chapter 3

Ecosystems: How They Work

Key Topics

1. Matter, Energy, and Life
2. Energy Flow in Ecosystems
3. The Cycling of Matter in Ecosystems
4. Implications for Human Societies

Pictured in the opening photo, the Serengeti is a vast tropical savanna ecosystem of 25,000 km^2 in northern Tanzania and southern Kenya. The rain falls bimodally: Short rains normally occur in November and December, long rains during March through May. A rainfall gradient passes from the drier southeastern plains (50 cm/yr) to the wet northwest in Kenya (120 cm/yr). The southeastern plains are a treeless grassland, and as the volcanic soils thicken to the north and west, the grasses gradually shift to woodlands—mixed *Acacia* trees and grassy patches. Large herbivores (wildebeest, zebra, and Thomson's gazelle) dominate the ecosystem. Herds of over 1.5 million animals are common on the plains during the rainy seasons. Just below the surface of the land, hordes of termites in extensive galleries process organic detritus as fast as it appears and restore nutrients to the soil.

Migration. As the rains fail, the large herds move to the woodlands in the north, where forage is available year-round. There, the animals face heavier predation from lions and hyenas, which need the woodlands for cover for raising young and for successful stalking. This migration, in which the animals travel 200 or more kilometers and back again each year, is energetically costly. Why do they do it if there is sufficient forage in the woodlands? The answer is still being investigated, but evidence points to two possible factors: (1) The vegetation in the plains is high in phosphorus, which the herbivores need for successful growth and lactation. Their annual presence there maintains the high phosphorus content as their wastes are broken down and nutrients are returned to the soils. (2) The presence of high numbers of predators in the woodlands may force the herds to migrate to the grasslands, where they are less vulnerable, especially when giving birth to their young.

In this ecosystem known as the Serengeti, producers, herbivores, carnivores, and scavengers or detritus feeders interact in a sustainable set of relationships. However, the Serengeti and its spectacular wildlife will continue to exist only as long as the land is protected. This World Heritage site is pressed on all sides by poaching, the population growth of pastoralists (cattle and goat herders), and

The Serengeti **A large herd of wildebeest and zebra graze on the lush grasses, with *Acacia* woodlands in the distance. Inset shows a map of the Serengeti ecosystem and the migration route taken by the large herds.**

mechanized agriculture, but the Kenyan and Tanzanian governments appear to be committed to maintaining the core national parks (which consist of 14,700 km^2).

You will learn in this chapter how ecosystems like the Serengeti work, starting at the fundamental level of chemicals and energy. You will also learn how natural ecosystems sustain human life, and you will look at an estimate of what ecosystem goods and services are worth to humankind. Studying how ecosystems work will give you some insight into why natural systems are sustainable and may suggest ways to make our human system more sustainable.

3.1 Matter, Energy, and Life

Matter in Living and Nonliving Systems

Atoms. The basic building blocks of all **matter** (all gases, liquids, and solids in both living and nonliving systems) are **atoms.** Only 94 different kinds of atoms occur in nature, and these are known as the naturally occurring **elements.** In addition, chemists and physicists have created 21 more in the laboratory, but they are so unstable that they break down into simpler elements. (See Table C–1, p. 670.)

How can these relatively few *building blocks* make up the countless materials of our world, including the tissues of living things? Picture each kind of atom as a different-sized Lego® block. Like Legos, atoms can build a great variety of things. Also like Legos, natural materials can be taken apart into their separate constituent atoms, and the atoms can then be reassembled into different materials. All chemical reactions, whether they occur in a test tube, in the environment, or inside living things, and whether they occur very slowly or very fast, involve rearrangements of atoms to form different kinds of matter.

Atoms do not change during the disassembly and reassembly of different materials. A carbon atom, for instance, will always remain a carbon atom. Furthermore, atoms are neither created nor destroyed during chemical reactions. The same number and kind of different atoms exist before and after any reaction. This constancy of atoms is regarded as a fundamental natural law, the *law of conservation of matter.*

A more detailed discussion of atoms—how they differ from one another, how they bond to form various gases, liquids, and solids, and how chemical formulas can be used to describe different chemicals—is given in Appendix C (p. 669). Studying Appendix C now may help you better understand the material we are about to cover.

How are atoms put together? Which atoms make up living organisms? Where are those atoms found in the environment? How do they become part of living organisms? Answers to these questions are presented next.

Molecules and Compounds. A **molecule** consists of two or more atoms bonded together in a specific way. The properties of a material depend on the specific way in which atoms are bonded to form molecules, as well as on the atoms themselves. Similarly, a **compound** consists of two or more *different kinds* of atoms bonded together. A *molecule*, therefore, may consist of two or more of the *same kind* of atoms, or two or more different kinds of atoms, bonded together, whereas at least two *different kinds* of atoms are always involved in a *compound*. For example, the fundamental units of oxygen gas, which consists of two oxygen atoms bonded together, are molecules, but not a compound. Water, by contrast, is both a molecule and a compound, because the fundamental units are two hydrogen atoms bonded to an oxygen atom.

On the chemical level, then, the cycle of growth, reproduction, death, and decay of organisms is a continuous process of taking various atoms from the environment (food), assembling them into living organisms (growth), disassembling them (decay), and repeating the process. Driving the cycle is the genetically programmed urge living things have to grow and reproduce.

Four Spheres. During growth and decay, atoms move from the environment into living things and then return to the environment. To picture this process, think of the environment as three open systems, or "spheres," occupied by living things—the **biosphere** (Fig. 3–1). The **lithosphere** is Earth's crust, made up of rocks and minerals. The **hydrosphere** is water in all of its liquid and solid compartments: oceans, rivers, ice, and groundwater. The **atmosphere** is the thin layer of gases (including water vapor) separating Earth from outer space. Matter is constantly being exchanged within and between these four spheres.

Key Elements. Living things are characterized by six key elements: **carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P),** and **sulfur (S).** These six elements are the essential ones in the organic molecules that make up the tissues of plants, animals, and microbes. By looking at the chemical nature of the spheres, you can see where the six key elements and others occur in the environment (Table 3–1).

Atmosphere. The lower atmosphere is a mixture of molecules of three important gases—oxygen (O_2), nitrogen (N_2), and carbon dioxide (CO_2)—along with water vapor and trace amounts of several other gases that have no immediate biological importance (Fig. 3–2). The gases in the atmosphere are normally stable, but under some circumstances they react chemically to form new compounds (for example, ozone is produced from oxygen in the upper atmosphere, as described in Chapter 20).

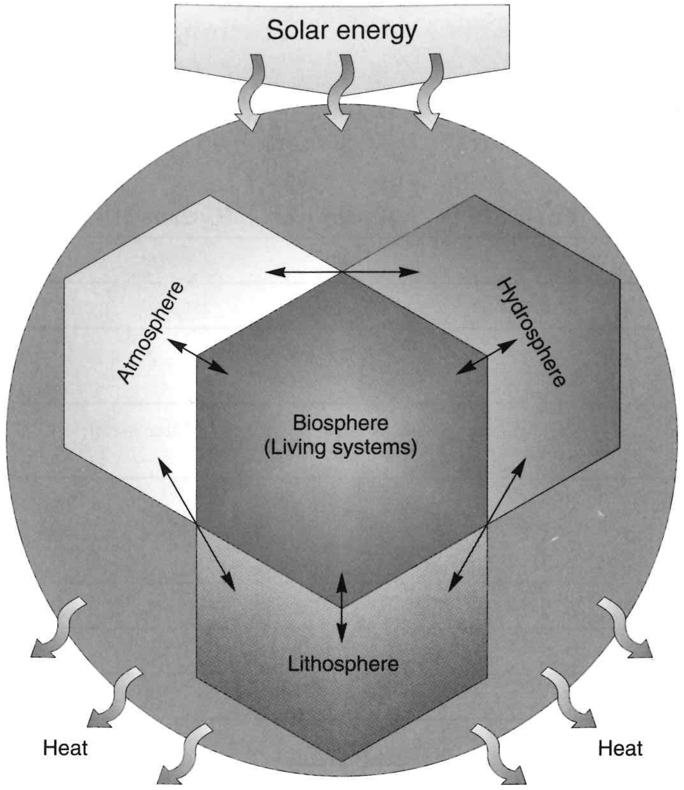


Figure 3–1 The four spheres of Earth's environment. The biosphere is all of life on Earth. It depends on, and interacts with, the atmosphere (air), the hydrosphere (water), and the lithosphere (soil and rocks). Adapted from *Geosystems,* 5e by Robert W. Christopherson. Copyright 2003 by Pearson Education, Inc.

Hydrosphere. While the atmosphere is a major source of *carbon* and *oxygen* for all organisms (and a source of *nitrogen* for a few of them), the hydrosphere is the source of *hydrogen*. Each molecule of water consists of two hydrogen atoms bonded to an oxygen atom, so the chemical formula for water is H_2O. A weak attraction known as *hydrogen bonding* exists between water molecules. At temperatures below freezing, hydrogen bonding holds the molecules in position with respect to one another, and the result is a solid (ice or snow). At temperatures above freezing, but below vaporization, hydrogen bonding still holds the molecules close, but allows them to move past one another, producing the liquid state. Vaporization occurs as hydrogen bonds break and water molecules move into the air independently. As temperatures are lowered again, all of these changes of state go in the reverse direction (Fig. 3–3). Despite the changes of state, the water molecules themselves retain their basic chemical structure of two hydrogen atoms bonded to an oxygen atom. Only the *relationship* between the molecules changes.

Lithosphere. All the other elements required by living organisms, as well as the 72 or so elements that are not required by them, are found in the lithosphere, in the form of rock and soil minerals. A **mineral** is any hard, crystalline, inorganic material of a given chemical composition. Most rocks are made up of relatively small crystals of two or more minerals, and soil generally consists of particles of many different minerals. Each mineral is made up of dense clusters of two or more kinds of atoms bonded together by an attraction between positive and negative charges on the atoms, as explained in Appendix C and shown in Fig. 3–4.

Interactions. Air, water, and minerals interact with each other in a simple, but significant, manner. Gases from the air and ions (charged atoms) from minerals may dissolve in water. Therefore, natural water is inevitably a *solution* containing variable amounts of dissolved gases and minerals. This solution is constantly subject to change, because any dissolved substances in it may be removed by various processes, or additional materials may dissolve in it. Molecules of water enter the air by evaporation and leave it again via condensation and precipitation. (See the hydrologic cycle, Chapter 7.) Thus, the amount of moisture in the air fluctuates constantly. Wind may carry dust or mineral particles, but the amount changes constantly, because the particles gradually settle out from the air. The various interactions are summarized in Fig. 3–5.

Organic Compounds. The chemical compounds making up the tissues of living organisms are referred to as **organic.** Unlike the relatively simple molecules that occur in the environment (such as CO_2, H_2O, and N_2), the key chemical elements in living organisms (C, H, O, N, P, S) bond to form very large, complex organic molecules, such as proteins, carbohydrates (sugars and starches), lipids (fatty substances), and nucleic acids (DNA and RNA). Some of these molecules may contain millions of atoms, and their potential diversity is infinite. Indeed, the diversity of living things reflects the diversity of these molecules.

The molecules that make up the tissues of living things are constructed mainly from carbon atoms bonded together into chains, with hydrogen and oxygen atoms attached. Nitrogen, phosphorus, and sulfur may be present

table 3-1 Elements Found in Living Organisms and the Locations of Those Elements in the Environment

Element (Kind of Atom)	Biologically Important Molecule or Ion in Which the Element Occurs[a]			Location in the Environment[b]		
	Symbol	**Name**	**Formula**	**Atmosphere**	**Hydrosphere**	**Lithosphere**
Carbon	C	Carbon dioxide	CO_2	X	X	X(CO_3^-)
Hydrogen	H	Water	H_2O	X	(Water itself)	
Atomic oxygen (required in respiration)	O	Oxygen gas	O_2	X	X	
Molecular oxygen (released in photosynthesis)	O_2	Water	H_2O		(Water itself)	
Nitrogen	N	Nitrogen gas	N_2	X	X	Via fixation
		Ammonium ion	NH_4^+		X	X
		Nitrate ion	NO_3^-		X	X
Sulfur	S	Sulfate ion	SO_4^{2-}		X	X
Phosphorus	P	Phosphate ion	PO_4^{3-}		X	X
Potassium	K	Potassium ion	K^+		X	X
Calcium	Ca	Calcium ion	Ca^{2+}		X	X
Magnesium	Mg	Magnesium ion	Mg^{2+}		X	X
Trace Elements[c]						
Iron	Fe	Iron ion	Fe^{2+}, Fe^{3+}		X	X
Manganese	Mn	Manganese ion	Mn^{2+}		X	X
Boron	B	Boron ion	B^{3+}		X	X
Zinc	Zn	Zinc ion	Zn^{2+}		X	X
Copper	Cu	Copper ion	Cu^{2+}		X	X
Molybdenum	Mo	Molybdenum ion	Mo^{2+}		X	X
Chlorine	Cl	Chloride ion	Cl^-		X	X

Note: These elements are found in *all* living organisms—plants, animals, and microbes. Some organisms require certain elements in addition to the ones listed. For example, humans require sodium and iodine.

[a] A molecule is a chemical unit of two or more atoms bonded together. An ion is a single atom or group of bonded atoms that has acquired a positive or negative charge as indicated.

[b] "X" means that element exists in indicated "sphere."

[c] Only small or trace amounts of these elements are required.

also, but the key common denominator is carbon–carbon and carbon–hydrogen or carbon–oxygen bonds (Fig. 3-6). Hence, the carbon-based molecules that make up the tissues of living organisms are called *organic molecules*. (The similarity between the words *organic* and *organism* is deliberate, not coincidental.) **Inorganic,** then, refers to all other molecules or compounds—that is, those with neither carbon–carbon nor carbon–hydrogen bonds.

All plastics and countless other human-made compounds are based on carbon–carbon bonding and are, chemically speaking, organic compounds. To resolve any confusion this may cause, the compounds making up living organisms are referred to as **natural organic compounds** and the human-made ones as **synthetic organic compounds.**

In conclusion, the elements essential to life (C, H, O, and so on) are present in the atmosphere, hydrosphere, or lithosphere in relatively simple molecules. In living *organisms* of the biosphere, on the other hand, they are *organized* into highly complex *organ*ic compounds. These organic compounds in turn make up the various parts of cells, which in their turn make up the tissues and organs of the organism, which in its turn is part of a population (Fig. 3-7). During growth and reproduction, then, the atoms from simple molecules in the environment are used to construct the complex organic molecules of an organism. Decomposition and decay is the reverse process. Each of these processes is discussed in more detail later in the chapter; first, however, we must consider another factor: *energy*.

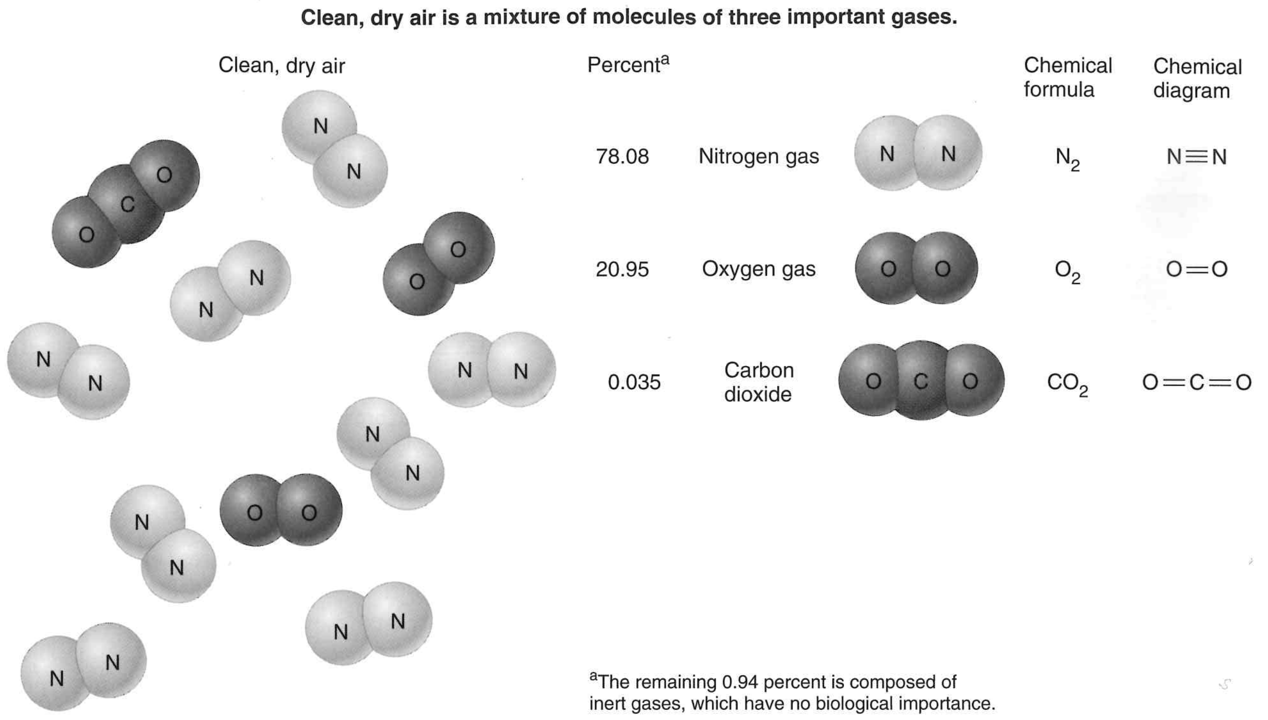


Figure 3-2 The major gases of clean, dry air. From a biological point of view, the three most important gases of the lower atmosphere are nitrogen, oxygen, and carbon dioxide. (Note that the proportion of carbon dioxide is deliberately overrepresented in the diagram.)

Energy Basics

In addition to rearranging atoms, chemical reactions absorb or release energy. To grasp this concept, you must be able to distinguish between matter and energy.

Matter and Energy. The universe is made up of *matter* and *energy*. A more technical definition of **matter** than the one given earlier in this chapter is *anything that occupies space and has mass*—that is, anything that can be weighed when gravity is present. This definition

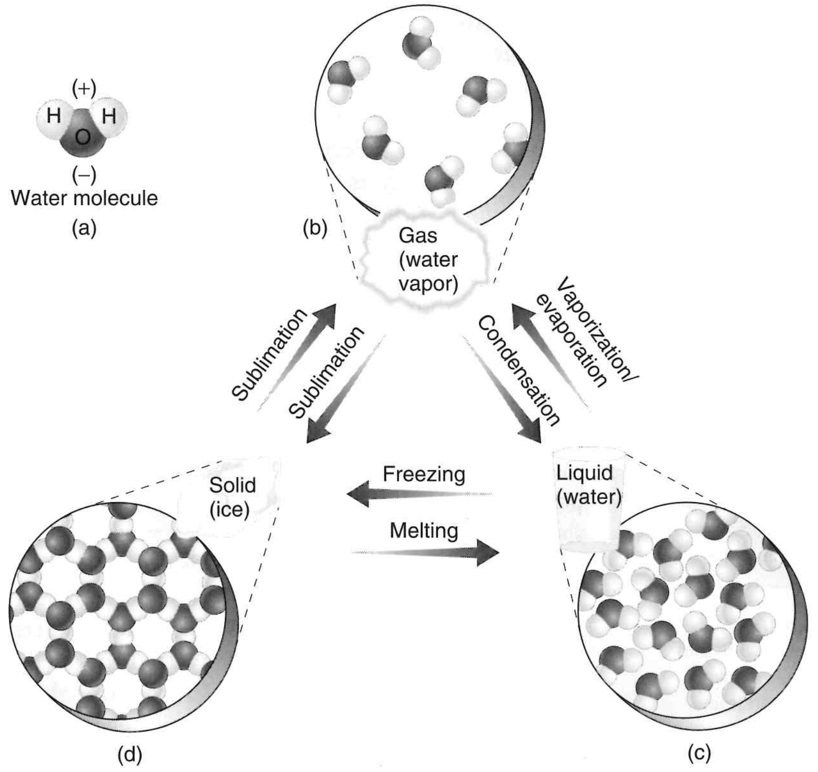


Figure 3-3 Water and its three states. (a) Water consists of molecules, each of which is formed when two hydrogen atoms bond to an oxygen atom (H_2O). (b) In water vapor, the molecules are separate and independent. (c) In liquid water, the weak attraction between water molecules known as hydrogen bonding gives the water its liquid property. (d) At freezing temperatures, hydrogen bonding holds the molecules firmly, giving the solid state—ice.

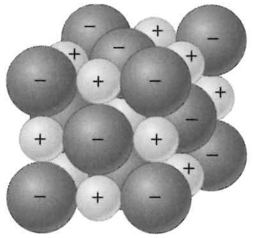
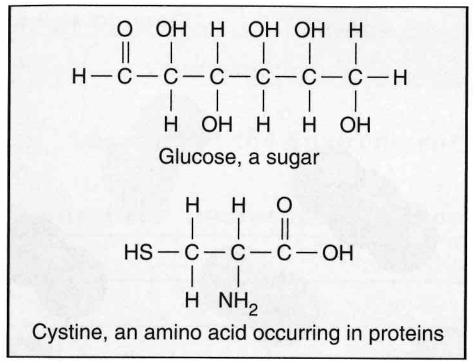


Figure 3-4 Minerals. Minerals (hard crystalline compounds) are composed of dense clusters of atoms of two or more elements. The atoms of most elements gain or lose one or more electrons, becoming negative (−) or positive (+) ions. Salt (sodium chloride, NaCl) is held together by the attraction between the positive sodium (Na+) and negative chloride (Cl−) charges.



$$\mathrm{H{-}\overset{O}{\overset{\|}{C}}{-}\underset{H}{\overset{OH}{C}}{-}\underset{OH}{\overset{H}{C}}{-}\underset{H}{\overset{OH}{C}}{-}\underset{H}{\overset{OH}{C}}{-}\underset{OH}{\overset{H}{C}}{-}H}$$

$$\mathrm{HS{-}\underset{H}{\overset{H}{C}}{-}\underset{NH_2}{\overset{H}{C}}{-}\overset{O}{\overset{\|}{C}}{-}OH}$$

Figure 3-6 Organic molecules. The organic molecules that make up living organisms are larger and more complex than the inorganic molecules found in the environment. Glucose, a sugar, and cysteine, an amino acid, show this relative complexity.

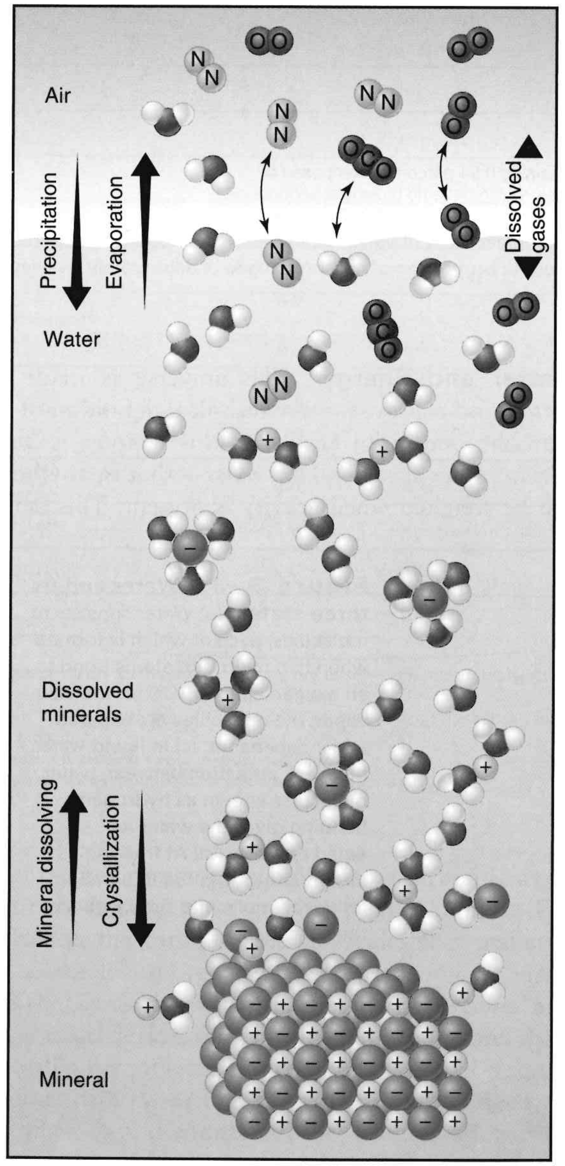


Figure 3-5 Interrelationship among air, water, and minerals. Minerals and gases dissolve in water, forming solutions. Water evaporates into air, causing humidity. These processes are all reversible: Minerals in solution recrystallize, and water vapor in the air condenses to form liquid water.

covers all solids, liquids, and gases, and living as well as nonliving things.

Atoms are made up of protons, neutrons, and electrons, which in turn are made of still smaller particles. Because atoms are the basic units of all elements and remain unchanged during chemical reactions, they can be treated as the basic units of matter.

In contrast to matter, *light*, *heat*, *movement*, and *electricity* do not have mass, nor do they occupy space. (Note that *heat*, as used here, refers not to a hot object, but to the heat energy you can feel radiating from the hot object.) These are the common forms of energy with which you are probably familiar. What do the various forms of energy have in common? They *affect* matter, causing changes in its *position* or its *state*. For example, the release of energy in an explosion causes things to go flying—a change in position. Heating water causes it to boil and change to steam, a change of state. On a molecular level, changes of state are actually movements of atoms or molecules. For instance, the degree of heat energy contained in a substance is a measure of the relative vibrational motion of the atoms and molecules of the substance. Therefore, we can define **energy** as *the ability to move matter*.

Kinetic and Potential Energy. Energy can be categorized as either *kinetic* or *potential* (Fig. 3-8). **Kinetic energy** is *energy in action or motion*. Light, heat energy, physical motion, and electrical current are all forms of kinetic energy. **Potential energy** is *energy in storage*. A substance or system with potential energy has the capacity, or *potential*, to release one or more forms of kinetic energy. A stretched rubber band has potential energy; it can send a paper clip flying. Numerous chemicals, such as gasoline and other fuels, release kinetic energy—heat energy, light, and movement—when ignited. The potential energy contained in such chemicals and fuels is called **chemical energy.**

Energy may be changed from one form to another in innumerable ways (Fig. 3-9). Besides understanding that potential energy can be converted to kinetic energy, it is especially important to recognize that kinetic energy can be converted to potential energy. (Consider, for example, charging a battery or pumping water into

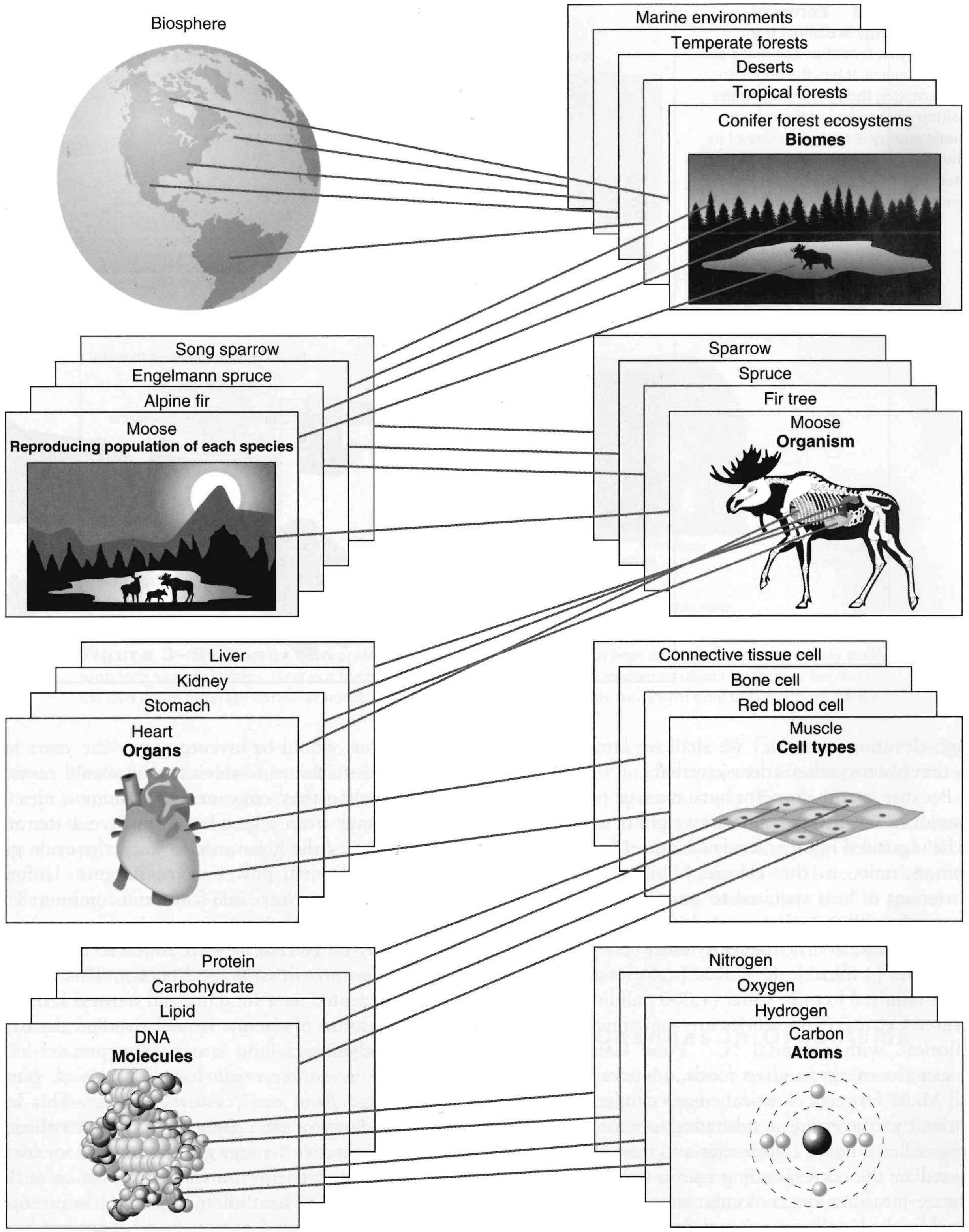
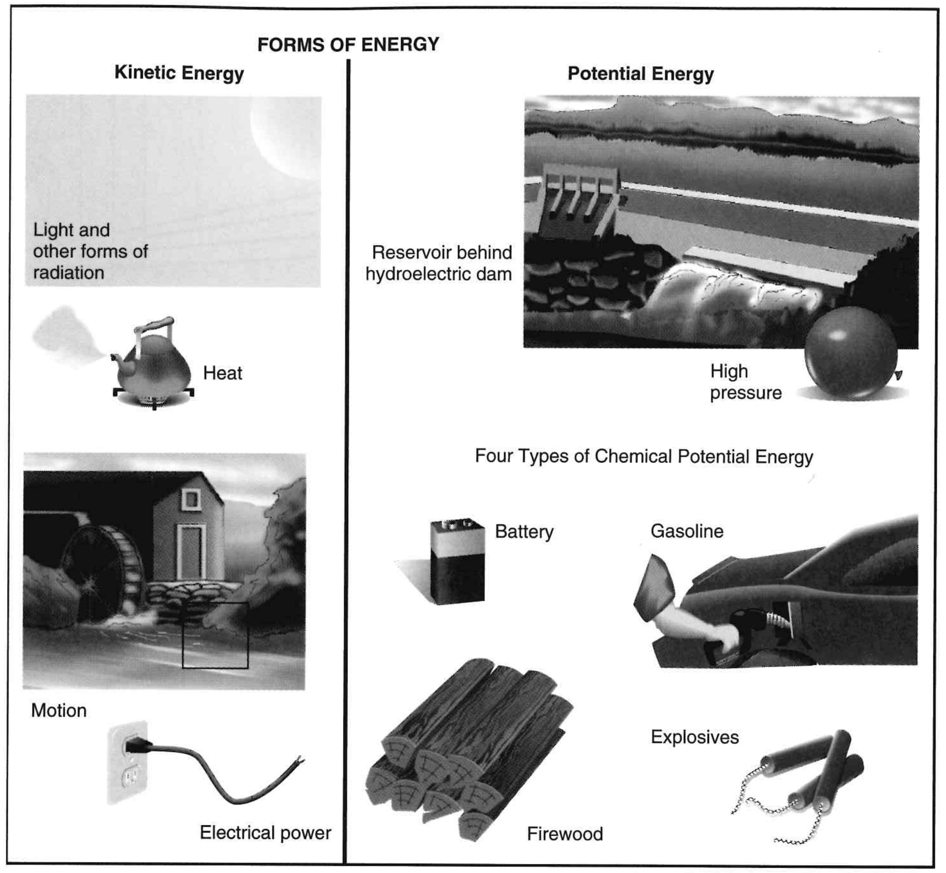


Figure 3-7 Life as a hierarchy of organization of matter. In the inorganic sphere, elements are arranged simply in molecules of the air, water, and minerals. In living organisms, they are arranged in complex organic molecules, which in turn make up cells that constitute tissues, organs, and, thus, the whole organism. Levels of organization continue up through populations, species, ecosystems, and, finally, the whole biosphere.

Figure 3-8 Forms of energy. Energy is distinct from matter in that it neither has mass nor occupies space. It has the ability to act on matter, though, changing the position or the state of the matter. Kinetic energy is energy in one of its active forms. Potential energy is the potential that systems or materials have to release kinetic energy.



a high-elevation reservoir.) We shall see later in this section that photosynthesis does just that.

Because energy does not have mass or occupy space, it cannot be measured in units of weight or volume, but it can be measured in other kinds of units. One of the most common units is the **calorie,** which is defined as the amount of heat required to raise the temperature of 1 gram (1 milliliter) of water 1 degree Celsius. This is a very small unit, so it is frequently more convenient to use kilocalories (1 kilocalorie = 1,000 calories), the amount of heat required to raise 1 liter (1,000 milliliters) of water 1 degree Celsius. (Kilocalories are sometimes denoted as "Calories" with a capital "C." Food Calories, which measure the energy in given foods, are actually kilocalories.) Many forms of chemical energy can be measured in calories by converting a substance to heat energy in a device called a bomb calorimeter and measuring the heat released by the corresponding rise in temperature. Temperature measures the molecular motion in a substance caused by the kinetic energy present in it.

If energy is defined as the ability to move matter, then no matter can be moved *without* the absorption or release of energy. Indeed, no *change* in matter—from a few atoms coming together or apart in a chemical reaction to a major volcanic eruption—can be separated from its respective change in energy.

Energy Laws: Laws of Thermodynamics. Because energy can be converted from one form to another, numerous would-be inventors over the years have tried to build machines or devices that would produce more energy than they consumed. A common idea is to use the output from a generator to drive a motor that, in turn, drives the generator to keep the cycle going and yields additional power in the bargain. Unfortunately, all such devices have one feature in common: They don't work. When all the inputs and outputs of energy are carefully measured, they are found to be *equal*. There is no net gain or loss in total energy. This observation is now accepted as a fundamental natural law, **the law of conservation of energy.** It is also called the **first law of thermodynamics,** and it can be expressed as follows: *Energy is neither created nor destroyed, but may be converted from one form to another.* This law really means that you can't get something for nothing.

Imaginative "energy generators" fail for two reasons: First, in every energy conversion, a portion of the energy is converted to heat energy (thermal infrared). Second, there is no way of trapping and recycling heat energy without expending even more energy in doing so. Consequently, in the absence of energy inputs, any and every system will sooner or later come to a stop as its energy is converted to heat and lost. This is now accepted as another natural law, the **second law of thermodynamics,** and it can be expressed as follows: *In any energy conversion, some of the usable energy is always lost.* Thus, you can't get something for nothing (the first law) and, in fact, you can't even break even (the second law)!

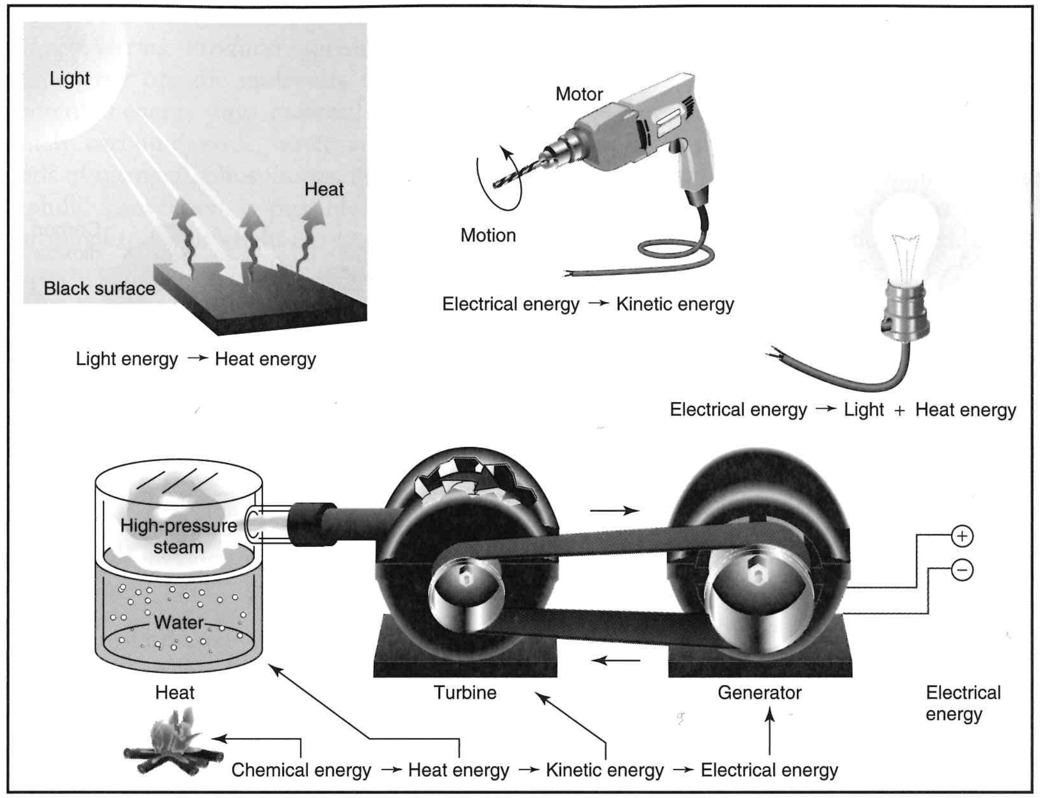


Figure 3-9 Energy conversions. Any form of energy except heat energy can spontaneously transform into any other form. Heat is a form of energy that flows from one system or object to another because the two are at different temperatures; therefore, heat can spontaneously transform only to something cooler.

Entropy. Underlying the loss of usable energy to heat is the principle of increasing *entropy*. **Entropy** is a measure of the degree of disorder in a system, so increasing entropy means increasing disorder. Without energy inputs, everything goes in one direction only—toward increasing entropy. This principle of ever-increasing entropy is the reason that all human-made things tend to deteriorate. The increasing disorder of your dormitory room as the semester wears on is one example of entropy.

The conversion of energy and the loss of usable energy to heat are both aspects of increasing entropy. Heat energy is the result of the random vibrational motion of atoms and molecules. Thus, it is the lowest (most disordered) form of energy, and its spontaneous flow to cooler surroundings is a way for that disorder to spread. Therefore, the second law of thermodynamics may be more generally stated as follows: *Systems will go spontaneously in one direction only—toward increasing entropy*. The second law also says that systems will go spontaneously only toward *lower* potential energy, a direction that releases heat from the systems (Fig. 3-10).

The word *spontaneously* is very important in this statement of the second law. It is possible to pump water uphill, charge a battery, stretch a rubber band, compress air, or otherwise increase the potential energy of a system. The verbs *pump, charge, stretch,* and *compress* tell us, however, that energy is being put into the system. In contrast, flow in the opposite direction, which releases energy, occurs spontaneously (Fig. 3-11a).

Whenever you see something gaining potential energy, therefore, keep in mind that the energy is being obtained from somewhere else (the first law). Moreover, the amount of energy lost from that "somewhere else" is greater than the amount gained (the second law). Let us now relate these concepts of matter and energy to organic molecules, organisms, ecosystems, and the biosphere.

Energy Changes in Organisms

All organic molecules, which make up the tissues of living organisms, contain *high potential energy*. When these molecules are burned, the heat and light of the flame are the potential energy being released as kinetic energy. By contrast, try as you might, you will not be able to get energy by burning inorganic compounds like carbon dioxide, water, or rock-based minerals. (Some minerals, such as magnesium and sulfur, can be burned.) Indeed, many of these materials are used as fire extinguishers. They are nonflammable because they have very *low potential energy*. Thus, the production of organic material from inorganic material represents a *gain* in potential energy. Conversely, the breakdown of organic matter *releases* energy.

This relationship between the formation and breakdown of organic matter on the one hand, and the gain

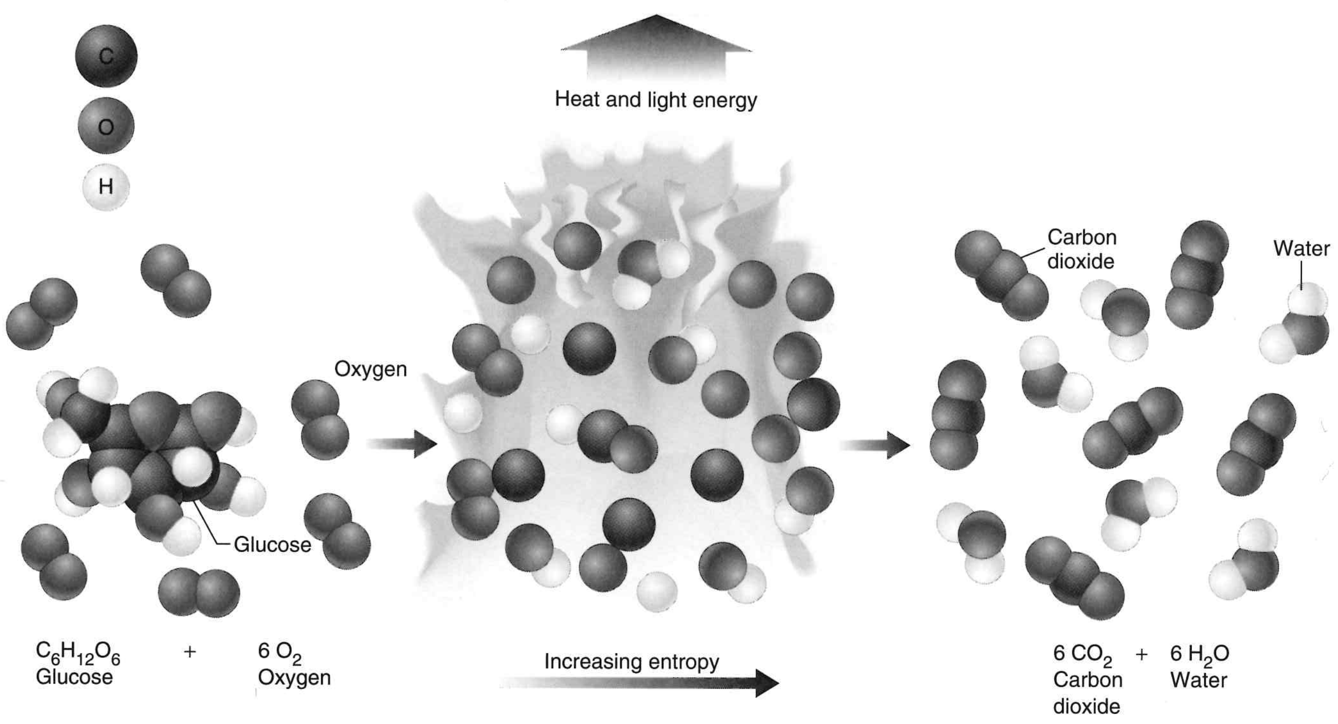


Figure 3-10 **Entropy.** Systems go spontaneously only in the direction of increasing entropy. When glucose, a major constituent of wood, is burned, heat is released, and the atoms become more disordered. Both of these phenomena are aspects of increasing entropy.

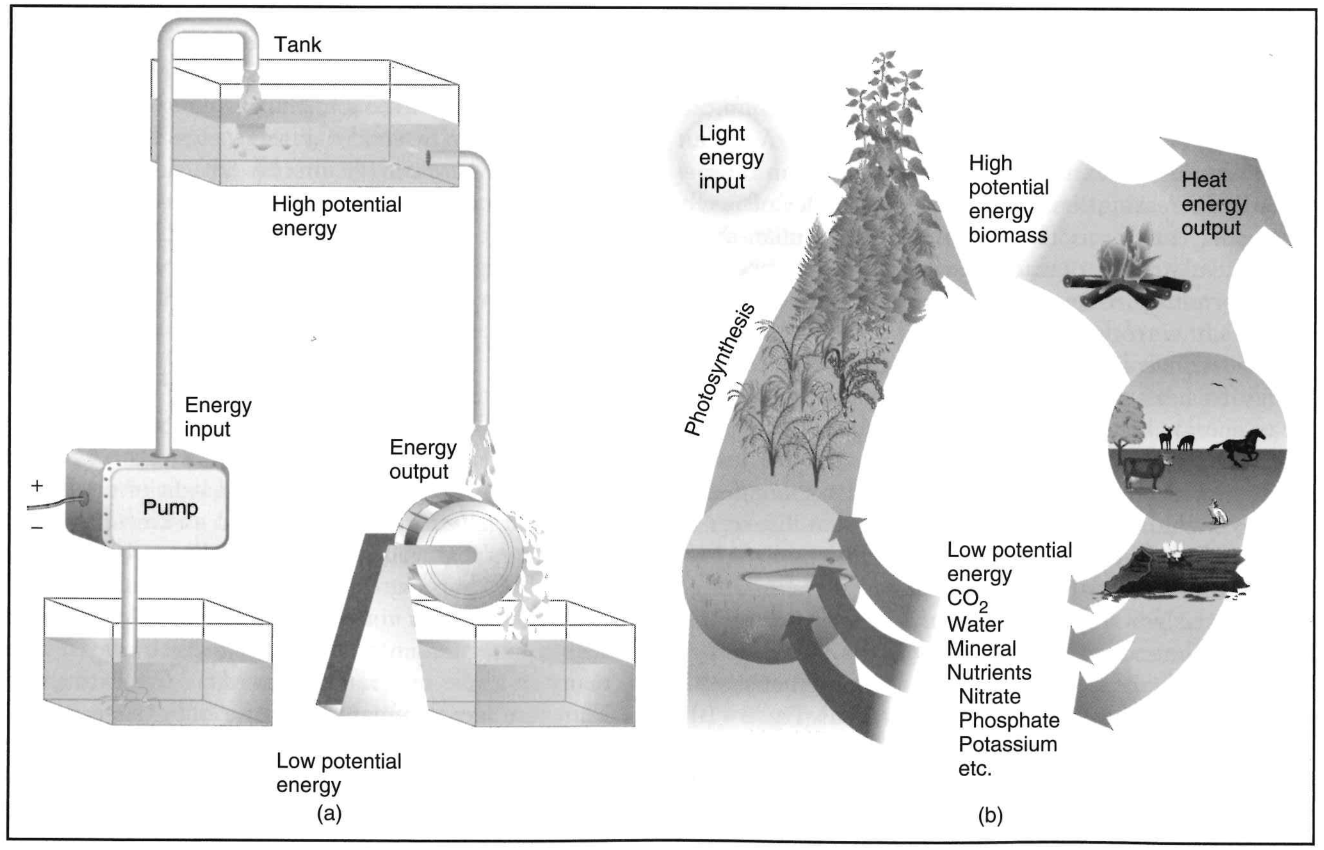


Figure 3-11 **Storage and release of potential energy.** (a) A simple physical example of the storage and release of potential energy. (b) The same principle applied to ecosystems.

and release of energy on the other, forms the basis of the *energy dynamics of ecosystems. Producers* (green plants) make high-potential-energy organic molecules for their needs from low-potential-energy raw materials in the environment—namely, carbon dioxide, water, and a few dissolved compounds of nitrogen, phosphorus, and other elements. This "uphill" conversion is possible because producers use chlorophyll to absorb light energy. On the other hand, all *consumers, detritus feeders,* and *decomposers* obtain energy for movement and growth from feeding on and breaking down organic matter made by producers (Fig. 3-11b).

Producers and Photosynthesis. Recall from Chapter 2 that producers (green plants) use *photosynthesis* to make sugar (glucose, stored chemical energy) from carbon dioxide, water, and light energy. This process, which also releases oxygen gas as a by-product, is described by the following chemical equation:

Photosynthesis
(An energy-demanding process)

$$\underset{\text{(low potential energy)}}{\underset{\substack{\text{carbon dioxide}\\ \text{(gas)}}}{6\,CO_2} + \underset{\text{water}}{12\,H_2O}} \;\xrightarrow[\substack{\uparrow\\ \text{light energy}\\ \text{input}}]{}\; \underset{\text{(high potential energy)}}{\underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\substack{\text{oxygen}\\ \text{(gas)}}}{6\,O_2} + \underset{\text{water}}{6\,H_2O}}$$

Chlorophyll in the cells of the plant absorbs the kinetic energy of light and uses it to remove the hydrogen atoms from water (H_2O) molecules. The hydrogen atoms combine with carbon atoms from carbon dioxide to form a growing chain of carbons that eventually turns into a glucose molecule. After the hydrogen atoms are removed from water, the oxygen atoms that remain combine with each other to form oxygen gas, which is released into the air. Water appears on both sides of the equation because 12 molecules are consumed and 6 molecules are newly formed during photosynthesis.

The key energy steps in photosynthesis remove the hydrogen from water molecules and join carbon atoms together to form the carbon–carbon and carbon–hydrogen bonds of glucose. These steps convert the low-potential-energy bonds in water and carbon dioxide molecules to the high-potential-energy bonds of glucose. The laws of thermodynamics are not violated in this process because much more energy goes into the reaction than comes out. Careful measurements show that the rate of photosynthesis (which determines the amount of glucose formed) is related to the intensity of light, but seems terribly inefficient: At best, 2 calories of sugar are formed for each 100 calories of light energy falling on the plant (2% efficiency).

Within the Plant. The glucose produced in photosynthesis serves three purposes in the plant: (1) Either by itself or combined with nitrogen, phosphorus, sulfur, and other mineral nutrients absorbed by the plant's roots, glucose is the raw material used for making all the other organic molecules (proteins, carbohydrates, and so on) that make up the stem, roots, leaves, flowers, and fruit of the plant. (2) The synthesis of all these organic molecules requires additional energy, as do the plant's absorption of nutrients from the soil and certain other functions. This energy is obtained when the plant breaks down a portion of the glucose to release its stored energy in a process called *cell respiration*, which is discussed later. (3) A portion of the glucose produced may be stored for future use. For storage, the glucose is generally converted to starch, as in potatoes, or to oils, as in seeds. These conversions are summarized in Fig. 3-12.

None of these reactions, from the initial capture of light by chlorophyll to the synthesis of plant structures,

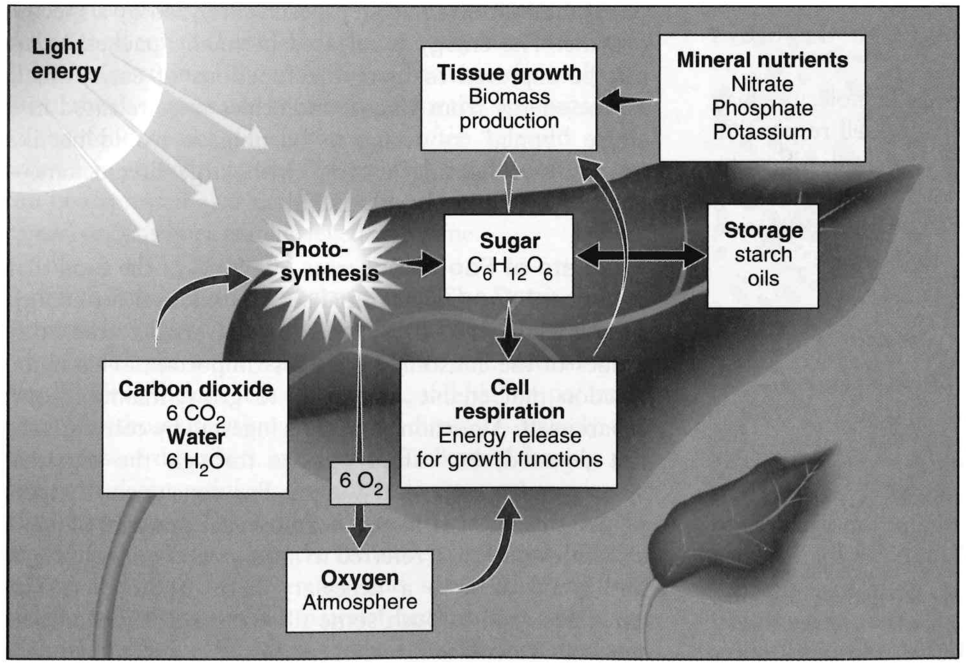


Figure 3-12 **Producers as chemical factories.** Using light energy, producers make glucose from carbon dioxide and water, releasing oxygen as a by-product. Breaking down some of the glucose to provide additional chemical energy, they combine the remaining glucose with certain nutrients from the soil to form other complex organic molecules that the plant then uses for growth.

take place automatically. Each step is catalyzed by specific **enzymes,** *proteins that promote the synthesis or breaking of chemical bonds.* The same is true of cell respiration.

Setting the Table. As the plants in an ecosystem convert sunlight into new organic matter, they are "setting the table" for the rest of the ecosystem—the herbivores, carnivores, and decomposers described in the food webs in Chapter 2. Because the plants are creating *new* organic matter for the ecosystem, they are the *primary* producers. Given suitable conditions and resources, the producers of an ecosystem will maintain their photosynthetic activity over time in the process called *primary production.* The total amount of photosynthetic activity in producers is called *gross primary production;* subtracting the energy consumed by the plants themselves yields the *net primary production.* Thus, net primary production is the *rate* at which new organic matter is made available to consumers in an ecosystem. In the Serengeti, the grasses in the plains have to produce at the rate of 560 kg dry weight per km^2 per day in order to keep up with the rate at which they are being grazed.

Consumers. Consumers need energy to move about and to perform such internal functions as pumping blood. In addition, consumers need energy to synthesize all the molecules required for growth, maintenance, and repair of their bodies. This energy comes from the breakdown of organic molecules in food (or from the body's own tissues if food is unavailable). Between 60 and 90% of the food that we and other consumers eat and digest acts as "fuel" to provide energy.

Digestion. First, the starches, fats, and proteins that you eat are digested—broken down into simpler molecules—in the stomach or intestine. Starches are broken down into sugar (glucose), for example. These simpler molecules are then absorbed from the intestine into the bloodstream and transported to the body's individual cells.

Respiration. Inside each cell, organic molecules may be broken down through a process called **cell respiration** to release the energy required for the work done by that cell. Most commonly, cell respiration involves the breakdown of glucose, and the overall chemical equation is basically the reverse of that for photosynthesis:

Cell Respiration
(An energy-releasing process)

$$\underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{oxygen}}{6\,O_2} \rightarrow \underset{\text{carbon dioxide}}{6\,CO_2} + \underset{\text{water}}{6\,H_2O} + \text{energy}$$

(high potential energy) (low potential energy)

The purpose of cell respiration is to release the potential energy contained in organic molecules to perform the activities of the organism. Note that *oxygen* is *released* in photosynthesis, but *consumed* in cell respiration to break down glucose to carbon dioxide and water. Oxygen is absorbed through the lungs with every inhalation (or through the gills, in the case of fish) and is transported to all the body's cells via the circulatory system. Carbon dioxide, which is formed as a waste product, moves from the cells into the circulatory system and is eliminated through the lungs (or gills) with every exhalation.

In keeping with the second law of thermodynamics, converting the potential energy of glucose to the energy required to do the body's work is not 100% efficient. Considerable waste heat is produced, and this is the source of *body heat.* This heat output can be measured in animals (cold-blooded or warm-blooded) and in plants. It is more noticeable in warm-blooded animals only because much of their body heat is used to maintain their body temperature.

Gaining Weight. The basis of weight gain or loss becomes apparent here. Organic matter is broken down in cell respiration only as it is needed to meet the energy demands of the body. This is why your breathing rate, the outer reflection of cell respiration, varies with changes in your level of exercise and activity. If you consume more calories from food than your body needs, the excess may be converted to fat and stored, and the result is a gain in weight. In contrast, the principle of dieting is to eat less and exercise more, to create an energy demand that exceeds the amount of energy contained in your food. This imbalance forces the body to break down its own tissues to make up the difference, and the result is a weight loss. Carried to an extreme, such an imbalance leads to *starvation* and even death when the body runs out of anything expendable to break down for its energy needs.

Oxidation. The overall reaction for cell respiration is the same as that for simply burning glucose. Thus, it is not uncommon to speak of "burning" our food for energy. Such a breakdown of molecules is also called **oxidation.** The distinction between burning and cell respiration is that in cell respiration the oxidation takes place in about 20 small steps, each catalyzed by a specific enzyme. The energy is released in small "packets" that can be captured to drive the functions of each cell. If all the energy from glucose molecules were released in a single "bang," as occurs in burning, it would be like heating and lighting a room with large firecrackers—energy indeed, but hardly useful.

The Fate of Food. Whereas 60–90% of the food that consumers eat, digest, and absorb is oxidized for energy, the remaining 10–40%, which is converted to the body tissues of the consumer, is no less important. This is the fraction that enables the body to grow, maintain, and repair itself. A portion of what is ingested by consumers is not digested, but simply passes through the digestive system and out as fecal wastes. For consumers that eat plants, this waste is largely **cellulose,** the material of plant cell walls. It is often referred to as *fiber, bulk,* or *roughage,* and some of it is a necessary part of the diet. The intestines need to push some fiber through them so that they can keep clean and open. Waste products can also

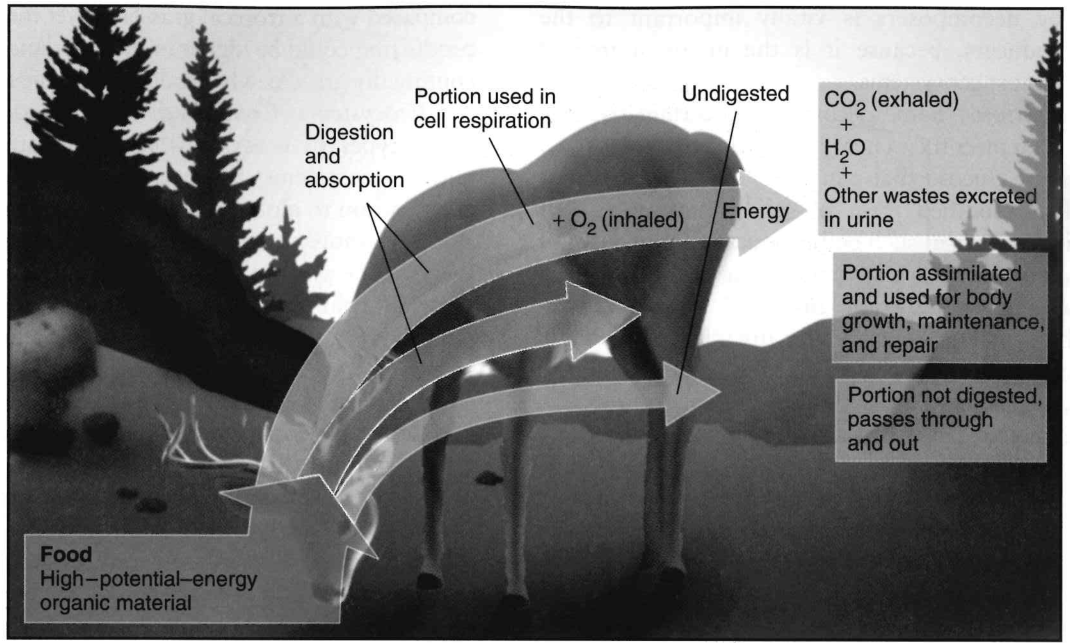


Figure 3–13 **Consumers.** Only a small portion of the food ingested by a consumer is assimilated into body growth, maintenance, and repair. A larger amount is used in cell respiration to provide energy; waste products are carbon dioxide, water, and various mineral nutrients. A third portion is not digested and becomes fecal waste.

include compounds of nitrogen, phosphorus, and any other elements present, in addition to the usual carbon dioxide and water. These by-products are excreted in the urine (or as similar waste in other kinds of animals) and returned to the environment.

In sum, organic material (food) eaten by any consumer follows one of three pathways: (1) More than 60% of what is digested and absorbed is oxidized to provide energy, and waste products are released back to the environment; (2) the remainder of what is digested and absorbed goes into body growth, maintenance and repair, or storage (fat); and (3) the portion that is not digested or absorbed passes out as fecal waste (Fig. 3–13). In an ecosystem, therefore, only that portion of the food which becomes the body tissue of the consumer can become food for the next organism in the food chain. This process is often referred to as *secondary* production, and like primary production, it also can be expressed as a rate (amount of growth of the consumer, or consumer trophic level) over time.

Detritus Feeders and Decomposers: The Detritivores. Detritus is largely cellulose because it consists mostly of dead leaves, the woody parts of plants, and animal fecal wastes. Nevertheless, it is still organic and high in potential energy for those organisms which can digest it—namely, the decomposers described in Chapter 2. Beyond having the ability to digest cellulose, decomposers (various species of fungi and bacteria, as well as a few other microbes) act as any other consumer, using the cellulose as a source of both energy and nutrients. Termites and some other detritus feeders can digest woody material because they maintain decomposer microorganisms in their guts in a mutualistic symbiotic relationship. The termite (a detritus feeder) provides a cozy home for the microbes (decomposers) and takes in the cellulose, which the microbes digest for both their own and the termites' benefit (Fig. 3–14).

Most decomposers use oxygen for cell respiration, which breaks the detritus down into carbon dioxide, water, and mineral nutrients. Likewise, there is a release of waste heat, which you may observe as the "steaming" of a manure or compost pile on a cold day. The release of

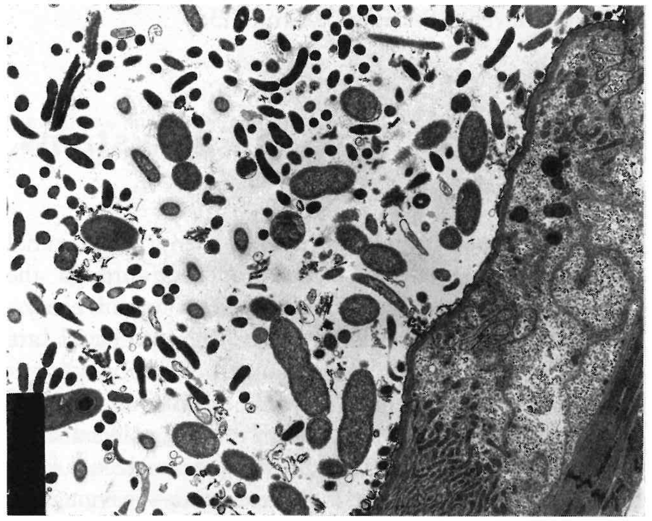


Figure 3–14 **Termite gut.** Termites can live on cellulose-based woody matter because their guts contain a consortium of symbiotic microbes able to digest cellulose. In this electron micrograph the symbionts are on the left, and the termite intestinal wall on the right.

nutrients by decomposers is vitally important to the primary producers, because it is the major source of nutrients in most ecosystems.

Fermentation. Some decomposers (certain bacteria and yeasts) can meet their energy needs through the partial breakdown of glucose that can occur in the absence of oxygen. This modified form of cell respiration, called **fermentation,** results in such end products as ethyl alcohol (C_2H_6O), methane gas (CH_4), and acetic acid ($C_2H_4O_2$). The commercial production of these compounds is achieved by growing the particular organism on suitable organic matter in a vessel without oxygen. In nature, **anaerobic,** or *oxygen-free,* environments commonly exist in the sediments of lakes, marshes, or swamps and in the guts of animals, where oxygen does not penetrate readily. Methane gas is commonly produced in these locations. A number of large grazing animals, including cattle, maintain fermenting bacteria in their digestive systems in a mutualistic, symbiotic relationship similar to that just described for termites. As a result, both cattle and termites produce methane.

For simplicity, the focus of this chapter is on terrestrial ecosystems. Keep in mind, though, that exactly the same processes occur in aquatic ecosystems. As aquatic plants and algae absorb dissolved carbon dioxide and mineral nutrients from the water, they use photosynthesis to produce food and dissolved oxygen that sustain consumers and other heterotrophs. Likewise, aquatic heterotrophs return carbon dioxide and mineral nutrients to the aquatic environment. Aquatic and terrestrial systems are never entirely isolated from one another, and they exchange materials all the time.

To summarize, the different biotic components of ecosystems function on the basis of two common processes: (a) the *flow of energy,* using sunlight as the basic energy source, and (b) the *cycling of nutrients.* These processes are examined in more depth at the ecosystem level in Sections 3.2 and 3.3.

3.2 Energy Flow in Ecosystems

Primary Production

In most ecosystems, sunlight, or solar energy, is the initial source of energy absorbed by producers through the process of photosynthesis. (The only exceptions are ecosystems near the ocean floor, where the producers are chemosynthetic bacteria.) As mentioned in Section 3.1, primary production captures only about 2%, at most, of incoming solar energy. Even though this seems like a small fraction, the resulting net production—estimated at some 115 billion tons of organic matter per year—is enough to fuel all of life on Earth. In a given ecosystem, the actual biomass of primary producers at any given time is referred to as the *standing-crop biomass.* Both biomass and primary production vary greatly in different ecosystems. For example, a forested ecosystem maintains a very large biomass compared with a tropical grassland, yet the rate of primary production could be higher in the grassland, where animals continually graze newly produced organic matter.

Ecosystems Compared. The productivity of different types of ecosystems (e.g., terrestrial biomes and aquatic ecosystems) has been examined to evaluate their contribution to global productivity and to investigate why some are more productive than others. Figure 3–15 presents (a) the average net primary productivity, (b) the percentage of different ecosystems over Earth's surface, and, subsequently, (c) the percentage of global net primary productivity attributed to 19 of the most important ecosystems. Some key relationships between abiotic factors and specific ecosystems can be seen in the data. Tropical rain forests are both highly productive and contribute considerably to global productivity; they cover a large area of the land and are characterized by ideal climatic conditions for photosynthesis—warm temperatures and abundant rainfall. The open oceans cover 65% of Earth's surface, so they account for a large portion of global productivity, yet their actual rate of production is low enough that they are veritable biological deserts. Although light, temperature, and water are abundant, primary production in the oceans is limited by the scarcity of nutrients—a good lesson in the significance of limiting factors (Chapter 2). (See Global Perspective, p. 70). The seasonal effects of differences in latitude can also be seen by comparing productivity in tropical, temperate, and boreal (coniferous) forests.

Energy Flow and Efficiency

As primary producers are consumed by herbivores, energy is transferred from producer to consumer. Recall from Chapter 2, Section 2.2, that each of these components is a *trophic level.* Thus, energy flow in an ecosystem can be characterized by how the energy moves from one trophic level to another. Figure 3–16 shows how energy flows through three trophic levels of a grazing food web. At each trophic level, some energy goes into growth (production), some is converted to heat (respiration), and some is given off as waste or is not consumed. As energy flows from one trophic level to the next, only a small fraction is actually passed on. This is due to three things: (1) Much of the preceding trophic level is standing biomass and is not consumed; (2) much of what is consumed is used for energy; and (3) some of what is consumed is undigested and passes through the organism.

Figure 3–16 shows that a very large proportion of the primary-producer trophic level is not consumed in the grazing food web. As this material dies (leaves drop, grasses wither and die, and so on), it is joined by the fecal wastes and dead bodies from higher trophic levels and represents the starting point for a separate food web, the detritus food web, pictured earlier in Fig. 2–10. In many cases, the majority of the energy in an ecosystem flows through the detritus food web.

Efficiency. Because energy is lost when it is transferred to the next higher trophic level, each successive trophic level captures only a fraction of the energy that entered the previous trophic level and is usually represented by a much smaller biomass. Calculations show that the efficiency of transfer in a number of ecosystems ranges from 5 to 20%, with 10% being the average. Thus, there is an approximate 90% *loss* of energy as it moves from one trophic level to the next. This loss gets quite critical at increasingly higher trophic levels and is the reason carnivores are much less abundant than herbivores, carnivores that eat other carnivores are even less abundant, and so forth. In any given ecosystem, therefore, there are usually only three to five trophic levels; there simply isn't enough energy left to pass along to "supercarnivores."

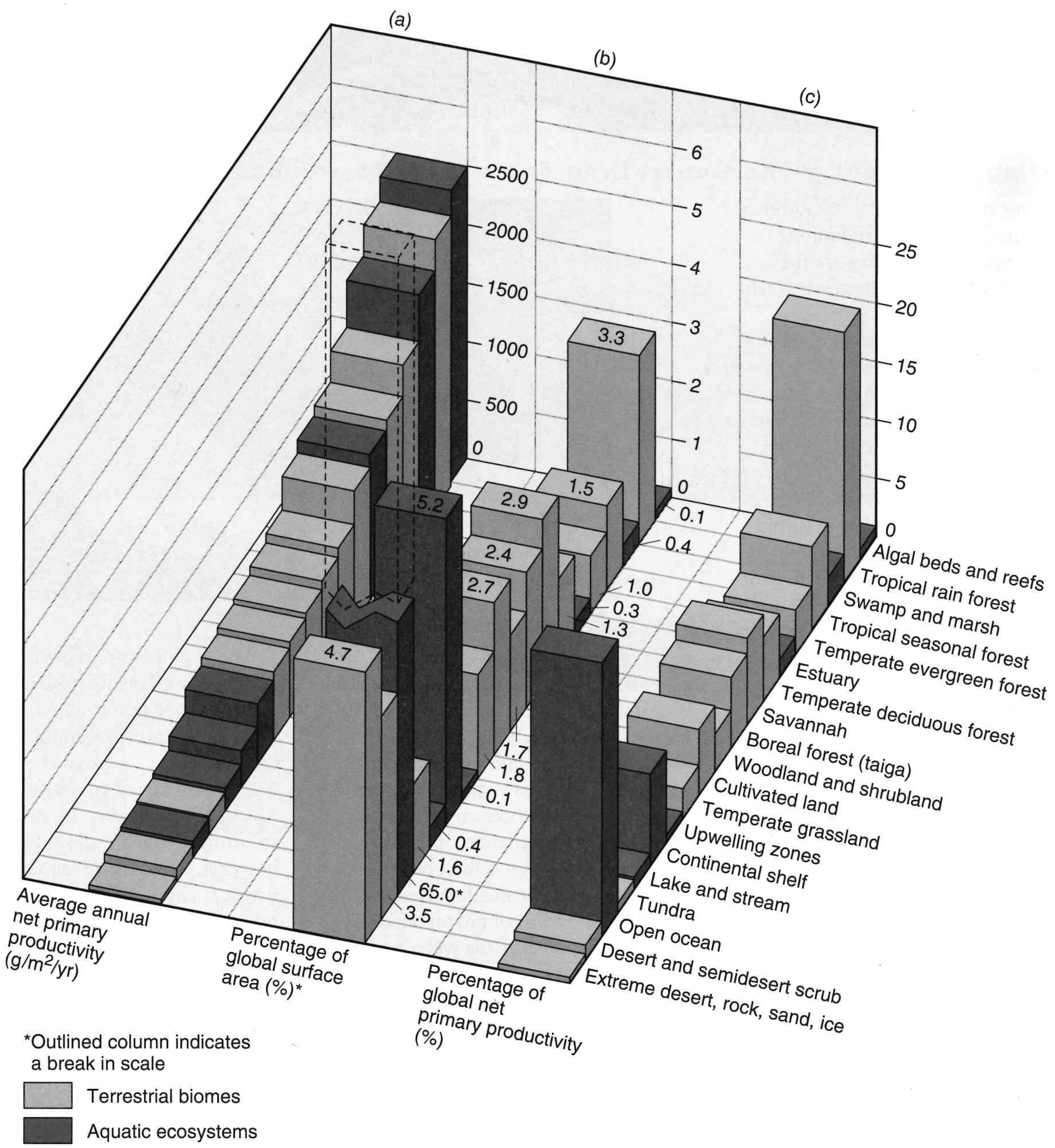
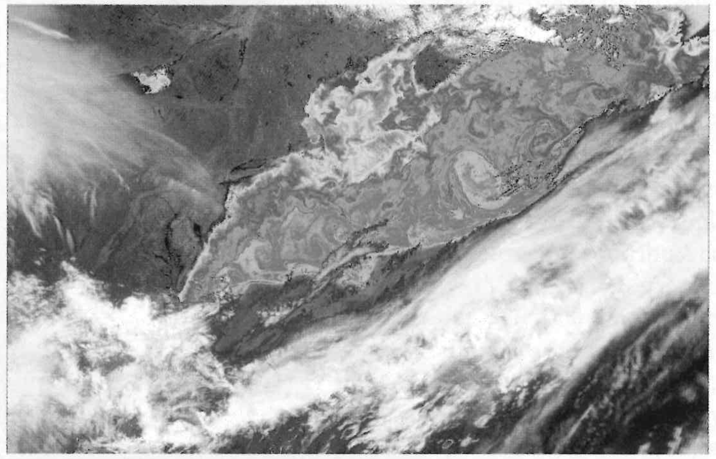


Figure 3–15 Productivity of different ecosystems. (a) The annual net primary productivity of different ecosystems; (b) the percentage of different ecosystems over Earth's surface area; and (c) the percentage of global net primary productivity.

What happens to all the solar energy entering ecosystems? Most of it is absorbed by the atmosphere, oceans, and land, thus heating them in the process. The small fraction (2–5%) captured by living plants is either passed along to the next trophic level or degraded into the lowest and most disordered form of energy—heat—as the plant decomposes. Eventually, all of the energy entering ecosystems escapes as heat. According to the laws of thermodynamics, no energy will actually be lost. So many energy conversions are taking place in ecosystem trophic activities, however, that entropy is increased and all the energy is degraded to a form unavailable to do further work. The ultimate result is that *energy flows in*

global perspective

Light and Nutrients: The Controlling Factors in Marine Ecosystems



Ecosystems run on solar energy and they recycle nutrients. The major limiting factors in marine ecosystems are the availabilities of light and nutrients. Light diminishes as water depth increases, because even clear water absorbs light. The layer of water from the surface down to the greatest depth at which there is adequate light for photosynthesis is known as the **euphotic zone**. Below the euphotic zone, photosynthesis does not occur. In clear water, the euphotic zone may be as deep as 600 feet (180 m), but in turbid (cloudy) water, it may be only a few centimeters. In coastal waters, where the euphotic zone extends to the bottom, the bottom may support abundant plant life in the form of aquatic vegetation attached to or rooted in sediments. If the euphotic zone does not extend to the bottom, the bottom will be barren of plant life.

Whether shallow or deep, the euphotic zone supports a diverse ecosystem. Phytoplankton—algae and photosynthetic bacteria that grow as single cells or in small groups of cells—can maintain themselves close to the surface in the euphotic zone. Phytoplankton support a diverse food web, from the zooplankton (small crustaceans and protozoans) that feed on them to many species of fish and sea mammals (whales and porpoises) at the higher trophic levels.

An entire ecosystem can also operate in the cold, dark depths below the euphotic layer. This ecosystem is nourished by detritus raining down from above and, closer to the ocean floor, by vents and fissures that produce mineral-rich water and warmth.

In a phytoplankton-based system, nutrients dissolved in the water become critically important. If the water contains too few dissolved nutrients such as phosphorus or nitrogen compounds, the growth of phytoplankton and, hence, the rest of the ecosystem will be limited. If the bottom receives light, it may support vegetation despite nutrient-poor water, because this kind of vegetation draws nutrients from the bottom sediments. Indeed, in some estuaries, nutrient-rich water inhibits the growth of bottom vegetation, because the dissolved nutrients support the growth of phytoplankton instead, which makes the water turbid and shades out the bottom vegetation.

The most productive areas of the ocean—the areas supporting the most abundant marine life of all sorts—are generally found within 200 miles (320 km) of shore. Either the bottom is within the euphotic zone and thus supports abundant vegetation, or nutrients washing in from the land support an abundant primary production of phytoplankton.

In the open ocean, there is less marine life the further you move from shore. Indeed, marine biologists consider most of the open ocean to be a "biological desert." Life is scarce here because the bottom is well below the euphotic zone and the water is nutrient poor.

When plants and animals die in the ocean, they sink to the bottom. Nutrients carried to the bottom with this settling detritus are released into solution by decomposers, primarily bacteria. This nutrient-rich bottom water is carried along by deep-running ocean currents. Where the currents hit underwater mountains or continental rims, the nutrient-rich water is forced to the surface. Phytoplankton flourish in these areas of **upwelling** (rising) and thus support a rich diversity of fish and marine mammals. As a result, the world's oceans are far from being uniformly stocked with fish. By far the richest marine fishing areas are continental shelves and regions of upwelling, as shown on the accompanying map of the North Atlantic. The yellow and green areas overlie Georges Bank and the Gulf of Maine and show the effects of nutrients from upwelling and local estuaries.

a one-way direction through ecosystems; it is not recycled, so it must be continually resupplied by sunlight.

Running on Solar Energy

No system can run without an input of energy, and living systems are no exception. For all major ecosystems, both terrestrial and aquatic, the initial source of energy is *sunlight*. As a basic energy source, sunlight is highly sustainable because it is both *nonpolluting* and *nondepletable*.

Nonpolluting. Light from the Sun is a form of pure energy; it contains no substance that can pollute the environment. All the matter and pollution involved in the production of light energy are conveniently left behind on the Sun some 93 million miles (150 million kilometers) away in space.

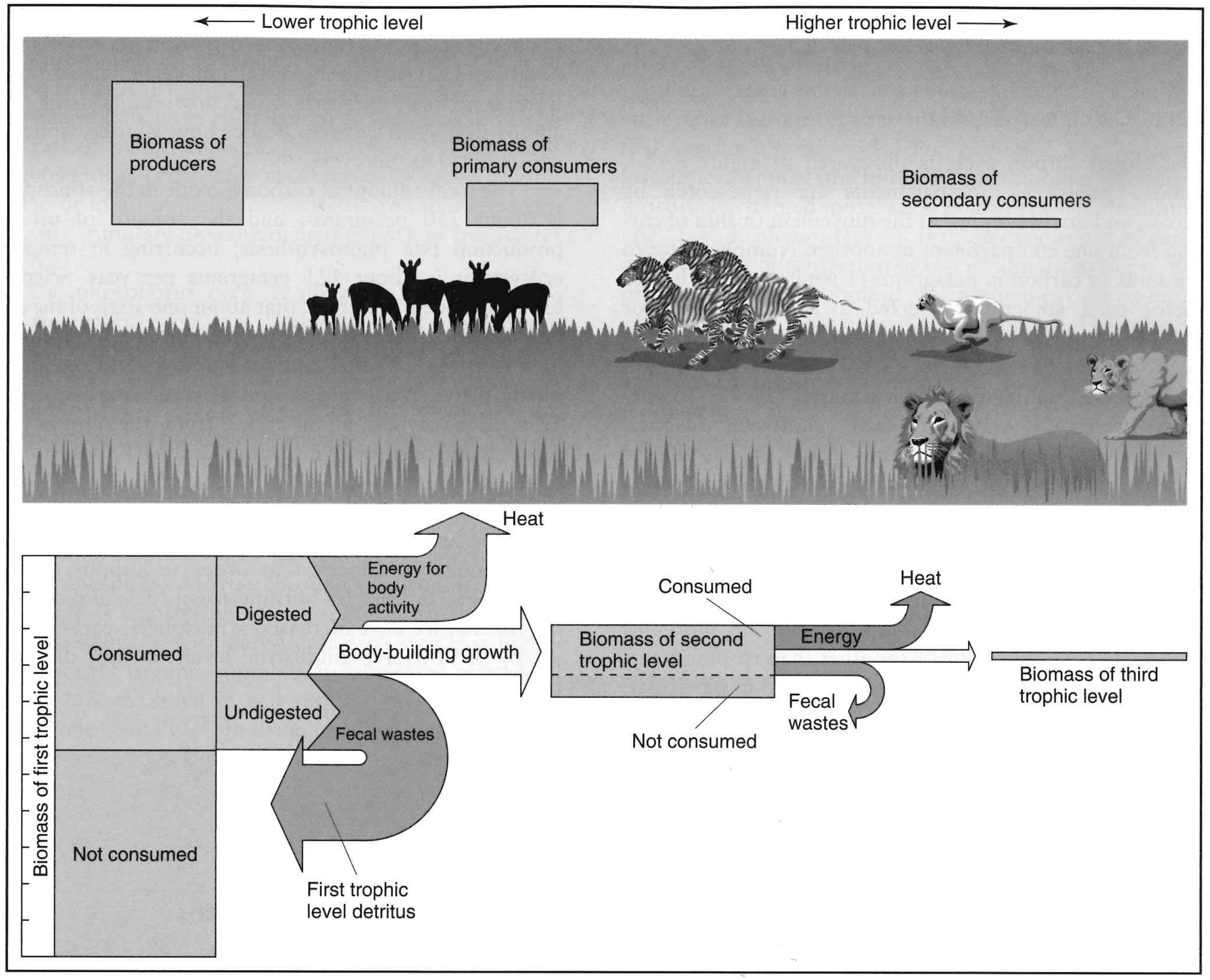


Figure 3-16 Energy flow through trophic levels in a grazing food web. Each trophic level is represented as biomass boxes, and the pathways taken by the energy flow are indicated with arrows.

Nondepletable. The Sun's energy output is remarkably constant; the radiant energy from the sun (called the solar constant) strikes Earth's atmosphere at about 2 calories per cm^2 per minute. How much or how little of this energy is used on Earth will not influence, much less deplete, the Sun's output. Even though cosmologists predict that the Sun will expire some day (a few billion years from now!), for all practical purposes the Sun is an everlasting source of energy.

Energy flow is one of the two fundamental processes that make ecosystems work. The second process is the cycling of nutrients and other elements.

3.3 The Cycling of Matter in Ecosystems

The various inputs and outputs of producers, consumers, detritus feeders, and decomposers fit together remarkably well. The products and by-products of each group are the food or essential nutrients for the other. Specifically, the organic material and oxygen produced by green plants are the food and oxygen required by consumers and other heterotrophs. In turn, the carbon dioxide and other wastes generated when heterotrophs break down their food are exactly the nutrients needed by green plants. This kind of recycling is fundamental to sustainability, for two reasons: (a) It prevents the accumulation of wastes that would cause problems (for example, ammonia is excreted by many animals and is toxic at relatively low concentrations), and (b) it guarantees that the ecosystem will not run out of essential elements.

According to the law of conservation of matter, atoms cannot be created, destroyed, or changed, so recycling is the only possible way to maintain a dynamic system. To see how well the biosphere has mastered recycling, we now focus on the pathways of three key elements heavily affected by human activities: carbon, phosphorus, and nitrogen. Because these pathways all lead in circles and involve biological, geological, and chemical processes, they are known as **biogeochemical cycles.** (Recall that energy is not recycled.)

The Carbon Cycle

The global carbon cycle is illustrated in Figure 3–17; major "pools" or compartments are represented by boxes, and arrows represent the movement or flux of carbon from one compartment to another. Numbers refer to amounts of carbon in petagrams (1 petagram = 1 billion metric tons, sometimes referred to as 1 gigaton). For descriptive purposes, it is convenient to start the carbon cycle with the "reservoir" of carbon dioxide (CO_2) molecules present in the air and bicarbonate (HCO_3^-) molecules present in water. Through photosynthesis and further metabolism, carbon atoms from CO_2 become the carbon atoms of the organic molecules making up a plant's body. The carbon atoms then move into food webs and become part of the tissues of all the other organisms in the ecosystem. At any point, a given atom may be respired and returned to the atmosphere; in aquatic systems, it will be returned to the inorganic carbonate in solution. Processes other than trophic transfer are significant. The figure indicates two in particular: (1) geological sedimentation and burial on the land and under the ocean and limestone formation of carbon in the ocean, and (2) weathering of calcium carbonate and combustion of fossil-fuel carbon laid down millions of years ago by biological systems. Notice how all four "spheres" are involved in this cycle.

The total amount of carbon dioxide in the atmosphere is about 750 petagrams, and the amount of primary production (via photosynthesis) occurring in terrestrial ecosystems is about 121 petagrams per year. Scientists have concluded, therefore, that about one-sixth of the total atmospheric carbon dioxide is taken up in photosynthesis in a year, but an equal amount is returned to the atmosphere, through cell respiration. This means that, on the average, a carbon atom cycles from the atmosphere, through one or more living things, and back to the atmosphere every six years.

Human intrusion into the carbon cycle is significant: We are diverting or canceling out 40% of terrestrial primary production in order to support human enterprises. Indeed, by burning fossil fuels and destroying forests, we have increased atmospheric carbon dioxide by 35% over preindustrial levels, a topic discussed in Chapter 20.

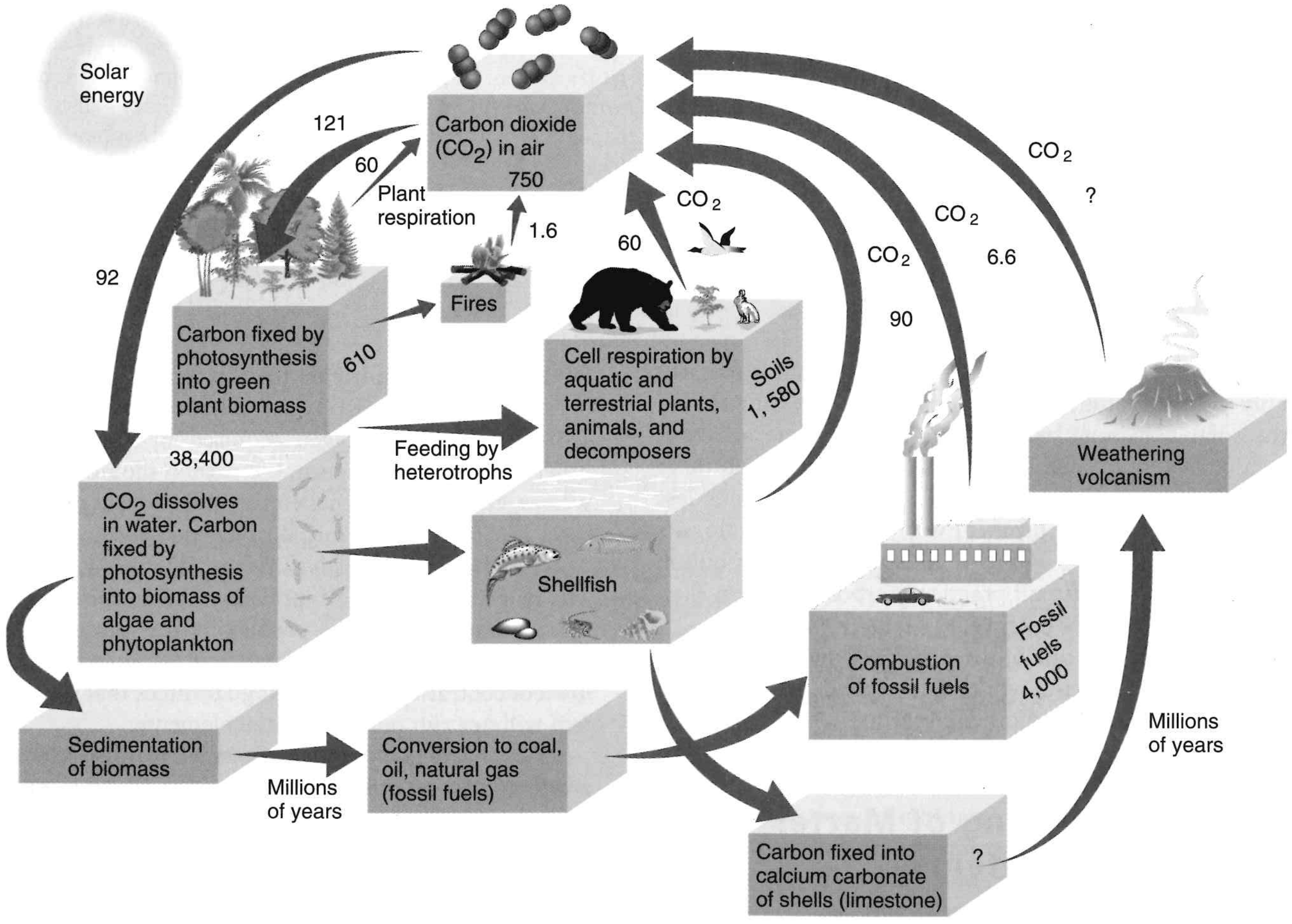


Figure 3–17 **The global carbon cycle.** Boxes in the figure refer to pools of carbon, and arrows refer to the movement, or flux, of carbon from one pool to another. Numbers are recorded in petagrams of carbon (1 petagram = 1 billion metric tons).

The Phosphorus Cycle

The phosphorus cycle is representative of the cycles of all the biologically important mineral nutrients—those elements which have their origin in the rock and soil minerals of the lithosphere. (See Table 3–1.) We focus on phosphorus because its shortage tends to be a limiting factor in a number of ecosystems and its excess can seriously stimulate unwanted algal growth in freshwater systems.

The phosphorus cycle is illustrated in Fig. 3–18. Like the carbon cycle, it is depicted as a set of pools and fluxes to indicate key processes. Phosphorus exists in various rock and soil minerals as the inorganic ion *phosphate* (PO_4^{3-}). As rock gradually breaks down, phosphate and other ions are released. This slow process is the normal means of replenishing phosphorus that is lost to runoff. Plants absorb PO_4^{3-} from the soil or from a water solution, and once the phosphate is incorporated into organic compounds by the plant, it is referred to as **organic phosphate.** Moving through food chains, organic phosphate is transferred from producers to the rest of the ecosystem. As with carbon, at each step it is highly likely that the organic compounds containing phosphate will be broken down in cell respiration or by decomposers, releasing PO_4^{3-} in urine or other waste material. The phosphate may then be reabsorbed by plants to start the cycle again.

Phosphorus enters into complex chemical reactions with other substances that are not shown in this simplified version of the cycle. For example, PO_4^{3-} forms insoluble chemical precipitates with a number of cations (positively charged ions), such as iron (Fe^{3+}), aluminum (Al^{3+}), and calcium (Ca^{3+}). If these cations are in sufficiently high concentration in soil or aquatic systems, the phosphorus can be bound up in chemical precipitates and rendered largely unavailable to plants. The precipitated phosphorus can slowly release PO_4^{3-} as plants withdraw naturally occurring PO_4^{3-} from soil, water, or sediments.

There is an important difference between the carbon cycle and the phosphorus cycle. No matter where CO_2 is released, it will mix into and maintain the concentration of CO_2 in the atmosphere. Phosphorus, however, does not have a gas phase, so it is recycled only if the wastes containing it are deposited in the *ecosystem from which it came*. The same holds true for other mineral nutrients. In natural ecosystems, wastes (urine, detritus) are deposited in the same area, so recycling occurs efficiently. As mentioned earlier, the rich growth of grasses on the plains of the Serengeti is traced to

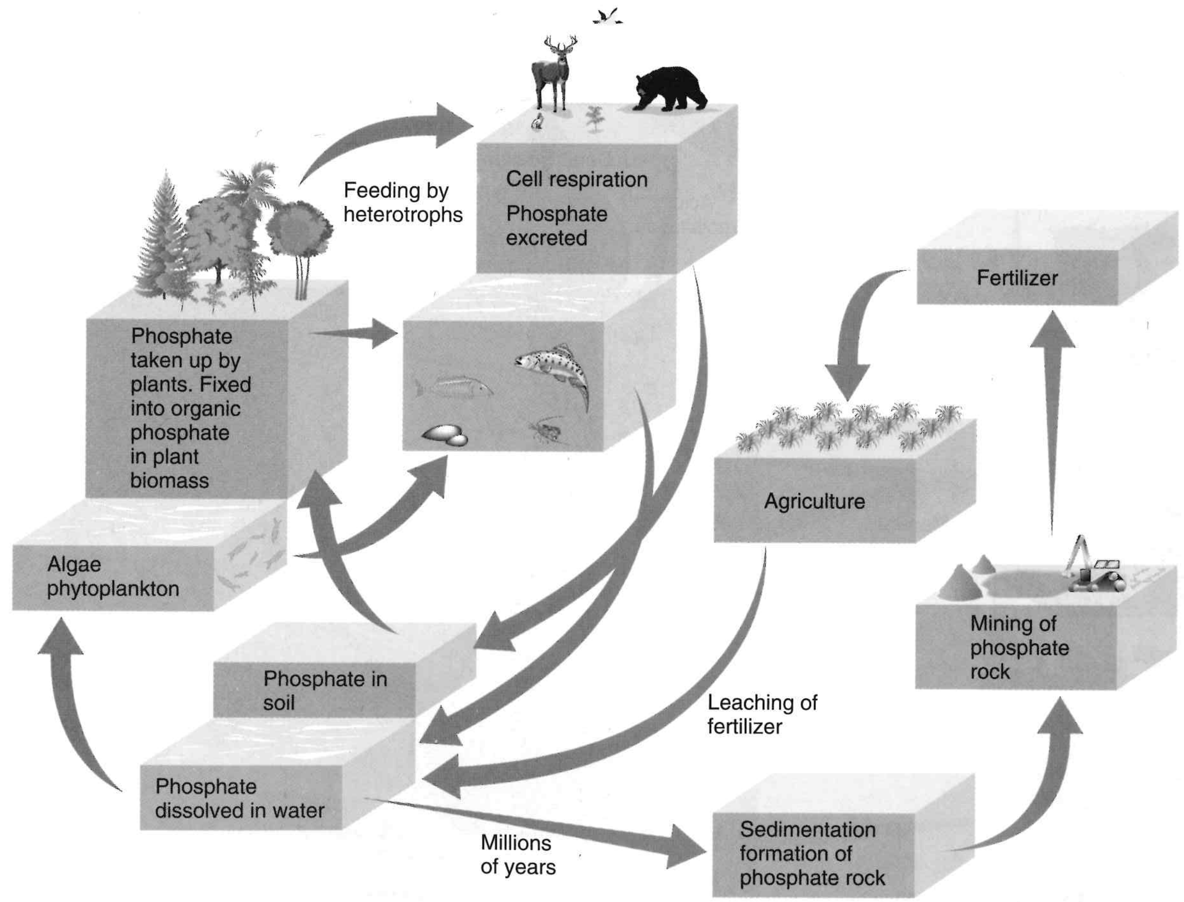


Figure 3–18 **The global phosphorus cycle.**

phosphorus brought and maintained there by the dense herbivore herds. Humans have been extremely prone to interrupt this cycle, however.

Human Impacts. The most serious intrusion into the phosphorus cycle comes from the use of phosphorus-containing fertilizers. Phosphorus is mined in several locations around the world (in the United States, Florida is a prominent source) and is then made into fertilizers, animal feeds, detergents, and other products. Much of the phosphorus applied to agricultural croplands and lawns makes its way into waterways—either directly, in runoff from the land, or indirectly, in sewage effluents. There is essentially no way to return this waterborne phosphorus to the soil, so the bodies of water end up overfertilized. This leads, in turn, to a severe water pollution problem known as eutrophication. (See Chapter 17.)

When we use manure, compost (rotted plant wastes), or sewage sludge (instead of chemical fertilizer) on crops, lawns, or gardens, the natural cycle is imitated. In too many cases, however, it is not. Human applications have almost quadrupled the amount of phosphorus annually entering soils and surface waters (normally around 3.5 teragrams per year [1 teragram = 1 million metric tons], to the present 13 teragrams per year). Therefore, we are accelerating the natural phosphorus cycle as we mine it from the earth and as it subsequently moves from the soil into aquatic ecosystems.

The Nitrogen Cycle

The nitrogen cycle (Fig. 3–19) has aspects of both the carbon cycle and the phosphorus cycle. Like carbon, nitrogen possesses a gas phase; like phosphorus, it acts as a limiting factor. The nitrogen cycle is otherwise unique. Most notably, bacteria in soils, water, and sediments perform many of the steps of the cycle. Like phosphorus, nitrogen is in high demand by both aquatic and terrestrial plants.

The main reservoir of nitrogen is the air, which is about 78% nitrogen gas (N_2). Plants cannot use nitrogen gas directly from the air. Instead, the nitrogen must be in mineral form, such as ammonium ions (NH_4^+) or nitrate ions (NO_3^-). Beginning with the uptake of nitrates by green plants, nitrogen is incorporated into essential organic compounds such as proteins and nucleic acids. The nitrogen then follows the classic energy-flow pattern from producers to herbivores to carnivores and, finally, to decomposers (referred to as heterotrophs in Fig. 3–19). At various points, nitrogen wastes are released, primarily as ammonium compounds. A group of soil bacteria, the nitrifying bacteria, oxidizes the ammonium to nitrate in a chemosynthetic process that yields energy for the bacteria. At this point, the nitrate is once again available for uptake by green plants—a local ecosystem cycle within the global cycle. In most ecosystems, the supply of nitrate or ammonium nitrogen is quite limited, yet there is an abundance of nitrogen gas—if it can be accessed.

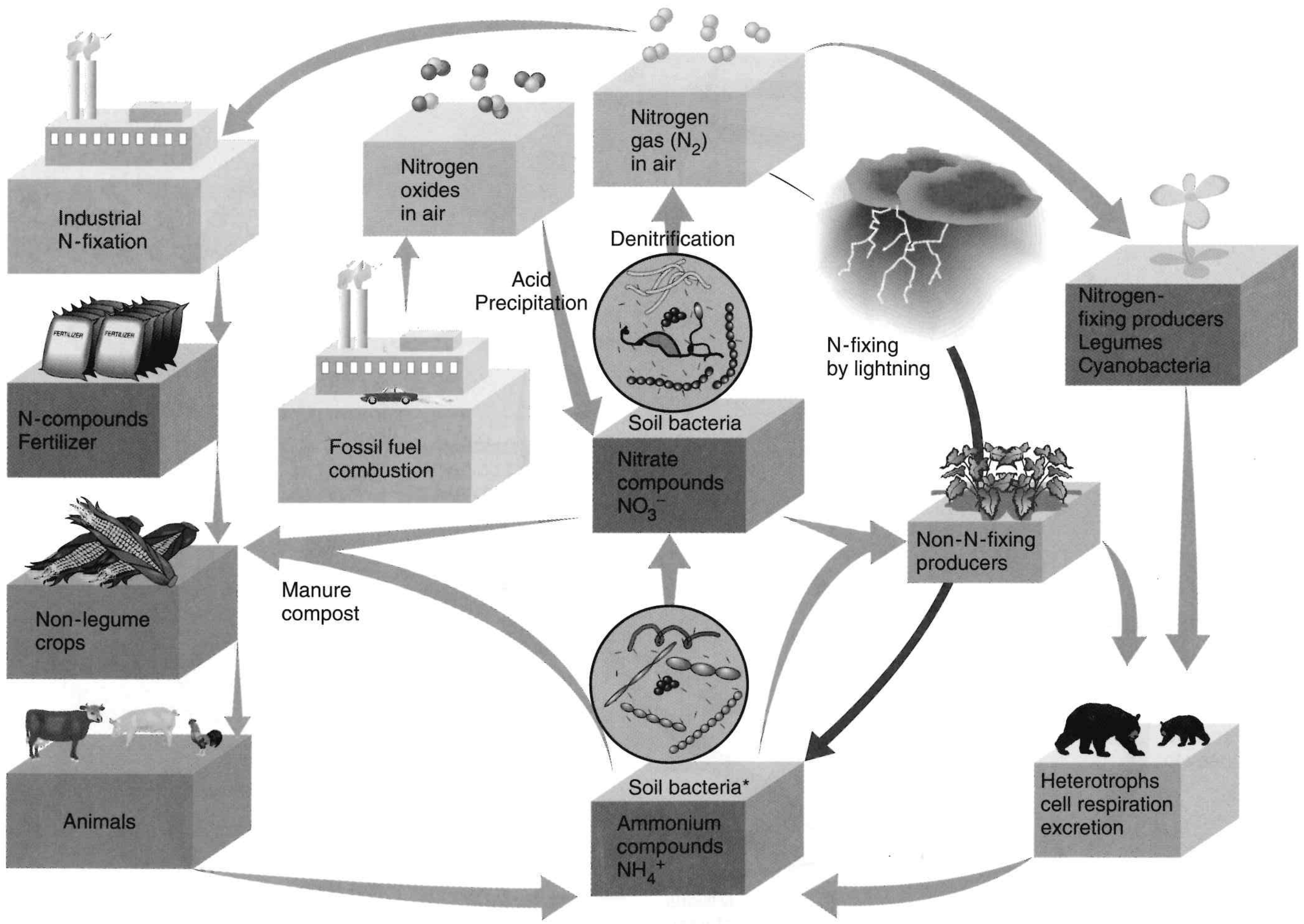


Figure 3–19 The global nitrogen cycle.

Nitrogen Fixation. A number of bacteria and cyanobacteria (chlorophyll-containing bacteria, formerly referred to as blue-green algae) can convert nitrogen gas to the ammonium form, a process called biological **nitrogen fixation.** In terrestrial ecosystems, the most important among these nitrogen-fixing organisms is a bacterium in the genus *Rhizobium*, which lives in nodules on the roots of legumes, the plant family that includes peas and beans (Fig. 3–20). [This is another example of mutualistic symbiosis. The legume provides the bacterium with a place to live and with food (sugar) and gains a source of nitrogen in return.] From the legumes, nitrogen enters the food web. Many ecosystems are "fertilized" by nitrogen-fixing organisms; legumes, with their symbiotic bacteria, are by far the most important. The legume family includes a huge diversity of plants, ranging from clovers (common in grasslands) to desert shrubs and many trees. Every major terrestrial ecosystem, from tropical rain forest to desert and tundra, has its representative legume species, and legumes are generally the first plants to recolonize a burned-over area. Without them, all production would be sharply impaired due to a lack of available nitrogen. The nitrogen cycle in aquatic ecosystems is similar. There, cyanobacteria are the most significant nitrogen fixers.

Three other important processes also "fix" nitrogen. One is the conversion of nitrogen gas to the ammonium form by discharges of lightning in a process known as *atmospheric nitrogen fixation*; the ammonium then comes down with rainfall. The second is the *industrial fixation* of nitrogen in the manufacture of fertilizer. (The Haber–Bosch process converts nitrogen gas and hydrogen to ammonia.) The third is a consequence of the *combustion of fossil fuels*, during which nitrogen from coal and oil is oxidized; some nitrogen gas is also oxidized during high-temperature combustion. Both of these processes lead to nitrogen oxides (NO_x) in the atmosphere, which are converted to nitric acid and then brought down to Earth as acid precipitation.

Denitrification. Denitrification is a microbial process that occurs in soils and sediments, where oxygen is unavailable for normal bacterial decomposition. A number of microbes can take nitrate (which is highly oxidized) and use it as a substitute for oxygen. In so doing, the nitrogen is reduced (it gains electrons) to nitrogen gas and released back into the atmosphere. Large amounts of organic matter are decomposed in this manner. Farmers seek to avoid denitrification because it reduces soil fertility. Accordingly, they plow as early as possible in the spring in order to restore oxygen to the soil. In sewage treatment systems, denitrification is a desirable process and is promoted to remove nitrogen from the wastewater before it is released in soluble form to the environment (Chapter 17).

Human Impacts. Human involvement in the nitrogen cycle is significant and a major cause for concern. Many agricultural crops are legumes (peas,

Figure 3–20 Nitrogen fixation. Bacteria in root nodules of legumes convert nitrogen gas in the atmosphere to forms that can be used by plants.

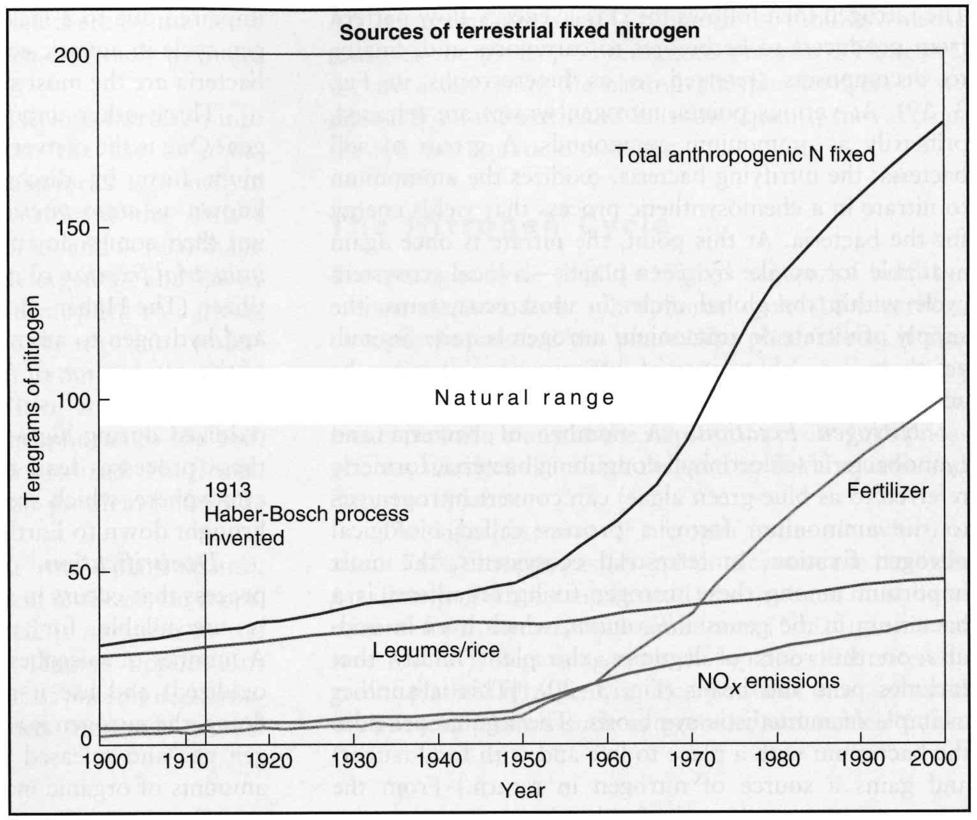


Figure 3–21 Terrestrial fixed nitrogen. Nitrogen fixed by human-promoted (anthropogenic) processes have surpassed the natural levels of nitrogen fixation, essentially fertilizing the global ecosystem.

beans, soybeans, alfalfa), so they draw nitrogen from the air, thus increasing the normal rate of nitrogen fixation on land. Crops that are nonleguminous (corn, wheat, potatoes, cotton, and so on) are heavily fertilized with nitrogen derived from industrial fixation. Also, fossil-fuel combustion fixes nitrogen from the air. All told, these processes add some 150 teragrams of nitrogen to terrestrial ecosystems annually (Fig. 3–21). This is approximately 1.5 times the natural rate of nitrogen fixation. In effect, we are more than doubling the rate at which nitrogen is moved from the atmosphere to the land.

The consequences of this global nitrogen fertilization are serious. Acid deposition has destroyed thousands of lakes and ponds and caused extensive damage to forests (Chapter 21). The surplus nitrogen has led to "nitrogen saturation" of many natural areas, whereby the nitrogen can no longer be incorporated into living matter and is released into the soil. There, it leaches cations (positively charged mineral ions) such as calcium and magnesium from the soil, which leads to mineral deficiencies in trees and other vegetation. Washed into surface waters, the nitrogen makes its way to estuaries and coastal oceans, where it promotes rich "blooms" of algae, some of which are toxic to fish and shellfish. When the algal blooms die, they sink to deeper water or sediments, where they reduce the oxygen supply and kill bottom-dwelling organisms like crabs, oysters, and clams, creating "dead zones." (See Chapter 17.) Of course, these are just the observable effects of nitrogen enrichment; there may be other effects that have not yet been well documented, such as a loss of biodiversity by encouraging luxuriant growth of a few dominant plant species.

Although we have focused on the cycles of carbon, phosphorus, and nitrogen, cycles exist for oxygen, hydrogen, and all the other elements that play a role in living things. Also, while the routes taken by distinct elements may differ, all of the cycles are going on simultaneously, and all come together in the tissues of living things. As the elements cycle through ecosystems, energy flows in from the Sun and through the living members of the ecosystems. The links between these two fundamental processes of ecosystem function are shown in Fig. 3–22.

3.4 Implications for Human Societies

Ecosystem Sustainability

Ecosystems have existed for thousands of years or more, maintaining natural populations of the biota and the processes that they carry out, processes that in turn sustain the ecosystems. In this chapter, we have focused on energy flow and nutrient cycling—how natural ecosystems work, *in theory*. In *reality*, however, it is the Earth's specific ecosystems that we depend on for goods and services (ecosystem capital). Is our use of natural and managed ecosystems a serious threat to their long-term sustainability? We will look briefly at how we are affecting energy flow and nutrient cycling, but a more detailed

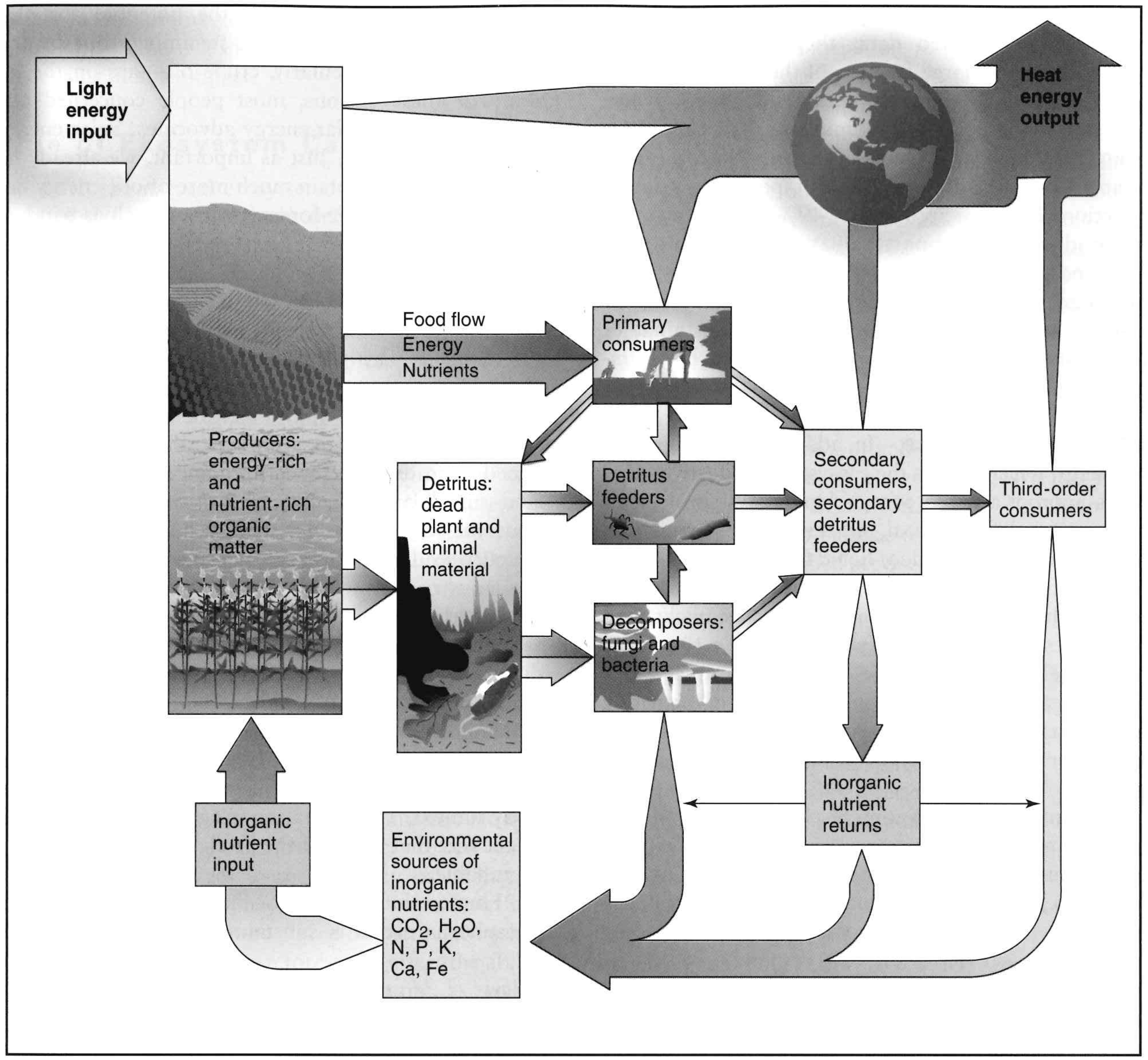


Figure 3–22 Nutrient recycling and energy flow through an ecosystem. Arranging organisms by feeding relationships and depicting the energy and nutrient inputs and outputs of each relationship shows a continuous recycling of nutrients (blue) in the ecosystem, a continuous flow of energy through it (red), and a decrease in biomass in it (thickness of arrows).

investigation of our use of specific types of ecosystems must wait until Chapter 11.

One of the reasons for studying natural ecosystems is that they are models of sustainability. As a result, we might benefit from understanding what it is that makes them sustainable and, where possible, how to emulate them. As Figure 3–22 shows, it is the Sun that energizes the processes of energy flow and nutrient cycling, and then the biological, geological, and chemical interactions within and between ecosystems are the drivers of change. One key to their sustainability, therefore, is that *ecosystems use sunlight as their source of energy.*

Significance of Energy Flow. Humans make heavy use of the energy that starts with sunlight and flows through natural and agricultural ecosystems. Agriculture, for example, provides most of our food. To accomplish this, we have converted almost 11% of Earth's land area from forest and grassland biomes to agricultural ecosystems. Grasslands provide animals for labor, meat, wool, leather, and milk. Forest biomes provide us with 3.3 billion cubic meters of wood annually for fuel, building material, and paper. Finally, some 15% of the world's energy consumption is derived directly from plant material.

Calculations of the total annual global net primary production of land ecosystems average out at 120 petagrams of dry matter, including agricultural as well as the more natural ecosystems. Two independent groups of researchers have calculated that humans currently appropriate 32% of this total production for agriculture, grazing, forestry, and human-occupied lands. Although these kinds of calculations require making a lot of estimates based on limited data, they do indicate that humans are using a large fraction of the whole, and that it is likely to grow. Further, because humans convert many natural and agricultural lands to urban and suburban housing, highways, dumps, factories, and the like, we cancel out an additional 8% of potential primary production. Thus, we appropriate 40% of the land's primary production to support human needs. In so doing, we have become the dominant biological force on Earth. As ecologist Stuart Pimm puts it, "Man eats Planet! Two-fifths already gone." Is this level of use sustainable? If so, and if our use increases, when do we reach the limits of sustainable use?

Another Energy Source. In addition to running on solar energy, which creates the ecosystem productivity that humans appropriate, the current human system depends heavily on fossil fuels—coal, natural gas, and crude oil. Crude oil is refined to produce liquid fuels such as gasoline, diesel fuel, fuel oil, and so on. Even in the production of food, which depends fundamentally on sunlight and photosynthesis, it is estimated that we use about 10 calories of fossil fuel for every calorie of food consumed. This additional energy is depleted in the course of preparing fields, fertilizing the plants, controlling pests, harvesting the food, and processing, preserving, transporting and, finally, cooking it.

The annual combustion of fossil fuels releases 6.6 petagrams of CO_2^- carbon, as well as some 35 teragrams of nitrogen and 50 teragrams of sulfur. The biosphere has a limited capacity to absorb these by-products, however, so air pollution problems result, including urban smog, acid rain, and the potential for global climate change. Also, problems stemming from the depletion of fuels—particularly, crude oil—are on the horizon. For these reasons, most people concerned about sustainability are solar-energy advocates. Solar energy is extremely abundant. Just as important, we already have the technology to obtain much more of our energy needs from sunlight and the forces it causes, such as wind. (See Chapter 14.)

Sustainability and Nutrient Cycling. *Ecosystems dispose of wastes and replenish nutrients by recycling the elements.* This maintains their sustainability, indefinitely. Human systems, by contrast, are based in large part on a *one-directional flow* of elements (Fig. 3–23). For example, the fertilizer–nutrient phosphate, which is mined from deposits, ends up going into waterways via land runoff and effluents from sewage treatment. The same one-way flow occurs with such metals as aluminum, mercury, lead, and cadmium, which are the "nutrients" of our industry. At one end, these resources are mined from the Earth; at the other, they end up in dumps and landfills as items containing them are discarded. As a result, there are depletion problems at the resource end and pollution problems at the other. The Earth has substantial (but not unlimited) deposits of most minerals; however, the capacity of ecosystems (even the whole biosphere) to absorb wastes without being disturbed is comparatively limited. This limitation is aggravated, furthermore, by the fact that many of the products we use are nonbiodegradable.

Human intrusion into the carbon, nitrogen, and phosphorus cycles is substantial and will undoubtedly intensify in the coming years. Is this level of impact sustainable? If so, and if it increases, when do we reach the limits of sustainable impact?

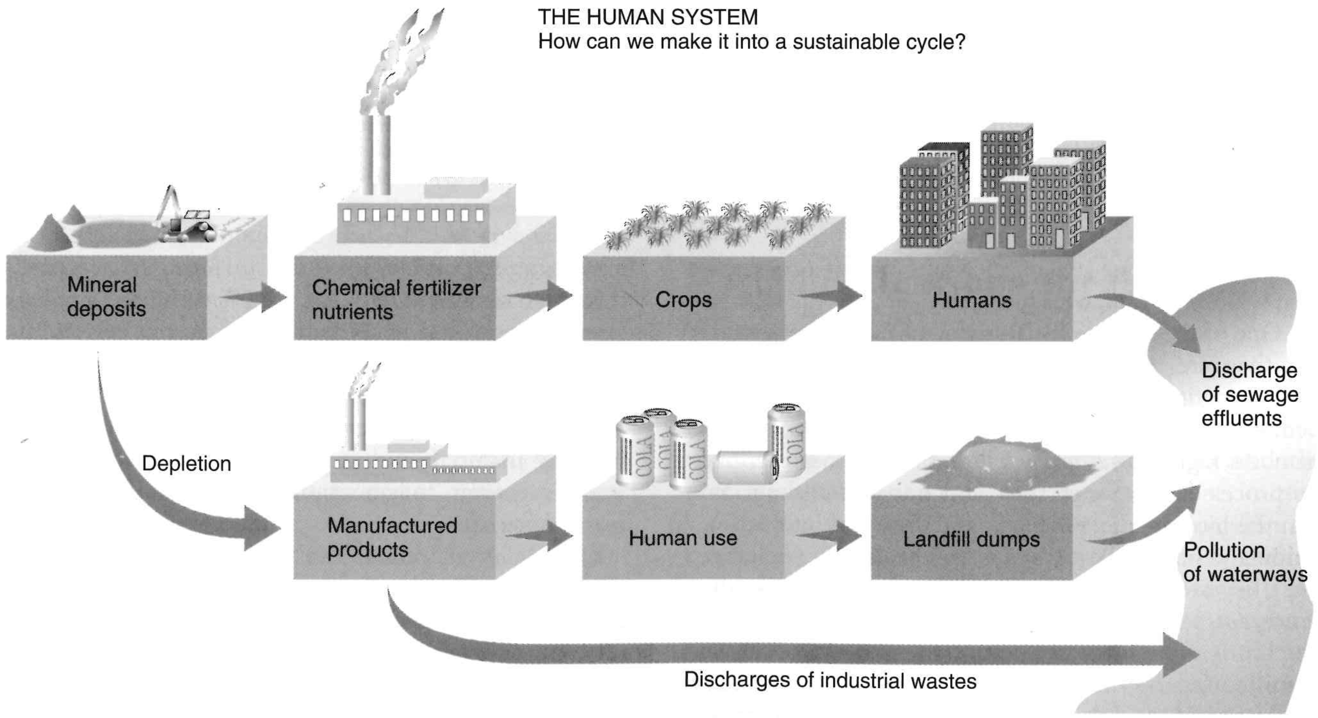


Figure 3–23 **One-directional nutrient flow in human society.**

Value of Ecosystem Capital

How much are natural ecosystems worth to us? Recall from Chapter 1 that we have defined the goods and services we derive from natural systems as *ecosystem capital.* In a first-ever attempt of its kind, a team of 13 natural scientists and economists[1] collaborated to produce a report entitled "The Value of the World's Ecosystem Services and Natural Capital." Their reason for making such an effort was that the goods and services provided by natural ecosystems are not easily seen in the market (meaning the market economy that normally allows us to place value on things) or may not be in the market at all. Thus, things such as clean air to breathe, the formation of soil, the breakdown of pollutants, and the like never pass through the market economy. People are often not even aware of their importance. Because of this, these things are undervalued or not valued at all.

The team identified 17 major ecosystem goods and services that provide vital functions we depend on. The team also identified the ecosystem functions that actually carry out the vital human support and gave examples of each (Table 3–2), making the point that it is useless to consider human welfare without these ecosystem services, so in one sense, their value as a whole is infinite. However, the **incremental value** of each type of service can be calculated. That is, changes in the quantity or quality of various types of services may influence human welfare, and an economic value can be placed on that relationship. For example, removing a given forest will affect the ability of the forest to provide lumber in the future, as well as perform other services, such as soil formation and promotion of the hydrologic cycle. The economic value of this effect can be calculated. So, by calculating incremental values, making many approximations, and collecting data from other researchers who have worked on individual processes, the research team tabulated the annual global value of ecosystem services performed. According to their calculations, the total value to human welfare of a year's services amounts to $38 trillion (in 2000 dollars), and that is considered a conservative estimate! This is significantly more than the $25 trillion calculated for the gross world product of the world economy.

The real power of the team's analysis lies in its use for making local decisions. Thus, the value of a wetlands cannot be represented solely by the amount of soybeans that could be grown on the land if it were drained. Instead, wetlands provide other vital ecosystem services, and these should be balanced against the value of the soybeans in calculating the costs and benefits of a proposed change in land use. The bottom line of their analysis is, in their words, "that ecosystem services provide an important portion of the total contribution to human welfare on this planet." For this reason, the ecosystem capital stock (the ecosystems and the populations in them, including the lakes and wetlands) must be given adequate weight in public-policy decisions involving changes to them. Because these services are outside the market and uncertain, they are too often ignored or undervalued, and the net result is human changes to natural systems whose social costs far outweigh their benefits. For example, coastal mangrove forests in Thailand are often converted to shrimp farms; an analysis showed that the economic value of the forests (for timber, charcoal, storm protection, and fisheries support) exceeded the value of the shrimp farms by 70%.

A New Look. In 2002, a new team looked at the 1997 team's calculation of value and examined the benefit–cost consequences of converting ecosystems to more direct human uses (e.g., a wetland to a soybean field).[2] In every case, the net balance of value was a loss. That is, services lost outweighed services gained. The team examined five different biomes and found consistent losses in ecosystem capital, running at −1.2% per year. Based on the calculated total ecosystem value of $38 trillion, this percentage represents an annual loss of $250 billion through habitat conversion alone. If so, the authors asked, why is conversion still happening? They suggested that the benefits of conversion were often exaggerated through various government subsidies, seriously distorting the market analysis. Thus, the market does not adequately measure many of the benefits from natural ecosystems, nor does it deal well with the fact that many major benefits are on regional or global scales, while the benefits of conversion are narrowly local. The authors argued strongly for a much greater global effort to conserve natural ecosystems. Beyond conservation, our tremendous dependence on natural systems should lead, logically, to proper management of those systems, a topic discussed in Chapter 4.

The Future

On a global scale, the future growth of the human population and rising consumption levels will severely challenge ecosystem sustainability. Over the next 50 years, for example, the world's population is expected to increase by at least 2.5 billion people. The needs and demands of this expanded human population will create unprecedented pressures on the ability of Earth's systems to provide goods and services. Estimates based on current trends indicate that impacts on the nitrogen and phosphorus cycles alone will raise the amounts of these nutrients being added to the land and water two to three times above current levels. Demands on agriculture will likely require at least 15% more agricultural land; irrigated land area is expected to double, greatly stressing an already strained hydrologic cycle. Such growing demands cannot be met without

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[1] Robert Costanza et al., "The Value of the World's Ecosystem Services and Natural Capital," *Nature* 387 (1997): 253–260.

[2] Andrew Balmford et al., "Economic Reasons for Conserving Wild Nature," *Science* 297 (August 9, 2002): 950–953.

table 3-2 **Ecosystem Services and Functions**

Ecosystem Service	Ecosystem Functions	Examples
Gas regulation	Regulation of atmospheric chemical composition	CO$_2$–O$_2$ balance, O$_3$ for UVB protection, and SO$_x$ levels
Climate regulation	Regulation of global temperature, precipitation, and other biologically mediated climatic processes at global or local levels	Greenhouse gas regulation, dimethylsulfoxide production affecting cloud formation
Disturbance regulation	Capacitance, damping, and integrity of ecosystem response to environmental fluctuations	Storm protection, flood control, drought recovery, and other aspects of habitat response to environmental variability controlled mainly by vegetation structure
Water regulation	Regulation of hydrological flows	Provisioning of water for agricultural (such as irrigation) or industrial (such as milling) processes or transportation
Water supply	Storage and retention of water	Provisioning of water by watersheds, reservoirs, and aquifers
Erosion control and sediment retention	Retention of soil within an ecosystem	Prevention of loss of soil by wind, runoff, or other removal processes; storage of silt in lakes and wetlands
Soil formation	Soil-formation processes	Weathering of rock and the accumulation of organic material
Nutrient cycling	Storage, internal cycling, processing, and acquisition of nutrients	Nitrogen fixation, N, P, and other elemental or nutrient cycles
Waste treatment	Recovery of mobile nutrients and removal or breakdown of excess nutrients and compounds	Waste treatment, pollution control, detoxification
Pollination	Movement of floral gametes	Provisioning of pollinators for the reproduction of plant populations
Biological control	Trophic-dynamic regulations of populations	Keystone predator to control prey species, reduction of herbivory by top predators
Refugia	Habitat for resident and transient populations	Nurseries, habitat for migratory species, regional habitats for locally harvested species, or overwintering grounds
Food production	That portion of primary production extractable as food	Production of fish, game, crops, nuts, and fruits by hunting, gathering, subsistence farming, or fishing
Raw materials	That portion of primary production extractable as raw materials	The production of lumber, fuel, or fodder
Genetic resources	Sources of unique biological materials and products	Medicine, products for materials science, genes for resistance to plant pathogens and crop pests, ornamental species (pets and horticultural varieties of plants)
Recreation	Provision of opportunities for recreational activities	Ecotourism, sport fishing, and other outdoor recreational activities
Cultural	Provision of opportunities for noncommercial uses	Aesthetic, artistic, educational, spiritual, or scientific values of ecosystems

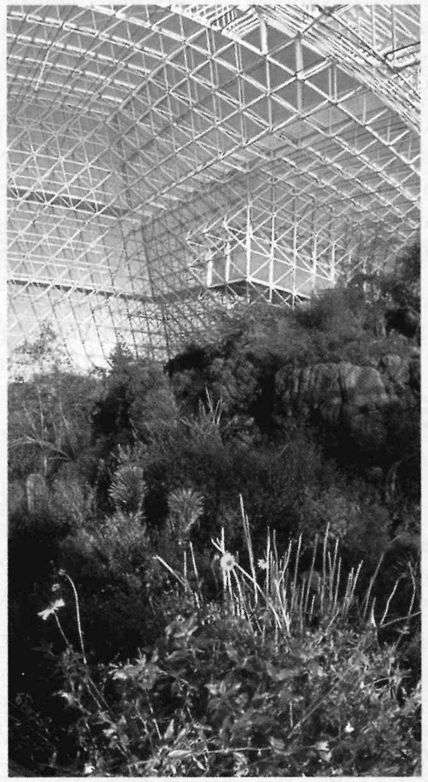
Source: Reprinted, by permission, from Robert Costanza, Ralph d'Arge, Rudolf de Groot, Stephen Farber, Monica Grasso, Bruce Hannon, Karin Limburg, Shahid Naeem, Robert V. O'Neill, Jose Paruelo, Robert G. Raskin, Paul Sutton, and Marjan van den Belt, "The Value of the World's Ecosystem Services and Natural Capital," *Nature* 387 (1997): 253–260.

earth watch

Biosphere 2

The proof of a theory lies in testing it. If the biosphere functions as we have described—running on solar energy and recycling all the elements from the environment through living organisms, and back to the environment—then we might be able to create an artificial biosphere that functions similarly.

The largest such experiment to date is Biosphere 2, constructed in Arizona, 30 miles north of Tucson. Biosphere 2 was developed entirely with private venture capital ($200 million), with a view toward gaining information and experience that might be used to create permanent space stations on the Moon or other planets or in long-distance space travel. In addition, it was hoped that Biosphere 2 would yield information that would further our understanding of our own biosphere—Biosphere 1.



As originally constructed, Biosphere 2 was a supersealed "greenhouse" enclosing an area of 2.5 acres (1 ha). Entry and exit were through a double air lock. Different environmental conditions within the containment supported several ecosystems. Accordingly, there were areas of tropical rain forest, savanna, desert, fresh- and saltwater marshes, and a miniocean complete with a coral reef, each stocked with representative species—over 4,000 in all. An agricultural area and living quarters for a crew of up to 10 "Biospherians" completed the arrangements.

All water, air, and nutrient recycling took place within the structure; wastes, including human and animal excrement, were treated and recycled to support the growth of plants. A crew of four men and four women began a two-year mission in September 1991. In addition to monitoring and collecting data on the natural systems, their main occupation was engaging in intensive organic agriculture to produce plant foods both for themselves and for feeding a few goats and chickens, which produced eggs, milk, and a little meat. The living quarters included the comforts and conveniences of modern living, but all communication with the outside world was via electronics. The crew's environment, including its plants and animals, was totally sealed from that of the outside world.

Not everything went perfectly; in fact, quite a few things went wrong. At one point, additional oxygen had to be introduced because oxygen was being absorbed by the huge concrete structure that supported the greenhouse. The amount of nitrous oxide rose to dangerous levels and had to be controlled in order to preserve the health of the inhabitants. Food production failed, so food had to be imported. Nearly all the birds and animals thought to be able to tolerate the enclosure died off, with the exception of cockroaches and ants.

At the end of their two-year experimental sojourn, the Biospherians emerged somewhat thinner, but all in good health. Grave doubts were cast on the scientific value of the experiment, however, because of the necessary interventions and the loss of so many species. Perhaps the greatest value of the experiment was to demonstrate that even $200 million could not reproduce a functioning, self-contained ecosystem capable of supporting just eight people.

Biosphere 2 received new life when Columbia University's Lamont–Doherty Earth Observatory agreed to take it over in 1996. The facility became an educational center for undergraduates and classroom teachers. It also became an important tourist site, entertaining 180,000 visitors annually. Its ecosystems, with the capability of controlling many environmental parameters, were used for major research projects. Next to Earth, it is the world's largest greenhouse—a suitable place to explore the greenhouse effect. In particular, researchers were investigating the effects of increased levels of atmospheric CO$_2$ on the coral reef ecosystem and on the tropical rain forest. Early results indicated that such increases will greatly affect these systems—negatively in the case of the coral reefs and only slightly positively in that of the rain forests. Unfortunately, Columbia University decided in September; 2003, to withdraw its support from Biosphere 2, leaving this huge facility to an uncertain future.

facing serious trade-offs between different goods and services. More agricultural land means more food, but less forest, and therefore less of the important services forests perform. More water for irrigation means more rivers will be diverted, so less water will be available for domestic use and for sustaining the riverine ecosystems. These dire projections are not necessarily predictions, and they don't have to be inevitable outcomes. By looking ahead, we may choose other alternatives if we clearly understand the consequences of simply continuing present practices.

The pressures on ecosystems illustrate why it is crucially important to understand how ecosystems work and how human societies interact with them (see Earth Watch, p. 81). Although these are broad-scale, even global, pressures, the decisions that will most directly determine ecosystem sustainability are local or regional. Figure 1–5, which shows the conceptual framework of the Millennium Ecosystem Assessment project, identifies a number of "drivers of change," both direct and indirect. People living within and adjacent to an ecosystem usually are those who benefit most directly from the ecosystem. For example, they may remove vegetation, harvest wood, add fertilizer, withdraw water, harvest game animals, and so on. Their local decisions will have both intended and unintended consequences. If they harvest firewood from a forest (intended), soil erosion may increase (unintended). If many local decision makers make similar decisions, the impacts may have cumulative regional and, eventually, global unintended and undesirable consequences. The private gain achieved by the local decision to exploit an ecosystem may have to be modified or overruled by governmental decision makers who are more concerned with maintaining the ecosystem as a public good. Thus, responsible public policy is needed to address how ecosystems will be exploited and managed.

In Chapter 4, we discuss how ecosystems are balanced and how they change over time. As we do so, we will examine the consequences of such ecosystem behavior for management purposes and will also encounter additional examples of ecosystem properties that maintain sustainability.

revisiting the themes

Sustainability

Ecosystems have existed for millennia because they are sustainable. Although ecosystems are highly diverse, they share two fundamental characteristics that are crucial to their sustainability. The first is their energy source: They depend on a nondepletable, nonpolluting source—the Sun. The other is the efficient recycling of nutrients and other chemicals through the activities of the organisms and numerous geological and chemical processes. As a result, wastes do not accumulate in ecosystems, and essential elements for plant primary production are continuously resupplied.

The human system makes heavy use of ecosystems, and to that extent, we also depend on solar energy and nutrient recycling. Because of this dependency, our use of ecosystem productivity and our intrusion into the nutrient cycles must both come under the scrutiny of sustainability. When do we reach the limits of sustainable use? When does our impact on nutrient cycles become unsustainable? These are hard questions to answer, particularly because the most direct impacts on ecosystems occur at the local level, yet it is the cumulative impacts of many local decisions that lead to global changes.

Sound Science

Virtually all of the information presented in this chapter was acquired through the application of sound scientific principles by countless scientists over many years. The basics of matter and energy and of ecosystem functioning have been well established for many years. Sound science is the basis of recent attempts to evaluate the human impact on ecosystem processes, too. A good example is the work of the teams trying to calculate the overall economic worth of ecosystem capital.

Stewardship

The Serengeti ecosystem is vulnerable because it exists in a setting of an expanding human population and increasing conversion to mechanized agriculture. So far, the countries involved are protecting the core of the ecosystem, although pressures are threatening the land on the margins. Sustaining this irreplaceable ecosystem will be a strong challenge to the stewardship of the governments and the people of Kenya and Tanzania.

Ecosystem Capital

This chapter, which describes the basics of how ecosystems work, is all about ecosystem capital. The goods and services ecosystems provide are essentially priceless, but the human system is so economically driven that it is helpful to estimate their economic value. When this is done, the calculated value exceeds the value of the entire gross world product, on an annual basis. Moreover, when natural ecosystems are converted to more managed systems like agriculture, studies indicate that this inevitably ends up as a net financial loss.

Policy and Politics

If public-policy decisions were made on the basis of the true value of the goods and services provided by ecosystems, then efforts to conserve natural ecosystems would be intensified. This is seldom the case, however; local decisions heavily favor exploitation and the conversion of ecosystems, often because unwise subsidies encourage these processes, as well