

42

Ecosystems and Energy

▼ **Figure 42.1** Why is this Antarctic ice blood red?



KEY CONCEPTS

- 42.1** Physical laws govern energy flow and chemical cycling in ecosystems
- 42.2** Energy and other limiting factors control primary production in ecosystems
- 42.3** Energy transfer between trophic levels is typically only 10% efficient
- 42.4** Biological and geochemical processes cycle nutrients and water in ecosystems
- 42.5** 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 24). 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 42.1**).

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 42.2**). 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 of the local ecosystems on Earth.

Regardless of an ecosystem's size, two key ecosystem processes cannot be fully described by the population or community phenomena you have studied so far: 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 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 plants and animals and by organisms such as bacteria and fungi that break down organic wastes and dead organisms.



▲ **Figure 42.2** A desert spring ecosystem.

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'll 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 measure how ecosystems respond. We'll also consider some of the impacts of human activities on energy flow and chemical cycling. Finally, we'll explore the growing science of restoration ecology, which focuses on returning degraded ecosystems to a more natural state.

CONCEPT 42.1

Physical laws govern energy flow and chemical cycling in ecosystems

Cells transform energy and matter, subject to the laws of thermodynamics (see Concept 6.1). Like cell biologists, ecosystem ecologists study how energy and matter are transformed 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 based on feeding relationships (see Concept 41.2), 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 states that energy cannot be created or destroyed but only transferred or transformed. 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 transfers within and across ecosystems, in part to understand how many organisms a habitat can support and how much 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. We can measure the efficiency of ecological energy conversions just as we measure the efficiency of light bulbs and car engines. Because the energy flowing through ecosystems is ultimately dissipated into space 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 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 can be released from the soil by a decomposer, taken up by 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 are important aspects of ecosystem ecology.

Although most elements are not gained or lost on a global scale, they can be gained by or lost from a particular ecosystem. In a forest, mineral nutrients—the essential elements that plants obtain from soil—typically 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 29.11). In terms of losses, some elements return to the atmosphere as gases, and 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.

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'll see later in this chapter.

Energy, Mass, and Trophic Levels

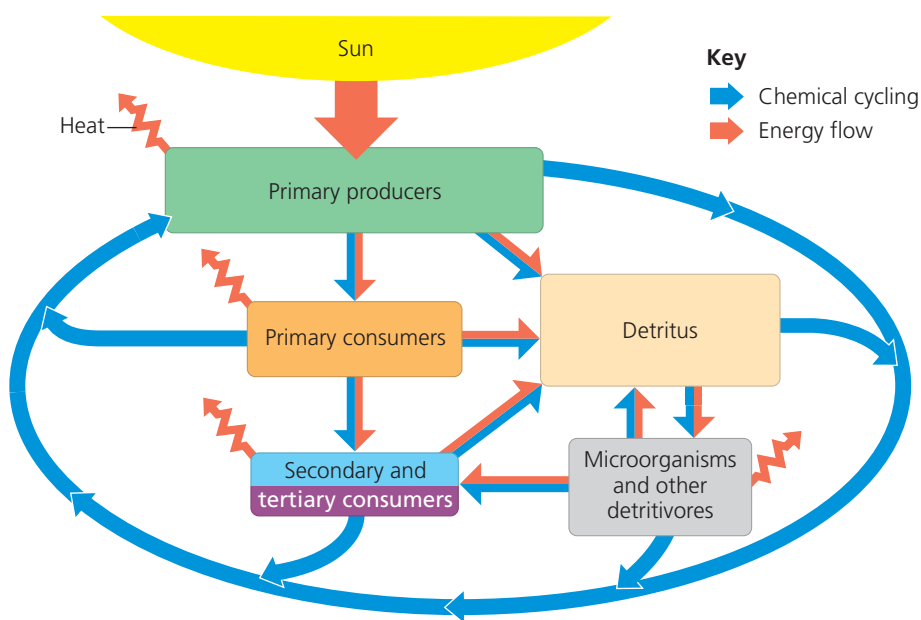
Ecologists group species into trophic levels based on their main source of nutrition and energy (see Concept 41.2). The trophic level that ultimately supports all others consists of autotrophs, also called the **primary producers** of the ecosystem. Most autotrophs are photosynthetic organisms that use light energy to synthesize sugars and other organic compounds, which they then use as fuel for cellular respiration and as building material for growth. Plants, algae, and photosynthetic prokaryotes are the most common autotrophs, although chemosynthetic prokaryotes are the primary producers in deep-sea hydrothermal vents (see Figure 40.10) and places deep underground or beneath ice (see Figure 42.1).

Organisms in trophic levels above the primary producers are heterotrophs, which depend directly or indirectly on the 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 42.3).

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.

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



▲ **Figure 42.4** 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.

to synthesize new organic matter was exhausted. Figure 42.4 summarizes the trophic relationships in an ecosystem.

CONCEPT CHECK 42.1

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** How does the second law of thermodynamics explain why an ecosystem's energy supply must be continually replenished? (See Concept 6.1 to review the laws of thermodynamics.)

For suggested answers, see Appendix A.



▲ **Figure 42.3** Fungi decomposing a dead tree.

CONCEPT 42.2 Energy and other limiting factors control primary production in ecosystems

The theme of energy transfer underlies all biological interactions (see Chapter 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**. 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, the initial energy input is chemical, 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 (see Figure 41.14). 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 ($1 \text{ J} = 0.239 \text{ cal}$). This is enough energy to supply the demands of the entire human population for approximately 20 years at 2010 energy consumption levels. The intensity of the solar energy striking Earth varies with latitude, with the tropics receiving the greatest input (see Figure 40.3). 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 8.9); 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 ($1.50 \times 10^{14} \text{ kg}$) 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):

$$\text{NPP} = \text{GPP} - R_a$$

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.

Net primary production can be expressed as energy per unit area per unit time ($\text{J}/\text{m}^2 \cdot \text{yr}$) or as biomass (mass of vegetation) added per unit area per unit time ($\text{g}/\text{m}^2 \cdot \text{yr}$). (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 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.

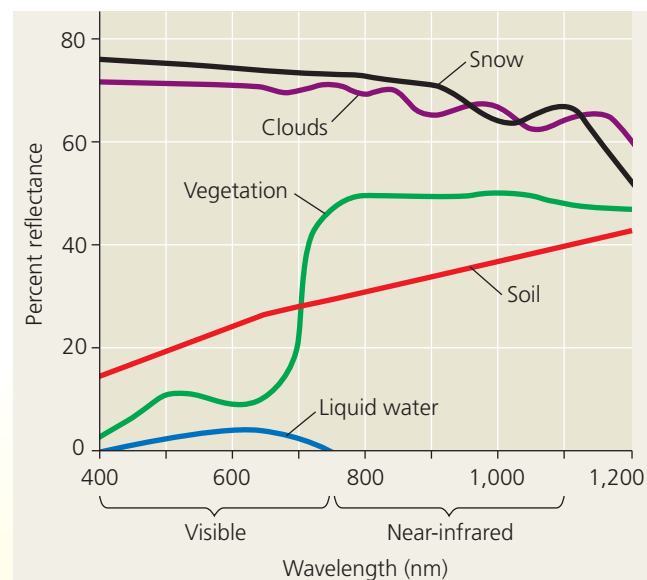
Satellites provide a powerful tool for studying global patterns of primary production (Figure 42.5). Images produced from satellite data show that different ecosystems vary considerably in their NPP. Tropical rain forests are among the most productive terrestrial ecosystems and contribute a large portion of the planet's NPP. Estuaries and coral reefs also have

▼ Figure 42.5 Research Method

Determining Primary Production with Satellites

Application Because chlorophyll captures visible light (see Figure 8.9), 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.

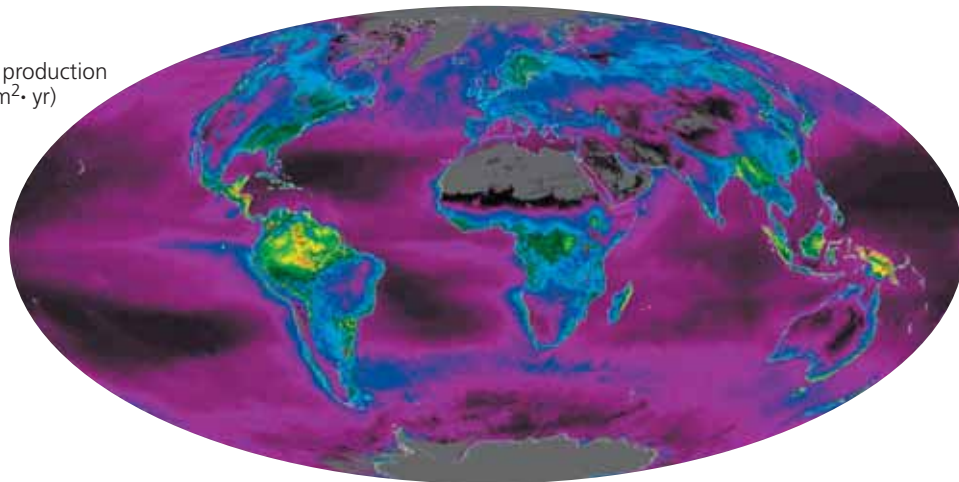
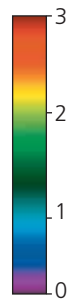


Results Scientists use the satellite data to help produce maps of primary production like the one in Figure 42.6.

► **Figure 42.6 Global net primary production.** This 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 illustrate the importance of some highly productive habitats, such as wetlands, coral reefs, and coastal zones? Explain.

Net primary production
(kg carbon/m²·yr)



very high NPP, 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 the open oceans are relatively unproductive (Figure 42.6), their vast size means that together they contribute about as much global NPP as terrestrial systems do.

Whereas NPP 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 CO₂ 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 CO₂ or O₂ entering or leaving the ecosystem. If more CO₂ enters than leaves, the system is storing carbon. Because O₂ release is directly coupled to photosynthesis and respiration (see Figure 7.2), a system that is giving off O₂ is also storing carbon. On land, ecologists typically measure only the net flux of CO₂ from ecosystems because detecting small changes in O₂ in a large atmospheric O₂ pool is difficult. In the oceans, researchers use both approaches.

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.

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 40.11). 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 42.6 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 42.7, 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.

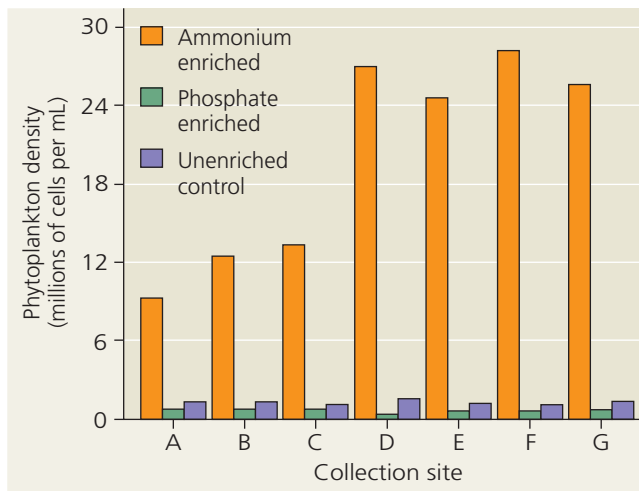
The macronutrients nitrogen and phosphorus are not the only nutrients that limit aquatic production. Several large areas of the ocean have low phytoplankton densities despite relatively high nitrogen concentrations. The Sargasso Sea,

▼ Figure 42.7 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.



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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.

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 42.1). 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.

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

Table 42.1 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).

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.

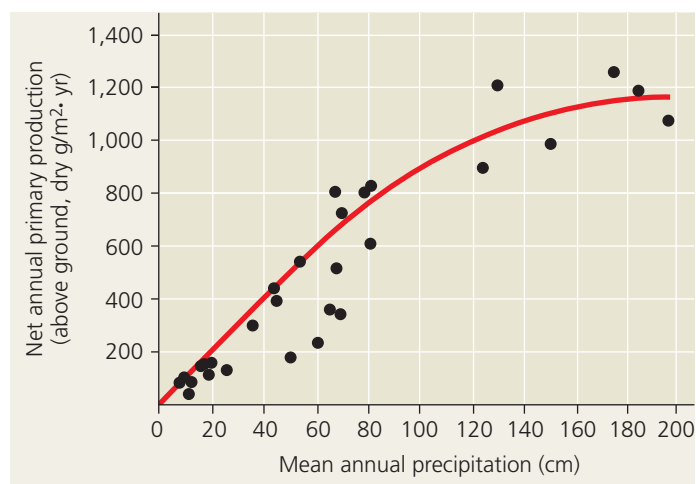
In freshwater lakes, nutrient limitation is also common. During the 1970s, scientists showed that sewage and fertilizer runoff from farms and lawns adds large amounts of nutrients to lakes. Cyanobacteria and algae grow rapidly in response to these added nutrients. When the primary producers die, detritivores can reduce or even use up the available oxygen in the water through decomposition, also reducing the 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 40.10).

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 limits 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 42.6). 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



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▲ Figure 42.8 A global relationship between net primary production and mean annual precipitation for terrestrial ecosystems.

plot of NPP and annual precipitation in **Figure 42.8**. 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.

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 the 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 adaptation is the symbiosis 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 Concept 29.4). Plants also have root hairs and other anatomical features that increase their area of contact with the soil (see Chapter 28). Many plants release enzymes and other substances into the soil that increase the availability of limiting nutrients; such enzymes include phosphatases, which cleave a phosphate group from larger molecules and make it 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 today.

CONCEPT CHECK 42.2

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** 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 8.3).

For suggested answers, see Appendix A.

CONCEPT 42.3

Energy transfer between trophic levels is typically only 10% efficient

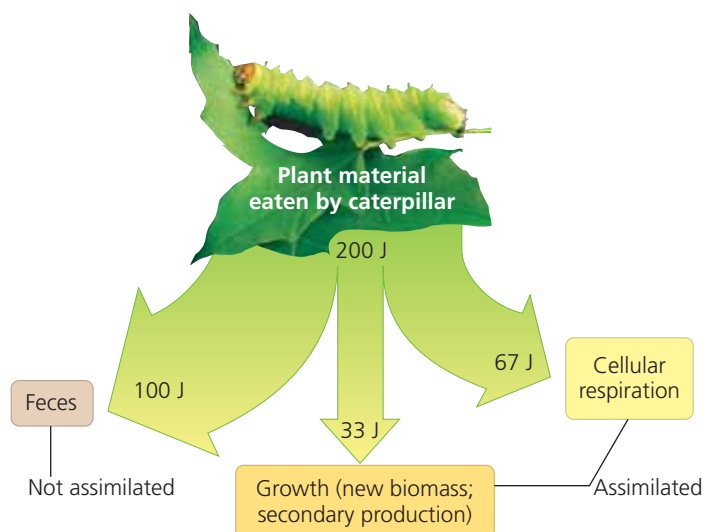
The amount of chemical energy in consumers' food that is converted to new biomass during a given period is called the **secondary production** of the ecosystem. Consider the transfer of organic matter from primary producers to herbivores, the primary consumers. In most ecosystems, herbivores eat only 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. Most 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 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 42.9**). 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. Most of the energy in feces is eventually lost as heat after the feces are consumed by detritivores. The energy used for the caterpillar's respiration is also lost from the 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:

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



▲ **Figure 42.9 Energy partitioning within a link of the food chain.** Less than 17% of the caterpillar's food is actually used for secondary production (growth).

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 42.9, 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. Insects and microorganisms are much 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%. 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%). In the **Scientific Skills Exercise**, you

Scientific Skills Exercise

Interpreting Quantitative Data in a Table

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

Interpret the Data

1. What proportion of the solar energy that reaches the marsh is incorporated into gross primary production? Into net primary production? (A proportion is the same as a percentage divided by 100. Both measures are useful for comparing relative efficiencies across different ecosystems.)
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 proportion of all net primary production leaves the marsh as detritus each year?

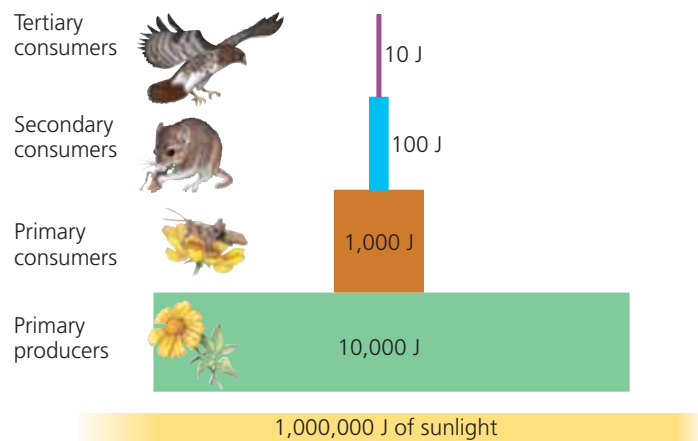
Data from J. M. Teal, Energy flow in the salt marsh ecosystem of Georgia, *Ecology* 43:614–624 (1962).

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

can calculate trophic efficiency and other measures of energy flow in a salt marsh ecosystem.

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 41).

The loss of energy with each transfer in a food chain can be represented by a *pyramid of net production*, in which the



▲ **Figure 42.10 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.

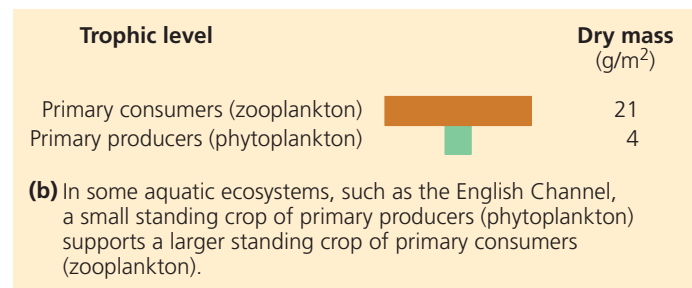
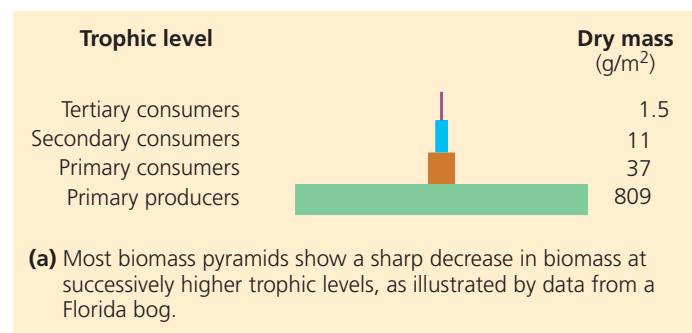
trophic levels are arranged in tiers (**Figure 42.10**). The width of each tier is proportional to the net production, expressed in joules, of each trophic level. The highest level, which represents top-level predators, contains relatively few individuals. The small population size typical of top predator species is one reason they tend to be vulnerable to extinction (as well as to the evolutionary consequences of small population size, discussed in Concept 21.3).

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 42.11a**). Certain aquatic ecosystems, however, have inverted biomass pyramids: Primary consumers outweigh the producers (**Figure 42.11b**). 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:

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

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 42.10.

The dynamics of energy flow through ecosystems have important implications for human consumers. Eating meat is a relatively inefficient way of tapping photosynthetic production. The same pound of soybeans that a person could eat for



▲ **Figure 42.11 Pyramids of biomass (standing crop).** Numbers denote the dry mass of all organisms at each trophic level.

protein produces only a fifth of a pound of beef or less when fed to a cow. Worldwide agriculture could, in fact, feed many more people and require less land if we all fed more efficiently—as primary consumers, eating plant material.

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

CONCEPT CHECK 42.3

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 42.10? For suggested answers, see Appendix A.

CONCEPT 42.4 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. Decomposition replenishes the pools of inorganic nutrients that plants and other autotrophs use to build new organic matter.

Decomposition and Nutrient Cycling Rates

Decomposition is controlled by the same factors that limit primary production in aquatic and terrestrial ecosystems (see Concept 42.2). These factors include temperature, moisture, and nutrient availability. Decomposers usually grow faster and decompose material more quickly in warmer ecosystems (**Figure 42.12**). In tropical rain forests, 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 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. 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 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 exchange between the bottom layers of water and the water at the surface.

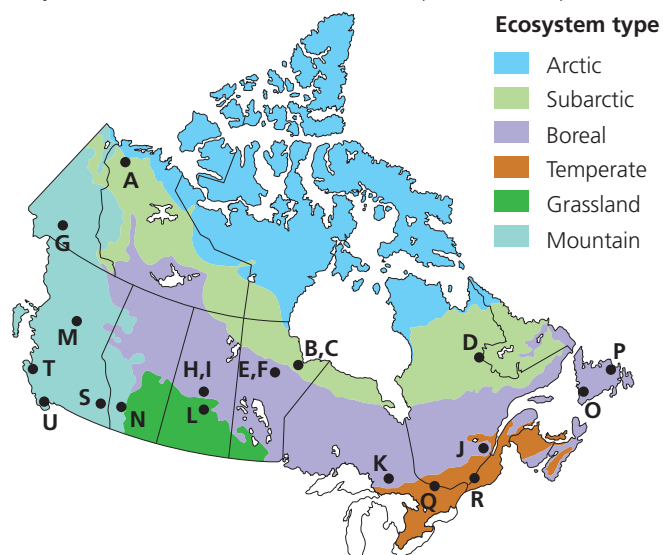
Biogeochemical Cycles

Because nutrient cycles involve both biotic and abiotic components, they are called **biogeochemical cycles**. For convenience, 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

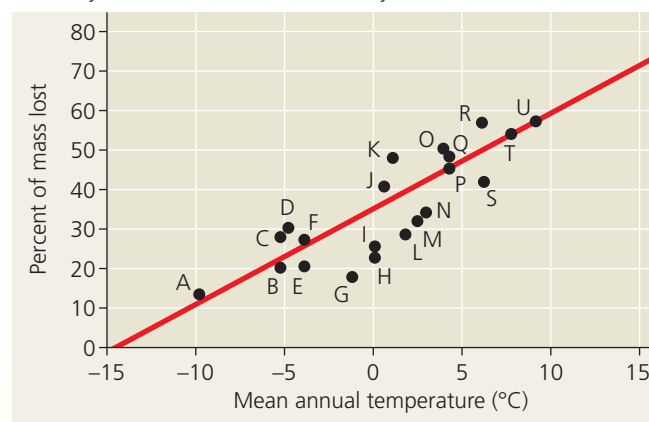
▼ Figure 42.12 Inquiry

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 (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?

cycles of these elements are essentially global. Other elements, including phosphorus, potassium, and calcium, are too heavy to occur as gases at Earth's surface. They cycle locally in terrestrial ecosystems and more broadly in aquatic ecosystems.

Figure 42.13 provides a detailed look at the cycling of water, carbon, nitrogen, and phosphorus. When you study each

▼ Figure 42.13 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.

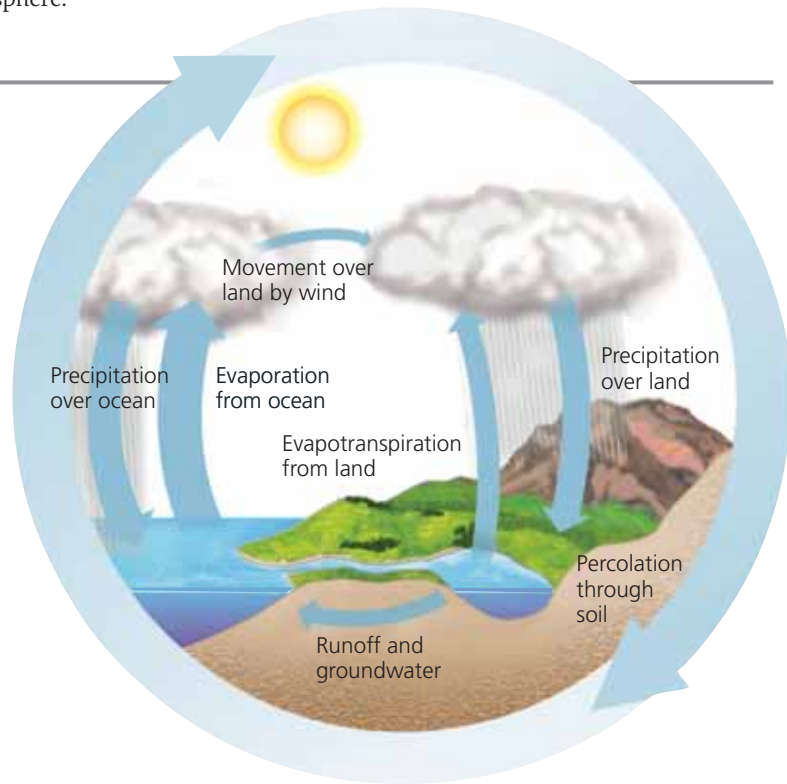
The Water Cycle

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.

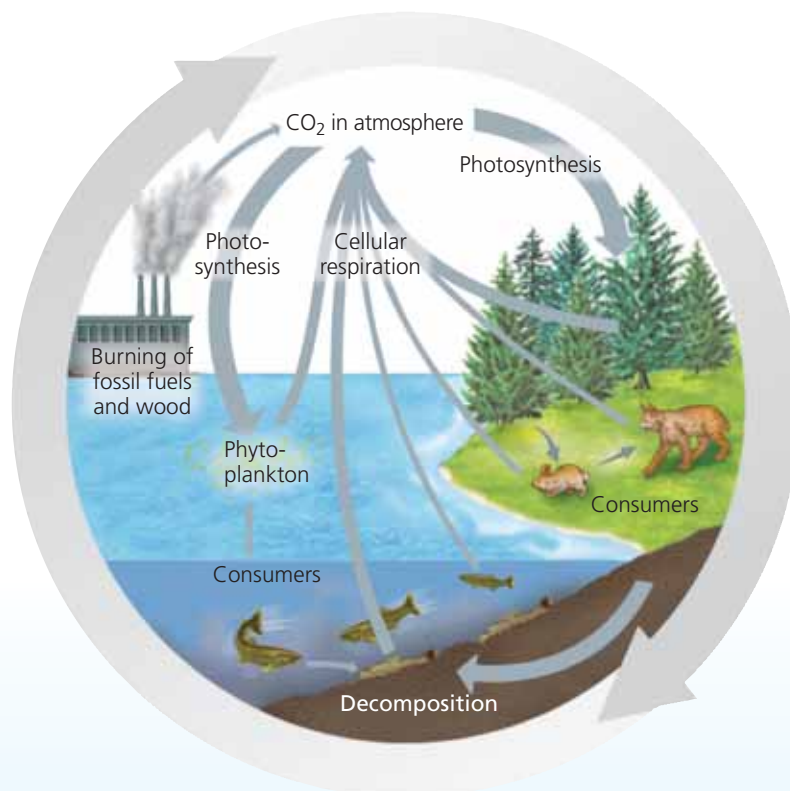
Forms available to life All organisms are capable of exchanging water directly with their environment. Liquid water is the primary physical phase in which water is used, though some organisms can harvest water vapor. Freezing of soil water can limit water availability to terrestrial plants.

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 CO₂ during photosynthesis and convert the carbon to organic forms that are used by consumers, including animals, fungi, and heterotrophic protists and prokaryotes.

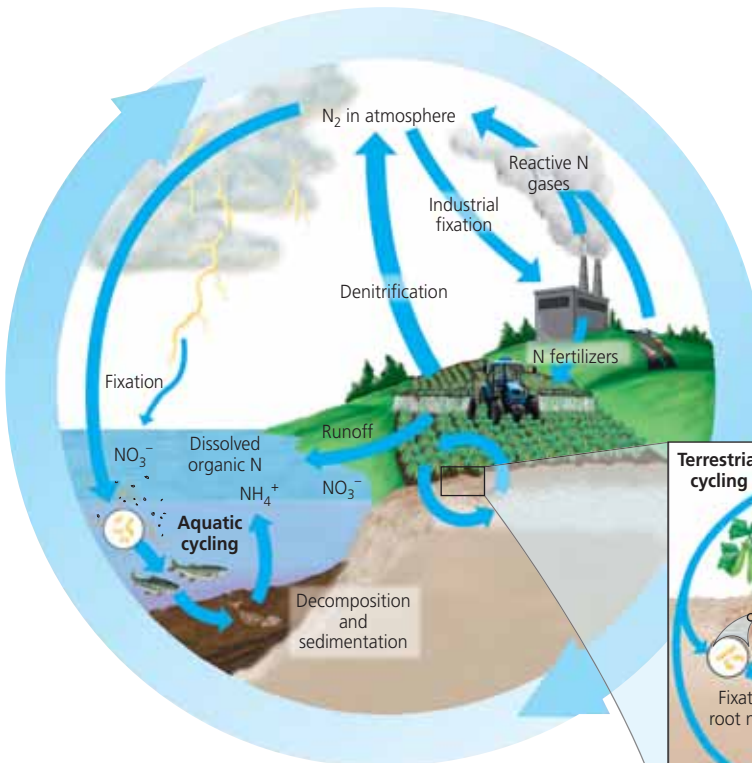
Reservoirs The major reservoirs of carbon include fossil fuels, soils, the sediments of aquatic ecosystems, the oceans (dissolved carbon compounds), plant and animal biomass, and the atmosphere (CO₂). The largest reservoir is sedimentary rocks such as limestone; however, this pool turns over very slowly. All organisms are capable of returning carbon directly to their environment in its original form (CO₂) through respiration.

Key processes Photosynthesis by plants and phytoplankton removes substantial amounts of atmospheric CO₂ each year. This quantity is approximately equaled by CO₂ added to the atmosphere through cellular respiration by producers and consumers. The burning of fossil fuels and wood is adding significant amounts of additional CO₂ to the atmosphere. Over geologic time, volcanoes are also a substantial source of CO₂.

ANIMATION **BioFlix** Visit the Study Area in **MasteringBiology** 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.

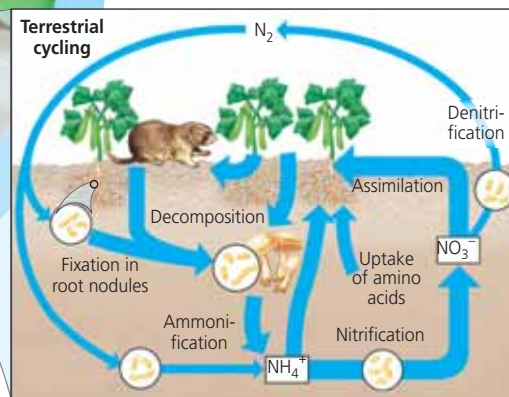


Forms available to life Plants can assimilate (use) two inorganic forms of nitrogen—ammonium (NH_4^+) and nitrate (NO_3^-)—and some organic forms, such as amino acids. Various bacteria can use all of these forms as well as nitrite (NO_2^-). Animals can use only organic forms of nitrogen.

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 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. 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.



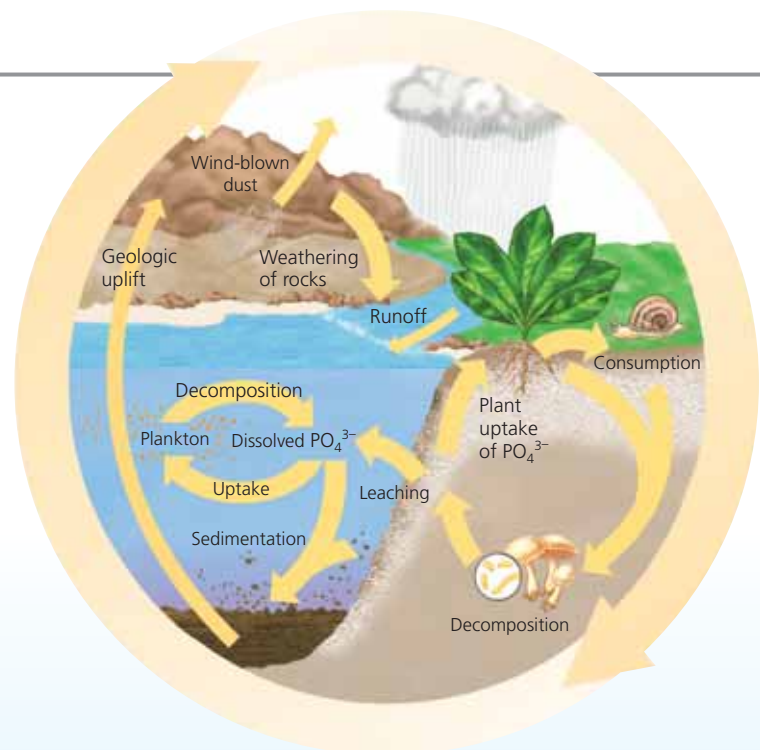
The Phosphorus Cycle

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.



cycle, consider which steps are driven primarily by 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.

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 and abiotic 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 the 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.

Case Study: Nutrient Cycling in the Hubbard Brook Experimental Forest

Since 1963, ecologists Herbert Bormann, Gene 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 42.14a). 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.

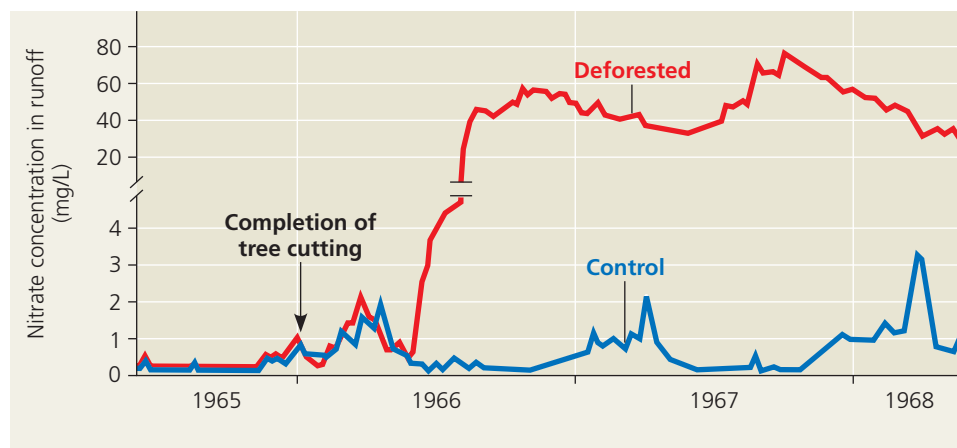
Experimental deforestation of a watershed dramatically increased the flow of water and minerals leaving the watershed (Figure 42.14b). Over three years, water runoff from the newly deforested watershed was 30–40% greater than in a control watershed, apparently because there were no plants to absorb and 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 42.14c). The Hubbard Brook deforestation study showed that the amount of nutrients leaving an intact forest ecosystem is controlled mainly by the plants. Retaining



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

A related Experimental Inquiry Tutorial can be assigned in MasteringBiology.

nutrients in ecosystems helps to maintain the productivity of the systems and, in some cases, to avoid problems caused by excess nutrient runoff (see Figure 42.7).

CONCEPT CHECK 42.4

1. **DRAW IT** For each of the four biogeochemical cycles detailed in Figure 42.12, 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 42.5

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 (see Concept 41.3). Sometimes that recovery takes centuries, though, particularly when human activities 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.

One of the basic assumptions of restoration ecology 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 42.15**).

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**. Some plants and lichens adapted to soils containing heavy metals can accumulate high concentrations of toxic metals such as zinc, 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 pigment, making it useful as a biological monitor and potentially as a remediator.



(a) In 1991, before restoration



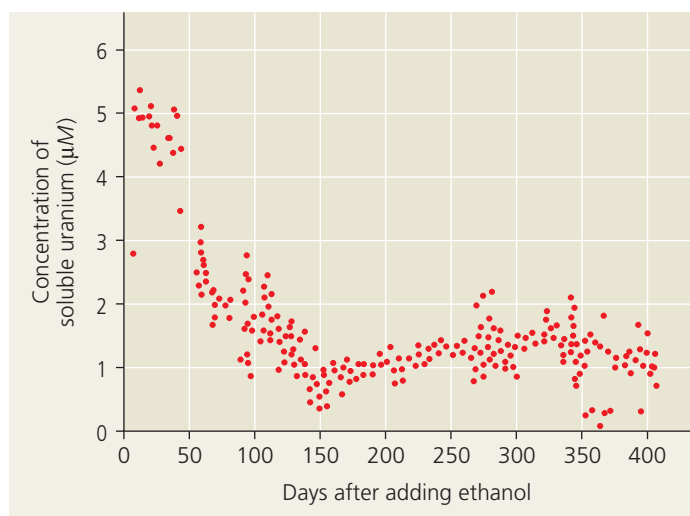
(b) In 2000, near the completion of restoration

▲ **Figure 42.15** A gravel and clay mine site in New Jersey before and after restoration.

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 42.16).



(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.

▲ **Figure 42.16 Bioremediation of groundwater contaminated with uranium at Oak Ridge National Laboratory, Tennessee.**

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 26). 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 provide critical ecosystem services, including pollination and seed dispersal, 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. Such 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, 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 42.17** explores four ambitious and successful restoration projects. The great number of such projects around the world and the dedication of the people engaged in them suggest that restoration ecology will continue to grow as a discipline for many years.

CONCEPT CHECK 42.5

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 42.17)?

For suggested answers, see Appendix A.

▼ Figure 42.17 Exploring Restoration Ecology Worldwide

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

► 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.



◀ 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.



◀ 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).



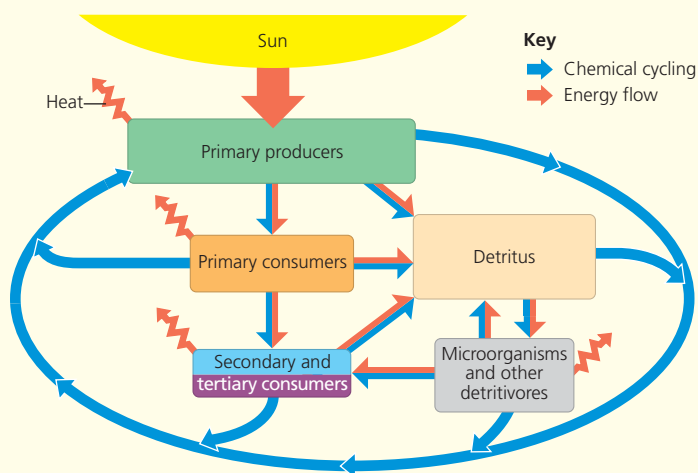
42 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 42.1

Physical laws govern energy flow and chemical cycling in ecosystems (pp. 865–866)

- An **ecosystem** consists of all the organisms in a community and the abiotic factors with which they interact. The laws of physics and chemistry apply to ecosystems, particularly for 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 42.2

Energy and other limiting factors control primary production in ecosystems (pp. 866–870)

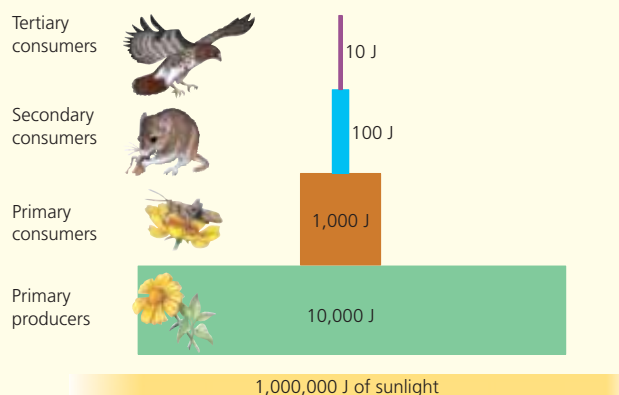
- Primary production** sets the spending limit for the global energy budget. **Gross primary production** is the total energy assimilated by an ecosystem in a given period. **Net primary production**, the energy accumulated in autotroph biomass, equals gross primary production minus the energy used by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

? 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 42.3

Energy transfer between trophic levels is typically only 10% efficient (pp. 870–872)

- 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 net production 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 42.4

Biological and geochemical processes cycle nutrients and water in ecosystems (pp. 872–877)

- Water moves in a global cycle driven by solar energy. The carbon cycle primarily reflects the reciprocal processes of photosynthesis and cellular respiration.
- 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.

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

CONCEPT 42.5

Restoration ecologists help return degraded ecosystems to a more natural state (pp. 877–879)

- 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

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

Level 2: Application/Analysis

- Nitrifying bacteria participate in the nitrogen cycle mainly by
 - converting nitrogen gas to ammonia.
 - releasing ammonium from organic compounds, thus returning it to the soil.
 - converting ammonia to nitrogen gas, which returns to the atmosphere.
 - converting ammonium to nitrate, which plants absorb.
 - incorporating nitrogen into amino acids and organic compounds.
- Which of the following has the greatest effect on the rate of chemical cycling in an ecosystem?
 - the ecosystem's rate of primary production
 - the production efficiency of the ecosystem's consumers
 - the rate of decomposition in the ecosystem
 - the trophic efficiency of the ecosystem
 - the location of the nutrient reservoirs in the ecosystem
- The Hubbard Brook watershed deforestation experiment yielded all of the following results *except*:
 - Most minerals were recycled within a forest ecosystem.
 - The flow of minerals out of a natural watershed was offset by minerals flowing in.
 - Deforestation increased water runoff.
 - The nitrate concentration in waters draining the deforested area became dangerously high.
 - Calcium levels remained high in the soil of deforested areas.
- Which of the following would be considered an example of bioremediation?
 - adding nitrogen-fixing microorganisms to a degraded ecosystem to increase nitrogen availability
 - using a bulldozer to regrade a strip mine
 - dredging a river bottom to remove contaminated sediments

- reconfiguring the channel of a river
 - adding seeds of a chromium-accumulating plant to soil contaminated by chromium
- If you applied a fungicide to a cornfield, what would you expect to happen to the rate of decomposition and net ecosystem production (NEP)?
 - Both decomposition rate and NEP would decrease.
 - Both decomposition rate and NEP would increase.
 - Neither would change.
 - Decomposition rate would increase and NEP would decrease.
 - Decomposition rate would decrease and NEP would increase.

Level 3: Synthesis/Evaluation

- 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 your drawing: ocean evaporation, 425 km³; ocean evaporation that returns to the ocean as precipitation, 385 km³; ocean evaporation that falls as precipitation on land, 40 km³; evapotranspiration from plants and soil that falls as precipitation on land, 70 km³; runoff to the oceans, 40 km³. Based on these global numbers, how much precipitation falls on land in a typical year?
- 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.
- FOCUS ON EVOLUTION** 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?
- FOCUS ON ENERGY AND MATTER** As described in Concept 42.4, 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?

For selected answers, see Appendix A.

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