp and marsh	15,000	2,000
Lake and stream	20	250
Marine Ecosystems		
Open ocean	3	125
Upwelling zones	20	500
Continental shelf	10	360
Kelp beds and reefs	2,000	2,500
Estuaries	1,000	1,500
World Average	3,600	333

From Whittaker, R.H. 1975. *Communities and Ecosystems*. 2nd ed. Macmillan.

cient; thus, some of the chemical energy liberated by cellular respiration is always converted to heat, which most organisms do not use.

Ecological efficiency is the ratio of net productivity at one trophic level to net productivity at the trophic level below it. For example, if the plants in an ecosystem have a net primary productivity of $100 \text{ g/m}^2/\text{year}$ of new tissue and the herbivores that eat those plants produce $10 \text{ g/m}^2/\text{year}$, the ecological efficiency of the herbivores is 10%. The efficiencies of three processes—harvesting food, assimilating ingested energy, and producing new biomass—determine the ecological efficiencies of consumers.

Harvesting efficiency is the ratio of the energy content of food consumed to the energy content of food available. Predators harvest food efficiently when prey are abundant and easy to capture (see Section 50.1).

Assimilation efficiency is the ratio of the energy absorbed from consumed food to the food's total energy content. Because animal prey is relatively easy to digest,

Ecosystem	Percentage of Earth's Surface Covered	Percentage of Total Producer Biomass	Percentage of Total Net Primary Productivity
Open ocean	65.1	0.05	24.40
Continental shelf	5.2	0.01	5.60
Extreme desert, rock, sand, ice	4.7	0.03	0.04
Desert and thornwoods	3.5	0.71	0.94
Tropical rain forest	3.3	41.60	22.00
Savanna	2.9	3.30	7.94
Cultivated land	2.7	0.76	5.35
Boreal forest (taiga)	2.4	13.03	5.64
Temperate grassland	1.8	0.76	3.18
Woodland and shrubland	1.7	2.71	3.53
Tundra	1.6	0.27	0.65
Tropical deciduous forest	1.5	14.12	7.05
Temperate deciduous forest	1.4	11.41	4.94
Temperate rain forest	1.0	9.51	3.82
Swamp and marsh	0.4	1.62	2.35
Lake and stream	0.4	0.003	0.29
Estuaries	0.3	0.08	1.23
Algal beds and reefs	0.1	0.07	0.94

Figure 51.5

Biomass and net primary productivity. The percentage of Earth's surface that an ecosystem covers is not proportional to its contribution to the total biomass of producers or its contribution to the total net primary productivity.

carnivores absorb between 60% and 90% of the energy in their food; assimilation efficiency is lower for prey with indigestible parts like bones or exoskeletons. Herbivores assimilate only 15% to 80% of the energy they consume because cellulose is not very digestible.

Production efficiency is the ratio of the energy content of new tissue produced to the energy assimilated from food. Production efficiency varies with maintenance costs. For example, endothermic animals often use less than 10% of their assimilated energy for growth and reproduction, because they use energy to generate body heat (see Section 46.8). Ectothermic animals, by contrast, channel more than 50% of their assimilated energy into new biomass.

The overall ecological efficiency of most organisms is between 5% and 20%. As a rule of thumb, only about 10% of the energy accumulated at one trophic level is converted into biomass at the next higher trophic level, as illustrated by energy transfers at Silver Springs, Florida (**Figure 51.6**). Producers in the Silver Springs ecosystem convert 1.2% of the solar energy they intercept into chemical energy (represented by 20,810 kcal of gross primary productivity). However, they use about two-thirds of this energy for respiration, leaving only one-third to be included in new plant biomass, the net primary productivity. All consumers in the grazing food web (on the right in Figure 51.6) ultimately depend on this energy source, which dwindles with each transfer between trophic levels. Energy is lost to respiration and export (that is, the transport of energy-containing materials out of the ecosystem by flowing water) at each trophic level. In addition, sub-

stantial energy, represented in organic wastes and uneaten biomass, flows into the detrital food web (on the left in Figure 51.6). To determine the ecological efficiency of any trophic level, we divide its productivity by the productivity of the level below it. For example, the ecological efficiency of midlevel carnivores at Silver Springs is $111 \text{ kcal/yr} \div 1103 \text{ kcal/yr} = 10.06\%$.

As energy works its way up a food web, energy losses are multiplied in successive energy transfers, greatly reducing the energy available to support the highest trophic levels. Consider a hypothetical example in which ecological efficiency is 10% for all consumers. Assume that the plants in a small field annually produce new tissues containing 100 kcal of energy. Because only 10% of that energy is transferred to new herbivore biomass, the 100 kcal in plants produces only 10 kcal of new herbivorous insects; only 1 kcal of new songbirds, which feed on insects; and only 0.1 kcal of new falcons, which feed on songbirds. Thus, after three energy transfers, only 0.1% of the energy from primary productivity remains at the highest trophic levels. If the energy available to each trophic level is depicted graphically, the result is a **pyramid of energy** with primary producers on the bottom and higher-level consumers on the top. We discuss ecological pyramids in detail in the next section.

The low ecological efficiencies that characterize most energy transfers illustrate one advantage of eating “lower on the food chain.” Even though humans digest and assimilate meat more efficiently than vegetables, we might be able to feed more people if we all ate more vegetables directly instead of first passing

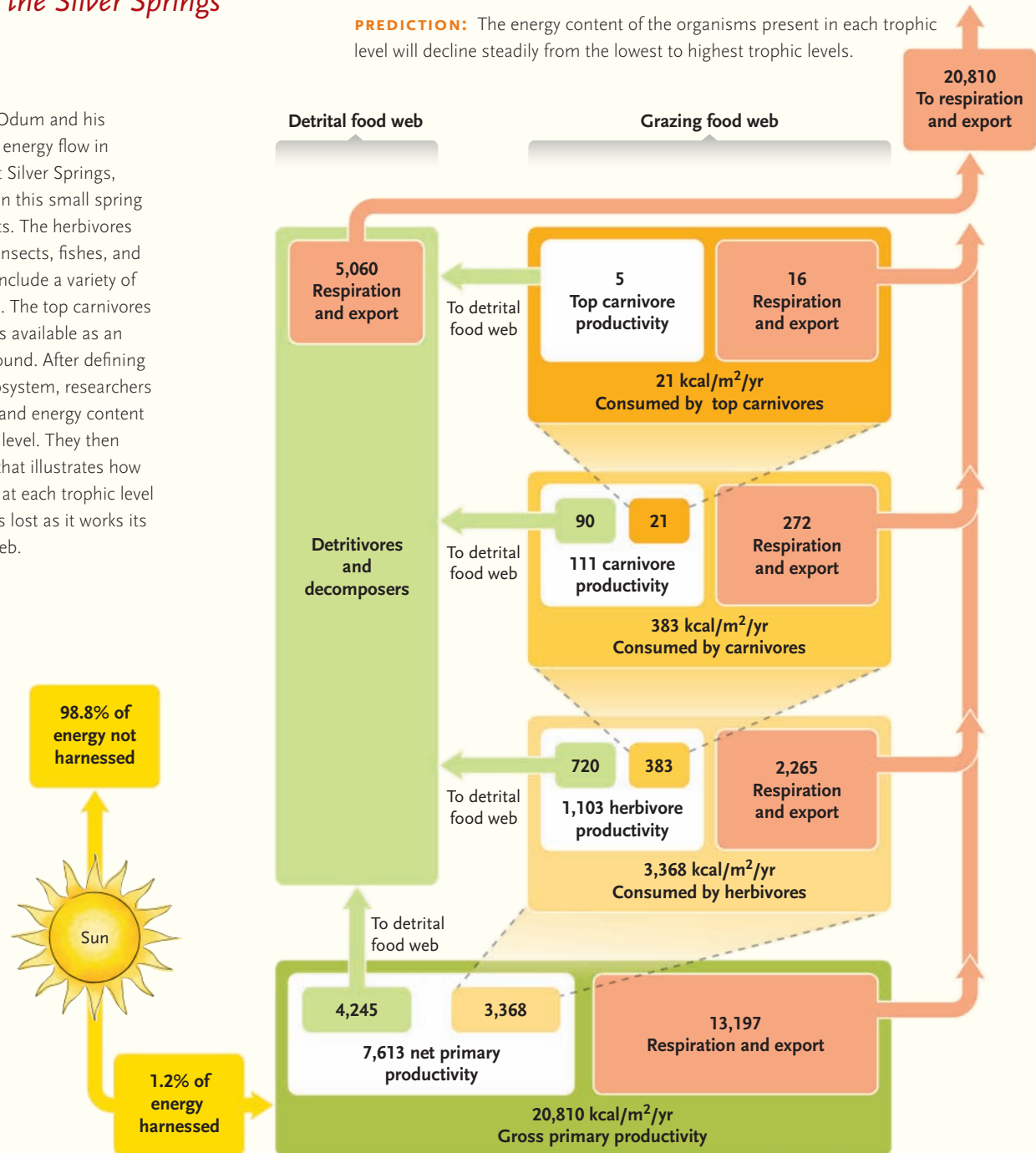
Figure 51.6 Observational Research

Energy Flow in the Silver Springs Ecosystem

METHOD: Howard T. Odum and his research team analyzed energy flow in an aquatic ecosystem at Silver Springs, Florida. The producers in this small spring are mostly aquatic plants. The herbivores include snails, shrimp, insects, fishes, and turtles. The carnivores include a variety of invertebrates and fishes. The top carnivores are large fish. Sunlight is available as an energy source all year round. After defining the food web in this ecosystem, researchers estimated the biomass and energy content (kcal/g) of each trophic level. They then constructed a diagram that illustrates how much energy is present at each trophic level and how much energy is lost as it works its way through the food web.

HYPOTHESIS: Only a small percentage of the energy present in a trophic level is transferred to the next higher trophic level in the ecosystem.

PREDICTION: The energy content of the organisms present in each trophic level will decline steadily from the lowest to highest trophic levels.



RESULTS: The diagram illustrates annual energy flow for the spring ecosystem at Silver Springs, Florida. Numbers on the diagram indicate the quantity of energy (kcal/m²/yr). Because the ecosystem is based on flowing water, small quantities of energy arrive from other ecosystems and small quantities are exported in material carried away by stream flow.

CONCLUSION: The study confirmed the hypothesis that only a small proportion of the energy present at a trophic level is transferred to the next higher trophic level. Ultimately, all of the energy that passes through the grazing and detrital food webs is released as metabolically generated heat.

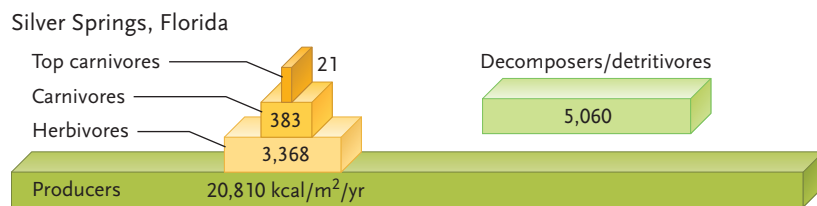


Figure 51.7
Pyramids of energy. The pyramid of energy for Silver Springs, Florida, shows that the amount of energy passing through each trophic level decreases as it moves up the food web.

these crops through another trophic level, such as cattle or chickens, to produce meat. The production of animal protein is costly because much of the energy fed to livestock is used for their own maintenance rather than the production of new biomass. But despite the economic—not to mention health-related—logic of a more vegetarian diet, a change in our eating habits alone won't eliminate food shortages or the frequency of malnutrition. Many regions of Africa, Australia, North America, and South America support vegetation that is suitable only for grazing by large herbivores. These areas could not produce significant quantities of edible grains and vegetables.

Ecological Pyramids Illustrate the Effects of Energy Losses

The inefficiency of energy transfer from one trophic level to the next has profound effects on ecosystem structure. Ecologists illustrate these effects in diagrams called **ecological pyramids**. Trophic levels are drawn as stacked blocks, with the size of each block proportional to the energy, biomass, or numbers of organisms present. We mentioned the pyramid of energy in the previous section. Pyramids of energy typically have wide bases and narrow tops (**Figure 51.7**) because each trophic level contains only about 10% as much energy as the trophic level below it.

The progressive reduction in productivity at higher trophic levels, as illustrated in Figure 51.6, usually establishes a **pyramid of biomass** (**Figure 51.8**). The biomass at each trophic level is proportional to the chemical energy temporarily stored there. Thus, in terrestrial ecosystems, the total mass of producers is generally greater than the total mass of herbivores, which is, in turn, greater than the total mass of predators (see Fig-

ure 51.8a). Populations of top predators—animals like mountain lions or alligators—contain too little biomass and energy to support another trophic level; thus, they have no nonhuman predators.

Freshwater and marine ecosystems sometimes exhibit inverted pyramids of biomass (see Figure 51.8b). In the open waters of a lake or ocean, primary consumers (zooplankton) eat the primary producers (phytoplankton) almost as soon as they are produced. As a result, the standing crop of primary consumers at any moment in time is actually larger than the standing crop of primary producers. Food webs in these ecosystems are stable, however, because the producers have exceptionally high **turnover rates**. In other words, the producers divide and their populations grow so quickly that feeding by zooplankton doesn't endanger their populations or reduce their productivity. And on an annual basis, the *cumulative total* biomass of primary producers far outweighs that of primary consumers.

The reduction of energy and biomass also affects the population sizes of organisms at the top of a food web. Top predators are often relatively large animals. Thus, the limited biomass present in the highest trophic levels is concentrated in relatively few animals (**Figure 51.9**). The extremely narrow top of this **pyramid of numbers** has grave implications for conservation biology. Top predators tend to be large animals with small population sizes. And because each individual must patrol a large area to find sufficient food, the members of a population are often widely dispersed within their habitats. As a result, they are subject to genetic drift (see Section 20.3) and are highly sensitive to hunting, habitat destruction, and random events, which can lead to extinction (see Chapter 53). Top predators may also suffer from the accumulation of poisonous materials that move through food webs (see *Focus on Research* on biological magnification in Chapter 53). Even predators that feed below the top trophic level often suffer the ill effects of human activities. *Insights from the Molecular Revolution* describes how researchers determined that fishing diminishes fragile populations of loggerhead sea turtles (*Caretta caretta*), a predator that routinely travels from one ecosystem to another.



Figure 51.8
Pyramids of biomass. (a) The pyramid of standing crop biomass for Silver Springs is bottom heavy, as it is for most ecosystems. (b) Some marine ecosystems, such as that in the English Channel, have an inverted pyramid of biomass because producers are quickly eaten by primary consumers. Only the producer and herbivore trophic levels are illustrated here. The data for both pyramids are given in grams of dry biomass per square meter.

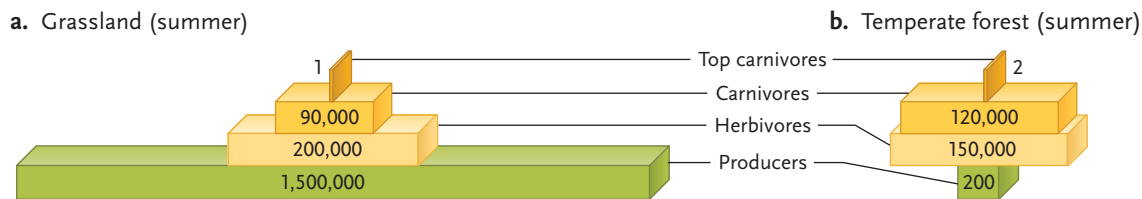


Figure 51.9
Pyramids of numbers. (a) The pyramid of numbers (number of individuals per 1000 m²) for temperate grasslands is bottom-heavy because individual producers are small and very numerous. (b) The pyramid of numbers for forests may have a narrow base because herbivorous insects often outnumber the producers, which are large trees. Data for both pyramids were collected in summer. Detritivores and decomposers (soil animals and microorganisms) are not included because they are difficult to count.

Consumers Sometimes Regulate Ecosystem Processes

As you know from the preceding discussion, numerous abiotic factors—the intensity and duration of sunlight, rainfall, temperature, and the availability of nutrients—have significant effects on primary productivity. Primary productivity, in turn, has profound effects on populations of herbivores and the predators that feed on them. But what effect does feeding by these consumers have on primary productivity?

Research conducted in the 1990s suggests that consumers may sometimes influence rates of primary productivity, especially in ecosystems with low species diversity and relatively few trophic levels. For example, food webs in lake ecosystems depend primarily on the productivity of phytoplankton (Figure 51.10). These producers are consumed by herbivorous zooplankton, which are in turn eaten by predatory invertebrates and fishes. The top nonhuman carnivore in these food webs is usually a predatory fish.

Herbivorous zooplankton play a central role in the regulation of lake ecosystems. Small zooplankton species consume only small phytoplankton. Thus, when small zooplankton are especially abundant, the large phytoplankton escape predation and survive, and the lake's primary productivity is high. By contrast, large zooplankton are voracious, eating both small and large phytoplankton. When large zooplankton are especially abundant, they reduce the overall biomass of phytoplankton, lowering the ecosystem's primary productivity.

In what has been termed a **trophic cascade**—predator–prey effects that reverberate through the population interactions at two or more trophic levels in an ecosystem—feeding by plankton-eating invertebrates and fishes has a *direct* impact on herbivorous zooplankton populations and an *indirect* impact on phytoplankton populations and the ecosystem's primary productivity. Invertebrate predators prefer small zooplankton. And when the invertebrates that eat small zooplankton are the dominant carnivores in the ecosystem, large zooplankton become more abundant;

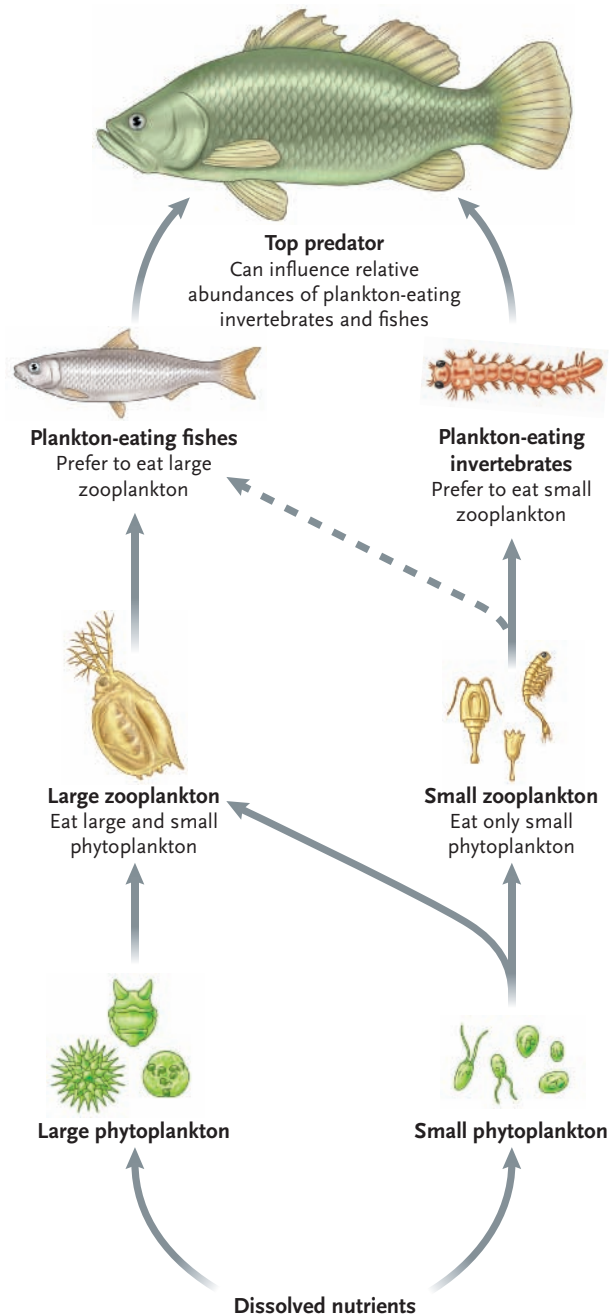


Figure 51.10
Consumer regulation of primary productivity. A simplified food web illustrates that lake ecosystems have relatively few trophic levels. The effects of feeding by top carnivores can cascade downward, exerting an indirect effect on phytoplankton and, thus, on primary productivity.



INSIGHTS FROM THE MOLECULAR REVOLUTION

Fishing Fleets at Loggerheads with Sea Turtles

Populations of loggerhead sea turtles (*Caretta caretta*) that nest on Western Pacific beaches in Australia and Japan have been in decline. A surprising recent discovery indicates that the explanation may lie many thousands of miles away. Loggerhead sea turtles hatch from eggs that females bury on sandy beaches. The hatchlings then scurry to the surf and migrate to distant feeding grounds. The turtles mature at the feeding grounds, and eventually return to their hatching beaches to lay eggs.

Recently, a population of loggerhead sea turtles was discovered feeding along the coast of Baja California. Nesting grounds for these turtles are known only in the western Pacific, in Australia and Japan; none had been identified in the eastern Pacific. Did these turtles really migrate across 10,000 km of open ocean from Japan and Australia to Baja California? If so, the trip would be the longest open ocean migration known for any marine animal.

Location	Sequence A	Sequence B	Sequence C
Australian nesting areas	26 turtles	0 turtles	0 turtles
Japanese nesting areas	0 turtles	23 turtles	3 turtles
Baja California feeding grounds	2 turtles	19 turtles	5 turtles
North Pacific	1 turtle	28 turtles	5 turtles

In addition, this long journey might explain the decline of the turtles in Japan and Australia. Scientists know that as many as 4000 loggerhead turtles drown in fishing nets in the north Pacific each year. Are these turtles intercepted on their way to Baja California from the Australian or Japanese feeding grounds? If so, the large numbers caught in fishing nets may contribute to the decline of loggerhead populations in the western Pacific.

Brian W. Bowen and his colleagues at the University of Florida, Gainesville, used mitochondrial DNA (mtDNA) sequences to answer these questions. One 350-base-pair segment of mtDNA was particularly useful because it includes sequence variations that are characteristic of different loggerhead populations.

The investigators took DNA samples from nesting populations in Australia and Japan, from feeding populations in Baja California, and from turtles drowned in fishing nets in the north Pacific. They used the polymerase chain reaction (PCR) to amplify the mtDNA segment from the DNA samples. Sequencing of the amplified segments revealed three major variants of mtDNA, which the researchers designated sequences A, B, and C. The sequences were distributed among loggerhead turtles as shown in the accompanying table.

The mtDNA of most turtles found in Baja California and in fishing nets in

the north Pacific match that of turtles from the Japanese nesting areas, supporting the idea that loggerhead turtles hatched in Japan make the long migration across the north Pacific to Baja California. The data also indicate that a few turtles hatched in Australia may follow the same migratory route.

The investigators propose that the North Pacific Current, which moves from west to east, aids the migration. The return trip from Baja to Japan could be made via the North Equatorial Current, which runs from east to west just north of the equator. Loggerhead turtles have been found in this current; further tests will reveal whether they have the mtDNA sequence characteristic of the individuals nesting in Japan and feeding in Baja California.

Because only 2000 to 3000 female loggerhead turtles nest in Japan, it is uncertain whether the Japanese nesting population can survive the loss of thousands of offspring to fishing in the north Pacific. The number of female loggerhead turtles nesting in Australia has declined by 50% to 80% in the last decade; the loss of only a few individuals in fishing nets could have a drastic impact on this population as well. To save the loggerhead turtles, wildlife managers and international agencies must establish and enforce limits on the number of migrating individuals trapped and killed in the ocean fisheries.

they consume many phytoplankton, causing productivity to decrease. By contrast, zooplankton-eating fishes prefer to eat large zooplankton (see Figure 50.2). Thus, when plankton-eating fishes are abundant, small zooplankton become the dominant herbivores. As a result, large phytoplankton become more numerous and the lake's productivity rises.

Large predatory fishes may add an additional level of control to the system because they feed on and regulate the population sizes of plankton-eating invertebrates and fishes. Thus, the effects of feeding by the top predator can cascade downward through the food web, affecting the densities of plankton-eating invertebrates and fishes, herbivorous zooplankton, and phytoplankton.

STUDY BREAK

1. What is the difference between gross primary productivity and net primary productivity?
2. What environmental factors influence rates of primary productivity in terrestrial and aquatic ecosystems?
3. Why is energy lost from an ecosystem at every transfer from one trophic level to the trophic level above it?
4. How can the presence of a top predator influence the interactions of organisms at lower trophic levels and an ecosystem's productivity?

51.2 Nutrient Cycling in Ecosystems

The availability of nutrients is as important to ecosystem function as the input of energy. Photosynthesis—the conversion of solar energy into chemical energy—requires carbon, hydrogen, and oxygen, which producers acquire from water and air. Producers also need nitrogen, phosphorus, and other minerals (see Table 33.1). A deficiency in any of these minerals can reduce primary productivity.

Earth is essentially a closed system with respect to matter. Thus, unlike energy, for which there is a constant cosmic input, virtually all the nutrients that will ever be available for biological systems are already present. Nutrient ions or molecules constantly circulate between the abiotic environment and living organisms in what ecologists describe as **biogeochemical cycles**. And unlike energy, which flows through ecosystems and is gradually lost as heat, matter is conserved in biogeochemical cycles. Although there may be local shortages of specific nutrients, Earth's overall supplies of these chemical elements are never depleted.

Ecologists Describe Nutrient Cycling with a Generalized Compartment Model

Nutrients take various forms as they pass through biogeochemical cycles. Some materials, such as carbon, nitrogen, and oxygen, form gases, which move through global *atmospheric cycles*. Geological processes move other materials, such as phosphorus, through local *sedimentary cycles*, carrying them between dry land and the seafloor. Rocks, soil, water, and air are the reservoirs where mineral nutrients accumulate, sometimes for many years.

Ecologists use a **generalized compartment model** to describe nutrient cycling (Figure 51.11). Two criteria divide ecosystems into four compartments where nutrients accumulate. First, nutrient molecules and ions are described as either *available* or *unavailable*, depending upon whether or not they can be assimilated by organisms. Second, nutrients are present either in *organic* material, the living or dead tissues of organisms, or in *inorganic* material, such as rocks and soil. For example, minerals in dead leaves on the forest floor are in the available-organic compartment because they are in the remains of organisms that can be eaten by detritivores. But calcium ions in limestone rocks are in the unavailable-inorganic compartment because they exist in a nonbiological form that producers cannot assimilate.

Nutrients move rapidly within and between the available compartments. Living organisms are in the available-organic compartment, and whenever heterotrophs consume food, they recycle nutrients within that reservoir (indicated by the oval arrow in the upper left of Figure 51.11). Producers acquire nutrients

from the air, soil, and water of the available-inorganic compartment. Consumers also acquire nutrients from the available-inorganic compartment when they drink water or absorb mineral ions through the body surface. Several processes routinely transfer nutrients from organisms to the available-inorganic compartment. As one example, respiration releases carbon dioxide, moving both carbon and oxygen from the available-organic compartment to the available-inorganic compartment.

By contrast, the movement of materials into and out of the unavailable compartments is generally slow. Sedimentation, a long-term geological process, converts ions and particles of the available-inorganic compartment into rocks of the unavailable-inorganic compartment. Materials are gradually returned to the available-inorganic compartment when rocks are uplifted and eroded or weathered. Similarly, over millions of years, the remains of organisms in the available-organic compartment were converted into coal, oil, and peat of the unavailable-organic compartment.

Except for the input of solar energy, we have described energy flow and nutrient cycling as though ecosystems were closed systems. In fact, most ecosystems exchange energy and nutrients with neighboring ecosystems. For example, rainfall carries nutrients into a forest ecosystem, and runoff carries nutrients from a forest into a lake or river. Ecologists have mapped the biogeochemical cycles of important elements, often by

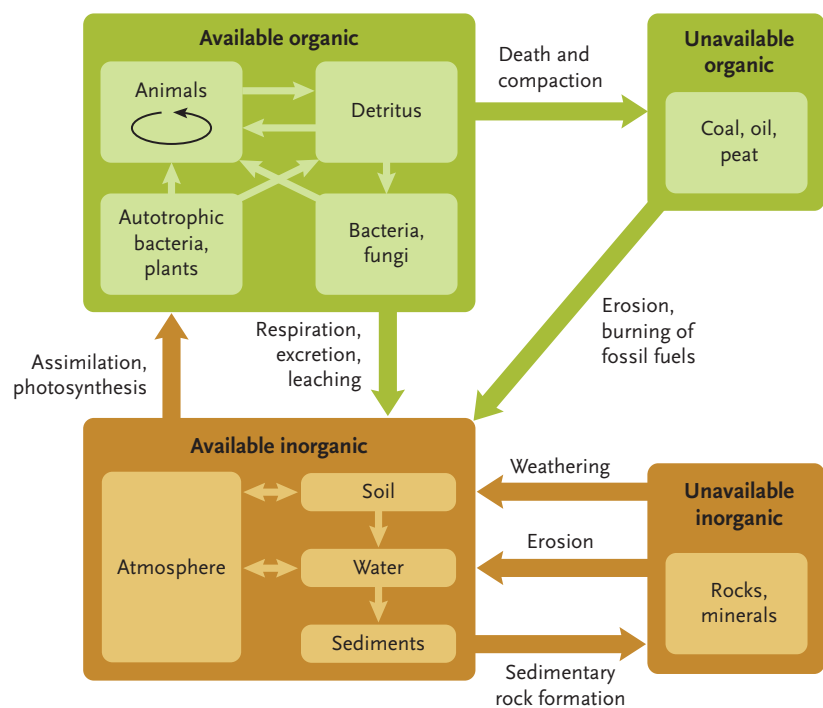


Figure 51.11 A generalized compartment model of nutrient cycling. Nutrients cycle through four major compartments within ecosystems. Processes that move nutrients from one compartment to another are indicated on the arrows. The oval arrow in the upper left of the figure represents animal predation on other animals.

using radioactively labeled molecules that they can follow in the environment. As you study the details of the four biogeochemical cycles described below, try to understand them in terms of the generalized compartment model of nutrient cycling.

The Hydrologic Cycle Recirculates All the Water on Earth

Although it is not a mineral nutrient, water is the universal intracellular solvent for biochemical reactions. Nevertheless, only a fraction of 1% of Earth's total water is present in biological systems at any time.

The cycling of water, called the **hydrologic cycle**, is global, with water molecules moving from the ocean into the atmosphere, to the land, through freshwater ecosystems, and back to the ocean (**Figure 51.12**). Solar energy causes water to evaporate from oceans, lakes, rivers, soil, and living organisms, entering the atmosphere as a vapor and remaining aloft as a gas, as droplets in clouds, or as ice crystals. It falls as precipitation, mostly in the form of rain and snow. When precipitation falls on land, water flows across the surface or percolates to great depth in the soil, eventually reentering the ocean reservoir through the flow of streams and rivers.

The hydrologic cycle maintains its global balance because the total amount of water that enters the atmosphere is equal to the amount that falls as precipitation. Most water that enters the atmosphere evaporates from the ocean, which represents the largest reservoir on the planet. A much smaller fraction evaporates from terrestrial ecosystems, and most of that results from transpiration in green plants.

The constant recirculation provides fresh water to terrestrial organisms and maintains freshwater ecosystems such as lakes and rivers. Water also serves as a transport medium that moves nutrients within and between ecosystems, as demonstrated in a series of classic experiments in the Hubbard Brook Experimental Forest, described in *Focus on Basic Research*.

The Carbon Cycle Includes a Large Atmospheric Reservoir

Carbon atoms provide the backbone of most biological molecules, and carbon compounds store the energy captured by photosynthesis (see Section 9.1). Carbon enters food webs when producers convert atmospheric carbon dioxide (CO_2) into carbohydrates. Heterotrophs acquire carbon by eating other organisms or detritus.

a. The water cycle

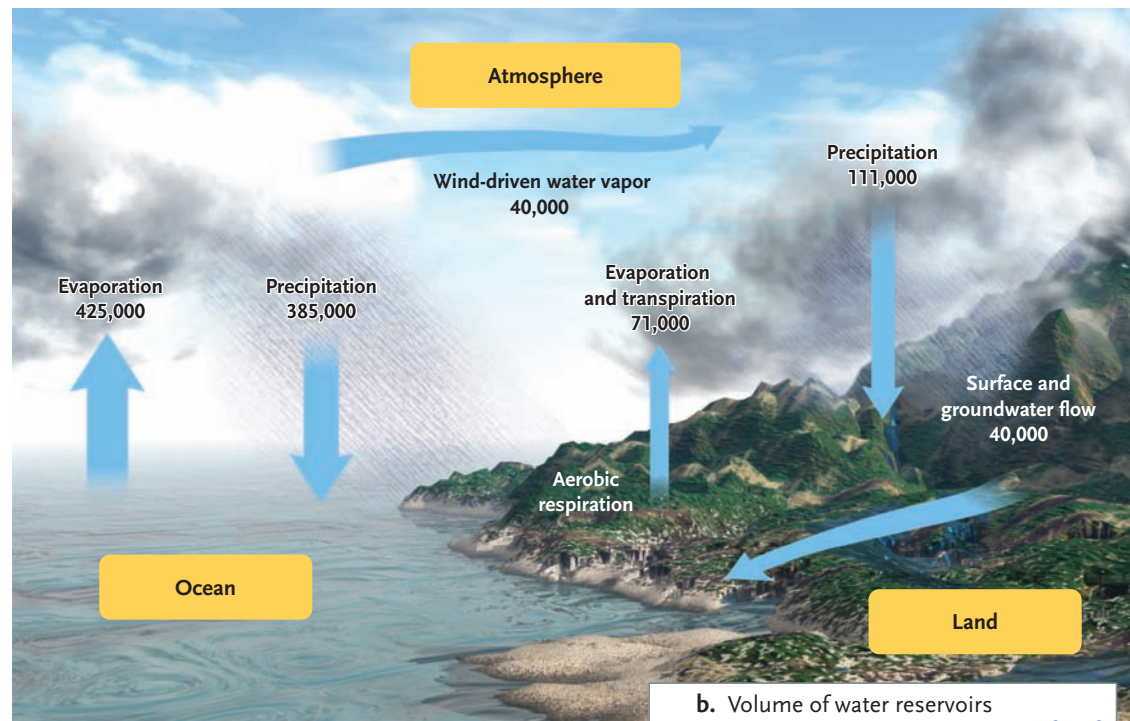


Figure 51.12

The hydrologic cycle. Water cycles through marine, atmospheric, and terrestrial reservoirs. **(a)** Data on the arrows list the amount of water (in km^3/yr) moved among reservoirs by various processes. **(b)** The oceans are by far the largest of the six major reservoirs of water on Earth.

b. Volume of water reservoirs	
Water reservoirs	Volume (10^3 km^3)
Oceans	1,370,000
Polar ice, glaciers	29,000
Groundwater	4,000
Lakes, rivers	230
Soil moisture	67
Atmosphere (water vapor)	14

FOCUS ON RESEARCH

Basic Research: Studies of the Hubbard Brook Watershed

Because water always flows downhill, local topography affects the movement of dissolved nutrients in terrestrial ecosystems. A **watershed** is an area of land from which precipitation drains into a stream or river system. Thus, each watershed represents a part of an ecosystem from which nutrients exit through a single outlet, much the way a bathtub empties through a single drain. When several streams join to form a river, the watershed drained by the river encompasses all of the smaller watersheds drained by the streams. For example, the Mississippi River watershed covers roughly one-third of the United States, and it includes watersheds drained by the Illinois, Missouri, and Tennessee Rivers as well as many other watersheds drained by smaller streams and rivers.

Because watersheds are relatively self-contained units, they are ideal for large-scale field experiments about nutrient flow in ecosystems. Herbert Bormann of Yale University and Gene Likens of Cornell University have conducted a classic experiment on this topic since the 1960s. Bormann and Likens manipulated small watersheds of temperate deciduous forest in the Hubbard Brook Experimental Forest in the White Mountain National Forest of New Hampshire. They measured precipitation and nutrient input into the watersheds, the uptake of nutrients by vegetation, and the amount of nutrients leaving the watershed via streamflow. Nutrients exported in streamflow were monitored in water samples collected from V-shaped concrete weirs built into bedrock below the streams that drained the watersheds (**Figure a**). Impermeable bedrock underlies the soil, preventing water from leaving the system by deep seepage.

After collecting several years of baseline data on six undisturbed watersheds, the researchers cut all the trees in one small watershed in 1965 and 1966. They also applied herbicides to prevent regrowth. After establishing

this experimental treatment, they monitored the output of nutrients in streams that drained experimental and control watersheds. They attributed differences in nutrient export between undisturbed watersheds (controls) and the clear-cut watershed (experimental treatment) to the effects of deforestation.

Bormann and Likens determined that vegetation absorbed substantial water and conserved nutrients in undisturbed watersheds. Plants used about 40% of the precipitation for transpiration. The rest contributed to runoff and groundwater. Control watersheds lost only about 8–10 kg of calcium per hectare each year, an amount that was replaced by the erosion of bedrock and input from rain. Moreover, control watersheds actually accumulated about 2 kg of nitrogen per hectare per year and slightly smaller amounts of potassium.

By contrast, the experimentally deforested watershed experienced a 40% annual increase in runoff. During a 4-month period in the summer, runoff increased 300%. Some mineral losses were similarly large. The net loss of calcium was 10 times higher than in the control watersheds (**Figure b**) and the loss of potassium 21 times higher. Phosphorus losses did not increase;



Figure a
Weir used to measure the volume and nutrient content of water leaving a watershed by streamflow.

this mineral was apparently retained by the soil. However, the loss of nitrogen was an astronomical 120 kg per hectare per year. So much nitrogen entered the stream draining the experimental watershed that the stream became choked with algae and cyanobacteria. Thus, the results of the Hubbard Brook experiment suggest that deforestation increases flooding and decreases the fertility of ecosystems.

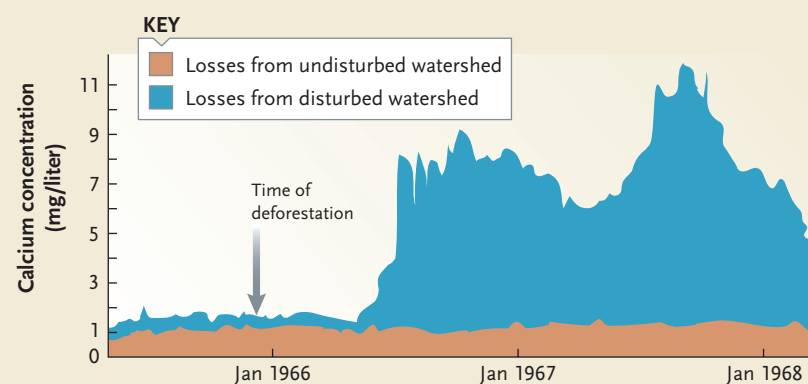


Figure b
Calcium losses from a deforested watershed were much greater than those from controls. The arrow indicates the time of deforestation in early winter. Mineral losses did not increase until after the ground thawed the following spring; increased runoff also caused large water losses from the watershed.

a. Amount of carbon in major reservoirs	
Carbon reservoirs	Mass (10^{15} g)
Sediments and rocks	77,000,000
Ocean (dissolved forms)	39,700
Soil	1,500
Atmosphere	750
Biomass on land	715

b. Annual global carbon movement between reservoirs	
Direction of movement	Mass (10^{15} g)
From atmosphere to plants (carbon fixation)	120
From atmosphere to ocean	107
To atmosphere from ocean	105
To atmosphere from plants	60
To atmosphere from soil	60
To atmosphere from burning fossil fuel	5
To atmosphere from burning plants	2
To ocean from runoff	0.4
Burial in ocean sediments	0.1

c. The global carbon cycle

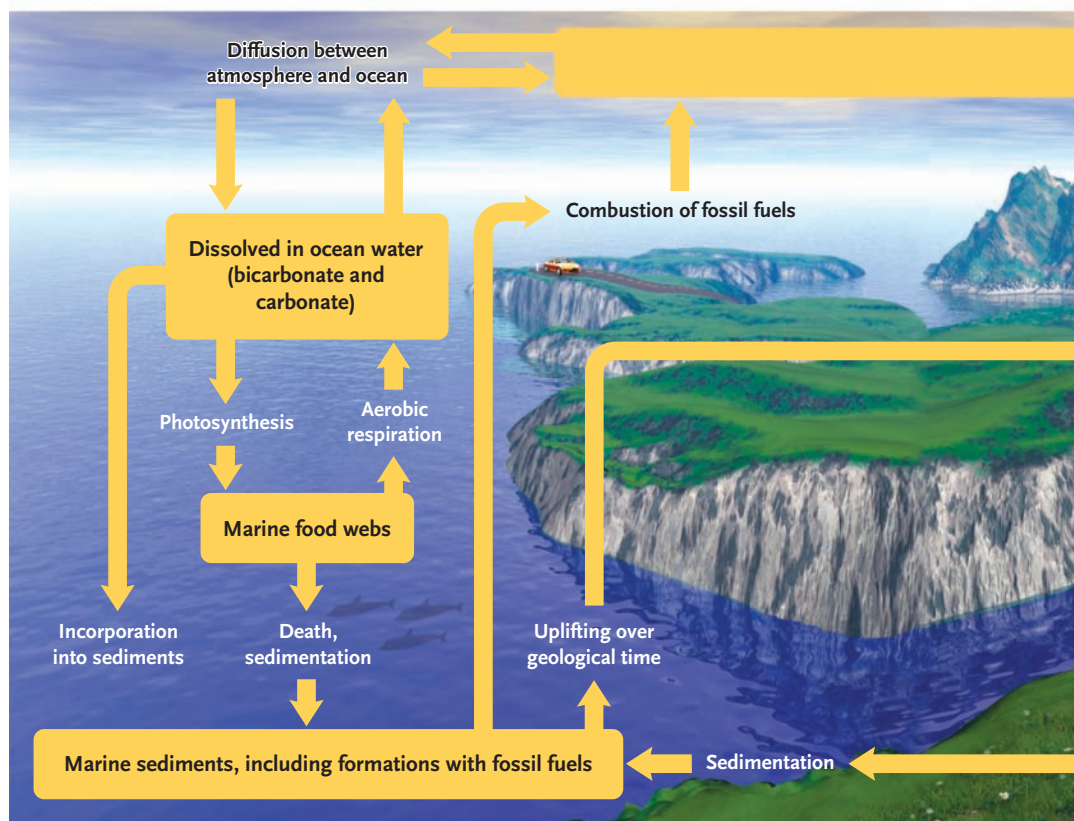


Figure 51.13

The carbon cycle. Marine and terrestrial components of the global carbon cycle are linked through an atmospheric reservoir of carbon dioxide. (a) By far, the largest amount of Earth's carbon is found in sediments and rocks. (b) Earth's atmosphere mediates most movements of carbon. (c) In this illustration of the carbon cycle, boxes identify major reservoirs, and labels on the arrows identify the processes that cause carbon to move between reservoirs.

Although carbon moves somewhat independently in the sea and on land, a common atmospheric pool of CO_2 creates a global carbon cycle (Figure 51.13).

The largest reservoir of carbon is sedimentary rock, such as limestone or marble. Rocks are in the unavailable-inorganic compartment, and they exchange carbon with living organisms at an exceedingly slow pace. Most available carbon is present as dissolved bicarbonate ions (HCO_3^-) in the ocean. Soil, the atmosphere, and plant biomass form other significant, but much smaller, reservoirs of available carbon. Atmospheric carbon is mostly in the form of molecular CO_2 , a product of aerobic respiration. Volcanic eruptions also release CO_2 into the atmosphere.

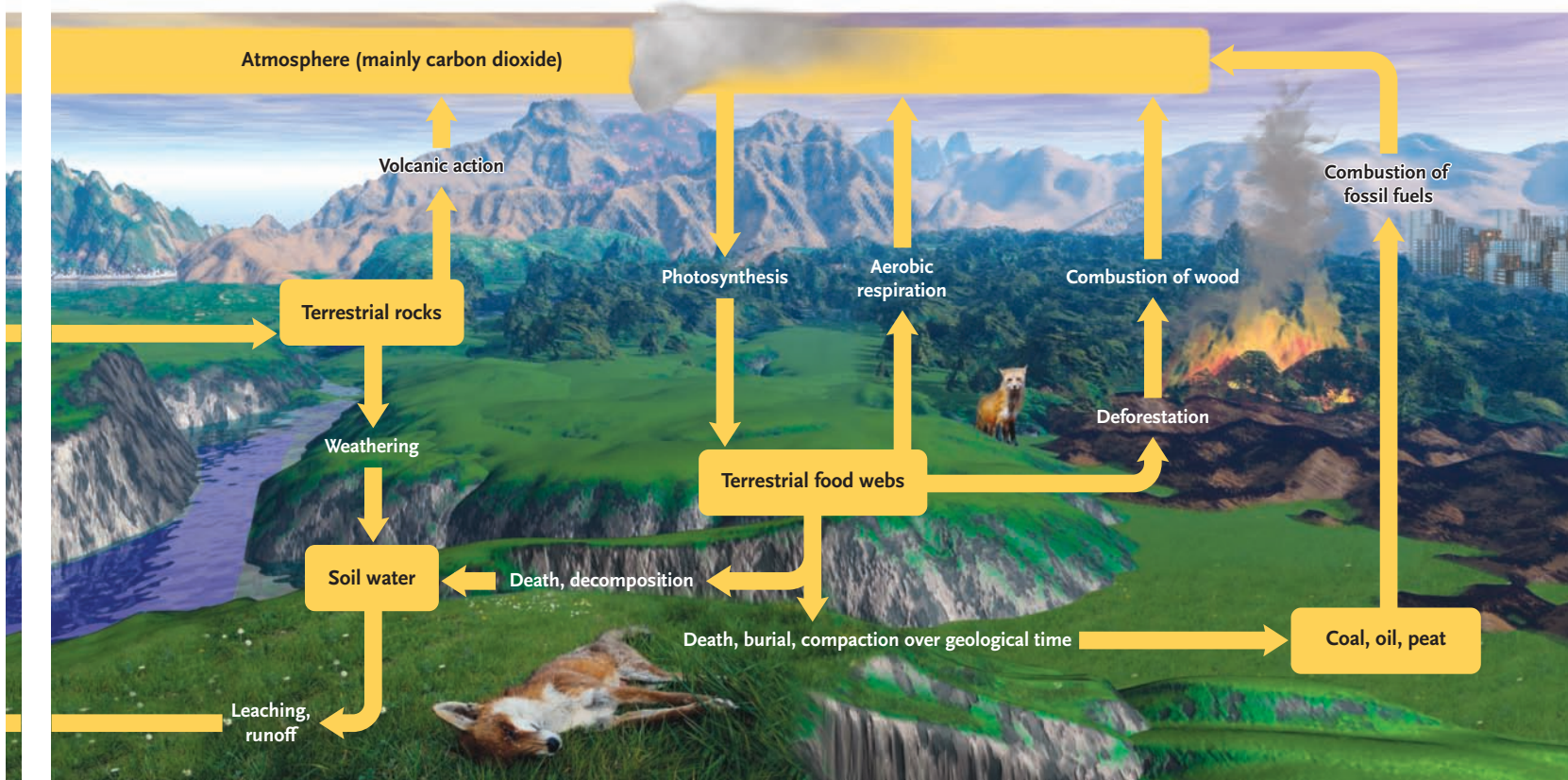
Sometimes carbon atoms leave the organic compartments for long periods of time. Some organisms in marine food webs build shells and other hard parts by incorporating dissolved carbon into calcium carbonate (CaCO_3) and other insoluble salts. When shelled organisms die, they sink to the bottom and are buried in sediments. The insoluble carbon that accumulates as rock in deep sediments may remain buried for millions of years before tectonic uplifting brings it to the surface,

where erosion and weathering dissolve sedimentary rocks and return carbon to an available form.

Carbon atoms were also transferred to the unavailable-organic compartment when soft-bodied organisms were buried in habitats where low oxygen concentration prevented decomposition. Under suitable geological conditions, these carbon-rich tissues were slowly converted to gas, petroleum, or coal, which humans now use as fossil fuels. Human activities, especially the burning of fossil fuels, are transferring carbon into the atmosphere at a high rate. The resulting change in the worldwide distribution of carbon is having profound consequences for Earth's atmosphere and climate, including a general warming of the climate and a rise in sea level, as described in *Focus on Applied Research*.

The Nitrogen Cycle Depends upon the Activity of Diverse Microorganisms

All organisms require nitrogen to construct nucleic acids, proteins, and other biological molecules. Earth's atmosphere had a high nitrogen concentration long



before life originated. Today, a global **nitrogen cycle** moves this element between the huge atmospheric pool of gaseous molecular nitrogen (N_2) and several much smaller pools of nitrogen-containing compounds in soils, marine and freshwater ecosystems, and living organisms (**Figure 51.14**).

Nitrogen Cycling within Ecosystems. Molecular nitrogen is abundant in the atmosphere, but triple covalent bonds bind its two atoms so tightly that most organisms cannot use it. However, three biochemical processes—nitrogen fixation, ammonification, and nitrification (**Table 51.2**)—convert nitrogen into nitrogen compounds that primary producers can incorporate into biological molecules such as proteins and nucleic acids. Secondary consumers obtain their nitrogen by consuming primary producers, thereby initiating the movement of nitrogen through the food webs of an ecosystem.

In **nitrogen fixation** (see Section 33.3), molecular nitrogen (N_2) is converted into ammonia (NH_3) and ammonium ions (NH_4^+). Certain bacteria, including *Azotobacter* and *Rhizobium*, which collect molecular nitrogen from the air between soil particles, are the major nitrogen fixers in terrestrial ecosystems. The cyanobacteria partners in some lichens (see Section 28.3) also fix molecular nitrogen. Other cyanobacteria, such as *Anabaena* and *Nostoc*, are important nitrogen fixers in

aquatic ecosystems; the water fern (genus *Azolla*) plays that role in rice paddies. Collectively, these organisms fix an astounding 200 million metric tons of nitrogen each year; nitrogen fixation can also result from lightning and volcanic action. Plants and other primary producers assimilate and use this nitrogen in the biosynthesis of amino acids, proteins, and nucleic acids, which then circulate through food webs.

Some plants, including legumes (such as beans and clover), alders (*Alnus* species), and some members of the rose family (Rosaceae), are mutualists with nitrogen-fixing bacteria. These plants acquire nitrogen from soils much more readily than plants that lack such mutualists. Although these plants have the competitive edge in nitrogen-poor soil, nonmutualistic species often displace them in nitrogen-rich soil.

In addition to nitrogen fixation, several other biochemical processes make large quantities of nitrogen available to producers. **Ammonification** of detritus by bacteria and fungi converts organic nitrogen into ammonia (NH_3), which dissolves into ammonium ions (NH_4^+) that plants can assimilate; some ammonia escapes into the atmosphere as a gas. **Nitrification** by certain bacteria produces nitrites (NO_2^-) that are then converted by other bacteria to usable nitrates (NO_3^-). All of these compounds are water-soluble, and water rapidly leaches them from soil into streams, lakes, and oceans.



FOCUS ON RESEARCH

Applied Research: Disruption of the Carbon Cycle

Concentrations of gases in the lower atmosphere have a profound effect on global temperature, which in turn has enormous impact on global climate. Molecules of carbon dioxide (CO_2), water, ozone, methane, nitrous oxide, and other compounds collectively act like a pane of glass in a greenhouse (hence the term *greenhouse gases*). They allow the short wavelengths of visible light to reach Earth's surface; but they impede the escape of longer, infrared wavelengths back into space, trapping much of that energy as heat. In short, greenhouse gases foster the accumulation of heat in the lower atmosphere, a warming action known as the **greenhouse effect**, which prevents Earth from being a cold and lifeless planet.

Since the late 1950s, scientists have measured atmospheric concentrations of CO_2 and other greenhouse gases at remote sampling sites, which are free of local contamination and reflect the average concentrations of these gases in the atmosphere. Results indicate that concentrations of greenhouse gases have increased steadily for as long as they have been monitored.

The graph for atmospheric CO_2 concentration (**Figure a**) has a regular zigzag pattern that follows the annual cycle of plant growth in the northern hemisphere. Photosynthesis withdraws so much CO_2 from the atmospheric available-inorganic pool during the northern hemisphere summer that

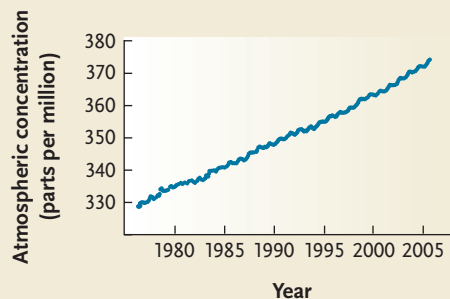


Figure a

Increases in atmospheric concentration of carbon dioxide, mid-1970s through 2004. The data were collected at a remote monitoring station in Australia (Cape Grim, Tasmania) and compiled by scientists at the Commonwealth Scientific and Industrial Research Organization, an agency of the Australian government.

its concentration falls. The concentration is higher during the northern hemisphere winter, when aerobic respiration continues, returning carbon to the atmospheric available-inorganic pool, and photosynthesis slows. The zigs and the zags in the data for CO_2 represent seasonal highs and lows, but the midpoint of the annual peaks and troughs has increased steadily for 40 years. Many scientists interpret these data as evidence of a rapid buildup of atmospheric CO_2 , which represents a shift in the distribution of carbon in the major reservoirs on Earth. The best estimates suggest that CO_2 concentration has increased by 35% in the last 150 years and by more than 10% in the last 30 years.

What has caused the increase in the atmospheric concentration of CO_2 ? Burning of fossil fuels and wood is the largest contributor, because CO_2 is a combustion product of this process. Today, humans burn more wood and fossil fuels than ever before. Vast tracts of tropical forests are being cleared and burned (see Section 53.2). To make matters worse, deforestation reduces the world's biomass of plants, which assimilate CO_2 and help maintain the carbon cycle as it existed before human activities disrupted it.

Why is an increase in the atmospheric CO_2 concentration so alarming? Recent research suggests that plants with C_3 metabolism will respond to increased CO_2 concentrations with increased growth rates, but that C_4 plants will not (review Section 9.4 on C_3 and C_4 plants). Thus, rising atmospheric levels of CO_2 will probably alter the relative abundances of many plant species, changing the composition and dynamics of their communities.

Simulation models by scientists who study the global climate suggest that increasing concentrations of any greenhouse gas may also intensify the greenhouse effect, contributing to a trend of global warming. Should we be alarmed about the prospect of a warmer planet? Some models predict that the mean temperature of the lower atmosphere will rise by 4°C ,

enough to increase ocean surface temperatures. Water expands when heated, and global sea level could rise as much as 0.6 m just from this expansion. In addition, atmospheric temperature is rising fastest near the poles. Thus, global warming may also foster melting of glaciers and the Antarctic ice sheet, which might raise sea level much more, inundating low coastal regions. Waterfronts in Vancouver, Los Angeles, San Diego, Galveston, New Orleans, Miami, New York, and Boston could be submerged. So might agricultural lands in India, China, and Bangladesh, where much of the world's rice is grown. Moreover, global warming could disturb regional patterns of precipitation and temperature. Areas that now produce much of the world's grains, including parts of Canada and the United States, would become arid scrub or deserts, and the now-forested areas to their north would become dry grasslands.

Many scientists believe that atmospheric levels of greenhouse gases will continue to increase at least until the middle of the twenty-first century and that global temperature may rise by several degrees. At the Earth Summit in 1992, leaders of the industrialized countries agreed to try to stabilize CO_2 emissions by the end of the twentieth century. We have already missed that target, and some countries, including the United States, which is the largest producer of greenhouse gases, have now abandoned that goal as too costly. Stabilizing emissions at current levels will not reverse the damage already done, nor will it stop the trend toward global warming. Many scientists agree that we should begin preparing for the consequences of global warming now. For example, we might increase reforestation efforts because a large tract of forest can withdraw significant amounts of CO_2 from the atmosphere. We might also step up genetic engineering studies to develop heat-resistant and drought-resistant crop plants, which may provide crucial food reserves in regions of climate change.

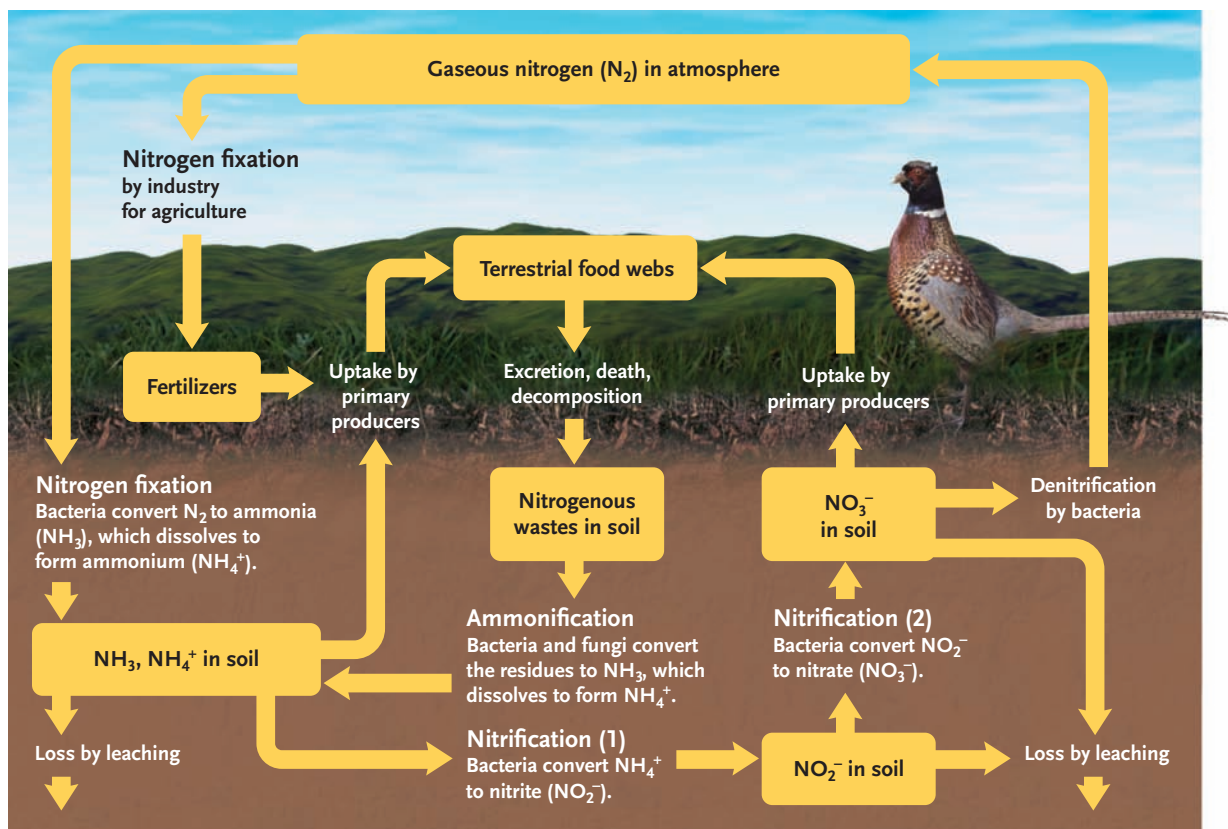


Figure 51.14

The nitrogen cycle in terrestrial ecosystems. Nitrogen cycles through terrestrial ecosystems when unavailable molecular nitrogen is made available through the action of nitrogen-fixing bacteria. Other bacteria recycle nitrogen within the available organic compartment through ammonification and two types of nitrification, converting organic wastes into ammonium ions and nitrates. Denitrification converts nitrate to molecular nitrogen, which returns to the atmosphere. Runoff carries various nitrogen compounds from terrestrial ecosystems into oceans, where it is recycled in marine food webs.

Under conditions of low oxygen availability, **denitrification** by still other bacteria converts nitrites or nitrates into nitrous oxide (N_2O) and then into molecular nitrogen (N_2), which enters the atmosphere, completing the cycle. This action can deplete supplies of soil nitrogen in waterlogged or otherwise poorly aer-

ated environments, such as bogs and swamps. In an interesting twist on the usual predator-prey relationships, several species of flowering plants that live in nitrogen-poor soils, such as Venus' fly trap (*Dionaea muscipula*), capture and digest small insects as their primary nitrogen source.

Table 51.2 Biochemical Processes That Influence Nitrogen Cycling in Ecosystems

Process	Organisms Responsible	Products	Outcome
Nitrogen fixation	Bacteria: <i>Rhizobium</i> , <i>Azotobacter</i> , <i>Frankia</i> Cyanobacteria: <i>Anabaena</i> , <i>Nostoc</i>	Ammonia (NH_3), ammonium ions (NH_4^+)	Assimilated by primary producers
Ammonification of organic detritus	Soil bacteria and fungi	Ammonia (NH_3), ammonium ions (NH_4^+)	Assimilated by primary producers
Nitrification			
(1) Oxidation of NH_3	Bacteria: <i>Nitrosomonas</i> , <i>Nitrococcus</i>	Nitrite (NO_2^-)	Used by nitrifying bacteria
(2) Oxidation of NO_2^-	Bacteria: <i>Nitrobacter</i>	Nitrate (NO_3^-)	Assimilated by primary producers
Denitrification of NO_3^-	Soil bacteria	Nitrous oxide (N_2O), molecular nitrogen (N_2)	Released to atmosphere

Human Disruption of the Nitrogen Cycle. Human activities are altering the nitrogen cycle, primarily through the application of nitrogen-containing fertilizers. Of all nutrients required for primary production, nitrogen is often the least abundant. Agriculture routinely depletes soil nitrogen: with each harvest, nitrogen is removed from fields through the harvesting of plants that have accumulated nitrogen. Soil erosion and leaching remove more. Traditionally, farmers rotated their crops, alternately planting legumes and other crops in the same fields. In combination with other soil-conservation practices, crop rotation stabilized soils and kept them productive, sometimes for thousands of years.

Until 50 years ago, nearly all the nitrogen in living systems was made available by nitrogen-fixing microorganisms. Today, however, agriculture relies on the application of synthetic fertilizers. Some yields have quadrupled over the past 50 years. But 50 years is just an instant in the history of agriculture, and such high yields may not be sustainable for very long. Moreover, the production of synthetic fertilizers is expensive. It uses fossil fuels both as a raw material and as an energy source, so that fertilizer becomes increasingly costly as supplies of fossil fuels dwindle. Furthermore, rain and runoff leach excess fertilizer from agricultural fields and carry it into aquatic ecosystems. Like the phosphorus in Lake Erie, nitrogen has become a

major pollutant of freshwater ecosystems, artificially enriching the waters and allowing producers to expand their populations.

The Phosphorus Cycle Includes a Large Sedimentary Reservoir

Phosphorus compounds lack a gaseous phase, and this element moves between terrestrial and marine ecosystems in a sedimentary cycle (**Figure 51.15**). Earth's crust is the main reservoir of phosphorus, as it is for other minerals such as calcium and potassium that undergo sedimentary cycles.

Phosphorus is present in terrestrial rocks in the form of phosphates (PO_4^{3-}). In the **phosphorus cycle**, weathering and erosion carry phosphate ions from rocks to soil and into streams and rivers, which eventually transport them to the ocean. Once there, some phosphorus enters marine food webs, but most of it precipitates out of solution and accumulates for millions of years as insoluble deposits, mainly on continental shelves. When parts of the seafloor are uplifted and exposed, weathering releases the phosphates.

Plants absorb and assimilate dissolved phosphates directly, and phosphorus moves easily to higher trophic levels. All heterotrophs excrete some phosphorus as a waste product in urine and feces, which are decom-

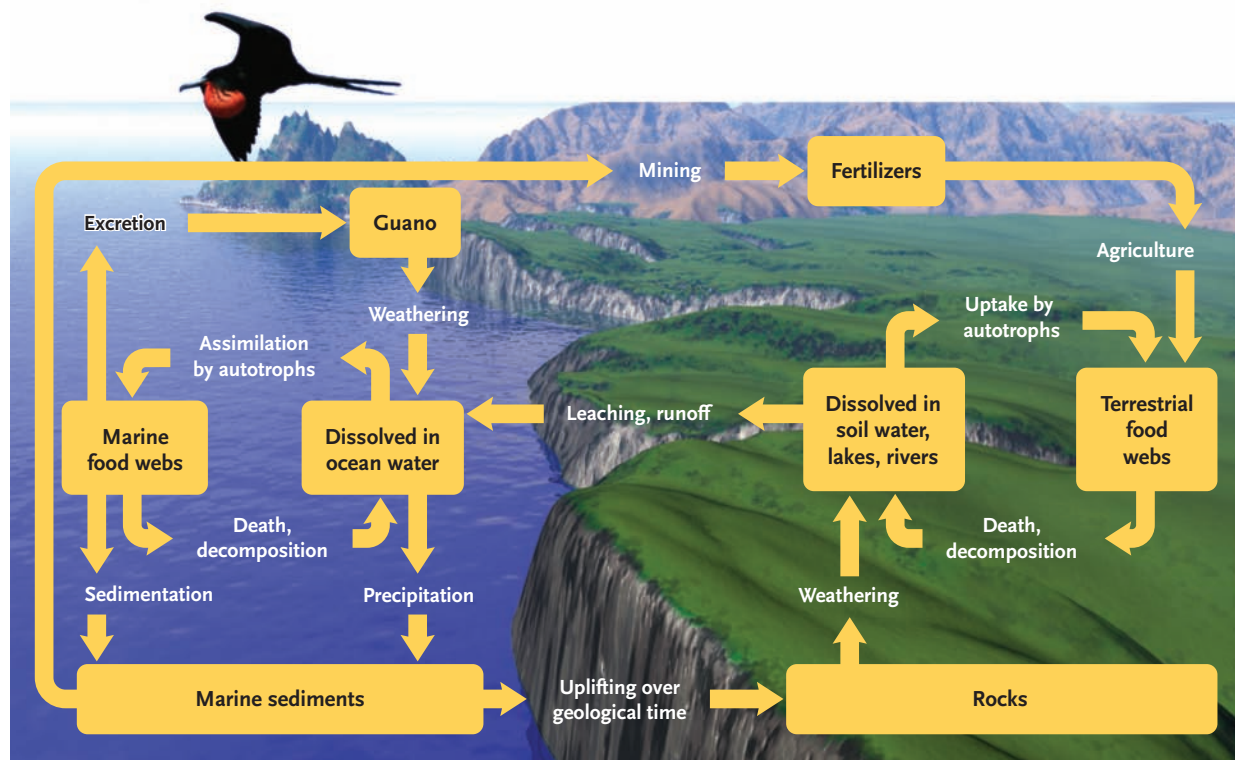


Figure 51.15

The phosphorus cycle. Phosphorus becomes available to biological systems when wind and rainfall dissolve phosphates in rocks and carry them into adjacent soil and freshwater ecosystems. Runoff carries dissolved phosphorus into marine ecosystems, where it precipitates out of solution and is incorporated into marine sediments.

posed, and producers readily absorb the phosphate ions that are released. Thus, phosphorus cycles rapidly *within* terrestrial communities.

Supplies of available phosphate are generally limited, however, and plants acquire it so efficiently that they reduce soil phosphate concentration to extremely low levels. Thus, like nitrogen, phosphorus is a common ingredient in agricultural fertilizers, and excess phosphates are pollutants of freshwater ecosystems. For many years, phosphate for fertilizers was obtained from *guano* (the droppings of seabirds that consume phosphorus-rich food), which was mined on small islands off the Pacific coast of South America. Most phosphate for fertilizer now comes from phosphate rock mined in Florida and other places with abundant marine deposits.

STUDY BREAK

1. In the generalized compartment model of biogeochemical cycling, how are the compartments where nutrients accumulate classified?
2. How does the global hydrologic cycle maintain its balance?
3. What process moves large quantities of carbon from an organic compartment to an inorganic compartment?
4. What microorganisms drive the global nitrogen cycle, and how do they do it?
5. What is Earth's main reservoir for phosphorus, and why is it recycled at such a slow rate from that reservoir?

51.3 Ecosystem Modeling

Ecologists Use Conceptual Models and Simulation Models to Understand Ecosystem Dynamics

To make predictions about how an ecosystem will respond to specific changes in physical factors, energy flow, or nutrient availability, ecologists turn to ecosystem modeling. Analyses of energy flow and nutrient cycling allow us to create a *conceptual model* of how ecosystems function (**Figure 51.16**). Energy that enters ecosystems is gradually dissipated as it flows through a food web. By contrast, nutrients are conserved and recycled among the system's living and nonliving components. This very general model does not include processes that carry nutrients and energy out of one ecosystem and into another.

Note that the conceptual model ignores the nuts-and-bolts details of exactly how specific ecosystems function. Although it is a useful tool, a conceptual

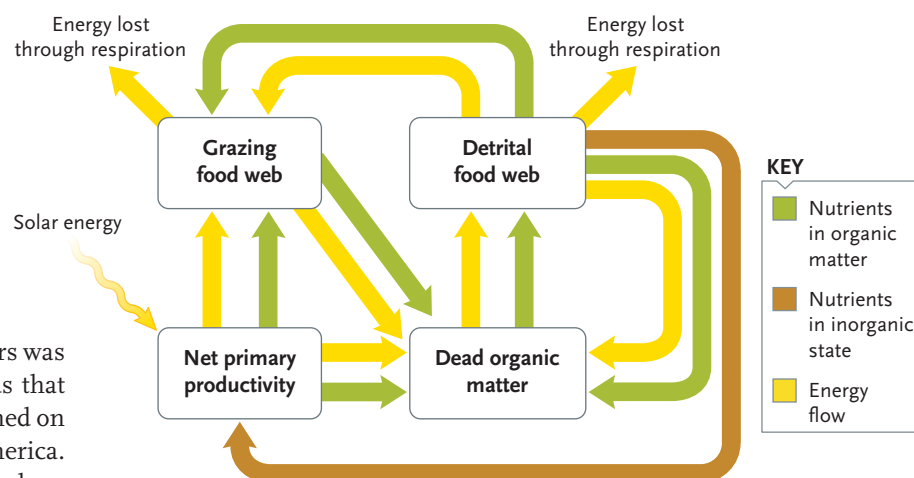


Figure 51.16

A conceptual ecosystem model. A simple conceptual model of an ecosystem illustrates how energy flows through the system and is lost from both detrital and grazing food webs. Nutrients are recycled and conserved.

model doesn't really help us predict what would happen, say, if we harvested 10 million tons of introduced salmon from Lake Erie every year. We could simply harvest the fishes and see what happens. But ecologists prefer less intrusive approaches to study the potential effects of disturbances.

One approach to predicting “what would happen if . . .” is **simulation modeling**. Using this method, researchers gather detailed information about a specific ecosystem. They then create a series of mathematical equations that define its most important relationships. For example, one set of equations might describe how nutrient availability limits productivity at various trophic levels. Another might relate population growth of zooplankton to the productivity of phytoplankton. Other equations would relate the population dynamics of primary carnivores to the availability of their food, and still others would describe how the densities of primary carnivores influence reproduction in populations at both lower and higher trophic levels. Thus, a complete simulation model is a set of interlocking equations that collectively predict how changes in one feature of an ecosystem might influence others.

Creating a simulation model is no easy task, because the relationships within every ecosystem are complex. First, you must identify the important species, estimate their population sizes, and measure the average energy and nutrient content of each. Next, you would describe the food webs in which they participate, measure the quantity of food each species consumes, and estimate the productivity of each population. And, for the sake of completeness, you would determine the ecosystem's energy and nutrient gains and losses caused by erosion, weathering, precipitation, and runoff. You would repeat these measurements seasonally to identify annual variation in these factors. Finally, you might repeat the measurements over several years to determine the effects of year-to-year variation in climate and chance events.

After collecting these data, you would write equations that quantify the relationships in the ecosystem,

including information about how temperature and other abiotic factors influence the ecology of each species. Having completed that job, you could begin to predict—possibly in great detail—the effects of harvesting 10 million or even 50 million tons of salmon annually from Lake Erie. Of course, you would have to refine the model whenever new data became available.

Some ecologists devote their professional lives to the study of ecosystem processes. The long-term initiative at the Hubbard Brook Forest provides a good example. As we attempt to understand larger and more complex ecosystems—and as we create larger and more complex environmental problems—modeling becomes an increasingly important tool. If a model is based on well-defined ecological relationships and good empirical data, it can allow us to make accurate predictions about ecosystem changes without the need for costly

and environmentally damaging experiments. But like all ideas in science, a model is only as good as its assumptions, and models must constantly be adjusted to incorporate new ideas and recently discovered facts.

In the next chapter we examine how interactions among ecosystems establish the global phenomena that characterize the biosphere.

STUDY BREAK

1. What are the advantages and disadvantages of relying on conceptual models that describe ecosystem function?
2. What data must ecologists collect before constructing a simulation model of an ecosystem?

UNANSWERED QUESTIONS

How does the carbon cycle of a forest respond to climate change and urbanization?

As you've read in this chapter, human influences on the environment can have dramatic unforeseen consequences for ecosystems, altering energy flow and nutrient cycling. Given the complexity of ecosystems—the myriad scales of influence and multiple interactions among the organisms, the physical environment, and climate change variables—the precise response of an ecosystem is difficult to predict, even with advanced ecosystem models. We do know with certainty, however, that the carbon, nitrogen, and water cycles of forested ecosystems in the northeastern United States are changing, and they are likely to continue to do so.

Carbon cycle research in forested ecosystems often entails building an ecosystem model from quantitative data on the various pools and fluxes of carbon in the ecosystem and how these change with time. Scientists then correlate these changes with the environmental conditions and derive a mechanistic understanding that they can use to make predictions about how the ecosystem will respond to future changes. In theory, *gross primary productivity* (GPP) should be predictable from a basic understanding of photosynthesis and a general description of the ambient environmental conditions. In practice, however, the complexity of canopy architecture and leaf positioning, the timing of recurring natural phenomena, and the effects of herbivory and leaf losses from abiotic factors all make accurate predictions more difficult. Furthermore, the problem is dynamic because age-related changes in stand structure, disturbance, invasion, drought, seasonality, and pests or pathogens all add spatial and temporal complexities. Scientists should be able to predict *net primary productivity* (NPP), a key parameter used by ecologists to classify the world's ecosystems, from measurements of the cellular respiration and the relative abundances of representative organisms from the ecosystem.

Quantifying GPP and NPP on a large spatial scale can be challenging, and discovering the underlying mechanisms that control ecosystem responses to changes in environmental conditions is difficult. For example, studies at Black Rock Forest, a deciduous-oak-dominated forest in New York State, revealed that temporal heterogeneity (seasonal variation

in leaf and stem respiration) and spatial heterogeneity (variations in canopy and hill slope position) are important factors that must be included in models of canopy respiration. Nevertheless, some simplifications may be possible. For example, while the basal rate of respiration is quite variable and subject to acclimation, it may be predictable from basic plant properties such as their nitrogen concentrations. Furthermore, the temperature coefficient of respiration is relatively constant, greatly simplifying the construction of an ecosystem model. To consider the impact of tree respiration on ecosystem form and function fully, my research team experimented with models that explicitly consider physiological linkages between photosynthesis and respiration, as mediated by leaf carbohydrate pools. We found that when we included direct linkages to carbon gain in the analysis, the model correctly predicted a large (23%) decrease in the estimated nighttime canopy respiration during the growing season. This result emphasizes the need for a process-based modeling approach when estimating forest productivity.

Our research at Black Rock Forest has also demonstrated that human activities in New York City (60 miles to the south) may be influencing tree growth in both urban and rural areas, with significant changes in seedling size, biomass allocation, herbivory, stomatal densities, nutrient concentrations, efficiency of water use, and rates of key physiological processes such as photosynthesis and respiration. Urbanization has a clear effect on the land area developed, but current research is showing that human activities in urban areas also influence forested ecosystems in the surrounding rural areas. Understanding how human activity, climate change, and forest ecosystems interact is crucial if we are to make prudent and sustainable development decisions, preserving the health of the ecosystems and the services they provide.



Kevin Griffin is an associate professor at Columbia University's Lamont-Doherty Earth Observatory. His research centers on processes in plant and ecosystem ecology, the goal of which is to increase our understanding of both the role of vegetation in the global carbon cycle and the interactions between the carbon cycle and Earth's climate system. To learn more about Dr. Griffin's research, go to <http://www.ldeo.columbia.edu/>.

Review

Go to **ThomsonNOW**™ at www.thomsonedu.com/login to access quizzing, animations, exercises, articles, and personalized homework help.

51.1 Energy Flow and Ecosystem Energetics

- Ecosystems include biological communities and the abiotic environmental factors with which they interact (Figure 51.1).
- Food webs define the pathways along which energy and nutrients move through the biological components of an ecosystem. Ecosystems include both grazing and detrital food webs, which are closely interconnected (Figure 51.2).
- Only a small portion of the solar energy that reaches Earth is converted into chemical energy through the process of photosynthesis.
- An ecosystem's gross primary productivity is the rate at which producers convert solar energy into chemical energy. Producers use some energy for respiration; some is converted to heat; and some remains in the ecosystem as net primary productivity.
- Primary productivity is measured in units of energy captured or biomass produced per unit area per unit time. Net primary productivity indexes the energy available to support heterotrophs. Ecosystems vary in productivity and in their contributions to Earth's total productivity (Figure 51.3, Table 51.1).
- On land, primary productivity is limited by the availability of sunlight, water, and nutrients; temperature; and how much photosynthetic tissue is present. In marine and aquatic ecosystems, primary productivity is limited when sunlight and nutrients are not available in the same place (Figures 51.4 and 51.5).
- Only a fraction of the energy at any trophic level is converted into biomass at higher trophic levels. Ecological efficiencies generally range from 5% to 20%. As energy passes through a food web, an average of 90% is lost at each transfer between trophic levels, limiting the number of trophic levels that a food web can support (Figure 51.6).
- Ecological pyramids portray the effects of energy losses. For terrestrial ecosystems, pyramids of energy, biomass, and numbers generally have broad bases and narrow tops (Figures 51.7–51.9).
- The food preferences of consumers can influence primary productivity through a trophic cascade (Figure 51.10).

[Animation: The role of organisms in an ecosystem](#)

[Animation: Food webs](#)

[Animation: Energy flow at Silver Springs](#)

51.2 Nutrient Cycling in Ecosystems

- Earth is a closed system with respect to matter.
- Nutrients circulate in biogeochemical cycles between living organisms and nonliving reservoirs. Nutrients accumulate in four

compartments, defined by whether the nutrients are available or unavailable and whether they are in organic or inorganic material (Figure 51.11). Nutrients move rapidly between available compartments. Exchange rates for the unavailable compartments are slow. Some biogeochemical cycles are atmospheric; others are sedimentary.

- Water circulates through the atmosphere, oceans, and terrestrial and freshwater ecosystems in a global hydrologic cycle. Water evaporates from the oceans and continents and falls as precipitation. Runoff and streamflow return excess precipitation from the land to the oceans (Figure 51.12).
- The carbon cycles in terrestrial and aquatic ecosystems are linked through an atmospheric pool of CO₂, which primary producers assimilate. Respiration returns carbon to the atmosphere as CO₂. Earth's largest reservoir of carbon is unavailable in sedimentary rock. Other large reservoirs include coal, oil, and peat as well as dissolved bicarbonate and carbonate ions in seawater (Figure 51.13).
- Nitrogen is cycled between living organisms and an atmospheric pool of nitrogen gas. Bacteria and cyanobacteria make nitrogen available to the food web through the processes of nitrogen fixation, ammonification, and nitrification. Denitrification converts nitrogen compounds to molecular nitrogen, which enters the atmosphere (Figure 51.14, Table 51.2). The use of synthetic fertilizers disrupts the nitrogen cycle.
- Phosphorus undergoes a sedimentary cycle. Weathering and erosion of rock make phosphorus available; it is leached from soil and carried to the ocean. Dissolved phosphates precipitate out of seawater, forming insoluble deposits, which are eventually uplifted by tectonic processes (Figure 51.15).

[Animation: Hydrologic cycle](#)

[Animation: Hubbard Brook experiment](#)

[Animation: Carbon cycle](#)

[Animation: Greenhouse effect](#)

[Animation: Greenhouse gases](#)

[Animation: Carbon dioxide and temperature](#)

[Animation: Nitrogen cycle](#)

[Animation: Phosphorus cycle](#)

51.3 Ecosystem Modeling

- Conceptual models describe energy flow and nutrient cycling in ecosystems (Figure 51.16).
- Simulation models are interlocking mathematical equations that define the relationships between populations and between populations and the physical environment. They allow users to predict the effects of changes in ecosystem structure and function.

Questions

Self-Test Questions

1. Which of the following events would move energy and material from a detrital food web into a grazing food web?
 - a. A beetle eats the leaves of a living plant.
 - b. An earthworm eats dead leaves on the forest floor.
 - c. A robin catches and eats an earthworm.
 - d. A crow eats a dead robin.
 - e. A bacterium decomposes the feces of an earthworm.
2. The total dry weight of plant material in a forest is a measure of the forest's:
 - a. gross primary productivity.
 - b. net primary productivity.
 - c. cellular respiration.

- d. standing crop biomass.
 - e. ecological efficiency.
3. Which of the following ecosystems has the highest rate of net primary productivity?
 - a. open ocean
 - b. temperate deciduous forest
 - c. tropical rain forest
 - d. desert and thornwoods
 - e. agricultural land
 4. Endothermic animals exhibit a lower ecological efficiency than ectothermic animals because:
 - a. endotherms are less successful hunters than ectotherms.
 - b. endotherms eat more plant material than ectotherms.
 - c. endotherms are larger than ectotherms.
 - d. endotherms produce fewer offspring than ectotherms.
 - e. endotherms use more of their energy to maintain body temperature than ectotherms.
 5. The amount of energy available at the highest trophic level in an ecosystem is determined by:
 - a. only the gross primary productivity of the ecosystem.
 - b. only the net primary productivity of the ecosystem.
 - c. the gross primary productivity and the standing crop biomass.
 - d. the net primary productivity and the ecological efficiencies of herbivores.
 - e. the net primary productivity and the ecological efficiencies at all lower trophic levels.
 6. Some freshwater and marine ecosystems exhibit an inverted pyramid of:
 - a. biomass.
 - b. energy.
 - c. numbers.
 - d. turnover.
 - e. ecological efficiency.
 7. Which process moves nutrients from the available-organic compartment to the available-inorganic compartment?
 - a. respiration
 - b. erosion
 - c. assimilation
 - d. sedimentation
 - e. photosynthesis
 8. Which of the following materials has a sedimentary cycle?
 - a. water
 - b. oxygen
 - c. nitrogen
 - d. phosphorus
 - e. carbon
 9. Which of the following statements is supported by the results of studies at the Hubbard Brook Experimental Forest?
 - a. Most of the energy captured by primary producers is lost before it reaches the highest trophic level in an ecosystem.
 - b. Deforested watersheds experience significantly less runoff than undisturbed watersheds.
 - c. Deforested watersheds lose more calcium and nitrogen in runoff than undisturbed watersheds.
 - d. Nutrients generally move through biogeochemical cycles very quickly.
 - e. Deforested watersheds generally receive more rainfall than undisturbed watersheds.
 10. Nitrogen fixation converts:
 - a. atmospheric molecular nitrogen to ammonia.
 - b. nitrates to nitrites.

- c. ammonia to molecular nitrogen.
- d. ammonia to nitrates.
- e. nitrites to nitrates.

Questions for Discussion

1. A lake near your home became overgrown with algae and pondweeds a few months after a new housing development was built nearby. What data would you collect to determine whether the housing development might be responsible for the changes in the lake?
2. Some politicians question whether recent increases in atmospheric temperature result from our release of greenhouse gases into the atmosphere. They argue that atmospheric temperature has fluctuated widely over Earth's history, and the changing temperature is just part of an historical trend. What information would allow you to refute or confirm their hypothesis? In addition, describe the pros and cons of reducing greenhouse gases as soon as possible versus taking a "wait and see" approach to this question.
3. If you could design the ideal farm animal—one that was grown as food for humans—from scratch, what characteristics would it have?
4. If you were growing a vegetable garden, identify the factors that might affect its primary productivity. How would you increase productivity? Identify some of the possible consequences of your gardening activities to nearby ecosystems.

Experimental Analysis

Design an experiment to test the hypothesis that the top predator in an aquatic ecosystem regulates the ecosystem's productivity. Establish as many experimental ponds as you wish, and imagine stocking them with organisms at different trophic levels. If the hypothesis is correct, describe the results you would expect to record from each of your experimental treatments.

Evolution Link

In the discussion of trophic cascades, we described how herbivorous zooplankton of different sizes eat phytoplankton of different sizes and how different types of predators preferentially feed on different sizes of zooplankton. Develop hypotheses about how these feeding preferences might establish different patterns of natural selection on the phytoplankton and zooplankton. How could you test your hypotheses?

How Would You Vote?

Emissions from motor vehicles are a major source of greenhouse gases. Many people buy large vehicles that use more fuel but are viewed as safer and more useful. Should such vehicles be taxed extra to discourage sales and offset their environmental costs? Can we expect the emergence of better fuels as well as more of the fuel-efficient, larger vehicles that are becoming available? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.