

Ecology and the Human Prospect

Hairy Solomon's seal (*Polygonatum pubescens*), a common herb of moist woods, thickets, and roadsides from Canada to South Carolina. With its leaves arranged along an arching stem,

Solomon's seal is well-adapted for light capture in shady conditions. On steep slopes, herbs with arching stems have an apparent advantage over herbs with erect stems (see page 676).



The Dynamics of Communities and Ecosystems

Ecology is the study of the interactions of organisms with one another and with all other components of their environment. As a science, ecology attempts to explain why particular plants and animals can be found living together in one area and not in others; why there are so many organisms of one sort and so few of another; what changes one might expect the interactions among them to produce in a particular area; and how ecosystems function, with particular reference to the flow of energy, the use of organic compounds, and the cycling of chemical elements.

A few definitions are necessary before we proceed. At the individual level, ecologists ask how the individual organism functions in and interacts with its environment. Individuals exist in **populations**, groups of individuals, usually of one species, that occur together at a given place. At the population level, ecologists ask what determined the abundance and distribution of individuals of a particular species.

Communities, in turn, consist of populations; they include the groups of plants, animals, and other organisms that live in a particular area. Although we can speak of an herb community or a community of vertebrate animals, the word "community" when unmodified is generally taken to mean *all* of the organisms that occur together at a particular place. An **ecosystem** includes not only these organisms but also their physical environment and their interactions, both with other organisms and with the environment. In this chapter, the properties of populations and individuals will be discussed in the context of interactions between organisms in communities and ecosystems. Once those interactions have been treated, we shall move on to consider properties of communities and ecosystems as a whole, centering our discussion on nutrient cycling, trophic levels, and the development of communities and ecosystems through time.

Biomes are large terrestrial complexes of communi-

ties of living organisms characterized by distinctive growth forms that have evolved in relation to a particular kind of climate. Examples include forests, grasslands, and deserts. The principal biomes are discussed in Chapter 30.

Interactions between Organisms

From the preceding discussion, it should be evident that interaction is central to the field of ecology. No organism living in a community—whether that community be a patch of woodland, a pasture, a pond, or a coral reef—exists in isolation. Each organism participates in a number of interactions, both with other organisms and with the nonliving components of the environment. We shall organize our discussion around three major kinds of interactions between species of organisms: mutualism, competition, and plant-herbivore (and plant-pathogen) interactions.

MUTUALISM

Mutualism is a biological interaction in which the growth, survival, and/or reproduction of both interacting species are enhanced. In many mutualisms, neither partner can survive without the other, particularly when competition from other plants and predation are taken into account. We have already come across several examples of mutualism in earlier chapters. Lichens are an outstanding example (Chapter 12). Others are the relationship between legumes and the nitrogen-fixing bacteria that live in nodules on the legume roots (see Chapter 27, pages 602–607) and some of the closely linked pollination relationships discussed in Chapter 19, such as that between the yucca moth and the yucca plant. Two additional examples of mutualism will now be discussed in greater detail.

Mycorrhizae

One of the most interesting and ecologically significant examples of mutualism concerns the interaction between fungi and plants. As discussed in Chapters 12 and 27, the roots of most vascular plants are associated with fungi, forming compound structures known as mycorrhizae. These fungi play a vital role in the absorption of phosphorus and other essential nutrients; without the fungi, the normal growth of the plants would be impossible. Mycorrhizae appear to have played a crucial role in the establishment of early plants on land.

In many vascular plants, nonmycorrhizal individuals are rarely encountered under natural conditions, even though growth may be possible without fungi if

nutrients are abundant. Most vascular plants are dual organisms in the same sense that lichens are dual organisms, although the relationship is not obvious above ground. 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 12, 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 dicots—mainly trees—the associations are mostly with basidiomycetes but also with certain ascomycetes; such associations are called ectomycorrhizae. Some of them are highly specific, with one species of fungus forming ectomycorrhizal associations only with a particular species or 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 nutrients particularly difficult to obtain.

Ants and Acacias

The most intricate examples of mutualism occur in the tropics, where many more kinds of organisms are found than in temperate regions. For example, trees and shrubs of the genus *Acacia* occur widely in tropical and subtropical regions. The interaction between certain species of *Acacia* in the lowlands of Mexico and Central America and the ants that inhabit their thorns (actually, stipular “thorns,” or spines) provides a remarkable example of the complexity that plant-animal interactions can entail. The particular relationship between the bull’s-horn acacias and the inhabitants of their thorns, ants of the genus *Pseudomyrmex*, is a good example (Figure 29–1).

The bull’s-horn acacias have a pair of greatly swollen thorns more than 2 centimeters long at the base of each leaf. Nectaries occur on the petioles, and small nutritive organs known as Beltian bodies are located at the tip of each leaflet. The ants live inside the hollow thorns and obtain sugars from the nectaries and fats and proteins by eating the Beltian bodies. The acacias grow extremely rapidly and are particularly common in disturbed areas, where the competition between rapidly growing colonizing plants is often intense.

Thomas Belt first described the relationship between *Pseudomyrmex* and the bull’s-horn acacias in his book,



(a)



(b)



(c)



(d)

29-1

Ants and acacias. (a) A queen ant cuts an entrance into a thorn on a seedling bull's-horn acacia (*Acacia cornigera*). She will hollow out the thorn and raise her first brood inside it. (b) The tip of an acacia leaf. The orange structures at

the tips of the leaflets are Beltian bodies. They are a source of food for the ants. (c) A worker ant (*Pseudomyrmex ferruginea*) drinking from a nectary at the base of a petiole of one of the compound leaves. (d) Warriors in a battle for

possession of an acacia. Obtaining all of their food from the acacia, the ants, in turn, kill most other insects that attempt to feed on it and girdle all plants that come into contact with it.

The Naturalist in Nicaragua (1874). Following his observations, there was a prolonged controversy about whether the presence of the ants actually benefited the acacia plants. This question was finally and definitively solved in 1964 by Daniel Janzen. Janzen found that the worker ants, which swarm over the surface of the plant, 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 rapidly growing tropical vegetation within which the acacia grows.

When Janzen removed the ants from a plant by poisoning them or clipping off the portions of the plant that contained ants or when an acacia was naturally unoccupied by ants (a situation that occurs rarely), the plant's growth was extremely slow, and the plant usually died after a few months as a result of insect damage and shading by other plants. Plants inhabited by ants grew very rapidly, soon reaching 6 meters or more in height and overtopping the other second-growth vegetation. These ants make their nests only in these particular acacias and are completely dependent on the acacias' nectaries and Beltian bodies for food. Thus the ant-acacia system is as much a dual biological entity as, for example, a lichen. One element usually cannot survive without the other in the community in which it occurs.

COMPETITION

Competition is defined as interaction between members of the same population or of two or more populations in order to obtain a mutually required resource available in limited supply. In competition, one species interferes with another species enough to keep the second species from gaining access to the resource.

Unlike animals, which ingest food, green plants are dependent on a single process, photosynthesis, to obtain their energy. Competition in plants is therefore manifested largely in terms of a "struggle for light." Those plants whose photosynthetic rate, growth form, and pattern of allocation of energy to leaves, roots, and stems result in the highest rate of growth in a particular environment will often have an advantage in this struggle. Those plants with a lower growth rate must either be able to photosynthesize at low light intensities, have a high growth rate relative to competitors elsewhere, or die. The evolution of plants with C_4 and CAM photosynthesis (pages 116 to 117) can be seen in this light: the physiological properties of such species enable them to dominate climatic areas where their C_3 ancestors would have either perished or else been competitively excluded by more rapidly growing C_4 or CAM species.

Differences in height, leaf arrangement, crown shape, and allocation to roots versus leaves affect a plant's growth rate relative to potential competitors.



(a)

29-2

Lullington Heath National Nature Reserve, East Sussex, England, an area of chalk grassland, before (a) and after (b) the elimination of rabbits by the viral



(b)

disease myxomatosis. The first photograph was taken in 1954, the second in 1978. In an effort to restore the diversity of herbaceous plants, the authorities have

introduced grazing programs for sheep and horses over much of the reserve, which has an area of 62 hectares.

Different combinations of these traits are likely to maximize growth in different environments; no single combination can produce the best competitor in all environments. As a consequence, vegetation in different climatic areas 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, photosynthetic physiology, and 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 yield in extreme environments, such as those that are relatively poor in nutrients or water, or are heavily shaded. These relationships are important in agriculture, therefore. Knowledge of these factors will also provide the information necessary to predict the performance of individual plant species and communities in a world that is rapidly changing, as by the global warming that is resulting from increased levels of CO₂ and certain other atmospheric gases, largely produced by human activities.

Competition between plant species can be visualized more easily under experimental conditions than in nature. From observations 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 what Garrett Hardin has called **the principle of competitive exclusion**. If the environment is complex, as it often is in nature, various organisms may relate to it in different ways, in effect subdividing the environment and achieving competitive success in different microenvironments. These various organisms may then continue to coexist indefinitely.

For example, Engelmann spruce (*Picea engelmannii*)

and subalpine fir (*Abies lasiocarpa*) coexist and form the dominant tree community in the subalpine zone of the central and northern Rocky Mountains. Careful field measurements suggest that these two tree species are maintained as codominants in this area because the greater longevity and size of the spruce are balanced by the faster growth in height and more flexible seedling-establishment requirements of the fir. 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. In other words, fir seedlings outcompete spruce in shaded understories (that is, they survive), whereas spruce seedlings outcompete fir in sunnier sites, by virtue of higher growth rates there and lower sensitivity to drought. Constant disturbance from storms, flooding, and avalanches, among other factors, and the relatively short lifespan of fir prevent it from taking over the entire landscape as succession proceeds. Patterns of this sort are frequent in different plant communities, but they are often not at all obvious on simple inspection. The different requirements of the species involved remove them from direct competition and allow them to coexist indefinitely.

If populations of coexisting species are kept at low levels, competitive exclusion may be avoided even though the species do, in principle, compete for the same limiting resources. Such a situation occurred in the chalk grasslands of England when the grasses were kept closely cropped by rabbits and many kinds of flowering plants were able to grow in this habitat. Diversity is enhanced in such situations when competitive dominant species—grasses and other tall herbs in this case—are attacked preferentially. This allowed many other kinds of shorter grasses and other herbs to coexist. However, the situation changed drastically earlier in this century, when a severe epidemic of myxomatosis, a disease caused by a virus, 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 (Figure 29-2). Similar effects are

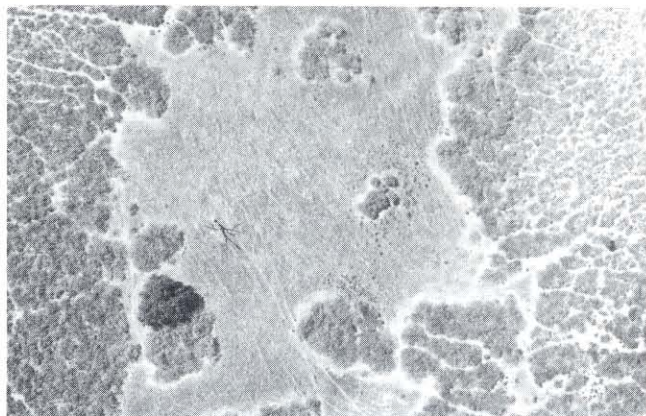
often seen when comparing grazed and ungrazed pastures or grasslands, and they also arise in areas where natural disasters, such as hurricanes, are common. Thus, as we might expect, the diversity of species is greater along a wave-lashed coast, where disturbance is continuous, than in a more stable environment.

Clonal reproduction, which is important in many plants, sometimes makes it difficult to define the limits of individual plants in nature. This, in turn, may make it difficult to evaluate the competitive interactions of specific genotypes within a species. Genetically identical individuals may be widely dispersed but still occur in widely separated but similar environments within a single complex habitat. This is characteristic not only of rhizomatous perennials, such as many grasses and sedges, but also of dandelions and other plants in which the seeds are produced asexually and contain embryos that are genetically identical to their parents. It is characteristic also of those plants, such as white clover (*Trifolium repens*), in which an original plant simply grows apart into distinct individuals.

Depletion of a shared resource, such as light or water, is not the only mechanism by which plants may compete. In some competitive interactions, one (or both) of the competing organisms produces chemical substances that inhibit either the growth of members of its own species, resulting in increased spacing of like individuals, or the growth of other species. 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 excellent example of this phenomenon is provided by the effects of black walnuts (*Juglans nigra*) on other plants, which are very sparse under the walnut trees. Tomatoes (*Lycopersicon esculentum*) and alfalfa (*Medicago sativa*) wilt when grown near black walnuts, and their seedlings die if their roots contact walnut roots. Similarly, white pine (*Pinus strobus*) and black locust (*Robinia pseudoacacia*) are often killed by black walnuts growing in their vicinity, especially in poorly drained soils, where the toxins leached from the walnuts apparently accumulate. The bare zones around sage (*Salvia leucophylla*) shrubs in California (Figure 29-3) may also occur in part because of allelopathic effects, although the birds and rodents that the shrubs shelter exert an important influence on the patterns observed (Figure 29-4).

Allelopathic effects are likewise being applied in agriculture. For example, a strip planted with sorghum will have two to four times fewer weeds the following



29-3

Purple sage (*Salvia leucophylla*) shrubs produce terpenes that evaporate and spread through the air, ultimately reaching the soil, where they inhibit the growth of other plants. In this aerial view, the bare zone around the individual *Salvia* shrubs and colonies can be seen plainly. Immediately around the shrubs is a completely bare zone, and then a zone of inhibited grassland with a few stunted annual herbs.

year than other strips. The sorghum plants evidently leave behind allelopathic compounds in the soil that depress the growth of weeds.



29-4

When mammals such as mice are excluded from the bare zone, annual plants grow luxuriantly right up to the edge of the shrubs in areas where they are normally absent. Such results, reported by Bruce Bartholomew of the California Academy of Sciences, indicate that the effect of these mammals would be sufficient to account for the bare zone, regardless of whether the plants are producing toxic chemicals.

PLANT-HERBIVORE AND
PLANT-PATHOGEN INTERACTIONS

We have already considered one important area of plant-herbivore interactions involving flowering plants—the relationships that exist between flowers and their visitors, and between fruits and their dispersers (Chapter 19). 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.

The important role of plant-herbivore and plant-pathogen interactions in determining the structure of natural communities is not always evident. 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 in Australia (Figure 29–5).

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 19, 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 plant products.” 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.

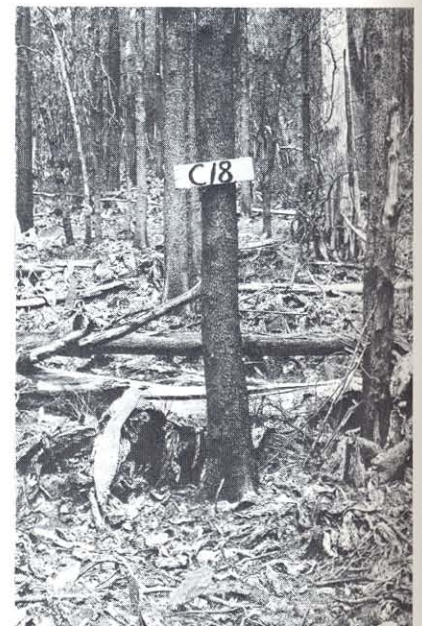
In the sea, many seaweeds have evolved comparable defenses. These marine algae are consumed by many different kinds of herbivores, including fishes, sea urchins, mollusks, and other animals; nearly all of the biomass is ultimately consumed in some habitats. To escape these herbivores, some seaweeds grow in cracks and holes or in other 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 against herbivores that is employed by seaweeds is virtually as extensive as that which occurs among flowering plants on land.

29–5

(a) Dense prickly-pear cactus (*Opuntia inermis*) growing in a mixed scrub forest in Queensland, Australia, in October 1926; (b) the same forest 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.



(a)



(b)

Pesticides and Ecosystems

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 either reaches soil, water, or nontarget organisms in the same ecosystem or spreads into neighboring ecosystems, where it may have important 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 (see pages 646 to 648). For example, chlorinated hydrocarbons, such as DDT (now outlawed in the United States for use but not for manufacture and export, unfortunately, and not in most 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. In addition, many

strains of insects, bacteria, and fungi have evolved that are resistant to the pesticides designed to control them. 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, predator species that naturally control 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 ecosystems 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 (the methods of genetic engineering described in Chapter 25 will be especially useful in achieving this goal), 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.

Plant-herbivore and plant-pathogen interactions may be quite complex. For example, 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; such 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 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.

When infected with fungi or bacteria, plants often defend themselves by producing natural antibiotics called **phytoalexins** (page 33). 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 more or less 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



(a)



(b)

29-6

(a) The monarch butterfly (*Danaus plexippus*) obtains cardiac glycosides from the plants of the milkweed family (*Asclepiadaceae*), upon which its larvae (b) feed. As a result, the monarch is unpalatable to birds and other vertebrates. It “advertises” this fact by bright orange-and-black adult coloration and by larvae that are conspicuously banded with white, yellow, and black. Even the eggs of the monarch, which are bright yellow and conspicuous, contain enough cardiac glycosides to be protected.

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 energetic 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 importance 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 Chapter 25), also offers new possibilities for enhancing crop resistance that do not carry a high energy cost.

Just as some plants produce phytoalexins, others produce tannins and other phenolic compounds, 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 marshalled 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 other 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 resins and phenolic compounds than the earlier shoots.

The secondary plant products ingested by herbivores may, in turn, play a role in the animals’ ecological relationships with other animals. For example, some insects store these poisons within their tissues and are thereby protected from their predators (Figure 29-6). 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 scientists are just beginning to understand.

Nutrient Cycling

With this section, we turn to the overall properties of ecosystems. As mentioned earlier, ecosystems have the property of regulating the flow of energy, originally derived from the sun, and regulating the cycling of nutrients. Aspects of these properties will be explored in the remaining pages of this chapter.

In terms of its nutrient supply, an ecosystem is more or less self-sustaining. One of the more important reasons for this autonomy is the continuous cycling of chemical elements between organisms and the environment. The pathways of some of these essential elements, known as nutrient cycles, were discussed in Chapter 27. Ideally, nothing is lost, so that the pool of nutrients is continually renewed and continually available for the growth of organisms. The rate of flow from the nonliving pool to the organisms and back again, the amount of available material in the nonliving pool, and the form of this pool differ among nutrients and from habitat to habitat.

By considering the interaction of organisms, it is easy to see that competition for nutrients can easily occur. In some cases, this competition has become so intense that organisms benefit from a mutualistic interaction, such as the formation of mycorrhizae, in which one partner assumes the responsibility of providing nutrients for the other.

RECYCLING IN A FOREST ECOSYSTEM

Studies of a deciduous forest ecosystem in the Hubbard Brook Experimental Forest of the White Mountain National Forest of New Hampshire have shown that the plants of this community play a major role in the retention of nutrient elements. The investigators first established a procedure for determining the mineral budget—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 29–7). A particular advantage of this site was that a granitic bedrock is present just below the soil surface, so that very little material leaches downward; that is, the soil water percolates only a short distance. In addition, few nutrients are added by dissolution of the highly resistant bedrock.

The investigators discovered that the natural forest was extremely efficient in conserving its 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 sys-



29–7

Weir in the Hubbard Brook Experimental Forest in New Hampshire. Water from each of six experimental ecosystems was channeled through a weir (such as this one, built where the water leaves the watershed) and was analyzed for chemical elements. The trees and shrubs in the watershed behind this weir 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.

tem. In the case of nitrogen, the ecosystem was actually accumulating this element 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.

At Hubbard Brook, the biological regulation of element cycling was tested by the following experiment. In the winter of 1965–1966, all trees, saplings, and shrubs in one 15.6-hectare area in one small 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. During the four months from June to September 1966, the runoff of water from the area was four times greater than in previous years. Net loss of calcium was 20 times higher than in the undisturbed forest, and potassium loss was 21 times higher. The most severe disturbance was seen in the nitrogen cycle. The tissues of dead plants and animals

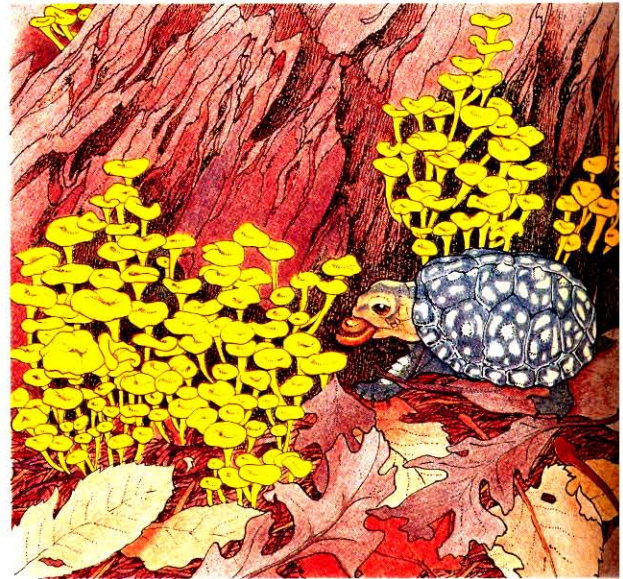
continued to be decomposed to ammonia or ammonium ions, which were then acted upon by nitrifying bacteria to produce nitrates, the form in which nitrogen is usually assimilated by plants. However, no plants were present, and the nitrate ions were not held in the soil. The net loss of nitrogen averaged 120 kilograms per hectare per year from 1966 to 1968. As a side effect, the stream that drained the area, polluted with nitrates, supported an algal bloom. The nitrate concentration of the stream increased to levels above those established by the U.S. Public Health Service as safe for drinking water.

Nitrogen is not always lost so readily from disturbed forest ecosystems. In the Hubbard Brook experiment, vegetation regrowth was prevented by herbicides so no uptake was possible; therefore, these results represent the maximum possible loss. The actual local rates of nitrogen loss depend on the details of the nitrogen cycle in the particular forest before the disturbance takes place. For example, if the microorganisms in the ecosystem have a high demand for the nitrogen released after forest clear-cutting, forest disturbance would not result in losses of the magnitude measured at Hubbard Brook.

Trophic Levels

In addition to its *physical* (or nonliving) components, each ecosystem includes two classes of *biotic* (or living) components—autotrophs and heterotrophs. Autotrophs are mainly photosynthetic organisms, which are able to use light energy to manufacture their own food; they are known as **primary producers**. Autotrophs consist of green plants, algae, and autotrophic bacteria. Because heterotrophs cannot manufacture their own food, they must use the organic molecules made by the autotrophs. Several feeding levels, or **trophic levels**, occur among the heterotrophs: **primary consumers**, or **herbivores**—animals that feed on living plants; **secondary consumers**, or parasites and carnivores—animals that feed on animals; and **decomposers**—fungi, bacteria, and various small animals that break down organic matter stored in the bodies of other organisms. All three levels are present in most ecosystems.

In a given ecosystem, organisms from each of the trophic levels make up what is called a **food chain** (Figure 29–8). The relationships between the organisms in a food chain regulate the flow of energy and nutrients through the ecosystem. The length and complexity of such food chains vary a great deal. Usually an organism has more than one source of food and is itself preyed on by more than one kind of organism. Under most circumstances, it is more nearly correct to speak of a **food**



29–8

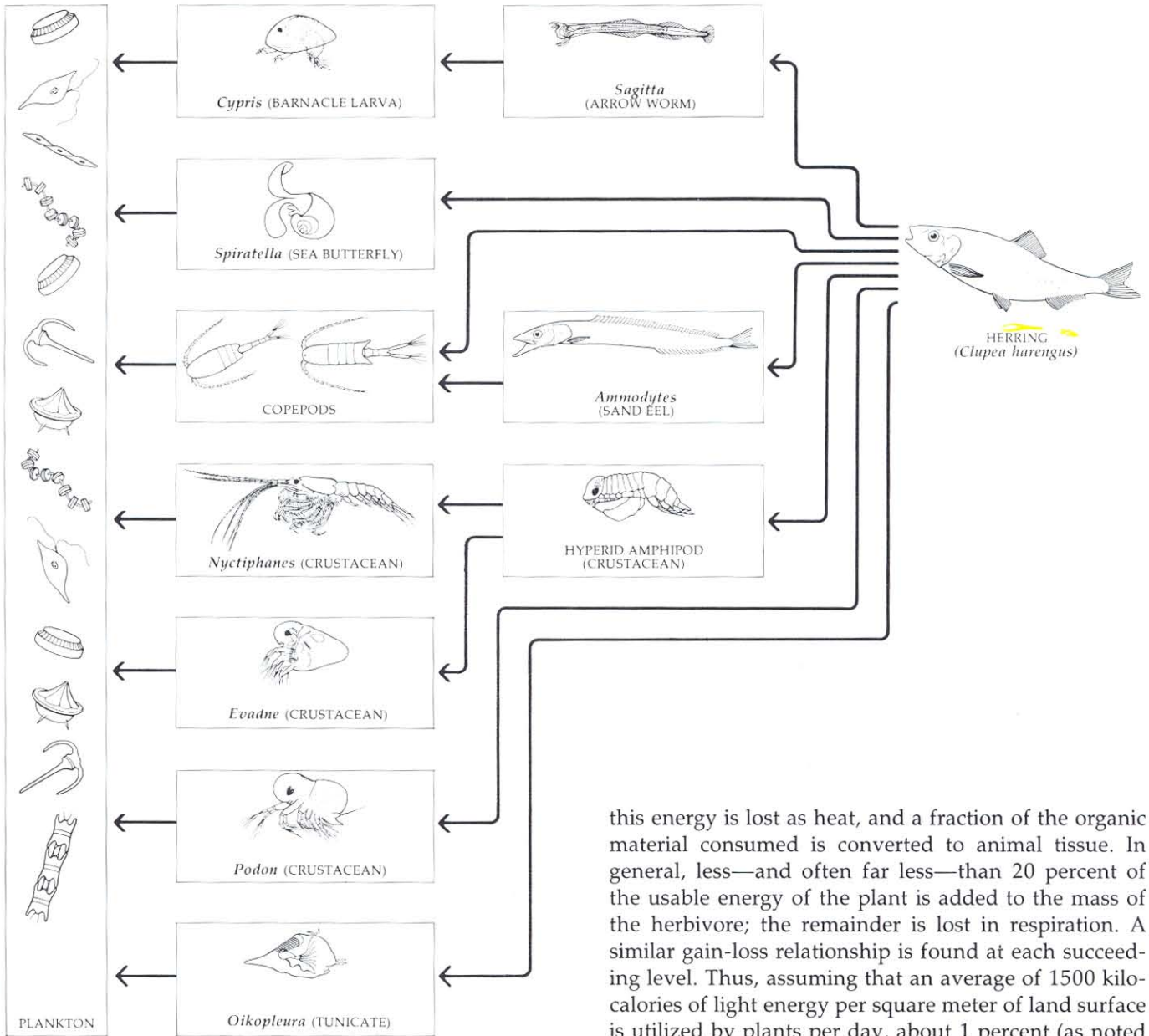
*A food chain. A three-toed box turtle (*Terrapene carolina triunguis*) feeds on a snail that has fed on the mushrooms that are decomposing organic matter in the soil.*

web (Figure 29–9). The complexity of trophic relationships has a number of important implications for the overall properties of that ecosystem.

THE FLOW OF ENERGY

In an ecosystem, the flow of energy typically begins with solar energy that is captured in photosynthesis and used to make carbohydrate molecules. Energy does not flow in a cycle in ecosystems; rather, it flows through autotrophs (usually photosynthetic organisms; that is, plants, algae, and some bacteria) to consumers (animals and heterotrophic protists) and then to decomposers. At each step, the great majority of the energy is dissipated in the form of heat energy, which eventually is returned to space as infrared radiation.

A very large amount of **biomass** is produced on earth each year. (“Biomass” is a convenient shorthand term for organic matter.) It is currently estimated that the earth’s annual production of biomass amounts to about 200 billion metric tons. Despite this enormous figure, photosynthetic organisms are not very efficient in converting the sun’s energy into organic compounds. Generally, less than 1 percent of the light that falls on a plant is utilized in biosynthesis (see Chapter 5). How-



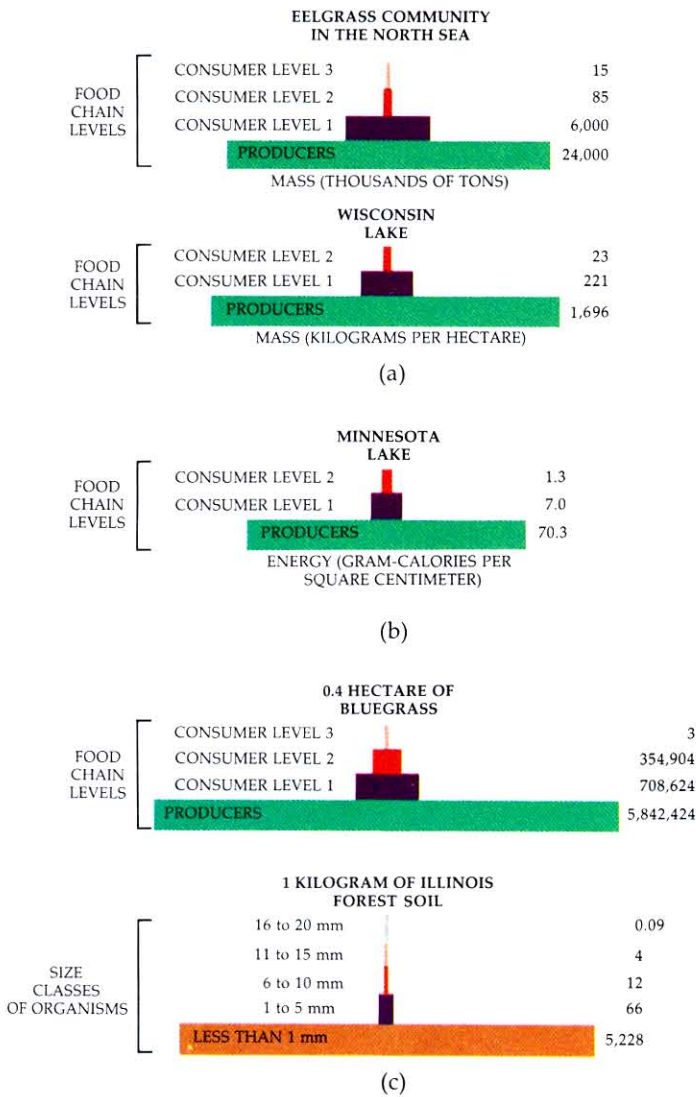
29-9
 The feeding relationships of the herring (*Clupea harengus*) in the North Atlantic, illustrating some of the complexities and interrelationships of a food web.

this energy is lost as heat, and a fraction of the organic material consumed is converted to animal tissue. In general, less—and often far less—than 20 percent of the usable energy of the plant is added to the mass of the herbivore; the remainder is lost in respiration. A similar gain-loss relationship is found at each succeeding level. Thus, assuming that an average of 1500 kilocalories of light energy per square meter of land surface is utilized by plants per day, about 1 percent (as noted above), or 15 kilocalories, is converted to plant material. Of this amount, perhaps 10 percent, or 1.5 kilocalories, is incorporated into the bodies of the herbivores that eat the plants, and 10 percent of that, or about 0.15 kilocalorie, is incorporated into the bodies of the carnivores that prey on the herbivores.

To give a concrete example, Lamont Cole of Cornell University, in his studies of Lake Cayuga, near the Cornell 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. In addition, of these 150 kilocalories, 30 kilocalories are reconstituted as smelt (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

ever, particularly productive stands of vegetation, and some aquatic systems, may convert up to 3 percent of the annual incident solar radiation into chemical energy.

When the organic material produced by plants is consumed by an herbivore, energy is released. Most of



29-10 Pyramids of mass (a), energy (b), and numbers of organisms (c) in various communities. A relatively small amount of mass or energy is transferred to each successively higher level. The units of measurement are listed at the bottom of each figure, with the quantities opposite each level, at the right of the figure.

the original 1000 kilocalories. Smelt are much more abundant, and constitute a much larger biomass, in Lake Cayuga than the trout. Thus, more of the original energy is available to us if we eat smelt rather than the trout that feed on the smelt; yet trout are considered a delicacy, smelt a much less desirable food for humans. Under conditions of starvation, people cannot afford the tenfold loss of energy that occurs when plants are fed to animals; they must then become herbivores to obtain as much food as possible.

Food chains are generally limited to three or four links; the amount of energy remaining at the end of a longer food chain is so small that few organisms can be supported by it. Body size also plays a role in the structure of food chains. For example, an animal constituting one link generally has to be large enough to capture prey from the previous, lower link on the food chain (though small insects do feed on large trees!). In the end, most of the biomass in an ecosystem is used by decomposers, such as fungi and bacteria.

Owing to the relationships just discussed, the total energy at successively higher trophic levels in an ecosystem generally decreases sharply, setting up the sort of relationship described by the expression "pyramid of energy" (Figure 29-10). This relationship may not hold if there is rapid turnover among the primary producers, such as algae in a lake; the turnover rate then becomes the controlling factor, and the total energy present at that level may be relatively small at any one time. A similar relationship is characteristic of mass, leading to the existence of "pyramids of mass." In general, there are also far more individuals at the lower levels than at the higher levels, which leads to a "pyramid of numbers." It also follows that, if all the organisms in an ecosystem are divided into size classes, the small animals will be far more numerous than the large ones.

A practical aspect of the flow of energy through ecosystems concerns human efforts to develop renewable sources of energy from plants, a process known as biological energy conversion. Plantings of fast-growing trees and other plants may provide a major, renewable energy source in the future, and they may constitute one of the most environmentally benign ways of efficiently capturing solar energy. Even now, scientists estimate that the waste materials available each year after the harvest of crop and forest products could provide an amount of energy equivalent to 1 percent of the gasoline consumed annually in the United States, or 4 percent of the nation's annual consumption of electrical energy. The potential is limited, however, by the energy costs of harvesting the material. In developing countries, more than 2 billion people rely on biomass for virtually all their cooking, heating, and lighting, so that the ability of plants to convert energy from the sun to a form useful to humans is a matter of central importance on a global scale.

Development of Communities and Ecosystems

SUCCESSION

Some plant communities appear to remain the same year after year, whereas others change rapidly. In the latter case, there is a progression of changes in the community called **succession**. A cleared woodlot is rapidly colonized by the remaining trees in the vicinity; in a similar fashion, a pasture eventually gives way to a forest. Analogous series of events occur in naturally disturbed areas, such as lakes, floodplain forests, or steep

hillsides. Natural disturbances (for instance, floods, windstorms, earthquakes, landslides, fires) are a pervasive feature of all ecosystems, even “pristine” wilderness areas that are little disturbed by humans. The process of succession is both continuous and world-wide in scope.

Succession occurs at a variable rate in all temporarily disturbed areas. Some ponds, for example, fill with aquatic plant remains and debris; emergent vegetation builds soil, while sediment washes in and contributes to filling in of the lake; the site is taken over by meadow; moisture-loving shrubs may become established; and finally the forest characteristic of the region develops in the meadow that formed earlier where there had been a pond (Figure 29–11). In another example, rocks



(a)



(b)



(c)



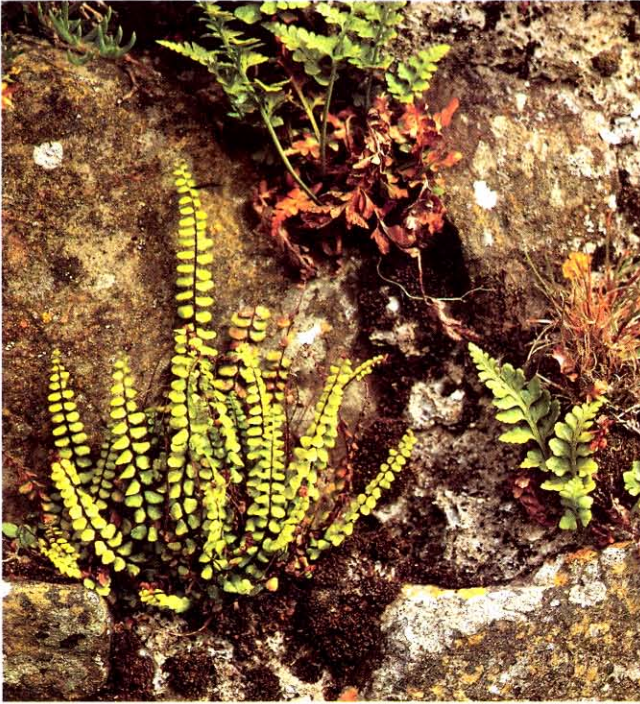
(d)

29-11

(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)

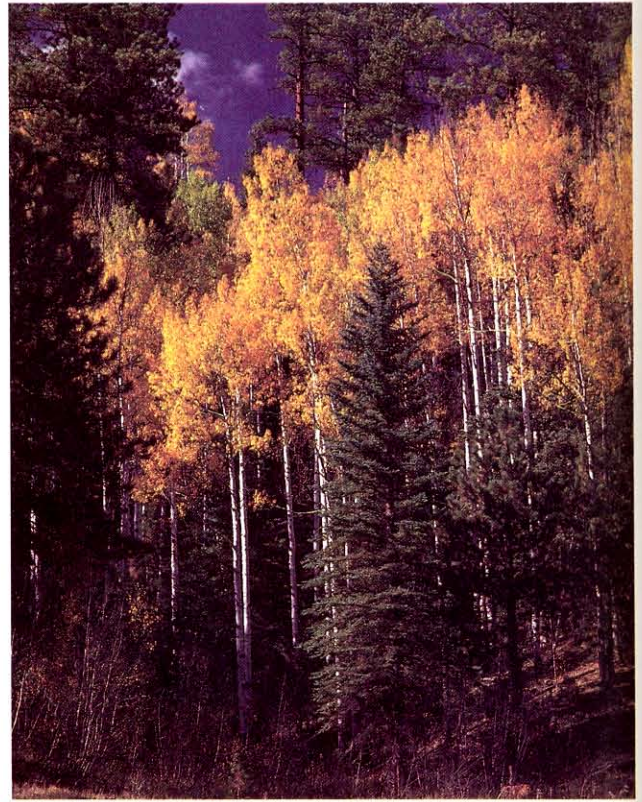
Marsh grasses, sedges, and cattails (*Typha* spp.) growing on an old pond bed continue the process of succession.



29-12
An early stage of succession. Lichens have begun to break down the rocks, while ferns and bryophytes are accumulating soil in a small crevice.

weather and break down because of freezing and thawing and other physical factors, and the process is sometimes expedited by the action of lichens, which secrete chemicals that erode the rocks directly, and by mosses, which expand when wet, continually breaking off little flakes of rock (Figure 29-12). Soil accumulates around the bases of the lichens and mosses, and flowering plant seedlings eventually may 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. In the early stages of succession, plants with symbionts that have the ability to fix nitrogen may be prominent, at least in certain areas. Another example of succession is shown in Figure 29-13.

The process of succession is often not completely unidirectional, particularly in its later stages. It is generally simple to observe the early stages of succession and very difficult to interpret the later ones. In more mature



29-13
Seedling trees of balsam fir (*Abies balsamea*) growing under and replacing quaking aspen (*Populus tremuloides*) in northern Arizona—a stage in forest succession leading to a climax community of white spruce (*Picea glauca*) and balsam fir.

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.

The creation and refilling of **gaps** created by natural disturbances are processes that play a key role in the process of succession and in the maintenance of species diversity in various plant communities. The gaps that occur when trees fall in a forest, for example, provide opportunities for many plant species with relatively high light requirements to flourish in such areas. In temperate North America, a number of species that characteristically occur in gaps, such as black cherries and blackberries, have fleshy fruits eaten by birds. The birds digest the fleshy parts of these fruits and drop the seeds in new gaps, which are thus colonized efficiently. Such pioneer species often have multilayered, diffuse crowns; light, nondurable wood; and high rates of growth under sunny conditions. The dominant, late successional trees in the same forest often have very different characteristics, such as more tightly packed crowns, heavy but durable wood, and slow rates of growth under sunny conditions; however, they can

29-14

(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*) in Yosemite National Park in California. With the prevention of forest fires by human beings, sugar pines are being replaced by other trees, such as white fir (*Abies concolor*), the trees seen here growing at the base of the sugar pines.



(a)

grow in the shade and live longer than the pioneers. Such differences between tree species play a major role in determining their local success and thus the structure of the mature forest.

One of the most significant forms of natural disturbance affecting plant communities is fire. 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 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 that occur burn, or one of controlled burning, can preserve the remaining groves of sugar pine in the open form that most people find so attractive (Figure 29-14b). Similar relationships are found in all vegetation types in which fires periodically burn, either naturally or caused by humans.



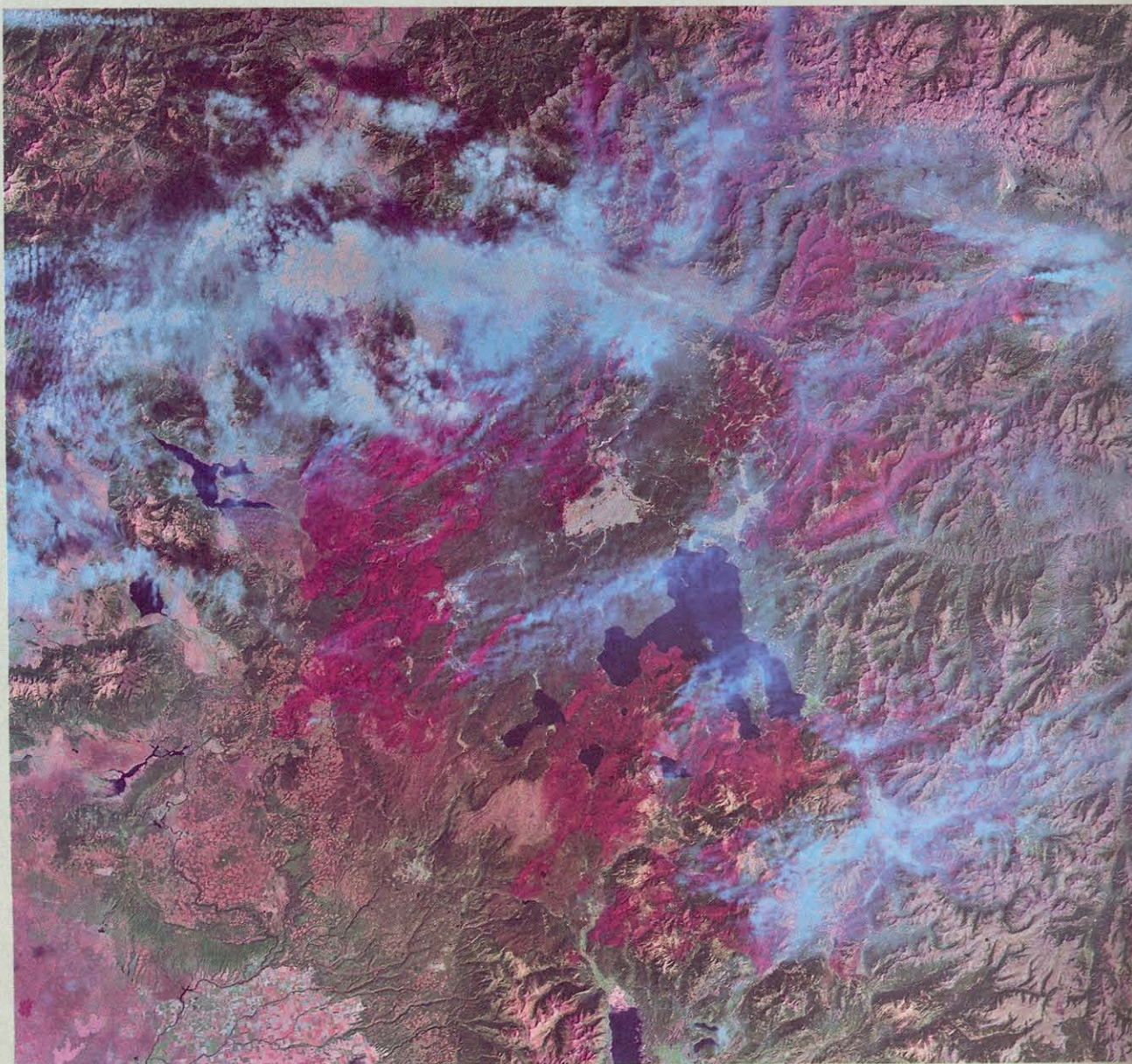
(b)

The Great Yellowstone Fire

It was an exceptionally dry summer in 1988, with the hottest, driest conditions since the Dust Bowl of the 1930s. But the park managers of Yellowstone National Park were confident that major fires could not happen. Yet in July of that year, Yellowstone broke into flames. Soon new fires were breaking out in every section of the park; they continued to spread throughout August and September. Park concessions were endangered. Tourists had to be evacuated. A holocaust had begun. What had gone wrong?

Yellowstone Park was established in 1872 in order to preserve its natural beauty, and that included protecting it

from fires. Eventually, however, scientists and managers realized that there was a gradual decrease in certain species, as seen in photographs taken through the years. This evidence, along with the existence of charred stumps, strongly suggested that fire was a normal part of the Yellowstone ecosystem. In 1972, park officials initiated a program in which they allowed natural fires in remote areas to burn without interference. The program had subsequently been extended throughout the park to all but 5 percent of the total area—places where people were living. This policy was widely viewed as a success.



But by October 1988, 4300 square kilometers lay charred, and nowhere in the park could you get a vantage point where there was no visible fire damage. Dry winds, gusting to more than 100 kilometers per hour, had frustrated the efforts of more than 9000 firefighters to control the spread of the flames. Was this havoc the result of buildup of abnormal amounts of biomass in the trees and shrubs? Could it have been prevented by controlled burning?

Fire scars among the annual growth rings of lodgepole pines (*Pinus contorta*) indicated that any one spot in Yellowstone had burned naturally about every 20 to 25 years, with a wide range of variation. Lodgepole pine, like other pines, is adapted to fire. Its cones open only in intense heat, and its seeds regenerate best following fires, benefit when the light-blocking mature trees are killed, and thrive on the nutrients released from burned pine needles. The beautiful, even-aged lodgepole pine stands that are such a characteristic feature of Yellowstone National Park are a direct consequence and reflection of periodical catastrophic fires.

At higher elevations, with cooler climates, mostly small fires had burned almost every decade. In areas where there were no significant fires, the lodgepole pines were eventually replaced by other tree species, such as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). These species usually succeed lodgepole pine, starting about 150 years after a fire, and become dominant during the following century. As the original lodgepole pines die, however, the forest canopy becomes uneven, with many gaps, and is highly flammable. Fires that occur at early stages of succession are usually small, but as the forest becomes more mature, fires are extensive and highly destructive.

In Yellowstone, fire usually intervenes and the climax fir-spruce communities are very rare. The extensive fires

of 1988 seem to have been similar to a series of fires that occurred around 1700 and perhaps should also be viewed as a natural feature of this area. Major efforts to suppress fires in the Yellowstone area may merely have delayed this natural cycle for a few years.

At any event, the great fire of 1988 appears to have had no major lasting effect on the ecosystem. Lush meadows feed healthy buffalo and deer. Colorful lupines help to replace the soil's depleted nitrogen. Pine seedlings thrive on the sunny flats and slopes. Lodgepole pines grow slowly in Yellowstone. In 30 years, these seedlings will be 2 to 4 meters tall; perhaps in 80 or 100 years, the forests will begin to resemble those that burned in 1988. In two or three centuries, the stage may have been set for a repeat of the events that occurred in the late summer of that year. Meanwhile, curiosity about the recovery of the Yellowstone ecosystem from the great fire has proved a great stimulus to tourism, and people have been visiting the area in record numbers.

In management terms, the continuation of a program in which lightning-set fires are allowed to burn is clearly an appropriate strategy for maintaining the natural ecosystems of Yellowstone, but the total area—like that of all protected areas—is so limited that fires cannot be allowed to burn completely freely. They affect too many interests both within the protected areas and beyond their boundaries to be treated with complete passivity. Scientists and managers currently are studying the possibility of burning areas near human habitation periodically to reduce the amount of natural fuel. The struggle between the interests of humans and the continuance of nature continues. In this context, fire is clearly seen as an example of a natural, pervasive influence affecting an apparently pristine ecosystem.

(a) Satellite image of Yellowstone area at the height of the fire activity, September 8, 1988. Red denotes the area within the burn perimeter, and green identifies unaffected vegetation. Yellowstone Lake is the dark blue shape on the right, just below the center. (b) Regeneration near Elk Park in Yellowstone, a year after the fire.



(b)



(a)



(b)

29-15

The most recent severe eruption of Mount St. Helens in Washington State took place on May 18, 1980. (a) What had been productive forests of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and firs (*Abies amabilis* and *A. procera*) were blown down by the lateral blast. (b) Over an area of more than 60 square kilometers, a deep layer of volcanic debris was deposited. (c) During the summer of 1981, many perennial plants, like the fireweed (*Epilobium angustifolium*) shown here, resprouted from ash-covered clearcuts on steep slopes, where erosion removed the overlying ash. Although there is blown-down forest in the background, the area of lush regrowth is an old clearcut where the fireweed had become well established prior to the eruption. (d) Douglas fir and many other plants with wind-dispersed seeds recolonized areas that had been so deeply covered by volcanic debris that the plants beneath were killed. This photograph was taken in 1984.

Following natural disasters, recolonization produces similar successional changes. For example, 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 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.

In the state of Washington, the violent eruption of Mount St. Helens on May 18, 1980, sent a massive avalanche of volcanic debris from the top and north side of the mountain 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 (Figure 29-15).

Life began to reappear on the slopes affected by the eruption almost immediately, however, with plants sprouting up through the volcanic debris the following spring. 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 terres-



(c)



(d)

trial vertebrates soon moved back into the area. The eruptive periods of Mount St. Helens have been separated by only 100 to 500 years in the last 35 centuries, and both the blast itself and the recovery from its effects that scientists were able to observe in the early 1980s were typical of natural phenomena that periodically affect living systems in volcanic areas.

A general property of successional processes is that, if climatic factors remain constant, the process of succession should ultimately slow and nearly stop, and terminate in a **climax community**. Such a community is self-perpetuating; its characteristics relate to the specific climatic conditions under which it is produced. A climax community, however, is an ideal concept that mainly serves as a reference point against which to measure community change. In reality, climatic conditions often change, natural disturbances such as hurricanes and landslides occur, and animals modify the nature of the changing communities. The communities that develop at a particular place reflect a balance of many different environmental factors.

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

Although the eruption of Mount St. Helens has provided a recent and 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.

Summary

Biomes are large terrestrial complexes of living organisms that are characterized by distinctive vegetation and climate. Specific growth features are characteristic of the dominant plants of each biome. Ecosystems are self-sustaining systems that include the aggregation of living organisms together with the nonliving (physical) elements of the environment with which they interact. Communities consist of all the organisms that live in a particular area, or of a subset of these organisms that is defined for a particular purpose.

Some of the relationships that occur in communities can be grouped under three headings: mutualism, competition, and plant-herbivore (and plant-pathogen) relationships. In mutualism, two populations 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, which obtain their food from the plants and protect them from most herbivores and from competition with other plants.

Competitive interactions are found between most kinds of plants that grow together 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; often plants with the highest growth rate relative to other species in a particular environment will be the most successful competitors there. Plants have also evolved chemical weapons with which to compete aggressively with nearby plants, and

such allelopathic relationships can also affect community composition. Finally, plants frequently compete for the services of pollinators and seed dispersers; such competition can have a profound impact on the reproduction and long-term abundance of different species.

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 may also utilize the toxic substances produced by the plant to gain a degree of protection from its own predators.

An ecosystem consists of nonliving elements and two different kinds of living elements—autotrophs and heterotrophs. 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 properties of ecosystems have been studied especially well 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. 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, less than 20 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 three or four 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, mass, and numbers.

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, for example. 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 occur when the gaps are formed grow rapidly under sunny conditions and have other characteristics different from those of the trees that dominate the mature forest. Eventually succession may result in the production of a climax community, which reproduces itself indefinitely unless there are major environmental changes.

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. Succession after volcanic eruptions, 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.