SECTION 7

ECOLOGY

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The Dynamics of Communities and Ecosystems

CHAPTER OUTLINE

E**cology** is often defined as the study of the interactions of organisms with each other and with their physical environment, but it is more simply defined as the study of ecological systems, or **ecosystems.** An ecosystem is all of the organisms that occur together at a particular place, as well as the environment with which they interact. The goals of ecology include seeking to understand the interactions among organisms and the interactions of organisms with all the nonliving components of their environment.

The great challenge in studying ecosystems is their complexity. Everything discussed in previous chapters of the textbook—cell physiology, genetics, growth, morphology, the diversity of plants—is important to how ecosystems function. When we look at the whole system, however, we need to think about many things that are of no immediate concern to a physiologist, who may, for example, be working on the details of enzyme function. Ecologists are expected to be able to answer questions such as: Why are grasslands common in some places, and forests in others? Why are there so many more species of plants and animals in the wet tropics than in the polar regions? A knowledge of enzyme chemistry may be necessary for the full explanation, but we will also have to think about climate, soils, geologic history, animals as both

predators and pollinators, interactions with microbial species, evolutionary biology, and much else besides.

It is the goal of ecology to provide an explanation of how ecosystems got to the state they are in, and to predict how they will change in the future. For both aspects, special attention is given to the human component. How have humans affected local and global ecosystems, and what will the future be like, given different assumptions about what we do and do not do in the coming years? Making accurate predictions has been extremely difficult in the past because the complexity of ecosystems makes it easy to overlook subtle interactions.

As in other areas of science, it is helpful in ecology to study components of the ecosystem rather than tackle the complexity of the entire system. One such analytical view is hierarchical. The living portion of an ecosystem is seen to consist of a set of populations, a **population** being a group of all individuals belonging to the same taxonomic unit, usually a species, within the area of interest. The set of all populations makes a **community.** Community can also be qualified to indicate subsets of the whole so that some studies may focus on the bird community, others the plant community, and so on.

We noted above that ecologists seek to understand why living systems are as they are. Putting this question in an open-ended way requires that ecologists join forces with evolutionists. As has been emphasized throughout the book, evolutionary processes shape organisms and therefore also determine the ways in which they interact. Evolution is therefore inextricably intertwined with ecology in what G. E. Hutchinson of Yale University aptly called "the ecological theater and the evolutionary play." In previous chapters of the book, we have considered the fundamental points of evolutionary theory and the major categories of evidence,

◀ *With its long, slender bill, the ruby-throated hummingbird* (Archilochus colubris) *extracts nectar from the elongated spurs of the wild columbine* (Aquilegia canadensis) *flower. As the hummingbird sips the nectar, which is abundant and rich in sugars sufficient to support the bird's high energy requirements, pollen from the yellow anthers may be dusted onto the bird's bill and head. As the hummingbird flies from flower to flower, some of this pollen adheres to the stigma and develops to fertilize the ovules. In obtaining its food, the hummingbird ensures genetic recombination for the columbine.*

CHECKPOINTS

By the time you finish reading this chapter, you should be able to answer the following questions:

1. What does the science of ecology encompass, and what is the difference between a population, a community, and an ecosystem?

2. What is a food chain, what types of organisms are found in each link of the chain, and how does energy flow through it?

3. What do ecologists mean by the term "competition," and how do plants compete with one another?

4. What is mutualism?

as well as the mechanisms by which the plot of the evolutionary play moves forward. Here and in the online Chapter 32, we shall place ourselves in the ecological theater to observe the actors—that is, all living things—in the variety of interactions with each other and the physical environment that together constitute the play.

Ecosystem Energetics—Trophic Levels

We have said that an ecosystem consists of a collection of interacting organisms. But what do we mean by "interact"? There are many aspects to interaction, but the most basic focuses on energy. As we have seen, living organisms require a constant supply of usable energy, and the same is true of ecosystems. They will function only if energy continuously flows through them. We say that energy flows, because ultimately all of the energy that is incorporated into the living organisms of the ecosystem will be dissipated as unusable heat, as dictated by the second law of thermodynamics (pages 90–92).

The process that is the engine of the ecosystem—the starting place for the energy flow—is the capturing of usable energy from the nonliving environment. Only some organisms are capable of doing this, and we have earlier introduced the term for such organisms—**autotrophs,** or "self-feeders." We also distinguished two types of autotrophs, *chemosynthesizers* and *photosynthesizers.* Chemosynthesizers, which are all microbial, are a fascinating group, both in the contemporary biosphere and in the evolution of life on Earth. Today, their importance is most apparent in extreme habitats, the most spectacular of which are the hydrothermal vent communities in the deep ocean, where the complete darkness makes photosynthesis impossible but where an abundance of reduced inorganic molecules offers the opportunity for extracting energy through their oxidation. Overall, however, chemosynthesizers make only a small contribution to the total energy extracted from nonliving sources.

The predominant autotrophs of aquatic and terrestrial systems are the photosynthesizers, which include bacteria, green algae, and the familiar vascular and nonvascular green plants that cover most land surfaces other than the very coldest, hottest, or driest. Autotrophs use the captured energy to produce organic materials that serve as a source of energy for the other major group—the **heterotrophs**—organisms that feed on others, either by consuming parts of, or entire, living organisms or waste products and organic detritus. Like autotrophs, heterotrophs are found in all sizes and in an astonishing array of functional types from heterotrophic bacteria and algae to mushrooms, scorpions, whales, and human beings.

These energy relationships provide a way of understanding how each organism contributes to the functioning of the whole. A basic sketch of ecosystem function focuses on the concept of **trophic level.** The first trophic level encompasses the autotrophs, also called **primary producers.** In a forest ecosystem, for example, the primary producers are trees, but also cyanobacteria, algae, mosses, ferns, grasses, and shrubs. The next trophic level, the **pr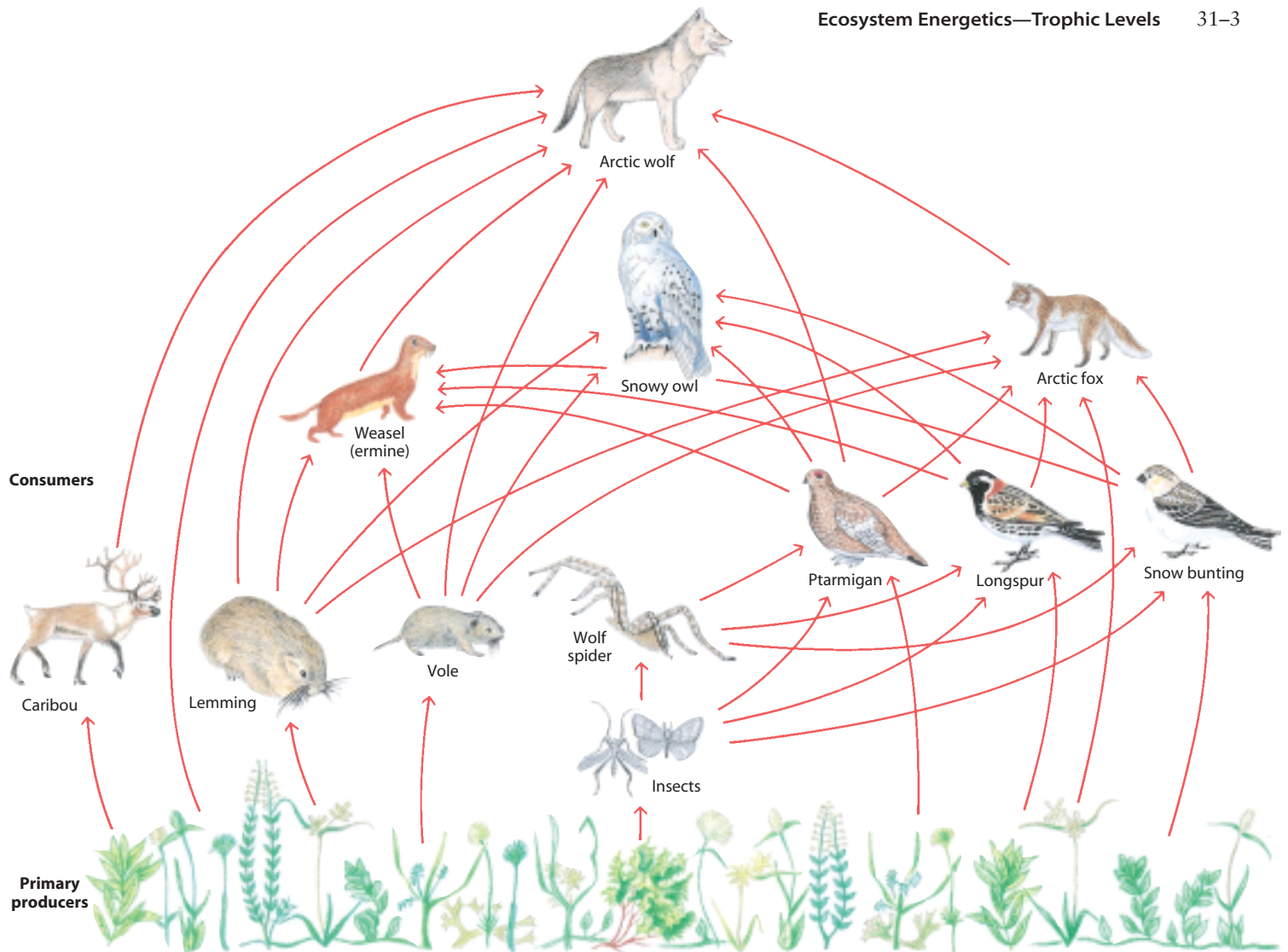imary consumers,** consists of heterotrophs that feed directly on the primary producers. These primary consumers are also, by definition, **herbivores,** or eaters of plants. The next trophic level, **secondary consumers,** includes heterotrophs that feed on the primary consumers. Thus, in a forest, a bark beetle is a primary consumer, and a woodpecker that eats the beetles is a secondary consumer. The number of trophic levels along the **food chain,** which consists of the primary producers and various levels of consumers, depends on the ecosystem. Under most circumstances, an organism has more than one source of food and is itself preyed on by more than one kind of organism; therefore, it is more nearly correct to speak of a **food web** (Figure 31–1).

In all but very unusual and limited ecosystems, however, there are at least four to six levels. That food chains do not extend to 50 or 100 levels is explainable on thermodynamic grounds. First, no more energy can flow through the system than is fixed by the primary producers. Second, at each transfer—from sunlight to plant, plant to herbivore, and so on—some energy is inevitably lost, which is the basic message of the second law of thermodynamics. Less energy is therefore available to each successive trophic level.

The loss at the primary production stage is substantial. Generally, less than 1 percent of the light that falls on a plant is utilized in photosynthesis (page 89). In some cases, vegetation that is particularly productive, as well as some aquatic systems, may convert up to 3 percent of the annual incident solar radiation into chemical energy. Beyond this, about one-tenth of the energy incorporated in one trophic level can be assimilated into the next. The annual growth of herbivores, therefore, is roughly one-tenth of the annual productivity of the plants, and the carnivores feeding on the herbivores grow about one-tenth as much as the herbivores. With such sharp declines in available energy at each step, it is clear that after only a few links in a food chain, little energy remains. So, for example, we could imagine a "super-raptor" bird that ate only eagles and large hawks, but there is no such bird, and the primary reason is that its prey would be so sparse and dispersed that the bird would require an immense range to sustain itself.

So far, we have followed the food chain from the primary producers to higher levels of consumers—from plant to top carnivore. There are two other important trophic categories in the ecosystem. The most important of these includes the **decomposers**—fungi, bacteria, and various small animals that feed on the waste products and dead bodies and body parts of other organisms. Decomposers are critical to ecosystem function, because without them the biosphere would be buried beneath organic debris. Elements and molecules that living organisms require in amounts far greater than can easily be obtained from the nonliving environment—most notably, nitrogen and phosphorus in usable forms—would be in very short supply. The recycling function of decomposers is essential.

A second special case is that of the **parasite,** defined as an organism that lives in or on an organism and derives its energy and nutrients from it. The association benefits the parasite and harms the host. Parasites are all heterotrophs and

Consumers

Arctic wolf

Snowy owl

Weasel (ermine)

Arctic fox

Ptarmigan

Longspur

Snow bunting

Wolf spider

Caribou

Lemming

Vole

Insects

Primary producers

31–1 Food web *Diagram of a food web in the Arctic tundra during the spring and summer. The arrows point in the direction of energy flow. This food web is simplified considerably. In reality, many more species of both plants and animals are involved. The fungi, bacteria, and small animals that function as decomposers (not shown here) also play an important role in food webs.*

include viruses, pathogenic bacteria and fungi, and a vast array of mostly invertebrate animals, such as insects and roundworms. Parasites are always one trophic level above their hosts. So, although there is no "super-raptor" that feeds exclusively on eagles and large hawks, there are parasites that feed on large raptors. And, wouldn't parasites have parasites? (To quote a poet, "Little fleas have smaller fleas upon their backs to bite 'em.") The answer is yes, and this example reveals the limitations of an oversimplified trophic scheme. We will provide a more general view in a later section.

The simple view of an ecosystem that lumps organisms into a few trophic levels is useful for doing summary book-keeping regarding energy. For example, Lamont Cole, in his classic studies of Lake Cayuga, near the Cornell University campus in New York State, calculated that, for every 1000 kilocalories of light energy utilized by algae in the lake, about 150 kilocalories are reconstituted as small aquatic animals. Of these 150 kilocalories, 30 kilocalories are reconstituted as smelt, which is a small fish. If we were

to eat these smelt, we would gain about 6 kilocalories from the original 1000 kilocalories used by the algae. But if trout eat the smelt and we then eat the trout, we gain only about 1.2 kilocalories from the original 1000 kilocalories. Smelt are much more abundant and constitute a much larger **bio-mass** (the total organic matter) in Lake Cayuga than do the trout. Thus, more of the original energy is available to us if we eat smelt rather than the trout that feed on smelt. Yet trout are considered a delicacy, and smelt a much less desirable food for humans. This simple example has profound implications for the future of our species. A human population that obtains most of its calories from meat cannot be as large as one that is primarily vegetarian.

In General, Ecosystems Can Be Described by Pyramids of Energy, Biomass, and Numbers

The basic organizing force imposed by the dissipation of energy as it flows to higher trophic levels is reflected in the

Pesticides and Ecosystems

As we have explained, chemical warfare wasn't invented by humans. Many organisms use chemicals in self-defense or to disadvantage competitors. But humans have taken chemical means of controlling the populations of other species to an extreme. Approximately half a billion metric tons of pesticides and herbicides are produced annually for application to crops in the United States alone. Of this enormous total, it has been estimated that only approximately 1 percent actually reaches the target organisms. Most of the remainder falls indiscriminately on nontarget organisms and drifts into neighboring ecosystems, where it may have significant detrimental effects. This residue may result in the elimination of certain species, for example, and the loss of those species may affect the functioning of the ecosystem as a whole or lead indirectly to the elimination of other species. The abundance of important decomposers, such as earthworms and other soil organisms, may be greatly reduced by pesticides and herbicides, so that the ecosystem as a whole ceases to function normally. The intensity of such effects depends on the toxicity of the chemicals and on their persistence in the environment.

One of the problems associated with some chemical pollutants is that they tend to be concentrated as they pass up through food chains, reaching their highest concentrations in the top predators *(a)*. For example, chlorinated hydrocarbons, such as DDT (now outlawed in the United States for use but not for manufacture and export, unfortunately, and not outlawed in many other industrialized countries), become concentrated in the tissues of predatory birds and cause the shells of their eggs to be abnormally thin. The shell of such an egg is likely to break before the chick is ready to hatch, causing its death *(b)*.

Another problem is predictable from natural selection. Repeated use of an insecticide, for example, eliminates the genetically susceptible individuals and increases the fitness, relatively, of the more resistant genotypes. Of the estimated 2000 species of major insect pests, about a quarter have already evolved strains that are resistant to one or more insecticides. Similarly, a number of species of weeds have evolved resistance to herbicides.

Other effects are less direct. For example, an insecticide toxic to a broad predator species

that naturally controls populations of pest species may be eliminated by pesticide poisoning, leading to outbreaks of the very pest organisms that the chemicals were employed to control in the first place. As with most human activities, the net effect of the application of pesticides and herbicides is to lessen the diversity of the ecosystem affected. Yet productive modern agriculture depends, to a large extent, on the application of these useful substances.

Because the effects of pesticides and herbicides are often so drastic, however, scientists are actively searching for less damaging methods of improving agricultural yields. These include selective breeding to produce crops that are resistant to pests, increased research to develop pesticides and herbicides that are less toxic and less persistent than those currently used, and integrated pest-management systems, involving combinations of control measures, including the encouragement of predators and diseases of pest species as well as the judicious application of pesticides.
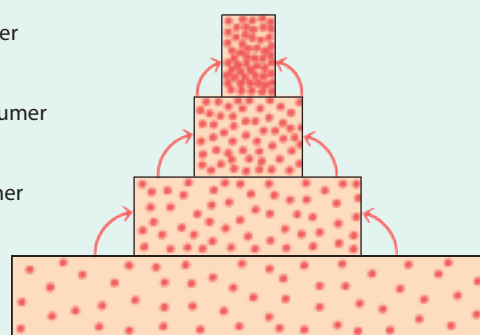

DDT:
In tertiary consumer (top carnivore)

In secondary consumer (carnivore)

In primary consumer (herbivore)

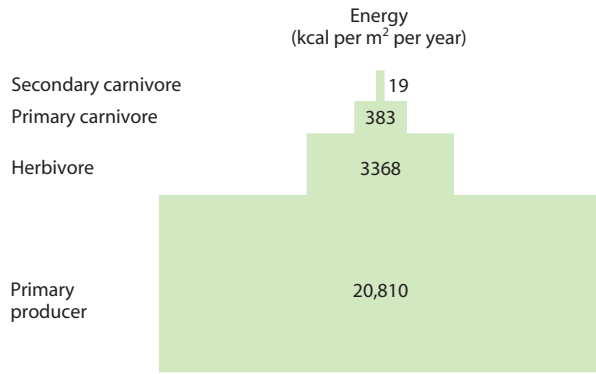In primary producers (plants and algae)

(a)

(b)

(a) Concentration of DDT residues being passed along a simple food chain. The concentration of DDT increases as the material passes up the chain, and high concentrations occur in the carnivores. *(b)* This dead peregrine falcon embryo, its development almost completed, was found with two broken, infertile eggs in a nest in southwestern Scotland in May of 1971. It is not known if the developing falcon died as a direct consequence of the high levels of DDT residue in its body or as a result of the collapse of its shell. Birds at the top of food chains, such as the peregrine falcon, the osprey, and the bald eagle, were the principal victims. With the banning of DDT in many countries, dramatic recoveries have been observed in populations of all three species.

"pyramid of energy" (Figure 31–2). Because the energy books must balance, in a system that is operating in a more or less consistent manner (so-called steady state) with inputs of energy balancing losses over the course of a year, the energy input to each successive trophic level will be less than the energy input to the level below it. Organisms at each trophic level cannot have more energy available to them than the level below, except for short periods of time. In fact, studies have shown that transfers of energy up the food chain involve substantial losses at each level.
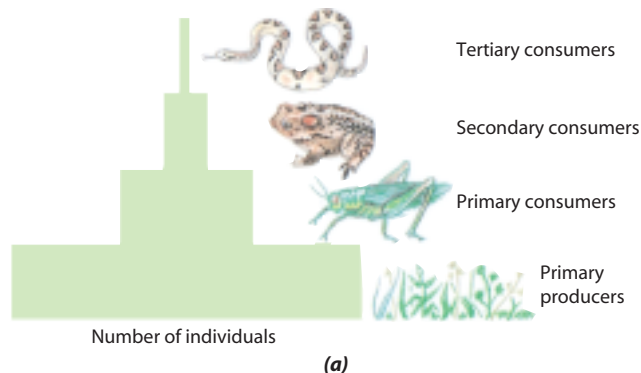
As we have noted, approximately one-tenth of the energy incorporated in one trophic level is incorporated into the next. The pyramid of energy is usually matched by a pyramid of biomass, the mass (usually expressed as dry weight) of living
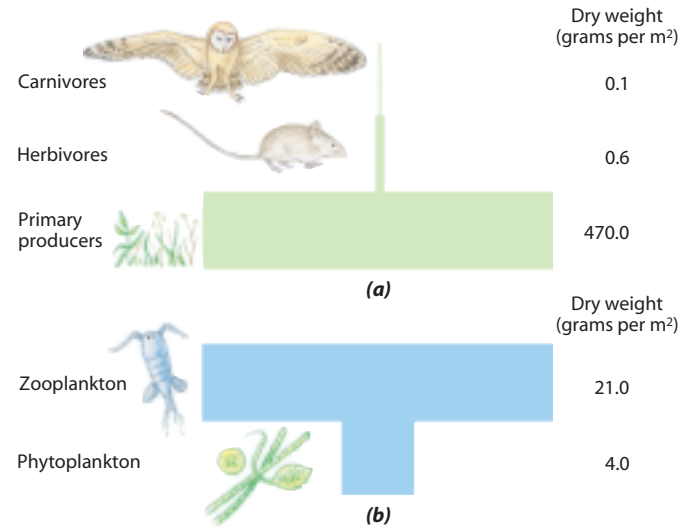
Energy
(kcal per m² per year)

Secondary carnivore	19
Primary carnivore	383
Herbivore	3368
Primary producer	20,810

31–2 Pyramid of energy flow *In this river ecosystem in Florida, a relatively small proportion of the energy in the system is transferred at each trophic level. Much of the energy is used metabolically and is measured as heat (in kilocalories) lost in respiration.*

Dry weight
(grams per m²)

Carnivores	0.1
Herbivores	0.6
Primary producers	470.0

(a)

Dry weight
(grams per m²)

| Zooplankton | 21.0 |
| Phytoplankton | 4.0 |

(b)

31–3 Pyramids of biomass *The pyramids shown here for **(a)** the plants and animals in a field in Georgia and **(b)** plankton in the English Channel reflect the biomass present at any one time. The seemingly paradoxical relationship between the biomass of phytoplankton and zooplankton exists because the high reproduction rate of the smaller phytoplankton population is sufficient to support a large zooplankton population.*

organisms. This biomass is very unequally divided among trophic levels. The usual pattern is for primary producers to have ten times (or more) the biomass of the herbivores, and so on up the chain (Figure 31–3a). But biomass does not have the absolute constraints of energy. It is possible for a system at steady state to have greater standing biomass in a higher trophic level if the rate of growth of the lower trophic level, and therefore the energy available per unit time, is sufficient to sustain this higher biomass. This situation is all but impossible for most terrestrial systems, but is often observed in aquatic systems in which algae multiply rapidly enough to sustain a greater biomass of herbivores (Figure 31–3b).

Ecologists sometimes also speak of "pyramids of numbers." If all organisms were of the same size and required the same amount of energy per unit time per unit biomass, then pyramids of numbers would resemble pyramids of biomass and energy. In fact, however, organism sizes and energy requirements per unit biomass are very different, with the result that pyramids of numbers can have a variety of shapes (Figure 31–4). It should also be clear that introducing microbial organisms into the pyramid of numbers would produce patterns even more divergent from the usual energy pyramid.
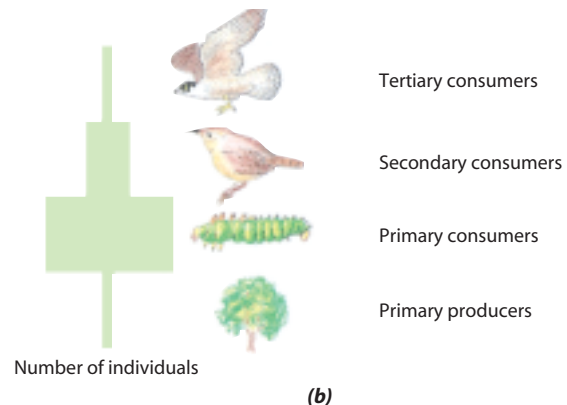
Even this rudimentary view of ecosystem energetics provides a useful perspective on practical aspects of energy use in the human-dominated ecosystem. We have noted that all of the organic materials produced are potentially the food of decomposers. In some systems, such as the tropical rainforests, the organic debris and dead organisms disappear rapidly and almost completely, but a small amount of organic material that is resistant to decay accumulates in the soil. In other ecosystems, however, decomposers are inhibited, primarily by the oxygen limitation that occurs when substrates are saturated or under water. In these cases, the input of organic matter can exceed the capacity of decay organisms to break it down, and thick layers of dead and discarded parts of primary producers can accumulate. These layers can remain relatively little changed (forming peat, for example), or they can undergo transformations when buried deep

Tertiary consumers

Secondary consumers

Primary consumers

Primary producers

Number of individuals

(a)

Tertiary consumers

Secondary consumers

Primary consumers

Primary producers

Number of individuals

(b)

31–4 Pyramids of numbers (a) *In a grassland ecosystem, the number of primary producers (grass plants) is large, and **(b)** for a* temperate forest, a single primary producer, a tree, can support a large number of herbivores.

under sediments to form organic-rich geologic formations of lignite, coal, oil, and gas. High levels of carbon dioxide in the atmosphere are also thought to have contributed to the rapid accumulation of organic layers in past epochs.

Since the middle of the nineteenth century, humans have been heavily exploiting these residues of past primary productivity as sources of energy. The most readily accessible of these are now depleted, and, although new discoveries will be made, it is agreed that they will be fewer or more costly to exploit, or both. The question then arises: Can we have a sustainable source of energy by using renewable sources of energy from plants, a process known as *biological energy conversion?* Before the nineteenth century, dead plants, such as wood and brush, and dried herbivore feces, such as "buffalo chips," were the only significant external energy source for humans. Today, they remain of critical importance in developing countries, where more than 2 billion people rely on biomass for virtually all their cooking, heating, and lighting.

Researchers are currently exploring ways of incorporating biomass utilization into industrialized economies. Planting fast-growing trees on marginal agricultural lands may constitute one of the most environmentally benign ways of efficiently capturing solar energy. Harvesting and transportation costs are a limiting factor, suggesting that power plants would need to be situated close to the production areas. But, as with natural ecosystems, human ecosystems cannot violate the laws of thermodynamics. By whatever means we obtain our energy, its rate of consumption cannot exceed the rate at which we capture it from such sources as fossil fuels, current biomass accumulation, and nuclear energy. And the environmental costs of each energy alternative must be carefully considered.

Food Webs Provide a More Nearly Complete Accounting of Trophic Relationships

The simple producer-herbivore-carnivore type of lumped description of trophic structure can provide only a summary description of an ecosystem. To understand ecosystem dynamics more fully, it is necessary to analyze the energy relations in more detail. If we consider each species population in an ecosystem, it can be seen that energy flow is much more complicated. A first complication is that many species fall into more than one trophic level. Our own species illustrates this—most humans are omnivorous, eating meat, animal products (milk, eggs), plants, and decomposers (for example, mushrooms). But the same is true of countless other species. Nor are the trophic relations of species constant over their lifespan. Many fish, for example, begin life feeding on zooplankton but end as large top carnivores eating other fish that may also be carnivores on still other fish. A second complication is that many species are specialized and able to utilize only one or a few species as sources of food, while others utilize many species, switching among them as their prey vary in abundance.

Such complexity can be diagrammed by representing species as nodes and indicating the trophic connections among species by connecting the nodes. For even a species-poor ecosystem a few hectares in size, such a complete diagram would contain hundreds of nodes and a mass of interconnecting lines. This is why the relatively simple ecosystems of the high Arctic, with fewer species than most areas, have been studied in an attempt to establish ecosystem energy flows in a reasonably complete manner (Figure 31–1).

The characteristics of the food web determine important aspects of ecosystem dynamics. Ecologists have devoted considerable time to theoretical studies that explore the consequences of different food-web qualities. One early hypothesis was that an ecosystem with more connections between species should be more stable than another ecosystem with the same number of species but fewer connections. The logic behind this deduction was simple. If there are multiple pathways for energy to flow through a system, the failure of one pathway—say, one species is nearly exterminated by a pathogen—can be compensated for by another pathway. This intuitively simple idea has been difficult to verify for real systems. A related question concerns how many of each kind of species a system "needs" to function. We have pointed out that, of course, there must be at least one primary producer species, but most ecosystems have many. Is this just chance, or is there some ecological and evolutionary process that leads inevitably to such redundancies? It is possible that the redundancy is only apparent, and that the various species of primary producers each fill subtly different roles.

Nutrient and Material Cycling

Ecosystems are energy-processing systems, but in order to capture and utilize energy, organisms must accumulate the right kinds of molecules and ions. In contrast to energy, which must flow into a system continuously, or nearly so, the material part of ecosystems is recycled. Nearly all the nitrogen atoms in our bodies have been used countless times before (a few new nitrogen atoms no doubt seep upward from deep within the Earth each year) and, we hope, will be used many times more. The scale of recycling and the transitions in the recycling process depend on the chemistry of the particular element or molecule.

The pathways of some of these essential elements, known as nutrient cycles, are discussed in Chapter 29 of the book. Elements with a significant gaseous phase, especially water, carbon, and nitrogen (Figure 29–8), have regional and global cycles. Elements that move mainly in solution or in particles may have more local cycles, such as phosphorus (Figure 29–14). For ecosystems to capture and process energy, and for the growth of the constituent organisms to approach optimum, the necessary elements and molecules must be available in sufficient amounts and in the right proportions. This is not usually the case, most obviously for water. Large parts of the land surface have drought-limited primary productivity and therefore limited energy flow, as in the Atacama Desert of coastal Peru and northern Chile, for example. Less obvious is the fact that carbon dioxide supplies are commonly below the levels that would allow maxi-

mum rates of photosynthesis, although human activities, by increasing global carbon dioxide supplies, are lessening this constraint, with unknown consequences.

Nitrogen, needed in large amounts by living organisms because of its central role in the chemistry of life, is often deficient, as has been shown repeatedly by experiments in which the addition of nitrogen to the soil causes a sharp increase in plant growth. It follows that plants must often compete for nitrogen. In some cases, this competition has become so intense that organisms benefit from a mutualistic interaction, such as the formation of nitrogen-fixing bacterial nodules, in which one partner assumes the responsibility of providing nutrients for the other (Figure 29–11).

Classic Experiments on Nutrient Recycling Were Performed at Hubbard Brook

In the last half of the twentieth century, ecologists devoted much attention to understanding nutrient and other material cycles in ecosystems and in the biosphere. Studies of a deciduous forest ecosystem in the Hubbard Brook Experimental Forest of the White Mountain National Forest of New Hampshire were landmarks in this effort. The purpose of the studies was to gain a quantitative understanding of nutrient storage and movement through ecosystems. Mass balance was used as the basic model, meaning that the inputs and outputs of the system as a whole and between compartments within the system must balance.

The investigators established a procedure for determining the mineral budget—measuring input and output, or "gain" and "loss"—of different areas in the forest. By analyzing the nutrient content of rain and snow, they were able to estimate atmospheric input, and by constructing concrete weirs that channeled the water flowing out of selected areas, they were able to calculate output (Figure 31–5). A particular advantage of this site was that an essentially impermeable granite bedrock, resistant to chemical weathering, is present just below the soil surface. This meant that nutrient-enriched water moving through the soil was trapped above the rock and could be intercepted as it flowed out of the catchment in stream water. In addition, few nutrients are added by dissolution of the highly resistant bedrock.

The study showed quantitatively what ecologists have always suspected, which is that forest ecosystems are extremely efficient in conserving their mineral elements. For example, annual net loss of calcium from the ecosystem was 9.2 kilograms per hectare. This represents only about 0.3 percent of the calcium in the system. Nitrogen, which can enter the system by fixation, and as nitrates, nitrites, and ammonium (Figure 29–8), was actually accumulating at a rate of about 2 kilograms per hectare per year. There was a similar, though somewhat smaller, net gain of potassium in the system.

Experiments at the ecosystem level are difficult, and one of the boldest ever attempted was undertaken at Hubbard Brook in an effort to clarify how elements are cycled through living organisms. In the winter of 1965–1966, all trees, saplings, and shrubs in one 15.6-hectare area in one small

31–5 Hubbard Brook weir *Water from each of six experimental ecosystems in the Hubbard Brook Experimental Forest in New Hampshire was channeled through weirs, built where the water leaves the watershed. The water was then analyzed for chemical elements. The trees and shrubs in the watershed behind the weir shown here have been cut down. The experiments showed that deforestation disrupted the tight cycling of nutrients by various living components of the ecosystem and greatly increased the loss of nutrient elements from that system.*

watershed of the forest were cut down. No organic materials were removed, however, and the soil was undisturbed. During the following spring, the area was sprayed with a herbicide to inhibit regrowth. With the primary producers largely shut down, the result was a massive loss of nutrients. During the four months from June through September 1966, the runoff of water was four times greater than in previous years. Net losses of calcium and potassium were both about 20 times higher than in the undisturbed forest.

The most severe disturbance was seen in the nitrogen cycle. The microbial decomposers continued to function, leading to the release of ammonia and ammonium ions, and in turn, nitrites and nitrates. Without plants to absorb them, these highly soluble ions were readily leached, and the net loss of nitrogen averaged 120 kilograms per hectare per year from 1966 to 1968. The nitrate concentration in the stream that drained the area increased to levels above those established by the U.S. Public Health Service as safe for drinking water, and an algal bloom developed.

Interactions between Organisms —Beyond Trophic Relationships

Understanding interactions is central to ecology. This is encapsulated in the often-repeated statement that the basic message of ecology is that everything is connected. No organism—whether in a patch of woodland, a pasture, a pond, a coral reef, or an urban gated community—exists in isolation. To this point, we have emphasized overall ecosystem function, that is, organisms as producers and consumers. But mass and energy balance provide only the background. The connections between organisms are much more complex than this. To grasp this complexity we need to delve deeper into the major categories of interaction. We shall organize our discussion around three major kinds of interactions between organisms: competition, mutualism, and predation for the special cases of plant-herbivore (and plant-pathogen) interactions.

Competition Results When Organisms Require the Same Limited Resource

Competition is of fundamental importance, primarily because it is seen as the force that drives natural selection. It is defined as an interaction in which two or more organisms are utilizing a *required* resource available in *limited* supply. "Required" means that without the resource the organism will eventually succumb, and "limited" means that there is a fixed supply. Consequently, not all of the competing organisms can have as much of the resource as would be optimal for their growth and reproduction. The experimental proof of competition is that an organism will perform better (grow faster, produce more offspring) when its competitors are removed, and that the improved performance can be shown to be due to its having obtained more resources. Many ecologists make a distinction between competition directly involving resources and *interference competition,* such as the interference competition of birds for territories. Although the reason for this interaction may ultimately be related to the need for each pair of birds to have adequate food for their nestlings, the negative interaction will take place even in circumstances where food is so abundant that it is not limiting.

Growth Rate Is an Important Factor Affecting Competition among Plants

The fact that green plants cannot move from place to place and that they are dependent on absorbing light sets the stage for their competitive interactions. In all cases, where other necessary resources (water and nutrients) are in good supply and the environment is relatively benign, light is a limiting factor. This is because plants are able to produce leaves that intercept very nearly all the direct light. In theory, if plants cooperated, they could absorb all the light there was to absorb by producing a carpet-like covering over the surface of the ground. With proper construction of this carpet—for example, providing a way to avoid light saturation during the middle of the day—there would be no need to raise the photosynthetic surface high above the ground, as is "wastefully" done in forests. But the reason why carpet plants are limited to special extreme situations, such as alpine tundra, rocky outcrops, deserts after rains, and putting greens, is easily explained by competition. Any plant that raises its canopy above that of its neighbors can intercept light, putting its competitors in shade and therefore at a severe disadvantage.

Competition in terrestrial plants in habitats generally favorable for plant growth (moist to wet tropics and temperate zones) is therefore largely a "struggle for light." The conspicuous winners in the evolutionary struggle are the tall woody plants—primarily trees. In these plants, physiological functions, such as photosynthetic rate and water-use strategies, are combined successfully with a growth form that allocates energy appropriately to the production of leaves, roots, and stems. This assures them a good chance of finding their "place in the sun" when opportunity presents itself.

Some plants were led down other evolutionary pathways, developing sets of traits that allowed them to utilize the lower light levels of the forest understory or to exploit brief windows of light availability. The best-known examples of the latter approach are the spring ephemerals, which are species of plants found in the temperate deciduous forests. Spring ephemerals develop early in the spring and accumulate much or all of their energy during the brief time that the light levels on the forest floor are high. These plants go dormant some time after expansion of the new tree leaves puts the ephemerals back in the shade. Such specialization also exists among trees. Some trees require high levels of light and can survive from seedling or sprout to become a tree only when other trees are absent or sparse, as after a fire. Other trees have seedlings that can survive during conditions of reduced light, until an opportunity in the form of increased light and perhaps other resources allows it to accelerate its growth and move into the canopy.

We have described the situation for portions of the Earth where water and nutrients are in good supply and where fires and other disturbances are not too frequent. Even in these environments, there is also some degree of competition for resources other than light. But as environments become drier or more nutrient deficient, light becomes less important. This is very apparent in deserts, where trees are absent—except where water is locally abundant, as in palm oases—and the perennial plants are widely spaced (see Figure 32–13). Ecologists have established that in such situations it is belowground competition for water that is important. Because of the limited water supply, there is more light than can be exploited.

A plant's growth rate relative to potential competitors is affected by differences in height, leaf arrangement, crown shape, and energy allocation to roots versus leaves. Different combinations of these traits are likely to maximize growth in various environments. No single combination can produce the best competitor in all environments, and consequently vegetation in areas with different climates is dominated by plants with different growth forms. Within a given area—indeed, within a single community, such as a temperate forest or prairie—differences in growth form, photosyn-

thetic physiology, and energy allocation may permit species to coexist by granting each a competitive advantage in different microenvironments.

The ways in which individual plants are able to enhance their overall growth and thus compete for light, water, and mineral nutrients largely determine their success in different habitats. An understanding of such factors is therefore the key to increasing agricultural yield in extreme environments, such as those that are relatively poor in nutrients or water or are heavily shaded. Knowledge of these factors will also provide the information necessary to predict the performance of individual plant species and communities. This is especially important in a world that is rapidly changing due to global warming, which is resulting from increased levels of carbon dioxide and other atmospheric gases produced largely by human activities (pages 136–137).

The Principle of Competitive Exclusion Provides a Baseline for Studying Competition

Ecologists have found that it is challenging to measure competition in nature. Consequently, much of our knowledge of competition depends on experiments, usually in very simplified settings. From observation of the growth of organisms in simple environments, it has been deduced that two species with similar environmental requirements cannot coexist indefinitely in the same habitat. This is a simplified version of the **principle of competitive exclusion,** which holds that one or the other species must eventually be eliminated. This principle has been demonstrated experimentally. A classic study was conducted with two species of duckweed, *Lemna polyrhiza* and *Lemna gibba.* When grown in individual pure cultures, *L. gibba* always grew more slowly than *L. polyrhiza,* yet when the two species were grown together *L. polyrhiza* was always replaced by *L. gibba.* The plant bodies of *L. gibba* have air-filled sacs that enable them to form a floating mass over the other species, cutting off the light. As a consequence, in mixed cultures the shaded *L. polyrhiza* died out (Figure 31–6).

Competition Favors Specialization

If the world were completely uniform, the principle of competitive exclusion would suggest that ecological and evolutionary forces would result in the emergence of one or a very few winners. But, of course, the world is not uniform, and we find different species dominating in different areas. This can be reconciled with the competitive exlusion principle by invoking specialization. As some of our preceding examples suggest, a set of traits that makes a species dominant in one place will not necessarily work well in another. We do not find sugar maple trees in the desert, because they would die from lack of water. Alternatively, saguaro cacti cannot survive in the forest, because their photosynthesis would be severely inhibited in the shade, and in moist environments, they would be susceptible to attack by decay organisms.

Specialization can also involve more subtle factors that allow species to coexist within a habitat in a kind of balance. For example, Engelmann spruce *(Picea engelmannii)* and subalpine fir *(Abies lasiocarpa)* coexist in roughly equal abundance and form the dominant tree community in the subalpine zone of the central and northern Rocky Mountains. The greater longevity and size of the spruce are balanced by the faster growth in height of firs and more flexible requirements for establishing fir seedlings. Spruce seedlings are found primarily in forest gaps or associated with a canopy of firs, whereas fir seedlings are found more commonly in the forest. Fir seedlings outcompete spruce in shaded understories by the simple fact that they survive. Spruce seedlings, however, outcompete fir in sunnier sites because of their higher growth rates and lower sensitivity to drought. Constant disturbance from storms, flooding, and avalanches, among other factors, and the relatively short life span of fir prevent it from taking over the entire landscape. Patterns of this sort are frequent in different plant communities, but they are often not so obvious. The different requirements of the species involved mitigate the competition and allow them to coexist indefinitely.
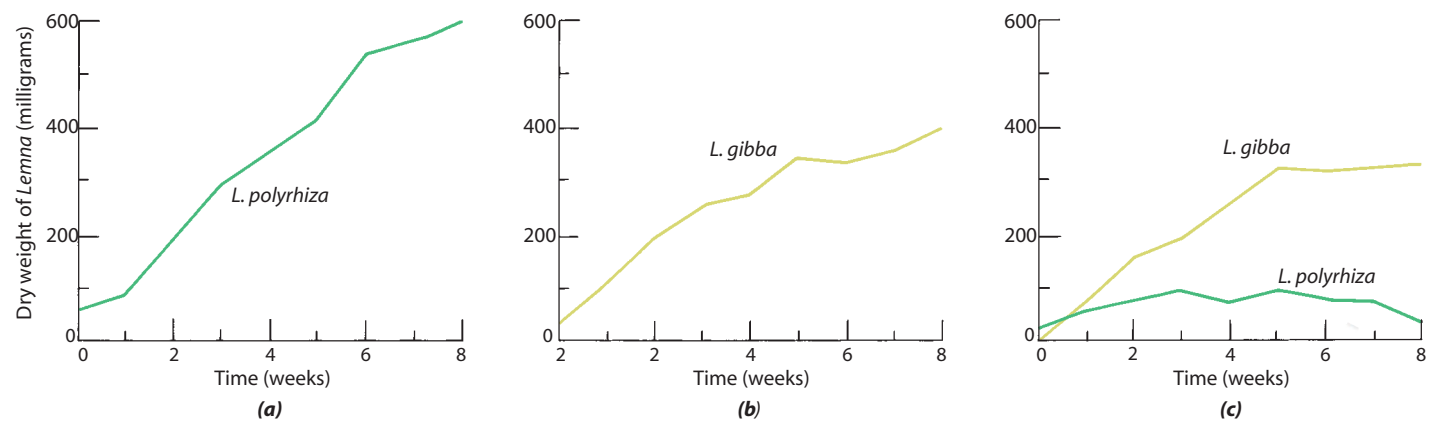
31–6 Competitive exclusion An experiment with two species of floating duckweed, which are tiny angiosperms found in ponds and lakes. One species, Lemna polyrhiza *(a),* grows more rapidly in pure culture than the other species, Lemna gibba *(b).* But L. gibba *has tiny* air-filled sacs that enable it to float on the surface. When the two species are grown together, L. gibba *shades* L. polyrhiza *and is the victor in the competition for light* *(c).*

One repeating pattern is that exclusion among competitors is relaxed when some factor limits growth. Herbivory can be such a factor. In the chalk grasslands of England, the grasses were historically kept closely cropped by rabbits, allowing many other kinds of shorter grasses and herbs to flourish. The situation changed drastically early in the twentieth century, however, when a severe epidemic of the viral disease myxomatosis drastically reduced the population of rabbits. After this decline, the grass cover of the chalk soils became deeper and more dense, and many of the formerly abundant species of flowering plants became rare. Nutrient deficiency and propensity for drought can have a similar effect. The greatest diversity of species in prairies of the midwestern United States tends to be found on sandy soils or on thin-soiled prairies on limestone hills. The assumption is that, on these more stressful sites, the most aggressive species (in this case, C_4 grasses) are kept in check by limited resources.

But biodiversity in some places seems greater than specialization can explain and competitive exclusion should allow. Species-rich tropical forests and the dense shrublands, or *fynbos,* of South Africa have posed a problem for oversimplified views of competition. Put simply, there seem to be many more species than should be necessary to fill all the essential ecological roles. Attempts to explain the coexistence of species on the basis of balancing specializations, as in the previous fir-spruce example, have had limited success. Current work suggests that the explanation may lie in recognizing that competitive exclusion describes only a tendency, and that it may be possible for evolutionary processes to generate new species faster than competitive forces can exclude the less fit. For one thing, fitness differences may be slight, and the more similar the fitness of two competing species, the longer it will take for the exclusion to occur. If, in addition, random or cyclical variation is imposed, competition can be prevented from acting uniformly and consistently. As a result, many species may be able to coexist despite substantial overlap in their patterns of resource use.

Some Organisms Produce Chemicals That Inhibit the Growth of Others
Plants mostly compete by appropriating resources directly, but there are other modes of negative interaction. In some instances, one (or both) of the competing organisms produces chemical substances that inhibit the growth of members of its own or other species. Interaction that seems to be a kind of chemical warfare is most clearly present in microbial interactions. For example, the fungus *Penicillium chrysogenum,* which grows on organic substrates such as seeds, produces significant quantities of penicillin in nature. Penicillin inhibits the growth of gram-positive bacteria, which might otherwise compete directly with the fungus for the same nutrients. However, bacteria that produce penicillinases (enzymes that break down penicillin), such as *Bacillus cereus,* often replace the *Penicillium.*

Analogous relationships among plants are grouped under the general heading of **allelopathy.** An example familiar to gardeners in the eastern part of the United States is that of black walnut *(Juglans nigra).* Many other plants cannot grow beneath, or in some cases even near, black walnut trees. Tomatoes *(Solanum lycopersicum)* and alfalfa *(Medicago sativa)* wilt when grown near black walnut trees, and their seedlings die if their roots contact walnut roots. Also white pine *(Pinus strobus)* and black locust *(Robinia pseudoacacia)* often die when near black walnut trees. This is especially true in poorly drained soils, where the toxic substances leached from the walnuts apparently accumulate.

Allelopathic effects are being applied in agriculture. For example, a strip planted with sorghum will have two to four times fewer weeds the following year than other strips. The sorghum plants evidently leave behind allelopathic compounds in the soil that depress the growth of weeds.

Mutualism Is an Interaction in Which Both Species Benefit
Mutualism is a biological interaction in which the growth, survival, and/or reproduction of both interacting species are enhanced. In many examples of mutualism, neither partner can survive without the other, particularly when competition from other plants and predation are taken into account. We discussed several examples of mutualism in earlier chapters of the book—lichens (Chapter 14), legumes and the nitrogen-fixing bacteria that live in nodules on their roots (Chapter 29), and the close relationships between plants and their pollinators and seed dispersers (Chapter 20). Here we provide two additional examples. One, a ubiquitous example involving many species of higher plants and fungi, is functionally very important (mycorrhizae); the other is a specific association involving an insect and a plant (ants and acacias). Both cases appear to have developed as the result of coevolution—species mutually evolving to exploit the benefits of cooperation.

Mycorrhizae Are Associations between Roots and Fungi
As discussed in Chapter 14, the roots of most vascular plants are associated with fungi, forming compound structures known as mycorrhizae (pages 291–294). The mycorrhizal fungi are not simply fungi that happen to be near plant roots. They are clearly specialized to grow closely on the roots or actually into the tissues without causing the damage that would be expected if they were pathogens. In this mutualistic relationship, it is easy to see the benefit to the heterotrophic fungi—they gain access to the proteins, sugars, and other organic products of the primary producers. But the advantage to the plants was not so obvious and had to be revealed through experimentation. It has been shown that fungi greatly enhance the ability of the plant's roots to absorb phosphorus and other essential nutrients. In some cases they also increase water uptake. The plant is utilizing the superior ability of the fungus to extract these resources. Without the fungi, the most strongly mycorrhizal plants grow only poorly or not at all. Other plants are "facultatively" mycorrhizal, meaning that they can grow without mycorrhizae in some circumstances.

The ubiquity of mycorrhizae means that most vascular plants are dual organisms in the same sense that lichens (pages 286–291) are dual organisms, although the relation-

ship is not obvious aboveground. As University of Wisconsin soil scientist S. A. Wilde stated, "A tree removed from the soil is only a part of the whole plant, a part surgically separated from its . . . absorptive and digestive organ."

The fungi that form mycorrhizal associations in most plants are zygomycetes. As discussed in Chapter 14, the associations are called *endomycorrhizae,* and they are characteristic of a majority of species of herbs, shrubs, and trees. In some groups of conifers and eudicots—mainly trees—the associations are mostly with basidiomycetes but also with certain ascomycetes; such associations are called *ectomycorrhizae.* Some of these associations are highly specific, with one species of fungus forming ectomycorrhizal associations with only a particular species, or a group of related species, of vascular plants. For example, the pore fungus *Boletus elegans* is known to associate only with larch *(Larix),* a conifer. Other fungi, such as *Cenococcum geophilum,* have been discovered living in ectomycorrhizal association with forest trees of more than a dozen genera. Ectomycorrhizae are particularly characteristic of relatively pure stands of trees growing at high latitudes in the Northern Hemisphere or at high elevations, two places where slow decomposition rates may make soil nutrients particularly difficult to obtain.

Acacia Trees and Ants Interact in a Mutually Beneficial Way Many striking examples of mutualism occur in the species-rich tropics. One of them involves species of *Acacia,* a large genus of leguminous trees and shrubs that is widely distributed in tropical and subtropical regions. Certain species of *Acacia* in the lowlands of Mexico and Central America possess conspicuous traits that were puzzling when first encountered, but are now understood as being a remarkable mutualism. Like many acacias, these have

"thorns" (technically stipular spines), but thorns that are excessively enlarged, up to 2 centimeters long at the base. Grasping a branch of one of these acacias quickly reveals a related peculiarity—the thorns are generally inhabited by ants, which will swarm out of the small holes they create in the thorns to attack anything, animal or vegetable, that disturbs their host plant. Nectaries (sugar-secreting structures) also occur on the petioles, and small protein-rich structures are located at the tip of each leaflet (Figure 31–7). These structures are called Beltian bodies after Thomas Belt, who described them in his book *The Naturalist in Nicaragua,* published in 1874. It seemed that the ants were protecting the plant, and the plant was providing food and shelter, but there were doubters.

This question was definitively answered in 1964 by Daniel Janzen. Janzen found that the worker ants *(Pseudomyrmex),* which swarm over the surface of the plant *(Acacia cornigera),* bite and sting animals of all sizes that contact the plant, thus protecting it from the activities of herbivores and ensuring a home for themselves. Moreover, whenever the branches of another plant touch an inhabited acacia tree, the ants girdle the other plant's bark, destroying the invading branches and producing a tunnel to the light through the dense surrounding tropical vegetation.

When Janzen removed the ants from a plant by poisoning them or clipping off the portions of the plant that contained ants, the plant grew very slowly and usually died within a few months as a result of insect damage and shading by other plants. On the other hand, plants inhabited by ants grew very rapidly, soon reaching 6 meters or more in height and overtopping the other second-growth vegetation.

Ants of the genus *Pseudomyrmex* make their nests only in these particular acacias and are completely dependent on

(a)

(b)

31–7 Ants and acacias (a) *A worker ant* (Pseudomyrmex ferruginea) *drinking from a nectary of a bull's-horn acacia* (Acacia cornigera). *At the right is an entrance hole into a thorn cut out by the queen ant. After hollowing out the thorn, the queen raises her brood within it.* **(b)** *Worker ants collecting Beltian bodies from the tips of* acacia leaflets. Rich in protein and oils, the Beltian bodies are an important food source for both adult and larval ants. The ants kill other insects that attempt to feed on the acacia and girdle plants that come into contact with it.

the acacias' nectaries and Beltian bodies for food. Thus the ant-acacia system is as much a dual biological entity as is a lichen. One element usually cannot survive without the other in the community in which it occurs, and it seems certain that both organisms have evolved toward this mutualistic relationship.

Plant-Herbivore and Plant-Pathogen Interactions Involve a Variety of Defense Mechanisms

In Chapter 20 of the text, we considered one important area of plant-herbivore interactions involving flowering plants— the relationships between flowers and their visitors, and between fruits and their dispersers. These specialized interactions arose during the course of evolution from the more general relationships between plants and the animals that consume them. Relationships between plants and pathogenic organisms, especially fungi and bacteria, are similar in their effects.

Knowledge of plant-herbivore interactions may have important applications in determining the structure of natural communities. For example, vast areas of Australia were at one time covered with spiny clumps of prickly-pear cactus *(Opuntia),* a plant that was introduced from Latin America. Fertile lands became useless for grazing, and the economy of great stretches of the interior was severely threatened. Today, the cactus has been nearly eliminated by a cactus moth *(Cactoblastis cactorum)* discovered in South America and deliberately introduced into Australia to control the cactus. The larvae of this moth destroy the cactus plants by eating them.

The moth, once abundant in Australia, can scarcely be found today, even by a careful inspection of the few remaining cactus clumps; yet there is no doubt that it continues to exert a controlling influence over the populations of this plant (Figure 31–8).

Plants Produce Toxic Chemicals in Response to Herbivores

The effects of herbivores on plants are profound, both in the short term and in the long term. Herbivores control the reproductive potential of plants by destroying their photosynthetic surfaces, their food-storage organs, or their reproductive structures. As discussed in Chapter 20, these interactions have led, over the course of time, to the evolution by plants of a wide variety of chemical defenses—in the form of molecules commonly referred to as secondary metabolites. The ability of plants to produce toxic chemicals and to retain them in their tissues gives the plants a tremendous competitive advantage. Indeed, these chemicals are apparently the most important factors in controlling herbivorous insects in nature. This advantage is analogous to the advantage achieved by the production of thorns or tough, leathery leaves, which obviously protect plants from grazing. Scientists working to improve the resistance of crops to herbivores are focusing much of their effort on these chemicals.

In the sea, many seaweeds have evolved comparable defenses. These marine algae are consumed by many different kinds of herbivores, including fishes, sea urchins, mollusks, and other animals. In fact, nearly all of the biomass is ultimately consumed in some habitats. To escape these herbivores, some seaweeds grow in cracks and holes or in other

(a)

(b)

31–8 *Plant-herbivore interaction* (a) *Dense prickly-pear cactus* (Opuntia inermis) *growing on a pasture in Queensland, Australia, in November 1926.* **(b)** *The same pasture in October 1929, after the cacti were destroyed by the deliberately introduced South American moth* Cactoblastis cactorum. *First introduced in May 1925, the larvae of this moth destroyed the cacti on more than 120 million hectares of rangeland.*

habitats that the herbivores do not visit. Palatable seaweeds may gain protection by growing intermixed with chemically protected ones. Many seaweeds produce chemical defenses that render them distasteful to herbivores, whereas others (for instance, coralline red algae) may be too tough to consume. In other words, the array of defenses employed by seaweeds against herbivores is virtually as extensive as that which occurs among flowering plants on land.

Plant-Herbivore and Plant-Pathogen Interactions May Be Quite Complex

Pea plants *(Pisum sativum)* are largely protected from parasitic fungi by a substance called pisatin, which the plants produce. Many strains of the important parasitic fungus *Fusarium,* however, have enzymes called monooxygenases, which convert pisatin into a less toxic compound. These fungi then have the ability to attack peas. Humans also utilize monooxygenases to detoxify certain chemicals that would otherwise be harmful to the body. In such ways, "chemical warfare" between plants and their herbivores is continuously being waged.

The protective chemicals that plants produce are often not only distasteful but may display still other features that deter herbivores. Chromenes, for example, can interfere with insect juvenile hormone (essential to an insect's life cycle) and thus can act as true insecticides. A Mexican sneezeweed *(Helenium* sp.*)* produces helanalin, which functions as a powerful insect repellent. Pyrethrum is another natural insecticide, which is produced commercially from a species of *Chrysanthemum.* Even the waxy surfaces of leaves, which are difficult to digest, may be important in retarding attacks by insects and fungi (Figure 2–10).

Phytoalexins Are Molecules Produced in Response to Invasion by Microorganisms

When infected with fungi or bacteria, plants often defend themselves by producing natural antibiotics called **phytoalexins** (page 27). These are lipidlike compounds whose synthesis can also be stimulated by leaf damage. They appear to be produced in response to the presence of specific carbohydrate molecules, called **elicitors,** that are present in fungal and bacterial cell walls. The elicitors, which are released from the fungal or bacterial cell walls by enzymes present in the plants being attacked, diffuse through the plant cells somewhat like hormones. Ultimately the elicitors bind to specific receptors on the plasma membranes of the plant cells, bringing about metabolic changes that result in the production of the phytoalexins.

In principle, it should be possible to spray elicitors onto crops before the crops become infected and thereby protect them from fungal and bacterial pests. Such a process would be analogous to vaccination in humans and domestic animals. One possible problem, however, is that the energy cost to the plant of producing large quantities of phytoalexins might lower the plant's ultimate yield more than would the fungal or bacterial infection. A natural advantage of the phytoalexins as defensive substances is that the plant does not need to expend the energy necessary to produce them unless it is actually attacked. Nevertheless, understanding phytoalexin production in plants is of considerable impor-

tance for crop protection, and several synthetic elicitors have already been produced and tested. Manipulating the genetic basis of resistance, now possible through the methods of genetic engineering (described in Chapters 1 and 10), also offers new possibilities for enhancing crop resistance that do not carry a high energy cost.

Tannins Provide a Static Chemical Defense

Just as some plants produce phytoalexins, others produce tannins and other phenolic compounds (pages 30 to 33), and these compounds seem to play a similar role in nature. Tannins are generally static defenses, always present in the plant parts where they occur. In some instances, however, they may be marshaled by the plant when it is attacked. For example, when gypsy moths *(Lymantria dispar)* attack and defoliate oak trees *(Quercus* spp.*),* the trees produce new leaves that are much higher in tannins and other phenolic compounds than normal. The new leaves produced under such conditions are also tougher, and they contain less water than those they replace. Indeed, the differences are great enough that larvae feeding on the new leaves experience reduced growth, and further outbreaks of gypsy moths are diminished in intensity. The tannins apparently interfere with digestion in the insects by combining with plant proteins, making them indigestible. Similar effects may be common in other plants as well. For example, when snowshoe hares heavily browse some trees and shrubs, such as paper birch *(Betula papyrifera),* these plants produce new shoots that are much richer in distasteful resins and phenolic compounds than the earlier shoots.

The secondary metabolites ingested by herbivores may, in turn, play a role in the animals' ecological relationships with other animals. For example, some insects, such as the monarch butterfly, store these poisons within their tissues and are thereby protected from their predators (Figure 2–25). In addition, some sex attractants in insects are derived from the plants on which they feed.

Viewed as a whole, the relationships within a community are incredibly complex. Organisms that coexist within a community often have evolved together. Within the community, they affect one another in an endless variety of ways, a few of which are just beginning to be understood.

Development of Communities and Ecosystems

Succession Is the Change in a Community over Time

Living systems are dynamic—their continuing requirement for energy ensures that. Changes in the environment that affect the capacity of an ecosystem to accumulate and utilize energy will inevitably cause some degree of change in the system. Hypothetically, the closest approach to stability that can be expected is that a constant supply of sunlight (or other source of fixable energy) will flow without disrupting events. In this case, a **steady state** could be approximated, with energy input equaling energy output and all ecosystem components at stable population levels. Some ecosystems can approach this, but usually over only short

(a)

(b)

(c)

(d)

31–9 *Succession* (a) *Emerging vegetation grows along the edge of a pond.* **(b)** *Aquatic plants with floating leaves, such as water lily* (Nymphaea odorata), *grow across the surface of a pond and eventually choke out bottom-dwelling plants.* **(c)** *Water hyacinths* (Eichhornia crassipes) *play a similar role in warmer climates.* **(d)** *Marsh grasses, sedges, and cattails* (Typha *spp.*) *growing on an old pond bed continue the process of succession.*

periods of time, and only when the condition of the system is averaged over quite large areas. The truth of these assertions will be evident to anyone who has tried to maintain an urban lawn in a steady state of green perfection. The most diligent regimen of care will not prevent the system from moving away from the desired steady state in ways that require intervention.

   One of the primary tasks of ecologists is to understand how systems change and to explain why some systems seem to evolve toward an approximate steady state, while others change in unexpected ways or undergo cycles of destruction and rebuilding. One of the major insights of the intellectual founders of ecology was that ecosystems often exhibited considerable resilience; they could be severely disturbed and yet return to something like their original condition over a period of time. This predictable process of recovery after disturbance came to be called **succession.** The destructive activ-

ities of humans provided many opportunities to observe succession in progress. Changes in agricultural economies led to the abandonment of fields, and if these were in or adjacent to natural vegetation, the former fields were observed to revert back to their preagricultural condition, such as forest. In forested regions, the sequence was from weedy field, to open grass or forb (nongrass) areas, to shrubby grasslands with tree seedlings, to forests of fast-growing trees, and ultimately to forests of longer-lived trees capable of being established in more closed conditions.

   Early ecologists, most notably F. E. Clements, seized upon the process of succession as the primary element in ecological theory. According to this view, each part of the Earth had vegetation that developed in response to the climate of that region, and each had a characteristic steady-state system that was the end point of succession. This end point he called a "climax community." Clements was empha-

sizing that a climax community, as the final stage of succession, was stable and self-maintaining unless subjected to very intense disturbance. Although human activities provided most of the clear examples, it was also recognized that succession would occur naturally. All communities experience disruptions of one kind or another from purely natural sources—fire, flood, windstorms, volcanoes, extreme drought, unseasonal frost, ice storms, and unusual outbreaks of pathogens and herbivores, among others.

Clements' scheme, even as amplified to cover situations that did not seem to exemplify the model of disturbance leading to succession leading to climax, ultimately failed because the underlying model was too simple to encompass all the ways in which ecosystems change. Today, ecologists tend to view ecosystems as continually changing, with rates and directions subject to many influences. In place of the organismlike concept that succession "heals" an injured climax community, ecologists speak of the more general properties of *resilience* (the ability to return to the original state after disruption) and *stability* (the degree to which a system will resist disturbances). The confidence of ecologists in the capacity of nature to heal has also been shaken, and many now believe that ecosystems can undergo catastrophic change if pushed too far. Ecosystems will still heal, but the new system may not be much like the old system. This is healing in the sense that a flat tire on your bicycle heals by collapsing between the rim and the asphalt.

One source of ecosystem change arises from the physical processes of landscape evolution. This is very apparent in areas of the world engulfed by ice in the last glacial epoch, which geologically speaking ended only yesterday. Continental glaciers override the pre-existing drainage networks and create many undrained or poorly drained depressions. The inexorable action of gravity ensures that many of these depressions will gradually fill with sediment and organic debris. Sometimes this will happen rapidly, sometimes slowly, and sometimes it will be forestalled because of limited sediment input or capture of the depression into a river system. Where it occurs, it is a kind of slow succession, with the original lake first developing marsh along its edges, then the marsh gradually closing in, and ending perhaps with forest cover over an area that 10,000 years earlier was a postglacial lake (Figure 31–9). In glaciated regions, one can see lakes, marshes, and swamps that exemplify the stages of the process, and paleoecologists have confirmed this by obtaining cores from swamps and marshes that were formerly open lakes.

In another example, geologic forces act to raise rocks up faster than they can weather into soil (volcanoes can do it almost instantaneously), and glaciers or other erosive forces can strip away surface debris to expose bedrock. These rock surfaces are not hospitable for higher plants, but exposed bedrock is not in equilibrium with the physical environment. Chemical weathering will attack the surface—rapidly for limestones and calcareous shales, and only very slowly for resistant rocks such as quartzite. Freezing and thawing and other physical factors will cause cracking and spalling. The challenge of living on bare rock has been met by mosses and lichens, which can endure the extremes. They also can hasten the dissolution of the rock by retaining water and secreting chemicals that erode the rock. The mosses, which expand when wet, continually break off little flakes of rock (Figure 31–10). Eventually, where these forces degrading the rock are not too severe, soil will develop around the bases of the lichens and mosses, and the ferns and flowering plants that cannot exist on barren rock will become established. Their roots penetrate cracks, breaking the rocks down further. Eventually, perhaps after many centuries, the rock may be completely reduced to a component of soil, which also includes organic matter from the generations of organisms that have grown in it. The soil will ultimately be occupied by forests or other types of vegetation characteristic of the region. The process by which essentially barren areas are colonized is often described as "primary succession" to distinguish it from the "secondary succession" in which nearly all of the physical environment and some of the organisms survive the disturbance. Another example of succession is shown in Figure 31–11.

Volcanic activity provides us with the most dramatic examples of succession on barren substrates. In August 1883, a violent volcanic eruption destroyed half of the island of Krakatau, in the Java Straits about 40 kilometers from Java, Indonesia. The remaining half of the island was

31–10 Early stage of succession Lichens have begun to erode the rocks, while ferns and bryophytes are accumulating soil in a small crevice.

31–11 Forest succession *Seedling trees of white fir* (Abies concolor) *growing under and replacing quaking aspen* (Populus tremuloides) *in northern Arizona—a stage in forest succession leading to the formation of a community of Engelmann spruce* (Picea engelmanii) *and white fir.*

covered by a layer of pumice and ash more than 31 meters thick. Neighboring islands were also buried, and the entire assemblage of plants and animals on these islands was wiped out. Soon afterward, however, the recolonization of Krakatau began, and the expected number (based on the number originally occupying the area) of about 30 species of land and freshwater birds was reached within about 30 years. Recolonization by plants also proceeded rapidly, with a total of more than 270 species being recorded for the island of Krakatau by 1934. Similar changes followed the catastrophic eruption of Mount St. Helens on May 18, 1980, in Washington State. A massive avalanche of volcanic debris from the top and north side of the mountain poured into the North Toutle River Valley. Within 15 minutes, more than 61,000 hectares of forest and recreation land were devastated by the lateral blast, which blew down forests on about 21,000 hectares and killed trees and other plants but left them standing on another 9700 hectares. In addition, the nine-hour eruption covered the whole area with up to 0.5 meter of ash, pumice, and rock pulverized by the blast.

Life began to reappear on the slopes affected by the eruption almost immediately, however, with plants sprouting

up through the volcanic debris in the following spring (Figure 31–12). Much of this debris soon eroded off, and wind-dispersed seeds and fruits blew back into the area. Such dispersal was especially important in areas that had been buried by debris avalanches, which were so deep that they killed the plants buried beneath them, and on the volcanic flows. Many small animals also survived, both underground and in lakes and streams, and terrestrial vertebrates soon moved back into the area.

Succession Blends into Change, in General, Particularly in Its Later Stages Massive disturbance sets in motion the kind of obvious and large-scale changes that clearly deserve to be called succession. But as the ecosystem recovers, it eventually enters a stage in which changes are not so easily detected. Forests provide a clear example. After the canopy is filled by trees capable of establishing in the understory, so-called shade-tolerant species, change does not cease. Rather, it moves to a new mode in which change is dominated by small- and medium-sized disturbances that open gaps in the

31–12 Recolonization after volcanic eruption *When Mount St. Helens in the state of Washington exploded on May 18, 1980, shock waves leveled all of the trees in an area of about 21,000 hectares, and a deep layer of ash was deposited. Fireweed* (Chamaerion augustifolium) *and grasses, as seen here four months after the eruption, were among the first plants to recolonize the area.*

canopy. Because these processes are slow relative to human life spans, and because they occur only in scattered locations, it is difficult to grasp the significance of the **gap** processes. Are the gaps merely a means by which the "climax" species are maintaining themselves (as Clements would have argued), or are they slowly changing the system in a new direction? Or, as some ecologists have suggested, might they involve a cyclical process in which A replaces B but then, at some time in the future, B replaces A? In more mature communities, reversals in the expected direction of succession often occur, and the ultimate outcome may be heavily influenced by the nature of the adjoining communities.

Because we know that "gravity works," gap processes are present to some degree in all forests. A measure of the frequency of gap disturbances can be gauged by calculating "turnover time," which can be estimated by dividing the area under study by the area of gap produced on average each year. It tells us approximately how long we would have to wait after a gap formed before there was another gap at the same spot. Ecologists have estimated this time to be

between 60 and 250 years in tropical forests, and on the order of 100 years in temperate deciduous forests.

The concept of gap is general. In prairies, the small disturbances caused by ground-inhabiting mammals, such as badgers, ground squirrels, and prairie dogs, maintain species that cannot persist for long against the competition of the more robust grasses and plants. These bare soil gaps create microhabitats in which ragweed, for example, can germinate and survive for a brief period before the gap is occupied once again by more dominant, competitive species. Before pervasive human disturbance, gap processes were probably the major kind of change, and it is therefore not surprising to find many species that seem to be well suited to exploiting gaps.

Fire is one of the most significant forms of natural disturbance affecting plant communities (Figure 31–13). For example, when European settlers first arrived in California, they found a magnificent forest of sugar pine *(Pinus lambertiana)* along much of the length of the Sierra Nevada. Although conservationists tried to preserve some of this

(a)

(b)

31–13 Recolonization after forest fire (a) *When fire sweeps through a forest, recolonization—with regeneration from nearby unburned stands of vegetation—is initiated. Some plants produce sprouts from the base, others seed abundantly on the burned area. In one group of pines, the closed-cone (serotinous) pines, the cones do not open to release their seeds until they have been exposed to fire.*

(b) *Sugar pines* (Pinus lambertiana), *seen here in Yosemite National Park in California, require periodic fires to reduce the brush and smaller trees that compete with the sugar pine seedlings for light. Limiting or preventing fires has allowed other species, such as the white fir* (Abies concolor) *trees seen here growing at the base of the stately sugar pines, to replace them.*

forest in national parks and forests, many of the stands of pines were eventually replaced by other trees, such as white fir *(Abies concolor)* and incense cedar *(Calocedrus decurrens)*. Why did this change take place?

Sugar pine was a member of a successional stage in the forests of this region that was maintained by periodic fires. These fires were greatly reduced in number and scope after the influx of settlers to the area. Without lightning-set fires of low intensity periodically racing through the groves, a thick growth of brush and smaller trees grew up, evidently creating conditions so shady that sugar pine seedlings could not compete effectively. Only a policy of letting the occasional fires burn, or conducting controlled burns, can preserve the remaining groves of sugar pine in the open form that most people find so attractive (Figure 31–13b). Similar relationships are found in all vegetation types in which fires periodically burn, either naturally or through human activity.

Restoration Ecology Reestablishes Natural Communities

As human beings become more and more numerous, and as their impact on ecosystems becomes correspondingly profound, the science of **restoration ecology** will become more and more important. This field of study attempts to better understand the process of succession and use its principles to reestablish natural communities. It is often not a simple matter to recreate natural communities once they have been destroyed; yet the process is one of great significance to an increasingly overcrowded world.

A well-known example of restoration ecology has taken place at the University of Wisconsin Arboretum in Madison (Figure 31–14). Begun in 1934 on damaged agricultural land, several distinct natural communities have been devel-

oped, among them a tallgrass prairie, a dry prairie, and several types of pine and maple forests. While restoration can be a costly and uncertain process, it provides a way of going on the offensive in the struggle to ensure the survival of classic ecosystems and the plants and animals within them. The Arboretum's Curtis Prairie, for example, supports more than 200 species of native plants, many of them now rare in the area. Early work on the Curtis Prairie provided new insights into the importance of fire in the prairie ecosystem. Fire plays a key role, not only by eliminating most species of trees, but also by influencing the nutrient economy of the prairie ecosystem, and in other ways as well. In fact, a prairie may be regarded as a highly flammable ecosystem that "uses" fire to maintain itself against encroachment by nonprairie species. In many parts of North America, the persistence of prairie depends on recurrent fires—set by Native Americans or lightning before the arrival of Europeans. If these fires do not occur, the prairie may quickly be colonized by trees and accompanying, shade-tolerant species. This, indeed, is what happened to many of the tallgrass prairies in the midwestern United States following European settlement and the elimination of fire from the landscape. Although fire played an important role in the management of vegetation in many areas, even after settlement, the ecological significance of this was not understood until relatively recently. Attempts to restore prairies, such as the Curtis Prairie at the University of Wisconsin Arboretum, have played a key part in clarifying this role.

Although volcanic eruption provides a very dramatic example of natural disturbance and the ensuing early stages of succession, these phenomena are typical of all communities and occur throughout the world. Disturbance and succession are two important factors that account for the full extent of the diversity of life on Earth.

(a)

(b)

31–14 Habitat restoration *A restored prairie at the University of Wisconsin Arboretum in Madison. (a) Late summer on the prairie, with purple blazing star* (Liatris pycnostachya), *white flowering spurge* (Euphorbia corollata), *and yellow prairie-coneflower* (Ratibida pinnata). *(b) A burn carried out in late fall plays an important role in maintaining the prairie ecosystem.*

SUMMARY

An Ecosystem Consists of a Community and Its Environment

Ecosystems are self-sustaining systems that include living organisms as well as the nonliving (physical) elements of the environment with which they interact. Communities consist of all the organisms that live in a particular area.

The Living Components of an Ecosystem Are the Primary Producers, Consumers, and Decomposers

An ecosystem consists of nonliving elements and two different kinds of living elements—autotrophs (primary producers) and heterotrophs (consumers). Among the heterotrophs are the primary consumers, or herbivores; the secondary consumers, or carnivores and parasites; and the decomposers. The organisms found at these levels are members of food chains or food webs.

The Flow of Energy through an Ecosystem Affects the Mass and Number of Its Component Organisms

Energy flows through ecosystems, with 1 percent or less of the incident solar energy converted into chemical energy by green plants. When these plants are consumed, about 10 percent of their potential energy is stored at the next trophic level; a similar degree of efficiency characterizes transfers farther up the food chain. The amounts of energy remaining after several transfers are so small that food chains are rarely more than four to six links long. In most ecosystems, more energy, biomass, and individuals occur at lower trophic levels, giving rise to the phenomena known as pyramids of energy, biomass, and numbers.

Hubbard Brook Has Provided an Outdoor Laboratory for Studying Nutrient Cycling

The properties of ecosystems have been studied experimentally at Hubbard Brook, in New Hampshire, where it has been shown that undisturbed natural communities control the cycling of nutrients but that the control tends to be lost when the ecosystem is disturbed.

Competition Results When Organisms Require the Same Limited Resource

Competitive interactions occur between most kinds of plants that grow in close proximity and between most individual plants also. The principle of competitive exclusion states that when two kinds of organisms occurring together compete for the same limiting resources, ultimately only one of them will survive in that area. One of the most important kinds of competition is competition for light. Frequently, plants with the highest growth rate relative to other species in a particular environment are the most successful competitors there. In the course of evolution, plants have also developed chemical weapons with which to compete aggressively with nearby plants, and such allelopathic relationships can also affect community composition.

Mutualism Is a Relationship That Benefits Both Species

In mutualism, two species interact to the benefit of both. Examples include lichens, mycorrhizal associations between fungi and the roots of plants, and the relationships between flowering plants and their pollinators and fruit and seed dispersers. In the bull's-horn acacias of Latin America, the thorns are inhabited by specialized ants that obtain their food from the plants and protect them from most herbivores and from competition with other plants.

Plants Have a Variety of Physical and Chemical Defense Mechanisms against Herbivores

Plants counter the effects of herbivores, which limit the reproductive potential of the plants, through the evolution of spines, tough leaves, and similar structures or structural alterations, and, most important, chemical defenses. An insect or other herbivore that has overcome a plant's chemical defenses not only has a new and often largely untapped food resource at its disposal, but it may also utilize the toxic substances produced by the plant to gain a degree of protection from its own predators.

Succession Is the Change in a Community over Time

Succession occurs in naturally open areas, such as lakes, ponds, or meadows in a forested region, and after an area has been denuded by artificial or natural means. In the course of succession, the kinds of plants and animals in the area change continuously, some being characteristic only of the early stages of succession. The creation and refilling of gaps created by natural disturbances play a key role in the process of succession and in the maintenance of species diversity in various forest communities. The pioneer species that arise in the gaps grow rapidly under sunny conditions and have other characteristics different from those of the trees that dominate the mature forest. At one time, ecologists viewed succession as resulting in a stable climax community, but now they speak of resilience (the ability to return to the original state after disruption) and stability (the degree to which a system will resist disturbances). The current thinking is that ecosystems can undergo catastrophic change, never returning to their former state, if the disruption is too profound.

Fire plays a very important role in the dynamics of many ecosystems, as in the maintenance of sugar pine forests in the Sierra Nevada of California and of prairie ecosystems. Succession after volcanic eruption, such as that of Krakatau in Java in 1883 or Mount St. Helens in Washington State in 1980, provides a spectacular example of the process, and these areas have been studied extensively.

QUESTIONS

1. Why are food chains generally limited to four to six links?
2. In general, ecosystems can be described by pyramids of energy, biomass, and numbers. Explain.

3. Comment on the importance of plants in the retention of nutrients in forest ecosystems.

4. Explain the role of growth rate in the competition among plants.

5. According to the principle of competitive exclusion, two species with similar environmental requirements cannot coexist indefinitely in the same habitat. How might competitive exclusion be avoided?

6. The diversity of species is greater in an environment where disturbance is continuous than in a more stable environment. Why?

7. In what way does the ant-acacia system resemble a lichen?

8. Explain the role of phytoalexins and tannins in the defense of plants against microorganisms and herbivores, respectively.

9. Disturbance and succession are two important factors that account for the full extent of the diversity of life on Earth. Explain.

10. What role do gaps play in succession?

11. How does a plant community change over time?