Chapter 26

Ecology, Ecosystems, and Plant Populations

KEY CONCEPTS

1. Each organism has one of three roles in any ecosystem: producer, consumer, or decomposer. (a) Producers are green plants or protists that manufacture their own carbohydrate food from inorganic water and carbon dioxide. (b) Consumers are animals, pathogens, or parasites that obtain food by ingesting other organisms. (c) Decomposers are nongreen protists or prokaryotes that digest dead organic remains of producers and consumers.

2. Only about 1% of the solar radiation that reaches vegetation is absorbed and converted into metabolic energy, which can be measured as the caloric content of tissue. The transfer of metabolic energy by herbivores from plant tissue consumed to herbivore tissue is incomplete; only about 10% of available plant tissue is browsed and the rest remains uneaten. A similar small fraction of energy is transferred from herbivores to predators. Because only 1% to 10% of available energy is transferred at each level up the food chain, the maximum biomass at each level declines steeply, from producers to herbivores to predators.

3. A population is a local group of organisms belonging to the same species. Each population is genetically distinct. Most species have hundreds to thousands of unique populations, with each population subtly adapted to variations in the local environment. Thus, the population is the basic ecological unit of any species.

4. Every species can be assigned to one of a relatively small number of life history patterns. Each pattern represents a unique budget of time, activities, and resources that allows a population to continue in existence from generation to generation. Some of the activities budgeted are germination, growth, and reproduction.

5. The distribution of a population is affected by abiotic factors such as soil nutrient level, soil moisture availability, intensity of solar radiation, or the incidence of wildfire. Every plant must solve a zero-sum budget for dissipating incoming solar radiation energy into reflection, re-radiation, convection, metabolism, storage, and transpiration.

6. Distribution also is determined by biotic interactions with other species, such as competition (in which a substance is removed from the environment), amensalism (in which a substance is added to the environment), herbivory (consumption by an animal), and mutualism (cooperative behavior in which the probability of survival is increased for both interacting populations).

26.1 ECOSYSTEMS AND BIOMASS PYRAMIDS

Plant ecologists seek to find an underlying order to the pattern of plant distribution over the earth's surface.

What threads link plants to each other and to their environment? How flexible are those threads, and how intertwined? How has the process of evolution selected plant behaviors that permit plants to acquire enough energy and nutrients to grow, compete, deter herbivores, reproduce, and disseminate seeds to appropriate habitats? Are there as many ways to budget time and energy during a life cycle as there are species, or are there instead only a small number of successful "strategies" that many species share (Fig. 26.1)? How do plants either resist episodic stresses and disturbances or recover from them? What can certain species tell us, by their presence, vigor, or abundance, about the past and the future of a habitat? Can plants be used as scientific probes to analyze the environment, or as tools to restore degraded landscapes?

Figure 26.1. A 1-year-old conifer seedling. During its life span of several hundred years, the plant that grows from this seedling must successfully budget time and resources to satisfy the demands of growth, maintenance, reproduction, competition, and herbivore defense.

All these questions, and more, are being investigated by plant ecologists. The word **ecology**, derived from the Greek roots *oikos* ("home") and *logos* ("study of") was coined more than a century ago by the German zoologist Ernst Haeckel. Ecology is the study of organisms in their home, the environment. More generally, ecology is the study of organisms in relation to their natural environment.

Environment is the sum of all biotic (living) and abiotic (nonliving) elements that surround and influence an organism. Environment is synonymous with the terms *habitat* and *ecosystem*. Examples of biotic elements in an ecosystem are neighboring plants, animals, and soil microbes; examples of abiotic elements in an ecosystem are temperature, moisture, wind, sunlight, soil nutrients, and episodic fires. Depending on the organisms being studied, a habitat or ecosystem can be a few square centimeters of bare rock being colonized by mosses, a small lake filling with sediment, or an entire mountain range.

All the hundreds of species within any one ecosystem can be conveniently placed in a few **trophic** (nutritional) categories. Photosynthetic plants, whether seed plants, algal protists, or prokaryotes, are considered **producers** because they generate carbohydrate compounds from sunlight and inorganic chemicals alone. Herbivorous animals and plant parasites are **primary consumers**. Carnivorous animals are **secondary consumers**, and carnivores that consume secondary consumers are **tertiary consumers**. Carrion feeders, non-photosynthetic protists, and microbes are decomposers. Consumers and decomposers need organic carbon compounds to survive, and they are ultimately manufactured by producers.

Each trophic level can be described in terms of the number of species that belong to it, in terms of the weight of all individuals belonging to it (biomass), or in terms of the total caloric energy contained in the individuals. As a general rule, 1 g dry weight of plant or animal tissue contains 5,000 calories.

The biomass or energy of trophic levels decreases sharply from solar energy to producers to herbivores to predators. For example (Fig. 26.2), 1 acre of grassland in southern Michigan receives 4,700,000,000 (four billion seven hundred million or 47 x 10^8) calories over the course of 1 year. The vegetation, however, is capable of absorbing and transforming no more than 1% of that energy into plant tissue. One acre of vegetation, at the end of a year's growth, has added only 47,000,000 (4.7 x 10^7) calories. Herbivores, in turn, do not consume all that vegetation, but rather only about 10% of it, and most of that energy is burned in respiration. One acre of mice will consume about 5,000,000 (5 x 10^4) calories. Finally, the primary predator on this particular acre is a weasel. It can consume 10% of the mice, but only a fraction of that energy, 1000 (1 x 10^3) calories, can be measured as growth. If mountain lion, bobcat, or wolf were a secondary predator in this system, it would have to forage over dozens of acres to find and consume enough weasels to show any gain in weight. Figure 26.2 is an example of a biomass pyramid (energy pyramid). Pyramids for an acre of rain forest, salt marsh, desert scrub, or alpine lake typically show the same steep reduction in biomass or energy through their trophic levels.

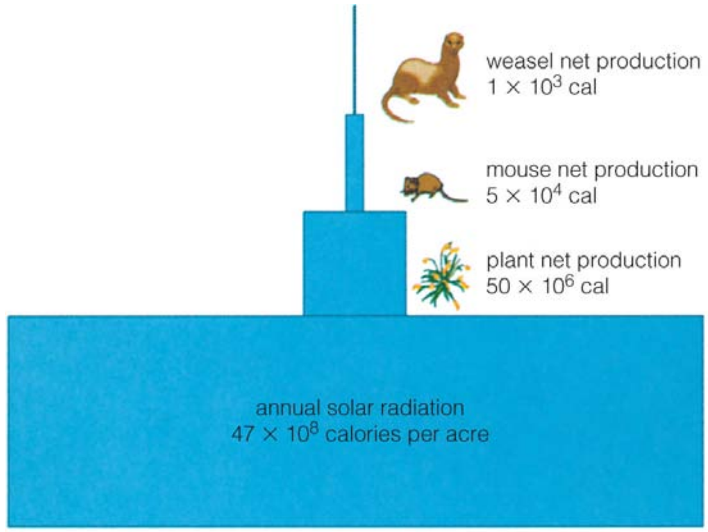


Figure 26.2. A biomass/energy pyramid for 1 acre of grassland in southern Michigan. Notice how steeply each trophic level's caloric content declines. In this particular ecosystem, solar energy reaching the vegetation over the course of 1 year totaled 47 x 10^8 calories per acre. Green plants transformed only a small fraction, about 1% of the solar energy, into growth. Mice were capable of transforming only about 10% of the vegetation into weight gain and reproduction. Weasels similarly transformed 10% of the mouse tissue into their own weight gain. Net weasel growth thus captured only 0.0002% of the solar radiation that fueled the base of the pyramid.

26.2 THE POPULATION: THE BASIC ECOLOGICAL UNIT

Ecologists usually do not study organisms as individuals; rather, they group them together into populations. A **population** is a group of freely interbreeding individuals belonging to the same species and occupying the same habitat. A plant population might consist of thousands of individuals, especially if they are small; or it might include only a few individuals, if they are rare. Not all individuals in a population actually interbreed every year, sharing pollen and genes, but they all grow close enough together so that they could potentially interbreed. Enough of them do interbreed to maintain a relatively homogeneous mix of genes throughout the population.

In special circumstances, a population can consist of many genetically identical individuals. Aspen (*Populus tremuloides*) reproduces not only sexually but also by underground roots and sucker shoots. A grove of aspen (Fig. 26.3) may have hundreds of trees, all connected underground, representing a single clone.

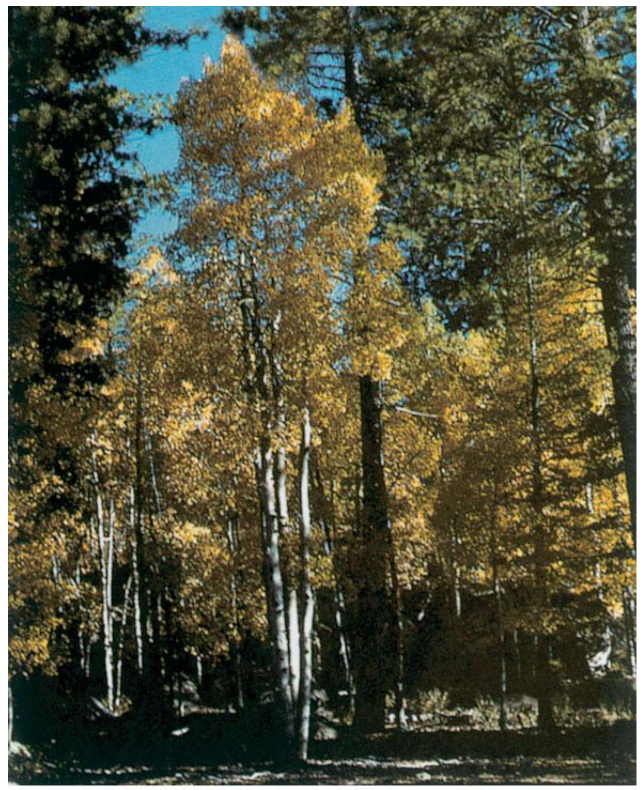


Figure 26.3. A population of aspen (*Populus tremuloides*). Aspen trees are capable of spreading asexually. This grove could all have the same genotype, but most aspen stands consist of a mixture of genotypes.

Although a population consists of only a single species, most species are made up of many populations. Each population occupies the same kind of habitat, scattered over a landscape or region. Some widespread species have thousands of populations, which range over many degrees of latitude or longitude and through hundreds of meters of elevation. In such a case, populations at the extremes of the species' territory are isolated from each other and have little opportunity to share genes. Over time, these outlier populations may evolve different structural or functional traits that allow the species to exploit new habitats.

Red maple (*Acer rubrum*) is a good example of a widespread species: it ranges throughout the entire eastern United States (Fig. 26.4) into habitats that vary from wet to dry. An uncommon species, such a California coast redwood (*Sequoia sempervirens*), has narrower habitat requirements than red maple. As a result, it has a smaller range and fewer populations (Fig. 26.4), although the number of individuals in each population is large. The rarest species with the narrowest habitat requirements may have only one or a few small populations. For instance, the closed-cone conifer Tecate cypress (*Cupressus forbesii*) occurs in only four little groves, all in southern California (Fig. 26.4).

Ecologists who study single populations and environmental factors that affect a population are engaged in population ecology. In contrast, community ecology or ecosystem ecology is the study of groups of different populations that coexist in the same habitat and of the environmental factors that affect them. This chapter discusses population ecology, and Chapter 27 discusses community and ecosystem ecology.

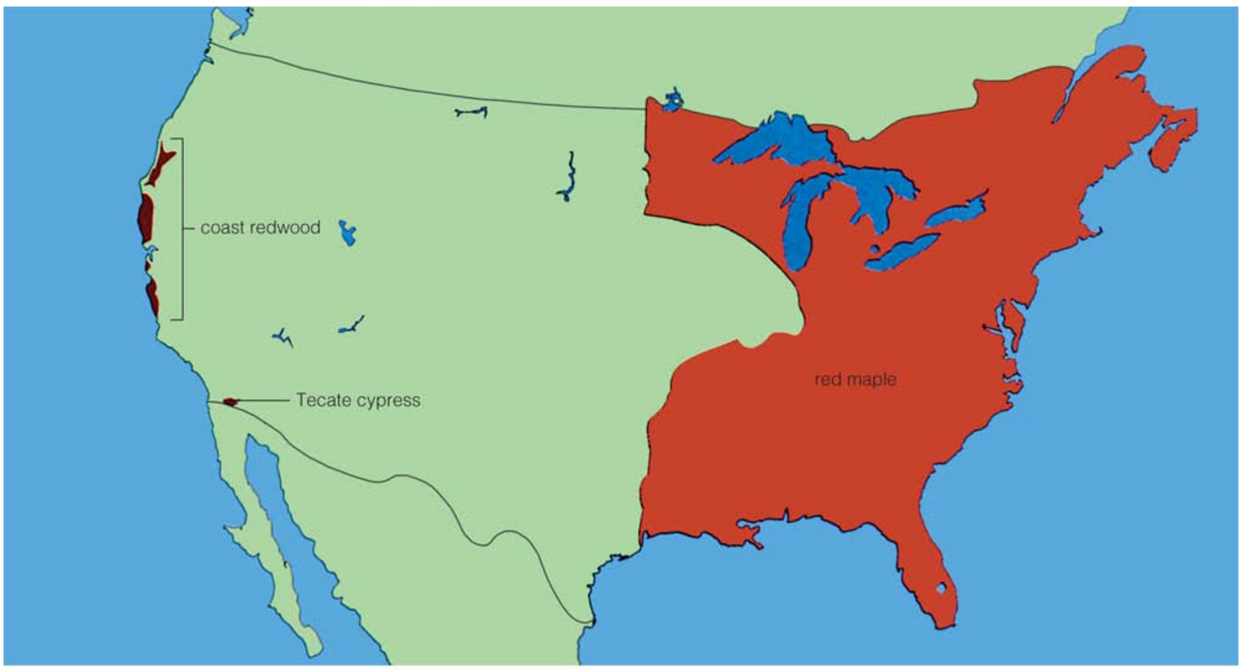


Figure 26.4. Distribution limits of a common species (red maple, *Acer rubrum*), an uncommon species (coast redwood, *Sequoia sempervirens*), and a rare species (Tecate cypress, *Cupressus forbesii*).

26.3 LIFE HISTORY PATTERNS

Every plant population has a problem to solve: how to allocate time and energy during the life cycle so as to maximize the probability of successful reproduction. Every plant has limits to its life span, its size, and the resources available to it; therefore, a plant's budget of time and energy is limited and finite.

Ecological research now indicates that there are only a few basic kinds of life cycle budgets and that each kind is shared by many species. We can think of each budget as a life history pattern: a collection of inherited traits and behaviors that permits a plant population to survive. Life spans, growth forms, timing of reproduction, and sexuality are the major components of life history patterns.

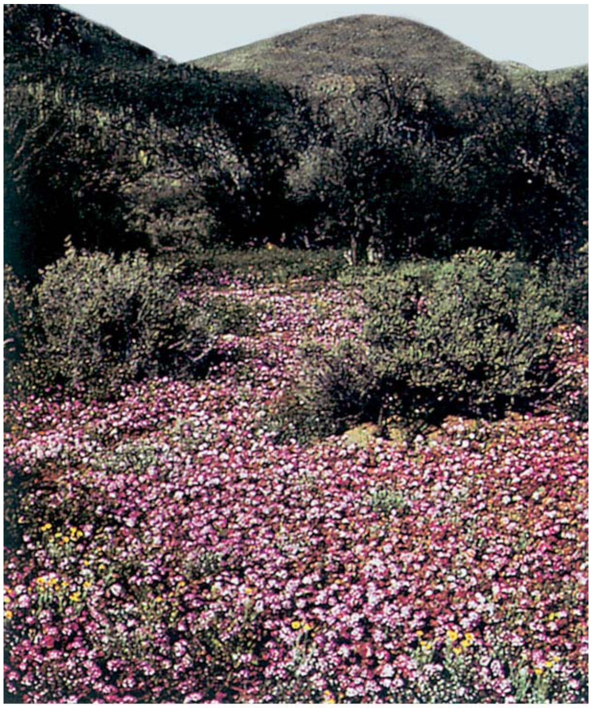


Figure 26.5. Desert ephemerals in flower. These annuals have a flexible life span, as short as 3 months or as long as 8 months, depending on temperature and rainfall.

Figure 26.6. Jack-in-the pulpit (*Arisaema triphylla*), a dioecious perennial herb. Plant sex depends on plant size, male plants being smaller than females, and juvenile (nonsexual) plants smallest of all.

Life Spans Are Annual, Biennial, or Perennial

Annual plants go from seed to seed in less than 1 year. They usually are small and inhabit open areas with short, unpredictable growing seasons. Desert annuals are good examples (Fig. 26.5): *Boerhaavia repens* (desert four o'clock) of the Sahara is a small annual that can go from seed to seed in only 10 to 14 days. But most annuals have a life span of 3 to 8 months. Perhaps the term **ephemeral** is more appropriate than annual, because it does not imply a full year of life.

Winter annuals in the Mojave Desert of California and Nevada usually germinate in November, with the onset of winter rains. They grow slowly during the winter, mainly developing a root system and a whorl of basal leaves. Warming temperatures in March and April bring rapid stem elongation and flower production. Seed maturity occurs by May, and the parent plant dies in June, killed by both the exhaustion of energy reserves that went into reproduction and the stresses of summer heat and drought. The total life span is about 8 months. However, the same winter annuals can complete their life cycle in only 3 to 4 months if winter rains are delayed until March. The plants then skip the winter phase of growth and go on to the reproductive stage; they flower as much smaller individuals but nevertheless complete seed set before dying on schedule in June.

Biennials live for 2 years. In the first year, growth takes place in the root system and a basal rosette of leaves. Cold temperatures during the first winter induce hormonal changes, so that during the second spring the shoot elongates and produces flowers. After setting seed, the plant dies. Carrot (*Daucas*) and lettuce (*Lactuca*) are examples of biennials. Most biennials can be induced experimentally to live longer than 2 years; therefore, we know that they are not genetically programmed to die in that span of time. If a biennial is kept warm over the winter, it remains in the vegetative state longer. Alternatively, biennials can be sprayed with gibberellin and experimentally induced to flower during the first year.

Perennials live for many years and usually flower repeatedly. Their growth form may be herbaceous or woody. **Herbaceous perennials** die back to underground parts each winter. Only their bulbs, corms, roots, or rhizomes are perennial; the aboveground leaves and stems are annual. *Iris, Gladiolus,* onion (*Allium*), potato (*Solanum*), the ferns, many wild grasses, and most spring-flowering herbs of the eastern deciduous forest (Fig. 26.6) are herbaceous perennials. They often occupy moderately harsh environments such as desert, seasonally dry grassland, shaded forest floors, or alpine regions.

It is difficult to determine the age of a herbaceous perennial because a woody stem with growth rings is absent. The perennial organs may retain a scar from each year's leaf system, however, and the scars can be counted to determine plant age. Other perennials spread outward vegetatively from rhizomes or runners, and their age can be estimated by knowing the annual rate of spread. From these types of evidence, we think that many herbaceous perennials live 20 to 30 years.

Woody perennials accumulate aboveground stem tissue year after year. What makes them woody is that the stems have secondary growth. The size and shape of the stems determine whether the plants are subshrubs, shrubs, vines, or trees. **Subshrubs** are multibranched and genetically dwarfed, seldom becoming taller than 30 cm. At the end of each growing season, their stems die back partially, but not all the way to the soil surface. They have short life spans, similar in length to those of herbaceous perennials. They often invade disturbed sites and are later overtopped and outcompeted by taller, longer living shrubs and trees. Rabbitbrush (several species of *Chrysothamnus*) is a common subshrub of the intermountain Great Basin.

Shrubs also are multibranched, but they do not die back annually. Sometimes an entire branch may die, but the tips of other, living branches continue to grow taller. Shrubs have life spans that may exceed a century. Some reproduce asexually with underground stems, and an entire clone can attain a very great age. Creosote bush (*Larrea tridentata*), for example, is a desert shrub capable of spreading vegetatively from the base. Some clones are old enough to form a ring several meters in diameter (Fig. 26.7), estimated to be several thousand years old.

Vines (called *lianas* in the tropics) have weak, single trunks. They require additional support from neighboring shrubs or trees, obtaining that support by twining about the host's trunk or literally sprawling on top of the host's leafy canopy. Common vines in the eastern deciduous forest include Virginia creeper (*Parthenocissus quinquefolia*) and Dutchman's pope (*Aristolochia durior*). Vines have

Figure 26.7. Creosote bush (*Larrea tridentata*), a common shrub of the warm deserts of North America. Individuals can live for more than 100 years. They can reproduce vegetatively, producing an ever-widening circle of offspring. Some of these clones are estimated to be several thousand years old.

secondary wood, but typically that wood is light because it contains many more vessels than tracheids and fibers. Such wood is metabolically inexpensive to build, leaving more energy to be allocated to the plant's growth in height. Consequently, vines have a relatively rapid growth rate. The life span of a vine is similar to that for subshrubs and shrubs.

Trees have strong, single trunks and an elevated branch system that does not die back annually. As with shrubs, individual branches or even a portion of the trunk may die, but the rest of the tree continues to grow in height and girth. Broadleaf trees, such as oak (*Quercus* species), are typically angiosperms; they also are called hardwoods because of the density of their secondary wood. Needleleaf trees, such as pine (*Pinus* species), are gymnosperms; they are called softwoods, because the uniform size and arrangement of tracheids in their secondary xylem make the wood relatively easy to cut through and work.

Hardwoods and softwoods can be either evergreen or deciduous. If they are evergreen, each individual leaf has a life span longer than 1 year; if they are deciduous, all leaves have a life span less than 1 year and fall synchronously (at the same time), leaving the tree bare for part of the year. Leaf life spans mirror the pattern for tree life spans, being longer for softwood trees than for hardwood trees. Broadleaf evergreens, such as some southern and western oaks, have leaf life spans of only 2 years; but needle-leaf evergreens, such as some mountain pines, have leaf life spans of 5 to 30 years.

Evergreen leaves, also called sclerophylls (hard leaves), are energetically more expensive to manufacture than deciduous leaves. They are thick, tough in texture, and bounded by a well-developed cuticle; they also have few air spaces in the mesophyll, exhibit a low surface-to-volume ratio, and contain high concentrations of metabolic byproducts. Collectively, these features mean that it takes more carbohydrates to build an evergreen leaf than a deciduous leaf.

Evergreen leaves are more drought tolerant than deciduous leaves, but at the same time they have a lower maximum rate of photosynthesis. Ecologists think that the long life of sclerophylls and their efficient use of water are compensations for their high expense and low photosynthetic rates.

Reproduction Can Be Semelparous or Iteroparous

Timing of reproduction is another component of a life history pattern.

Annuals, biennials, and some herbaceous perennials reproduce sexually only once, at the end of their life spans. This is called **semelparous** reproduction (derived from the Latin *semel* ["once"] and *parere* [to "bear"]). An advantage of semelparous reproduction is that a single burst of reproduction, delayed to the time of maximum plant size, yields so many seeds that some are likely to germinate and live long enough to produce the next generation. The California chaparral plant , our Lord's candle (*Yucca whipplei*, Fig. 26.8), is a semelparous perennial that flowers at the end of its 20-year life span. Semelparous plants spend 25% of their stored caloric resources on their single massive reproductive event. It is possible that they die by exhausting their food reserves in setting so many flowers and seeds in such a short time.

Figure 26.8. Our Lord's candle (*Yucca whipplei*), a semelparous perennial plant. It flowers only once, at the end of its 20-year life span. This species grows in coastal hills of central and southern California.

In contrast, **iteroparous** plants reproduce many times during their lives (*itero-* means "repeat"). Each reproductive event uses 5% to 15% of the plant's food reserves. Iteroparous plants go through a juvenile period before that first reproductive event. The length of the juvenile period depends on the species; in general, it accounts for 10% of the entire life span. In commercial fruit trees, the juvenile phase lasts 4 to 6 years, but wild trees often have a much longer juvenile period. Some iteroparous species reproduce at a constant rate once the juvenile period is over. Others, such as oak, pine, and fir, reproduce more abundantly some years than others. The years of high reproduction are called **mast** years.

Sexual Identity Is Not Always Fixed

The distribution of sexual identity among individuals is yet another component of life history patterns. Most species of angiosperms are **monoecious**, with male and female flower parts (stamens and pistils) on the same individual. Other species that have only male or only female flower parts on one individual are **dioecious**. We can imagine that the advantage of being dioecious is that cross-pollination is absolutely required; thus, genetic recombination and variation are high. The advantage of being monoecious is that a single isolated individual can reproduce successfully. Most weedy, invasive species are monoecious.

In dioecious species, the sex of the individual plant is usually genetically determined, but not by X and Y chromosomes, as in humans. Sometimes sex is not under any genetic control but is a consequence of plant size or habitat conditions. Jack-in-the-pulpit (see Fig. 26.6) is a herbaceous perennial in which the sex of an individual is environmentally controlled. Very young individuals go through a juvenile phase during which they grow vegetatively and become larger but do not reproduce. Plants exhibiting sexuality are older and larger in size than the juveniles, as measured by total area of leaves produced and volume of perennial underground parts. Of these adult plants, the largest--but not necessarily the oldest--are female. Sexuality in this case is actually a function of size, not of age. If a female plant is manipulated so that it does not accumulate much stored food one year, it will produce fewer leaves the next year, and the size of its underground system will shrink. If the loss in size is significant, the plant will become male. As it accumulates stored food over the years, it will become female again. If male plants are similarly starved the following year they may become non-reproductive, like juveniles. As they grow, they will become male again.

Some species segregate sex by habitat. Female plants tend to occupy moister or nutritionally richer soils, whereas male plants tend to occupy drier, sterile sites. Female plants require better sites because so much stored food must go into seeds and fruits, but male plants can occupy marginal sites because less energy is needed to produce pollen. Dioecious species thus subdivide the habitat and take advantage of all sites.

Another advantage of the dioecious state is that seed predation by animals is reduced. Female plants--with their energy-rich seeds and fruits--are mixed with male plants across the landscape; thus, an herbivore that finds a female plant may not encounter another female plant nearby, making it unlikely that the herbivore will devour all the seeds in a locale. Patterns of sexuality in other species are less obvious. Some red maple (*Acer rubrum*) individuals, for example, seem to change sex randomly from year to year, with few remaining constantly male or female. We still have much to learn about the allocation of sexuality in plants of dioecious species.

Life History Patterns Range from r to K

When life span, growth-form traits, timing of reproduction, and allocation of sexuality are put together, some concrete life history patterns emerge. It is useful to recognize two extremes because all other types can be arranged between the extremes. Those extremes are call r and K life history patterns (Table 26.1).

Typically, **r-selected** species are annuals or biennials that grow in open habitats. They have a rapid growth rate, deciduous leaves, and a short juvenile period. They are semelparous and allocate considerable caloric energy to reproduction. All of the common weeds that inhabit frequently disturbed locations are r-selected species: ragweed, wild radish, vetch, pigweed, dock, wild oats, and bindweed.

Table 26.1 Some Traits of r- and K-selected Species

Trait	r-selected	K-selected
Habitat	Often disturbed	More constant
Population	Variable size	More constant, often near the carrying capacity
Survivorship	Type I or II	Typically type III
Competition	Variable; not an important factor	Usually keen
Life span and reproductive effort	Usually short; semelparous; high reproductive effort	Long; iteroparous; low reproductive effort (except in mast years)
Growth pattern	Rapid growth and development	Slower growth and development
Body size	Small	Large
Juvenile period	Short; several months for herbs, 5 years for trees	Long (10% or more of entire life span)

K-selected species usually are perennials with a larger body size. These plants occupy more stable habitats that may be buffered from wind, sun, and frost by an overstory leaf canopy. Good examples are herbs, shrubs, and trees, such as hemlock, red oak, sugar maple, viburnum, false Solomon's seal, and Virginia creeper, in old-growth forests. They may be evergreen or deciduous. Compared with r-selected species, they have a slower growth rate and a longer juvenile stage; they expend less energy on reproductive events and are iteroparous. Basically, r-selected species maximize reproduction in unstable habitats at the expense of long life and large body size, whereas K-selected species maximize long-term occupation of a site and competitive abilities at the expense of rapid growth and early reproduction. Most species lie somewhere along a continuum between these extremes.

It is important to remember that r and K strategies are relative, not absolute, categories. For example, one might think that all annual herbs are r-selected and that all trees are K-selected. But tree species include some that are r-selected and other that are K-selected. Cottonwood trees (*Populus* species) grow rapidly, produce very light and easily decayed wood, have thin deciduous leaves with low concentrations of herbivore-deterring metabolic byproducts; they generate many seeds every year that are distributed randomly by the wind; and the trees favor disturbed, open habitats. All of these characteristics are r-type traits. Red oak trees (*Quercus rubra*), in contrast, grow slowly, produce dense and decay-resistant wood, have tougher leaves rich in tannins, produce large numbers of acorns only every several years, use animals to disperse the large seeds non-randomly, and favor undisturbed, shaded habitats. All of these characteristics are K-type traits. In a similar manner, some herbaceous plants are K-selected, whereas other are r-selected.

Another classification of life history patterns recognizes three extremes (Fig. 26.9) instead of two. In this system, the **R type** (abbreviation for ruderal, or roadside) is equivalent to the r in the r-K continuum described above. The **C type** (for competitive) is equivalent to the K. The **S type** (stress-tolerant) is a new category, representing species that grow in stressful habitats such as salt marshes, rock outcrops, moving sand, and deserts. Plant density in such habitats is low; thus, a tolerance of biotic stresses, such as competition, is less important than a tolerance of abiotic stresses.

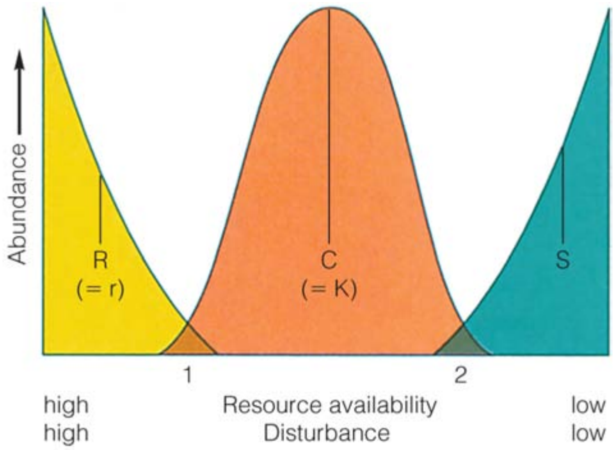


Figure 26.9. Diagram of the abundance of R, S, and C-type plants along a gradient of decreasing resource availability and frequency of disturbance. At point 1, disturbance becomes rare enough to favor C types over R types; at point 2, resources become so limiting that S types are favored over C types.

Figure 26.10. C, S, and R-selected plants may occur in the same local habitat, separated only by microenvironmental gradients. Rock outcrops in the Appalachian Mountains show a concentric zonation of plants, with S types at the outermost fringe, R types in a middle zone, and C types in the very center.

R, C, and S species can sometimes grow in close association. For example, rock outcrops in the Appalachian Mountains often are occupied by islands of vegetation (Fig. 26.10). At the outermost edge, growing on bare rock, are the mosses *Grimmia*, *Polytrichum*, and *Bryum*. These slow-growing plants are S types. Farther into the island of vegetation, growing on top of a thin layer of soil that mosses have accumulated, occur herbaceous R-type plants such as hair grass (*Deschampsia flexuosa*). In the center, with deepest soil, grow C-type shrubs and trees such as *Rhododendron* and chestnut oak (*Quercus prinus*). Most ecologists agree that this tripartite division is a concept that has improved our understanding of life history patterns.

26.4 PLANT DEMOGRAPHY: POPULATION AGE STRUCTURE OVER TIME

A population usually contains individuals of all ages: seedlings, juveniles, reproductive adults, and senescent oldsters. The proportion of the population in each age category tells us something about the history and future of that population. For example, Figure 26.11 is a summary of the ages of all pine and hardwood individuals in a forest near Gainesville, FL. (Actually, ages are not shown; rather, the diameter at breast height [dbh] of the trunks is indicated. However, tree age is generally proportional to dbh. A tree with a 25-cm dbh is about 100 years old in this forest; a tree with a 45-cm dbh is about 200 years old.)

Notice that the pine population in the figure has many mature trees 15 to 30 cm in dbh, but it has no seedlings, saplings, or young trees smaller than 5 cm in dbh. From this, we conclude that the pine population has not been reproducing itself for some decades. The hardwood population, in contrast, has only seedlings and saplings, with no large, mature individuals. This suggests that the hardwood population is a recent invader of the forest.

Putting the two population trends together, we can predict that the pine forest will be replaced by a hardwood forest. The current overstory pines eventually will reach their natural life span limits, about 200 years, and die. As they leave the canopy, they will be replaced by the young hardwoods growing beneath them.

In time, the forest will become a hardwood forest, and pines will be rare or absent. When that happens, we can predict that the distribution of ages is likely to follow the ideal curve shown in Figure 26.11. There will be many young hardwoods and fewer of the older ones. Such an age structure will be stable over time because as each old tree dies, the probability is great that youngsters of the same population are already growing beneath it and they will grow up to maintain the same overstory composition.

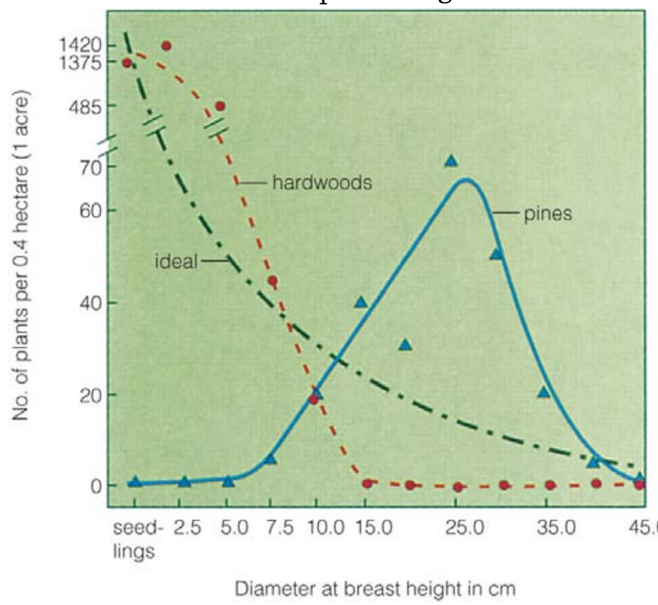


Figure 26.11. Age distribution (on the basis of trunk diameters at breast height) for pines and hardwoods in a forest near Gainesville, FL. The pine population is senescent, and the hardwood population is invading. The green line shows the expected age distribution of a stable population.

Plant demography is the study of changes in population age structure over time. By examining age structure, a demographer can create a mathematical model for predicting how long an average individual will live, when it will enter and leave reproductive age, how many seeds it will shed in its lifetime, and how many of those seeds will survive to germinate.

Figure 26.12 is a diagram summarizing the demography of one particular species. Let us tease apart that model. On the left, represent by small orange circles, are all the seeds currently in the ground; this is the seed pool. These seeds are 26 in number (N = 26). Environmental and physiological stresses, such as being eaten by animals, parasitized by soil microbes, or kept dormant by some internal mechanisms, take their toll, so that only a fraction of those seeds (9 of 26) germinate this year. The nine that germinate together are part of a single cohort, a segment of the population that is the same age. Of the nine germinated seeds, environmental stresses--such as heat, drought, or disease--kill four before they can reproduce, represented in the figure by short, truncated lines. The remaining five plants of the cohort all reach sexual maturity and produce flowers, indicated as large orange circles. One member of the cohort reproduces vegetatively before this event, producing an additional sixth plant, which also flowers. Notice that not all the

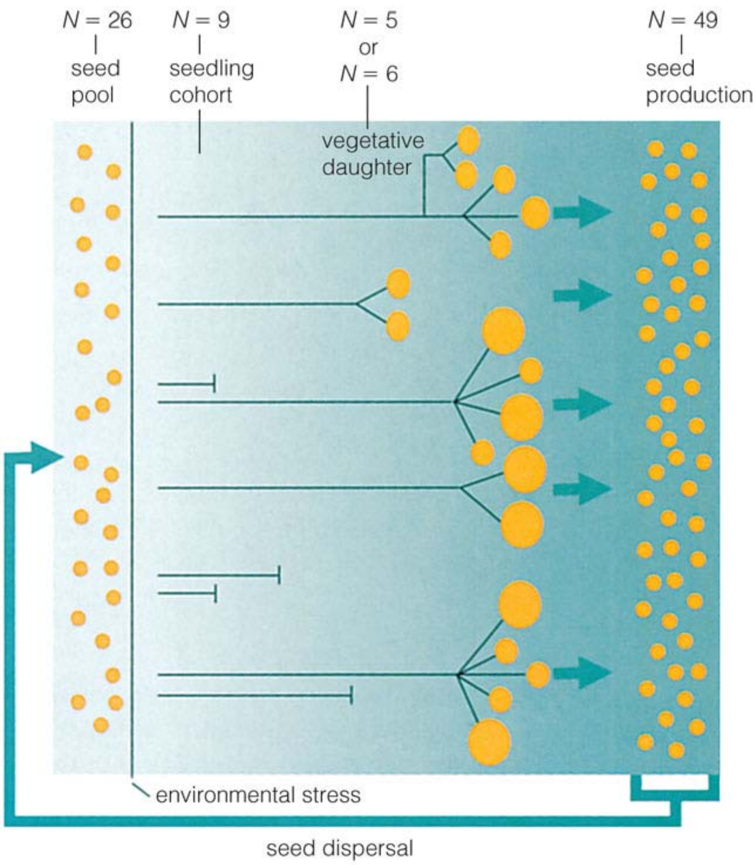
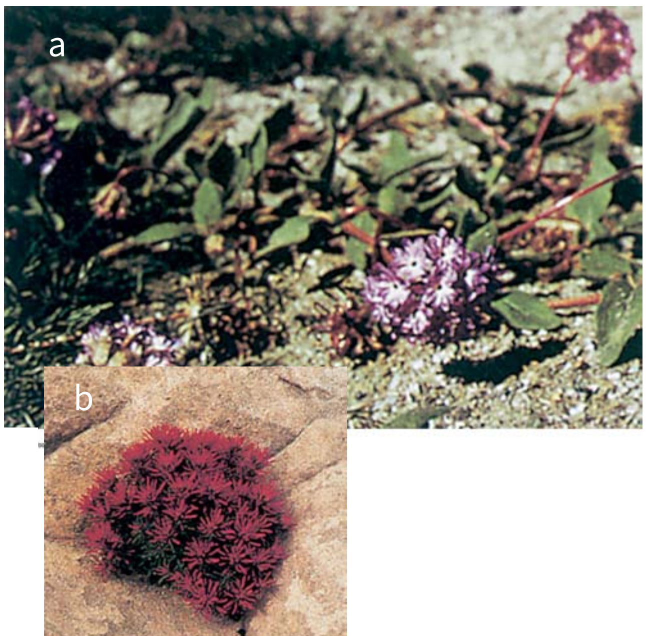


Figure 26.12. A model of one population's life history. Time increases from left to right. This species is semelparous and flowers only once at the end of its life span. It is capable of vegetative production during this life span. Note that not all seeds germinate and that not all seedlings reach maturity. *N* is the number of living individuals in the cohort at the times shown. Because seed output is larger than the initial seed pool, this population is growing.

plants produce the same number or sizes of flowers. Their reproductive effort probably correlates with the particular patch of ground each plant occupies.

This particular model is for a semelparous species because all six plants die on release of seeds (the horizontal lines stop). Notice that the number of seeds released (49) is much greater than the number at the start (26). Therefore, we might predict that this population will grow in number. Because about 35% of the original seed pool germinated, we can predict that next year's cohort of seedlings should total about 17 (35% of 49 seeds).

Another way of presenting changes in population age structure over time is in the form of a **survivorship curve** (Fig. 26.13). Plant and animal populations have three basic kinds of survivorship curves. A *type I* curve is characteristic of r-selected (or R-type) populations, such as annual plants. There is high survivorship (low mortality) for most of the life span; then all the individuals die within a relatively short time. A *type III* curve is characteristic of K-selected (or C-type) populations, such as forest trees. There is high mortality early in life, but then very low mortality once the individuals reach maturity. A *type II* curve is characteristic of S-type populations such as alpine herbaceous perennials. There is constant mortality throughout the life span because of the overwhelming importance of abiotic environmental stress at all stages of the life cycle.



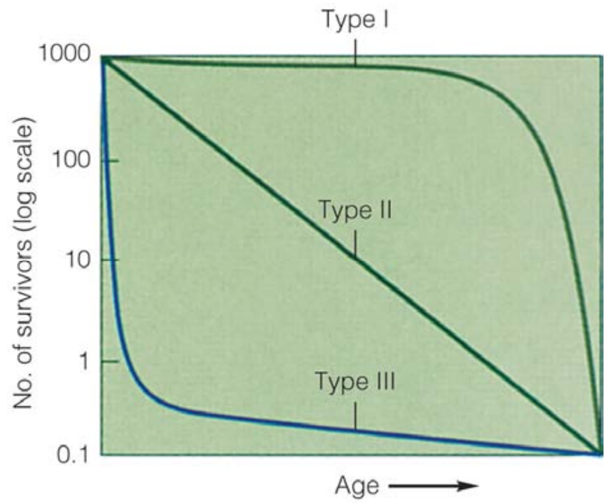


Figure 26.13. Three different survivorship curves. (a) A type I curve is characteristic of annual plants. (b) A type II curve is characteristic of plants in extreme environments. (c) A type III curve is characteristic of large perennial plants. Note that the vertical axis of the graph is logarithmic, meaning that each population unit changes by an order of magnitude.

26.5 POPULATION INTERACTIONS WITH THE ENVIRONMENT

We have already divided the environment into biotic and abiotic components, but an additional division is useful. The **macroenvironment** is that part of the environment determined by the general climate, elevation, and latitude of the region. Weather bureau data on rainfall, wind speed, and temperature are measurement of the macroenvironment. Such measurements are taken at a standard height above the ground, in cleared areas well away from buildings or trees.

The **microenvironment** is that part of the environment close to the surface of a plant, animal, structure, or the ground. The microenvironment is modified by nearby surfaces. For example, bare soil tends to absorb heat; consequently, on a clear day the temperature just above or below the soil surface is much greater than air temperature. Prostrate plants with basal leaves will experience microenvironmental temperatures much warmer than those recorded by the weather bureau 1.5 m above the ground. Microenvironmental air as far as 10 mm from the surface of a leaf on a still day is less turbulent, greater in humidity, and warmer than free air farther from the leaf.

Light quality and quantity are much different for herbs in the microenvironment beneath a forest canopy than for the leaves of the canopy itself. Herbs on the forest floor sense perhaps only 1% to 5% of the light received at the top of tree canopies. Moreover, the light that passes through the canopy is relative enriched in green and far-red wavelengths because photosynthetic pigments in the canopy leaves absorb in the blue and red portions of the spectrum.

Plants growing in shallow depressions experience frost more frequently than those growing on higher ground because cold air flows downhill. Soils may also be wetter and more anaerobic in depressions.

Water and Soil Are Important Environmental Factors

Probably no single abiotic factor is as significant in the distribution of plant populations as the supply of water. So important are plant-water relationships that species have been formally classified into **xerophytes** (plants able to grow in very dry places), **mesophytes** (those that grow best in moist soil), **helophytes** (those able to grow in saturated soil such as marshes and bogs), and **hydrophytes** (those able to grow rooted, submerged, emergent, or floating in standing water).

Plants in each category have unique morphological, anatomical, and physiological traits that adapt them to a particular moisture regimen. Xerophytes, for example, may have small, hard leaves; an epidermis with thick cuticle, light color, and hairlike trichomes; stomates that are sunken in epidermal depressions and that close early during the day; and, sometime, **succulent** tissue, the cells of which contain large, water-filled vacuoles. Leaves may be permanently absent or seasonally absent. If they are permanently absent, green stems conduct photosynthesis. If leaves are seasonally absent and they fall off during hot rainless periods, rather than during cold winter periods, the plants are called **drought-deciduous**.

Xerophytes can live in humid environments, provided that their roots are in dry microenvironments. Some xerophytes live in tropical rain forests as **epiphytes**--plants that grow on tree trunks or branches with their roots twining through relatively dry bark; they obtain all their water by trapping rainfall in leaf axils. Many of them have succulent leaves and stems and specialized water-storing tissue on root surfaces. One common group of tropical epiphytes belongs to the Cactaceae, or cactus family (Fig. 26.14). Cacti probably evolved in the tropics, later moving into dry deserts as those habitats appeared in the late Cenozoic. Other important epiphytic families are the Bromeliaceae and the Orchidaceae, to which the pineapple (*Ananas*) and the orchid, respectively, belong.

Other xerophytes live on soil in which the physical or chemical properties limit the amount of free water available to plant roots. Very coarse soils, high in sand or gravel, permit most rainwater to percolate rapidly, leaving an island of aridity within a climate that might seem wet and adequate for luxurious plant growth. Similarly, shallow soils or rock outcrops store little water in the root zone. Soils high in clay can potentially store much water, but the rate at which they can absorb water is slow; if rains come in torrential bursts, much of the precipitation will run off, rather than percolate. Saline soils are said to be physiologically arid because dissolved salts decrease the water potential of soil water, making the water less available. Again, locally dry islands of vegetation are the result.

Figure 26.14. An epiphytic cactus in a New Zealand semitropical forest.

The seasonal timing of precipitation can be as critical to vegetation as the annual amount. In the tropical latitudes, annual precipitation is generally more than 200 cm. When that precipitation is evenly divided among 12 months, a three-storied, evergreen forest results; but if the same annual precipitation is divided into wet and dry seasons, a less complex forest with many deciduous trees is the result. The form of precipitation also is important. Through the mid-elevations of California mountains, annual precipitation changes little, averaging 150 cm. Below an elevation of 2,000 m, however, most of that 150 cm falls as rain. Above 2,000 m elevation, most of it falls as snow, building a winter snowpack 3 to 4 m deep. As a result, the species of trees, shrubs, and herbs are dramatically different in the two zones, even though total and seasonal precipitation is the same.

Solar Radiation Is Another Environmental Factor

Solar radiation strikes the outer limits of our atmosphere with an energy content of about 2 calories per square centimeter per minute, a value called the *solar constant*. Solar wavelengths of the electromagnetic spectrum range from 300 to more than 10,000 nm. Technically, light is the portion of the solar spectrum visible to the human eye: wavelengths from 400 (violet light) to 740 nm (red light). Plants can use the same range of wavelengths in photosynthesis.

Only half of the solar constant reaches the lower atmosphere and vegetation within it because certain wavelengths are absorbed or reflected back to space. In particular, a significant amount of shortwave ultraviolet radiation is removed by ozone in the stratosphere.

Solar radiation is further depleted as it passes through foliage. Below a forest canopy, sunlight is reduced to 5% of what its level was just above the foliage. Many shade-tolerant herbs, shrubs, and tree saplings can still grow in this level of sunlight.

Long-living plants must be flexible in their light requirement because, as they grow, they experience different levels of light intensity. As saplings they may grow in dense shade, but as adults they are exposed to full sun. Furthermore, adult trees are so large that not all the leaves experience the same amount of sunlight. Leaves high in the canopy, **sun leaves**, receive high amounts of solar radiation, whereas those lower in the canopy, **shade leaves**, receive less. Shade leaves exhibit a different morphology, anatomy, and physiology from those that develop in sunlight, even when both are attached to the same plant. Shade leaves are broader, thinner, contain less chlorophyll per gram of tissue, and have less well-defined palisade and spongy mesophyll layers. They reach their maximum rate of photosynthesis at much lower light intensities than sun leaves (Fig. 26.15).

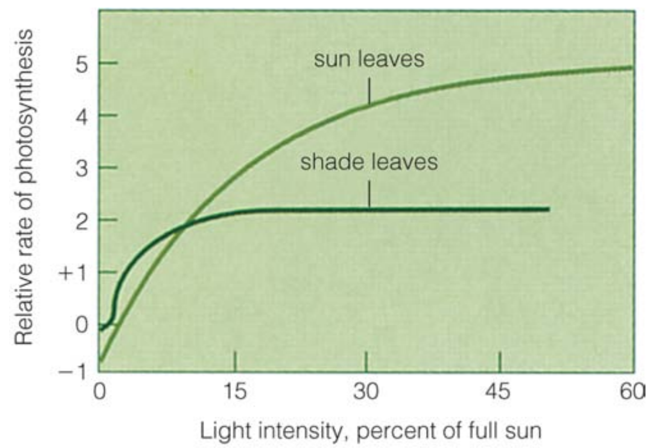


Figure 25.15. The rate of photosynthesis in sun leaves and shade leaves of beech trees (*Fagus sylvaticus*) at different light intensities.

Eastern hemlock (*Tsuga canadensis*) is a good example of a long-living, shade-tolerant tree species: it can grow in deep shade as a sapling but continues growth in full sun as an adult. Mature trees live for 1,000 years. Saplings grow slowly while shaded. Saplings only 2 m in height and 2 to 3 cm in dbh may have a ring count indicating an age of 60 years. Juveniles can remain alive in deep shade for as long as 400 years. If the canopy opens up because of the death of a mature tree, the increased light releases a juvenile into a fast growth made, and it soon fills the canopy gap. Many other trees, especially pines, are not shade tolerant, and their juveniles can grow only in open habitats.

Solar radiation also is depleted when it passes through water. At about 170 m below the surface of clear ocean water, sunlight is reduced to 0.5% of its level at the surface. Light level sets the compensation depth for most aquatic plants--the depth at which they can just maintain positive net photosynthesis.

BALANCING INCOMING AND OUTGOING SOLAR RADIATION If we assume that a plant is neither cooling down nor heating up, we can conclude that what comes in also goes out; that is, the its energy budget equals zero. Let us examine the energy budget of an imaginary plant leaf as an example (Fig. 26.16).

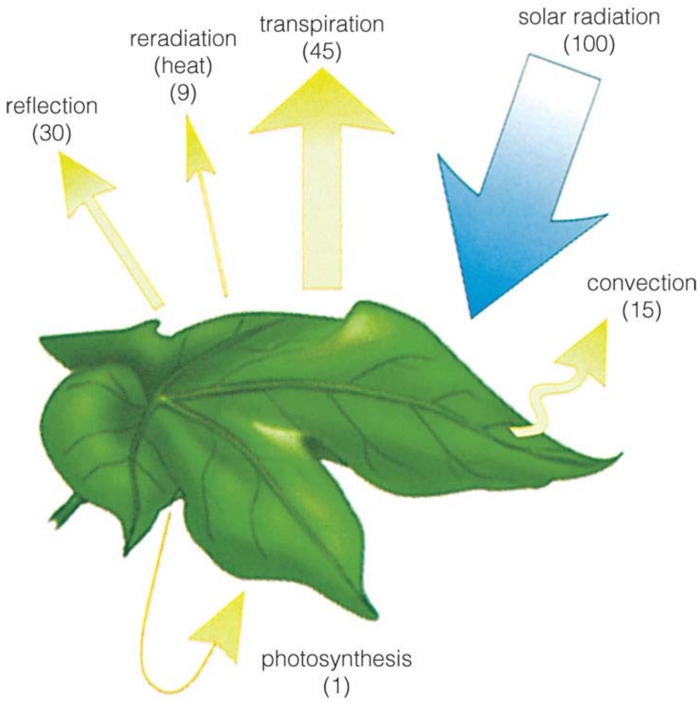


Figure 26.16. Energy budget of a leaf. Incoming solar radiation is given a relative value of 100 energy units. The leaf gives back 99 units in the forms of reflected light, re-radiation, transpiration, and convection (heating the air). Only 1 unit was assimilated in the process of photosynthesis.

Some of the solar radiation that reaches the leaf will be reflected. Perfectly white leaves reflect all radiation, but typical green leaves reflect only 30% of the energy. The energy that is absorbed is converted to long-wave energy (wavelengths greater than 740 nm), which is felt as heat--thus, the leaf warms up. This heat is dissipated in four ways: transpiration, convection, re-radiation, and metabolism (photosynthesis).

Transpiration is the conversion of water into gas and its loss from the leaf. When water changes state to gas, it uses up a significant amount of energy. For our imaginary leaf, with well-hydrated tissues and open stomata, transpiration accounts for 45% of the energy budget. In a desert, transpiration would account for less of the energy budget. **Convection** is the transfer of heat energy back to air. For out imaginary large, entire leaf, convection accounts for only 15% of the energy budget. In a desert plant, with smaller leaves, convection would account for more of the energy budget. **Re-radiation** is the loss of long-wave radiation back to space; its effect is best seen at night, when the temperature of the leaf decreases. Under the cover of a forest canopy, re-radiation accounts for only 9% of our imaginary leaf's heat budget. In a desert, under a cloudless sky, re-radiation would count for more of the energy budget. The overall remainder of the solar radiation, 1%, is converted into chemical energy by photosynthesis. Photosynthesis does not vary much, regardless of the plant or habitat.

This particular energy budget formula is:

Incoming solar radiation = (100 units)

= reflection + transpiration + convection + re-radiation + photosynthesis
= 30 units + 45 units + 15 units + 9 units + 1 unit .

The equation is balanced: 100 incoming units = 100 outgoing units, and there is zero gain or loss.

THE EFFECT OF SOLAR RADIATION ON TEMPERATURE As noted earlier, heat is a consequence of solar radiation. Long-wave radiation is experience as heat, and it is an important environmental factor. Heat can be measured with thermometers and expressed in many ways, temperature being just one.

Latitude and topography greatly influence solar radiation and heat. As we move north or south from the latitude at which the sun is overhead, the angle at which solar radiation strikes the ground becomes less direct and more oblique; this means that radiation travels through more of the earth's atmosphere and that more of it is absorbed or reflected. Light at the poles in summer may last 25 hours a day, but it is a weak light compared to the intensity at the equator. One consequence is that polar summer days are not very warm.

Because temperature tolerance differs among plant species, different species prosper at different latitudes and elevations. For instance, some plants are restricted to certain belts of elevation in mountains, and the elevation of those belts changes with latitude. Plants that grow in mountains respond to the diminishing amount of heat away from the equator by shifting their habitat lower and lower. Mountain hemlock (*Tsuga mertensiana*), for example, grows at high sub-alpine elevations (2,700 m) in the Sierra Nevada of California, but its habitat drops toward the north until it reaches sea level along the Alaskan coast (Fig. 16.17)l.

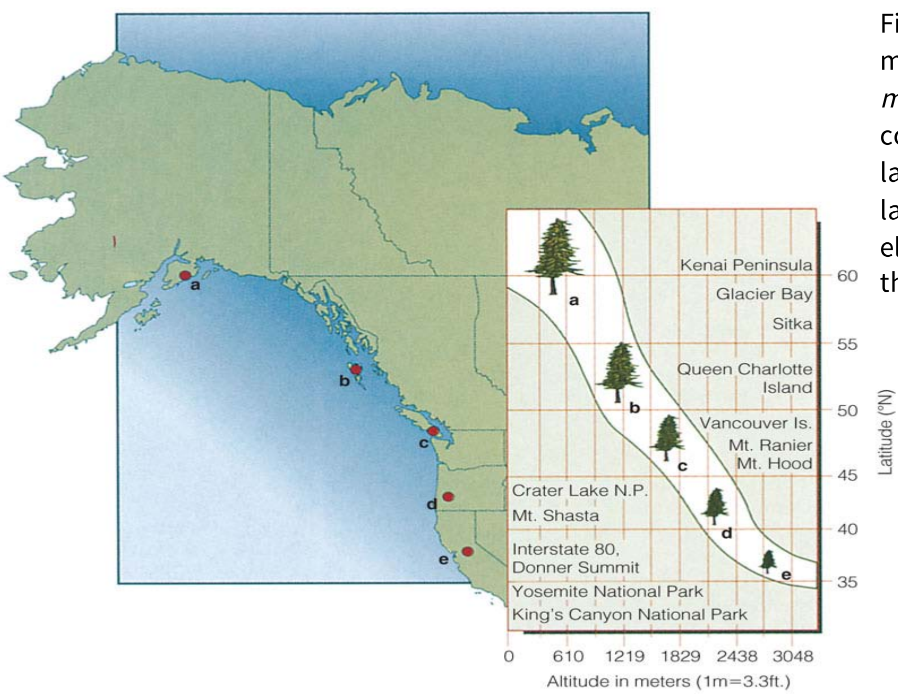


Figure 26.17. Distribution of mountain hemlock (*Tsuga mertensiana*) along the west coast of North America from latitude 62°N to 38°N. As latitude decreases, the elevation zone of the tree rises.

The direction a slope faces also affects solar radiation and heat. In the northern hemisphere, south-facing slopes receive more sunlight than north-facing slopes; consequently, they have higher temperatures and drier soils. These microenvironmental differences affect plant population distribution and behavior. A canyon gorge running east-west through an Indiana forest illustrates the magnitude of this effect. The gorge is 65 m in width at the top and 45 m in depth; its sides support scattered trees, shrubs, and herbs. Microenvironmental instruments were placed 15 cm above and below the soil surface midway down each side. In spring, the south-facing slope had a larger daily range of soil and air temperature, a greater average air temperature, a greater rate of soil water evaporation, lower soil moisture, and lower relative air humidity than the north-facing slope. Of nine spring-flowering species present on both slopes, the flowering time averaged 6 days earlier on the south-facing side. To gain a similar difference in flowering time on level land, one would have to pick sites 180 km apart.

Some species are sensitive to brief extremes of high or low temperature, and their distributions are determined more by the extremes of temperature than by long-term averages. Most species of palms and cacti, for example, are sensitive to frost and do not occur in regions that experience yearly frost, even if the duration of freezing temperature is short.

Other species are sensitive to variation in temperature over seasons or days, and it is this amplitude of temperature difference that is more important than the average temperature. The difference between maximum daytime temperature and minimum nighttime temperature within a 24-hour cycle is called a **thermoperiod**. California coast redwood (*Sequoia sempervirens*) grows best under the almost constant day-night and winter-summer temperatures of its habitat, near the temperature-buffering Pacific Ocean and bathed by summer fogs (Fig. 26.4). Experiments with seedling redwoods in growth chambers have shown that the optimum thermoperiod for coast redwood is close to zero. In contrast, conifers that grow inland in the Sierra Nevada have optimum thermoperiods greater than l3°C.

Fire Can Be a Natural Part of the Environment

In the last several decades, fire has been rediscovered as a natural environmental factor in North America. We say "rediscovered" because Native Americans were well aware of the occurrence and its effects, and they learned how to use it for their own purposes. Early Euro-American explorers and colonists invariably commented on the frequency of fires in forests and grasslands, but the pervasiveness of natural fire was ignored by land use managers until recently.

Most natural fires are started by lightning strikes unaccompanied by rain, which occur after a prolonged spell of dry weather. Climates that have such conditions are said to be fire-type climates, and they are widespread through North America. Each year in the United States, lightning accounts for 5,000 fires; this is two thirds of all our wild-fires. Human-caused fires are in the minority. Grasslands, chaparral scrub, the northern boreal forest, southeastern forests (Fig. 26.18), some

Figure 26.18. Fire in the southeastern coastal plain.

mountain conifer forests, and even desert palm oases owe their presence in large measure to climates with episodic natural fires.

When humans suppress fires in the mistaken notion that all fires are unnatural and catastrophic, they begin to change the mix of species and the shape of the landscape (see the endnote "PLANTS, PEOPLE, AND THE ENVIRONMENT: The Natural Fire Cycle in the Southeastern Pine Savanna"). This is because many species not only tolerate fire but depend on it, either to complete their life cycle or to maintain dominance over other species. Despite our current understanding of fire's importance and the creation of programs to use it in national parks and forests, only a small fraction of the land that should burn each year actually does burn. Thus, the accumulated magnitude of environmental change get larger year by year, and we have not returned North America to the landscapes seen by the first explorers.

Each Population Is Ecologically and Genetically Unique

We now realize that each population interacts with its local environment so that over evolutionary time it becomes genetically better adapted to that microenvironment. Each population within a given species, then, is probably genetically different from all others. The genetic differences can be expressed as plant morphology, timing of life cycle events such as flowering or leaf drop, or plant metabolism.

Not so long ago, botanists did not understand that species could contain such genetic diversity. In the 1920s, the botanist Gote Turesson collected seeds of species that had a wide range of habitats--from lowland, southern, and central Europe to northeastern Russia in the Ural Mountains--and he germinated them all in a garden in Åkarp, Sweden. He was the first to demonstrate that members of a wide-spread species were not genetically homogeneous. Despite the uniform environment of the common garden, plants that grew from seeds collected in warm, lowland sites often were taller and flowered later in the year than those that grew from seeds collected in cold, northern sites. They different in frost tolerance, leaf traits, and onset of dormancy. Yet, these variants all had the same flower traits and all could be cross-pollinated; therefore, they were members of the same species.

Turesson called these variants within species **ecotypes**. Today, after more research, we now understand that every population is its own ecotype.

One example of ecotypes involves alpine sorrel (*Oxyria digyna*), a small perennial herb that grows in rocky places above timberline. Some populations grow at high elevations in mountains; these are alpine populations (Fig. 26.19a). Others grow in the far north at low elevations; there are the arctic populations (Fig. 26.19b). Both populations experience certain environmental stresses in common, but they differ in other stresses. For example, they both are exposed to long periods of freezing winter weather, but during summer days alpine plants receive more solar

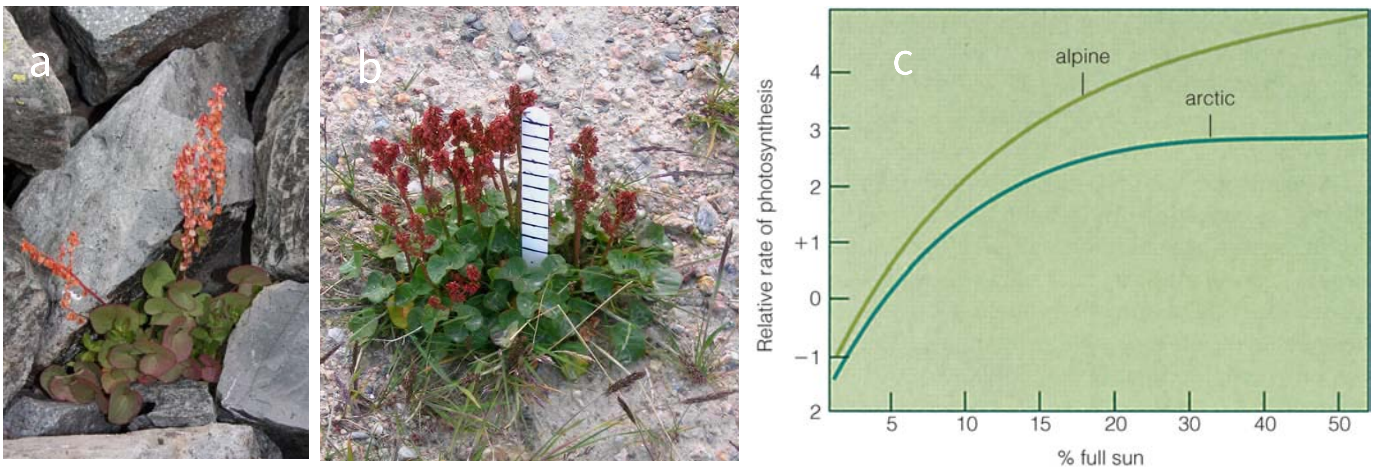


Figure 26.19. Ecotypes of alpine sorrel (*Oxyria digyna*). (a) Alpine ecotype. (b) Arctic ecotype. (c) Photosynthesis of each type at different light intensities.

radiation. Researchers have demonstrated that the alpine and arctic populations are separate ecotypes and that they differ in such physiological ways as the amount of light that is optimum for photosynthesis (Fig. 26.19c). Alpine plants photosynthesize best at 50% of full sun, whereas artic plants do best in lower light at 25% of full sun.

The ecotype concept is important in forestry. After logging, sites may be planted with tree seedlings. The seedlings come from seeds that were collected as close (in distance and elevation) to the logged area as possible. In mountainous terrain, seed sources must be within 100 m of elevation of the planting site. The Forest Service recognizes that the probability of seedling survival will be greatest for a population that is already genetically adapted to the local region.

26.6 INTERACTIONS AMONG NEIGHBORING POPULATIONS

Rarely does a single population, to the exclusion of all others, occupy a habitat. Usually, several plant, animal, and microbe populations--representing as many different species--coexist. Individuals of the various populations intermingle, growing next to each other, and this proximity allows them to affect each other. Sometimes the results are positive, with the organisms showing enhanced growth or survival; sometimes the results are negative, with the organisms suffering a decline.

There are four basic kinds of interactions: competition, amensalism, herbivory, and mutualism.

Competition Creates Stress by Reducing the Amount of a Commonly Required Resource

Competition may be defined as the decreased growth of two interacting populations because of an insufficient supply of a necessary resource such as light, moisture, space, nutrients, or pollinators. Sometimes the limitation lies with a single resource, but most often several resources are lacking. Competition may be equal, allowing the two populations to coexist indefinitely, or it may be unequal, eventually resulting in the displacement of one population and the occupation of its space by the other population.

Competition may be the most important biotic factor affecting plant distribution. Many populations restricted to saline, dry, or nutritionally poor soils, for example, would actually grow better on normal soil if other populations were first removed. These restricted populations are more tolerant of stress but are poor competitors in comparison with the plants that populate normal soil. When planted together, the restricted populations have slower root and shoot growth rates; consequently, they obtain less soil water and sunlight, and fewer of them survive to produce seeds. In time, they are completely eliminated from all but the most stressful sites, where plants from normal soils cannot maintain themselves.

The intensity of competition lessens in a process called divergent evolution. Over time two populations of different species become more different in such traits as the time of germination or flowering, tolerances for soil aridity or depth, nature of pollination or seed-dispersal vectors, or degree of shade tolerance. The portion of the microenvironment each population uses is called its **niche**. Over time, each population's niche becomes more distinct and separate from the niches of nearby populations. Theoretically, it is impossible for two populations to have the same niche because competition would be too intense; hence, the expression "One niche, one population."

Amensalism Creates Stress by Adding Something to the Environment

Amensalism (sometimes the word **allelopathy** is substituted) may be defined as the inhibition of one population by another through the addition of something to the environment. The added material can be a metabolic byproduct exuded from a living root or the decomposition products from dead litter. It can be a solid that accumulates beneath the parent plant, a liquid carried into the soil by percolating rainwater, or a volatile molecule carried off by the wind. A striking pattern of avoidance by two species in nature often is taken as evidence of amensalism (Fig. 26.20).

Amensalism may be common because plants are leaky systems, passively contributing all sorts of chemicals into the environment. One investigator grew seedlings representing 150 different flowering plant species in a nutrient culture. Water around the roots contained several radioactive elements as markers. The plants took up the isotopes through their roots and transported them to all organs, including the leaves. The plants then were exposed to a mist, and the water that condensed and ran off the leaves was collected for analysis. The investigator found that 14 elements, 7 sugars, 23 amino acids, and 15 organic acids--all radioactive--had leached from the plants.

Another study showed that roots are similarly leaky. Root tips were collected from mature trees in a New Hampshire forest and rinsed in distilled water. Analysis of the water revealed sugars, amino acids, organic acids, and various cations and anions. Birch (*Betula alleghaniensis*) exuded five times the amount of substance as maple (*Acer saccharum*). In nature, such substances from leaves, roots, or litter would accumulate in the soil, where they might affect microbial decomposers, soil pH, soil physical structure, and the growth of nearby plants.

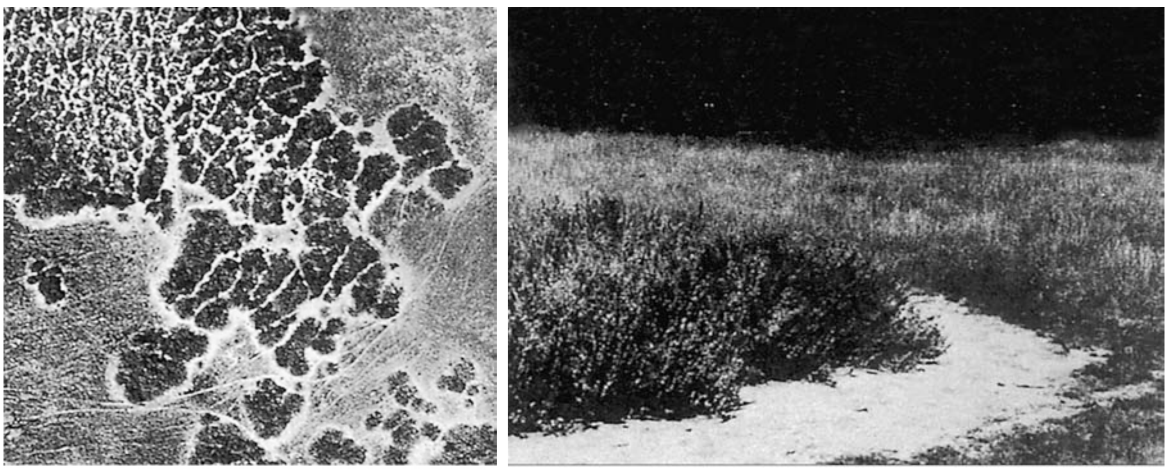


Figure 26.20. Possible amensalism between sage shrubs (*Salvia* and *Artemisia* species) and grasses in coastal areas of southern California. (a) Aerial photograph of a patch of sage. Note the bare soil beneath the shrubs and for some distance away from them. (b) View along the edge of a patch of shrubs, showing a zone of bare soil and stunted grasses several meters in width. Some researchers speculate that a volatile chemical exuded by shrub leaves prevents the grasses from germinating or growing normally.

Herbivory Is the Consumption of Plant Biomass by Animals

Herbivory is the harvesting by an animal of vegetative or reproductive parts of a plant; it may leave the plant alive or kill it. Herbivory can play a striking role in plant distribution. A glance along a pasture fence shows that certain palatable species are absent inside the pasture yet common outside it. Grazing animals are responsible for the difference.

Although plants often are thought of as passive organisms, unable to move as easily as animals, they are able to defend themselves against herbivores. The defenses are slowly elaborated over evolutionary time. One defense is the dispersal of population members over space, making it difficult for herbivores to locate and damage all the individuals. Dispersal can be achieved by vegetative runners or rhizomes, by explosive fruits, or by the use of wind as a vector. Another defense is the dispersal of population members over time. This can be accomplished by seeds with complicated dormancies or by reproduction that is irregular from year to year, as with masting or semelparous flowering. A third defense is the development of physical barriers such as sclerophylls, spines, thick bark, and hard fruits or seed coats.

A fourth defense is amensal: the manufacture and accumulation of metabolic byproducts that are distasteful or that otherwise inhibit herbivores from feeding. There has been much recent research into chemical herbivore defenses. The type of chemical a plant manufactures varies with its life history pattern: r-selected plants tend to manufacture toxins, whereas K-selected plants tend to accumulate tannins or terpenes. Toxins repel herbivores by interfering with nerve and muscle activity, hormone function, or liver and kidney metabolism. Toxins are small, relatively energetically inexpensive molecules of less than 500 molecular weight. They are effective in small concentrations, and they account for less than 2% of leaf dry weight. In contrast, tannins and terpenes repel herbivores by their bitter, unpleasant taste. They are large, complex molecules of 500 to 3,000 molecular weight and may account for 6% of leaf dry weight. Animals attempting to feed on plant tissue that is rich in tannins or terpenes move away to other plants.

Some chemical herbivore defenses are induced in response to an attack by an herbivore, parasite, or pathogen. Such chemical are called **phytoalexins**. The plant's chemical defense is analogous to antibody formation in animals. Humans are herbivores, too, and therefore plant toxins can and do poison humans, as well as grazing animals or insects. Humans, however, have learned to use some poisons as medicines or psychotropic drugs, and we cultivate the plants that manufacture them. The nicotine that accumulates in tobacco (*Nicotiana*) leaves inhibits herbivores, but humans use nicotine as a drug. Cocaine functions as an herbivore deterrent in coca shrubs (*Erythroxylon*), but Andean Indians learned to chew the leaves for stimulation while during strenuous activity at high elevations.

Mutualism Increases the Success of Both Populations

The previous examples of interactions were all negative, causing depressed growth or reproductive success in one or both interacting populations. **Mutualism** is an interaction that benefits both partners; furthermore, it is essential in the sense that the success of both partners is reduced when one of the partners is absent.

Several examples of mutualism already have been described earlier in this textbook. Animal partners form mutualistic relationships with plants. Bees, moths, and beetles--which cross-pollinate flowers while themselves feeding on nectar, pollen, or flower parts--are familiar examples. Ants, birds, and mammals that consume fruits while dispersing seeds are other examples. Sea anemones, which mutualistically harbor algae in their cells, provide yet another example. Lichens are mutualistic associations of fungi and algae, mycorrhizae are mutualistic associations of fungi and higher plants, and nitrogen-fixing bacteria live symbiotically in the root nodules of legumes.

If the benefits are not shared by both interacting populations, the relationship is not mutualistic but **commensal**. Epiphytes growing in a tropical tree, for example, form a commensal relationship with the tree. The host tree gains no benefit from the epiphyte. At the same time, the host tree is not usually hindered by the epiphyte, because the epiphyte is not a parasite and it is not so large that it shades the tree or breaks off limbs. The tree neither benefits nor loses by the association, whereas the epiphyte gains, greater exposure to light or perhaps protection from herbivores.

KEY TERMS

amensalism (allelopathy)
annual
biennials
C type
commensal
competition
convection
dioecious
drought-deciduous
ecotypes
environment
ephemeral
epiphytes
helophytes
herbaceous perennials
herbivory
hydrophytes
iteroparous
K-selected
macroenvironment
mast
mesophytes
microenvironment
monoecious
mutualism
niche
perennials
phytoalexins
plant demography
population
primary consumers
producers
r-selected
R type
re-radiation
secondary consumers
semelparous
shade leaves
shrubs
S type
subshrubs
succulent
sun leaves
survivorship curve
tertiary consumers
thermoperiod
transpiration
trees
trophic
vines
woody perennials
xerophytes

SUMMARY

1. Ecology is the study of organisms in relation to their natural environment. The environment contains all the biotic and abiotic elements that surround and influence an organism. The macroenvironment reflects the general, regional climate; the microenvironment reflects conditions near the surface of organisms or objects. Ecosystems consist of organisms and their environment. The organisms participate in trophic functions within the ecosystem: they produce food, they consume it, or they decompose it.

2. The basic ecological unit is the population. Every species typically has many populations, each one genetically distinct and adapted to its particular habitat. A population may be equivalent to an ecotype, unique in its morphology, physiology, or behavior. Population ecology is the study of a population, together with the environmental factors affecting that population.

3. A life history pattern is the budget of time and energy that carries a population through all phases of its life span. Plant life spans are annual (ephemeral), biennial, or perennial. Herbaceous perennials die back to below-ground organs each year. They occupy stressful habitats and commonly live for 20 to 30 years. Woody perennials include subshrubs, shrubs, vines, and trees. Trees include broadleaf angiosperm and needle-leaf gymnosperm categories. Broadleaf trees are shorter lived, have shorter-living leaves, and build harder wood than needle-leaf trees.

4. Semelparous populations reproduce only once, at the end of a plant's life span. Iteroparous populations reproduce repeatedly. Each pattern has its own advantages. Sexuality is sometimes determined by environmental factors or plant size; it is not necessarily under genetic control. The dioecious condition promotes cross-pollination, allows a population to occupy a wider array of sites, and reduces the loss of seeds to herbivores. The monoecious condition permits weedy, aggressive plants to disperse into new habitats, even when only a single individual has arrived.

5. Species with an r-selected life history pattern typically are small, fast-growing annuals adapted for open habitats; they are semelparous and allocate a great deal of caloric energy to reproduction. K-selected species typically are slow-growing, but ultimately large and long-lived forest trees in more stable habitats; they are iteroparous and allocate less energy to reproductive events. Most species lie somewhere along a continuum between these extremes.

6. Plant demography is the study of population age structure over time. It uses mathematical models to summarize the life span of individuals and cohorts in a population, their reproductive potential, their mortality rate over time, and future changes in the size of the population.

7. The intensity and quality of solar radiation change as the radiation passes through the atmosphere, plant leaves, and water. Light, the wavelength of solar

radiation visible to humans, is used by plants in photosynthesis. Large, long-living, K-selected plants successively live through different light environments and therefore must be flexible in their light requirements. This flexibility is enhanced by an ability to produce sun leaves and shade leaves and to be shade tolerant when young.

8. Every organism and organ has an energy budget with a zero sum. Solar radiation striking a leaf, for example, is first partitioned into reflected and absorbed energy. Absorbed energy is dissipated as transpiration, convection, re-radiation, and photosynthesis. Mesophytes expend most solar radiation by transpiration; xerophytes expend most solar radiation by convection, re-radiation, and reflection.

9. Fire caused by dry lightning strikes is a natural occurrence in many parts of North America. When natural fires are suppressed, the distribution of many plant populations is affected. Open pine savannas of the southeastern coastal plant, for example, change into dense oak forests if fires are not allowed to burn every 3 to 15 years. Currently, our use of prescribed fire is too limited to restore all North American landscapes to conditions before fire suppression.

10. Neighboring populations in the same habitat interact and affect each other through competition, amensalism, herbivory, and mutualism. Competition, amensalism, and herbivory are negative interactions, limiting the population size of one or both partners. Competition is caused by a deficient amount of an essential resource. Amensalism is caused by the addition of a deleterious substance into the microenvironment. Herbivory is the consumption of vegetative or reproductive plant material by an animal. Plants have evolved herbivore defenses in the following forms: (a) dispersal over space and time; (b) repulsive physical structures; and (c) toxic or unpalatable metabolic byproducts. The latter mechanism is a form of amensalism. Mutualism is a positive interaction, with the partners showing enhanced growth or survival.

Questions

1. A grassy acre in southern Michigan receives 47×10^8 calories of solar radiation over the course of one year. Plants fix, in photosynthesis, about 58×10^6 calories of that radiation. They retain 50×10^6 calories, and of these, mice consume 25×10^4 calories. The mice retain 5×10^4 calories, and of these, weasels consume 5×10^3 calories. Weasel net growth is 1×10^3 calories. If a young weasel must gain 2,000 g of weight in that year, and each gram is equivalent to 5×10^3 calories, how many acres of grassland must be its range?

2. Can a species be rare and in danger of extinction if its only population has thousands of individuals? Can a species be rare and in danger of extinction if it has thousands of populations, each population of which has only a few individuals?

3. Why do semelparous plants die after their single reproductive event? What are possible advantages to reproduction in this way? Shrubs and trees are rarely semelparous. Do you know of any in your region?

4. Is a single habitat inhabited by only r-selected or only K-selected species, or can they coexist in the same habitat?

5. What is the definition of plant demography? Try to diagram the demography of a human population using the same model shown for a plant population in Figure 26.12.

6. In an irrigated, dark green pasture in Texas, what fraction of annual solar radiation do you guess would be dissipated by transpiration, by reflection, by convection, and by photosynthesis? If that same pasture were allowed to revert to semiarid, non-irrigated natural grassland, how might those figures change?

7. How did Turesson show that species were not ecologically and genetically homogeneous? Is ecotype a synonym for population?

8. Describe the difference between competition and amensalism. Why are both of these interactions called negative, whereas mutualism is said to be positive?

PLANTS, PEOPLE, AND THE ENVIRONMENT: ***The Natural Fire Cycle in the Southeastern Pine Savanna***

One of the first vegetation types in the United States shown to be dependent on fire for its maintenance was the pine savanna of the southeastern coastal plain (Figure). Tall, scattered loblolly, slash, shortleaf, and longleaf pines dominate the region, and a thick growth of grasses, mainly *Andropogon* and *Aristida*, with some broad-leaved herbs, cover the ground beneath. Euro-American settlers found the pines to be valuable for lumber and turpentine and the grass to be valuable for grazing livestock. Wildfires were thought to be dangerous; therefore, during the nineteenth century some of this vegetation was protected from fire. Gradually, however, the pines gave way to oaks, and in time a dense oak forest with little grass replaced the pine savanna.

Longleaf pine (*Pinus palustris*) savanna in North Carolina (a) Aspect of the savanna. Overstory trees are widely spaced and average 50 years in age. Beneath them are grasses and broad-leafed herbs. (b) Close-up view of a young longleaf pine in the "grass" stage.

Ecological studies in the 1930s revealed the importance of fire to the pines, especially to longleaf pine (*Pinus palustris*). Longleaf pine is not only tolerant of fire, it is dependent on fire. Its seeds germinate in the fall, soon after dropping to the ground from cones. During their first year of growth, the seedlings are very sensitive to even the lightest fire. However, during the next several years, longleaf pine seedlings are in a "grass" stage (Fig. 1). Food reserves are shunted to the root system, the stem remains stunted, and a dense cluster of long needles surrounds the apical meristem, which is located at the ground surface. If a fire sweeps through the area at this time, the apical bud is insulated, and the seedling remains alive. A fire actually improves seedling survival because the high temperatures kill a common fungus that otherwise parasitizes the needles.

After the grass stage, longleaf pine saplings enter a 4- to 5-year period of rapid stem elongation. By the time the sapling is 8 to 9 years old, its canopy is high enough above the ground that it is beyond the reach of surface fire flames. In addition, the bark is thick enough to insulate the cambium from damage.

Pine savanna systems maintain themselves naturally so long as ground fires sweep through every several years. However, if fires are suppressed for as long as 15 years, hardwood seeds carried into the area by animals will germinate and produce young saplings. Hardwood saplings are very sensitive to ground fire; they would not be able to invade an area where burns occurred every few years. In the absence of fire, however, they compete well with grasses and pines, and they are tolerant of shade from the overstory pines. As the oaks grow, they create more shade, which inhibits pine seedling establishment, growth, and survival. When overstory pines die, they are replaced by hardwoods, not by pines. In time, an oak forest exists where a pine savanna used to be.

In addition to pines, many herbaceous plant species decline in abundance because fire no longer keeps down competing grass and smothering litter. Other species disappear because their life cycles somehow require fire. Their seeds can germinate only after the seed coat is scarified by high temperatures, or they flower profusely only after fire has released a pulse of nutrients into the soil. In addition, certain grazing animals, birds, and insects that live best in open savanna will be absent from this oak forest. In other words, a whole community of organisms will change in the absence of fire.

Standard land management practice currently is to set a prescribed surface fire purposely every 4 years if a natural fire has not visited the area. Under this system, the pine savanna maintains itself indefinitely, just as it would with natural wildfires.

The use of natural or prescribed fire as a management tool is still not widely practiced because it affects air quality, is expensive, and can be conducted only during narrow windows of time when there is a low probability that a fire will escape. The infamous Yellowstone fire in 1988 is a good example of a natural fire that was allowed to burn but that got out of control when the weather changed. It caused a great deal of economic damage to surrounding communities and resulted in a congressional investigation of the whole concept of fire management. The congressional report ratified the concept that natural fire is beneficial, but it recommended additional restrictions as to when natural fires would be allowed to burn.

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