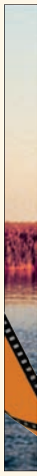
47 ECOSYSTEMS

Bye-Bye, Blue Bayou



Each Labor Day, the coastal Louisiana town of Morgan City celebrates the region's economic mainstays with the Louisiana Shrimp and Petroleum Festival. The state is the nation's third-largest petroleum producer and the leader in shrimp harvesting. But the petroleum industry's success may be contributing indirectly to the possible disappearance of the state's fisheries.

The global air temperature is rising, and fossil fuel burning is a contributing factor. Warmer air heats water near the sea surface, heated water expands, and so the sea level is rising. Warmer air also is melting ancient glaciers and ice caps, and meltwater is adding to the sea volume.

Since the 1940s, Louisiana has lost an area the size of Rhode Island to the sea. Low elevations along the United States coastline—including *14,720,000 acres* next to the Gulf of Mexico and Atlantic Ocean—may be one to three feet under water within fifty years.

Given that it has more than 40 percent of the nation's saltwater marshes, Louisiana has the most to lose (Figure 47.1). Its wetlands are already sinking, because extensive dams and levees interfere with the deposition of sediments that could replace those washed out to sea. In time, a rise in sea level will make 70 percent of the nation's wetlands *really* wet, with no land at all.

Are ecological and economic disasters now unfolding? What will happen to the livelihoods of people who harvest more than 3 billion dollars' worth of shellfish and fish from Louisiana's wetlands each year? What will happen to the more than 5 million birds—about 40 percent of North America's migratory ducks—that overwinter here? What will happen to villages, cities, and natural ecosystems at the low inland elevations, which Louisiana's wetlands buffer from storm surges and hurricanes?

More bad news: Warmer water may promote algal blooms and huge fish kills. Also, populations of many pathogenic bacteria increase in warmer water, so more people might get sick after swimming in contaminated water or eating contaminated shellfish.

Inland, heat waves and wildfires will become more intense. Deaths related to heat stroke will climb. Warmer temperatures will permit mosquitoes to extend their inland ranges. Some mosquitoes are vectors for agents of malaria, West Nile virus, and other diseases.

For some time, researchers have been predicting that global warming will raise evaporation rates, alter weather patterns, and cause prolonged drought for some regions and severe flooding for others, including Louisiana. They worry that 3 billion people may run out of fresh drinking

Figure 47.1 Cypress swamp in Louisiana. Inland saltwater intrusions threatening these trees, which are actually adapted to freshwater habitats. *Facing page*, Dawn on the bayou.

IMPACTS, ISSUES

water within twelve years. Reflect on Katrina, the category 5 hurricane that made a direct hit on Gulf Coast lowlands in 2005. Reflect on the devastation, flooding, contaminated freshwater sources, displaced populations, and impact on the nation's economy. Are predictions becoming reality?

This chapter can get you thinking about energy flow through ecosystems, starting with energy inputs from the sun. It will show how ecosystems depend on inputs, cycling, and outputs of nutrients—and how nutrients are cycled on a global scale.

The chapter also can get you thinking more about a related concept of equal importance. We have become players in the global flows of energy and nutrients even before we fully comprehend how the game plans work. Decisions we make today about global warming and other environmental issues may affect the quality of human life and the environment far into the future.

How Would You Vote?

Emissions from motor vehicles are a major source of greenhouse gases. Many people buy large vehicles that use more fuel but are viewed as safer and more useful. Should such vehicles be additionally taxed to discourage sales and offset their environmental costs? Can we expect better fuels as well as more of the fuel-efficient, larger vehicles that are becoming available? See BiologyNow for details, then vote online.

Key Concepts

ORGANIZATION OF ECOSYSTEMS

An ecosystem is a community and its physical environment. It is maintained by a one-way flow of energy and a cycling of materials through its interacting participants. It is an open system, with inputs, internal transfers, and outputs of both energy and nutrients. Section 47.1

FOOD WEBS

Food chains are linear sequences of feeding relationships, from producers through consumers, decomposers, and detritivores. The chains cross-connect, as food webs.

Most of the energy that enters a food web returns to the environment, mainly as metabolic heat. Most of the nutrients are cycled, but some are lost to the environment.

Biological magnification is the increasing concentration of a substance in the tissues of organisms as it moves up food chains. Sections 47.2, 47.3

PRIMARY PRODUCTIVITY

An ecosystem's primary productivity is the rate at which its producers capture and store energy in their tissues during a given interval. The amount stored depends on the number of producers and on the balance between photosynthesis and aerobic respiration. Section 47.4

CYCLING OF WATER AND NUTRIENTS

Primary productivity is influenced by the availability of water, carbon, nitrogen, phosphorus, and other substances, the ions or molecules of which move slowly from environmental reservoirs, among organisms of food webs, then back to the reservoirs. Human activities intervene in these cycles in measurable ways. Sections 47.5–47.12

Links to Earlier Concepts

This chapter takes a closer look at the main participants in ecosystems, especially the autotrophs (Sections 1.2, 7.8). It builds on your understanding of how the one-way flow of energy in nature shapes the organization of life (6.1, 6.2). You will place nitrogen-fixing microbes as well as soil erosion and leaching in the context of a global nitrogen cycle (30.1, 30.2). You will revisit pesticides (32.2), algal blooms (22.6), and methane hydrates (Chapter 3 introduction). You will come across more effects of deforestation (23.10).

47.1 The Nature of Ecosystems

LINKS TO SECTIONS 1.2, 6.1, 7.8, 46.1

In the preceding chapter, you focused on the dynamic nature of community structure. Turn now to the ways in which the energy and raw materials available in the physical environment help organize the interactions among species in that community. By identifying these interactions, ecologists can make predictions about whether they will remain stable and how they might change over the long term.

OVERVIEW OF THE PARTICIPANTS

Diverse natural systems abound on Earth's surface. In climate, landforms, soil, vegetation, animal life, and other features, deserts differ from hardwood forests, which differ from tundra and the prairies. Reefs differ from the open ocean, which differs from streams and lakes. *Even so, despite their differences, all of the systems are alike in many aspects of their structure and function.*

These systems run on energy that autotrophs—the self-feeders—capture. The most familiar autotrophs, remember, are plants and phytoplankton (Sections 7.8 and 22.6). As you know, both convert energy from the sun to chemical bond energy and use it to synthesize organic compounds from simple inorganic materials. These photoautotrophs are the **primary producers** for the system (Figure 47.2).

All other organisms in the system are **consumers**. They are different kinds of heterotrophs that feed on the tissues, products, and remains of other organisms. We may describe consumers by their diets. *Herbivores* eat plants. *Carnivores* eat flesh. *Parasites* live in or on a host and feed on its tissues. Earthworms, crabs, and other **detritivores** eat particles of decomposing organic matter (detritus), such as decaying bits of fallen leaves. **Decomposers** break down organic remains and wastes of all organisms. Hundreds of thousands of species of bacteria, protists, and fungi are decomposers.

Bear in mind, we cannot place some consumers in simple categories. Different kinds are *omnivores*, which may feed on animals, plants, fungi, protists, and even bacteria. A red fox is an example (Figure 47.3). It also scavenges when the opportunity presents itself. In the natural world, a full-time *scavenger* is a type of animal that feeds on the flesh of dead and decaying animals. Vultures are full-time scavengers. Hyenas hunt to kill but, like foxes, are opportunistic scavengers.

How does a system cycle nutrients? First, primary producers get hydrogen, oxygen, and carbon atoms from water and carbon dioxide in their environment. They also take up minerals, such as phosphorus and nitrogen. These are materials for biosynthesis. Later on, decomposition of organic wastes and remains releases

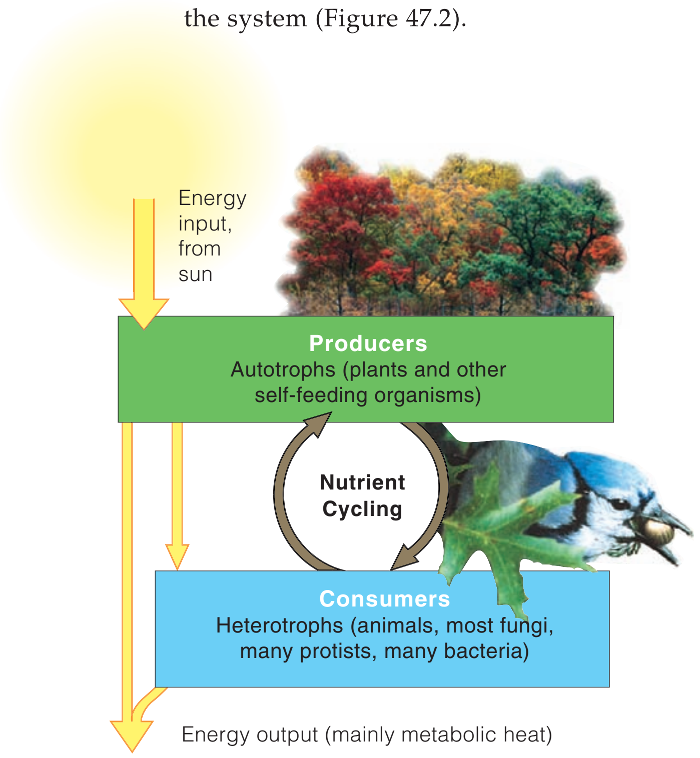


Figure 47.2 ***Animated!*** Model for ecosystems. Energy flows one way: into an ecosystem and out from it. Nutrients are cycled among autotrophs and heterotrophs. In nearly all ecosystems, energy flow starts with autotrophs that capture energy from the sun.

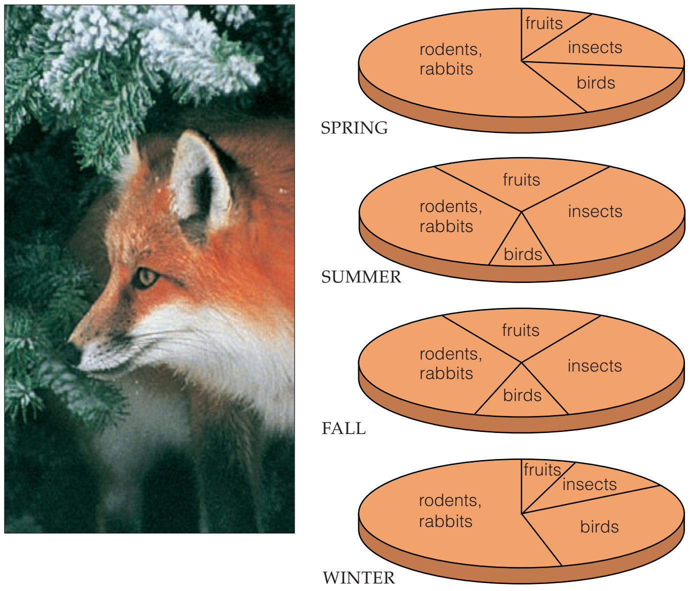


Figure 47.3 Red fox, an omnivore. Its diet shifts with seasonal changes in available food. Rodents, rabbits, and some birds make up the bulk of its diet in spring and winter. It eats more fruits and insects in the summer and fall.

nutrients back into the environment. Unless released substances move out of the system, as when mineral ions become dissolved in a stream that flows from a meadow, producers usually take them up again.

What we have just outlined is the **ecosystem**. We define each ecosystem as an array of organisms and their physical environment, all interacting through a one-way flow of energy and a cycling of the materials required to sustain life. It is an open system, in that it cannot sustain itself.

Energy inputs to most ecosystems are in the form of sunlight. There may be *nutrient inputs*, as from a creek delivering dissolved minerals to a lake. There are also *energy outputs* and *nutrient outputs*.

Energy transfers, remember, cannot be 100 percent efficient (Section 6.1). Over time, the energy originally harnessed by producers escapes to the environment, mainly as metabolically generated heat.

STRUCTURE OF ECOSYSTEMS

We can classify all organisms of an ecosystem by their functional roles in a hierarchy of feeding relationships called **trophic levels** (*troph*, nourishment). "Who eats whom?" we might ask. If organism B eats organism A, energy is transferred from A to B. All organisms at a given trophic level are the same number of transfer steps away from the energy input into an ecosystem.

As one example, think about some organisms of a tallgrass prairie ecosystem. The flowering plants and other producers that tap energy from the sun are at the first trophic level. Plants are eaten by herbivores, such as cutworms, which are at the next trophic level. Cutworms are one of the primary consumers that are eaten by carnivores at the third trophic level, and so on up through tiers of trophic levels.

At each trophic level, organisms interact with the same sets of predators, prey, or both. Omnivores feed at several levels, so we would partition them among different levels or assign them to a level of their own.

A **food chain** is a straight-line sequence of steps by which energy originally stored in autotroph tissues moves to higher trophic levels. In one tallgrass prairie food chain, for instance, energy from a plant flows to a cutworm that eats its juicy parts and on to a garter snake that eats the cutworm, to a crow that eats snake eggs and hatchlings, and finally to a marsh hawk that eats crow eggs and hatchlings (Figure 47.4).

Identifying a food chain is a simple way to start thinking about who eats whom in ecosystems. Bear in mind, many different species are usually competing for food in complex ways. Tallgrass prairie producers (mainly flowering plants) feed grazing mammals and herbivorous insects. But many more species interact in the tallgrass prairie and nearly all other ecosystems, particularly at the lower trophic levels. A number of food chains *cross-connect* with one another—as **food webs**—and that is the topic of the next section.

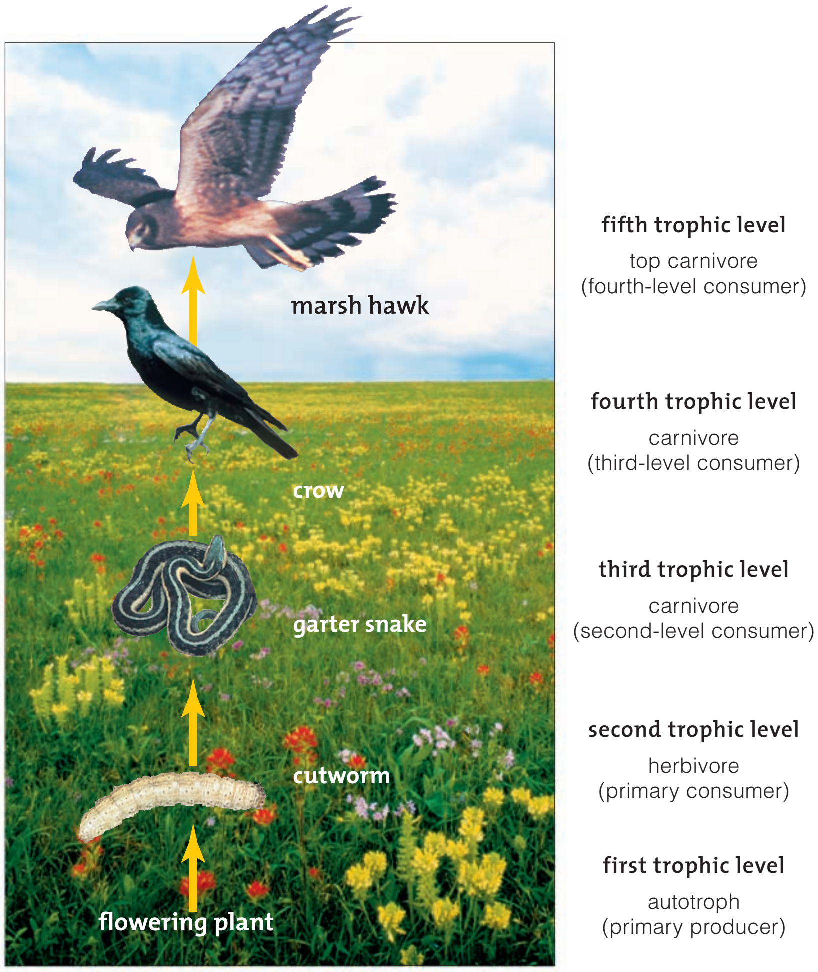


Figure 47.4 *Animated!* Example of a simple food chain and its corresponding trophic levels in a tallgrass prairie.

An ecosystem is a community of organisms that interconnect with one another and with their physical environment by a one-way energy flow and a cycling of materials.

Autotrophs tap into an environmental energy source and make their own organic compounds from inorganic raw materials. They are the ecosystem's primary producers.

Autotrophs are at the first trophic level of a food chain, a straight-line sequence of feeding relationships that proceeds through one or more levels of heterotrophs, or consumers.

In ecosystems, food chains cross-connect, as food webs.

47.2 The Nature of Food Webs

LINKS TO SECTIONS 6.1, 6.2

Food chains cross-connect with one another in food webs. By untangling the chains of many food webs, ecologists discovered patterns of organization. Those patterns reflect environmental constraints and the inefficiency of energy transfers from one trophic level to the next.

Recall, from Section 6.1, that energy concentrated in one place tends to spread out, or disperse, on its own. The collective strength of chemical bonds resists this spontaneous direction of energy flow. Every organism in an ecosystem must tap into a concentrated energy source and use it to build complex molecules even as they continually lose energy, as metabolic heat.

Plants capture energy that is concentrated in rays from the sun. They use some of it to drive metabolism, store about half of it in new plant tissues, and lose the rest as heat. Consumers tap into energy that became stored in plant tissues, remains, and wastes. They too, lose metabolic heat. *Taken together, all of the heat losses represent a one-way flow of energy out of the ecosystem.*

HOW MANY TRANSFERS?

When ecologists compared food chains in different kinds of food webs, a pattern emerged. In most cases, energy initially captured by producers passes through no more than four or five trophic levels. Even the rich ecosystems with complex food webs, such as the one in Figure 47.5, do not have lengthy food chains. The inefficiency of energy transfers may limit the sequence.

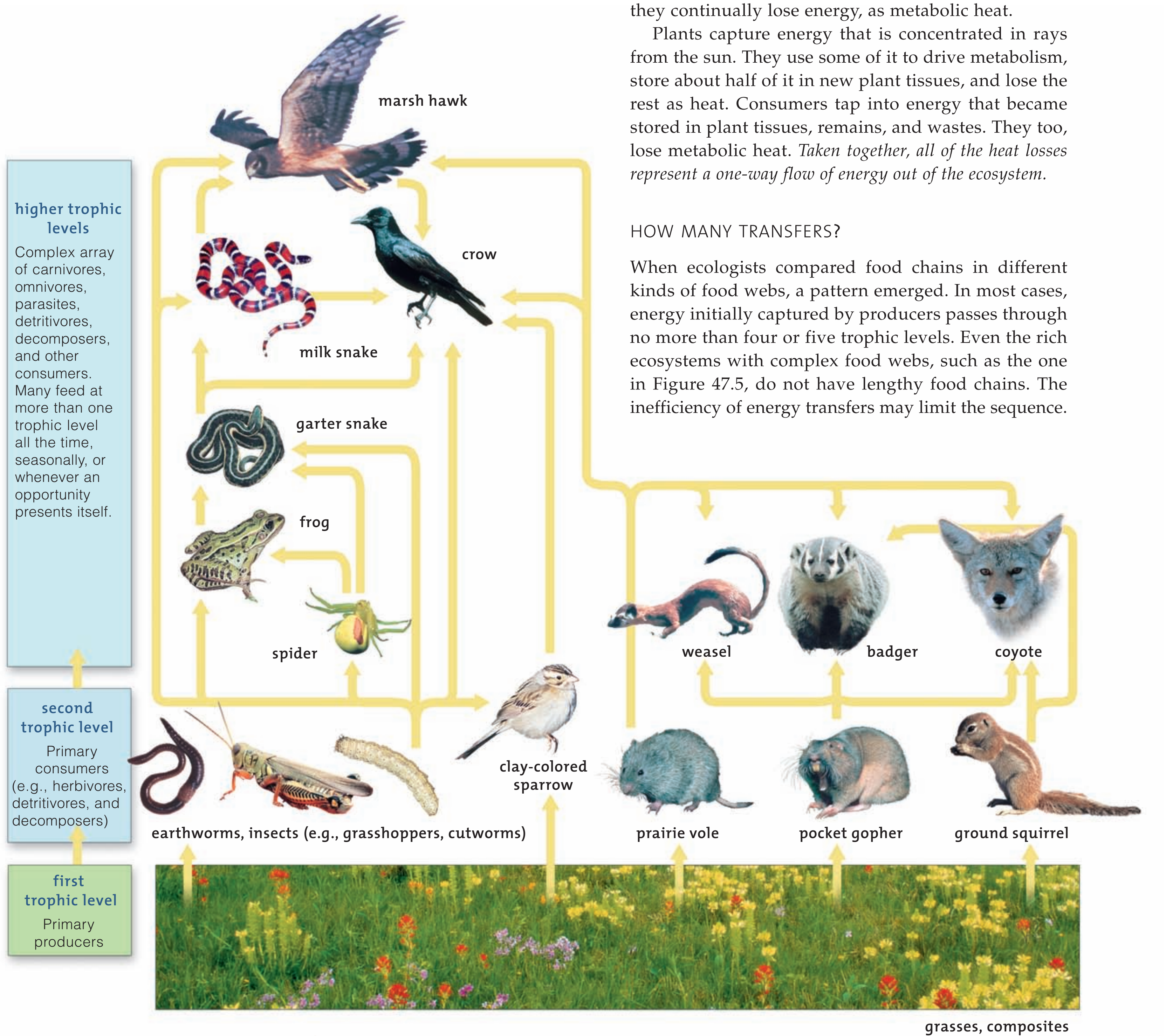
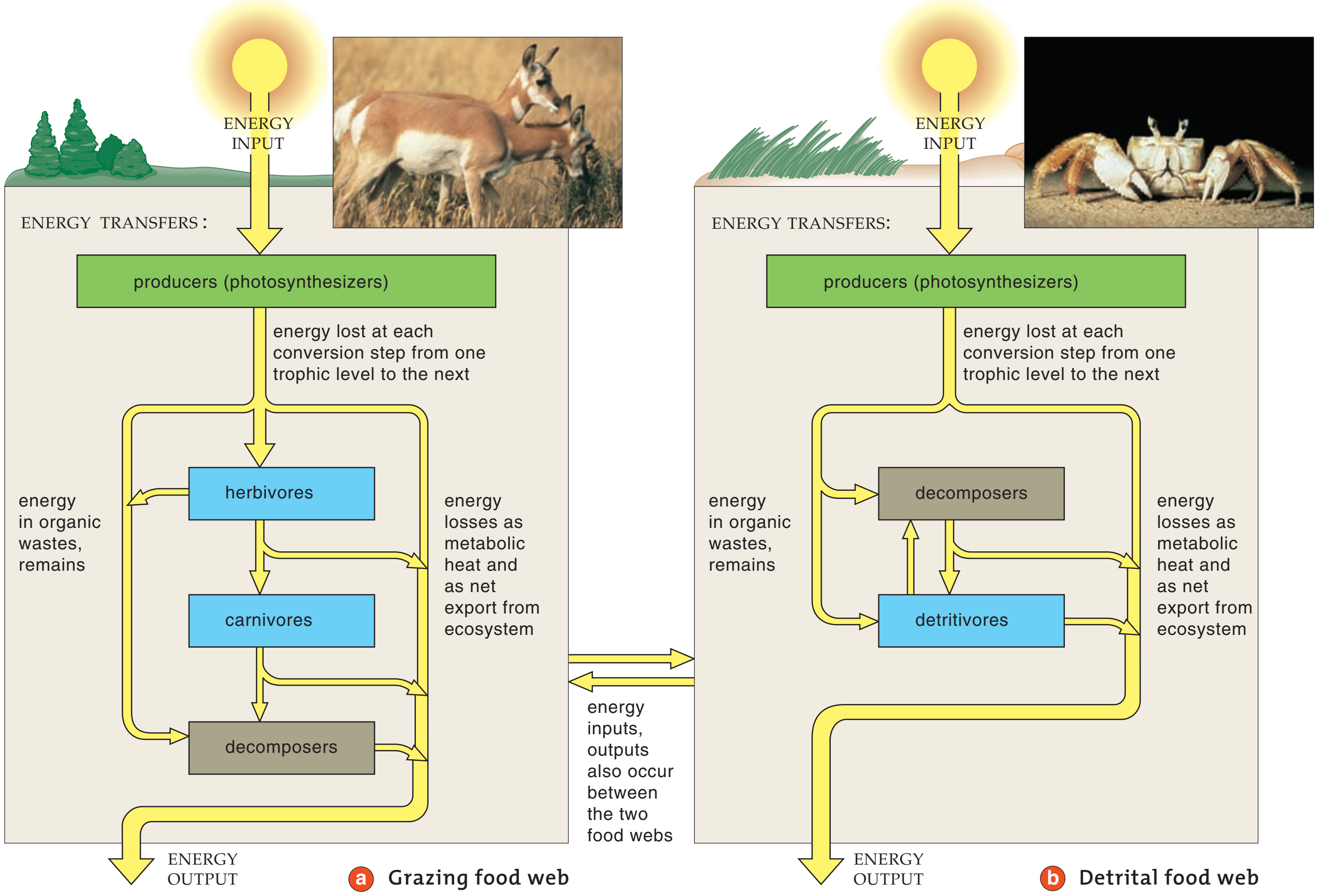


Figure 47.5 ***Animated!*** A small sampling of the organisms at successively higher trophic levels for a tallgrass prairie food web.



ⓐ **Grazing food web**

ⓑ **Detrital food web**

Figure 47.6 Generalized sketches of the one-way flow of energy through the participants of (**a**) a grazing food web and (**b**) a detrital food web.

Field studies and computer simulations of aquatic and land food webs reveal more patterns. Chains in food webs tend to be shortest where environmental conditions usually vary widely over time. Food chains tend to be longer in habitats that are more stable, such as ocean depths. The most complex webs tend to have many herbivorous species, as happens in grasslands. By comparison, the food webs with fewer connections tend to have more carnivores.

TWO CATEGORIES OF FOOD WEBS

Energy from producers—the organisms closest to a primary source—flows in one direction through two kinds of webs. In a **grazing food web**, energy flows mostly into herbivores, carnivores, then decomposers. In a **detrital food web**, energy from producers flows mainly into detritivores and decomposers. Figure 47.6 summarizes the flow through these food webs.

In nearly all ecosystems, both kinds of webs cross-connect. For example, in a rocky intertidal ecosystem, energy captured by algae flows to snails, which are eaten by herring gulls as part of a grazing food web. However, gulls also hunt crabs, which are among the primary consumers in the detrital food web.

The amount of energy that moves through the two kinds of food webs differs among ecosystems, and it often varies with the seasons. In most cases, however, most of the energy stored in producer tissues moves through *detrital* food webs. Think of cattle that graze heavily in a pasture. About half the energy stored in the grass plants enters the grazers. But cattle cannot access all of the stored energy. A lot is still present in undigested plant parts and in feces, and decomposers and detritivores go to work. Similarly, in marshes, most of the energy initially stored in the marsh grass tissues enters detrital food webs when the plants die.

The inherent inefficiency in energy transfers between trophic levels limits the length of food chains.

Tissues of living photosynthetic organisms are the basis for grazing food webs. Remains and wastes of these organisms are the basis for detrital food webs. In nearly all ecosystems, both types of food webs prevail and interconnect.

47.3 Biological Magnification in Food Webs

LINKS TO SECTIONS 27.3, 28.4, 32.2, 46.5

We turn now to a premise that opened this chapter—that disturbances to one part of an ecosystem often can have unexpected effects on other, seemingly unrelated parts.

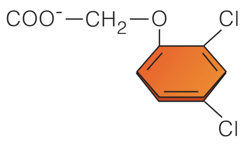
Ecosystem Analysis Many programs in ecology devise models as a way to monitor and predict the outcome of disturbances to ecosystems. Researchers work to identify all of the interacting biological, physical, chemical, and geologic factors that determine an ecosystem's processes and patterns. They might gather information by direct observations, satellite imaging and other remote sensing devices, and tests. Often they use mathematical models and computer programs to integrate pieces of available information on how the factors interact. Analysis of the results help them predict how the ecosystem will react to forces of change.

Results are most useful when all of the factors have been identified and accurately incorporated into a model for the ecosystem. The most crucial factor may be one that researchers do not yet know. A case in point follows.

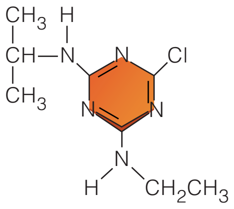
Some Chemical Background As you read in Sections 28.4 and 46.5, many plants repel herbivorous animals with natural toxins. They themselves are not harmed by these organic compounds, but the chemical effects may repel or kill individuals of a different species. We encounter traces of natural plant toxins, even in such familiar foods as hot peppers, potatoes, figs, celery, rhubarb, and alfalfa sprouts. We do not get sick or die in droves from hot peppers, often because toxicity is a function of concentration.

Just a few thousand years ago, farmers used sulfur, lead, arsenic, and mercury to help protect crop plants against insects. They freely dispensed these highly toxic metals until the late 1920s, when someone figured out they were poisoning people. Traces of toxic metals still turn up in contaminated croplands.

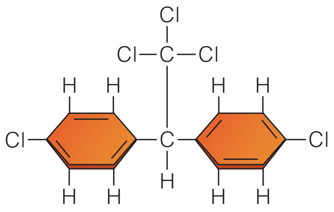
Farmers also used organic compounds extracted from leaves, flowers, and roots as natural pesticides. In 1945, scientists started to make synthetic toxins and to identify mechanisms by which toxins attack pests. *Herbicides*, such as synthetic auxins, kill weeds by disrupting metabolism and growth (Section 32.2). *Insecticides* clog the airways of a target insect, disrupt its nerves and muscles, or prevent its reproduction. *Fungicides* work against harmful fungi, including a mold that makes aflatoxin, one of the deadliest poisons. By 1995, people in the United States were spraying or spreading more than 1.25 billion pounds of toxins each year through fields, gardens, homes, and industrial and commercial sites (Figure 47.7).



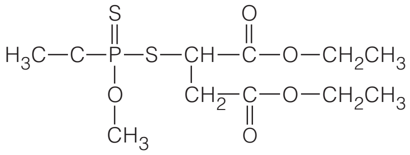
a *2,4-D* (2,4-dichlorophenoxyacetic acid), a synthetic auxin widely used as a herbicide. Enzymes of weeds and microbes cannot easily degrade 2,4-D, compared to natural auxins.



b *Atrazine*, the best-selling herbicide, kills weeds within a few days, as do glyphosate (Roundup), alachlor, (Lasso), and daminozide (Alar). It now appears that atrazine causes abnormal sexual development in frogs, even in trace amounts below the level allowed in drinking water.

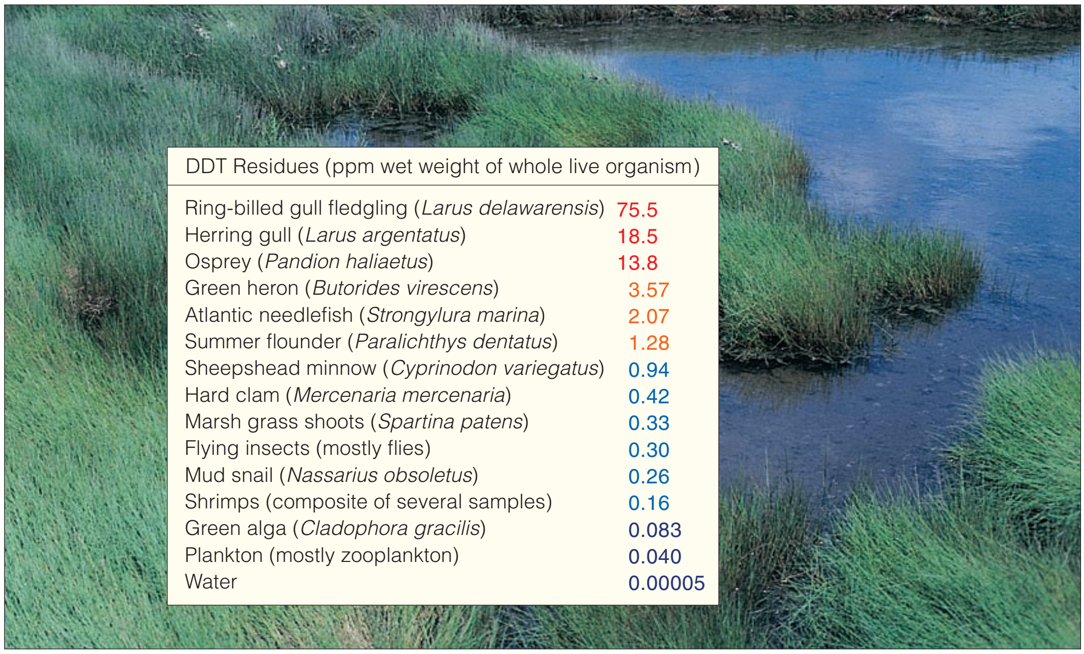


c Dichlorodiphenyltrichloroethane, or *DDT*. It takes two to fifteen years for this nerve cell poison to break down. Chlordane, another type of insecticide, also persists for a long time in the environment.



d *Malathion*. Like other organophosphates, it is cheap, breaks down faster than chlorinated hydrocarbons, and is more toxic. Organophosphates represent half of all insecticides used in the United States. Some are now banned for crops; application of others must end at least three weeks before harvest. Farmers who contest this policy want the Environmental Protection Agency to consider economic and trade issues as well as human health.

Figure 47.7 A few pesticides, some more toxic than others. The photograph shows one of the crop dusters that intervene in the competition for nutrients between crop plants and pests, including weeds.



DDT Residues (ppm wet weight of whole live organism)	
Ring-billed gull fledgling (*Larus delawarensis*)	75.5
Herring gull (*Larus argentatus*)	18.5
Osprey (*Pandion haliaetus*)	13.8
Green heron (*Butorides virescens*)	3.57
Atlantic needlefish (*Strongylura marina*)	2.07
Summer flounder (*Paralichthys dentatus*)	1.28
Sheepshead minnow (*Cyprinodon variegatus*)	0.94
Hard clam (*Mercenaria mercenaria*)	0.42
Marsh grass shoots (*Spartina patens*)	0.33
Flying insects (mostly flies)	0.30
Mud snail (*Nassarius obsoletus*)	0.26
Shrimps (composite of several samples)	0.16
Green alga (*Cladophora gracilis*)	0.083
Plankton (mostly zooplankton)	0.040
Water	0.00005

Figure 47.8 Biological magnification in an estuary on the south shore of Long Island, New York, as reported in 1967 by George Woodwell, Charles Wurster, and Peter Isaacson. The researchers knew of broad correlations between the extent of DDT exposure and mortality. For instance, residues in birds known to have died from DDT poisoning were 30–295 ppm, and they were 1–26 ppm in several fish species. Some DDT concentrations measured during this study were below lethal thresholds but were still high enough to interfere with reproductive success.

Figure 47.9 Peregrine falcon, a top carnivore in some food webs. This raptor almost became extinct as a result of biological magnification of DDT. A wildlife management program successfully brought back its population sizes. Peregrine falcons were reintroduced into wild habitats. They have adapted to cities. There, they hunt pigeons, large populations of which are a messy nuisance.

DDT in Food Webs The DDT molecule highlighted in Figure 47.7*c* is a fairly stable hydrocarbon that is nearly insoluble in water. Therefore, you might think—as many others did—that it would exert its toxic effects only where it was applied. However, winds can easily disperse DDT in vapor form, and water can disperse fine particles of it.

Given its molecular properties, DDT is highly soluble in fats, and so it can accumulate in the tissues of organisms. That is why DDT can show **biological magnification**. By this occurrence, a substance that degrades slowly or not at all becomes ever more concentrated in tissues of organisms at higher trophic levels of a food web.

Most of the DDT that becomes concentrated in all of the organisms that a consumer eats during its lifetime ends up in the consumer's own tissues. DDT and its modified forms disrupt metabolic activities and are toxic to many aquatic and terrestrial animals.

Several decades ago, DDT started to infiltrate food webs and exert its effects on diverse organisms in ways that no one had predicted. Where people sprayed DDT to control Dutch elm disease, songbirds died (Section 27.3). In forests where DDT was sprayed to kill budworm larvae, fish in the forest streams died. In fields sprayed to control one kind of pest, new pests moved in. *DDT was indiscriminately killing the natural predators that keep pest populations in check.*

Then side effects of biological magnification started to show up in habitats far removed from where the DDT had been applied—*and much later in time*. Most vulnerable were brown pelicans, bald eagles, peregrine falcons, and other top carnivores of some food webs (Figures 47.8 and 47.9). Why? A product of DDT breakdown interferes with some physiological processes. As one outcome, bird eggs developed brittle shells; many chick embryos did not even hatch. Some species were facing extinction.

In the United States, DDT has been banned since the 1970s except where necessary to protect public health. Many species hit hardest have recovered. Some birds still lay thin-shelled eggs because they pick up DDT at their winter ranges in Latin America. As late as 1990, a fishery near Los Angeles was closed. DDT from industrial waste discharges that had stopped twenty years earlier was still contaminating that ecosystem.

Today, ecologists are monitoring more than pesticides in ecosystems. Radioisotopes and heavy metals, including copper, zinc, lead, and mercury, also can become ever more concentrated in organisms. For example, in fields near heavily trafficked highways, ecologists found out that the soil concentration of lead can be as high as 1,200 parts per million (ppm)—and it gets magnified as it moves up food chains. The longer the chain, the greater the magnification.

47.4 Studying Energy Flow Through Ecosystems

LINKS TO SECTIONS 7.8, 8.7

Ecologists measure the amount of energy and nutrients entering an ecosystem, how much is captured, and the proportion stored in each trophic level.

WHAT IS PRIMARY PRODUCTIVITY?

The rate at which producers capture and store energy in their tissues during a given interval is the **primary productivity** of an ecosystem. How much energy gets stored depends on (1) how many producers there are and (2) the balance between photosynthesis (energy trapped) and aerobic respiration (energy used). *Gross* primary production is all energy initially trapped by the producers. *Net* primary production is the fraction of trapped energy that producers funnel into growth and reproduction. **Net ecosystem production** is the gross primary production *minus* the energy used by the producers and soil detritivores and decomposers. That amount of energy is subtracted because it cannot be transferred to herbivores at the next trophic level.

On land and in the water provinces, many factors impact net production, its seasonal patterns, and its distribution through a habitat (Section 7.8 and Figure 47.10). For instance, the size and form of the primary producers, the temperature range, the availability of mineral ions, and the amount of sunlight and rainfall in each growing season affect energy acquisition and storage. The harsher the conditions are, the less new growth plants add in a given season, and the lower the primary productivity.

ECOLOGICAL PYRAMIDS

Ecologists often represent the trophic structure of an ecosystem in the form of an ecological pyramid. In such pyramids, all primary producers form a base for successive tiers of consumers above them.

A **biomass pyramid** depicts the dry weight of all of an ecosystem's organisms at each tier. Figure 47.11 shows a biomass pyramid for one aquatic ecosystem. The amounts measured are grams per square meter at some specified time. Most commonly, the primary producers have most of the biomass in pyramids like this, and top carnivores are few. But some biomass pyramids are "upside-down," in that the smallest tier is on the bottom. This happens in springtime blooms of phytoplankton, which grow and reproduce quickly. The primary producers of these aquatic communities support a larger biomass of zooplankton, which eat them about as fast as they can reproduce.

An **energy pyramid** illustrates how the amount of usable energy diminishes as it is transferred through an ecosystem. Sunlight energy is captured at the base (first trophic level) and declines through successive levels to its tip (the top carnivores). Energy pyramids have a large energy base at the bottom, so they are always "right-side up." Such pyramids can provide a clear picture of energy flow from an outside source

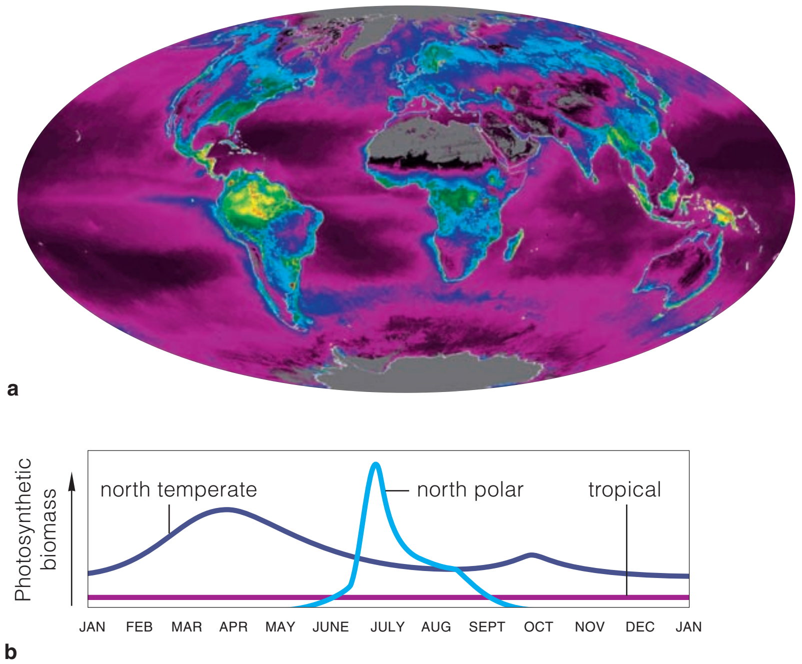


Figure 47.10 (**a**) Summary of satellite data on net primary productivity during 2002. Productivity is coded as *red* (highest) down through *orange*, *yellow*, *green*, *blue*, and *purple* (lowest). Although average productivity per unit of sea surface is lower than it is on land, total productivity on land and in seas is about equal, because most of Earth's surface is covered by water. (**b**) Examples of seasonal shifts in net primary productivity for three categories of ocean ecosystems.

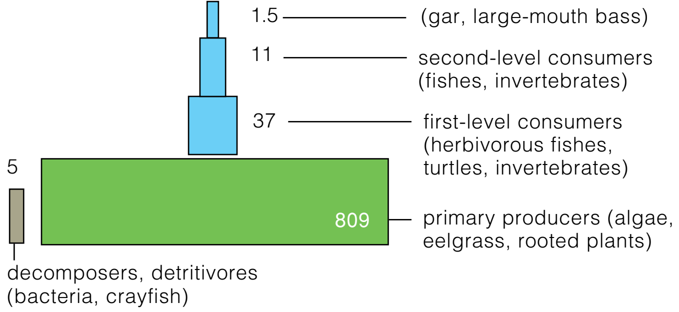


Figure 47.11 Biomass pyramid for Silver Springs, a small aquatic ecosystem in which biomass decreases in successively higher tiers. In different ecosystems, autotrophs are eaten almost as fast as they grow and reproduce. In such cases, biomass accumulates faster in consumers, so the biomass pyramid would be upside down.

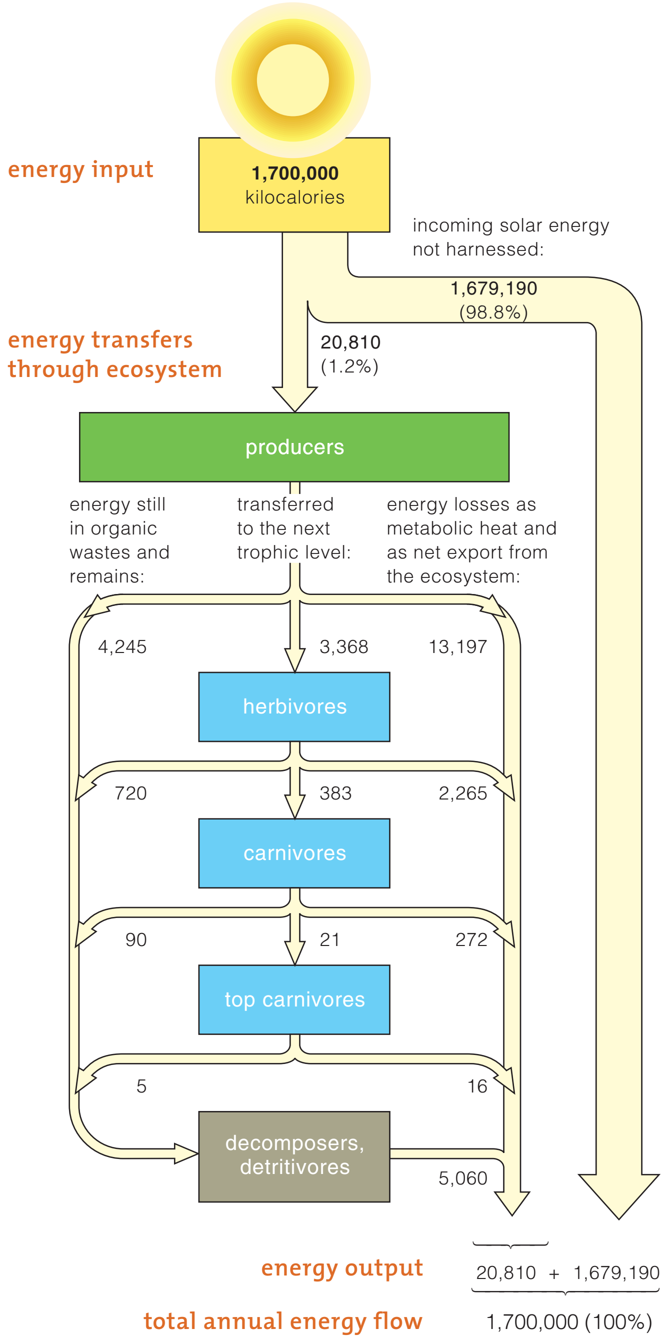


Figure 47.12 ***Animated!*** Breakdown of the annual energy flow through Silver Springs, Florida, as measured in kilocalories/square meter/year. Most of the primary producers in this small spring are aquatic plants. Most carnivores are insects and small fishes; the top carnivores are larger fishes. The original energy source, sunlight, is available all year. Detritivores and decomposers cycle organic compounds from the other trophic levels.

Producers trapped 1.2 percent of the incoming solar energy, and only a little more than a third of that became fixed in new plant biomass. The producers used more than 63 percent of the fixed energy for their own metabolism.

About 16 percent of the fixed energy was transferred to herbivores. Most was used for metabolism or transferred to detritivores and decomposers. Of the energy that transferred to herbivores, only 11.4 percent reached the next trophic level (carnivores). About 5.5 percent of the energy in the lower-level carnivores flowed to the top carnivores.

By the end of the specified interval, all 20,810 kilocalories of energy that flowed through the system appeared as metabolically generated heat.

and on through its departure, mainly by losses of the metabolic heat that each organism generates.

ENERGY FLOW THROUGH SILVER SPRINGS

Visualize yourself with ecologists who are gathering data to construct an energy pyramid for a freshwater spring over the course of one year. They measure how much energy one individual of each species takes in, loses as metabolic heat, stores in its body tissues, and then loses as wastes. They multiply the energy per individual by population size, then calculate energy inputs and outputs. Then they express the energy flow per unit of water (or land) per unit of time. Figure 47.12 was constructed from data that were gathered this way during a long-term study of a grazing food web in this type of aquatic ecosystem. It shows some calculations that ecologists used to depict the energy flow in pyramid form in Figure 47.13.

Based on many such studies, ecologists arrived at this generalization: Given the metabolic demands of organisms and the amount of energy lost in organic wastes, only 6 to 16 percent of the energy entering one trophic level is available for organisms at the next.

Gross primary productivity is an ecosystem's total rate of photosynthesis during a specified interval. The net amount is the rate at which primary producers store energy in tissues in excess of their rate of aerobic respiration. Heterotrophic consumption affects the rate of energy storage.

The trophic structure of an ecosystem may be represented by an ecological pyramid. Biomass pyramids may be top- or bottom-heavy depending on the ecosystem. In contrast, an energy pyramid always has the largest tier on the bottom.

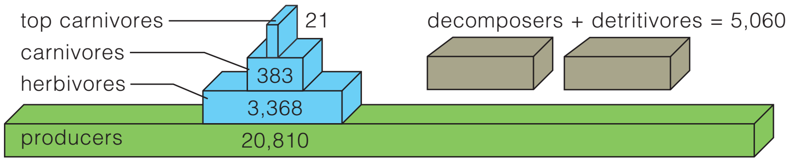


Figure 47.13 Pyramid of energy flow through Silver Springs, in kilocalories/square meter/year. This is a summary of the data used to construct Figure 47.12. Compare Figure 47.11, the biomass pyramid for this same ecosystem.

47.5 Overview of Biogeochemical Cycles

Without water and the nutrients dissolved in it, there would be no primary productivity, and no life.

In a **biogeochemical cycle**, an essential element moves from the environment, through ecosystems, then back to the environment. No other element can directly or indirectly fulfill the metabolic role of such elements, or **nutrients**, which is why we call them essential. As you read earlier, oxygen, hydrogen, carbon, nitrogen, and phosphorus are among them.

Figure 47.14 is one model for these cycles. Transfers to and from environmental reservoirs are usually far slower than rates of exchange among organisms of an ecosystem. Water is the main source for hydrogen and oxygen. Gaseous or ionized forms of other elements are dissolved in it. Solid forms of elements are tied up in rocks or sediments.

Nutrients move into and out of ecosystems by way of natural geologic processes. Weathering of rocks is a common source of nutrient inputs into an ecosystem. Erosion and runoff put nutrients into streams that carry them away. Most often, the quantity of a nutrient being cycled through an ecosystem each year is greater than the amount entering and leaving.

Decomposers help cycle the nutrients in ecosystems. Various prokaryotic species help transform solids and ions into gases, then back again. Through their action, they convert some elements that function as nutrients to forms that primary producers can take up.

In three types of biogeochemical cycles, portions of the environment are reservoirs for specific elements. In the *hydrologic* cycle, oxygen and hydrogen move, on a grand scale, in molecules of water. In *atmospheric* cycles, some gaseous form of the nutrient is the one available to ecosystems. Carbon and nitrogen cycles are examples. Phosphorus and other solid nutrients that have no gaseous form move in *sedimentary* cycles. They accumulate on the seafloor and eventually return to land through geological uplifting, which typically has taken millions of years. Earth's crust is the biggest reservoir for nutrients that have sedimentary cycles.

Primary productivity depends on water and nutrients that become dissolved in it. In a biogeochemical cycle, a nutrient moves slowly through the environment, then rapidly among organisms, and back to environmental reservoirs.

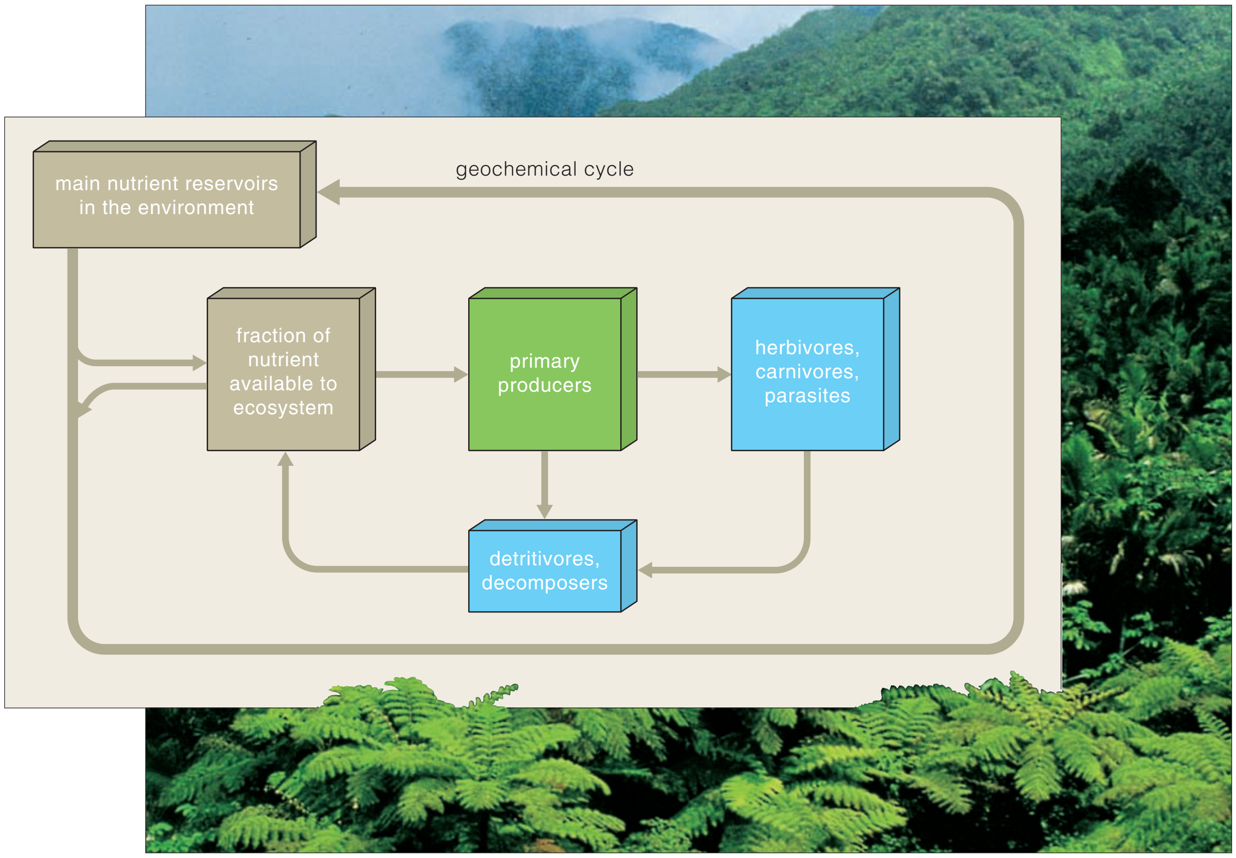


Figure 47.14 One generalized model of nutrient flow through an ecosystem on land. The overall movement of nutrients from the physical environment, through organisms, and then back to the environment is a biogeochemical cycle.

47.6 Hydrologic Cycle

On land, the availability of water, and nutrients dissolved in it, is not plentiful all of the time in all ecosystems. The variation affects primary productivity.

Driven by solar energy, Earth's waters slowly move from the ocean into the atmosphere, to land, and back to the ocean—the main reservoir. Figure 47.15 shows this **hydrologic cycle**. Water that evaporates into the lower atmosphere stays aloft as vapor, clouds, and ice crystals, then falls mainly as rain and snow. Ocean circulation and wind patterns influence the cycle.

Water moves nutrients into and out of ecosystems. A **watershed** is any region where precipitation flows into a single stream or river. Watersheds may be as small as the area that drains into a stream or as vast as the Amazon River or Mississippi River basin. Most water entering a watershed seeps into soil or joins surface runoff into streams. Plants take up water from soil and lose it by transpiration (Figure 47.16).

In the hydrologic cycle, water slowly moves on a global scale from the world ocean—the main reservoir—through the atmosphere, onto land, then back to the ocean.

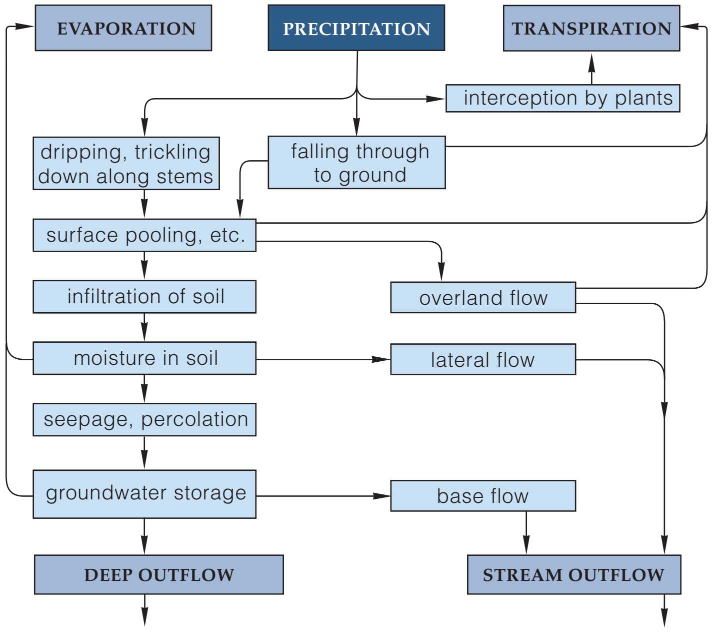


Figure 47.16 Model for how water moves through watersheds in general. *Dark blue* box is the input to the watershed; *light blue*, the distribution within it; and *medium blue*, outputs from it. Transpiration is the name for evaporation of water from leaves and other plant parts exposed to air (Section 30.3). Plants absorb water from soil and groundwater stores.

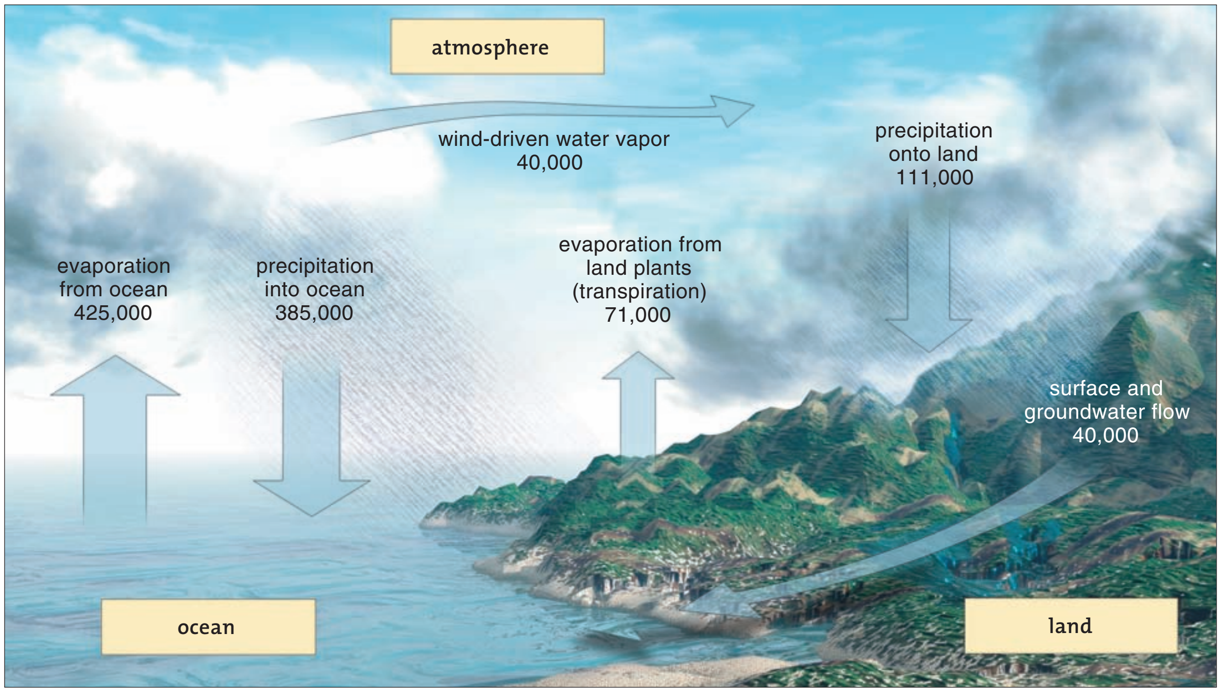


Figure 47.15 ***Animated!*** Hydrologic cycle. Water moves from the ocean to the atmosphere, land, and back. Arrows identify processes that move water, as measured in cubic kilometers per year. With 1,370,000,000 cubic kilometers, the ocean is the main reservoir. The next largest, polar ice and glaciers, locks up 29,000,000. Groundwater makes up only 4,000,000, lakes and rivers only 241,000, soil 67,000, and the atmosphere 14,000 cubic kilometers.

47.7 Watershed Experiments

FOCUS ON SCIENCE

LINKS TO SECTIONS 23.10, 30.1

Water is vital for all organisms. It also is a transport medium; it moves nutrients into and out of ecosystems. Its role in moving nutrients became clear in long-term studies of watersheds.

A watershed, again, is any region in which the precipitation becomes funneled into just one stream or one river. Figure 47.17*a* shows part of an experimental forest in the Hubbard Brook Valley of New Hampshire. The watersheds in this forest have a surface area of 14.6 hectares (36 acres), on average. Over the years, ecologists have painstakingly measured nutrient inputs and outputs in this forest. Such measurements have many practical applications.

For instance, cities that draw from a watershed's supply of surface water can adjust their usage in compliance with seasonal shifts in the volume of water. Measurements also reveal the extent to which vegetation cover influences the movement of nutrients through the ecosystem phase of biogeochemical cycles.

For example, you might think that surface runoff in a watershed would swiftly leach out calcium ions and other minerals dissolved in soil water. (Here you may wish to review the Section 30.1 explanation of leaching.) However, in the young, undisturbed forests of the Hubbard Brook watersheds, each hectare lost only eight kilograms or so of its calcium. The weathering of rocks and rainfall were replacing the lost calcium. In addition, tree roots were "mining" the soil by absorbing dissolved mineral ions, so calcium was being stored in a growing biomass of tree tissues.

In experimental watersheds in the Hubbard Brook Valley, deforestation caused a shift in nutrient outputs. The results, summarized in Figure 47.17*d*, are sobering. Calcium and other nutrients cycle very slowly, which means that deforestation may disrupt the availability of nutrients for an entire ecosystem. This is especially the case for forests that cannot regenerate themselves over the short term because of their soil properties and other characteristics. As you will see in the next chapter, the northern coniferous forests and tropical rain forests require long recovery times.

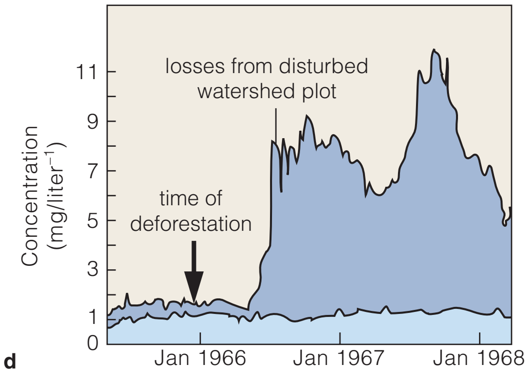


Figure 47.17 (**a**) Experimental deforestation in the Hubbard Brook watershed of New Hampshire. Researchers monitor surface runoff flowing over concrete catchments (**b**) on its way to a stream below. For some experiments, they stripped vegetation from forest plots but did not disturb the soil. They applied herbicides for three years to prevent regrowth. (**c**) They compared concentrations of calcium ions and other minerals in runoff over a control catchment against concentrations in runoff from an undisturbed area.

(**d**) Calcium losses were *six times* greater in deforested plots. Removing all vegetation from such forests clearly alters nutrient outputs in ways that can disrupt nutrient availability for an entire ecosystem.

47.8 A Global Water Crisis

Most of Earth's water is too salty to drink or use for agriculture. The skyrocketing increases in human population size make this a big problem.

Two-thirds of the fresh water that humans use goes directly into irrigating fields (Figure 47.18). Ironically, irrigation makes the land less suitable for agriculture. Piped-in water commonly has high concentrations of mineral salts. Where soil drains poorly, evaporation results in **salinization**, or a build-up of salt in soil that stunts crop plants and decreases yields.

Soil and aquifers hold **groundwater**. About half of the United States population taps into groundwater as a source of drinking water. Chemicals leached from landfills, hazardous waste dumps, and underground tanks that store gasoline, oil, and some solvents often contaminate it. Unlike flowing streams, which recover fast, polluted groundwater is difficult and expensive to clean up.

Groundwater overdrafts, or the amount that nature has not replenished, are high in many areas. Figure 47.19 shows some regions of aquifer depletion in the United States. Overdrafts have now depleted half of the great Ogallala aquifer, which supplies irrigation water for 20 percent of the Midwest's croplands.

Inputs of sewage, animal wastes, and many toxic chemicals from power-generating plants and factories make water unfit to drink. Sediments and pesticides run off from fields into water, along with phosphates and other nutrients that promote algal blooms. The pollutants accumulate in lakes, rivers, and bays before reaching the ocean. Many cities all over the world are still dumping untreated sewage into coastal waters.

If current rates of human population growth and water depletion continue, the amount of fresh water available for everyone will soon be 55 to 66 percent less than it was in 1976. In this past decade, thirty-three nations have already engaged in conflicts over reductions in water flow, pollution, and silt buildup in aquifers, rivers, and lakes. Among the squabblers are the United States and Mexico, Pakistan and India, and Israel and the Palestinian territories.

Could we meet our water needs by **desalinization**, or removal of salt from seawater? Salt can be removed by distillation or pushing water through membranes. The processes require fossil fuels, which makes them more feasible in Saudi Arabia and other countries with small populations and big fuel reserves. Most likely, desalinization will not be cost-effective for large-scale agriculture. It also produces mountains of salts.

Figure 47.18 If the world has so little fresh water, why are we irrigating deserts?

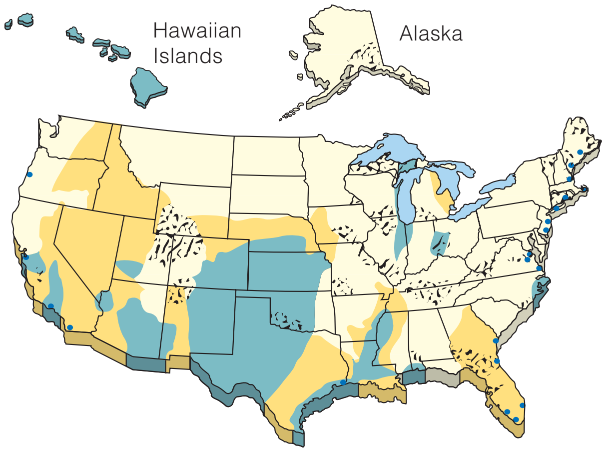


Figure 47.19 Aquifer depletion, seawater intrusion, and groundwater contamination in the United States. *Green* signifies high overdrafts, *gold*, moderate overdrafts, and *pale yellow*, insignificant withdrawals. Shaded areas are sites of major groundwater pollution. *Blue* squares indicate saltwater intrusion from nearby seas.

We may be in for upheavals and wars over water rights. Does this sound far-fetched? Consider the new dam across the Euphrates River. By building immense irrigation systems and dams at the headwaters of the Tigris and Euphrates rivers, Turkey can, in the view of one of its dam site managers, shut off water flow into Syria and Iraq for as long as eight months "to regulate their political behavior." One might say that regional, national, and global planning is overdue.

Agriculture accounts for about two-thirds of the human population's use of freshwater.

Aquifers that supply much of the world's drinking water are becoming polluted and depleted. Regional conflicts over access to clean, drinkable water are likely to increase.

47.9 Carbon Cycle

LINKS TO SECTIONS 7.8, 23.10, INTRODUCTIONS CHAPTERS 3, 22

Most of the world's carbon is locked in ocean sediments and rocks. It moves into and out of ecosystems in gaseous form, so its movement is said to be an atmospheric cycle.

In the **carbon cycle**, carbon moves through the lower atmosphere and all food webs on its way to and from its large reservoirs (Figure 47.20). Earth's crust holds the most carbon—66 million to 100 million gigatons, of which 4,000 are present in fossil fuels. (One gigaton is a billion tons.) Remember Chapter 22? Many single-celled organisms of ancient aquatic habitats, including foraminiferans and coccolithophores, formed shells of calcium carbonate. Uncountable numbers of cells died, sank, and were buried in seafloor sediments. Carbon in their remains have been cycled exceedingly slowly, after geologic forces uplift part of the seafloor. Such cycling cannot be measured in years, obviously.

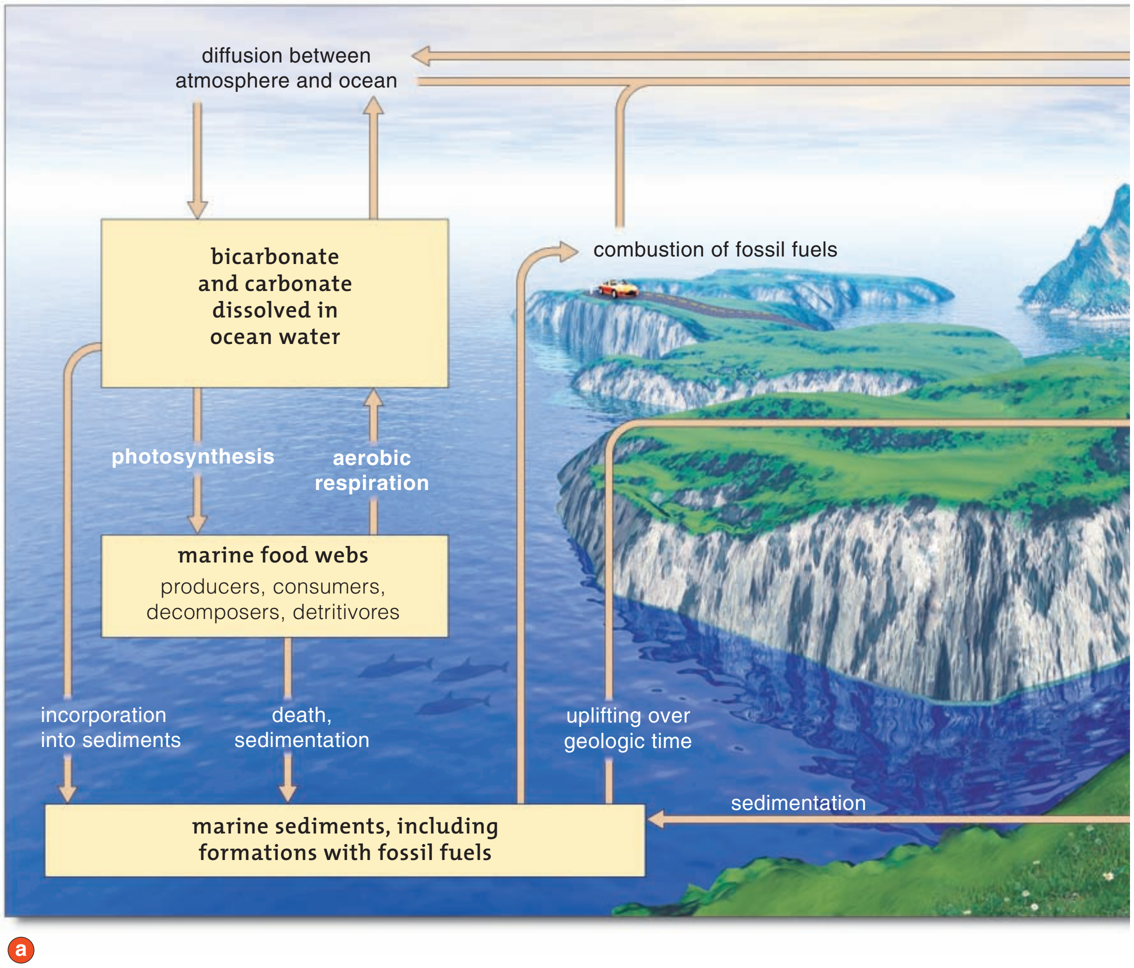
Most of the annual cycling takes place between the ocean and atmosphere. The ocean holds 38,000–40,000 gigatons of dissolved carbon, primarily in the form of bicarbonate and carbonate ions. The atmosphere holds about 766 gigatons of carbon, mainly combined with oxygen in the form of carbon dioxide (CO_2).

Detritus in soil holds another 1,500–1,600 gigatons of carbon atoms. Another 540–610 gigatons is present in biomass. Methane hydrates form a huge reservoir that was, oddly, overlooked in the past. Between 10,000 and 11,000 gigatons are sequestered off the coasts of continents and in permafrost. As explained in Section 48.10, permafrost consists of perpetually frozen peat bogs that are sometimes more than 500 meters thick. You read about methane hydrates in the introduction to Chapter 3. Also, on page 865 of this chapter, you are invited to consider how unstable deposits on the seafloor can have big impact on the carbon cycle.

Why doesn't all of the CO_2 dissolved in warm sea surface waters escape into the atmosphere? Driven by winds and regional differences in water density, ocean water makes a gigantic loop from the surface of the Pacific and Atlantic oceans down to the Atlantic and

Figure 47.20 ***Animated!*** Global carbon cycle through typical marine ecosystems (**a**) and land ecosystems (**b**). *Gold* boxes show the main carbon reservoirs. The vast majority of carbon atoms are in sediments and rocks, followed by ever lesser amounts in ocean water, soil, the atmosphere, and biomass. Here are typical annual fluxes in the global distribution of carbon, in gigatons:

From atmosphere to plants by carbon fixation	120
From atmosphere to ocean	107
To atmosphere from ocean	105
To atmosphere from plants	60
To atmosphere from soil	60
To atmosphere from fossil fuel burning	5
To atmosphere from net destruction of plants	2
To ocean from runoff	0.4
Burial in ocean sediments	0.1



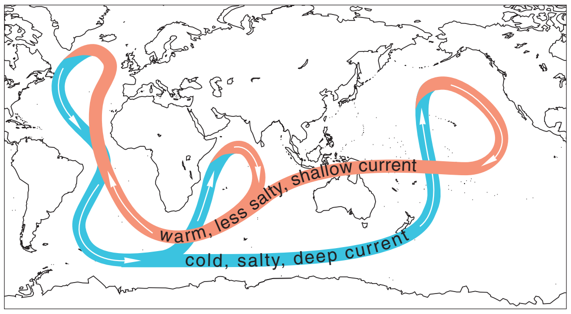


Figure 47.21 Ocean loop that moves carbon dioxide to carbon's deep ocean reservoir. It sinks in the cold, salty North Atlantic and rises in the warmer Pacific.

Antarctic seafloors. The CO_2 moves into deep storage reservoirs before water loops back up (Figure 47.21). The loop effectively mediates the annual fluxes in the global distribution of carbon.

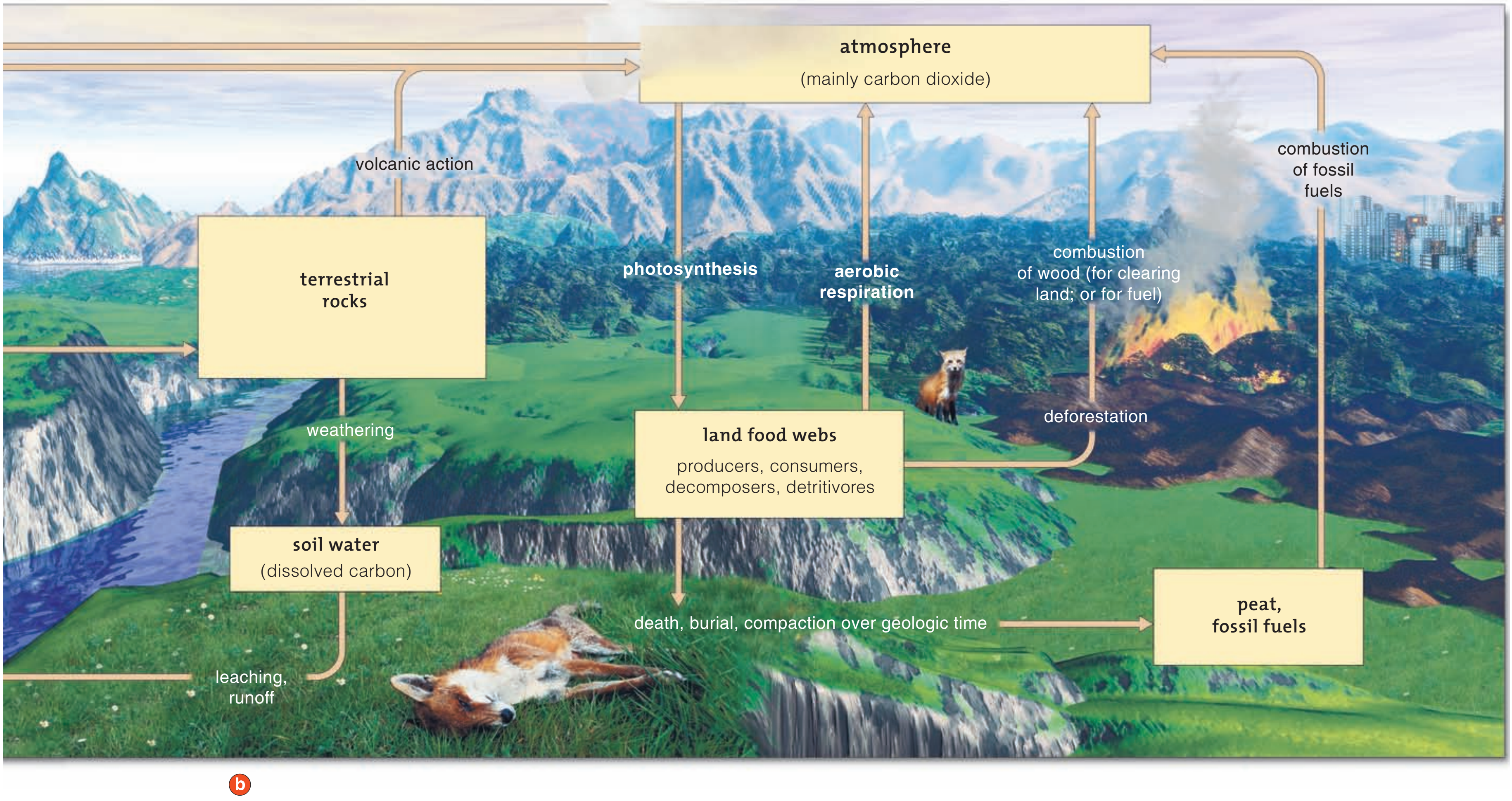
As you know, CO_2 is the key source of carbon for autotrophs, and for food webs in ecosystems on land and in the seas. That is why biologists often refer to the glocal cycling of carbon as the *carbon–oxygen cycle*. When photosynthetic autotrophs fix carbon, they lock up billions of metric tons of carbon atoms in organic compounds annually (Section 7.8). When aerobic cells engage in aerobic respiration, they release CO_2. More CO_2 is released when fossil fuels or forests burn and when volcanoes erupt.

The average time that an ecosystem holds a given carbon atom varies. As examples, organic wastes and remains decompose so fast in tropical rain forests that carbon does not build up at the soil surface. Bogs and other anaerobic habitats do not favor decomposition, so the organic material is not degraded to smaller bits and carbon accumulates in peat. Humans withdraw 4 to 5 gigatons from fossil fuel reservoirs every year. At the same time, human activities put about 6 gigatons more carbon in the atmosphere than can be cycled to the ocean reservoirs by natural processes.

Only about 2 percent of the excess carbon entering the atmosphere will become dissolved in ocean water. Most researchers now suspect that the carbon build-up in the atmosphere is amplifying the greenhouse effect. In other words, the increase might be contributing to global warming. The next section takes a look at this possibility and its environmental implications.

Earth's crust holds the vast majority of carbon. The ocean is the next largest reservoir. Most of the annual cycling of carbon occurs between the ocean and atmosphere.

Carbon moves into and out of ecosystems mainly when combined with oxygen, as in carbon dioxide, bicarbonate, and carbonate. We refer to this as the carbon–oxygen cycle.



CYCLING OF WATER AND NUTRIENTS

47.10 Greenhouse Gases, Global Warming

LINKS TO SECTIONS 7.1, 21.5, 23.10

The atmospheric concentrations of gaseous molecules help determine the average temperature near Earth's surface. Human activities are contributing to increases that may cause dramatic climate change.

Concentrations of a variety of gaseous molecules in Earth's atmosphere profoundly influence the average temperature near its surface. Temperature, in turn, has far-reaching effects on global and regional climates.

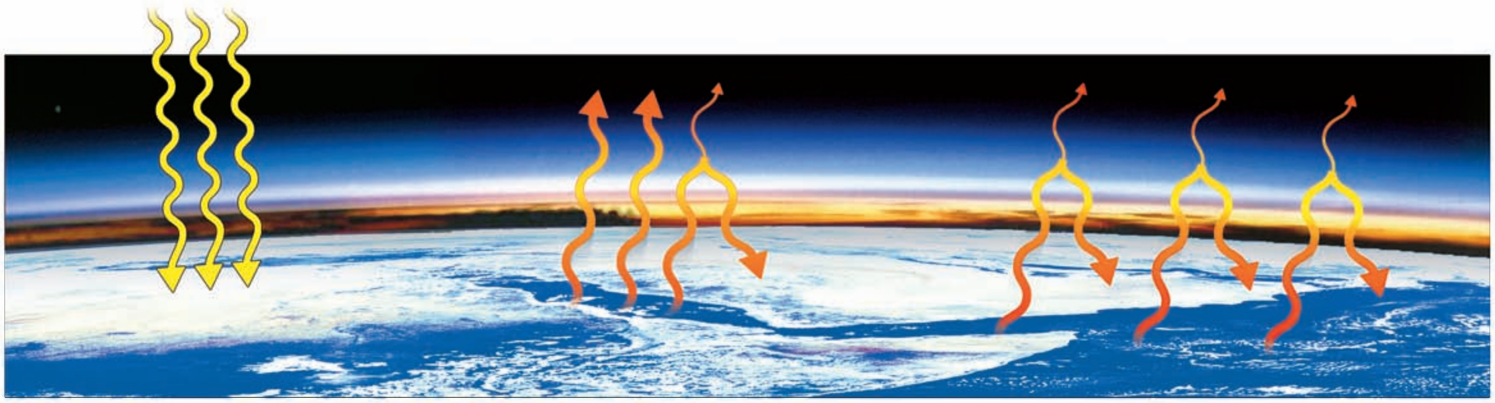
Atmospheric molecules of carbon dioxide, water, nitrous oxide, methane, and chlorofluorocarbons are among the main players in interactions that affect global temperature. Collectively, these gases function like the panes of glass in a greenhouse—hence their name, "greenhouse gases." The wavelengths of visible light pass through these gases to Earth's surface, which absorbs them and then emits longer, infrared wavelengths—heat. Greenhouse gases impede the escape of heat energy from Earth into space. How? The gaseous molecules absorb the longer wavelengths, then radiate much of it back toward Earth (Figure 47.22).

Constant reradiation of heat by greenhouse gases occurs lockstep with the constant bombardment and absorption of wavelengths from the sun. As heat builds up in the lower atmosphere, the air temperature near Earth's surface rises. The warming action is known as the **greenhouse effect**. Without it, Earth's surface would be so cold that it could not support life.

In the 1950s, laboratory researchers on Hawaii's highest volcano set out to measure the atmospheric concentrations of greenhouse gases. That remote site is almost free of local airborne contamination; it is also representative of overall atmospheric conditions for the Northern Hemisphere. What did they find? Briefly, carbon dioxide concentrations follow annual cycles of primary production. They drop during the summer, when photosynthesis rates are highest. They rise in winter, when photosynthesis rates decline but aerobic respiration is still going on.

Figure 47.23 *Facing page*, graphs of recent increases in four categories of atmospheric greenhouse gases. A key factor is the sheer number of gasoline-burning vehicles in large cities. *Above*, Mexico City on a smoggy morning. With 10 million residents, it is the world's largest city.

Alternating troughs and peaks along the graph line in Figure 47.23*a* are annual lows and highs of global carbon dioxide concentrations. For the first time, we could see the integrated effects of carbon balances for an entire hemisphere. Notice the midline of the troughs and peaks in the cycle. It shows that carbon dioxide concentration is steadily increasing—as are the concentrations of other major greenhouse gases.

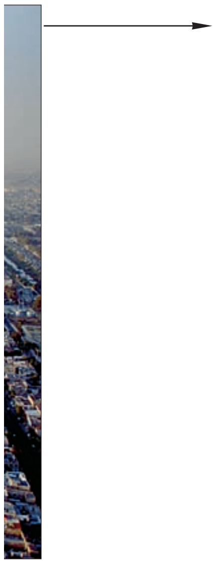


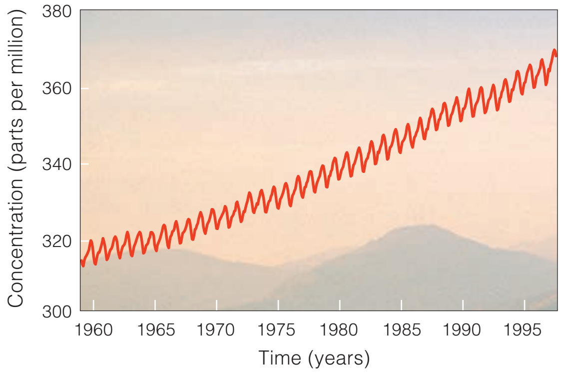
ⓐ Wavelengths in rays from the sun penetrate the lower atmosphere, and they warm the Earth's surface.

ⓑ The surface radiates heat (infrared wavelengths) to the atmosphere. Some heat escapes into space. But greenhouse gases and water vapor absorb some infrared energy and radiate a portion of it back toward Earth.

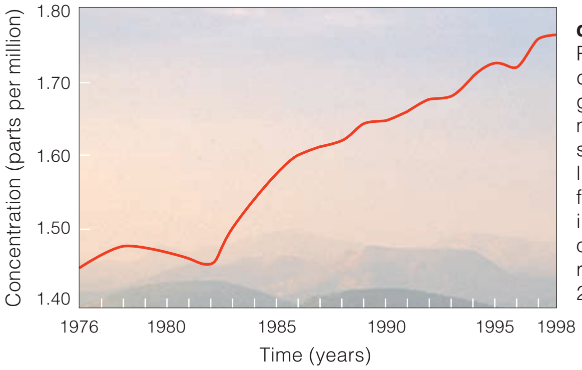
ⓒ Increased concentrations of greenhouse gases trap more heat near Earth's surface. Sea surface temperatures rise, so more water evaporates into the atmosphere. Earth's surface temperature rises.

Figure 47.22 ***Animated!*** The greenhouse effect.

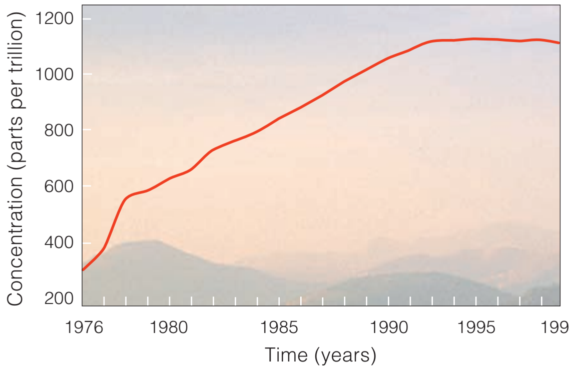




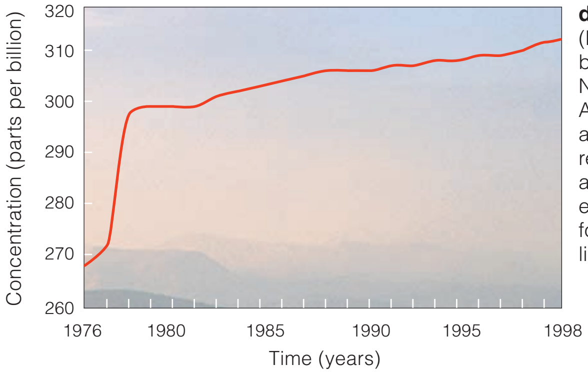
a Carbon dioxide (CO_2). Of all human activities, the burning of fossil fuels and deforestation (Section 23.10) contribute the most to rising atmospheric levels.



c Methane (CH_4). Production and distribution of natural gas as fuel adds to methane released by some bacteria that live in swamps, rice fields, landfills, and in the digestive tract of cattle and other ruminants (Section 21.5).



b CFCs. Until restrictions were in place, CFCs were widely used in plastic foams, refrigerators, air conditioners, and industrial solvents.



d Nitrous oxide (N_2O). Denitrifying bacteria produce N_2O in metabolism. Also, fertilizers and animal wastes release enormous amounts; this is especially so for large-scale livestock feedlots.

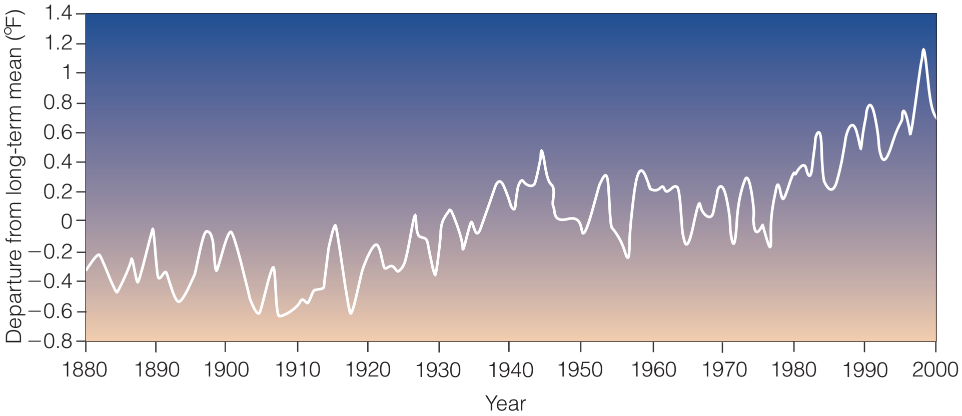


Figure 47.24 Recorded changes in global temperature between 1880 and 2000. At this writing, the hottest year on record was 1998.

Atmospheric levels of greenhouse gases are far higher than they were in most of the past. Carbon dioxide may be at its highest level since 420,000 years ago, and possibly since 20 million years ago. There is a growing consensus that the rise in greenhouse gases is caused by some human activities, mainly burning of fossil fuels. The big worry is that the increase may have far-reaching environmental consequences.

The increase in greenhouse gases may be a factor in **global warming**, a long-term increase in temperature near Earth's surface. Since direct atmospheric readings started in 1861, the lower atmosphere's temperature has risen by more than 1°F, mostly since 1946 (Figure 47.24). Also since then, nine of the ten hottest years on record occurred between 1990 and the present. Data from satellites, weather stations and balloons, research ships, and supercomputer programs suggest that irreversible climate changes are already under way. Polar ice is melting; glaciers are retreating. This past century, the sea level may have risen as much as twenty centimeters (eight inches).

We can expect continued temperature increases to have drastic effects on climate. As evaporation increases, so will global precipitation. Intense rains and flooding are expected to become more frequent in some regions.

It bears repeating: As investigations continue, a key research goal is to investigate all of the variables in play. With respect to the consequences of global warming, the most crucial variable may be the one we do not know.

47.11 Nitrogen Cycle

LINKS TO
SECTIONS 21.4,
22.6, 24.6, 30.2

Gaseous nitrogen makes up about 80 percent of the lower atmosphere. Successively smaller reservoirs are seafloor sediments, ocean water, soil, biomass on land, nitrous oxide in the atmosphere, and marine biomass.

INPUTS INTO ECOSYSTEMS

Gaseous nitrogen (N_2) travels in an atmospheric cycle called the **nitrogen cycle**. Triple covalent bonds join its two atoms ($N \equiv N$). Volcanic action and lightning convert some N_2 into forms that enter food webs. Far more enters by **nitrogen fixation**. With this metabolic process, bacteria split all three bonds in N_2 and use the atoms to form ammonia (NH_3). Later, ammonia is converted to ammonium (NH_4^+) and nitrate (NO_3^-). Most plants easily take up these two forms of nitrogen.

Figure 47.25 shows the nitrogen cycle. Its nitrogen fixers include cyanobacteria in aquatic habitats and in many lichens. *Rhizobium* is a nitrogen fixer in nodules on legume roots (Sections 24.6 and 30.2). Collectively, these nitrogen-fixing bacteria fix about 200 million metric tons of nitrogen each year. The plants do pay a high metabolic cost for the interaction. They give up sugars and other photosynthetic products that take large investments of ATP and NADPH. Such plants have a competitive edge in nitrogen-poor soil. Other plants that do not pay the metabolic price commonly displace them in nitrogen-rich soil.

The nitrogen incorporated into plant tissues moves through trophic levels of ecosystems and ends up in nitrogen-rich wastes and remains, where bacteria and fungi go to work on them (Sections 21.4 and 24.6). By

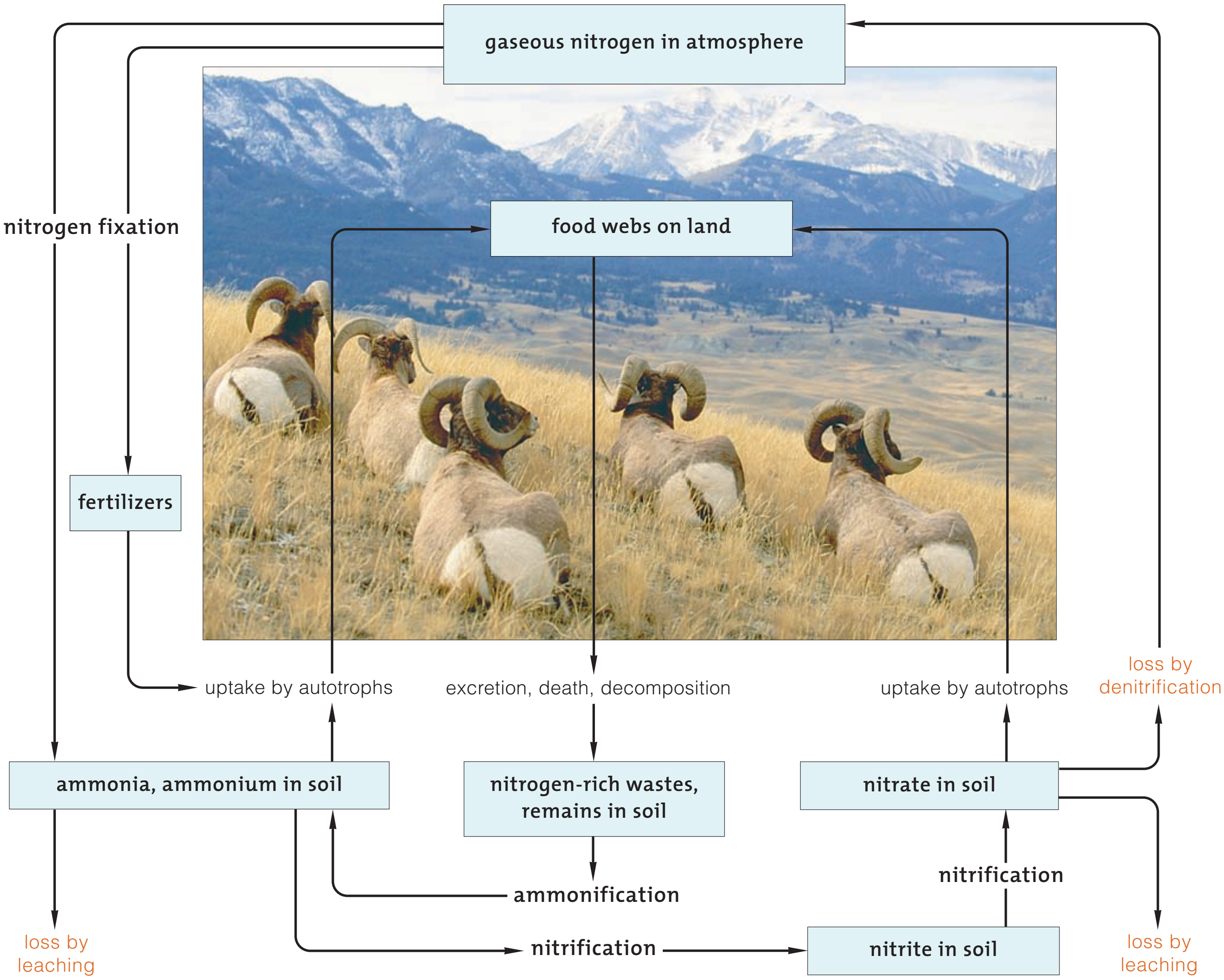


Figure 47.25 ***Animated!*** The nitrogen cycle in an ecosystem on land. Activities of nitrogen-fixing bacteria make nitrogen available to plants. Other bacterial species cycle nitrogen to plants. They break down organic wastes to ammonium and nitrates.

the process of **ammonification**, these microbes break down nitrogenous materials, and ammonium forms. They use some of the ammonium and release the rest to soil. Plants take it up, as do some nitrifying bacteria. In the first step of **nitrification**, certain bacteria cause nitrite (NO_2^-) to form when they strip electrons from ammonium. Different nitrifying bacteria use the nitrite in reactions that form nitrate (NO_3^-).

NATURAL LOSSES FROM ECOSYSTEMS

Ecosystems lose nitrogen through **denitrification**. By this process, denitrifying bacteria convert nitrate or nitrite to gaseous nitrogen or to nitrogen oxide (NO_2). Most denitrifying bacteria are anaerobic; they live in waterlogged soils and aquatic sediments.

Ammonium, nitrite, and nitrate are also lost from a land ecosystem in runoff and by leaching, the removal of some nutrients as water percolates through the soil (Section 30.1). Leaching removes nitrogen from land ecosystems and adds it to aquatic ones.

DISRUPTIONS BY HUMAN ACTIVITIES

Deforestation and grassland conversion for agriculture also cause big nitrogen losses. With each clearing and harvest, nitrogen in plant tissues is removed. Soil also becomes more vulnerable to erosion and leaching.

Many farmers counter nitrogen losses by rotating crops, as by alternating wheat with legumes. Rotation can help keep soil stable and productive. In developed countries, farmers also spread nitrogen-rich fertilizers. They even select new strains of crop plants that have a greater capacity to take up fertilizers from soil. By such practices, crop yields per hectare have doubled and sometimes quadrupled over the past forty years.

High temperature and pressure converts nitrogen and hydrogen gases to ammonia fertilizers. The use of these manufactured fertilizers greatly increases crop yields. It also can alter soil chemistry by disrupting a pH-dependent process called **ion exchange**. By this process, ions dissociate from soil particles, and then other ions in soil water replace them (Section 30.2). The most abundant exchangeable ions are calcium and magnesium. The hydrogen ions in nitrogen fertilizers makes soil water more acidic, and they displace other ions from binding sites on soil particles. Too many calcium and magnesium ions, which also are required for plant growth, trickle away in soil water.

Deposition of nitrogen in acid rains can have the same effect as overfertilization. Fossil fuel burned in power plants and vehicles releases nitrogen oxides, which contribute to global warming and to acid rain. Winds often carry these air pollutants far from their sources (Figure 47.26). By some estimates, pollutants are putting ten times the normal amounts of nitrogen into certain forests in eastern Europe.

Figure 47.26 Dead and dying trees in Smoky Mountain National Park. Forests are among the casualties of nitrogen oxides and other forms of air pollution.

Different plant species respond in different ways to high nitrogen levels. Increases in nitrogen can disrupt the balance among competing species in a community (Section 46.1), and diversity may decline. The impact can be pronounced in forests at high elevations and high latitudes, which have nitrogen-poor soils.

Some human activities disrupt aquatic ecosystems through nitrogen enrichment. Crop plants cannot take up all of the nitrogen in fertilizers. About half of the nitrogen applied to fields runs off into rivers, lakes, and estuaries. Sewage from cities and animal wastes puts even more nitrogen into the water provinces. As one outcome, nitrogen inputs promote algal blooms. So does the phosphorus in fertilizers, as explained in Sections 22.6 and 47.12.

The ecosystem phase of the nitrogen cycle starts with nitrogen fixation. Bacteria convert gaseous nitrogen in the air to ammonia and then to ammonium, which is a form that plants easily take up.

By ammonification, bacteria and fungi make additional ammonium available to plants when they break down nitrogen-rich organic wastes and remains.

By nitrification, bacteria convert nitrites in soil to nitrate, which also is a form that plants easily take up.

The ecosystem loses nitrogen when denitrifying bacteria convert nitrite and nitrate back to gaseous nitrogen, and when nitrogen is leached from soil.

47.12 Sedimentary Cycles

LINKS TO SECTIONS 3.8, 22.6

Unlike carbon and nitrogen, phosphorus does not cycle into and out of ecosystems in gaseous form. Like nitrogen, phosphorus can be taken up by plants only in ionized form, and it, too, is often a limiting factor on plant growth.

In the **phosphorus cycle**, phosphorus passes quickly through food webs as it moves from land to ocean sediments, then slowly back to dry land. Earth's crust is the largest reservoir of phosphorus.

The phosphorus in rock formations is mainly in the form of phosphate (PO_4^{3-}). Weathering and erosion deliver these ions to streams and rivers, which move them onward to the sea (Figure 47.27). The phosphates gradually accumulate and form insoluble deposits on submerged continental shelves. After many millions of years, crustal movements might uplift part of the seafloor and expose the phosphates on land surfaces. There, weathering and erosion will release phosphates from exposed rocks and start the cycle over again.

Phosphates are required building blocks for ATP, phospholipids, nucleic acids, and other compounds. Plants take up dissolved phosphates from soil water. Herbivores get them by eating plants; carnivores get them by eating herbivores. Animals lose phosphate in urine and in feces. Bacterial and fungal decomposers release phosphate from organic wastes and remains, then plants take them up again.

The hydrologic cycle helps move phosphorus and other minerals through ecosystems. Water evaporates from the ocean and falls on land. As it flows back to the ocean, it transports silt and dissolved phosphates that the primary producers require for growth.

Of all minerals, phosphorus is often the limiting factor in ecosystems. Only newly weathered, young soils are high in phosphorus. In aquatic habitats, most phosphorus is locked up in sediments. Not much is in gaseous form, so little is lost to the atmosphere.

Phosphorus is being lost from many tropical and subtropical ecosystems, many of which already have phosphorus-poor soils. Phosphorus stored in biomass and released from decomposing organic matter can sustain undisturbed forests or grasslands. As trees are harvested or land is cleared, phosphorus is lost. Crop yields start out low and soon are nonexistent. After fields are abandoned, natural regrowth is sparse. In developing countries especially, 1 to 2 billion hectares may be already depleted of phosphorus.

What about the developed countries? After years of fertilizer applications, many soils have phosphorus overloads. It is concentrated in eroded sediments and

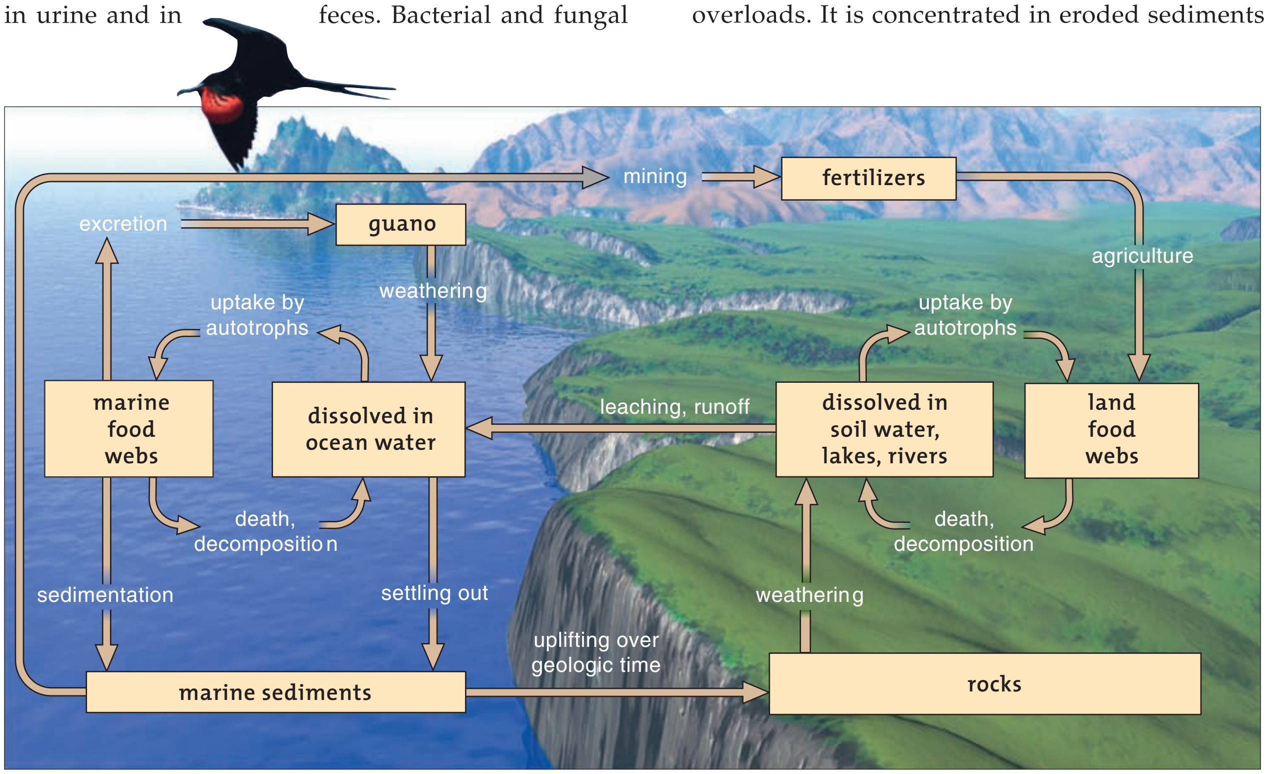


Figure 47.27 ***Animated!*** Phosphorus cycle. In this sedimentary cycle, phosphorus moves mainly in the form of phosphate ions (PO_4^{3-}) to the ocean. It moves through phytoplankton of marine food webs, then to fishes that eat plankton. Seabirds eat the fishes, and their droppings (guano) accumulate on islands. Humans collect and use guano as a phosphate-rich fertilizer.

runoff from agricultural fields. Phosphorus also is a waste in the outflows from sewage treatment plants and factories, and in the runoff from fields. Dissolved phosphorus that gets into streams, rivers, lakes, and estuaries can promote destructive algal blooms. Like plants, all photosynthetic algae require phosphorus, nitrogen, and other ions to grow. In many freshwater ecosystems, nitrogen-fixing bacteria keep the nitrogen levels high, so phosphorus becomes the limiting factor. When phosphate-rich pollutants pour in, populations of algae soar. As aerobic decomposers break down the remains of the algae, the water becomes depleted of the oxygen that fishes and other organisms require.

Eutrophication refers to the nutrient enrichment of any ecosystem that is otherwise low in nutrients. It is a process of natural succession. Phosphorus inputs as from agriculture can accelerate it, as the experiment shown in Figure 47.28 demonstrated.

Sedimentary cycles, in combination with the hydrologic cycle, move most mineral elements, such as phosphorus, through terrestrial and aquatic ecosystems.

Agriculture, deforestation, and other human activities upset the nutrient balances of ecosystems.

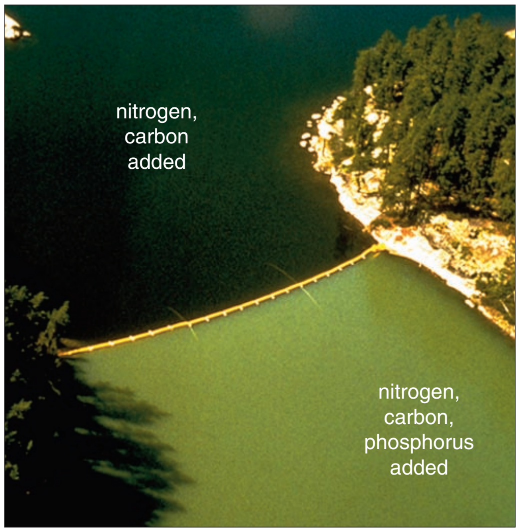


Figure 47.28 One of the eutrophication experiments. Researchers put a plastic curtain across a channel between two basins of a natural lake. They added nitrogen, carbon, and phosphorus on one side of the curtain (here, the *lower* part of the lake) and added nitrogen and carbon on the other side. Within months, the phosphorus-rich basin was eutrophic, with a dense algal bloom (green) covering its surface.

Summary

Section 47.1 An ecosystem consists of an array of organisms together with their physical and chemical environment. There is a one-way flow of energy into and out of an ecosystem, and a cycling of materials among the organisms. All ecosystems have inputs and outputs of energy and nutrients.

Sunlight is the initial energy source for almost all ecosystems. Primary producers capture energy from the sun. They also assimilate nutrients that they, and all consumers, require. Consumers include herbivores, carnivores, omnivores, decomposers, and detritivores.

Organisms in an ecosystem are classified by trophic levels. Those at the same level are the same number of steps away from the energy input into the ecosystem.

Biology Now

Learn about energy flow and material cycling with the animation on BiologyNow.

Section 47.2 Linear sequences by which energy and nutrients move through ever higher trophic levels are food chains, which interconnect as food webs. The efficiency of energy transfers is always low, so most ecosystems support no more than four or five trophic levels away from an original energy source. In a grazing food web, energy captured by producers flows directly to consumers. In a detrital food web, it flows directly to detritivores and decomposers. In nearly all ecosystems, both types of food webs interconnect.

Biology Now

Explore a food web with the animation on BiologyNow.

Section 47.3 By biological magnification, some chemical substance is passed from organisms at one trophic level to those above and becomes increasingly concentrated in body tissues. DDT is an example.

Section 47.4 A system's primary productivity is the rate at which producers capture and store energy in their tissues. It varies with climate, season, nutrient availability, and other factors.

Ecologists construct energy pyramids and biomass pyramids to show how energy and organic compounds are distributed in an ecosystem. Energy pyramids are largest at their base. The lowest trophic level has the greatest proportion of the energy in an ecosystem.

Long-term studies of the Silver Springs ecosystem in Florida illustrate the inefficiency of energy transfers. At each trophic level, far more energy was lost to the environment or in wastes and remains than was passed on to the next trophic level.

Biology Now

See how energy flows through one ecosystem with the animation on BiologyNow.

Section 47.5 In a biogeochemical cycle, water or a nutrient moves through the environment, then through organisms, then back to an environmental reservoir.

Sections 47.6–47.8 In the hydrologic cycle, water moves from the ocean into the atmosphere, to land, and back to the ocean—the main reservoir. Human actions are disrupting the cycle in ways that result in shortages and pollution of water.

Biology Now
Learn about the hydrologic cycle with the animation on BiologyNow.

Section 47.9 The carbon cycle moves carbon from its main reservoirs in rocks and seawater, through its gaseous form (carbon dioxide) in the atmosphere, and then through ecosystems. Deforestation and the burning of wood and fossil fuels are adding more carbon dioxide to the atmosphere than the oceans can absorb.

Biology Now
Observe the flow of carbon through its global cycle with the animation on BiologyNow.

Section 47.10 Collectively, greenhouse gases trap heat in the lower atmosphere, which helps make Earth's surface warm enough to support life. Natural processes and human activities are adding more greenhouse gases, including carbon dioxide, CFCs, methane, and nitrous oxide, to the atmosphere. The rise correlates with a rise in global temperatures and other climate changes.

Biology Now
Explore the causes of the greenhouse effect and global warming with the animation on BiologyNow.

Section 47.11 The atmosphere is the main reservoir for N_2, a gaseous form of nitrogen that plants cannot use. In nitrogen fixation, some soil bacteria degrade N_2 and assimilate the two nitrogen atoms into ammonia. Other reactions convert ammonia to ammonium and nitrate, which plants are able to take up. Some nitrogen is lost to the atmosphere by the action of denitrifying bacteria.

Human activities add nitrogen to ecosystems; for example, through fertilizer applications and fossil fuel burning, which releases nitrogen oxides.

Biology Now
Learn how nitrogen is cycled with the animation on BiologyNow.

Section 47.12 The phosphorus cycle is the main sedimentary cycle. Earth's crust is the largest reservoir. Phosphorus is often the limiting factor on the population growth of producers. Excess inputs of phosphorus to aquatic ecosystems contribute to eutrophication.

Biology Now
Learn how phosphorus is cycled with the animation on BiologyNow.

Self-Quiz

Answers in Appendix II

1. Ecosystems have ______ .
   a. energy inputs and outputs
   b. one trophic level
   c. no nutrient outputs; all nutrients are cycled
   d. a and b

2. Organisms at the lowest trophic level in a tallgrass prairie are all ______ .
   a. at the first step away from the original energy input
   b. autotrophs
   c. heterotrophs
   d. both a and b
   e. both a and c

3. Decomposers are commonly ______ .
   a. fungi
   b. animals
   c. bacteria
   d. a and c

4. Trophic levels are ______ .
   a. structured feeding relationships
   b. a case of who eats whom in an ecosystem
   c. a hierarchy of energy transfers
   d. all of the above

5. Primary productivity on land is affected by ______ .
   a. nutrient availability
   b. amount of sunlight
   c. temperature
   d. all of the above

6. If biological magnification occurs, the ______ will have the highest levels of toxins in their systems.
   a. producers
   b. herbivores
   c. primary carnivores
   d. top carnivores

7. Disruption of the ______ cycle is depleting aquifers.
   a. hydrologic
   b. carbon
   c. nitrogen
   d. phosphorus

8. Earth's largest carbon reservoir is ______ .
   a. the atmosphere
   b. sediments and rocks
   c. seawater
   d. living organisms

9. The ______ cycle is a sedimentary cycle.
   a. hydrologic
   b. carbon
   c. nitrogen
   d. phosphorus

10. ______ is often a limiting factor for plant growth.
   a. Nitrogen
   b. Carbon
   c. Phosphorus
   d. both a and c
   e. all of the above

11. Nitrogen fixation converts ______ to ______ .
   a. nitrogen gas; ammonia
   b. nitrates; nitrites
   c. ammonia; nitrogen gas
   d. ammonia; nitrates
   e. nitrites; nitrogen oxides

12. Match the terms with suitable descriptions.
   ____ producers
   ____ herbivores
   ____ decomposers
   ____ detritivores
   a. feed on plants
   b. feed on small bits of organic matter
   c. degrade organic wastes and remains to inorganic forms
   d. capture sunlight energy

Additional questions are available on **Biology Now**™

Critical Thinking

1. Visualize and then describe an extreme situation in which you are a participant in a food chain rather than a food web.

2. Marguerite is growing a vegetable garden in Maine. Eduardo is growing arugula in Spain. What are some of the variables that influence primary production in each of these locations?

3. Look around you and name all of the objects, natural or manufactured, that might be contributing to amplification of the greenhouse effect.

4. Polar ice shelves are vast, thickened sheets of ice that float on seawater. In March 2002, 3,200 square kilometers (1,410 square miles) of Antarctica's largest ice shelf broke free from the continent and shattered into thousands of icebergs (Figure 47.29). Scientists knew the ice shelf was shrinking and breaking up, but this was the single largest loss ever observed at one time. Why should this concern people who live in more temperate climates?

5. Fishes are a fine source of protein and of *omega-3 fatty acids*, which are necessary for the normal development of the nervous system. This would seem to make fish a good choice for pregnant women. But coal-burning power plants put mercury into the environment, and some of it ends up in fish. Eating mercury-tainted fish during pregnancy can adversely affect development of a fetal nervous system.

Tissues of predatory marine fishes, such as swordfishes, tunas, marlins, and sharks, have especially high levels of mercury. The Environmental Protection Agency has issued health advisories to pregnant women, suggesting that they limit their consumption of fish species most likely to be tainted with mercury. Although sardines are harvested from the same ocean, they have lower mercury levels and are not on the warning list. Explain why two species of fishes that live in the same place can have very different levels of mercury in their tissues.

6. Methane, remember, is a gaseous molecule of one carbon atom to which four hydrogens are attached (Section 3.1). *Methane hydrate* is a methane molecule surrounded by an icelike lattice of water molecules, and it forms only at low temperatures, high pressures, and high concentrations of methane. Such conditions prevail beneath the seafloor and in the arctic tundra, where vast deposits of methane hydrate have formed in frozen peat bogs. The deposits typically are hundreds of meters thick.

Over millions of years, ancient organisms that died and sank to the ocean floor were buried in sediments. Their carbon-rich remains are food for anaerobic archaeans living far beneath the seafloor. The archaeans produce methane, which bubbles up to the seafloor. There, the high pressures and low temperatures freeze the methane into solid blocks of methane hydrates (Figure 47.30).

Again, ocean deposits of methane hydrate hold 10,000 to 11,000 gigatons of methane. The next largest deposit, in arctic regions, only amounts to hundreds of gigatons. Significant amounts of carbon continually enter and leave the deposits. For instance, bacterial activity continually converts some of the methane to carbon dioxide, which helps control the amount of methane that can escape into the atmosphere.

The oceanic reservoir of methane hydrates may contain more carbon than all of the known reserves of oil, coal, and natural gas. However, the deposits are highly unstable; ice fills spaces in sediments, so increases in pressure or ocean water temperature can trigger catastrophic landslides and tsunamis. Reflect again on the global carbon cycle, then list some of the consequences of a catastrophic release of methane in terms of global temperature, climate, glaciation and sea level changes, and the composition of ocean water.

7. Reflect once more on Figure 47.30. The methane-eating and sulfate-eating bacteria near seeps on the seafloor are the start of food webs. Do some research and identify the producers and consumers in these deep-sea communities. Before you start, would you expect the food chains to be short or long? Make a list that organizes the participants by trophic levels.

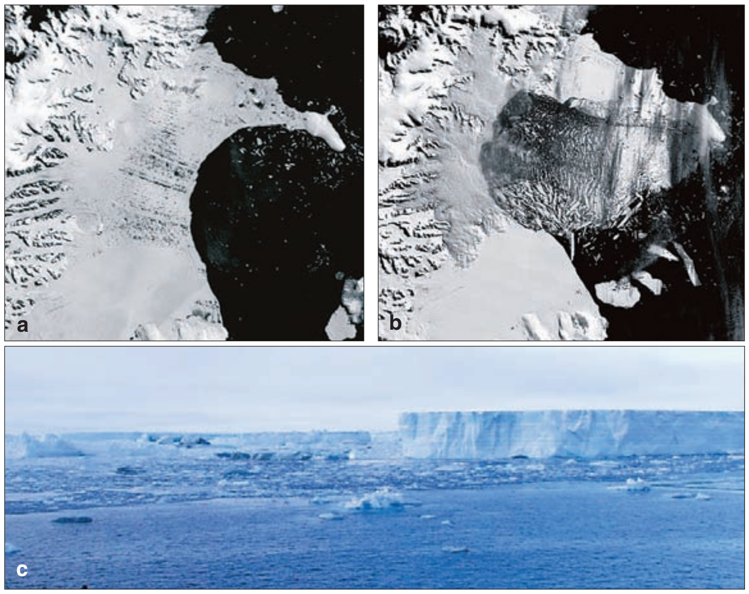


Figure 47.29 Antarctica's Larson B ice shelf in (**a**) January and (**b**) March 2002. About 720 billion tons of ice broke from the shelf, forming thousands of icebergs. (**c**) These are the just the tips of the icebergs, projecting twenty-five meters (eighty-two feet) above the sea surface.

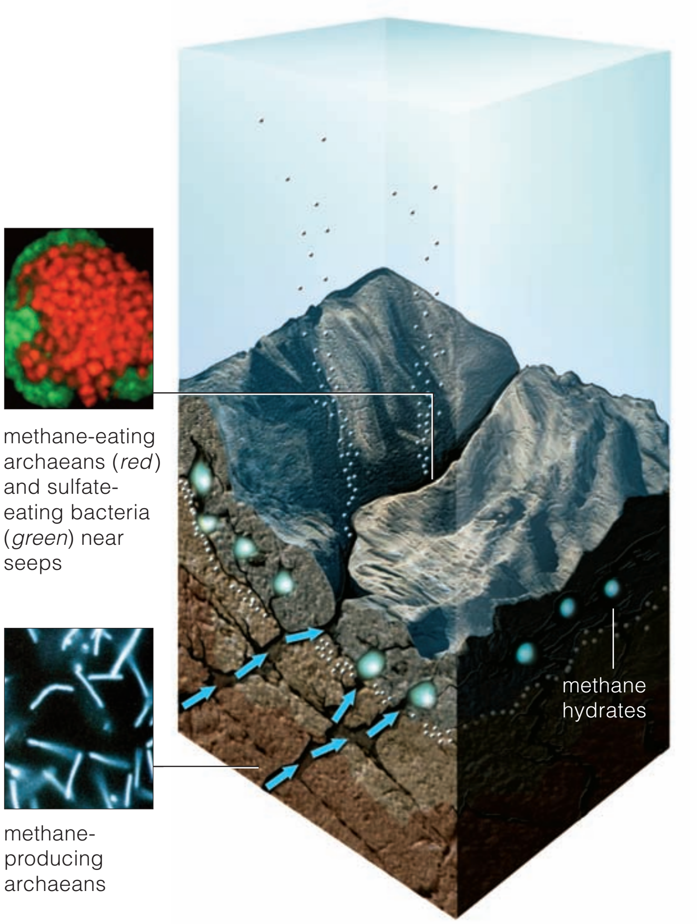


Figure 47.30 Methane cycling on the seafloor. Archaeans beneath the seafloor produce methane that seeps out from seafloor sediments. There, methane-eating microbes release carbon dioxide as well as hydrogen sulfide as metabolic products that become the basis of deep-sea food webs.