Chapter 27

Ecology and Plant Communities

THE NATURE OF PLANT COMMUNITIES

Each Plant Community Has Unique Attributes
Plant Communities Change over Time

VEGETATION TYPES

Tundra Vegetation Occurs beyond Timberline
Boreal Forest Is the Taiga of North America
Eastern Deciduous Forest Has a Complex Physiognomy
Grasslands Cover One-Fifth of North America
Desert Scrub Is Dominated by Shrubs
Chaparral and Woodland Are Mediterranean Vegetation Types
Pacific Coast Conifer Forests Are the Most Massive in the World
Upland Conifer Forests Have a Wide Distribution
Wetlands and Aquatic Ecosystems Are Productive

CONSERVATION BIOLOGY

Ecosystem Restoration

SUMMARY

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Nature in Flux or Nature in Balance?*

KEY CONCEPTS

1. A plant community is a group of recurring species that: share a characteristic habitat; collectively create a unique physiognomy; attain a typical range of species richness, annual productivity, and standing biomass; and through which nutrients and energy pass at predictable rates and with predictable efficiency. North America contains thousands of plant communities.

2. A vegetation type is composed of many communities that differ only in the identity of dominant or associated species, or both, but that otherwise share a similar physiognomy and environment. Two-thirds of North America is covered by only three major vegetation types: boreal forest, grassland, and tundra.

3. Successional plant communities change over time, whereas climax plant communities do not show any directional change, although they may fluctuate from year to year.

4. Conservation biology is a relatively new science that investigates ways to preserve, restore, and maintain biotic diversity in the face of human exploitation of natural ecosystems.

27.1 THE NATURE OF PLANT COMMUNITIES

Most plant populations do not grow in isolation. Single populations do not usually monopolize a habitat to the exclusion of all other organisms. Normally, there is a mixture of coexisting plant and animal populations, as well as of many less visible fungal, algal, and bacterial populations.

Wherever a particular habitat repeats itself within a region, many of the same species recur. The species composition does not replicate itself completely, but there is a nucleus of species that do repeat. These clustered species are said to be associated with each other and to be members of a biotic **community**. For simplicity, we can break down any community into its complement of animal, plant, or microbial species. Because this is a plant biology textbook, this chapter discusses communities from the standpoint of the plants they contain--that is, the plant community is discussed.

Every plant community is named after its dominant species and is characterized by its own roster of associated species and their combined architecture. For example, high peaks in the Great Smoky Mountains of North Carolina all have red spruce *(Picea rubens*) and Fraser fir (*Abies fraseri*) trees as the tallest layer of vegetation. The conifers are rather dense, and their canopies usually touch, creating a deep shade (Fig. 27.1). Beneath this needle-leaf canopy is a second, much more open layer of vegetation of scattered mountain ash trees (*Sorbus americana*). Mountain ash is a deciduous broadleaf species that sheds its leaves in the fall. A final layer of vegetation carpets the ground and consists mainly of ferns, mosses, and broad-leaved herbaceous perennials.

The spruce and fir populations are said to **dominate** the community because they contain the largest individuals and contribute the most biomass. By being the largest, they create the microenvironment within which smaller associated species live.

The architecture of this red spruce-Fraser fir community can be summarized as having three canopy layers: the uppermost is almost continuous and is made up of needle-leaf evergreens; the second is open and is made up of shorter, broadleaf trees; and the third is a continuous ground layer of herbs. The habitat is high-elevation, north-temperate, winter-cold, with well-drained soils. Wherever this habitat appears in the Appalachian Mountains, the spruce-fir community recurs.

Figure 27.1. A red spruce (*Picea rubens*)-Fraser fir (*Abies fraseri*) forest community in the Appalachian Mountains of North Carolina.

There are many other plant communities in the Appalachian Mountains. They are dominated by different species with different growth forms--such as shrubs, grasses, broad-leaved evergreen trees, or broad-leaved herbs. If we expand our vision to the entire North American continent, we could identify thousands of different plant communities. In addition, we could discern blendings or mixtures in **ecotones**, where two or more communities and environments grade into each other.

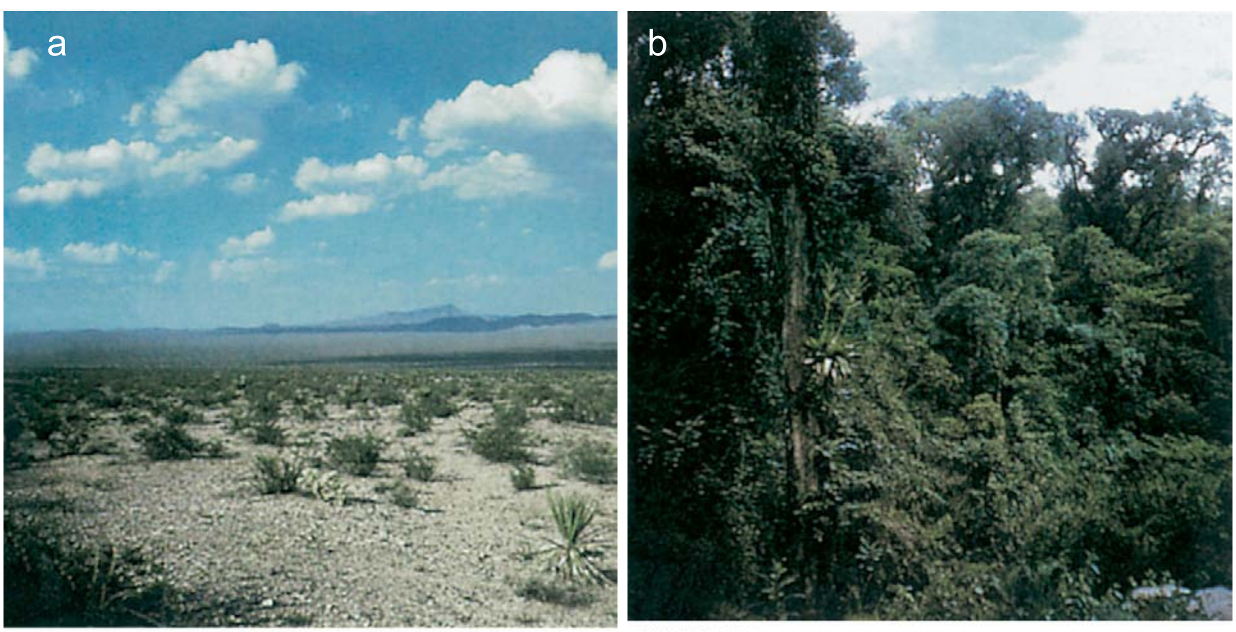
Each Plant Community Has Unique Attributes

Each plant community has features that transcend a mere list of member species. These features, or **attributes**, have to do with community architecture, species richness, the spatial patterns in which individuals are arranged, the efficiency with which they trap sunlight and cycle energy or nutrients through the community, and the stability of the associated species in the face of environmental stress or change. These attributes are summarized in Table 27.1; a few of the attributes also are discussed in the following paragraphs.

PHYSIOGNOMY   The architecture of an Appalachian spruce-fir community was described earlier in this chapter. A technical synonym for community architecture is physiognomy. **Physiognomy** is the external appearance of the community, its vertical structure, and the growth forms that dominate each canopy layer. A desert community, consisting of only a single canopy layer of widely scattered shrubs (Fig. 27.2a), might have 10% canopy cover or less--that is, 10% of the ground is directly beneath the foliage of the shrubs; 90% is open and unshaded. A tropical rain forest, with several overlapping tree layers (Fig. 27.2b), has 100% canopy cover.

Table 27.1 Some Attributes of Plant Communities
Physiognomy (architecture)
Canopy cover and leaf area index
Growth forms of dominant species
Spatial pattern
Timing of life cycle events (germination, bud break, flowering, leaf drop)
Species diversity and richness
Productivity
Biomass
Efficiency
Allocation of biomass (roots, stems, leaves, reproduction)
Nutrient cycling
Nutrient demand
Location and size of storage pools
Efficiency
Change over time (succession)
Primary vs. secondary
Progressive vs. retrogressive

Figure 27.2. (below) Communities with different physiognomies. (a) Desert scrub in southern Nevada, dominated by creosote bush (*Larrea tridentata*), has a single open canopy layer. (b) A tropical rain forest in northern Argentina has several tree canopy layers.



Another attribute of the canopy has to do with its thickness--that is, the number of layers of overlapping leaves through which light must pass on its way to the ground. Canopy cover does not measure this attribute, but leaf area index (LAI) does. LAI is the total area of leaf surface (one side only) for all leaves that project over a given area of ground. If the leaf and ground areas are measured in the same units (so many square meters of leaf surface per square meter of ground), then LAI becomes a dimensionless number. The desert community mentioned earlier in this chapter has an LAI of 1, and the tropical rain forest has an LAI of 10. The optimal LAI for crops such as corn is 4. Plant corn so densely that the LAI is greater creates too much shading for the lowest leaves.

SPECIES RICHNESS Biotic diversity, a term often used by the news media, simply means the total number of species that occur in a given community or region. In this sense **species richness** is synonymous with **diversity**. Communities differ in the number of associated species they contain. Tropical rain forests appear to have the greatest diversity of plant species, up to 365 per 10,000 m^2. Temperate forest and woodland communities have more moderate diversities of 50 to 100 species in a similar area, and desert communities have less than 50 species in the same area.

Not every species in a community is equally important. A few species are represented by many individuals, a few species are rare, and most are intermediate in abundance. It is the relative scale of importance of each species that collectively gives the community its unique physiognomy. The importance of each species can be quantified by counting the **density** of individuals (the number per square area), its canopy cover, its biomass, or its **frequency** of occurrence in the community. A widely dispersed population has individuals that would be frequently encountered, whereas individuals that are clumped together would be encountered less often (Fig. 27.3).

BIOMASS AND PRODUCTIVITY Communities differ in the amount of biomass that they have above and below ground. Tropical rain forests, for example, may have up to 500,000 kg of aboveground biomass per hectare, whereas desert communities have only 1% of that amount. Allocation of biomass above and below ground also varies with the community. Forest communities typically have five times as much biomass above as below ground. Another way of saying this is that the **root-to-shoot biomass ratio** of a forest is 0.2. In contrast, scrub communities have equal amounts of biomass above and below ground--the ratio is 1.0. Grassland communities have more biomass below ground than above ground--the ratio is 3.0.

Communities also differ in the amount of biomass they produce each year, their **productivity**. Those communities with the greatest biomass usually are the most productive because they have a great LAI with which to trap solar radiation. High-biomass communities also tend to live where the growing season is longest, another factor contribution to productivity. Thus, tropical rain forest communities have an annual productivity of 20,000 kg per hectare, compared to only 2,000 kg per hectare for deserts.

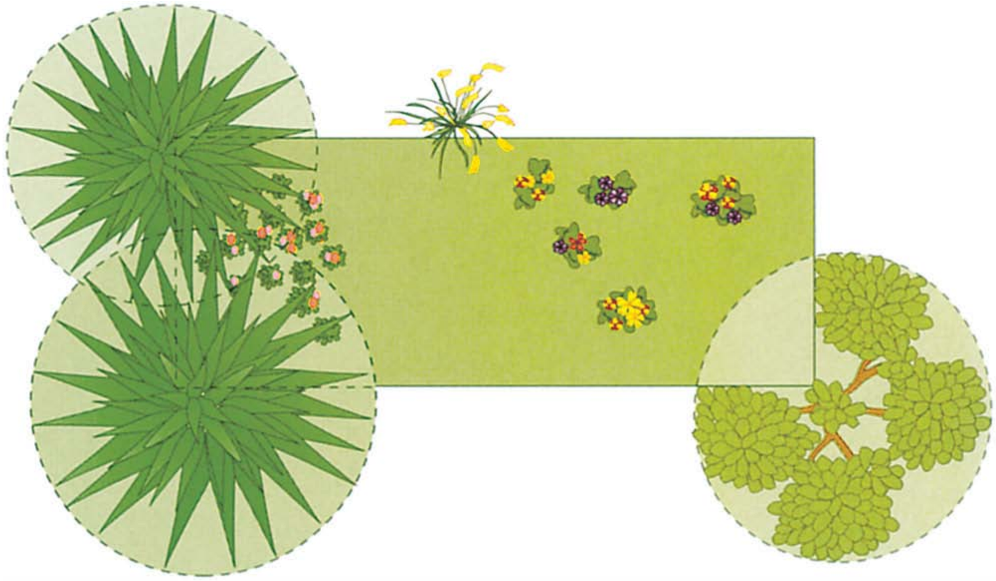


Figure 27.3. The importance of a species to its community can be measured by its density, canopy cover, and frequency. A rectangular frame outlines a sample within a desert scrub community, as seen from above. Density is the number of individuals of a species within the sample area. Cover is the percentage of the sample area shaded by each species. Frequency is a measure of the dispersion of members of a species and it cannot be estimated from one quadrat (counting frame). A species present in three out of four quadrats would have a 75% frequency. Dotted lines show rounded out canopy edges.

NUTRIENT CYCLING Communities differ in their demand for mineral nutrients from the soil, in the locations where such nutrients travel and accumulate, and in the rate at which they are returned to the soil or are lost from the ecosystem by erosion. This process of nutrient uptake, use, and return is called a **nutrient cycle**.

The nitrogen cycle (Fig. 27.4) for example, moves nitrogen from inorganic to organic forms and back again. Nitrogen gas (N_2) in the air is ordinarily not available to plants, which can absorb nitrogen only as ammonium (NH_4^+) or nitrate (NO_3^-). The biological process of nitrogen fixation accomplished by certain bacteria converts nitrogen gas into ammonium. Volcanic action also creates ammonium, as does lightning; this ammonium is then brought to the ground (and to plant roots) as ions dissolved in rainwater. Certain bacteria are capable of converting ammonium into nitrate.

Once in plants, the ammonium or nitrate is metabolically altered, moved onto amino acids, and then incorporated into proteins, nucleic acids, alkaloids, and many other molecules. Some of the nitrogen returns to the soil when leaves are shed or when the plant dies. Certain soil microbes convert the organic forms of nitrogen in litter back into ammonium, and others change the ammonium into nitrite (NO_2^-) and then into nitrate. Above 10% of the nitrogen in a plant is passed on to the next generation in the form of stored food in fruits and seeds; another 10% is ingested by grazing animals and becomes part of their metabolism. When they excrete waste or

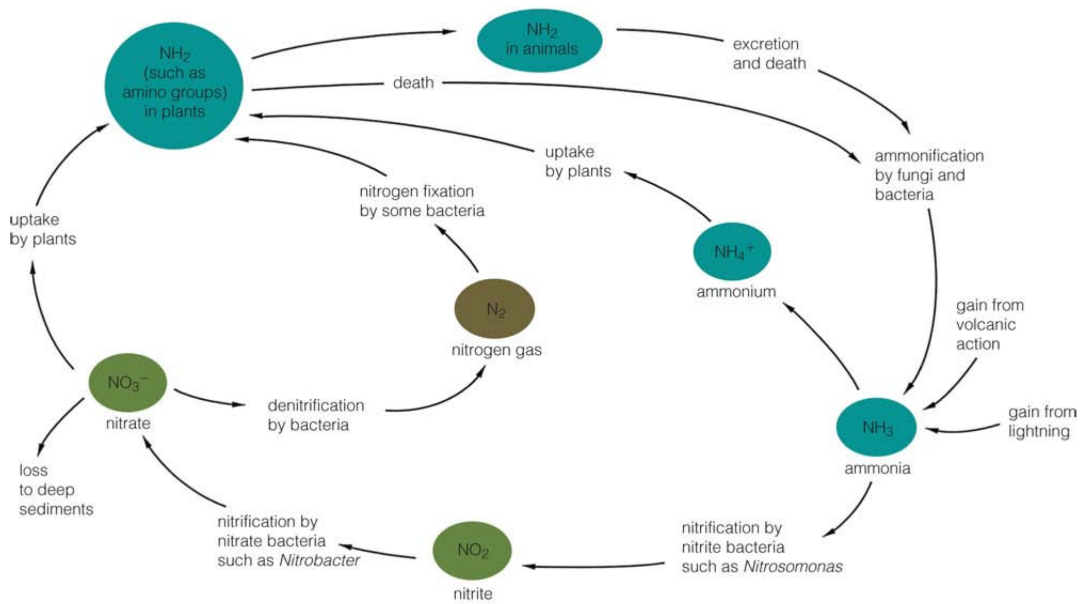


Figure 27.4. The nitrogen cycle. Blue: reduced forms of N; green: oxidized forms of N.

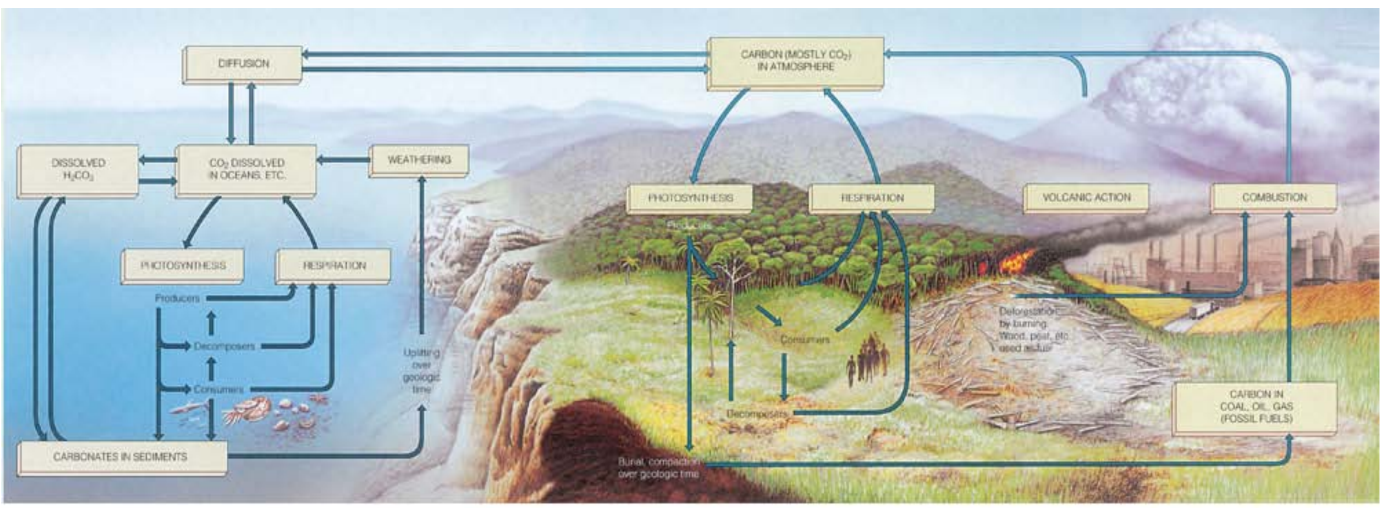


Figure 27.5. The global carbon cycle. The portion of the left shows movements of carbon through the marine ecosystem; on the right, movement of carbon through land ecosystems.

die, their nitrogen is converted into ammonium, nitrite, and nitrate by the same microbes that decompose plant remains.

Similar nutrient cycle diagrams could be prepared for sulfur, carbon (Fig. 27.5), water, and phosphorus. The details of each cycle, the rates of nutrient movement within it, and the overall efficiency are different from community to community.

Tropical forest communities, for example, contain broadleaf trees with a high demand for nitrogen and other nutrients. The forest trees store nutrients in trunks for long periods, and they return only a small fraction of the nutrients to the soil each year through leaf shedding and decomposition. The largest pool of nutrients in this particular ecosystem (80%) is in the wood. Decomposition, from litter to humus to soil, is rapid, the half-life of litter decomposition being less than 1 year because of continuously warm temperatures and adequate moisture. Most nutrients released to the soil are rapidly taken back up by a dense network of fine roots in the topsoil. Consequently, topical soils tend to be low in residual nutrients. There is little loss of nutrients from erosion, because the soil is covered with vegetation and anchored in place by dense roots. Most minerals are said to have a long residence time in the ecosystem, and the cycling of nutrients is "tight."

Northern forest communities, in contrast, contain conifer trees with a low demand for nutrients. These trees have a small pool of nutrients in their wood (33%), and they return more nutrients to the soil in an annual rain of litter. The half-life of litter decomposition is slow (10 years) because of cold temperatures; therefore, litter accumulates in a thick layer. The largest pool of nutrients in this ecosystem (60%) is in semi-decomposed litter called humus. Soils tend to be low in nutrients because they are acidic. Conifer foliage contains high amounts of organic acids, which dissolve cations in the soil, allowing them to be leached from the root zone. The cycling of nutrients in such a community is "loose."

Plant Communities Change Over Time

The microenvironment within a plant community is very different from that outside. Temperature, humidity, soil moisture, and light are all affected and modified. A stable community consists of K-selected species whose seedlings can survive to maturity in this unique microenvironment. Seedlings of species from other communities are at a disadvantage and cannot normally invade.

CHARACTERISTICS OF SUCCESSION If the stable community is removed by some disturbance--such as landslide, storm, canopy fire, or logging--then the soil surface is exposed, and the microenvironment has changed. The first species to colonize the site after the disturbance usually are not those of the old community. They are seedlings of r-selected species adapted to open sites. Only after a passage of time, when the biomass of invasive species had altered the microenvironment, will species of the old, stable community gradually return. The process of community change at one place over time is called *plant succession*.

Succession has limiting characteristics at population and community scales. For example, the death of one individual and its replacement by another is not succession. For evidence of succession we must instead look to change over a larger area than just the space taken up by one individual. Succession also has a maximum area limit because it must occur with a uniform macroenvironment. When we begin to cross soil boundaries or zones of elevation or latitude, the area is not longer homogeneous, so the changes that we see from place to place are not the result of succession. Succession generally occurs over an area from one hectare to several square kilometers (10^4 to 10^7 m^2).

Succession usually is measured over the course of several years to several hundred years. Thus, plant changes from season to season are not succession because they merely reflect life cycle phases. Succession does not occur over time periods shorter than a year. Furthermore, we all know that the environment is not constant from year to year. In good years, the biomass, productivity, and species richness of a community will be different from those in poor years. These random fluctuations in a community over relative short periods are not part of succession. There also is a maximum time--certainly shorter than 1,000 years--because succession must occur within a constant macroenvironment. Once we reach scales of time that incorporate global climate change, the community changes we see are not part of succession.

STAGES OF SUCCESSION Succession proceeds from pioneer to climax phases. For example, in parts of the southeastern United States, oak-hickory forests seem to be stable. If such a forest is cleared and then abandoned, the path of succession is as follows: the first plants to invade are annual and perennial herbs that grow well in high light intensity, such as horseweed (*Conyza canadensis*), *Aster pilosus*, and broomsedge (*Andropogon virginicus*). These make up a **pioneer stage** (Fig. 27.6a).

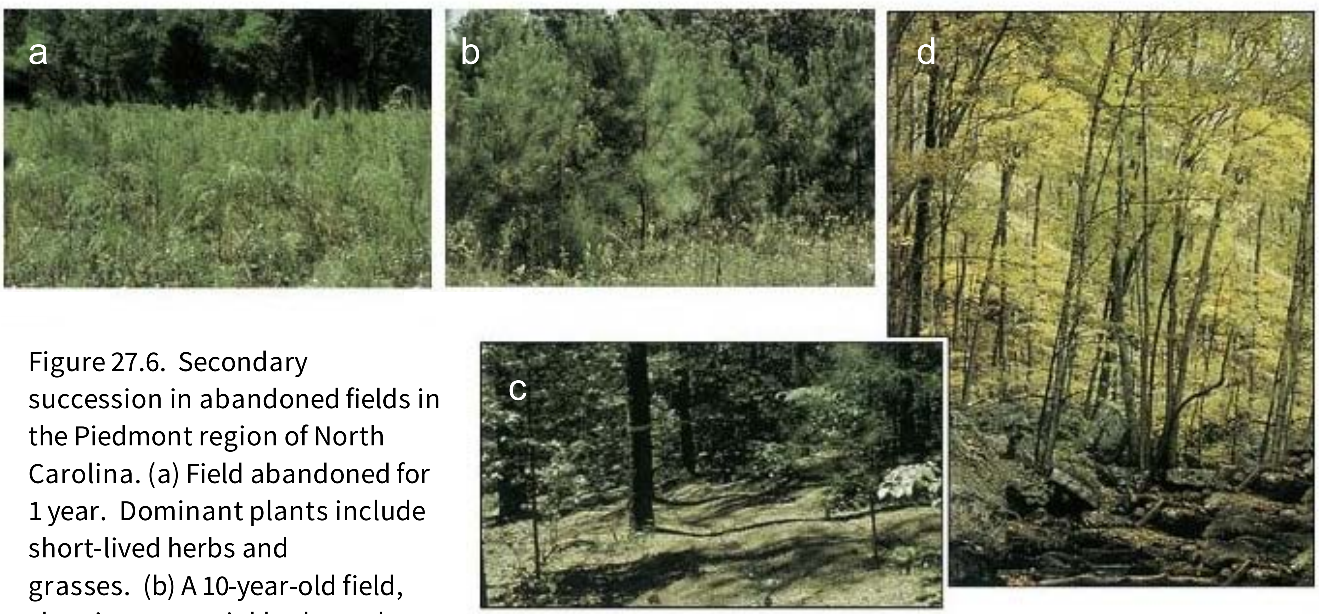


Figure 27.6. Secondary succession in abandoned fields in the Piedmont region of North Carolina. (a) Field abandoned for 1 year. Dominant plants include short-lived herbs and grasses. (b) A 10-year-old field, showing perennial herbs and pine saplings in the background. (c) Pine stand on field abandoned for 50 years. Old furrows are still obvious in the picture. The understory is dominated by broad-leaved tree seedlings. (d) Mature deciduous forest that has developed on a field abandoned for 150 years.

Pine seeds blow in from large, old pines that grow as scattered individuals in the surrounding oak-hickory forest. They are more readily dispersed than the heavier seeds of oak (*Quercus*) and hickory (*Carya*). They also germinate and grow well in semi-open habitats. Within 10 years of the disturbance, many short pine saplings are visible (Fig. 27.6b). As the pines grow, their emerging canopies begin to alter the microenvironment. Some of the pioneer herbs do not maintain their populations and disappear from the community or become rare. Within 30 years of the disturbance, a pine savanna has grown up (Fig. 27.6c).

Examination of the herb layer beneath the pines shows many oak and hickory seedlings and few pine seedlings. Pine seedlings grow poorly in shade and under conditions of root competition for moisture from other trees, but those of oak and hickory are more tolerant of shade and competition.

As described in Chapter 26, if fire sweeps through the pine savanna community frequently enough, the oaks and hickories are selectively eliminated. But if fire does not visit this community, succession continues. In this case, within 50 years of disturbance, a well-defined understory of hardwood saplings and young trees exists beneath the pines (Fig. 27.6b). Whenever a pine dies, it is replaced in the upper canopy by a maturing oak or hickory. Within 200 years of the disturbance, the forest again consists of mature oak and hickory trees with an occasional old pine. The dense grass understory of the pine savanna has disappeared and been replaced by shrubs and herbs associated with oak and hickory (Fig. 27.6d). The stable oak-hickory forest community is the end point of succession and is called the **climax stage**.

The succession just described is an example of **secondary succession**, which takes place on vegetated land. **Primary succession** occurs on newly exposed ground not previously occupied by plants. Examples of new land include mobile sand dunes, volcanic lava flows, mud exposed by a drop in lake water level, bare rock scraped clean by a retreating glacier, or the infilling of a small lake. The rate of succession is slower in primary succession for several reasons. First, the parent materials may be bedrock, coarse sand, or wind-blown silt--all of which lack clay particles and thus essential nutrients. Second, there is no bank of plant seeds, bulbs, or rhizomes already in the soil, left over from a predisturbance community. Primary successions often take several hundred years, whereas secondary successions may take only decades.

Many community traits change during succession, and these are summarized in Table 27.2. Basically, these changes make the community more complex and massive, the cycles of energy and nutrients more efficient, and the microenvironment less stressful. These changes are the result of **progressive succession**.

But not all succession is progressive. For example, Figure 27.7 is a summary of primary succession on Alaskan floodplains left dry when a river meanders and changes form. A first, progressive succession (clockwise in Fig. 27.7) leads to increasing herb cover and then to invasion by willow (*Salix*) and alder (*Alnus*) shrubs. Alders can fix nitrogen in their roots, so soils become richer. Biomass increases, shading the site. K-selected white spruce (*Picea glauca*) then invades the shade and slowly grows through the shrub canopy. As the spruce creates an overarching tree canopy, the r-selected alders decline in the deepening shade.

Now **retrogressive succession** begins, reversing the process, so that the community becomes simpler and less massive, cycles of energy and nutrients less efficient, and the microenvironment more severe. The mature spruce canopy creates a cold, dense shade. One consequence is that *Sphagnum* moss invades the ground surface; this moss has the capacity to retain large amounts of water, and it

Table 27.2 Comparison of Some Community Traits during Early and Late Stages of Progressive Succession

Trait	Early Stages	Later Stages
Biomass	Small	Large
Architecture	Simple	Complex
Nutrient pool	Soil	Vegetation
Mineral cycling	Loose	Tight
Productivity	High	Low
Stability	Low	High
Species diversity	Low	High
Life history	r-selected	K-selected
Site quality (microenvironment)	Extreme and not well-developed	Moderate and well-developed

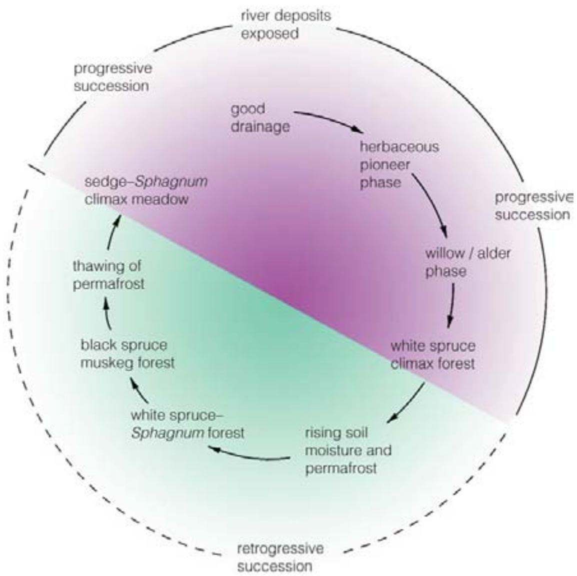


Figure 27.7. Progressive (purple) and retrogressive (green) succession on an Alaskan floodplain.

literally raises the water table. The shade and think layer of *Sphagnum* cools the soil, allowing a permanently frozen layer (**permafrost**) to rise toward the surface. White spruce requires well-drained soil and a deep water table, so it begins to die. Scattered, stunted black spruce (*Picea mariana*) trees replace the declining white spruce. Black spruce woodland permits more light to reach the ground, heating the soil and melting back the permafrost, creating an even wetter habitat. Consequently, the soil becomes shallow and soggy, and an open bog or muskeg replaces the spruce forest. Retrogressive succession ends in a meadow with dwarf shrubs, grasses, and sedges as the dominant growth forms.

27.2 VEGETATION TYPES

Plant communities blend into each other. Every species has its range limits, and at those limits each can be replaced by some other species that may have a similar growth form and niche. Therefore, the name of the plant community will change as the species range limits are crossed, but the architecture of the vegetation and the general habitat might stay the same. So long as the architecture and environment remain constant, several sequential communities all belong to a single vegetation type.

The term **vegetation** refers to the dominant growth form, not to the dominant species. Each vegetation type has a two-part name that describes the dominant growth form and the habitat; the name does not include any information about species. Thus, we have upland conifer forest, tropical rain forest, alpine tundra, eastern deciduous forest, tidal marsh, and desert scrub (scrub = shrub) vegetation types, among many others. The Appalachian red spruce-Fraser fir community fits within a more widespread vegetation type called subalpine conifer forest, which includes spruce-fir communities from the Rocky Mountains and the Cascade Range, as well as pine-hemlock communities from the Sierra Nevada.

There are, then, many fewer vegetation types than communities. North American has thousands of communities but fewer than a dozen major vegetation types (Fig. 27.8). Most of the world's major vegetation types are represented in North American, except for extremely arid deserts and several tropical grassland, savanna, and forest types. This chapter describes nine of North American's major vegetation types, beginning in the north and moving clockwise through the continent. The vegetation, of course, is simply one component of the regional ecosystem, but because of limited space, our descriptions will not dwell on such other ecosystem components as animals, microbes, and certain environmental factors. These large, regional, climatically controlled ecosystems often are called **biomes**.

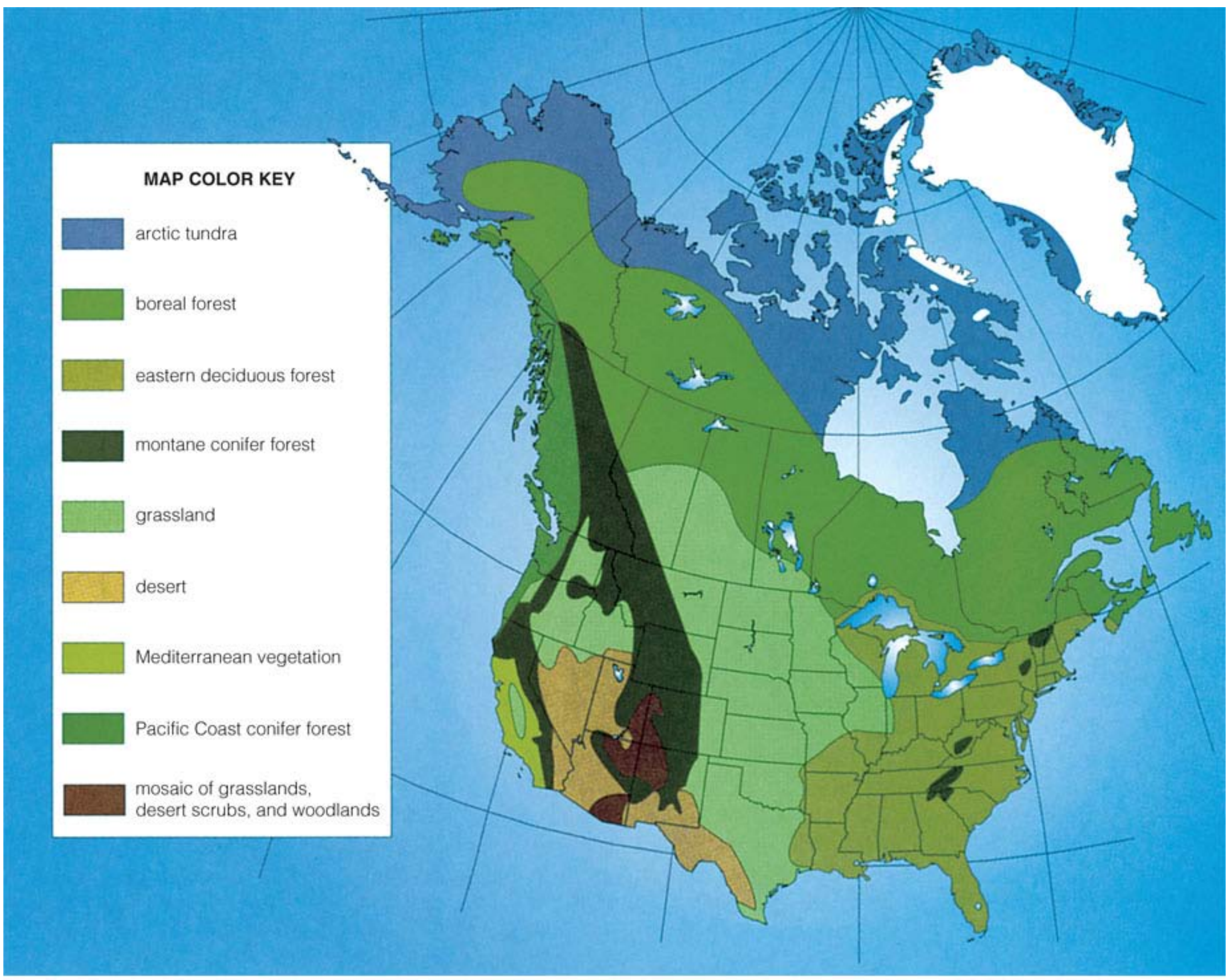


Figure 27.8. Major vegetation types of North America.

Tundra Vegetation Occurs Beyond Timberline

As one travels north toward the pole, trees gradually become scattered, stunted, and less common. They finally disappear completely in a zone called timberline. At the same time, low shrubs, perennial herbs, grasses, and sedges become dominant. Most of the biomass is below the soil surface and the root-to-shoot ratio is high (about 4). Shrubs are dwarfed, gaining normal height only in the protection of boulders or small hills. The winter wind, carrying drying air and ice, acts like a sandblast, pruning back stems wherever they project above the top of snow or beyond a protecting object. Perennials produce many large flowers, but the most successful reproduction is by rhizomes. Annuals are rare. This is **tundra**, a word derived from Finnish or Lapp, meaning a "marshy hill." Vegetation ecologists, however, use the word to describe vegetation (Fig. 27.9a), not topography. This vegetation type covers 19% of North America's land area.

Tundra is one-layered vegetation with nearly 100% cover at its southern extent, but decreasing to 5% to 50% cover at its northern limits. Similar vegetation occurs at lower latitudes in mountains, at elevations above timberline (Fig. 27.9b). The climates of the two tundra regions--arctic and alpine--have both similarities and differences. In both regions the warmest month has an average daily mean temperature of 10ºC or less. The growing season is short, only 2 to 3 months of the year having average daily temperatures above freezing. During the growing season, the top 30 cm of soil thaws, and roots may freely penetrate it; below this depth, soil and water are frozen year-round in an impermeable, meters-thick permafrost layer. Annual precipitation is less than 25 cm; thus, winter snowpacks are shallow and only deep enough to cover and insulate the low-growing vegetation. Few plants have evolved to tolerate this environment. Only 700 species in North America have ranges that extend into the arctic tundra.

Figure 27.9. Tundra vegetation. (a) Arctic tundra at high latitudes in Alaska, north of timberline. The antlers are from a caribou. (b) Alpine tundra at high elevation above timberline at 3,500 m in southern Colorado.

The **alpine tundra** differs from the **arctic tundra** in that summertime solar radiation and temperatures near the soil surface are greater; also, **thermoperiods** have a broader range than in arctic tundra. An alpine plant could experience leaf temperatures of 30ºC at midday and -5ºC at night, for a 35ºC thermoperiod. During the same 24-hour period, an arctic plant would experience a weak sun that never sets and temperature extremes of only 15ºC maximum and 5ºC minimum, for only a 10ºC thermoperiod. Alpine tundra plants share many of the environmental stresses felt by desert shrubs thousands of meters lower in elevation: strong winds, high solar radiation, short growing season, low soil moisture, and widely fluctuating temperatures.

Boreal Forest Is the Taiga of North America

South of the arctic tundra lies a broad belt of low-elevation conifer forest, the **boreal forest**. It covers 28% of North America. At the forest's northern limit, trees meet and mingle with the tundra, and they can be shrublike and slow growing. The critical environmental factor determining the location of timberline is the amount of heat received during the growing season. The growing season in the boreal forest is 3 to 4 months in duration, and temperatures can be much warmer than in the tundra. Annual precipitation is 30 to 90 cm, most of it falling in summer, so water is not limiting. Winter temperatures, however, can be even lower than they are in the tundra because oceans--with their moderating effect on temperature--are more distant. Soils are relatively young, acidic, and leached of nutrient. Some soils beneath the northern portion of the boreal forest have a permafrost layer.

This vegetation has a two-layered architecture. Trees are slender, short (15-20 m in height), and relatively short-lived (less than 300 years), but they are densely packed (Fig. 27.10). The Eurasian term for this vegetation, **taiga**, means "dense forest." Carpeting the ground beneath the overstory canopy is a continuous layer of bryophytes, seedless vascular plants, and herbaceous perennial angiosperms. Disturbance by storms and wildfires recurs every 200 or more years, affecting large areas and initiating secondary succession. Black spruce (*Picea mariana*), one of the most widespread trees in the boreal forest, is a **closed-cone conifer** well-adapted to fire. As an intense fire sweeps through a black spruce forest,

Figure 27.10. Boreal forest in northern Canada, adjacent to a clear-cut.

killing all aboveground vegetation, the millions of sealed cones are forced open by the heat, and for days after the burn a quiet rain of seeds falls on an ash-rich seed bed. A new black spruce forest will replace the old one.

Eastern Deciduous Forest Has a Complex Physiognomy

In the east at about 45°N latitude, boreal softwoods give way to deciduous hardwoods as the growing season increases to 6 months and annual precipitation climbs above 100 cm. Wingers are cold, but they are neither as intensely cold nor as long as in the boreal forest. Soils are richer in nutrients and less acidic. This is the **eastern deciduous forest**, a vegetation type dominated by a diversity of broadleaf, winter-deciduous tree species (Fig. 27.11a). Along the southern limits of the forest, at about 30°N latitude, winters are mild enough for evergreen broadleaf trees to mix, as a minor element, with deciduous trees. Precipitation declines to the west, where arid grassland exists as a boundary to the forest. Sometimes the transition from forest to grassland is abrupt, and sometimes it is many kilometers wide. The important ecotone between woody and herbaceous vegetation meanders north to south along the line at 95°W longitude.

The eastern deciduous forest, which covers 11% of North America, is a complex mix of communities. Little of this forest has escaped human impact. Native Americans influenced its structure for thousands of years by burning the understory. They maintained an open forest to encourage populations of birds and grazing animals used for food. Before the forest changes brought about by European colonists, forest buffalo and grouse grazed as far east as New York State. In 200 to 300 years, Euro-Americans modified the forest further by clearing, selective cutting, grazing, or accidentally introducing foreign pathogens and weeds. The modern forest no longer resembles the descriptions by early explorers. The forest overstory of Ohio and Pennsylvania, for example, was once dominated by 400-year-old oaks (*Quercus*), sugar maples (*Acer saccharum*), and chestnuts (*Castanea*) 1 to 2 m in diameter at breast height, with straight trunks rising 25 m before the first side branch. Black walnuts (*Juglans*), shagbark hickories (*Carya*), and cottonwoods (*Populus*) grew in flood plains near rivers and were big enough to be made into dugout canoes 20 m long and more than 1 m across. Currently, only a few forest reserves contain remnants of this ancient forest.

Seasonality is a striking feature of eastern deciduous forests. Overstory leaves turn brilliant yellow, red, and orange in autumn. After winter dormancy, the first green of spring comes from a diversity of herbaceous perennials on the forest floor (Fig. 27.11b). These species take advantage of a narrow time window when light and temperature permit rapid growth. As the overstory canopy completes its expansion of new leaves, these spring-flowering herbs shed seeds and enter dormancy. Two intermediate canopy layers--between the ground herbs and overstory trees--consist of scattered shrubs (many in the heath family) and small trees such as dogwood (*Cornus*). In addition, many vines (such as Virginia creeper, *Parthenocissus quinquefolia*), grow up through all of the tree and shrub canopies.

Figure 27.11. The eastern deciduous forest. (a) The leafy overstory canopy changes color in autumn, just before leaves drop. (b) Active spring growth of perennial herbs occurs before the new overstory completely leafs out.

Grasslands Cover One-Fifth of North America

Across an east-west expanse of perhaps 100 km, we pass through a gradient of increasing aridity and a series of vegetation types. At the west edge of the deciduous forest, the overstory tree canopy becomes discontinuous, and herbaceous plants begin to form a continuous ground cover. Forest becomes woodland and then savanna, steppe, and finally grassland. **Woodland** is grassland with overtopping trees whose canopies cover 30% to 60% of the ground; **savanna** is grassland with overtopping trees that are regularly present but whose canopies cover less than 30% of the ground; **steppe** is grassland interspersed with shrubs. **Grassland** (synonym, **prairie**), finally, is vegetation dominated by herbaceous plants growing in a climate too dry for trees (Fig. 27.12). Trees may be present, but they are restricted to special, localized topography, such as along waterways or on rocky ridgelines with thin soil. Perennial and annual grasses dominate the biomass, but broad-leaved dicot herbs (forbs) dominate in terms of numbers of species.

Some plant geographers have concluded that there is no such thing as a grassland climate. Their argument is that grasslands replace woodlands for reasons other than gradients in climate. A certain annual precipitation--for example, 50 cm--could support grassland, savanna, woodland, or forest. Grassland is favored in those places where variation in rainfall from year to year is high, creating years of

Figure 27.12. Grassland on rolling hills in North Dakota.

drought that alternate with years of above-average precipitation. Grassland also is favored in fire-type climates, where the probability of wildfire revisiting the same hectare of land every 1 to 3 years is high. In addition, grassland is favored where growing temperatures are high enough and air humidity low enough to promote transpiration. In forest, the ratio of incoming precipitation to outgoing transpiration is greater than 1; but in grasslands, the ratio decreases to 1 or just below. Finally, grassland is favored where soils are deep and texture is loamy to clayey.

Grasslands once covered 21% of North America. The largest area of grassland occupies the center of North America, from Alberta, Saskatchewan, and Manitoba in the north to Texas in the south. It consists of tall-grass, mixed-grass, and short-grass prairies. Other major grass-lands include: (1) along the edge of warm deserts in Texas, New Mexico, and Arizona; (2) scattered through the intermountain Great Basin (with a finger extending into the Palouse area of southeastern Washington and outliers in the Willamette Valley of Oregon); and (3) within the Central Valley of California.

All of our grasslands have been significantly modified by Euro-Americans in the last 200 years. Most of the central grasslands have been cleared and plowed, converted into farmland. The desert grasslands have been overgrazed and fire has been suppressed; as a result, desert shrubs have invaded. The intermountain, Palouse, and California grasslands have been overgrazed and invaded by aggressive annuals from Eurasia (for example, cheatgrass, *Bromus tectorum*), as well as having had many hectares converted to farmland, pasture, and urban sprawl.

Desert Scrub Is Dominated by Shrubs

Scrub is any vegetation dominated by shrubs. It occurs where either precipitation or the water storage capacity of the soil is too low to support grassland. Thorn scrub, chaparral, and desert scrub are examples. **Desert scrub** occurs where annual rainfall is less than 25 cm and a pronounced dry season exists every year. The annual precipitation-to-transpiration ratio decreases to 0.1. Another feature of desert climate is the high variation in rainfall from year to year, so that the concept of an average rainfall is meaningless. Desert vegetation covers only 5% of North America.

Deserts generally are warm to hot during the summer, but they may be quite cold in winter. The high-elevation intermountain desert, for example, regularly receives snow and hard frost every winter; this stress reduces species and growth form diversity (Fig. 27.13). The low-elevation and more southerly Sonoran desert has almost no frost; it has a greater diversity of species and growth forms. The two other North American deserts--the Mojave of southern California and Nevada, and the Chihuahua of Texas, New Mexico, and Mexico--are intermediate in elevation and temperature regimens.

Figure 27.13. The Great Basin desert vegetation has a uniform one-layered scrub architecture dominated by sagebrush shrubs (*Artemisia tridentata*). Warm desert vegetation is more diverse and includes succulents, trees, and drought-deciduous shrubs.

Associated with shrubs in the warm deserts may be succulent cacti, green-stemmed trees, subshrubs, herbaceous perennials, and ephemerals. Total ground cover may be 50% at the maximum and 5% at a minimum. Other parts of the world have more extremely arid climates than North America and in those places plant cover may be less than 1%.

All plants in desert scrub must be adapted to survive extended droughts. There are five basic techniques for drought tolerance or avoidance. One is the **phreatophyte** syndrome, a suite of traits shared by woody plants hat have deep roots in permanent contact with groundwater. These plants have green stems and leaves that are winter deciduous. Their leaves are well supplied with water during the hot summer, and therefore they are under stress (of cold temperature) only in wintertime, which is when the leaves are shed.

Other shrubs with shallower roots retain their leaves only during the wet season and drop them during dry seasons; this is the **drought-deciduous** syndrome. Drought-deciduous leaves are thin and energetically inexpensive; they can be cast off and remade several times a year (Fig. 27.14).

A few shrubs, the true xerophytes, have evergreen leaves. They are able to tolerate the desert dry season because their metabolism proceeds at a slow rate the entire year. Under prolonged drought, some of the leaves may be shed; but if all fall, the plant dies. Their leaves are typically small and have many anatomical features that retard transpiration.

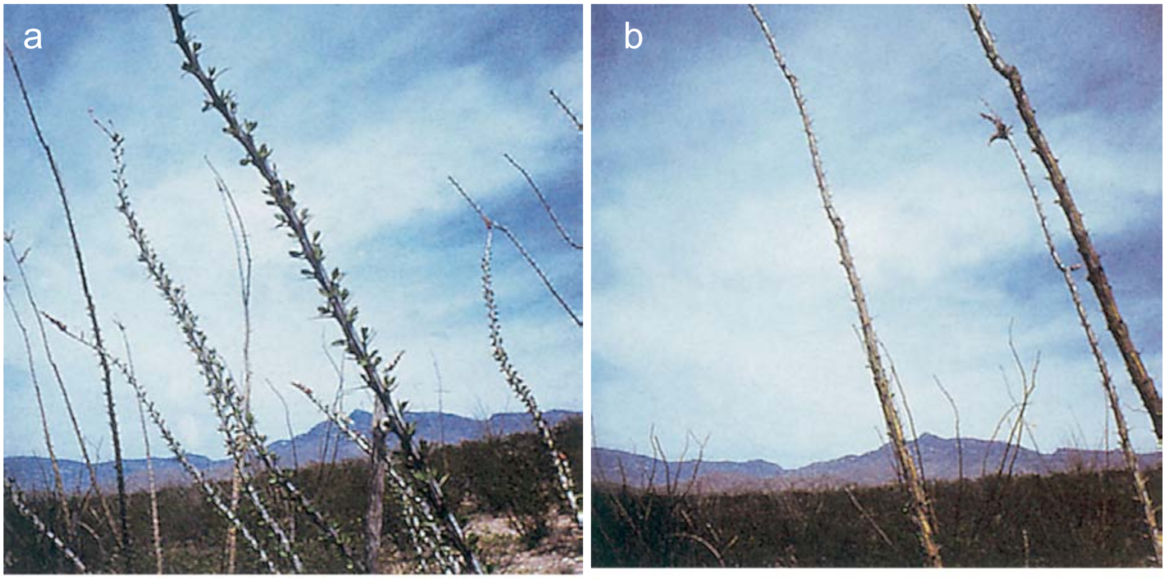


Figure 27.14. Coachwhip (*Fouquieria splendens*), a drought-deciduous plant that is able to shed and remake several crops of leaves each year. (a) Plant with leaves, soon after heavy rains. (b) Same plants, leafless during a later dry period.

Succulents, such as cacti, store water in the vacuoles of large cells. They typically exhibit *crassulacean acid metabolism,* which features stomata that open at night and close in the day, thereby lowering transpiration. Their leaves and bodies also minimize the amount of surface of a given volume or mass, another feature that reduces transpiration. Cacti have shallow root systems, capable of absorbing moisture from even light rains. Succulent plants appear to avoid drought, rather than tolerate it.

Ephemerals exhibit a fifth syndrome: they live for 6 weeks to 6 months and complete their life cycle during the wettest, least stressful part of the year. They avoid the drought season by passing through it in a state of dormancy, as seeds. Although woody plants dominate the desert biomass, ephemerals contribute the most species.

Chaparral and Woodland Are Mediterranean Vegetation Types

Mediterranean climates and vegetation are found in five locations throughout the world: (1) the Mediterranean rim of southern Europe, the Middle East, and northern Africa; (2) the Cape region of South Africa; (3) southern and south-western Australia; (4) central Chile; and (5) California. All these regions lie between 40 and 32 degrees N or S latitude. They occupy western or southwestern edges of continents, receive 27 to 90 cm of annual precipitation (mainly winter rainfall), have minimal frost, and experience episodic wild-fire. Mediterranean climates are fire-type climates, basically with hot, dry summers and cool, wet winters.

Vegetation is remarkably similar in these five areas, even though different families of plants predominate in each. Mediterranean vegetation ranges from forest (in the wettest locations) to woodland to scrub (in the driest locations). All these vegetation types are dominated by broad-leaved, evergreen, woody flowering plants, with a relatively high percentage of canopy cover.

Mediterranean scrub is called **chaparral**, derived from the Spanish as a term that generally means "low-growing" woody vegetation (in contrast to *forestal,* tall vegetation dominated by trees). Chaparral is dense, one-layered, and about 1 to 3 m in height; it is composed of rigidly branched shrubs with small, hard leaves and an extensive root system (Fig. 27.15a). In contrast to open desert scrub, chaparral has 100% cover and an LAI twice that of desert scrub. Herbs are uncommon.

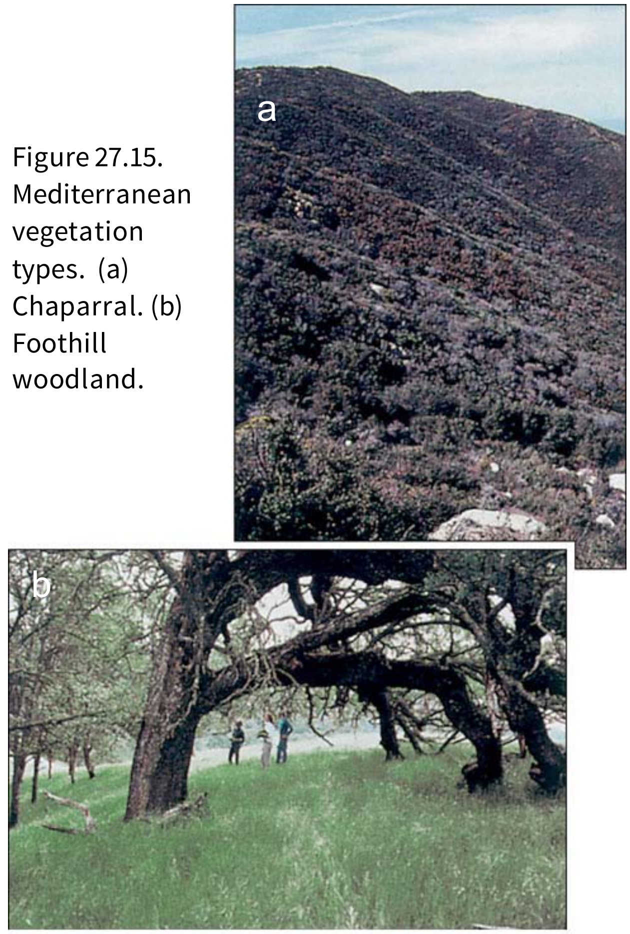


Figure 27.15. Mediterranean vegetation types. (a) Chaparral. (b) Foothill woodland.

Wildfire recurs every 20 to 50 years, consuming all the aboveground vegetation and producing very high temperatures. Chaparral shrubs respond to fire in several ways. Some are capable of sprouting from the root crown, which is buried beneath the soil surface and thus is insulated from high temperatures during the fire. Other have hard-coated seeds that lie dormant until cracked by moderately high temperatures. Some have seeds that are stimulated to germinate by some active ingredient in smoke. By both re-sprouts and seedlings, the chaparral community recovers its preburn cover and species composition within half a dozen years.

Chaparral grows on steep slopes with coarse, shallow soils, at elevations below 1,000 m. Nearby, within the same macroenvironment, are foothill woodlands, dominated by oak (*Quercus*) trees and underlain by grasses and forbs (Fig. 27.15b). Tree canopy cover is 30% to 60%. Woodland and chaparral vegetation types are spatially separated according to microenvironmental factors, not macroenvironmental ones. The woodland occupies gentler slopes, with deeper, less coarse soil, as well as moist north-facing or east-facing slopes, which burn less frequently than the drier chaparral sites.

Before the arrival of Euro-Americans, the woodland understory consisted mainly of perennial bunchgrasses. Because of the introduction of aggressive, weedy annuals in the last 150 years, the understory today consists mostly of annual grasses. These woodlands once supported the greatest population densities of Native Americans in all of North America. Oak acorns were the major resource that supported them. Acorns were easily collected every fall, leached of tannin, ground into flour, stored, and used the entire year, much as grains are used in other cultures.

Mediterranean vegetation covers only 1% of North America, but many people are familiar with it because California landscapes often are in the news--witness the ever-recurring catastrophes of wildfires, floods, landslides, earthquakes, and droughts--and because they serve as backdrops to many popular films and television programs.

Pacific Coast Conifer Forests Are the Most Massive in the World

The conifer forests of the Pacific coast are the most luxuriant, most productive, most massive vegetation type in the world. They are dominated by a rich diversity of big, long-living tree species underlain by equally rich canopies of shrubs, herb, bryophytes, and epiphytes (Fig. 27.16). The Pacific Coast conifer forests are situated in a low elevation strip of coastline that extends from Cook Inlet, Alaska, south to

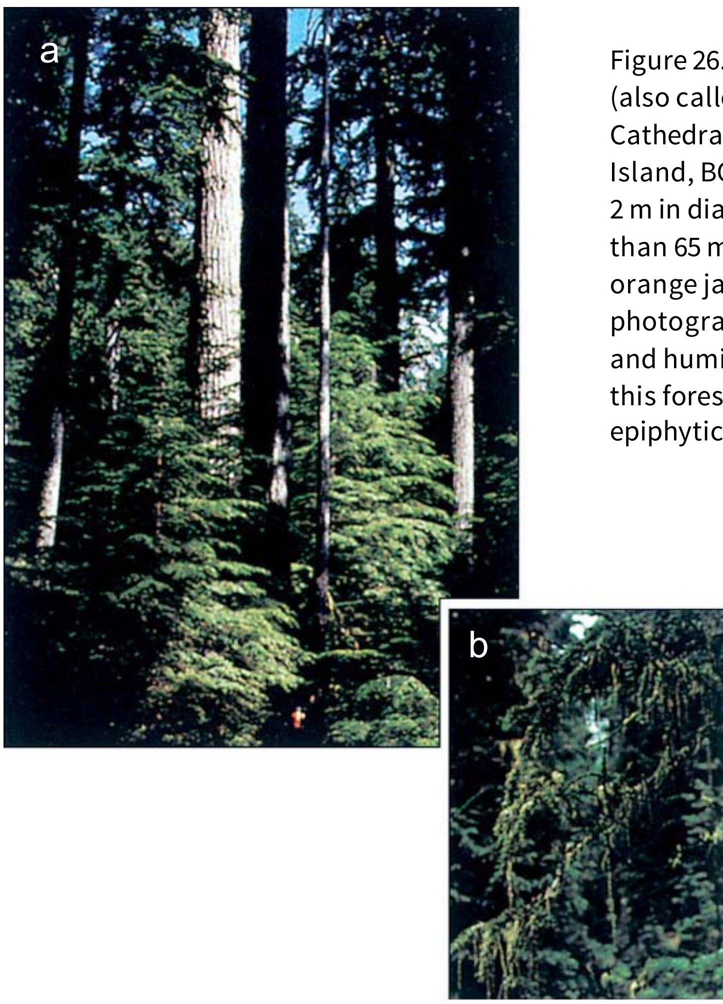


Figure 26.16. Pacific Coast conifer forest (also called a temperate rain forest). (a) Cathedral Grove Provincial Park, Vancouver Island, BC, Canada. The dominant trees are 2 m in diameter at breast height and more than 65 m in height. Note the person in the orange jacket near the bottom of the photograph. (b) Because of the high rainfall and humidity, tree trunks and branches in this forest support a rich assortment of epiphytic mosses and lichens.

Monterey, California. The climate is mild, buffered by the nearby ocean and summer fog banks; therefore, thermoperiods are only 6 to 10°C. Hard frosts are uncommon. Annual precipitation is very high, 80 to 300 cm, most of which falls in wintertime. Because of the climate, this type of forest often is called a **temperate rain forest**.

Dominant tree species include coast redwood (*Sequoia sempervirens*), Douglas fir (*Pseudotsuga menziesii*), lowland white fir (*Abies grandis*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). These trees all commonly live for 400 to 1,200 years and attain heights of 100 m. Annual productivity is as high as 25 metric tons per hectare. Standing biomass is typically 85 metric tons per hectare; in one particular location, it is as high as 230 metric tons per hectare. Tropical rain forest vegetation has a similar productivity, but its biomass is significant less.

Although this vegetation type covers only 3% of North America, its timber volume and value have been highly significant to both local human communities and distant corporations during the past century. Logging has had a heavy impact on the region. Conservationists, using the endangered northern spotted owl as a symbol of logging threats to biotic diversity have managed to decrease the intensity of logging in the United States in recent years. Canada has not yet reduced its harvest of coastal forests in British Columbia, however, and clear-cuts in British Columbia are said to be among the few human artifacts visible from orbiting spacecraft.

Upland Conifer Forests Have a Wide Distribution

Coniferous forests clothe the slopes of the higher Appalachian peaks, the Rocky Mountains, the Cascade-Sierra Nevada axis, the Coast Ranges of Washington and Oregon, and the Transverse and Peninsular Ranges of southern California. These upland forests are called **montane conifer forests**. The range from 65 to 19 degrees N latitude (well south, into the Sierra Madre of Mexico), and they cover 7% of North America. Annual precipitation increases from 60 cm at lowest elevations to more than 200 cm at highest elevations. Precipitation in winter is in the form of snow, and deep snowpacks can accumulate. Summers are warm and relatively dry. Montane conifer forests of the West are in a fire-type climate.

The structure, diversity, and productivity of montane conifer forests are intermediate between the two other conifer-dominated vegetation types described earlier, the boreal forest and the Pacific Coast forest. Many of our most popular national parks, the jewels of the park system, are located in this vegetation type: Glacier, Great Basin, Great Smoky Mountains (uppermost elevations), North Cascades, Rocky Mountains, Yellowstone, and Yosemite National Parks (Fig. 27.17).

Figure 27.17. Mid-montane conifer forest, Yosemite National Park, CA, about 2,000 m elevation.

Zonation of forest communities along elevation gradients is a common phenomenon. Lower montane (low-elevation) forests tend to be rather open savannas or woodlands, intermingled with species from adjacent grasslands, Mediterranean woodlands and chaparral, or deserts. Frequent wildfires seem to be essential to the maintenance of some of these communities, and they have been significantly degraded by overgrazing and changes in fire frequency over the last 150 years. Pinyon pines (*Pinus monophylla* and others), ponderosa pine (*Pinus ponderosa*), and junipers (*Juniperus scopulorum* and others) are common woodland trees.

Mid-montane (intermediate-elevation) forests are typically rich in overstory species, such as Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine (*P. ponderosa*), and many regionally limited tree species. A variety of shrubs in the heath and rose families also are common, as are seasonally present herbaceous perennials.

These are complex, four-layered forests that often require wildfire to maintain their structure. They need surface fires that burn relatively cool, consuming only litter, shrubs, and young trees. Under fire suppression management, these forests change their physiognomy, becoming denser. Then, when a surface fire does start, and the presence of a fire-type climate assures us that it will eventually start, the surface fire will "ladder" up the younger trees and become a raging, destructive crown fire (Fig. 27.18).

The mid-montane elevation belt contains many other vegetation types besides forest. Perhaps half the area is interrupted by meadow or scrub vegetation. **Meadow** is grassland that occurs within a climate capable of supporting forest vegetation. Forbs often dominate meadows, grasses being reduced to associate status. Forest is absent here because of local topography or soil that creates seasonally wet conditions. **Montane scrub** occurs on rocky ridges, on south-facing slopes, or as a temporary successional stage after wildfire. In the latter case, forests will slowly reclaim the site by growing through the scrub and shading it out.

Figure 27.18. Forest fires can be surface fires (left) or crown fires (right). Recurrent natural wildfires keep many montane forests open, so first remain on the ground and consume only litter, shrubs, and young trees. Fire temperatures are moderate, and mature trees usually survive. Fire suppression, however, allows more trees of all sizes to coexist; thus a surface fire can ladder up to the crowns of the tallest trees, becoming hotter and killing all above-ground vegetation.

Upper montane and **subalpine** (highest-elevation) **forests** are densest and simplest and experience the deepest snow packs. Fir (*Abies*), hemlock (*Tsuga*), pine (*Pinus*), and spruce (*Picea*) are the dominant genera. This is the elevation zone of the oldest individual plants in the world, the bristlecone pines (*Pinus longaeva*; Fig 27.19).

Figure 27.19. Bristlecone pine (*Pinus longaeva*) in the subalpine zone of the White Mountains of California. This species occurs on high peaks throughout the Great Basin, and individuals can reach 5,000 years of age.

Wetlands and Aquatic Ecosystems Are Productive

SALINE WETLANDS Wetlands are terrestrial sites where the upper soil is saturated by saline or fresh water for at least a few weeks of the year. Tidal wetlands, or salt marshes, are coastal meadows subject to periodic flooding by the sea (Fig. 27.20). They occupy nearly level shores that receive only low-energy waves, such as are found along estuaries or tidal flats behind barrier islands or sandy peninsulas. Environmental stresses include flooding--bringing mechanical disturbance and anerobic conditions--and salinity. As the ground slopes up toward land, however, these two stresses decline in frequency and intensity.

Figure 27.20. Tidal wetland (salt marsh) vegetation.

The vegetation is usually a single, low-growing, nearly closed layer of perennial herbs. The soil beneath is crowded with rhizomes and roots. The flora is rather simple, with only a handful of species coexisting in a given local wetland. Tidal wetlands along the entire Atlantic and Gulf coasts of the United States support less than 350 vascular plant species, and those along the entire Pacific coast, from Point Barrow to the tip of the Baja California peninsula, contain less than 80 species. Apparently, not many species have the genetic capacity to tolerate tidal marsh stresses. A few have enormous ranges that extend through nearly all coastlines of North America: arrow-grass (*Triglochin maritimum*), cord-grass (*Spartina aterniflora*), pickleweed (*Salicornia virginica*), saltbush (*Atriplex patula*), and salt grass (*Distichlis spicata*).

Some of the traits these successful species exhibit are succulence, asexual reproduction by rhizomes, and **aerenchymna tissue** in stems and roots that channels oxygen down into the anaerobic soil.

Enormous losses of acreage in tidal wetlands have occurred during the twentieth century. Tidal wetlands have been diked, drained, filled, and converted to farmland, ports, and cities. We have discovered their ecological value rather late. One ecological function these wetlands serve is as a biological filter for runoffs from the land, which contain pollutants and excessive nutrients. The marsh and its soil act as a sieve, cleaning the water before passing it on the ocean. Another ecological function is as a nursery for the young of many aquatic animals, including commercially valuable fish. Although salt-marsh vegetation has a low profile, its annual productivity is as great as that of a tropical rain forest. The plants are herbaceous, however; therefore, this tremendous amount of new plant biomass does not accumulate as woody tissue. Instead, it is shed each year into the water, where it fuels an extensive food chain through microbes, algae, plankton, invertebrates, fish, and humans.

Along exposed coasts that receive the full brunt of wave action, a **rocky intertidal** ecosystem replaces the salt marsh. Flowering plants are few in the rock intertidal zone, but they include surf grass (*Phyllospadix*), a relative of other sea grasses more commonly found in quieter harbor waters. Many seaweeds and a few kelps also are attached to rocks in this habitat, each at its own particular depth within the intertidal zone. The different depths at which they are distributed probably reflect different degrees of adaptation to the stresses of exposure.

Below the intertidal zone is the **neritic zone**. This aquatic ecosystem is a rocky shelf always covered by water but shallow enough to admit adequate sunlight for attached algae to grow along the bottom. Many kelps grow in the neritic zone, especially in cool-temperate oceans. As in the intertidal zone, different species of algae dominate at different depths (Fig. 27.21). The pattern of distribution probably reflects differing tolerance among algal species to low light. Both quality and quantity of light change with passage through water. The compensation depth, where positive growth is not longer possible, is usually shallower than 170 m.

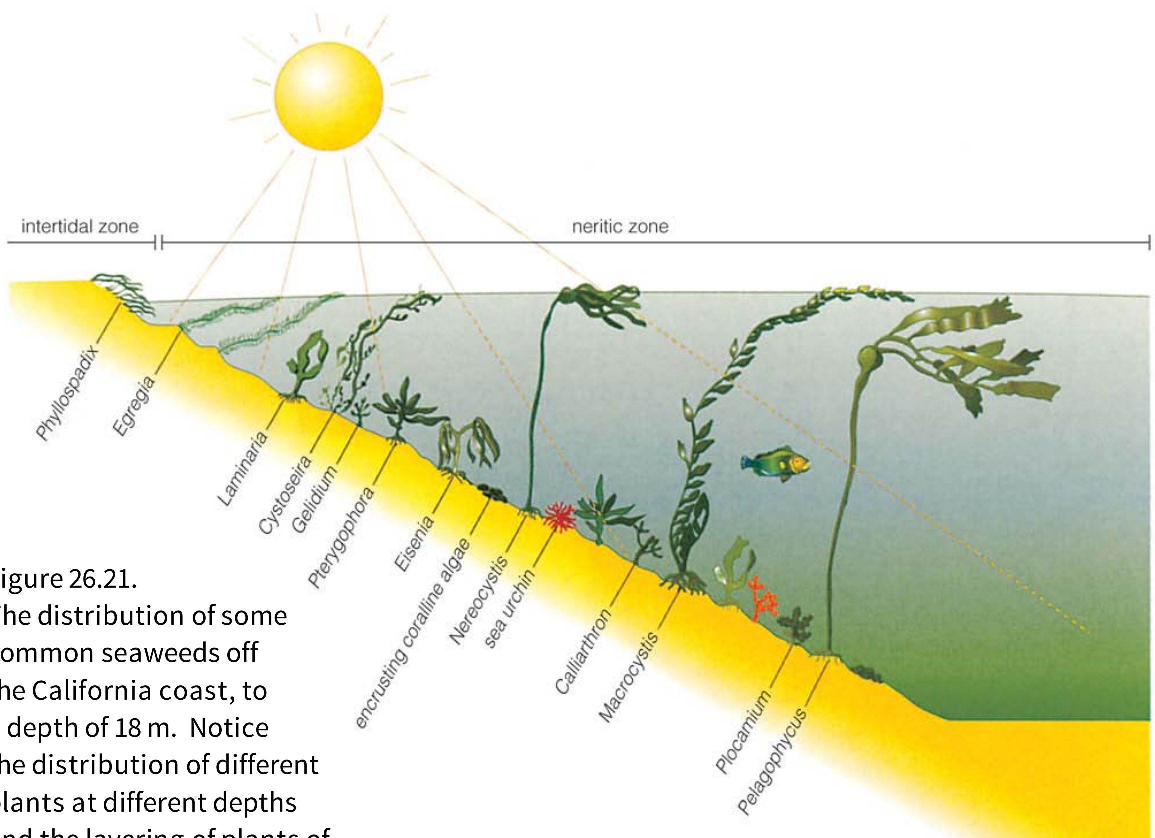


Figure 26.21.
The distribution of some common seaweeds off the California coast, to a depth of 18 m. Notice the distribution of different plants at different depths and the layering of plants of different sizes.

In deep oceanic bodies of water, the habitat between the surface and the compensation depth is dominated by phytoplankton. One exception is the Sargasso Sea off Bermuda, where large, floating masses of *Sargassum* seaweed are present. This seaweed may play an important role in the survival of young sea turtles, giving them a place to feed and hide from predators until they become large adults.

FRESHWATER WETLANDS **Freshwater wetlands** are found along the shorelines of lakes, rivers, sinks, seeps, and springs. Trees, shrubs, and herbs that occupy these habitats must be tolerant of occasional flooding, and they must be resilient to the physical disturbance of floodwater. They often have fast growth rates, produce abundant wind-distributed seed, and are capable of vegetative reproduction. This fringe of vegetation is ecologically important as a filter of eroded soil and nutrients that otherwise would enter adjacent aquatic ecosystems and degrade them. The filtering function is exceptionally important in the modern landscape because intensive agricultural practices add fertilizers and pesticides to the land.

At shallow margins of freshwater aquatic ecosystems (Fig. 27.22) are flowering plants such as sedge (*Scirpus, Carex, Cyperus*), cattail (*Typha*), pondweed

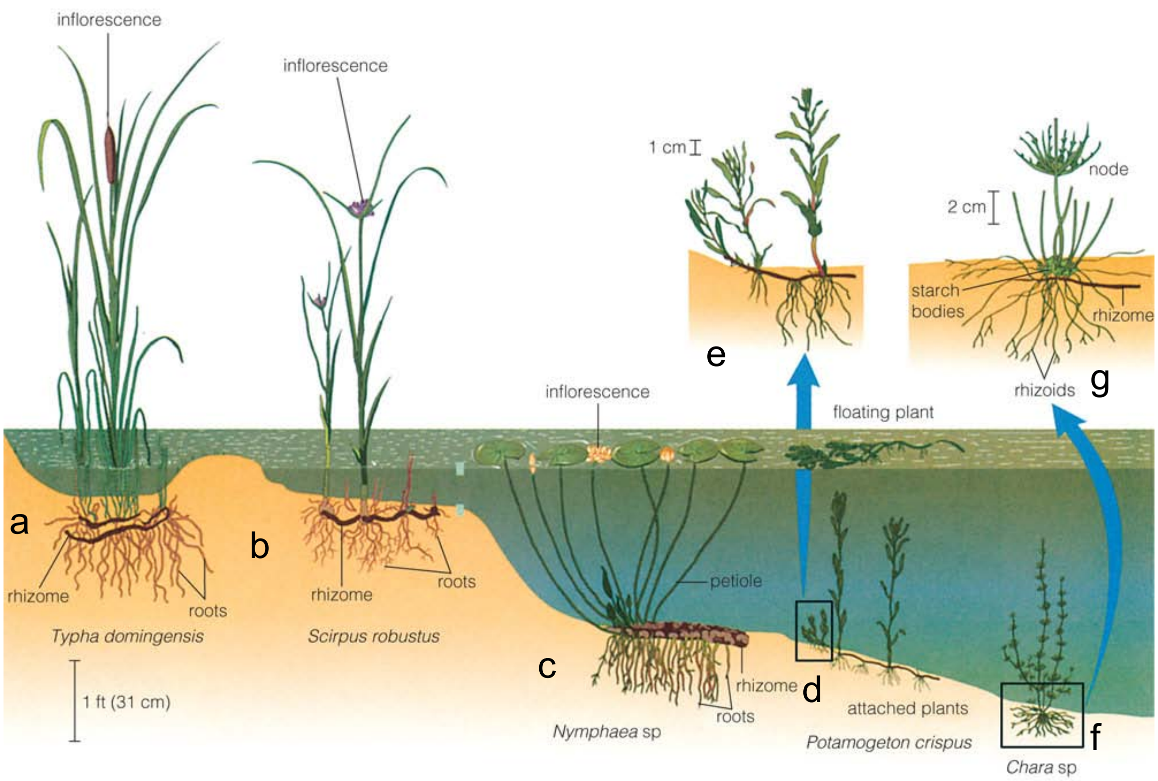


Figure 17.22. Freshwater ecosystems support flowering plants and algae. (a) Cattail (*Typha domingensis*). (b) Sedge (*Scirpus robustus*), more tolerant of flooding than cattail. (c) Water lily (*Nymphaea*), with floating leaves and flowers. (d,e) Submerged and floating segments of pondweed (*Potamogeton crispus*). (f,g) The stonewort *Chara*, a complex alga differentiated into rootlike rhizoids and rhizome-like and stem-like regions.

(*Potamogeton*), and water lily (*Nymphaea*). These are called emergent aquatic plants because, although rooted under water, some part of the plant body extends above the water surface. Associated with them are algae (diatoms, green algae, golden algae) that grow attached to the muddy surface or epiphytically to other plants.

In somewhat deeper water, submerged or floating flowering plants are common, associated with larger algae such as stonewort (*Chara*). If lakes are deep enough, their water may stagnate into zones. An upper zone, the **epilimnion**, is relative warm, and sunlight is intense enough to support large phytoplankton populations. Oxygen levels in the epilimnion are high. Below the epilimnion is a narrow transition zone where temperature declines rapidly with depth, on the order of $4^{o}C$ per meter. This is the **thermocline**, and it serves as a barrier to any mixing between the upper epilimnion and the lower **hypolimnion**, which extends to the bottom of the lake. Phytoplankton may occur in the hypolimnion, but only at low densities.

This chapter concludes with some thoughts about how this diversity of vegetation may be maintained into the future.

27.3 CONSERVATION BIOLOGY

Each year, the extent of natural vegetation grows smaller. Vast areas of some vegetation types, such as tundra and boreal forest, still remain as wilderness, but many of our deciduous forests, grasslands, deserts, woodlands, montane conifer forests, and tidal wetlands are endangered. They are threatened by timber harvest, land conversion, water diversion, the spread of weeds and pathogens, and even by the recreational impact of too many people in too small a place.

Only a generation ago, **conservation** meant a rate of natural resource consumption that would result in sustained, continued existence of that resource far into the future. We are beginning to understand that humans have great difficultly in staying within boundaries that would sustain a particular resource. Our species has had a sad, consistent history of overshooting these balance points. Our farming, fishing, and forestry activities have consistently led to overexploitation and decline of natural resources. Consequently, conservation now usually means the restricted use, nonuse, or preservation of some natural resources.

Conservation biology is a relatively new science that studies the impact of human societies on the nonhuman landscape. Conservation biologists ask the question: can a growth-oriented, technological culture coexist with its surrounding natural systems? We know that non-technological cultures, such as those of Native Americans, did coexist with their surrounding natural systems for thousands of years, but we recognize that their demands on nature were much different from ours.

Conservation biologists are investigating ways to measure sustainability. How do we know when a plant or animal population is maintaining itself? How do we measure biotic diversity? How do we design parks so that the probability of extinction for any rare population is as low as possible? How do we restore degraded habitats and their plant and animal communities? How do our technological activities interweave with the biosphere in unexpected ways to create global stresses (acid rain, ozone depletion, climate change, pollutants carried through food chains)? And how might we best modify these technological activities to reduce the stress?

Conservation biology is an exciting field, but its contributions will be limited if our human population continues to increase. In the middle of the twentieth century we numbered 3 billion, and we reached 6 billion by the start of the twenty-first century. Sustainability is an unattainable myth in the face of such climbing population pressure on the Earth. Without a doubt, the control of human population growth as been and remains the greatest challenge our species must solve.

Ecosystem Restoration

Some vegetation types and entire ecosystems cannot be conserved because they have been largely changed by recent human activities. Exotic weedy plants and animals have invaded and become widely established, reducing the abundance or even eliminating some native species. Domesticated livestock have caused severe surface erosion. Dams no longer permit the seasonal fluctuation in the volume of water that previously characterized a river. The program of fire suppression management has led to forest thickening, loss of species richness, and epidemic tree mortality during period droughts. Perhaps relictual, unchanged examples of a particular ecosystem exist in small, scattered, remote locations, but for all practical purposes, these ecosystems have been completely degraded.

In such cases, active management techniques have to be used to reverse the human-caused changes and bring back the previous ecosystem. Such a reversal is called **ecosystem restoration**, and it is a rapidly developing area of research and practice. One advantage of restoring a habitat, vegetation type, or ecosystem is that the restored system tends to be self-maintaining, requiring less investment in terms of human attention. Another advantage of restoration is that **ecosystem services** increase; such valuable attributes of an ecosystem include soil stabilization, protection against catastrophic fire, the filtering of contaminants from agricultural runoff, the provision of maximum biodiversity, and the moderation of temperature.

Restoration techniques imitate natural successional or disturbance processes. For example, if a forest type has become too dense because of decades of fire suppression management, then a fraction of the trees are cut and removed (the stand is thinned), followed by the setting of a prescribed fire that imitates a natural (lightning-started) fire. The prescribed fire is started during weather conditions that keep the flame front short and moving slowly. Thereafter, at set intervals of years that imitate the natural fire-return interval, prescribed fires continue to be set (Fig. 27.23). Grasslands can be similarly restored to their previous species richness and composition by purposely setting fires every several years, or instead by instituting livestock grazing practices or mowing that imitates the seasonality and intensity of native animal herds--herds now depleted or even extinct.

Restoration has been somewhat successful in wetlands, grasslands, and certain forest types. It has been much less successful in such stressful settings as deserts, subalpine meadows, on mine spoil, and in areas damaged by smog or acid deposition. Restoration is a young science, and it will require decades of more experimentation and accumulated wisdom before we can confidently presume that a given degraded ecosystem can be restored. Until that time, the wiser course of action is to conserve what still remains.

Figure 27.23. Paired photographs taken before and after 64 years of fire suppression management near Ebbetts Pass in the Sierra Nevada of California. (a) In 1929. (b) In 1993. Thinning, followed by prescribed fire, has restored a similar forest (c) back to a condition that resembles the natural vegetation.

KEY TERMS

aerenchymna tissue
alpine tundra
arctic tundra
attributes
biomes
boreal forest
chaparral
climax stage
closed-cone conifer
community
conservation
density
desert scrub
diversity
dominate
drought-deciduous
eastern deciduous forest
ecosystem restoration
ecosystem services
ecotone
epilimnion
frequency
freshwater wetland
grassland (prairie)
hypolimnion
meadow
mediterranean climates
montane conifer forests
montane scrub
neritic zone
nutrient cycle
permafros
phreatophyte
physiognomy
pioneer stage
primary succession
productivity
progressive succession
retrogressive succession
rocky intertidal
root-to-shoot biomass ratio
savanna
scrub
secondary succession
species richness
steppe
subalpine forests
succulents
taiga
temperate rain forest
thermocline
thermoperiods
tundra
vegetation
woodland

SUMMARY

1. A plant community consists of a cluster of associated species that is similar wherever a particular habitat repeats itself. Plant communities are named after their dominant or characteristic species.

2. Plant communities have a characteristic architecture, or physiognomy, which is a combination of the external appearance of the community, its vertical structure, and the growth forms of each canopy layer.

3. Other community attributes include percent cover, LAI, species richness, productivity, biomass, allocation of biomass (to roots, woody tissue, leaves, reproductive organs), rate of nutrient cycling, and relative stability.

4. Plant communities change over time in a process called succession. Technically, succession is cumulative, directional change in a homogeneous area over several years to several hundred years. Secondary succession takes place on already vegetated land that is disturbed; primary succession takes place on new land not previously occupied by plants. Primary succession is much slower than secondary succession.

5. Progressive succession leads to increasingly complex and massive communities, in which the cycles of energy and nutrient flow become tighter and more efficient and the microenvironment becomes less stressful and more buffered. Retrogressive succession exhibits the reverse trends.

6. Plant communities blend gradually into each other over space because every species has its own range limits. However, the architecture and habitat may remain constant. All plant communities that share the same architecture and habitat belong to the same vegetation type. Vegetation types are named after location and dominant growth form, not after the dominant species. North American has thousands of plant communities, but many fewer vegetation types.

7. The major vegetation types of North America differ profoundly in their productivity, biomass, physiognomy, habitat traits, and in the portion of North America that they occupy.

8. Two-thirds of North America is covered by boreal forest, grassland, and tundra. Tundra is herbaceous vegetation that occurs where the growing season is too cool and short for trees. Arctic tundra is at low elevations in far northern latitudes, whereas alpine tundra is at high elevations in mountain chains at more southern latitudes. Grassland vegetation lacks trees because of periodic droughts, a low precipitation-to-evaporation ratio, recurring wildfire, and a fine soil texture. Boreal forest (taiga) is dense, short, and relatively low in biotic diversity. It occurs in a wide band just south of arctic tundra, where the growing season is 3 to 4 months long and the difference between winter and summer temperatures is relatively high.

9. Other North American forest types include the eastern deciduous forest, dominated by winter-deciduous broadleaf trees; the Pacific Coast temperate rain forest, the most massive vegetation type in the world; and montane conifer forests.

10. Nonforest vegetation types include Mediterranean scrub and woodlands, desert scrub, and wetlands. Mediterranean climate occurs in only five small parts of the world; in North America, it dominates California. Characteristic vegetation includes a dense scrub called chaparral and an open woodland of evergreen and drought-deciduous small trees.

11. Desert scrub plants are more dispersed than chaparral shrubs, and they grow in a more arid environment. All desert plants either tolerate or avoid drought, and

they do so by being phreatophytes, drought deciduous, true xerophytes, succulents, or ephemerals.

12. Wetlands are very productive vegetation types, and they play important filtering roles as a buffer between terrestrial and aquatic ecosystems. Wetlands may be saline or freshwater. Saline wetlands include salt marshes and rocky intertidal habitats; freshwater wetlands include riparian vegetation along the banks of rivers, lakes, springs, and sinks.

13. Conservation biology is a relatively new science that investigates ways to preserve, restore, and maintain biotic diversity in the face of human exploitation of natural ecosystems. Given the current global population growth, it will be difficult to develop a resource management plan capable of sustaining our natural ecosystems.

14. Restoration ecology seems to offer great promise in our ability to restore degraded ecosystems to health, but in fact, most successful restorations have been limited to wetlands or grasslands, both dominated by herbs. The restoration of scrub and forest vegetation types on stressful substrates has been far less successful. It will be several decades before the science and technology of restoration will be more useful.

Questions

1. Some ecologists believe that plant communities are very tightly organized, with the associated species being somehow interdependent on one another. How could you test this idea, either by observation of experimentation?

2. What traits do communities exhibit that individual plants or plant populations do not?

3. When Mount St. Helens erupted in the 1980s, the explosion blew down forest trees and covered the ground with a deep deposit of volcanic ash. Succession has been studied since the eruption, and it is proceeding slowly. Is this primary or secondary succession, or both?

4. In the boreal forest, storms often uproot and blow down every tree in a stand. Over time, herbs and shrubs invade and cover the site; then aspen may dominate, and conifers reinvade the site under the shade of the aspen. Later, the conifers overtop the aspen, and a boreal forest is re-established. Explain why this succession is progressive, rather than retrogressive.

5. Why is it critically important for tundra plants to be low-growing perennial herbs?

6. Describe the physiognomy (architecture and dominant growth forms) of the eastern deciduous forest.

7. Consider a desert phreatophyte, a cactus, and an evergreen shrub all growing near each other in a hectare of desert. Which one do you think would grow the least in 1 year, and why?

8. Why is wetland vegetation important to an adjacent aquatic ecosystem?

9. Do you think it is possible for humans to do all four of the following simultaneously: continue economic growth, continue population growth, maintain biological diversity, and attain sustainability in natural resource use? If not, how many of these four could be simultaneously achieved?

PLANTS, PEOPLE, AND THE ENVIRONMENT: ***Nature in Flux or Nature in Balance?***

A **paradigm** is any widely accepted viewpoint. In science, a paradigm is made up of a family of related theories that seem to explain some behavior in nature. Until recently, one classical paradigm in ecology was the **equilibrium paradigm**, which defined nature as dominated by stable, long-undisturbed climax ecosystems. An old-growth montane forest, one acre of central prairie, or a strip of undisturbed salt marsh was each seen to be in equilibrium, or in balance, with its environment. This paradigm and its metaphor, "the balance of nature," suggest that any climax unit in a landscape will maintain itself, especially if isolated from direct human interference.

An example of the application of this paradigm is Mettler's Woods, the last remaining uncut upland forest in central New Jersey. The forest, which had been protected since colonial days and eventually became a part of Rutgers University, is now know as the Hutcheson Memorial Forest Center. The forest was considered to be climax and thus self-perpetuating. No human disturbance was to be permitted. Visitors were only allowed entrance when accompanied by a qualified guide and restricted to a single trail.

The last 30 years of research have tended to show that this paradigm is incorrect. In the case of Mettler's Woods, merely protecting the forest from humans has not been sufficient to maintain it. The old oaks (*Quercus* sp.), the average age of which is 250 years, are senescing, falling, and leaving gaps in the canopy. The overstory is quite open, the mid-layer dogwoods (*Cornus florida*) have succumbed to a regional epidemic of the fungal disease anthracnose, and many species of shade-tolerant wildflowers have become rare. After severe defoliation of the oaks caused by gypsy moth caterpillars in the early 1980s, several sun-loving shrubs and herbs invaded the forest understory and today they continue to maintain large populations. Using insecticides to manage the gypsy moth population was considered to be inappropriate in a nature reserve, and so was not done. Although the oaks do produce large seed crops, there is an almost complete failure of seedling oaks to survive into the sapling category.

It is now understood that surface fires had been a regular part of the history of the forest before fire protection policies were adopted in 1711. Fire scars preserved in the trunks of the oldest oaks document that light surface fires used to occur every 10 years. Perhaps these fires cleared away competing herbs and shrubs, thereby permitting seedlings to survive. Thus, the paradigm--and the conservation strategy derived form it--have failed to preserve the forest.

Failures of the equilibrium paradigm became so numerous and well-known by 1980 that ecologists developed a new paradigm, the nonequilibrium paradigm. First it accepts natural systems as being open, meaning that they must be put into the context of their surroundings. Second, it recognizes that natural systems are subject to physical disruption from a wide range of natural forces and events such as fire, drought, windstorm, earth movement, volcanism, herbivore outbreak, disease epidemics, and so on. Third, the new paradigm permits the inclusion of humans in the scope of conservation. Once the importance of natural disturbances is recognized, it is a short logical step to include humans as just another agent of change. A metaphor for this new viewpoint is "nature in flux."

The simplest translation of the contemporary paradigm into conservation biology would state that conservation cannot always be passive, but must often involve active management. If natural disturbance had been a characteristic that preserved a particular ecosystem, then managed disturbances that mimic natural one must be created. Managed disturbances might include setting a prescribed fire, thinning and mulching young trees, biologically controlling certain insects or pathogens, weeding out invasive plants, or permitting seasonal flooding. The size of the reserve must be large enough to permit such episodic disturbances to run their course within a least a portion of the reserve.

The location of a reserve must be chosen in appropriate relation to the land use practices, politics, and social attitudes within adjoining parcels. All pieces of an ecosystem are not equally capable of preservation, and active management cannot be practiced safely everywhere. Preserves must be large enough to permit episodic wildfires to burn some patches and to permit the movement of displaced animals to adjacent, unburned areas. In addition, adjacent parcels must be compatible with a "let-burn" policy for wildfires. We need to demarcate entire landscapes as parks, preferably with surrounding buffers and with corridors that connect parks so that biota can move more widely. The complexities of compromise and management required for preserve management today are very challenging.

A modern approach to regional preserve planning is being attempted in southern California, where decades of residential development have displaced and fragmented a major regional vegetation type called southern coastal scrub (Figure). A number of rare plant and animal species are at risk for extinction if development continues on the scale of the past several decades. As an alternative to continued future habitat and biotic diversity loss, a consortium of federal, state, and local government agency planners, developers, environmentalists, and citizens of several counties joined together. Their object is to locate the best and largest remnants of the scrub, then to suggest optimal boundary shapes, to design corridors between preserves, to designate appropriate human activities within buffer lands next to the corridors and preserves, and to identify developable areas and transportation routes within the context of this mosaic of regional open space. Will this approach be successful? At the present time, we still do not know. But conservationists are hopeful that it will work because the old method of conservation has not been successful, when the ecosystems of focus have been close to urban centers.

(Portions of this essay were condensed from Pickett, STA, Parker VT, Fiedler PL. 1992. The new paradigm in ecology: Implications for conservation biology above the species level. In Fiedler PI, Jain SK, eds. *Conservation biology*. New York, Chapman and Hall, pp. 65-88.)

Photo Credits

CO T.M. Murphy
Fig. 27.1 Michael G. Barbour
Fig. 27.2 (a-b) Michael G. Barbour
Fig. 27.6 Norm Christensen, Duke University
Fig. 27.7 Redrawn from Drury WH Jr. 1956. Contributions from the *Gray Herbarium* 178:1-30 with permission.
Fig. 27.8 Redrawn from Barbour MG, Christensen N. Vegetation of North America. In: *Flora of North America*, Vol. 1. New Yourk: Oxford University Press, with permission
Fig. 27.9 (a) James McGraw (b) Michael G. Barbour
Fig. 27.10 Michael G. Barbour
Fig. 27.11 (a-b) Michael G. Barbour
Fig. 27.12 Michael G. Barbour
Fig. 27.13 Michael G. Barbour
Fig. 27.14 (a-b) Michael G. Barbour
Fig. 27.15 (a-b) Michael G. Barbour
Fig. 27.16 Michael G. Barbour
Fig. 27.17 Greg Vaughn/Tom Stack & Associates
Fig. 27.18 Drawing by M. Yuval from Marbour M et al. 1993. *California's Changing Landscapes*. Sacramento: California native Plant Society, with permission.
Fig. 26.19 Michael G. Barbour
Fig. 27.20 Michael G. Barbour
Fig. 27.21 Redrawn from M. Foster, with permission
Fig. 27.23 (a,b) From Gruell GE. *Fire in Sierra Nevada Forests*. Missoula, MT: Mountain Press, 2001. (c) Michael G. Barbour
PLANTS, PEOPLE, AND THE ENVIRONMENT Michael G. Barbour