# 55

# Ecosystems and Restoration Ecology

▲ **Figure 55.1** **Why is this Antarctic ice blood red?**

**KEY CONCEPTS**

**55.1** Physical laws govern energy flow and chemical cycling in ecosystems

**55.2** Energy and other limiting factors control primary production in ecosystems

**55.3** Energy transfer between trophic levels is typically only 10% efficient

**55.4** Biological and geochemical processes cycle nutrients and water in ecosystems

**55.5** Restoration ecologists help return degraded ecosystems to a more natural state

**OVERVIEW**

## Cool Ecosystem

Three hundred meters below Taylor Glacier, in Antarctica, an unusual community of bacteria lives on sulfur- and iron-containing ions. These organisms thrive in harsh conditions, without light or oxygen and at a temperature of −10°C, so low that the water would freeze if it weren't three times as salty as the ocean. How has this community survived, isolated from Earth's surface for at least 1.5 million years? The bacteria are chemoautotrophs, which obtain energy by oxidizing sulfur taken up from their sulfate-rich environment (see Chapter 27). They use iron as a final electron acceptor in their reactions. When the water flows from the base of the glacier and comes into contact with air, the reduced iron in the water is oxidized and turns red before the water freezes. The distinctive color gives this area of the glacier its name—Blood Falls **(Figure 55.1)**.

Together, the bacterial community and surrounding environment make up an **ecosystem**, the sum of all the organisms living in a given area and the abiotic factors with which they interact. An ecosystem can encompass a vast area, such as a lake or forest, or a microcosm, such as the space under a fallen log or a desert spring **(Figure 55.2)**. As with populations and communities, the boundaries of ecosystems are not always discrete. Many ecologists view the entire biosphere as a global ecosystem, a composite of all the local ecosystems on Earth.

Regardless of an ecosystem's size, its dynamics involve two processes that cannot be fully described by population or community phenomena: energy flow and chemical cycling. Energy enters most ecosystems as sunlight. It is converted to chemical energy by autotrophs, passed to heterotrophs in the organic compounds of food, and dissipated as heat. Chemical elements, such as carbon and nitrogen, are cycled among abiotic and biotic components of the ecosystem. Photosynthetic and chemosynthetic organisms assimilate these elements in inorganic form from the air, soil, and water and incorporate them into their biomass, some of which is consumed by animals. The elements are returned in inorganic form to the environment by the metabolism of plants and animals and by organisms such as bacteria and fungi that break down organic wastes and dead organisms.

Both energy and matter are transformed in ecosystems through photosynthesis and feeding relationships. But unlike matter, energy cannot be recycled. An ecosystem must be powered by a continuous influx of energy from an external source—in most cases, the sun. Energy flows through ecosystems, whereas matter cycles within and through them.

Resources critical to human survival and welfare, ranging from the food we eat to the oxygen we breathe, are products of ecosystem processes. In this chapter, we will explore the dynamics of energy flow and chemical cycling, emphasizing the results of ecosystem experiments. One way to study ecosystem processes is to alter environmental factors, such as temperature or the abundance of nutrients, and study how ecosystems respond. We will also consider some of the impacts of human activities on energy flow and chemical cycling. Finally, we will explore the growing science of restoration ecology, which focuses on returning degraded ecosystems to a more natural state.

▲ **Figure 55.2 A desert spring ecosystem.**

CONCEPT 55.1

## Physical laws govern energy flow and chemical cycling in ecosystems

In Unit Two, you learned how cells transform energy and matter, subject to the laws of thermodynamics. Like cell biologists, ecosystem ecologists study the transformations of energy and matter within a system and measure the amounts of both that cross the system's boundaries. By grouping the species in a community into trophic levels of feeding relationships (see Chapter 54), we can follow the transformations of energy in an ecosystem and map the movements of chemical elements.

### Conservation of Energy

Because ecosystem ecologists study the interactions of organisms with the physical environment, many ecosystem approaches are based on laws of physics and chemistry. The first law of thermodynamics, which we discussed in Chapter 8, states that energy cannot be created or destroyed but only transferred or transformed. Thus, we can potentially account for the transfer of energy through an ecosystem from its input as solar radiation to its release as heat from organisms. Plants and other photosynthetic organisms convert solar energy to chemical energy, but the total amount of energy does not change: The amount of energy stored in organic molecules must equal the total solar energy intercepted by the plant, minus the amounts reflected and dissipated as heat. One area of ecosystem ecology involves computing energy budgets and tracing energy flow through ecosystems in order to understand the factors that control these energy transfers. Such transfers help determine how many organisms a habitat can support and the amount of food humans can harvest from a site.

One implication of the second law of thermodynamics, which states that every exchange of energy increases the entropy of the universe, is that energy conversions are inefficient; some energy is always lost as heat (see Chapter 8). We can measure the efficiency of ecological energy conversions just as we measure the efficiency of light bulbs and car engines. Energy flowing through ecosystems is ultimately dissipated into space as heat, so if the sun were not continuously providing energy to Earth, most ecosystems would vanish.

### Conservation of Mass

Matter, like energy, cannot be created or destroyed. This **law of conservation of mass** is as important for ecosystems as the laws of thermodynamics are. Because mass is conserved, we can determine how much of a chemical element cycles within an ecosystem or is gained or lost by that ecosystem over time.

Unlike energy, chemical elements are continually recycled within ecosystems. A carbon atom in $CO_2$ is released from the soil by a decomposer, taken up by a grass through photosynthesis, consumed by a bison or other grazer, and returned to the soil in the bison's waste. The measurement and analysis of chemical cycling within ecosystems and in the biosphere as a whole are an important aspect of ecosystem ecology.

Although elements are not significantly gained or lost on a global scale, they can be gained by or lost from a particular ecosystem. In a forest ecosystem, most mineral nutrients—the essential elements that plants obtain from soil—enter as dust or as solutes dissolved in rainwater or leached from rocks in the ground. Nitrogen is also supplied through the biological process of nitrogen fixation (see Figure 37.10). In terms of losses, some elements return to the atmosphere as gases, and others are carried out of the ecosystem by moving water. Like organisms, ecosystems are open systems, absorbing energy and mass and releasing heat and waste products.

In nature, most gains and losses to ecosystems are small compared to the amounts recycled within them. Still, the balance between inputs and outputs determines whether an ecosystem is a source or a sink for a given element. If a mineral nutrient's outputs exceed its inputs, it will eventually limit production in that system. Human activities often change the balance of inputs and outputs considerably, as we will see later in this chapter and in Chapter 56.

### Energy, Mass, and Trophic Levels

As you read in Chapter 54, ecologists assign species to trophic levels based on their main source of nutrition and energy. The trophic level that ultimately supports all others consists of autotrophs, also called the **primary producers** of the ecosystem. Most autotrophs are photosynthetic organisms that use light energy to synthesize sugars and other organic compounds, which they then use as fuel for cellular respiration and as building material for growth. Plants, algae, and photosynthetic prokaryotes are the biosphere's main autotrophs, although chemosynthetic prokaryotes are the primary producers in ecosystems such as deep-sea hydrothermal vents (see Figure 52.16) and places deep under the ground or ice (see Figure 55.1).

Organisms in trophic levels above the primary producers are heterotrophs, which depend directly or indirectly on the outputs of primary producers for their source of energy. Herbivores, which eat plants and other primary producers, are **primary consumers**. Carnivores that eat herbivores are **secondary consumers**, and carnivores that eat other carnivores are **tertiary consumers**.

Another group of heterotrophs is the **detritivores,** or **decomposers**, terms we use synonymously in this text to refer to consumers that get their energy from detritus. **Detritus** is nonliving organic material, such as the remains of dead organisms, feces, fallen leaves, and wood. Many detritivores are in turn eaten by secondary and tertiary consumers. Two important groups of detritivores are prokaryotes and fungi **(Figure 55.3)**. These organisms secrete enzymes that digest organic material; they then absorb the breakdown products, linking the consumers and primary producers in an ecosystem. In a forest, for instance, birds eat earthworms that have been feeding on leaf litter and its associated prokaryotes and fungi.

▲ **Figure 55.3 Fungi decomposing a dead tree.**

Detritivores also play a critical role in recycling chemical elements back to primary producers. Detritivores convert organic matter from all trophic levels to inorganic compounds usable by primary producers, closing the loop of an ecosystem's chemical cycling. Producers can then recycle these elements into organic compounds. If decomposition stopped, life would cease as detritus piled up and the supply of ingredients needed to synthesize new organic matter was exhausted. **Figure 55.4** summarizes the trophic relationships in an ecosystem.

### CONCEPT CHECK 55.1

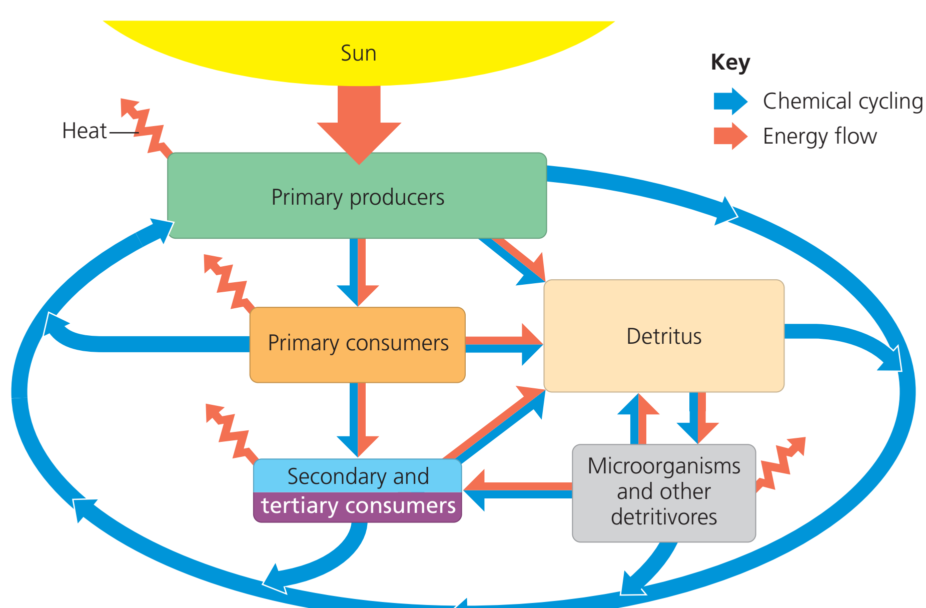
1. Why is the transfer of energy in an ecosystem referred to as energy flow, not energy cycling?
2. **WHAT IF?** You are studying nitrogen cycling on the Serengeti Plain in Africa. During your experiment, a herd of migrating wildebeests grazes through your study plot. What would you need to know to measure their effect on nitrogen balance in the plot?
3. **MAKE CONNECTIONS** Review the discussion of the second law of thermodynamics in Concept 8.1 (p. 144). How does this physical law explain why an ecosystem's energy supply must be continually replenished?

For suggested answers, see Appendix A.

## CONCEPT 55.2

## Energy and other limiting factors control primary production in ecosystems

As you read in Chapter 1, the theme of energy transfer underlies all biological interactions. In most ecosystems, the amount of light energy converted to chemical energy—in the form of organic compounds—by autotrophs during a given time period is the ecosystem's **primary production**. These photosynthetic products are the starting point for most studies of ecosystem metabolism and energy flow. In ecosystems where the primary producers are chemoautotrophs, as described in the Overview on page 1218, the initial energy input is chemical,




▶ **Figure 55.4 An overview of energy and nutrient dynamics in an ecosystem.** Energy enters, flows through, and exits an ecosystem, whereas chemical nutrients cycle primarily within it. In this generalized scheme, energy (dark orange arrows) enters from the sun as radiation, moves as chemical energy transfers through the food web, and exits as heat radiated into space. Most transfers of nutrients (blue arrows) through the trophic levels lead eventually to detritus; the nutrients then cycle back to the primary producers.

and the initial products are the organic compounds synthesized by the microorganisms.

## Ecosystem Energy Budgets

Since most primary producers use light energy to synthesize energy-rich organic molecules, consumers acquire their organic fuels secondhand (or even third- or fourthhand) through food webs such as that in Figure 54.15. Therefore, the total amount of photosynthetic production sets the spending limit for the entire ecosystem's energy budget.

### *The Global Energy Budget*

Each day, Earth's atmosphere is bombarded by about $10^{22}$ joules of solar radiation (1 J = 0.239 cal). This is enough energy to supply the demands of the entire human population for approximately 25 years at 2009 energy consumption levels. As described in Chapter 52, the intensity of the solar energy striking Earth varies with latitude, with the tropics receiving the greatest input. Most incoming solar radiation is absorbed, scattered, or reflected by clouds and dust in the atmosphere. The amount of solar radiation that ultimately reaches Earth's surface limits the possible photosynthetic output of ecosystems.

Only a small fraction of the sunlight that reaches Earth's surface is actually used in photosynthesis. Much of the radiation strikes materials that don't photosynthesize, such as ice and soil. Of the radiation that does reach photosynthetic organisms, only certain wavelengths are absorbed by photosynthetic pigments (see Figure 10.9); the rest is transmitted, reflected, or lost as heat. As a result, only about 1% of the visible light that strikes photosynthetic organisms is converted to chemical energy. Nevertheless, Earth's primary producers create about 150 billion metric tons ($1.50 \times 10^{14}$ kg) of organic material each year.

### *Gross and Net Production*

Total primary production in an ecosystem is known as that ecosystem's **gross primary production (GPP)**—the amount of energy from light (or chemicals, in chemoautotrophic systems) converted to the chemical energy of organic molecules per unit time. Not all of this production is stored as organic material in the primary producers because they use some of the molecules as fuel in their own cellular respiration. **Net primary production (NPP)** is equal to gross primary production minus the energy used by the primary producers for their "autotrophic respiration" ($R_a$):

$$NPP = GPP - R_a$$

On average, NPP is about one-half of GPP. To ecologists, net primary production is the key measurement because it represents the storage of chemical energy that will be available to consumers in the ecosystem.

Net primary production can be expressed as energy per unit area per unit time (J/m$^2$·yr) or as biomass (mass of vegetation) added per unit area per unit time (g/m$^2$·yr). (Note that biomass is usually expressed in terms of the dry mass of organic material.) An ecosystem's NPP should not be confused with the total biomass of photosynthetic autotrophs present, a measure called the *standing crop*. Net primary production is the amount of *new* biomass added in a given period of time. Although a forest has a large standing crop, its net primary production may actually be less than that of some grasslands; grasslands do not accumulate as much biomass as forests because animals consume the plants rapidly and because grasses and herbs decompose more quickly than trees do.

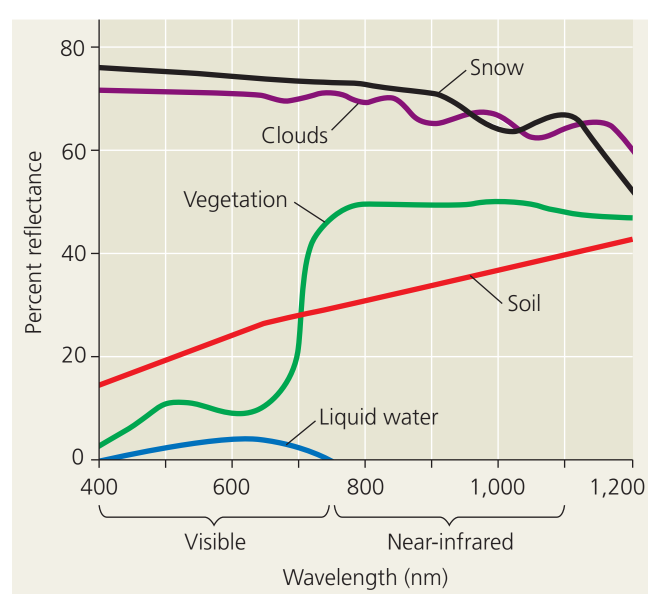
Satellites provide a powerful tool for studying global patterns of primary production **(Figure 55.5)**. Images produced from satellite data show that different ecosystems vary considerably in their net primary production. Tropical rain forests are among the most productive terrestrial ecosystems and contribute a large portion of the planet's net primary production. Estuaries and coral reefs also have very high net primary production, but their contribution to the global total is small because these ecosystems cover only about one-tenth the area covered by tropical rain forests. In contrast, while

▼ **Figure 55.5** **RESEARCH METHOD**

**Determining Primary Production with Satellites**

**APPLICATION** Because chlorophyll captures visible light (see Figure 10.9), photosynthetic organisms absorb more light at visible wavelengths (about 380–750 nm) than at near-infrared wavelengths (750–1,100 nm). Scientists use this difference in absorption to estimate the rate of photosynthesis in different regions of the globe using satellites.

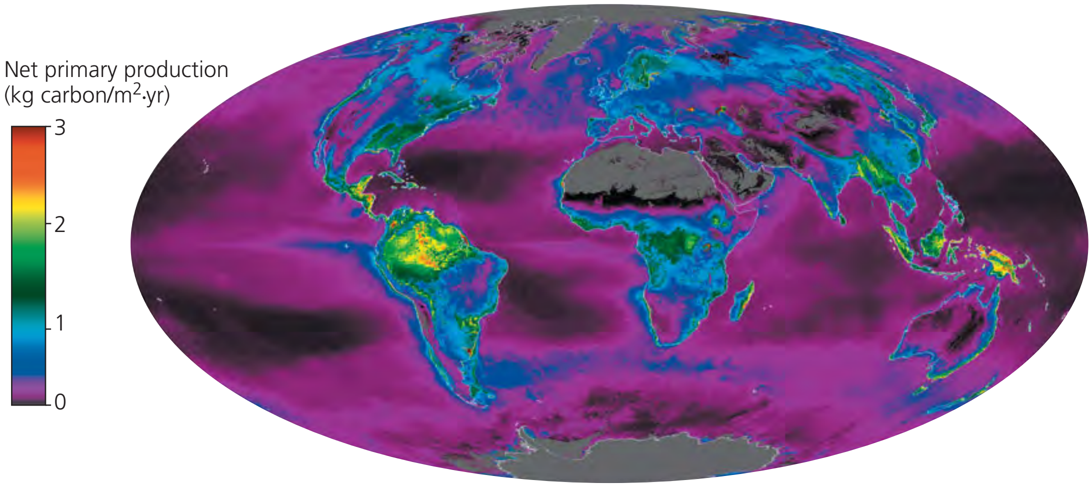
**TECHNIQUE** Most satellites determine what they "see" by comparing the ratios of wavelengths reflected back to them. Vegetation reflects much more near-infrared radiation than visible radiation, producing a reflectance pattern very different from that of snow, clouds, soil, and liquid water.




**RESULTS** Scientists use the satellite data to help produce maps of primary production like the one in Figure 55.6.

▶ **Figure 55.6 Global net primary production.** The map is based on data collected by satellites, such as amount of sunlight absorbed by vegetation. Note that tropical land areas have the highest rates of production (yellow and red on the map).

? *Does this global map accurately reflect the importance of some highly productive habitats, such as wetlands, coral reefs, and coastal zones? Explain.*




the oceans are relatively unproductive **(Figure 55.6)**, their vast size means that together they contribute as much global net primary production as terrestrial systems do.

Whereas net primary production can be stated as the amount of new biomass added in a given period of time, **net ecosystem production (NEP)** is a measure of the *total biomass accumulation* during that time. Net ecosystem production is defined as gross primary production minus the total respiration of all organisms in the system ($R_T$)—not just primary producers, as for the calculation of NPP, but decomposers and other heterotrophs as well:

$$NEP = GPP - R_T$$

NEP is useful to ecologists because its value determines whether an ecosystem is gaining or losing carbon over time. A forest may have a positive NPP but still lose carbon if heterotrophs release it as $CO_2$ more quickly than primary producers incorporate it into organic compounds.

The most common way to estimate NEP is to measure the net flux (flow) of $CO_2$ or $O_2$ entering or leaving the ecosystem. If more $CO_2$ enters than leaves, the system is storing carbon. Because $O_2$ release is directly coupled to photosynthesis and respiration (see Figure 9.2), a system that is giving off $O_2$ is also storing carbon. On land, ecologists typically measure only the net flux of $CO_2$ from ecosystems; detecting small changes in $O_2$ in a large atmospheric $O_2$ pool is difficult. In the oceans, researchers use both approaches. New marine research using $O_2$ measurements has revealed surprisingly high NEP in some of the nutrient-poor waters that cover much of the open ocean **(Figure 55.7)**. This result is causing biologists to reevaluate regional and global estimates of ocean productivity and to examine the constraints to marine productivity.

What limits production in ecosystems? To ask this question another way, what factors could we change to increase production for a given ecosystem? We'll address this question first for aquatic ecosystems.

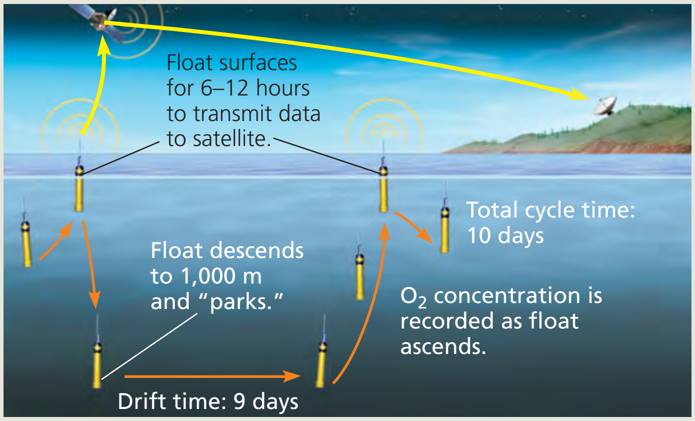
▼ **Figure 55.7**

# IMPACT

## Ocean Production Revealed

Net ecosystem production (NEP) is difficult to measure in the low-nutrient regions that make up most of Earth's oceans. Rates of primary production and total respiration are low, and the difference between them—NEP—is even lower. In principle, scientists could estimate NEP by measuring the amounts of $O_2$ present in the water. Until recently, though, they lacked a means of obtaining the necessary data. But in 2008, researchers were able to measure NEP in parts of the Pacific Ocean using high-resolution oxygen sensors deployed on floats. The floats were "parked" about 1,000 m deep and, after drifting for 9 days, automatically rose to the surface, measuring $O_2$ concentrations as they went. Overall, the researchers observed an average NEP of 25 g C/m$^2$ over the three-year study.

**WHY IT MATTERS** Phytoplankton communities in extensive regions of the oceans are more productive than scientists believed even a few years ago. Biologists have a new understanding of Earth's carbon cycle and what limits marine productivity around the world.




**FURTHER READING** S. C. Riser and K. S. Johnson, Net production of oxygen in the subtropical ocean, *Nature* 451:323–325(2008).

**MAKE CONNECTIONS** Review the discussion in Concept 28.7 (p. 597) of the role of photosynthetic protists as producers in aquatic ecosystems. What factors in addition to light availability are likely to limit primary production in the oceans?

## Primary Production in Aquatic Ecosystems

In aquatic (marine and freshwater) ecosystems, both light and nutrients are important in controlling primary production.

### *Light Limitation*

Because solar radiation drives photosynthesis, you would expect light to be a key variable in controlling primary production in oceans. Indeed, the depth of light penetration affects primary production throughout the photic zone of an ocean or lake (see Figure 52.13). About half of the solar radiation is absorbed in the first 15 m of water. Even in "clear" water, only 5–10% of the radiation may reach a depth of 75 m.

If light were the main variable limiting primary production in the ocean, we would expect production to increase along a gradient from the poles toward the equator, which receives the greatest intensity of light. However, you can see in Figure 55.6 that there is no such gradient. Another factor must strongly influence primary production in the ocean.

### *Nutrient Limitation*

More than light, nutrients limit primary production in most oceans and lakes. A **limiting nutrient** is the element that must be added for production to increase. The nutrient most often limiting marine production is either nitrogen or phosphorus. Concentrations of these nutrients are typically low in the photic zone because they are rapidly taken up by phytoplankton and because detritus tends to sink.

As detailed in **Figure 55.8**, nutrient enrichment experiments confirmed that nitrogen was limiting phytoplankton growth off the south shore of Long Island, New York. One practical application of this work is in preventing algal "blooms" caused by excess nitrogen runoff that fertilizes the phytoplankton. Prior to this research, phosphate contamination was thought to cause many such blooms in the ocean, but eliminating phosphates alone may not help unless nitrogen pollution is also controlled.

The macronutrients nitrogen and phosphorus are not the only nutrients that limit aquatic production. Several large areas of the ocean have low phytoplankton densities despite relatively high nitrogen concentrations. The Sargasso Sea, a subtropical region of the Atlantic Ocean, has some of the clearest water in the world because of its low phytoplankton density. Nutrient enrichment experiments have revealed that the availability of the micronutrient iron limits primary production there **(Table 55.1)**. Windblown dust from land supplies most of the iron to the oceans but is relatively scarce in this and certain other regions compared to the oceans as a whole.

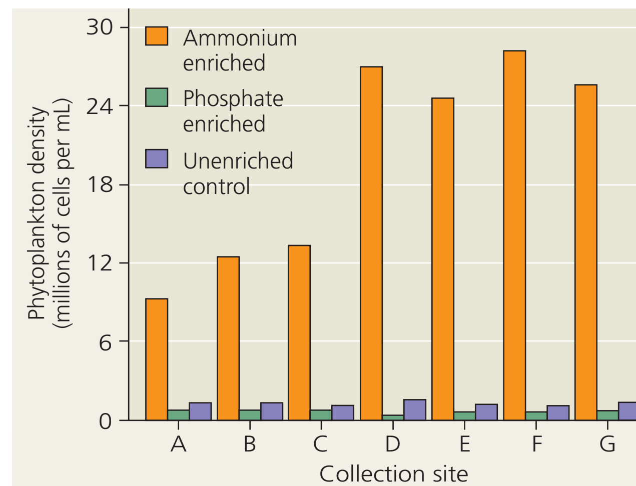
The finding that iron limits production in some oceanic ecosystems encouraged marine ecologists to carry out recent large-scale ocean fertilization experiments in the Pacific Ocean—research that might also shed light on ocean fertilization as a tool to remove the greenhouse gas carbon dioxide from the atmosphere. In one study, researchers spread low concentrations of dissolved iron over 72 km$^2$ of ocean and

▼ **Figure 55.8** INQUIRY

**Which nutrient limits phytoplankton production along the coast of Long Island?**

**EXPERIMENT** Pollution from duck farms concentrated near Moriches Bay adds both nitrogen and phosphorus to the coastal water off Long Island, New York. To determine which nutrient limits phytoplankton growth in this area, John Ryther and William Dunstan, of the Woods Hole Oceanographic Institution, cultured the phytoplankton *Nannochloris atomus* with water collected from several sites, identified as A–G. They added either ammonium ($NH_4^+$) or phosphate ($PO_4^{3-}$) to some of the cultures.

**RESULTS** The addition of ammonium caused heavy phytoplankton growth in the cultures, but the addition of phosphate did not.




**CONCLUSION** Since adding phosphorus, which was already in rich supply, did not increase *Nannochloris* growth, whereas adding nitrogen increased phytoplankton density dramatically, the researchers concluded that nitrogen is the nutrient that limits phytoplankton growth in this ecosystem.

**SOURCE** J. H. Ryther and W. M. Dunstan, Nitrogen, phosphorus, and eutrophication in the coastal marine environment, *Science* 171:1008–1013 (1971).

**WHAT IF?** How would you expect the results of this experiment to change if new duck farms substantially increased the amount of pollution in the water? Explain your reasoning.

**Table 55.1 Nutrient Enrichment Experiment for Sargasso Sea Samples**

| Nutrients Added to Experimental Culture | Relative Uptake of $^{14}C$ by Cultures* |
|---|---|
| None (controls) | 1.00 |
| Nitrogen (N) + phosphorus (P) only | 1.10 |
| N + P + metals (excluding iron) | 1.08 |
| N + P + metals (including iron) | 12.90 |
| N + P + iron | 12.00 |

*$^{14}C$ uptake by cultures measures primary production.

Source: D. W. Menzel and J. H. Ryther, Nutrients limiting the production of phytoplankton in the Sargasso Sea, with special reference to iron, *Deep Sea Research* 7:276–281 (1961).

then measured the change in phytoplankton density over a seven-day period. A massive phytoplankton bloom occurred, as indicated by increased chlorophyll concentration in the water. Adding iron had stimulated growth of cyanobacteria that fix additional atmospheric nitrogen (see Chapter 27), and the extra nitrogen stimulated proliferation of phytoplankton.

As a tool to remove carbon dioxide from air, iron fertilization remains controversial. There is little evidence from iron fertilization experiments that organic carbon sinks into deep-ocean water and sediments. Instead, it tends to be recycled by secondary consumers and decomposers in shallow waters, returning eventually to the atmosphere. Ecologists also have concerns about the overall effects of large-scale fertilization on marine communities. Iron fertilization is therefore unlikely to be widely applied anytime soon.

Areas of upwelling, where deep, nutrient-rich waters circulate to the ocean surface, have exceptionally high primary production. This fact supports the hypothesis that nutrient availability determines marine primary production. Because upwelling stimulates growth of the phytoplankton that form the base of marine food webs, upwelling areas typically host highly productive, diverse ecosystems and are prime fishing locations. The largest areas of upwelling occur in the Southern Ocean (also called the Antarctic Ocean), along the equator, and in the coastal waters off Peru, California, and parts of western Africa.

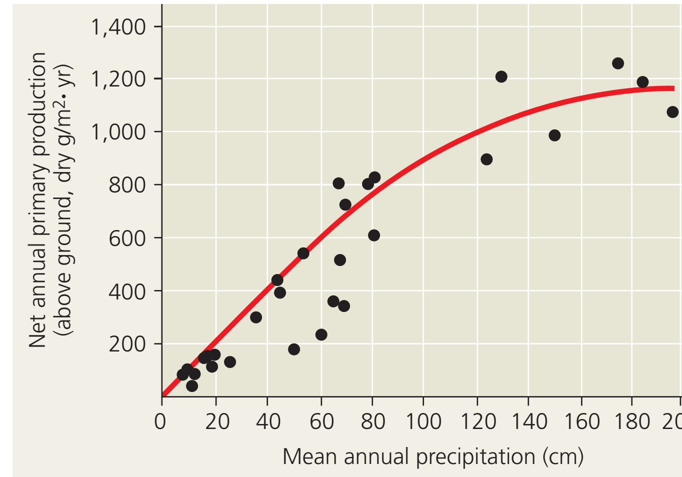
In freshwater lakes, nutrient limitation is also common. During the 1970s, scientists showed that sewage and fertilizer runoff from farms and lawns added large amounts of nutrients to lakes. Cyanobacteria and algae grow rapidly in response to these added nutrients, ultimately reducing the oxygen concentration and clarity of the water. The ecological impacts of this process, known as **eutrophication** (from the Greek *eutrophos*, well nourished), include the loss of many fish species from the lakes (see Figure 52.16).

Controlling eutrophication requires knowing which polluting nutrient is responsible. While nitrogen rarely limits primary production in lakes, a series of whole-lake experiments showed that phosphorus availability limited cyanobacterial growth. This and other ecological research led to the use of phosphate-free detergents and other important water quality reforms.

## Primary Production in Terrestrial Ecosystems

At regional and global scales, temperature and moisture are the main factors controlling primary production in terrestrial ecosystems. Tropical rain forests, with their warm, wet conditions that promote plant growth, are the most productive of all terrestrial ecosystems (see Figure 55.6). In contrast, low-productivity systems are generally hot and dry, like many deserts, or cold and dry, like arctic tundra. Between these extremes lie the temperate forest and grassland ecosystems, which have moderate climates and intermediate productivity.

The climate variables of moisture and temperature are very useful for predicting NPP in terrestrial ecosystems. Primary production is greater in wetter ecosystems, as shown for the plot of NPP and annual precipitation in **Figure 55.9**. Along with mean annual precipitation, a second useful predictor is *actual evapotranspiration*, the total amount of water transpired by plants and evaporated from a landscape. Evapotranspiration increases with the temperature and amount of solar energy available to drive evaporation and transpiration.




▲ **Figure 55.9 A global relationship between net primary production and mean annual precipitation for terrestrial ecosystems.**

### *Nutrient Limitations and Adaptations That Reduce Them*

**EVOLUTION** Mineral nutrients in the soil also limit primary production in terrestrial ecosystems. As in aquatic systems, nitrogen and phosphorus are the nutrients that most commonly limit terrestrial production. Globally, nitrogen limits plant growth most. Phosphorus limitations are common in older soils where phosphate molecules have been leached away by water, such as in many tropical ecosystems. Phosphorus availability is also often low in soils of deserts and other ecosystems with a basic pH, where some phosphorus precipitates and becomes unavailable to plants. Adding a nonlimiting nutrient, even one that is scarce, will not stimulate production. Conversely, adding more of the limiting nutrient will increase production until some other nutrient becomes limiting.

Various adaptations have evolved in plants that can increase their uptake of limiting nutrients. One important mutualism that you have already studied is the symbiosis between plant roots and nitrogen-fixing bacteria. Another important mutualism is mycorrhizal association between plant roots and fungi that supply phosphorus and other limiting elements to plants (see Chapters 36 and 37). Plants have root hairs and other anatomical features that increase the area of the soil that roots contact (see Chapter 35). Also, many plants release enzymes and other substances into the soil that increase the availability of limiting nutrients; examples include phosphatases, enzymes that cleave a phosphate group from larger molecules, and chelating agents that make micronutrients such as iron more soluble in the soil.

Studies relating nutrients to terrestrial primary production have practical applications in agriculture. Farmers maximize their crop yields by using fertilizers with the right balance of nutrients for the local soil and type of crop. This knowledge of limiting nutrients helps us feed billions of people on Earth today.

**CONCEPT CHECK 55.2**

1. Why is only a small portion of the solar energy that strikes Earth's atmosphere stored by primary producers?
2. How can ecologists experimentally determine the factor that limits primary production in an ecosystem?
3. **MAKE CONNECTIONS** Concept 10.3 (pp. 198–199) describes the Calvin cycle of photosynthesis. Explain how nitrogen and phosphorus, the nutrients that most often limit primary production, are necessary for the Calvin cycle to function.

For suggested answers, see Appendix A.

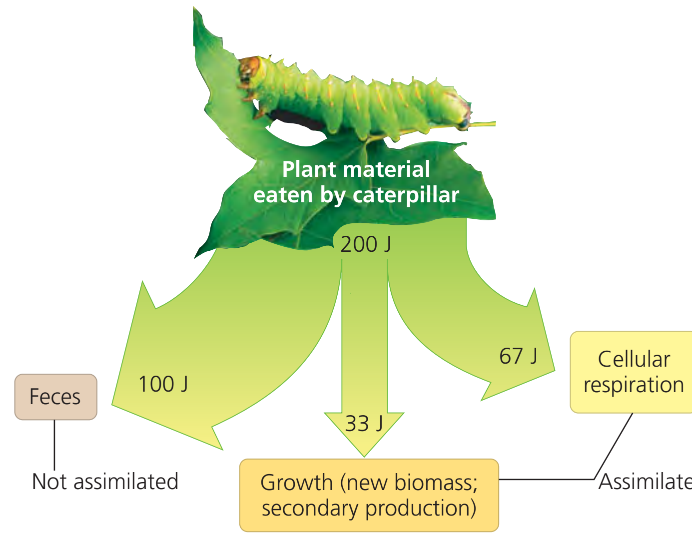
CONCEPT 55.3

## Energy transfer between trophic levels is typically only 10% efficient

The amount of chemical energy in consumers' food that is converted to their own new biomass during a given period is called the **secondary production** of the ecosystem. Consider the transfer of organic matter from primary producers to herbivores, the primary consumers. In most ecosystems, herbivores eat only a small fraction of plant material produced; globally, they consume only about one-sixth of total plant production. Moreover, they cannot digest all the plant material that they *do* eat, as anyone who has walked through a dairy farm will attest. The vast majority of an ecosystem's production is eventually consumed by detritivores. Let's analyze the process of energy transfer and cycling more closely.

### Production Efficiency

First we'll examine secondary production in an individual organism—a caterpillar. When a caterpillar feeds on a plant leaf, only about 33 J out of 200 J (48 cal), or one-sixth of the potential energy in the leaf, is used for secondary production, or growth **(Figure 55.10)**. The caterpillar uses some of the remaining energy (stored in organic compounds) for cellular respiration and passes the rest in its feces. The energy contained in the feces remains in the ecosystem temporarily, but most of it is lost as heat after the feces are consumed by detritivores. The energy used for the caterpillar's respiration is also eventually lost from the




▲ **Figure 55.10 Energy partitioning within a link of the food chain.** Less than 17% of the caterpillar's food is actually used for secondary production (growth).

ecosystem as heat. This is why energy is said to flow through, not cycle within, ecosystems. Only the chemical energy stored by herbivores as biomass, through growth or the production of offspring, is available as food to secondary consumers.

We can measure the efficiency of animals as energy transformers using the following equation:

$$\text{Production efficiency} = \frac{\text{Net secondary production} \times 100\%}{\text{Assimilation of primary production}}$$

Net secondary production is the energy stored in biomass represented by growth and reproduction. Assimilation consists of the total energy taken in, not including losses in feces, used for growth, reproduction, and respiration. **Production efficiency**, therefore, is the percentage of energy stored in assimilated food that is *not* used for respiration. For the caterpillar in Figure 55.10, production efficiency is 33%; 67 J of the 100 J of assimilated energy is used for respiration. (The 100 J of energy lost as undigested material in feces does not count toward assimilation.) Birds and mammals typically have low production efficiencies, in the range of 1–3%, because they use so much energy in maintaining a constant, high body temperature. Fishes, which are ectotherms (see Chapter 40), have production efficiencies around 10%. Insects and microorganisms are even more efficient, with production efficiencies averaging 40% or more.

### Trophic Efficiency and Ecological Pyramids

Let's scale up now from the production efficiencies of individual consumers to the flow of energy through trophic levels.

**Trophic efficiency** is the percentage of production transferred from one trophic level to the next. Trophic efficiencies must always be less than production efficiencies because they take into account not only the energy lost through respiration and contained in feces, but also the energy in organic material in a lower trophic level that is not consumed by the next trophic level. Trophic efficiencies are generally only about 10% and range from approximately 5% to 20%, depending on the type of ecosystem. In other words, 90% of the energy available at one trophic level typically is *not* transferred to the next. This loss is multiplied over the length of a food chain. For example, if 10% of available energy is transferred from primary producers to primary consumers, such as caterpillars, and 10% of that energy is transferred to secondary consumers, called carnivores, then only 1% of net primary production is available to secondary consumers (10% of 10%).

The progressive loss of energy along a food chain severely limits the abundance of top-level carnivores that an ecosystem can support. Only about 0.1% of the chemical energy fixed by photosynthesis can flow all the way through a food web to a tertiary consumer, such as a snake or a shark. This explains why most food webs include only about four or five trophic levels (see Chapter 54).

The loss of energy with each transfer in a food chain can be represented by a *pyramid of net production*, in which the trophic levels are arranged in tiers **(Figure 55.11)**. The width of each tier is proportional to the net production, expressed in joules, of each trophic level. The highest level, which represents top-level predators, contains relatively few individuals. The small population size typical of top predator species is one reason they tend to be vulnerable to extinction (as well as to the evolutionary consequences of small population size, discussed in Chapter 23).

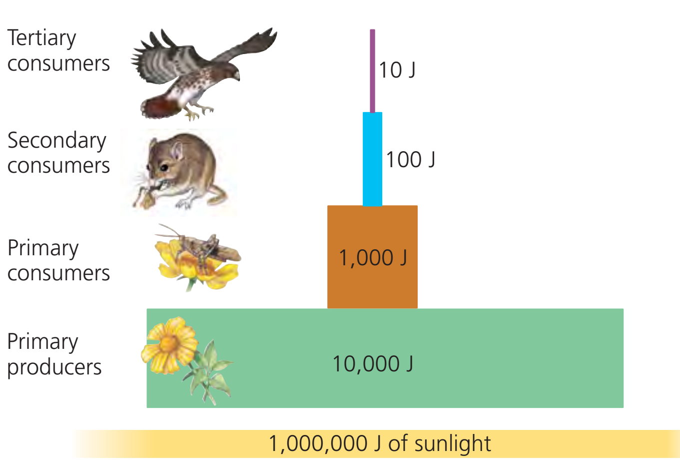
One important ecological consequence of low trophic efficiencies is represented in a *biomass pyramid*, in which each tier represents the standing crop (the total dry mass of all organisms) in one trophic level. Most biomass pyramids narrow sharply from primary producers at the base to top-level carnivores at the apex because energy transfers between trophic levels are so inefficient **(Figure 55.12a)**. Certain aquatic ecosystems, however, have inverted biomass pyramids: Primary consumers outweigh the producers **(Figure 55.12b)**. Such inverted biomass pyramids occur because the producers—phytoplankton—grow, reproduce, and are consumed so quickly by the zooplankton that they never develop a large population size, or standing crop. In other words, the phytoplankton have a short **turnover time**, which means they have a small standing crop compared to their production:

$$\text{Turnover time} = \frac{\text{Standing crop (g/m}^2)}{\text{Production (g/m}^2\cdot\text{day)}}$$

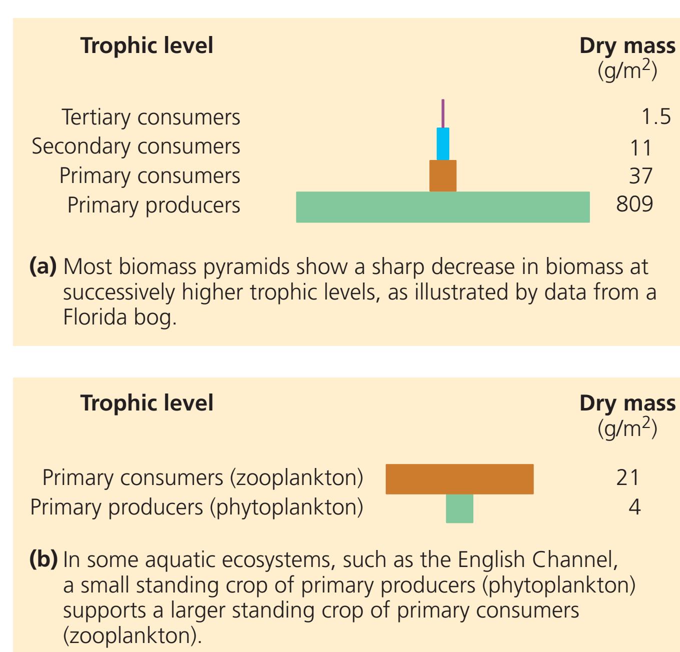
Because the phytoplankton continually replace their biomass at such a rapid rate, they can support a biomass of zooplankton bigger than their own biomass. Nevertheless, because phytoplankton have much higher production than zooplankton, the pyramid of *production* for this ecosystem is still bottom-heavy, like the one in Figure 55.11.

The dynamics of energy flow through ecosystems have important implications for humans. Eating meat is a relatively inefficient way of tapping photosynthetic production. The same pound of soybeans that a person could eat for protein produces only a fifth of a pound of beef or less when fed to a cow. Worldwide agriculture could, in fact, successfully feed many more people and require less cultivated land if humans all fed more efficiently—as primary consumers, eating plant material. Consequently, estimates of Earth's human carrying capacity (see Chapter 53) depend greatly on our diet and on the amount of resources each of us consumes.

In the next section, we will look at how the transfer of nutrients and energy through food webs is part of a larger picture of chemical cycling in ecosystems.




▲ **Figure 55.11 An idealized pyramid of net production.** This example assumes a trophic efficiency of 10% for each link in the food chain. Notice that primary producers convert only about 1% of the energy available to them to net primary production.




**(a)** Most biomass pyramids show a sharp decrease in biomass at successively higher trophic levels, as illustrated by data from a Florida bog.

**(b)** In some aquatic ecosystems, such as the English Channel, a small standing crop of primary producers (phytoplankton) supports a larger standing crop of primary consumers (zooplankton).

▲ **Figure 55.12 Pyramids of biomass (standing crop).** Numbers denote the dry mass of all organisms at each trophic level.

**CONCEPT CHECK 55.3**

1. If an insect that eats plant seeds containing 100 J of energy uses 30 J of that energy for respiration and excretes 50 J in its feces, what is the insect's net secondary production? What is its production efficiency?
2. Tobacco leaves contain nicotine, a poisonous compound that is energetically expensive for the plant to make. What advantage might the plant gain by using some of its resources to produce nicotine?
3. **MAKE CONNECTIONS** Figure 40.20 describes relative energy budgets for four animals. What are some ways in which the energy expenditures of the caterpillar described in Figure 55.10 would differ from the woman pictured in Figure 40.20?

For suggested answers, see Appendix A.

**CONCEPT 55.4**

# Biological and geochemical processes cycle nutrients and water in ecosystems

Although most ecosystems receive an abundant supply of solar energy, chemical elements are available only in limited amounts. Life on Earth therefore depends on the recycling of essential chemical elements. Much of an organism's chemical stock is replaced continuously as nutrients are assimilated and waste products released. When the organism dies, the atoms in its complex molecules are returned in simpler compounds to the atmosphere, water, or soil by the action of decomposers. Decomposition replenishes the pools of inorganic nutrients that plants and other autotrophs use to build new organic matter. Because nutrient cycles involve both biotic and abiotic components, they are called **biogeochemical cycles**.

## Biogeochemical Cycles

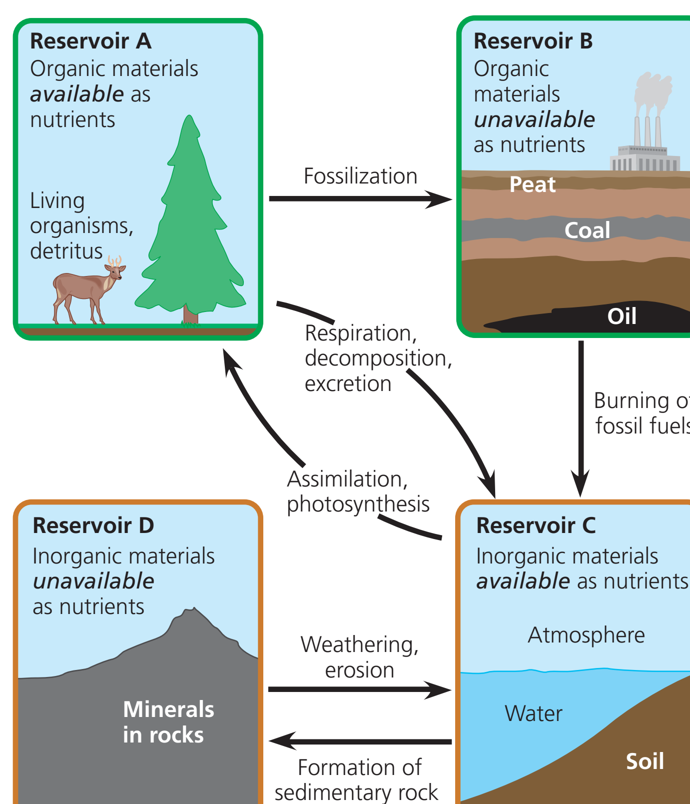
An element's specific route through a biogeochemical cycle depends on the element and the trophic structure of the ecosystem. For convenience, however, we can recognize two general categories of biogeochemical cycles: global and local. Gaseous forms of carbon, oxygen, sulfur, and nitrogen occur in the atmosphere, and cycles of these elements are essentially global. For example, some of the carbon and oxygen atoms a plant acquires from the air as $CO_2$ may have been released into the atmosphere by the respiration of an organism in a distant locale. Other elements, including phosphorus, potassium, and calcium, are too heavy to occur as gases at Earth's surface, although they are transported in dust. In terrestrial ecosystems, these elements cycle more locally, absorbed from the soil by plant roots and eventually returned to the soil by decomposers. In aquatic systems, however, they cycle more broadly as dissolved forms carried in currents.

Let's first look at a general model of nutrient cycling that includes the main reservoirs of elements and the processes that transfer elements between reservoirs (**Figure 55.13**). Each reservoir is defined by two characteristics: whether it contains organic or inorganic materials and whether or not the materials are directly available for use by organisms.

The nutrients in living organisms and in detritus (reservoir A in Figure 55.13) are available to other organisms when consumers feed and when detritivores consume nonliving organic matter. Some living organic material moved to the fossilized organic reservoir (reservoir B) long ago, when dead organisms were converted to coal, oil, or peat (fossil fuels). Nutrients in these deposits generally cannot be assimilated directly.

Inorganic materials (elements and compounds) that are dissolved in water or present in soil or air (reservoir C) are available for use. Organisms assimilate materials from this reservoir directly and return chemicals to it through the relatively rapid processes of cellular respiration, excretion, and decomposition. Although most organisms cannot directly tap into the inorganic elements tied up in rocks (reservoir D), these nutrients may slowly become available through weathering and erosion. Similarly, unavailable organic materials move into the available reservoir of inorganic nutrients when fossil fuels are burned, releasing exhaust into the atmosphere.

**Figure 55.14**, on the next two pages, provides a detailed look at the cycling of water, carbon, nitrogen, and phosphorus.




▲ **Figure 55.13 A general model of nutrient cycling.** Arrows indicate the processes that move nutrients between reservoirs.

▼ **Figure 55.14**

# Exploring Water and Nutrient Cycling

Examine each cycle closely, considering the major reservoirs of water, carbon, nitrogen, and phosphorus and the processes that drive each cycle. The widths of the arrows in the diagrams approximately reflect the relative contribution of each process to the movement of water or a nutrient in the biosphere.

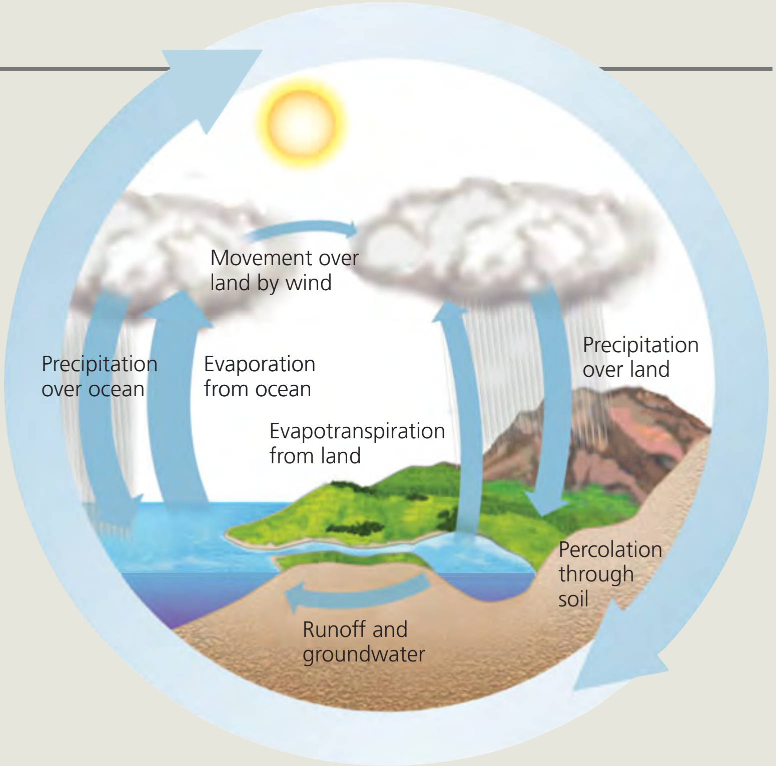
## The Water Cycle

**Biological importance** Water is essential to all organisms (see Chapter 3), and its availability influences the rates of ecosystem processes, particularly primary production and decomposition in terrestrial ecosystems.

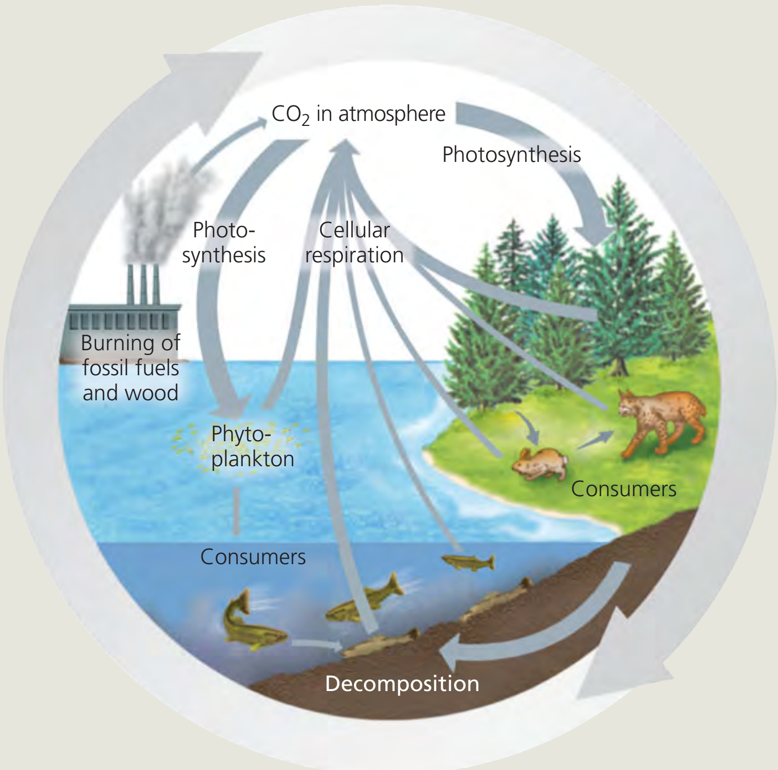
**Forms available to life** Liquid water is the primary physical phase in which water is used, though some organisms can harvest water vapor. Freezing of soil water can limit water availability to terrestrial plants.

**Reservoirs** The oceans contain 97% of the water in the biosphere. Approximately 2% is bound in glaciers and polar ice caps, and the remaining 1% is in lakes, rivers, and groundwater, with a negligible amount in the atmosphere.

**Key processes** The main processes driving the water cycle are evaporation of liquid water by solar energy, condensation of water vapor into clouds, and precipitation. Transpiration by terrestrial plants also moves large volumes of water into the atmosphere. Surface and groundwater flow can return water to the oceans, completing the water cycle.




## The Carbon Cycle

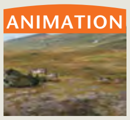



**Biological importance** Carbon forms the framework of the organic molecules essential to all organisms.

**Forms available to life** Photosynthetic organisms utilize $CO_2$ during photosynthesis and convert the carbon to organic forms that are used by consumers, including animals, fungi, and heterotrophic protists and prokaryotes.

**Reservoirs** The major reservoirs of carbon include fossil fuels, soils, the sediments of aquatic ecosystems, the oceans (dissolved carbon compounds), plant and animal biomass, and the atmosphere ($CO_2$). The largest reservoir is sedimentary rocks such as limestone; however, this pool turns over very slowly.

**Key processes** Photosynthesis by plants and phytoplankton removes substantial amounts of atmospheric $CO_2$ each year. This quantity is approximately equaled by $CO_2$ added to the atmosphere through cellular respiration by producers and consumers. The burning of fossil fuels and wood is adding significant amounts of additional $CO_2$ to the atmosphere. Over geologic time, volcanoes are also a substantial source of $CO_2$.




Visit the Study Area at **www.masteringbiology.com** for the BioFlix® 3-D Animation on The Carbon Cycle.

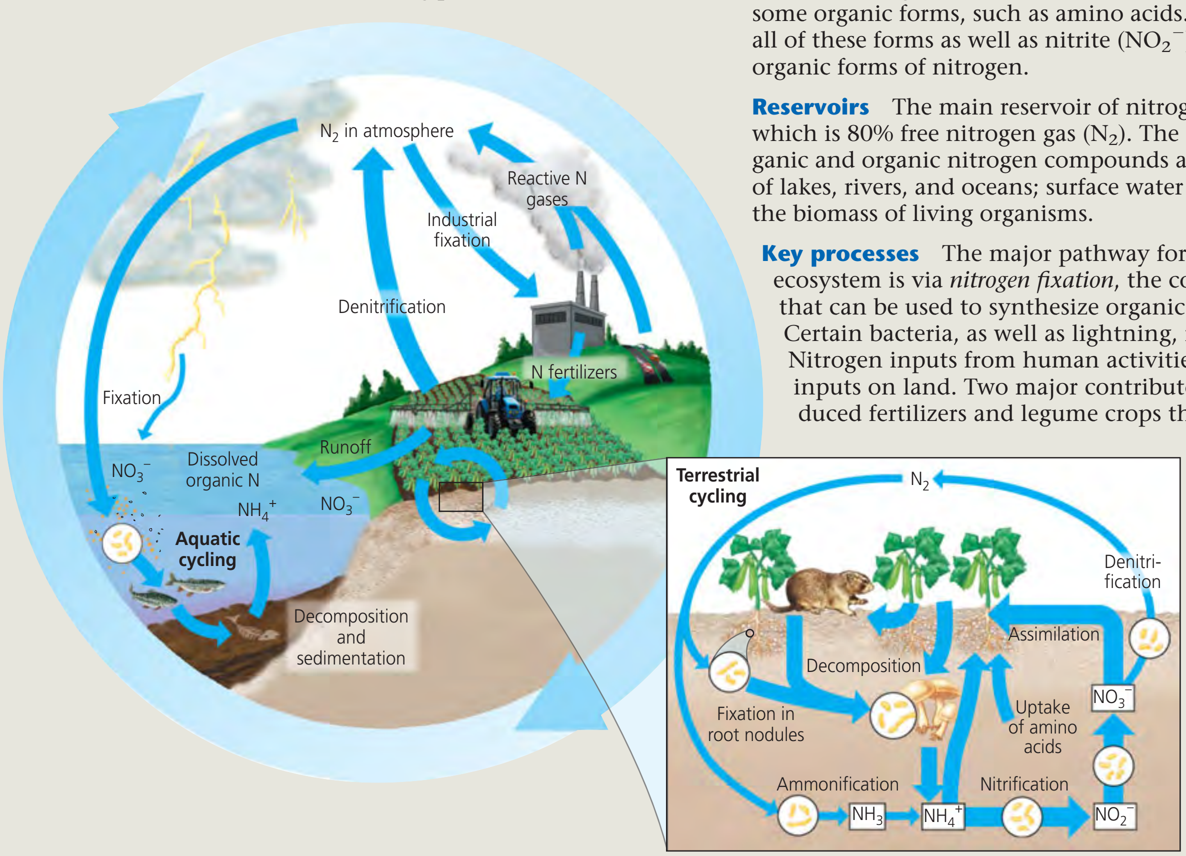
## The Nitrogen Cycle

**Biological importance** Nitrogen is part of amino acids, proteins, and nucleic acids and is often a limiting plant nutrient.

**Forms available to life** Plants can assimilate (use) two inorganic forms of nitrogen—ammonium ($NH_4^+$) and nitrate ($NO_3^-$)—and some organic forms, such as amino acids. Various bacteria can use all of these forms as well as nitrite ($NO_2^-$). Animals can use only organic forms of nitrogen.

**Reservoirs** The main reservoir of nitrogen is the atmosphere, which is 80% free nitrogen gas ($N_2$). The other reservoirs of inorganic and organic nitrogen compounds are soils and the sediments of lakes, rivers, and oceans; surface water and groundwater; and the biomass of living organisms.

**Key processes** The major pathway for nitrogen to enter an ecosystem is via *nitrogen fixation*, the conversion of $N_2$ to forms that can be used to synthesize organic nitrogen compounds. Certain bacteria, as well as lightning, fix nitrogen naturally. Nitrogen inputs from human activities now outpace natural inputs on land. Two major contributors are industrially produced fertilizers and legume crops that fix nitrogen via bacteria in their root nodules. Other bacteria in soil convert nitrogen to different forms (see also Figure 37.9). Some bacteria carry out *denitrification*, the reduction of nitrate to nitrogen gases. Human activities also release large quantities of reactive nitrogen gases, such as nitrogen oxides, to the atmosphere.



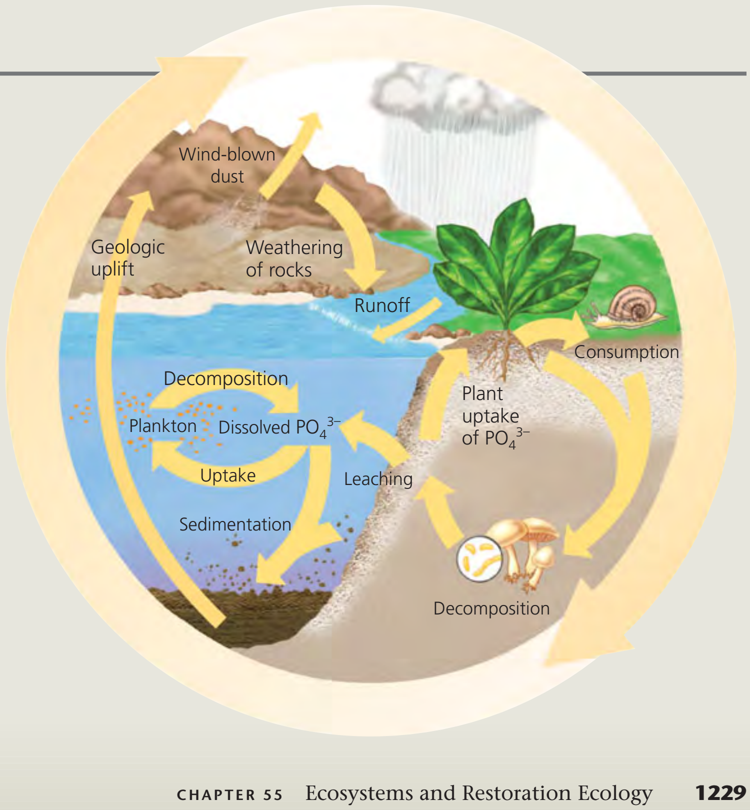

## The Phosphorus Cycle

**Biological importance** Organisms require phosphorus as a major constituent of nucleic acids, phospholipids, and ATP and other energy-storing molecules and as a mineral constituent of bones and teeth.

**Forms available to life** The most biologically important inorganic form of phosphorus is phosphate ($PO_4^{3-}$), which plants absorb and use in the synthesis of organic compounds.

**Reservoirs** The largest accumulations of phosphorus are in sedimentary rocks of marine origin. There are also large quantities of phosphorus in soil, in the oceans (in dissolved form), and in organisms. Because soil particles bind $PO_4^{3-}$, the recycling of phosphorus tends to be quite localized in ecosystems.

**Key processes** Weathering of rocks gradually adds $PO_4^{3-}$ to soil; some leaches into groundwater and surface water and may eventually reach the sea. Phosphate taken up by producers and incorporated into biological molecules may be eaten by consumers. Phosphate is returned to soil or water by either decomposition of biomass or excretion by consumers. Because there are no significant phosphorus-containing gases, only relatively small amounts of phosphorus move through the atmosphere, usually in the forms of dust and sea spray.



How have ecologists worked out the details of chemical cycling in various ecosystems? Two common methods use isotopes. One method is to follow the movement of naturally occurring, nonradioactive isotopes through the biotic and abiotic components of an ecosystem. The other method involves adding tiny amounts of radioactive isotopes of specific elements and tracing their progress. Scientists have also been able to make use of radioactive carbon ($^{14}C$) released into the atmosphere during atom bomb testing in the 1950s and early 1960s. Scientists use this "spike" of $^{14}C$ to trace where and how quickly carbon flows into ecosystem components, including plants, soils, and ocean water.

## Decomposition and Nutrient Cycling Rates

The diagrams in Figure 55.14 illustrate the essential role that decomposers (detritivores) play in recycling carbon, nitrogen, and phosphorus. The rates at which these nutrients cycle in different ecosystems are extremely variable, mostly as a result of differences in rates of decomposition.

Decomposition is controlled by the same factors that limit primary production in aquatic and terrestrial ecosystems (see Concept 55.2). These factors include temperature, moisture, and nutrient availability. Decomposers usually grow faster and decompose material more quickly in warmer ecosystems **(Figure 55.15)**. In tropical rain forests, for instance, most organic material decomposes in a few months to a few years, while in temperate forests, decomposition takes four to six years, on average. The difference is largely the result of the higher temperatures and more abundant precipitation in tropical rain forests.

Because decomposition in a tropical rain forest is rapid, relatively little organic material accumulates as leaf litter on the forest floor; about 75% of the nutrients in the ecosystem is present in the woody trunks of trees, and only about 10% is contained in the soil. Thus, the relatively low concentrations of some nutrients in the soil of tropical rain forests result from a short cycling time, not from a lack of these elements in the ecosystem. In temperate forests, where decomposition is much slower, the soil may contain as much as 50% of all the organic material in the ecosystem. The nutrients that are present in temperate forest detritus and soil may remain there for fairly long periods before plants assimilate them.

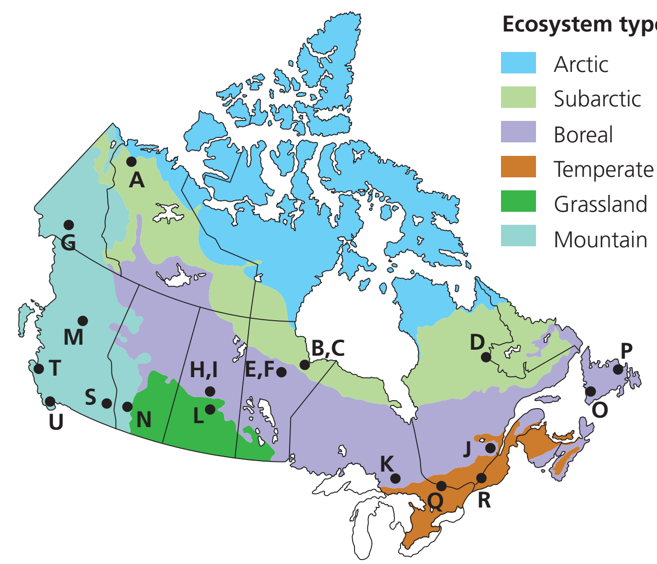
Decomposition on land is also slower when conditions are either too dry for decomposers to thrive or too wet to supply them with enough oxygen. Ecosystems that are both cold and wet, such as peatlands, store large amounts of organic matter (see Figure 29.11). Decomposers grow poorly there, and net primary production greatly exceeds decomposition.

In aquatic ecosystems, decomposition in anaerobic muds can take 50 years or longer. Bottom sediments are

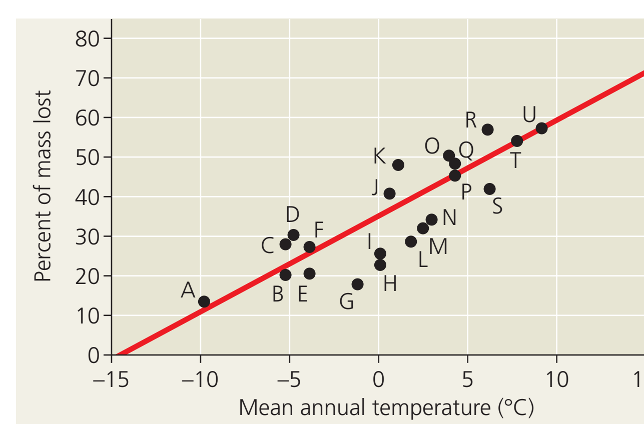
▼ **Figure 55.15** **INQUIRY**

### How does temperature affect litter decomposition in an ecosystem?

**EXPERIMENT** Researchers with the Canadian Forest Service placed identical samples of organic material—litter—on the ground in 21 sites across Canada (marked by letters on the map below). Three years later, they returned to see how much of each sample had decomposed.




**RESULTS** The mass of litter decreased four times faster in the warmest ecosystem than in the coldest ecosystem.




**CONCLUSION** Decomposition rate increases with temperature across much of Canada.

**SOURCE** T. R. Moore et al., Litter decomposition rates in Canadian forests, *Global Change Biology* 5:75–82 (1999).

**WHAT IF?** What factors other than temperature might also have varied across these 21 sites? How might this variation have affected the interpretation of the results?

comparable to the detritus layer in terrestrial ecosystems; however, algae and aquatic plants usually assimilate nutrients directly from the water. Thus, the sediments often constitute a nutrient sink, and aquatic ecosystems are very productive only when there is interchange between the bottom layers of water and the water at the surface (as occurs in the upwelling regions described earlier).

## *Case Study*: Nutrient Cycling in the Hubbard Brook Experimental Forest

Since 1963, ecologists Herbert Bormann, Eugene Likens, and their colleagues have been studying nutrient cycling at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire. Their research site is a deciduous forest that grows in six small valleys, each drained by a single creek. Impenetrable bedrock underlies the soil of the forest.

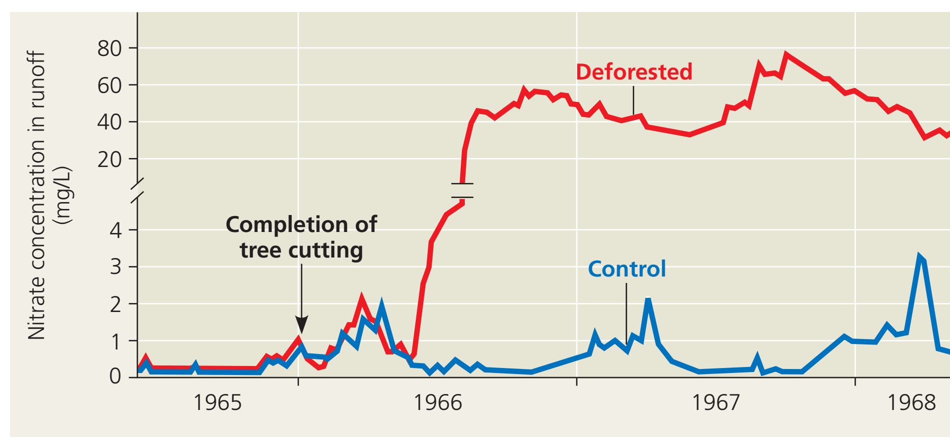
The research team first determined the mineral budget for each of six valleys by measuring the input and outflow of several key nutrients. They collected rainfall at several sites to measure the amount of water and dissolved minerals added to the ecosystem. To monitor the loss of water and minerals, they constructed a small concrete dam with a V-shaped spillway across the creek at the bottom of each valley (**Figure 55.16a**). They found that about 60% of the water added to the ecosystem as rainfall and snow exits through the stream, and the remaining 40% is lost by evapotranspiration.

Preliminary studies confirmed that internal cycling conserved most of the mineral nutrients in the system. For example, only about 0.3% more calcium ($Ca^{2+}$) leaves a valley via its creek than is added by rainwater, and this small net loss is probably replaced by chemical decomposition of the bedrock. During most years, the forest even registers small net gains of a few mineral nutrients, including nitrogen.

Experimental deforestation of a watershed dramatically increased the flow of water and minerals leaving the watershed (**Figure 55.16b** and **c**). Over three years, water runoff from the newly deforested watershed was 30–40% greater than in a control watershed, apparently because there were no plants to absorb and transpire water from the soil. The concentration of $Ca^{2+}$ in the creek increased 4-fold, and the concentration of $K^{+}$ increased by a factor of 15. Most remarkable was the loss of nitrate, whose concentration in the creek increased 60-fold, reaching levels considered unsafe for drinking water (Figure 55.16c). The Hubbard Brook deforestation study showed that the amount of nutrients leaving an intact forest ecosystem is controlled mainly by the plants. Retaining nutrients in ecosystems helps to maintain the productivity of the systems and, in some cases, to avoid problems cause by excess nutrient runoff (see Figure 55.8).

**(a)** Concrete dams and weirs built across streams at the bottom of watersheds enabled researchers to monitor the outflow of water and nutrients from the ecosystem.

**(b)** One watershed was clear-cut to study the effects of the loss of vegetation on drainage and nutrient cycling. All of the original plant material was left in place to decompose.




**(c)** The concentration of nitrate in runoff from the deforested watershed was 60 times greater than in a control (unlogged) watershed.

▲ **Figure 55.16 Nutrient cycling in the Hubbard Brook Experimental Forest: an example of long-term ecological research.**

MB See the related Experimental Inquiry Tutorial in MasteringBiology.

## CONCEPT CHECK 55.4

1. **DRAW IT** For each of the four biogeochemical cycles detailed in Figure 55.14, draw a simple diagram that shows one possible path for an atom of that chemical from abiotic to biotic reservoirs and back.
2. Why does deforestation of a watershed increase the concentration of nitrates in streams draining the watershed?
3. **WHAT IF?** Why is nutrient availability in a tropical rain forest particularly vulnerable to logging?

For suggested answers, see Appendix A.

## CONCEPT 55.5

# Restoration ecologists help return degraded ecosystems to a more natural state

Ecosystems can recover naturally from most disturbances (including the experimental deforestation at Hubbard Brook) through the stages of ecological succession that we discussed in Chapter 54. Sometimes that recovery takes centuries, though, particularly when humans have degraded the environment. Tropical areas that are cleared for farming may quickly become unproductive because of nutrient losses. Mining activities may last for several decades, and the lands are often abandoned in a degraded state. Ecosystems can also be damaged by salts that build up in soils from irrigation and by toxic chemicals or oil spills. Biologists increasingly are called on to help restore and repair ecosystem damage.

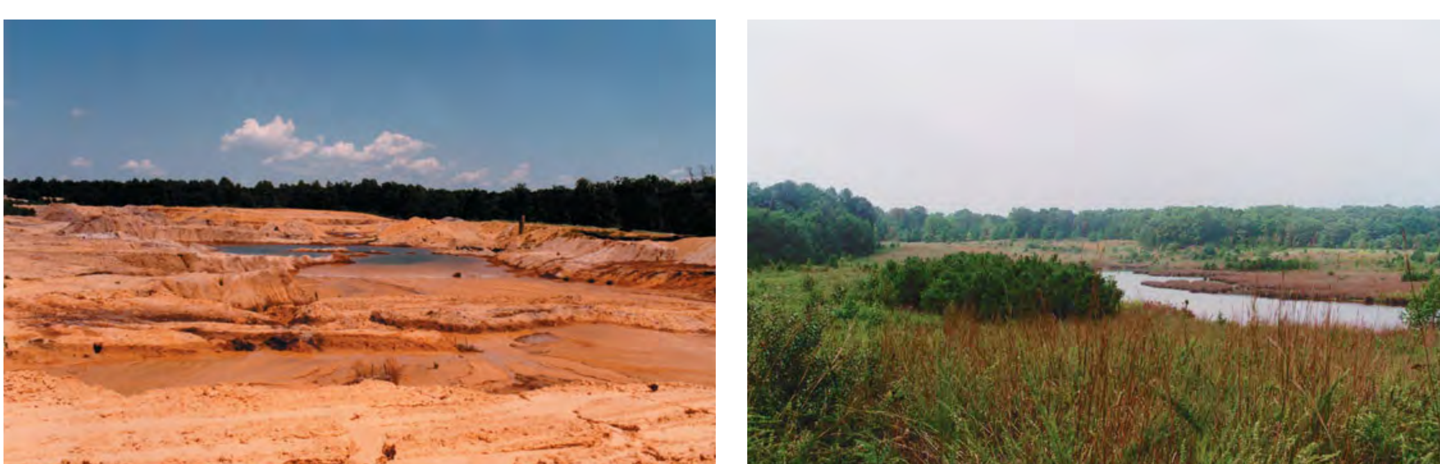
Restoration ecologists seek to initiate or speed up the recovery of degraded ecosystems. One of the basic assumptions is that environmental damage is at least partly reversible. This optimistic view must be balanced by a second assumption—that ecosystems are not infinitely resilient. Restoration ecologists therefore work to identify and manipulate the processes that most limit recovery of ecosystems from disturbances. Where disturbance is so severe that restoring all of a habitat is impractical, ecologists try to reclaim as much of a habitat or ecological process as possible, within the limits of the time and money available to them.

In extreme cases, the physical structure of an ecosystem may need to be restored before biological restoration can occur. If a stream was straightened to channel water quickly through a suburb, restoration ecologists may reconstruct a meandering channel to slow down the flow of water eroding the stream bank. To restore an open-pit mine, engineers may first grade the site with heavy equipment to reestablish a gentle slope, spreading topsoil when the slope is in place (**Figure 55.17**).

Once physical reconstruction of the ecosystem is complete—or when it is not needed—biological restoration is the next step. Two key strategies in biological restoration are bioremediation and biological augmentation.

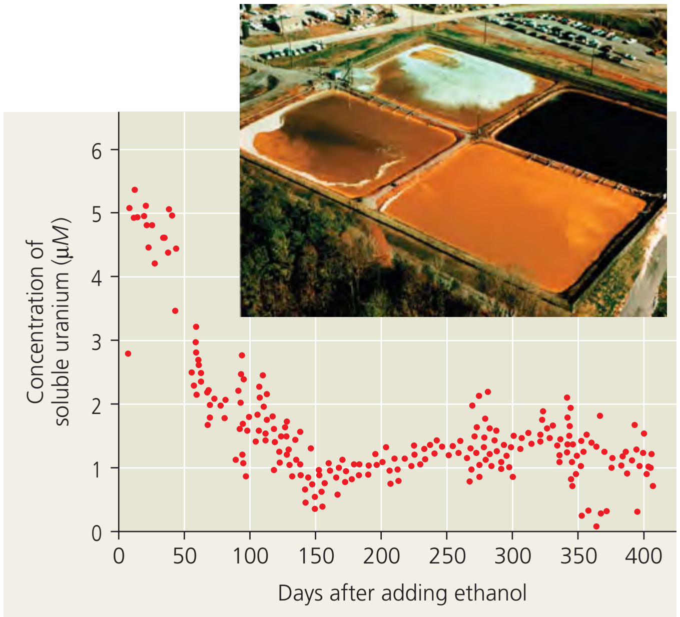
### Bioremediation

Using organisms—usually prokaryotes, fungi, or plants—to detoxify polluted ecosystems is known as **bioremediation** (see Chapter 27). Some plants and lichens adapted to soils containing heavy metals can accumulate high concentrations of potentially toxic metals such as zinc, nickel, lead, and cadmium in their tissues. Restoration ecologists can introduce such species to sites polluted by mining and other human activities and then harvest these organisms to remove the metals from the ecosystem. For instance, researchers in the United Kingdom have discovered a lichen species that grows on soil polluted with uranium dust left over from mining. The lichen concentrates uranium in a dark



**(a)** In 1991, before restoration **(b)** In 2000, near the completion of restoration

▲ **Figure 55.17 A gravel and clay mine site in New Jersey before and after restoration.**




▲ **Figure 55.18 Bioremediation of groundwater contaminated with uranium at Oak Ridge National Laboratory, Tennessee.** Wastes containing uranium were dumped in four unlined pits (inset) for more than 30 years, contaminating soils and groundwater. After ethanol was added, microbial activity decreased the concentration of soluble uranium in groundwater near the pits.

pigment, making it useful as a biological monitor and potentially as a remediator.

Ecologists already use the abilities of many prokaryotes to carry out bioremediation of soils and water. Scientists have sequenced the genomes of at least ten prokaryotic species specifically for their bioremediation potential. One of the species, the bacterium *Shewanella oneidensis*, appears particularly promising. It can metabolize a dozen or more elements under aerobic and anaerobic conditions. In doing so, it converts soluble forms of uranium, chromium, and nitrogen to insoluble forms that are less likely to leach into streams or groundwater. Researchers at Oak Ridge National Laboratory, in Tennessee, stimulated the growth of *Shewanella* and other uranium-reducing bacteria by adding ethanol to groundwater contaminated with uranium; the bacteria can use ethanol as an energy source. In just five months, the concentration of soluble uranium in the ecosystem dropped by 80% **(Figure 55.18)**. In the future, genetic engineering could be increasingly useful as a tool for improving the performance of prokaryotes and other organisms as bioremediators.

## Biological Augmentation

In contrast to bioremediation, which is a strategy for removing harmful substances from an ecosystem, **biological augmentation** uses organisms to *add* essential materials to a degraded ecosystem. To augment ecosystem processes, restoration ecologists need to determine which factors, such as chemical nutrients, have been lost from a system and are limiting its recovery.

Encouraging the growth of plants that thrive in nutrient-poor soils often speeds up succession and ecosystem recovery. In alpine ecosystems of the western United States, nitrogen-fixing plants such as lupines are often planted to raise nitrogen concentrations in soils disturbed by mining and other activities. Once these nitrogen-fixing plants become established, other native species are better able to obtain enough soil nitrogen to survive. In other systems where the soil has been severely disturbed or where topsoil is missing entirely, plant roots may lack the mycorrhizal symbionts that help them meet their nutritional needs (see Chapter 31). Ecologists restoring a tallgrass prairie in Minnesota recognized this limitation and enhanced the recovery of native species by adding mycorrhizal symbionts to the soil they seeded.

Restoring the physical structure and plant community of an ecosystem does not necessarily ensure that animal species will recolonize a site and persist there. Because animals aid critical ecosystem services, including pollination, seed dispersal, and herbivory, restoration ecologists sometimes help wildlife reach and use restored ecosystems. They might release animals at a site or establish habitat corridors that connect a restored site to other places where the animals are found. They sometimes establish artificial perches for birds or dig burrows for other animals to use at the site. These and other efforts can improve the biodiversity of restored ecosystems and help the community persist.

## Restoration Projects Worldwide

Because restoration ecology is a relatively new discipline and because ecosystems are complex, restoration ecologists generally learn as they go. Many restoration ecologists advocate adaptive management: experimenting with several promising types of management to learn what works best.

The long-term objective of restoration is to return an ecosystem as much as possible to its predisturbance state. **Figure 55.19**, on the next two pages, identifies several ambitious and successful restoration projects around the world. The great number of such projects, the dedication of the people engaged in them, and the successes that have been achieved suggest that restoration ecology will continue to grow as a discipline for many years.

**CONCEPT CHECK 55.5**

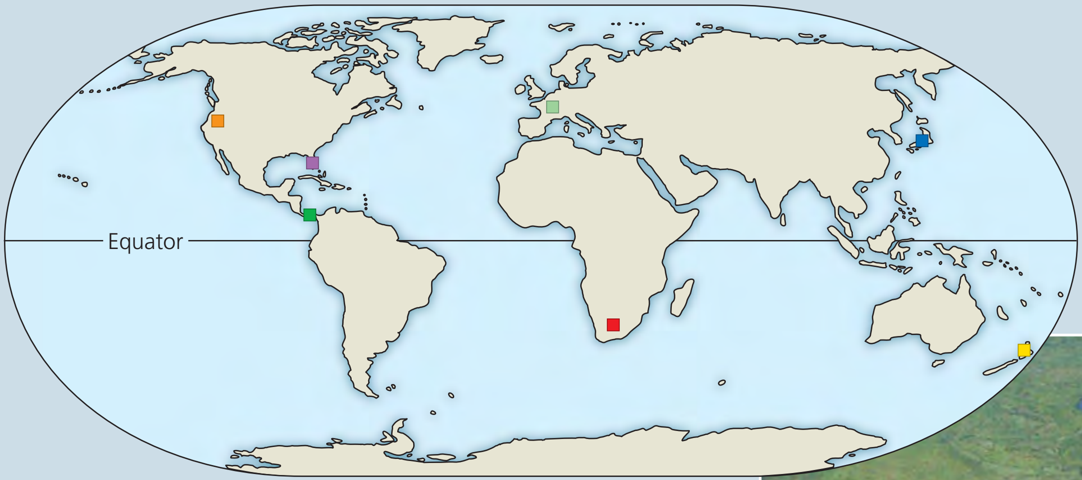
1. Identify the main goal of restoration ecology.
2. How do bioremediation and biological augmentation differ?
3. **WHAT IF?** In what way is the Kissimmee River project a more complete ecological restoration than the Maungatautari project (see Figure 55.19)?

For suggested answers, see Appendix A.

▼ Figure 55.19

# Exploring Restoration Ecology Worldwide

The examples highlighted on these pages are just a few of the many restoration ecology projects taking place around the world. The color-coded dots on the map indicate the locations of the projects.




## Kissimmee River, Florida

The Kissimmee River was converted from a meandering river to a 90-km canal, threatening many fish and wetland bird populations. Kissimmee River restoration has filled 12 km of drainage canal and reestablished 24 km of the original 167 km of natural river channel. Pictured here is a section of the Kissimmee canal that has been plugged (wide, light strip on the right side of the photo), diverting flow into remnant river channels (center of the photo). The project will also restore natural flow patterns, which will foster self-sustaining populations of wetland birds and fishes.

## Truckee River, Nevada

Damming and water diversions during the 20th century reduced flow in the Truckee River, leading to declines in riparian (riverside) forests. Restoration ecologists worked with water managers to ensure that sufficient water would be released during the short season of seed release by the native cottonwood and willow trees for seedlings to become established. Nine years of controlled-flow release led to the result shown here: a dramatic recovery of cottonwood-willow riparian forest.

## Tropical dry forest, Costa Rica

Clearing for agriculture, mainly for livestock grazing, eliminated approximately 98% of tropical dry forest in Central America and Mexico. Reversing this trend, tropical dry forest restoration in Costa Rica has used domestic livestock to disperse the seeds of native trees into open grasslands. The photo shows one of the first trees (right center), dispersed as seed by livestock, to colonize former pastureland. This project is a model for joining restoration ecology with the local economy and educational institutions.

## Rhine River, Europe

Centuries of dredging and channeling for navigation (see the barges in the wide, main channel on the right side of the photo) have straightened the once-meandering Rhine River and disconnected it from its floodplain and associated wetlands. The countries along the Rhine, particularly France, Germany, Luxembourg, the Netherlands, and Switzerland, are cooperating to reconnect the river to side channels, such as the one shown on the left side of the photo. Such side channels increase the diversity of habitats available to aquatic organisms, improve water quality, and provide flood protection.

## Coastal Japan

Seaweed and seagrass beds are important nursery grounds for a wide variety of fishes and shellfish. Once extensive but now reduced by development, these beds are being restored in the coastal areas of Japan. Techniques include constructing suitable seafloor habitat, transplanting from natural beds using artificial substrates, and hand seeding (shown in this photograph).

## Succulent Karoo, South Africa

In this desert region of southern Africa, as in many arid regions, overgrazing by livestock has damaged vast areas. Private landowners and government agencies in South Africa are restoring large areas of this unique region, revegetating the land and employing more sustainable resource management. The photo shows a small sample of the exceptional plant diversity of the Succulent Karoo; its 5,000 plant species include the highest diversity of succulent plants in the world.

## Maungatautari, New Zealand

Weasels, rats, pigs, and other introduced species pose a serious threat to New Zealand's native plants and animals, including kiwis, a group of flightless, ground-dwelling bird species. The goal of the Maungatautari restoration project is to exclude all exotic mammals from a 3,400-ha reserve located on a forested volcanic cone. A specialized fence around the reserve eliminates the need to continue setting traps and using poisons that can harm native wildlife. In 2006, a pair of critically endangered takahe (a species of flightless rail) were released into the reserve in hopes of reestablishing a breeding population of this colorful bird on New Zealand's North Island.

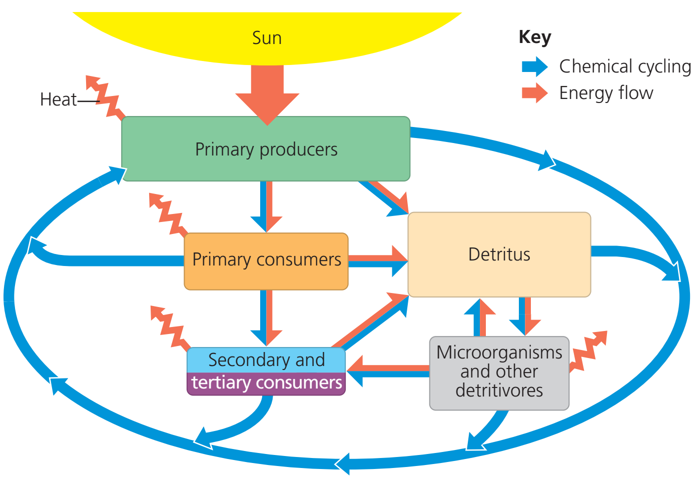
# 55 CHAPTER REVIEW

## SUMMARY OF KEY CONCEPTS

### CONCEPT 55.1

**Physical laws govern energy flow and chemical cycling in ecosystems (pp. 1219–1220)**

- An **ecosystem** consists of all the organisms in a community and all the abiotic factors with which they interact. The laws of physics and chemistry apply to ecosystems, particularly in regard to the conservation of energy. Energy is conserved but degraded to heat during ecosystem processes.
- Based on the **law of conservation of mass**, ecologists study how much of a chemical element enters and leaves an ecosystem and cycles within it. Inputs and outputs are generally small compared to recycled amounts, but their balance determines whether the ecosystem gains or loses an element over time.




*Based on the second law of thermodynamics, would you expect the typical biomass of primary producers in an ecosystem to be greater than or less than the biomass of secondary producers in the same ecosystem? Explain your reasoning.*

### CONCEPT 55.2

**Energy and other limiting factors control primary production in ecosystems (pp. 1220–1225)**

- **Primary production** sets the spending limit for the global energy budget. **Gross primary production** is the total energy assimilated by an ecosystem in a given period. **Net primary production**, the energy accumulated in autotroph biomass, equals gross primary production minus the energy used by the primary producers for respiration. **Net ecosystem production** is the total biomass accumulation of an ecosystem, defined as the difference between gross primary production and total ecosystem respiration.
- In aquatic ecosystems, light and nutrients limit primary production.
- In terrestrial ecosystems, climatic factors such as temperature and moisture affect primary production on a large geographic scale. More locally, a soil nutrient is often the limiting factor in primary production.

*What additional variable do you need to know the value of in order to estimate NEP from NPP? Why might measuring this variable be difficult, for instance, in a sample of ocean water?*

### CONCEPT 55.3

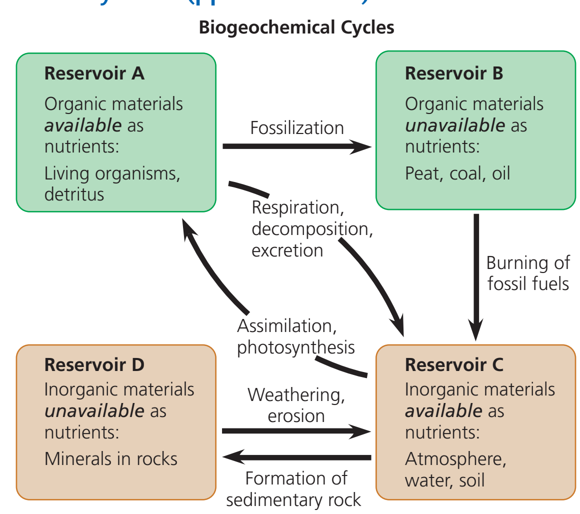
**Energy transfer between trophic levels is typically only 10% efficient (pp. 1225–1227)**

- The amount of energy available to each trophic level is determined by the net primary production and the **production efficiency**, the efficiency with which food energy is converted to biomass at each link in the food chain.
- The percentage of energy transferred from one trophic level to the next, called **trophic efficiency**, is generally 5–20%, with 10% being the typical value. Pyramids of net production and biomass reflect low trophic efficiency.

*Why would a long-distance runner typically have a lower production efficiency than a more sedentary person?*

### CONCEPT 55.4

**Biological and geochemical processes cycle nutrients and water in ecosystems (pp. 1227–1232)**




- Water moves in a global cycle driven by solar energy. The carbon cycle primarily reflects the reciprocal processes of photosynthesis and cellular respiration. Nitrogen enters ecosystems through atmospheric deposition and nitrogen fixation by prokaryotes, but most of the nitrogen cycling in natural ecosystems involves local cycles between organisms and soil or water. The phosphorus cycle is relatively localized.
- The proportion of a nutrient in a particular form and its cycling in that form vary among ecosystems, largely because of differences in the rate of decomposition.
- Nutrient cycling is strongly regulated by vegetation. The Hubbard Brook case study showed that logging increases water runoff and can cause large losses of minerals. It also demonstrated the importance of long-term ecological measurements in documenting the occurrence of and recovery from environmental problems.

*If decomposers usually grow faster and decompose material more quickly in warmer ecosystems, why is decomposition in hot deserts so slow?*

### CONCEPT 55.5

**Restoration ecologists help return degraded ecosystems to a more natural state (pp. 1232–1235)**

- Restoration ecologists harness organisms to detoxify polluted ecosystems through the process of **bioremediation**.

- In **biological augmentation**, ecologists use organisms to add essential materials to ecosystems.

**?** *In preparing a site for surface mining and later restoration, what would be the advantage of removing the shallow topsoil first and setting it aside separately from the deeper soil, rather than removing all soil at once and mixing it in a single pile?*

## TEST YOUR UNDERSTANDING

### LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Which of the following organisms is *incorrectly* paired with its trophic level?
   a. cyanobacterium—primary producer
   b. grasshopper—primary consumer
   c. zooplankton—primary producer
   d. eagle—tertiary consumer
   e. fungus—detritivore
2. Which of these ecosystems has the *lowest* net primary production per square meter?
   a. a salt marsh
   b. an open ocean
   c. a coral reef
   d. a grassland
   e. a tropical rain forest
3. The discipline that applies ecological principles to returning degraded ecosystems to a more natural state is known as
   a. population viability analysis.
   b. landscape ecology.
   c. conservation ecology.
   d. restoration ecology.
   e. resource conservation.

### LEVEL 2: APPLICATION/ANALYSIS

4. Nitrifying bacteria participate in the nitrogen cycle mainly by
   a. converting nitrogen gas to ammonia.
   b. releasing ammonium from organic compounds, thus returning it to the soil.
   c. converting ammonia to nitrogen gas, which returns to the atmosphere.
   d. converting ammonium to nitrate, which plants absorb.
   e. incorporating nitrogen into amino acids and organic compounds.
5. Which of the following has the greatest effect on the rate of chemical cycling in an ecosystem?
   a. the ecosystem's rate of primary production
   b. the production efficiency of the ecosystem's consumers
   c. the rate of decomposition in the ecosystem
   d. the trophic efficiency of the ecosystem
   e. the location of the nutrient reservoirs in the ecosystem
6. The Hubbard Brook watershed deforestation experiment yielded all of the following results *except*:
   a. Most minerals were recycled within a forest ecosystem.
   b. The flow of minerals out of a natural watershed was offset by minerals flowing in.
   c. Deforestation increased water runoff.
   d. The nitrate concentration in waters draining the deforested area became dangerously high.
   e. Calcium levels remained high in the soil of deforested areas.
7. Which of the following would be considered an example of bioremediation?
   a. adding nitrogen-fixing microorganisms to a degraded ecosystem to increase nitrogen availability
   b. using a bulldozer to regrade a strip mine
   c. dredging a river bottom to remove contaminated sediments
   d. reconfiguring the channel of a river
   e. adding seeds of a chromium-accumulating plant to soil contaminated by chromium
8. If you applied a fungicide to a cornfield, what would you expect to happen to the rate of decomposition and net ecosystem production (NEP)?
   a. Both decomposition rate and NEP would decrease.
   b. Both decomposition rate and NEP would increase.
   c. Neither would change.
   d. Decomposition rate would increase and NEP would decrease.
   e. Decomposition rate would decrease and NEP would increase.

### LEVEL 3: SYNTHESIS/EVALUATION

9. **DRAW IT** Draw a simplified global water cycle showing ocean, land, atmosphere, and runoff from the land to the ocean. Add these annual water fluxes to the figure: ocean evaporation, 425 $km^3$; ocean evaporation that returns to the ocean as precipitation, 385 $km^3$; ocean evaporation that falls as precipitation on land, 40 $km^3$; evapotranspiration from plants and soil that falls as precipitation on land, 70 $km^3$; runoff to the oceans, 40 $km^3$. Based on these global numbers, how much precipitation falls on land in a typical year?
10. **EVOLUTION CONNECTION**
    Some biologists have suggested that ecosystems are emergent, "living" systems capable of evolving. One manifestation of this idea is environmentalist James Lovelock's Gaia hypothesis, which views Earth itself as a living, homeostatic entity—a kind of superorganism. If ecosystems are capable of evolving, would this be a form of Darwinian evolution? Why or why not?
11. **SCIENTIFIC INQUIRY**
    Using two neighboring ponds in a forest as your study site, design a controlled experiment to measure the effect of falling leaves on net primary production in a pond.
12. **WRITE ABOUT A THEME**
    **Energy Transfer** As described in Concept 55.4, decomposition typically occurs quickly in moist tropical forests. However, waterlogging in the soil of some moist tropical forests results in a buildup of organic matter ("peat"; see Figure 29.11) over time. In a short essay (100–150 words), discuss the relationship of net primary production, net ecosystem production, and decomposition for such an ecosystem. Are NPP and NEP likely to be positive? What do you think would happen to NEP if a landowner drained the water from a tropical peatland, exposing the organic matter to air?

*For selected answers, see Appendix A.*

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*BioFlix* **Tutorial** The Carbon Cycle
**Tutorial** Energy Flow Through Ecosystems
**Activities** Pyramids of Production • GraphIt!: Animal Food Production Efficiency and Food Policy • Energy Flow and Chemical Cycling • The Carbon Cycle • The Nitrogen Cycle • The Global Carbon Cycle
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