Ecosystems and Restoration Ecology

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Figure 55.1 How can foxes transform a grassland into tundra?

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 return degraded ecosystems to a more natural state

Arctic terns, major guano generators

Transformed to Tundra

The arctic fox (*Vulpes lagopus*) is a predator native to arctic regions of North America, Europe, and Asia **(Figure 55.1)**. Valued for its fur, it was introduced onto hundreds of subarctic islands between Alaska and Russia around 1900 in an effort to establish populations that could be easily harvested. The fox's introduction had a surprising effect: It transformed many habitats on the islands from grassland to tundra.

How did the presence of foxes transform the islands' vegetation from one biome to another? The foxes fed voraciously on the islands' seabirds, decreasing their density almost 100-fold compared to that on fox-free islands. Fewer seabirds meant less bird guano (waste), a primary source of essential nutrients for plants on the islands. Researchers suspected that the scarcity of nutrients reduced the growth of nutrient-hungry grasses, favoring instead the slower-growing forbs (nonwoody plants other than grasses) and shrubs typical of tundra. To test this explanation, the scientists added fertilizer to plots of tundra on one of the fox-infested islands. Three years later, the fertilized plots had reverted back to grassland.

Each of these "fox islands" and the community of organisms on it is an example of 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 large area, such as a lake, forest, or island, or a microcosm, such as the space under a fallen log or a small desert spring **(Figure 55.2)**. As with populations and communities, the boundaries of ecosystems are not always discrete. Many ecologists view the entire

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MB **Get Ready for This Chapter**

Figure 55.2 **A desert spring ecosystem.**

biosphere as a global ecosystem, a composite of all the local ecosystems on Earth.

An ecosystem, regardless of its size, has two key emergent properties: energy flow and chemical cycling. Energy enters most ecosystems as sunlight. This light energy is converted to chemical energy by autotrophs, passed to heterotrophs in the organic compounds of food, and dissipated as heat. As for chemical cycling, elements such as carbon and nitrogen are passed between the biotic and abiotic components of the ecosystem. Photosynthetic and chemosynthetic organisms take up 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 organisms and by decomposers that break down organic wastes and dead organisms.

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

Ecosystem processes yield resources critical to human survival and welfare, ranging from the food we eat to the oxygen we breathe. In this chapter, we'll explore the dynamics of energy flow and chemical cycling, emphasizing the results of ecosystem experiments. We'll also consider how human activities have affected energy flow and chemical cycling. Finally, we'll examine the growing science of restoration ecology, which focuses on returning degraded ecosystems to a more natural state.

CONCEPT 55.1

Physical laws govern energy flow and chemical cycling in ecosystems

Cells transform energy and matter, subject to the laws of thermodynamics (see Concept 8.1). Cell biologists study these transformations within organelles and cells and measure the amounts of energy and chemical compounds that cross the cells' boundaries. Ecosystem ecologists do the same thing, except in their case the "cell" is an entire ecosystem. By determining trophic levels of feeding relationships (see Concept 54.2) and studying how organisms interact with their physical environment, ecologists can follow the transformations of energy in an ecosystem and map the movements of chemical elements.

Conservation of Energy

To study energy flow and chemical cycling, ecosystem ecologists use approaches based on laws of physics and chemistry. The first law of thermodynamics states that energy cannot be created or destroyed but only transferred or transformed (see Concept 8.1). 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. Ecosystem ecologists often measure energy transfers within and across ecosystems, in part to understand how many organisms a habitat can support and the amount of food humans can harvest from a site.

The second law of thermodynamics states that every exchange of energy increases the entropy of the universe. One implication of this law is that energy conversions are inefficient. Some energy is always lost as heat. As a result, each unit of energy that enters an ecosystem eventually exits as heat. Thus, energy flows through ecosystems—it does not cycle within them for long periods of time. Because energy flowing through ecosystems is ultimately lost as heat, most ecosystems would vanish if the sun were not continuously providing energy to Earth.

Conservation of Mass

Matter, like energy, cannot be created or destroyed. This **law of conservation of mass** is as important for ecosystems as are the laws of thermodynamics. 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. For example, a carbon atom in CO_2 might be released from the soil by a decomposer, taken up by a blade of grass through photosynthesis, consumed by a grazing animal, and returned to the soil in the animal's waste.

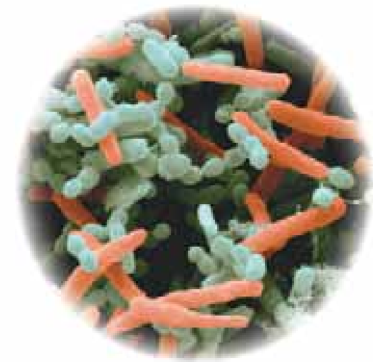
In addition to cycling within ecosystems, elements can also be gained or lost by an ecosystem. For example, a forest gains mineral nutrients—the essential elements that plants obtain from soil—that enter as dust or as solutes dissolved in rainwater or leached from rocks in the ground. Nitrogen is also supplied through the biological process of nitrogen fixation (see Figure 37.12). In terms of losses, some elements return to the atmosphere as gases, while others are carried out of the ecosystem by moving water or by wind. Like organisms, ecosystems are open systems, absorbing energy and mass and releasing heat and waste products.

Most gains and losses to ecosystems are small compared to the amounts that cycle within them. Even so, the balance between inputs and outputs is important because it determines whether an ecosystem stores or loses a given element. In particular, if a nutrient's outputs exceed its inputs, that nutrient will eventually limit production in that ecosystem. Human activities often change the balance of inputs and outputs considerably, as we'll see later in this chapter and in Concept 56.4.

Energy, Mass, and Trophic Levels

Ecologists group species in an ecosystem into trophic levels based on feeding relationships (see Concept 54.2). 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 use as fuel for cellular respiration and as building material for growth. The most common autotrophs are plants, algae, and photosynthetic prokaryotes, although chemosynthetic prokaryotes are the primary producers in ecosystems such as deep-sea hydrothermal vents (see Figure 52.15) and places deep under the ground or ice.

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**.



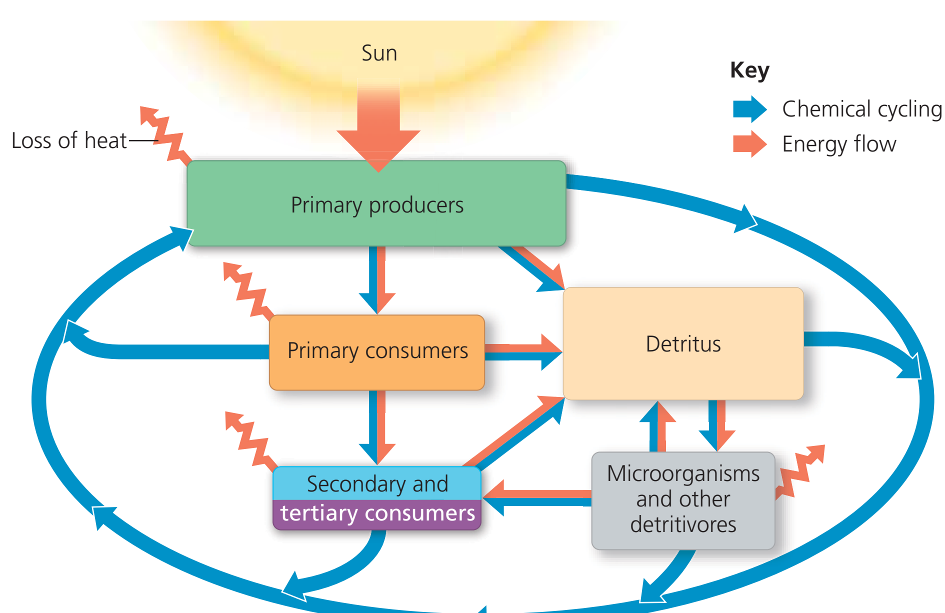
▲ **Rod-shaped and spherical bacteria in compost (colorized SEM)**

▼ **Fungi decomposing a dead tree**

▲ **Figure 55.3 Detritivores.**

Another group of heterotrophs is the **detritivores**, or **decomposers**, terms used 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. Although some animals (such as earthworms) feed on detritus, the main detritivores are prokaryotes and fungi **(Figure 55.3)**. These organisms secrete enzymes that digest organic material; they then absorb the breakdown products. Many detritivores are in turn eaten by secondary and tertiary consumers. In a forest, for instance, birds eat earthworms that have been feeding on leaf litter and its associated prokaryotes and fungi. As a result, chemicals originally synthesized by plants pass from the plants to leaf litter to detritivores to birds.

By recycling chemical elements to producers, detritivores also play a key role in the trophic relationships of an ecosystem **(Figure 55.4)**. Detritivores convert organic matter from all trophic levels to inorganic compounds usable by primary



➤ **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 within it. Energy (dark orange arrows) entering from the sun as radiation is transferred as chemical energy through the food web; each of these units of energy ultimately exits as heat radiated into space. Most transfers of nutrients (blue arrows) through the food web lead eventually to detritus; the nutrients then cycle back to the primary producers.

VISUAL SKILLS ➤ *In this diagram, one blue arrow leads to the box labeled "Primary consumers," and three blue arrows come out of this box. For each of these four arrows, describe an example of nutrient transfer that the arrow could represent.*

producers. When the detritivores excrete waste products or die, those inorganic compounds are returned to the soil. Producers can then absorb these elements and use them to synthesize organic compounds. If decomposition stopped, life as we know it would cease as detritus piled up and the supply of ingredients needed to synthesize organic matter was exhausted.

MB **Animation: Energy Flow and Chemical Cycling**

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** ➤ Use the second law of thermodynamics to explain why an ecosystem's energy supply must be continually replenished (see Concept 8.1).

For suggested answers, see Appendix A.

CONCEPT 55.2

Energy and other limiting factors control primary production in ecosystems

The theme of energy transfer underlies all biological interactions (see Concept 1.1). 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**. In ecosystems where the primary producers are chemoautotrophs, the initial energy input is chemical, and the initial products are the organic compounds synthesized by the microorganisms.

Ecosystem Energy Budgets

In most ecosystems, primary producers use light energy to synthesize energy-rich organic molecules, and consumers acquire their organic fuels secondhand (or even third- or fourth-hand) through food webs (see 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 approximately 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 19 years at 2013 energy consumption levels. The intensity of the solar energy striking Earth varies with latitude, with the tropics receiving the greatest input (see Figure 52.3). About 50% of 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.

However, 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 (1.50×10^{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 for their own cellular respiration. **Net primary production (NPP)** is equal to gross primary production minus the energy used by the primary producers (autotrophs) for their cellular respiration (R_a, where "a" stands for autotrophs):

$$NPP = GPP - R_a$$

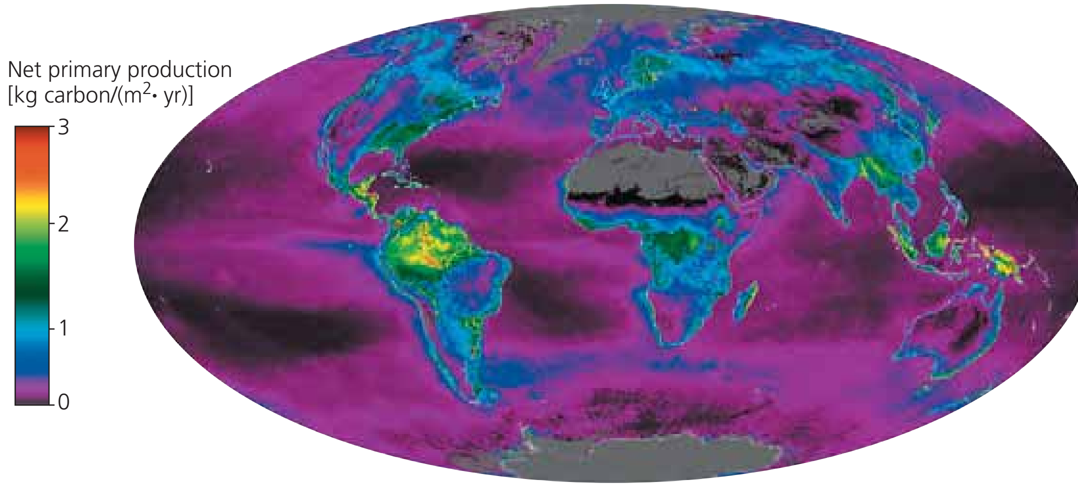
On average, NPP is about one-half of GPP. To ecologists, NPP is the key measurement because it represents the storage of chemical energy that will be available to consumers in the ecosystem. Using the analogy of a paycheck, you can think of net primary production (NPP) as the take-home pay, which equals gross primary production (GPP), the gross pay, minus respiration (R_a), the taxes.

Net primary production can be expressed as energy per unit area per unit time [$J/(m^2 \cdot yr)$] or as biomass (mass of vegetation) added per unit area per unit time [$g/(m^2 \cdot yr)$]. (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. The net primary production is the amount of *new* biomass added in a given period of time. Although the total biomass of a forest is large, its NPP 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. Images produced from satellite data show that different ecosystems vary considerably in

Figure 55.5 Global net primary production. The map is based on satellite-collected data, 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).

VISUAL SKILLS *Does this map accurately reflect the significance of wetlands, coral reefs, and coastal zones, which are highly productive habitats? Explain.*



their NPP **(Figure 55.5)**. For example, tropical rain forests are among the most productive terrestrial ecosystems and contribute a large portion of the planet's NPP. Estuaries and coral reefs also have very high NPP, but their contribution to the global total is smaller because these ecosystems cover only about one-tenth the area covered by tropical rain forests. In contrast, while the open oceans are relatively unproductive, their vast size means that together they contribute as much global NPP as terrestrial systems do.

Whereas NPP can be expressed as the amount of new biomass added by producers in a given period of time, **net ecosystem production (NEP)** is a measure of the *total biomass accumulation* during that time. NEP 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 because detecting small changes in O_2 flux in a large atmospheric O_2 pool is difficult.

Next, we'll examine factors that limit production in ecosystems, focusing first on aquatic ecosystems.

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, you 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 55.5 that there is no such gradient. What other factor strongly influences 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 nutrients that most often limit marine production are nitrogen and 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.

In one study, detailed in **Figure 55.6**, nutrient enrichment experiments found 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. Preventing such blooms is critical because their occurrence can lead to the formation of large marine "dead zones," regions in which oxygen concentrations drop to levels that are fatal to many organisms (see Figure 56.24).

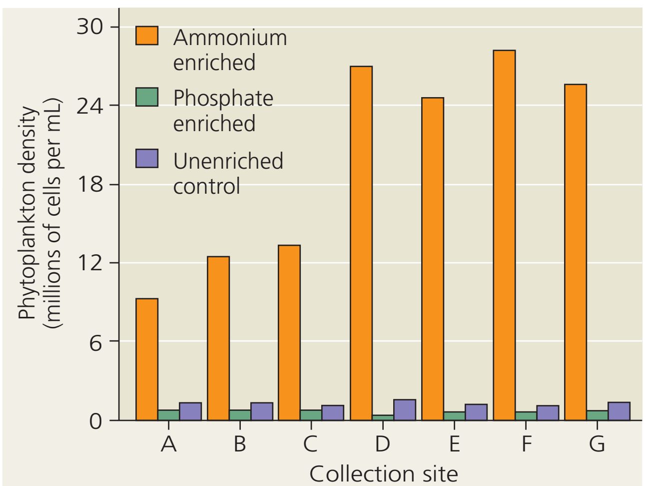
The macronutrients nitrogen and phosphorus are not the only nutrients that limit aquatic production. Several large areas of the ocean have low phytoplankton densities despite relatively high nitrogen concentrations. The Sargasso Sea, a subtropical region of the Atlantic Ocean, has some of the

Figure 55.6

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 through 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 The researchers concluded that nitrogen is the nutrient that limits phytoplankton growth in this ecosystem because adding phosphorus did not increase *Nannochloris* growth, whereas adding nitrogen increased phytoplankton density dramatically.

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

WHAT IF? ➤ *Predict how the results would change if water samples were drawn from areas where new duck farms had greatly increased the amount of pollution in the water. Explain.*

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 the Sargasso Sea and certain other regions compared to the oceans as a whole.

On the flip side, 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

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 (Fe)	1.08
N + P + metals, including Fe	12.90
N + P + Fe	12.00

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

Data from 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).

INTERPRET THE DATA ➤ *The element molybdenum (Mo) is another micronutrient that can limit primary production in the oceans. If the researchers found the following results for additions of Mo, what would you conclude about its relative importance for growth?*

N + P + Mo	6.0
N + P + Fe + Mo	72.0

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.

Nutrient limitation is also common in freshwater lakes. During the 1970s, scientists showed that the sewage and fertilizer runoff from farms and lawns adds considerable nutrients to lakes, promoting the growth of primary producers. When the primary producers die, detritivores decompose them, depleting the water of much or all of its oxygen. 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 52.15).

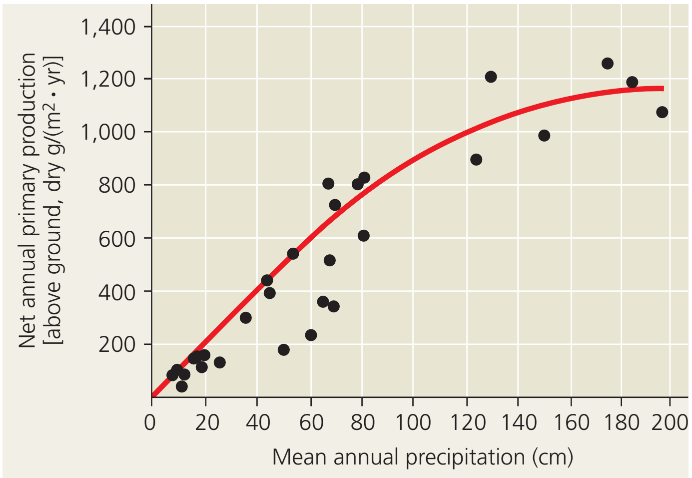
To control eutrophication, scientists need to know which nutrient is responsible. While nitrogen rarely limits primary production in lakes, many whole-lake experiments showed that phosphorus availability limited cyanobacterial growth. This and other ecological research led to the use of phosphate-free detergents and other 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 terrestrial ecosystems (see Figure 55.5). 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, with moderate climates and intermediate productivity.

The climate variables of precipitation and temperature are very useful for predicting NPP in terrestrial ecosystems. For example, primary production is greater in wetter ecosystems, as shown for the plot of NPP and annual precipitation

Figure 55.7 A global relationship between net primary production and mean annual precipitation for terrestrial ecosystems.



in **Figure 55.7**. NPP also increases with temperature and the amount of solar energy available to drive evaporation and transpiration.

Nutrient Limitations and Adaptations That Reduce Them

EVOLUTION Soil nutrients can 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. Note that 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.

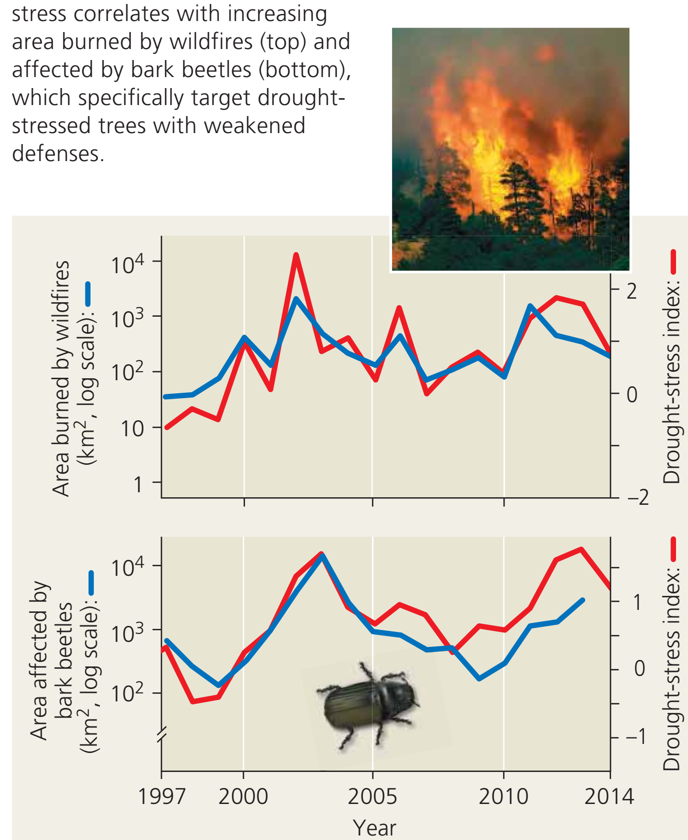
Various adaptations have evolved in plants that can increase their uptake of limiting nutrients. One important adaptation is the mutualism between plant roots and nitrogen-fixing bacteria. Another is the mycorrhizal association between plant roots and fungi that supply phosphorus and other limiting elements to plants (see Figure 37.15). Plant roots also have hairs and other anatomical features that increase the area of soil in contact with the roots (see Figures 33.9 and 35.3). Many plants release enzymes and other substances into the soil that increase the availability of limiting nutrients; such substances include phosphatases, which cleave a phosphate group from larger molecules, and certain molecules (called chelating agents) that make micronutrients such as iron more soluble in the soil.

Effects of Climate Change on Production

As we've seen, climatic factors such as temperature and precipitation affect terrestrial NPP. Thus, we might expect that climate change could affect production in terrestrial ecosystems—and it does. For example, satellite data showed that from 1982 to 1999, NPP increased by 6% in terrestrial ecosystems. Nearly half of this increase occurred in the tropical forests of the Amazon, where changing climate patterns had caused cloud cover to decrease, thereby increasing the amount of solar energy available to primary producers. Since 2000, however, these gains in NPP have been erased. This reversal was affected by another aspect of climate change: a series of major droughts in the southern hemisphere.

Another effect of climate change on NPP can be seen in the impact of "hotter droughts" on wildfires and insect outbreaks. Consider forests in the American southwest. In recent decades, the forests of this region have experienced droughts driven by climate warming and changing patterns of precipitation. These ongoing droughts, in turn, have led to increases in the area burned by wildfires and the area affected by outbreaks of bark beetles such as the mountain pine beetle *Dendroctonus ponderosae* (**Figure 55.8**). As a result, tree mortality has increased and NPP has decreased in these forests.

Figure 55.8 Climate change, wildfires, and insect outbreaks. Forests in the American southwest are experiencing hotter droughts caused by rising temperatures in the summer and reduced snowfall in the winter. The drought-stress index indicates how greatly trees are stressed by these conditions; rising values of this index correspond to increasing drought. Higher drought stress correlates with increasing area burned by wildfires (top) and affected by bark beetles (bottom), which specifically target drought-stressed trees with weakened defenses.



PROBLEM-SOLVING EXERCISE

Can an insect outbreak threaten a forest's ability to absorb CO_2 from the atmosphere?

One way to combat climate change is to plant trees, since trees absorb large amounts of CO_2 from the atmosphere, converting it to biomass through photosynthesis. But what happens to the carbon stored as biomass in trees when an insect population explodes in number? Such insect outbreaks have become more frequent with climate change.

▲ A tree with dozens of "pitch tubes," indications of a damaging outbreak of mountain pine beetles

Instructors: A version of this Problem-Solving Exercise can be assigned in MasteringBiology.

In this exercise, you will test whether an outbreak of the mountain pine beetle (*Dendroctonus ponderosae*) alters the amount of CO_2 that a forest ecosystem absorbs from and releases to the atmosphere.

Your Approach The principle guiding your investigation is that every ecosystem both absorbs and releases CO_2. Net ecosystem production (NEP) indicates whether an ecosystem is a carbon sink (absorbing more CO_2 from the atmosphere than it releases; this occurs when NEP > 0) or a carbon source (releasing more CO_2 than it absorbs; NEP < 0). To find out if the mountain pine beetle affects NEP, you will determine a forest's NEP before and after a recent outbreak of this insect.

Your Data From 2000 to 2006, an outbreak of the mountain pine beetle killed millions of trees in British Columbia, Canada. The impact of such outbreaks on whether forests gain carbon (NEP > 0) or lose carbon (NEP < 0) was poorly understood. To find out, ecologists estimated net primary production (NPP) and cellular respiration by decomposers and other heterotrophs (R_h), before and after the outbreak. These data allow forest NEP to be calculated from the equation NEP $=$ NPP $-$ R_h.

	NPP $[g/(m^2 \cdot yr)]$	R_h $[g/(m^2 \cdot yr)]$
Before outbreak	440	408
After outbreak	400	424

Your Analysis

1. Before the outbreak, was the forest a carbon sink or a carbon source? After the outbreak?
2. NEP is often defined as NEP $=$ GPP $-$ R_T, where GPP is gross primary production and R_T equals cellular respiration by autotrophs (R_a) *plus* cellular respiration by heterotrophs (R_h). Use the relation NPP $=$ GPP $-$ R_a to show that the two equations for NEP introduced in this exercise are equivalent.
3. Based on your results in question 1, predict whether the mountain pine beetle outbreak could have feedback effects on the global climate. Explain.

Climate change can also affect whether an ecosystem stores or loses carbon over time. As discussed earlier, net ecosystem production, or NEP, reflects the total biomass accumulation that occurs during a given period of time. When NEP > 0, the ecosystem gains more carbon than it loses; such ecosystems store carbon and are said to be a carbon *sink*. In contrast, when NEP < 0, the ecosystem loses more carbon than it gains; such ecosystems are a carbon *source*.

Recent research shows that climate change can cause an ecosystem to switch from a carbon sink to a carbon source. For example, in some arctic ecosystems, climate warming has increased the metabolic activities of soil microorganisms, causing an uptick in the amount of CO_2 produced in cellular respiration. In these ecosystems, the total amount of CO_2 produced in cellular respiration now exceeds what is absorbed in photosynthesis. As a result, these ecosystems—which once were carbon sinks—are now carbon sources. When this happens, an ecosystem may contribute to climate change by releasing more CO_2 than it absorbs. In the **Problem-Solving Exercise**, you can examine how outbreaks of an insect population may affect the NEP of forest ecosystems.

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. **WHAT IF? ➤** Suppose a forest was heavily burned by a wildfire. Predict how NEP of this forest would change over time.
4. **MAKE CONNECTIONS ➤** Explain how nitrogen and phosphorus, the nutrients that most often limit primary production, are necessary for the Calvin cycle to function in photosynthesis (see Concept 10.3).

For suggested answers, see Appendix A.

CONCEPT 55.3

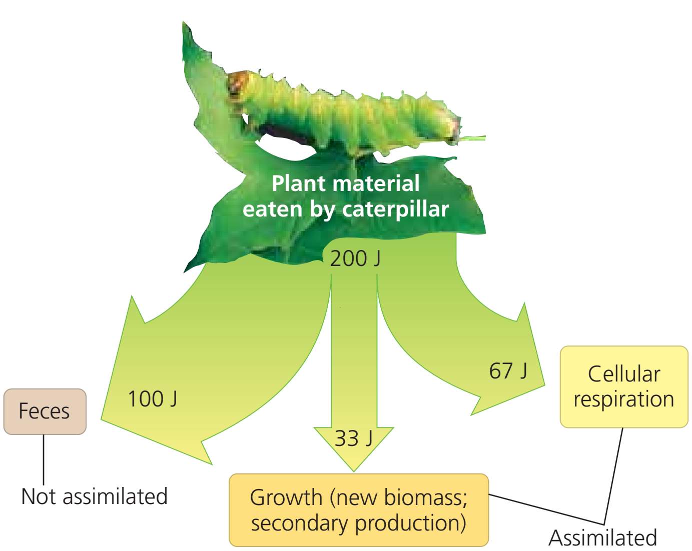
Energy transfer between trophic levels is typically only 10% efficient

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 field where cattle have been grazing will attest. Most of an ecosystem's production is eventually consumed by detritivores. Let's analyze the process of energy transfer more closely.

Production Efficiency

We'll begin by examining secondary production in one organism—a caterpillar. When a caterpillar feeds on a leaf, only about 33 J out of 200 J, or one-sixth of the potential energy in the leaf, is used for secondary production, or growth **(Figure 55.9)**. The caterpillar stores some of the remaining energy in organic compounds that will be used for cellular respiration and passes the rest in its feces. The energy 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 ecosystem as heat. Only the chemical energy stored by herbivores as biomass, through growth or the production of offspring, is available as food to secondary consumers.

▼ Figure 55.9 Energy partitioning within a link of the food chain.



INTERPRET THE DATA ➤ *What percentage of the energy in the caterpillar's food is actually used for secondary production (growth)?*

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 amount of energy an organism has consumed and used for growth, reproduction, and respiration. **Production efficiency**, therefore, is the percentage of energy stored in assimilated food that is used for growth and reproduction, *not* respiration. For the caterpillar in Figure 55.9, 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 mainly ectothermic (see Concept 40.3), 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.

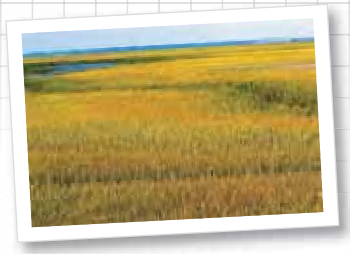
Trophic efficiency is the percentage of production transferred from one trophic level to the next. Trophic efficiencies must always be less than production efficiencies because they take into account not only the energy lost through respiration and contained in feces, but also the energy in organic material in a lower trophic level that is not consumed by the next trophic level. Trophic efficiencies range from roughly 5% to 20% in different ecosystems, but on average are only about 10%. 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. 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 (carnivores), then only 1% of net primary production is available to secondary consumers (10% of 10%). In the **Scientific Skills Exercise**, you can calculate trophic efficiency and other measures of energy flow in a salt marsh ecosystem.

The progressive loss of energy along a food chain 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 Figure 54.15).

The loss of energy with each transfer in a food chain can be represented by an *energy pyramid*, in which the net productions of different trophic levels are arranged in tiers **(Figure 55.10)**. The width of each tier is proportional to the

SCIENTIFIC SKILLS EXERCISE

Interpreting Quantitative Data



How Efficient Is Energy Transfer in a Salt Marsh Ecosystem? In a classic experiment, John Teal studied the flow of energy through the producers, consumers, and detritivores in a salt marsh. In this exercise, you will use the data from this study to calculate some measures of energy transfer between trophic levels in this ecosystem.

How the Study Was Done Teal measured the amount of solar radiation entering a salt marsh in Georgia over a year. He also measured the aboveground biomass of the dominant primary producers, which were grasses, as well as the biomass of the dominant consumers, including insects, spiders, and crabs, and of the detritus that flowed out of the marsh to the surrounding coastal waters. To determine the amount of energy in each unit of biomass, he dried the biomass, burned it in a calorimeter, and measured the amount of heat produced.

Data from the Study

Form of Energy	kcal/(m^2 · yr)
Solar radiation	600,000
Gross grass production	34,580
Net grass production	6,585
Gross insect production	305
Net insect production	81
Detritus leaving marsh	3,671

Data from J. M. Teal, Energy flow in the salt marsh ecosystem of Georgia, *Ecology* 43:614–624 (1962).

INTERPRET THE DATA

1. What percentage of the solar energy that reaches the marsh is incorporated into gross primary production? Into net primary production?
2. How much energy is lost by primary producers as respiration in this ecosystem? How much is lost as respiration by the insect population?
3. If all of the detritus leaving the marsh is plant material, what percentage of all net primary production leaves the marsh as detritus each year?

Instructors: A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

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 predators is one reason they tend to be vulnerable to extinction (and to the evolutionary consequences of small population size; see Concept 23.3).

One important ecological consequence of low trophic efficiencies is represented in a *biomass pyramid*, in which each tier represents 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 55.11a)**. Certain aquatic ecosystems, however, have inverted biomass pyramids: Primary consumers outweigh the producers in these ecosystems **(Figure 55.11b)**. Such inverted biomass pyramids occur because the producers—phytoplankton—grow, reproduce, and are consumed so quickly by the zooplankton that their total biomass remains at comparatively low levels. However, because the phytoplankton continually replace their biomass

Figure 55.10 An idealized pyramid of energy. 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.

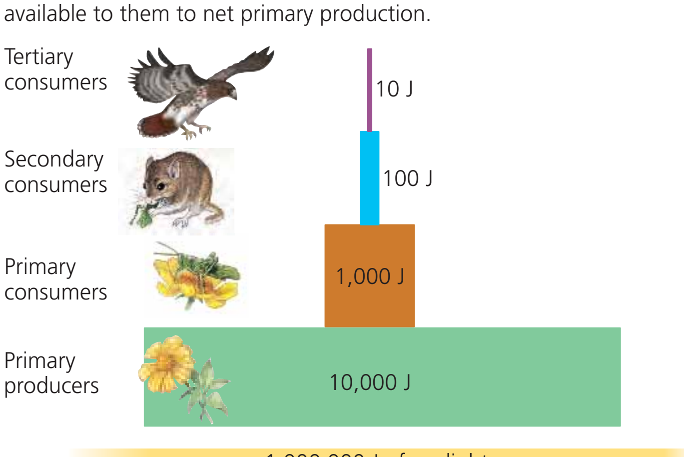
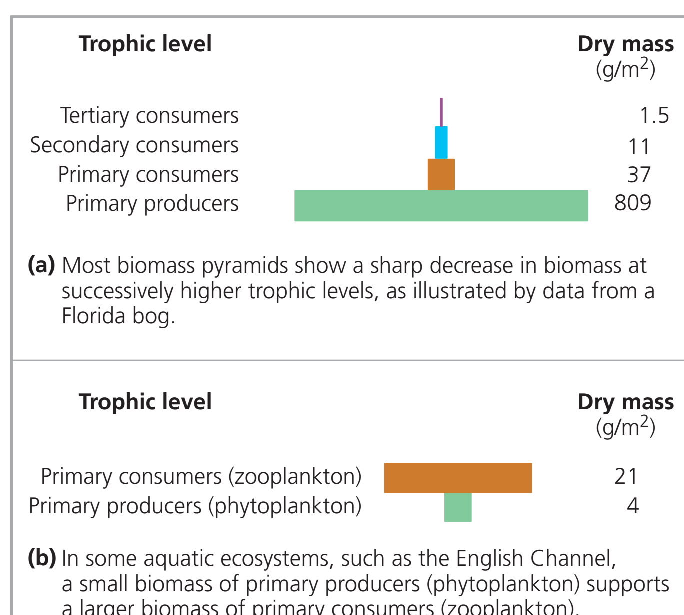


Figure 55.11 Pyramids of biomass. Numbers denote the dry mass of all organisms at each trophic level.



(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 biomass of primary producers (phytoplankton) supports a larger biomass of primary consumers (zooplankton).

at such a rapid rate, they can support a biomass of zooplankton bigger than their own biomass. Likewise, because phytoplankton reproduce so quickly and have much higher production than zooplankton, the pyramid of *energy* for this ecosystem is still bottom-heavy, like the one in Figure 55.10.

The dynamics of energy flow through ecosystems have implications for human consumers. For example, 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. Agriculture worldwide could, in fact, feed many more people and require less land if we all fed more efficiently—as primary consumers, eating plant material.

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. **WHAT IF?** ➤ Detritivores are consumers that obtain their energy from detritus. How many joules of energy are potentially available to detritivores in the ecosystem represented in Figure 55.10?

For suggested answers, see Appendix A.

CONCEPT 55.4

Biological and geochemical processes cycle nutrients and water in ecosystems

Although most ecosystems receive abundant solar energy, chemical elements are available only in limited amounts. Life 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 are released. When the organism dies, the atoms in its body are returned to the atmosphere, water, or soil by decomposers. By liberating nutrients from organic matter, decomposition replenishes the pools of inorganic nutrients that plants and other autotrophs use to build new organic matter.

Decomposition and Nutrient Cycling Rates

Decomposers are heterotrophs that get their energy from detritus. Their growth is controlled by the same factors that limit primary production in ecosystems, including temperature, moisture, and nutrient availability. Decomposers usually grow faster and decompose material more quickly in warmer ecosystems **(Figure 55.12)**. In tropical rain forests, most organic material decomposes in a few months to a few years, whereas 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 ecosystem's nutrients 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 years 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 cold and wet, such as peatlands, store large amounts of organic matter. Decomposers grow poorly there, and net primary production greatly exceeds the rate of decomposition.

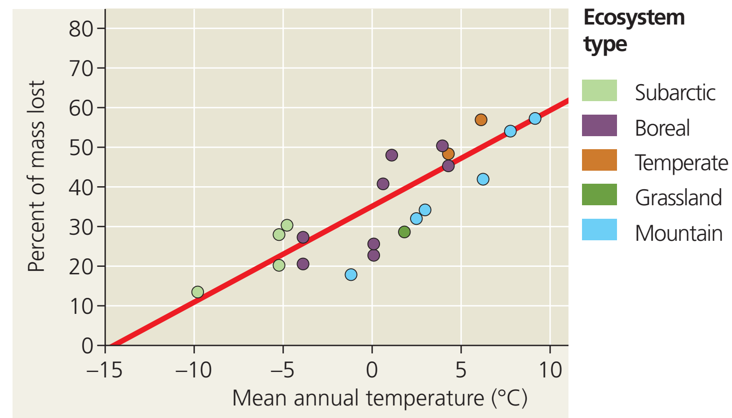
In aquatic ecosystems, decomposition in anaerobic muds can take 50 years or longer. Bottom sediments are comparable

Figure 55.12

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. Three years later, they returned to see how much of each sample had decomposed.

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



Conclusion Decomposition rate increases with temperature across much of Canada.

Data from J. A. Trofymow and the CIDET Working Group, *The Canadian Intersite Decomposition Experiment: Project and Site Establishment Report* (Information Report BC-X-378), Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre (1998) and 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?*

to the detritus layer in terrestrial ecosystems, but 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 exchange between the bottom layers of water and surface waters (as occurs in the upwelling regions described earlier).

Biogeochemical Cycles

Because nutrient cycles involve both biotic and abiotic components, they are called **biogeochemical cycles**. We can recognize two general scales 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.

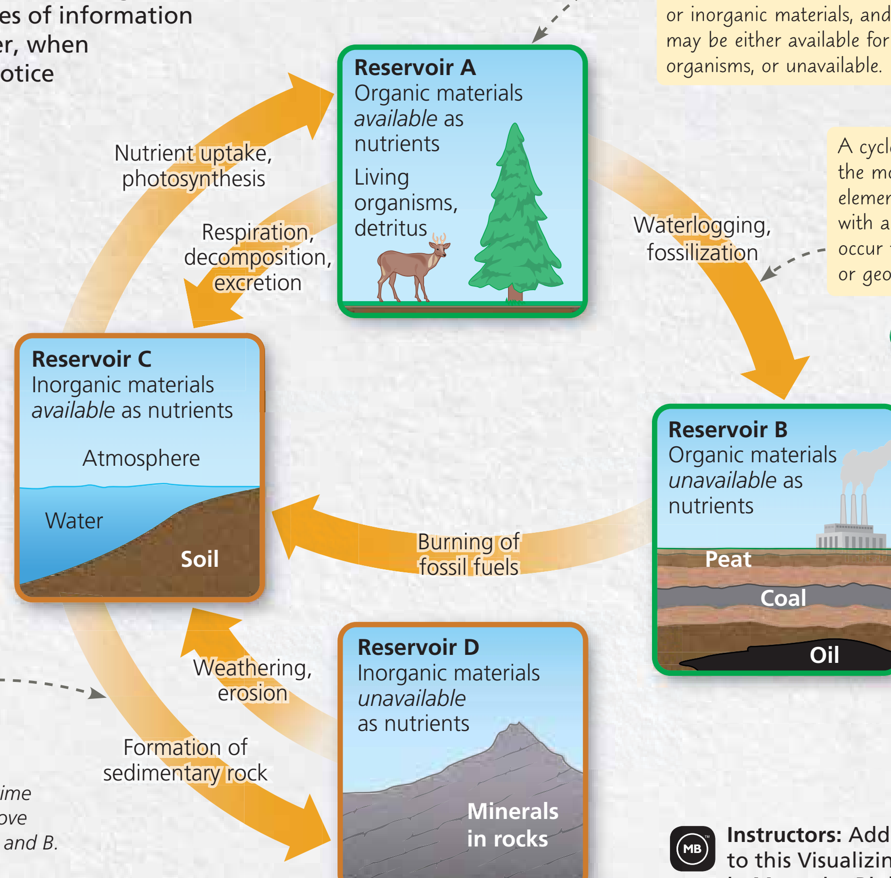
Let's first look at a general model of nutrient cycling that includes reservoirs where elements exist and processes that transfer elements between them **(Figure 55.13)**. The nutrients in living organisms and detritus (reservoir A) are available to other organisms when consumers feed and when detritivores consume nonliving organic matter. The low pH and low oxygen levels found in the waterlogged sediments of swamps can inhibit decomposition, leading to the formation of peat. When this occurs, organic materials from dead organisms can be transferred from reservoir A to reservoir B; eventually, peat may be converted to fossil fuels such as coal or oil. Inorganic materials that are dissolved in water or present in soil or air (reservoir C) are available for use. 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.

Figure 55.14 provides a detailed look at the cycling of water, carbon, nitrogen, and phosphorus. When you study each cycle, consider which steps are driven primarily by

▼ Figure 55.13 Visualizing Biogeochemical Cycles

A biogeochemical cycle diagram summarizes the movements of a chemical element between living and nonliving components of the biosphere. This figure uses a generic model of nutrient cycling to show what types of information may be represented. Later, when you study Figure 55.14, notice how this information is depicted in the specific nutrient cycles.

Cycle diagrams include a representation of the **reservoirs** in which the chemical element is found. A reservoir can consist of either organic or inorganic materials, and those materials may be either available for direct use by organisms, or unavailable.



A cycle diagram also represents the movements of the chemical element between reservoirs, usually with arrows. These movements occur through biological, chemical, or geologic processes.

1 *Suppose decomposition rates slowed greatly. Use the diagram to hypothesize how that might affect the transfer of materials from reservoir A to reservoirs B and C.*

Nutrient cycle diagrams may not represent the time scale of the different processes. Thus, it's important to keep in mind that some processes, such as photosynthesis, occur on a short time scale within an individual's lifespan, while others, such as rock formation, occur on a long geologic time scale.

2 *Compare and contrast the time scales at which materials move into and out of reservoirs A and B.*

Instructors: Additional questions related to this Visualizing Figure can be assigned in MasteringBiology.

▼ 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.

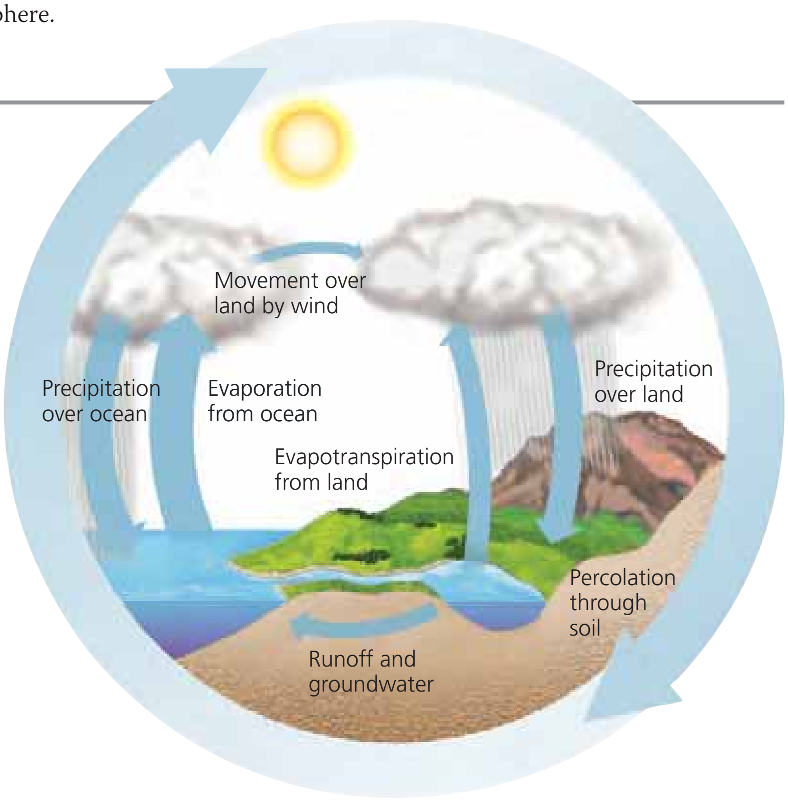
The Water Cycle

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

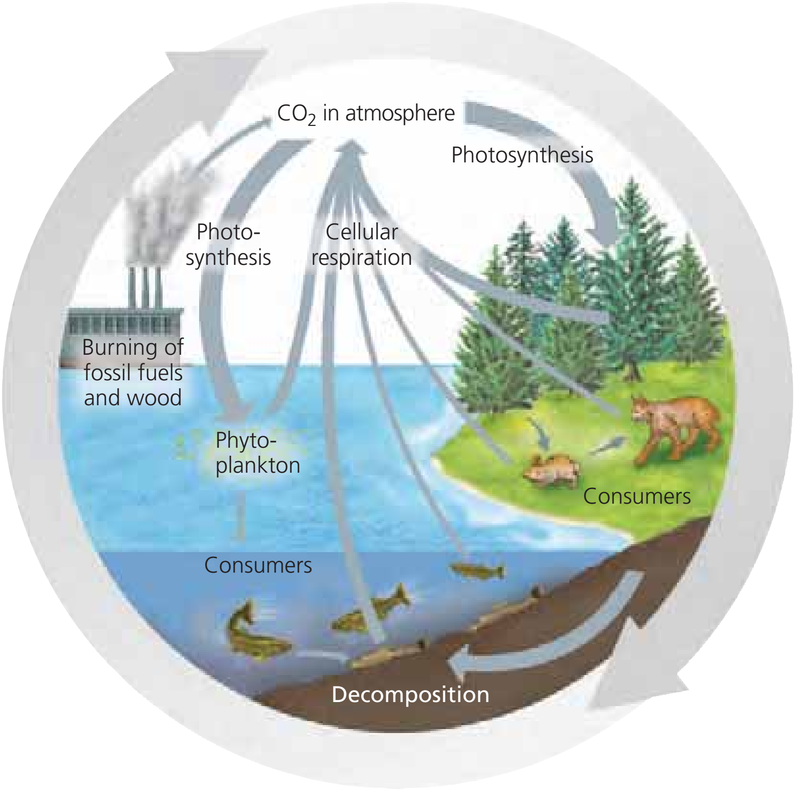
Forms available to life All organisms are capable of exchanging water directly with their environment. Liquid water is the primary physical phase in which water is used, though some organisms can harvest water vapor. Freezing of soil water can limit water availability to terrestrial plants.

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, carbon remains in this pool for long periods of time. All organisms are capable of returning carbon directly to their environment in its original form (CO_2) through respiration.

Key processes Photosynthesis by plants and phytoplankton removes substantial amounts of atmospheric CO_2 each year. This quantity is approximately equal to the 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.

MB **BioFlix® Animation: The Carbon Cycle**

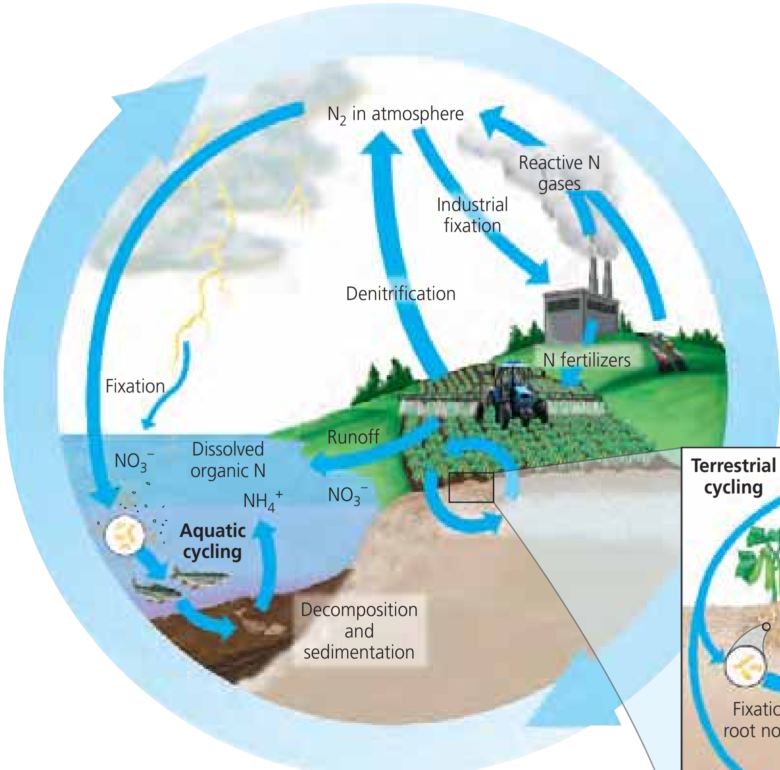
The Nitrogen Cycle

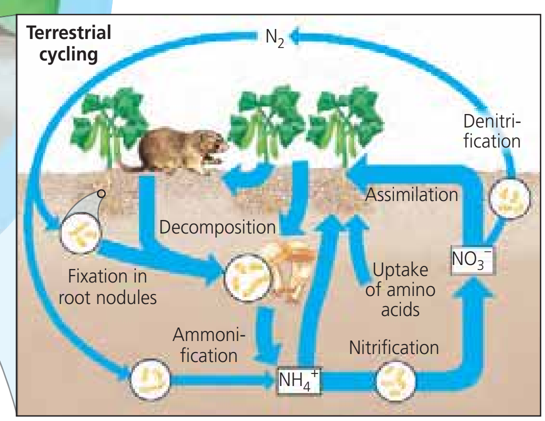
Biological importance Nitrogen is part of amino acids, proteins, and nucleic acids and is often a limiting plant nutrient.

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 and volcanic activity, 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. Examples include nitrifying bacteria, which convert ammonium to nitrate, and denitrifying bacteria, which convert nitrate to nitrogen gas. Human activities also release large quantities of reactive nitrogen gases, such as nitrogen oxides, to the atmosphere.





Animation: The Nitrogen Cycle

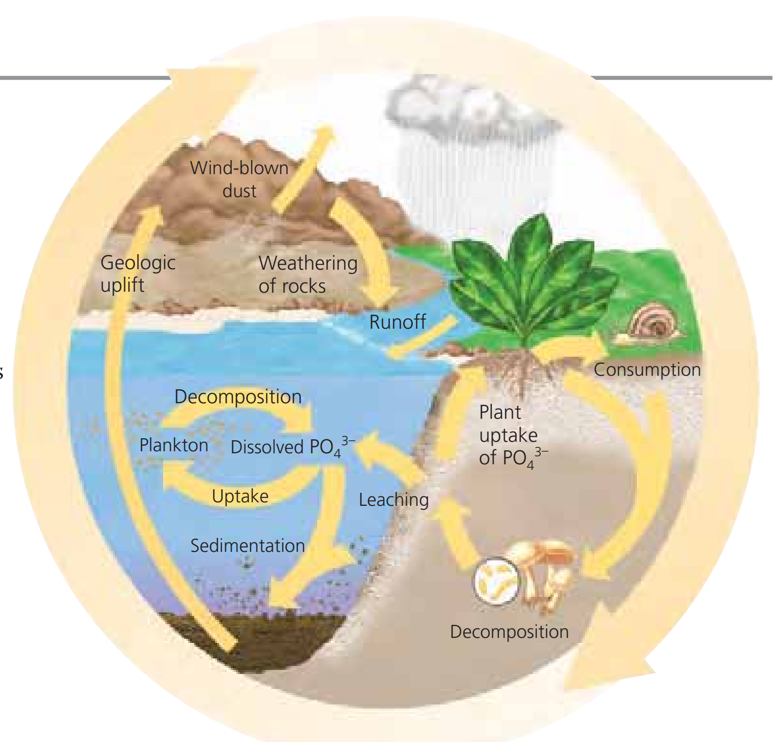
The Phosphorus Cycle

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.



biological processes. For the carbon cycle, for instance, plants, animals, and other organisms control most of the key steps, including photosynthesis and decomposition. For the water cycle, however, purely physical processes control many key steps, such as evaporation from the oceans. Note also that human actions, such as the burning of fossil fuels and the production of fertilizers, have had major effects on the global cycling of carbon and nitrogen.

How have ecologists worked out the details of chemical cycling in various ecosystems? One common method is to follow the movement of naturally occurring, nonradioactive isotopes through the biotic (organic) and abiotic (inorganic) components of an ecosystem. Another 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. This "spike" of ^{14}C can reveal where and how quickly carbon flows into ecosystem components, including plants, soils, and ocean water.

Case Study: Nutrient Cycling in the Hubbard Brook Experimental Forest

Since 1963, ecologist Gene Likens and 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. Impermeable 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 55.15a)**. 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.

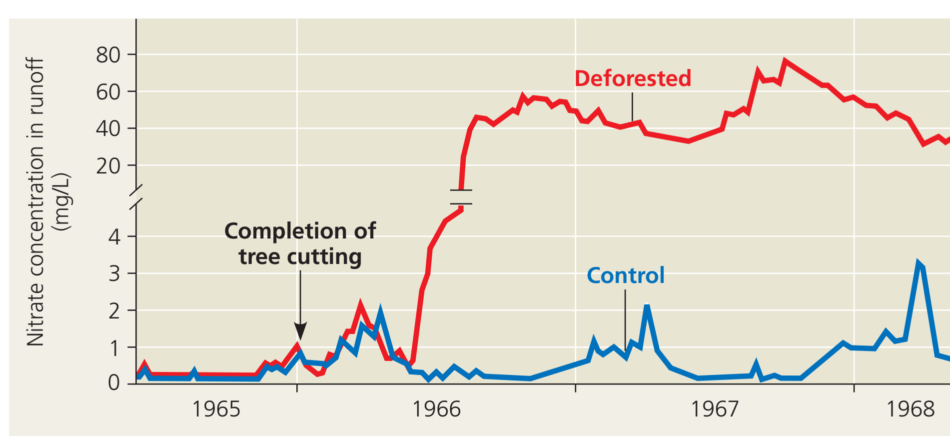
Preliminary studies confirmed that internal cycling conserved most of the mineral nutrients in the system. For example, only about 0.3% more calcium (Ca^{2+}) leaves a valley via its creek than is added by rainwater, and this small net loss is probably replaced by chemical decomposition of the bedrock. 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 55.15b)**. 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. Most remarkable was the loss of nitrate, whose concentration in the creek increased 60-fold, reaching levels considered unsafe for drinking water **(Figure 55.15c)**. The Hubbard Brook deforestation study showed that the amount of nutrients leaving an intact

Figure 55.15 Nutrient cycling in the Hubbard Brook Experimental Forest: an example of long-term ecological research.

(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.

MB **Instructors**: A related Experimental Inquiry Tutorial can be assigned in MasteringBiology.

forest ecosystem is controlled mainly by the plants. Retaining nutrients in an ecosystem helps to maintain the productivity of the system, as well as to avoid algal blooms and other problems caused by excess nutrient runoff.

Interview with Eugene Likens: Co-founder of the Hubbard Brook Forest Study

CONCEPT CHECK 55.4

1. **DRAW IT ➤** For each of the four biogeochemical cycles 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 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 (see Concept 54.3). Sometimes, however, that recovery takes centuries, 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 damaged ecosystems.

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, 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 grade the site with heavy equipment to reestablish a gentle slope, spreading topsoil when the slope is in place **(Figure 55.16)**.

After any physical reconstruction of the ecosystem is complete, the next step is biological restoration. The long-term objective of restoration is to return an ecosystem as closely as possible to its predisturbance state. **Figure 55.17** explores four ambitious and successful restoration projects. These and the many other such projects throughout the world often employ two key strategies: bioremediation and biological augmentation.

Bioremediation

Using organisms—usually prokaryotes, fungi, or plants—to detoxify polluted ecosystems is known as **bioremediation**. Some plants and lichens adapted to soils containing heavy metals can accumulate high concentrations of toxic metals such as 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

▼ **Figure 55.16 A gravel and clay mine site in New Jersey before and after restoration.**

(a) In 1991, before restoration

(b) In 2000, near the completion of restoration

▼ Figure 55.17 Exploring Restoration Ecology Worldwide

The examples highlighted in this figure are just a few of the many restoration ecology projects taking place around the world.

Kissimmee River, Florida

In the 1960s, the Kissimmee River was converted from a meandering river to a 90-km canal to control flooding. This channelization diverted water from the floodplain, causing the wetlands to dry up, 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.

Succulent Karoo, South Africa

In the Succulent Karoo 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 with the hope of reestablishing a breeding population of this colorful bird on New Zealand's North Island.

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 seaweeds and seagrasses from natural beds using artificial substrates, and hand seeding (shown in this photograph).

species that grows on soil polluted with uranium dust left over from mining. The lichen concentrates uranium in a dark 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 (see Concept 27.6). 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)**.

Biological Augmentation

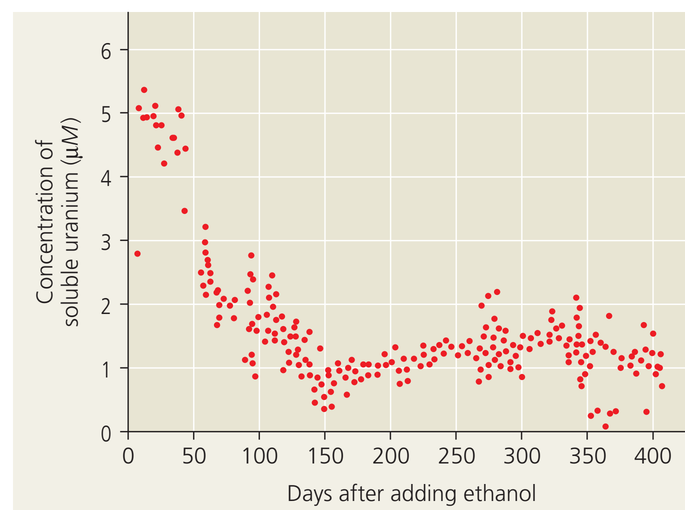
In contrast to bioremediation, which is a strategy for removing harmful substances from an ecosystem, **biological augmentation** uses organisms to *add* essential materials to a degraded ecosystem. To augment ecosystem processes, restoration ecologists need to determine which factors, such as chemical 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 Concept 31.1). 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 always ensure that animal species will recolonize a site and persist there. Because animals provide critical ecosystem services, including pollination and seed dispersal, restoration ecologists sometimes help wildlife to reach and use restored ecosystems. They might release animals at a site or establish habitat corridors that connect a restored site to places where the animals are found. They sometimes establish artificial perches for birds to use. These and other efforts can increase the biodiversity of restored ecosystems and help the community persist.

▼ Figure 55.18 Bioremediation of groundwater contaminated with uranium at Oak Ridge National Laboratory, Tennessee.

(a) Wastes containing uranium were dumped in these four unlined pits for more than 30 years, contaminating soils and groundwater.



(b) After ethanol was added, microbial activity decreased the concentration of soluble uranium in groundwater near the pits.

Ecosystems: *A Review*

Figure 55.19 illustrates energy transfer, nutrient cycling, and other key processes for an arctic tundra ecosystem. Note the conceptual similarities between this figure and Make Connections Figure 10.23, "The Working Cell." The scale of the two figures is different, but the physical laws and biological rules that govern life apply equally to both systems.

CONCEPT CHECK 55.5

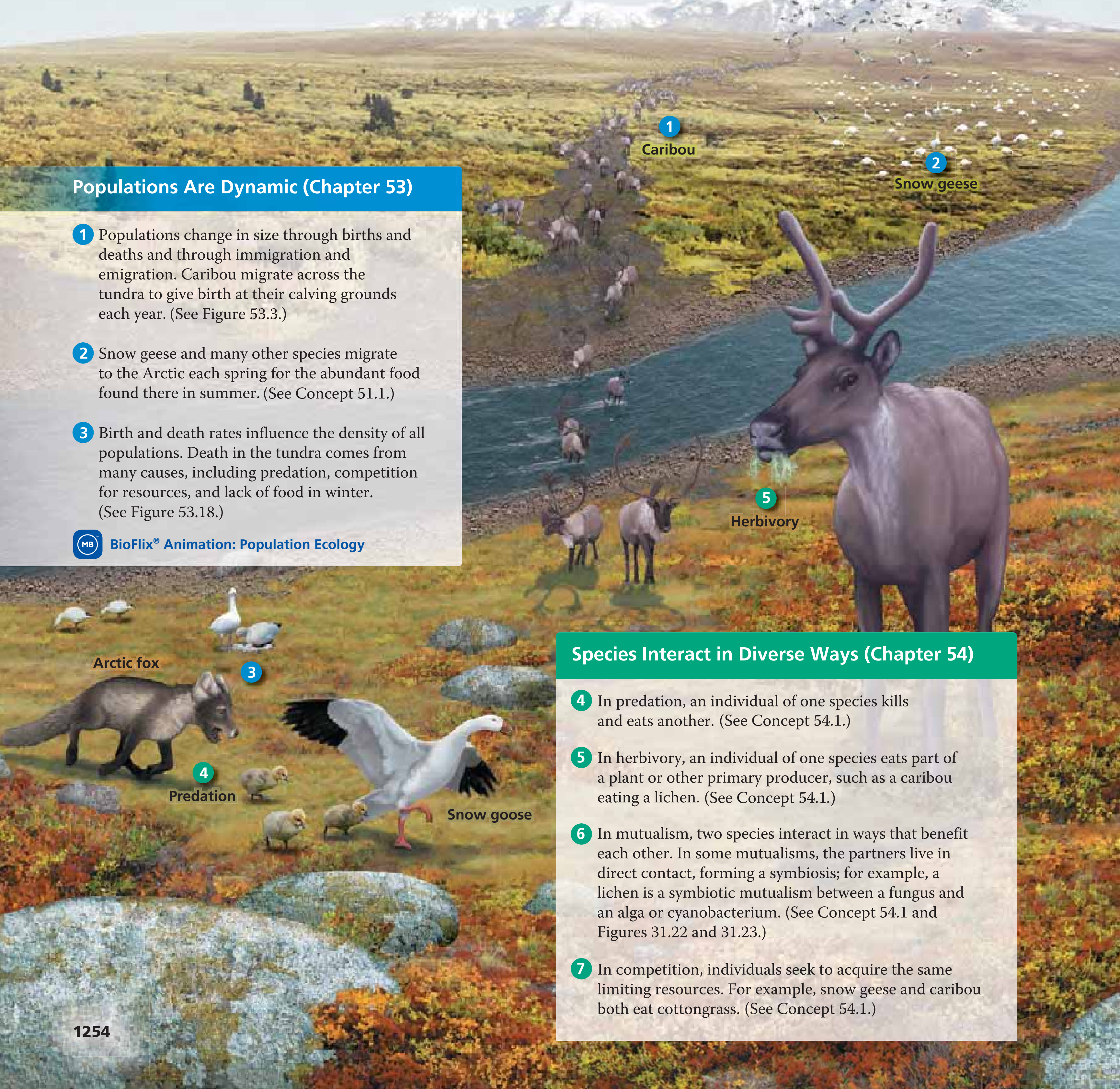
1. Identify the main goal of restoration ecology.
2. **WHAT IF? ➤** In what way is the Kissimmee River project a more complete ecological restoration than the Maungatautari project (see Figure 55.17)?

For suggested answers, see Appendix A.

▼ **Figure 55.19** **MAKE CONNECTIONS**

The Working Ecosystem

This arctic tundra ecosystem teems with life in the short two-month growing season each summer. In ecosystems, organisms interact with each other and with the environment around them in diverse ways, including those illustrated here.



Populations Are Dynamic (Chapter 53)

1. Populations change in size through births and deaths and through immigration and emigration. Caribou migrate across the tundra to give birth at their calving grounds each year. (See Figure 53.3.)

2. Snow geese and many other species migrate to the Arctic each spring for the abundant food found there in summer. (See Concept 51.1.)

3. Birth and death rates influence the density of all populations. Death in the tundra comes from many causes, including predation, competition for resources, and lack of food in winter. (See Figure 53.18.)

MB **BioFlix® Animation: Population Ecology**

Species Interact in Diverse Ways (Chapter 54)

4. In predation, an individual of one species kills and eats another. (See Concept 54.1.)

5. In herbivory, an individual of one species eats part of a plant or other primary producer, such as a caribou eating a lichen. (See Concept 54.1.)

6. In mutualism, two species interact in ways that benefit each other. In some mutualisms, the partners live in direct contact, forming a symbiosis; for example, a lichen is a symbiotic mutualism between a fungus and an alga or cyanobacterium. (See Concept 54.1 and Figures 31.22 and 31.23.)

7. In competition, individuals seek to acquire the same limiting resources. For example, snow geese and caribou both eat cottongrass. (See Concept 54.1.)

Organisms Transfer Energy and Matter in Ecosystems (Chapter 55)

8 Primary producers convert the energy in sunlight to chemical energy through photosynthesis. Their growth is often limited by abiotic factors such as low temperatures, scarce soil nutrients, and lack of light in winter. (See Figures 10.6, 52.12, and 55.4.)

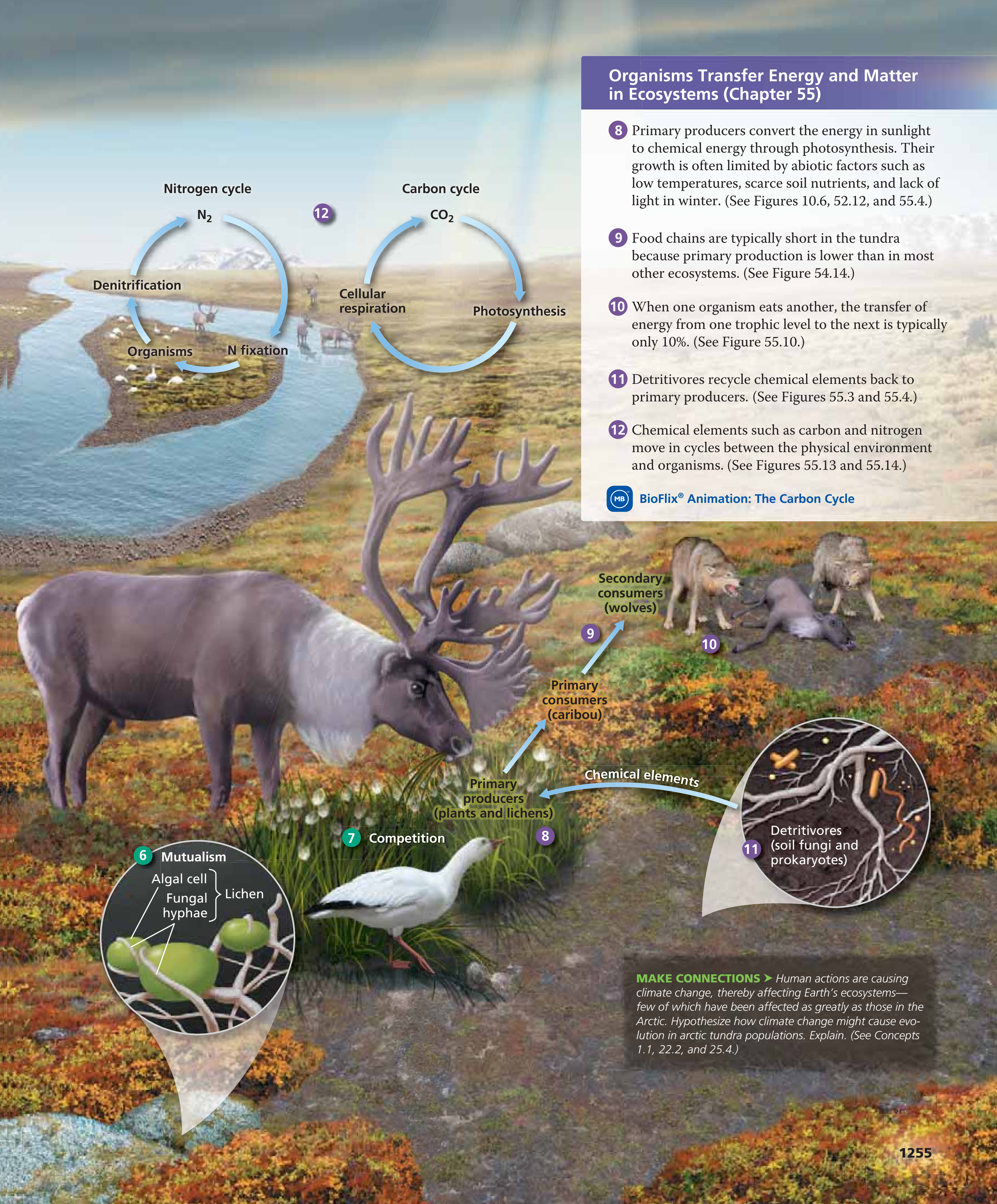
9 Food chains are typically short in the tundra because primary production is lower than in most other ecosystems. (See Figure 54.14.)

10 When one organism eats another, the transfer of energy from one trophic level to the next is typically only 10%. (See Figure 55.10.)

11 Detritivores recycle chemical elements back to primary producers. (See Figures 55.3 and 55.4.)

12 Chemical elements such as carbon and nitrogen move in cycles between the physical environment and organisms. (See Figures 55.13 and 55.14.)

BioFlix® Animation: The Carbon Cycle



MAKE CONNECTIONS ➤ *Human actions are causing climate change, thereby affecting Earth's ecosystems—few of which have been affected as greatly as those in the Arctic. Hypothesize how climate change might cause evolution in arctic tundra populations. Explain. (See Concepts 1.1, 22.2, and 25.4.)*

55 Chapter Review

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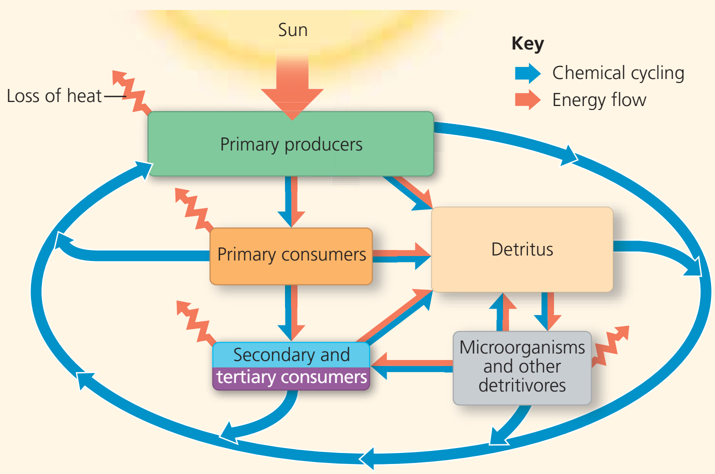
SUMMARY OF KEY CONCEPTS

CONCEPT 55.1

Physical laws govern energy flow and chemical cycling in ecosystems *(pp. 1237–1239)*

VOCAB SELF-QUIZ goo.gl/6u55ks

- An **ecosystem** consists of all the organisms in a community and all the abiotic factors with which they interact. Energy is conserved but released as heat during ecosystem processes. As a result, energy flows through ecosystems (rather than being recycled).
- Chemical elements enter and leave an ecosystem and cycle within it, subject to the **law of conservation of mass**. Inputs and outputs are generally small compared to recycled amounts, but their balance determines whether the ecosystem gains or loses an element over time.



Considering 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 system? Explain your reasoning.

CONCEPT 55.2

Energy and other limiting factors control primary production in ecosystems *(pp. 1239–1243)*

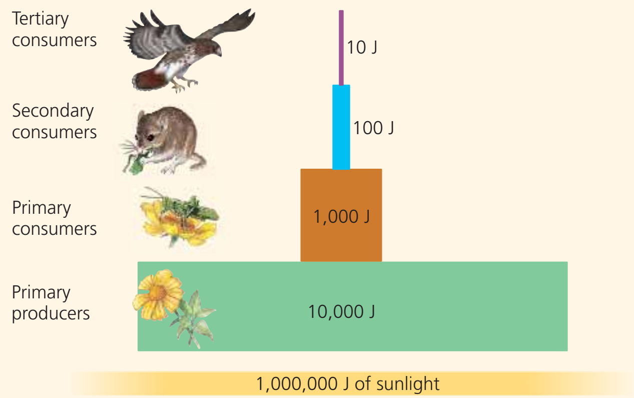
- **Primary production** sets the spending limit for the global energy budget. **Gross primary production** is the total energy assimilated by an ecosystem in a given period. **Net primary production**, the energy accumulated in autotroph biomass, equals gross primary production minus the energy used 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 at large scales, but a soil nutrient is often the limiting factor locally.

If you know NPP for an ecosystem, what additional variable do you need to know to estimate NEP? 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. 1244–1246)*

- 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 typically 10%. Pyramids of energy and biomass reflect low trophic efficiency.



Why would runners have a lower production efficiency when running a long-distance race than when they are sedentary?

CONCEPT 55.4

Biological and geochemical processes cycle nutrients and water in ecosystems *(pp. 1246–1251)*

- 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.
- The proportion of a nutrient in a particular form varies 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.

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

CONCEPT 55.5

Restoration ecologists return degraded ecosystems to a more natural state *(pp. 1251–1255)*

- 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, why would engineers separate the topsoil 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

PRACTICE TEST
goo.gl/CUYGKD

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) 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 tropical rain forest

3. The discipline that applies ecological principles to returning degraded ecosystems to a more natural state is known as
(A) restoration ecology.
(B) thermodynamics.
(C) eutrophication.
(D) biogeochemistry.

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 ammonium to nitrate, which plants absorb.
(D) 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 rate of decomposition in the ecosystem
(B) the production efficiency of the ecosystem's consumers
(C) the trophic efficiency of the ecosystem
(D) the location of the nutrient reservoirs in the ecosystem

6. The Hubbard Brook watershed deforestation experiment yielded all of the following results *except* which of the following?
(A) Most minerals were recycled within a forest ecosystem.
(B) Calcium levels remained high in the soil of deforested areas.
(C) Deforestation increased water runoff.
(D) The nitrate concentration in waters draining the deforested area became dangerously high.

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) reconfiguring the channel of a river
(D) 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) Neither would change.
(C) Decomposition rate would increase and NEP would decrease.
(D) Decomposition rate would decrease and NEP would increase.

Level 3: Synthesis/Evaluation

9. DRAW IT (a) Draw a simplified global water cycle showing ocean, land, atmosphere, and runoff from the land to the ocean. Label your drawing with these annual water fluxes:
- 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

(b) What is the ratio of ocean evaporation that falls as precipitation on land compared with runoff from land to the oceans? (c) How would this ratio change during an ice age, and why?

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. Are ecosystems capable of evolving? If so, would this be a form of Darwinian evolution? Why or why not? Explain.

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 AND MATTER Decomposition typically occurs quickly in moist tropical forests. However, waterlogging in the soil of some moist tropical forests results over time in a buildup of organic matter called "peat." 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?

13. SYNTHESIZE YOUR KNOWLEDGE

This dung beetle (genus *Scarabaeus*) is burying a ball of dung it has collected from a large mammalian herbivore in Kenya. Explain why this process is important for the cycling of nutrients and for primary production.

For selected answers, see Appendix A.

For additional practice questions, check out the **Dynamic Study Modules** in MasteringBiology. You can use them to study on your smartphone, tablet, or computer anytime, anywhere!