Life Histories and Evolutionary Fitness

Trade-offs in the allocation of resources provide a basis for understanding life histories.

Phenotypic plasticity allows an individual to adapt to environmental change.

Life histories vary along a slow–fast continuum.

A life history represents the best resolution of conflicting demands on the organism.

Life histories balance trade-offs between current reproduction and future reproduction.

Semelparous organisms are those that breed once and then die.

Senescence is a decline in physiological function with increasing age.

One of the remarkable facts concerning reproductive success is that the end result is always approximately the same. That is, each individual, on average, produces one offspring that lives to reproduce. This must be so, for otherwise populations would either dwindle rapidly to extinction because individuals failed to replace themselves, or they would grow out of all bounds.

Nonetheless, how organisms grow and produce offspring also varies in all imaginable ways. A female sockeye salmon, after swimming up to 5,000 km from her Pacific Ocean feeding ground to the mouth of a coastal river in British Columbia, faces another 1,000-km upriver journey to her spawning ground. There she lays thousands of eggs, and then promptly dies, her body wasted from the exertion. A female African elephant produces a single offspring at intervals of several years, lavishing intense care on her baby until it is old enough and large enough to fend for itself in the world of elephants (Figure 10.1).

Thrushes start to reproduce when they are 1 year old, and may produce several broods of three or four young each year, but rarely live beyond 3 or 4 years. Storm petrels, which are seabirds the size of thrushes, do not begin to reproduce until they are 4 or 5 years old, and rear at most a single chick each year, but may live for 30 or 40 years.

Such attributes of the schedule of an individual’s life—age at maturity, number of offspring, life span—make up what ecologists call the life history of the individual. Life histories are complex phenomena influenced by factors in the environment, the general body plan and lifestyle of organisms, and their individual and evolutionary responses to physical conditions, food supply, predators, and other aspects of the environment.
As we have seen, organisms are generally well suited to the conditions of their environments. Form and function vary in parallel with the ranges of temperature, water availability, salinity, oxygen, and other factors encountered by each species. We have seen how organisms choose their activity spaces and make foraging decisions in response to temporal and spatial variation in their environments. Whether modifications of form and function have evolved or result from individual responses to different environments, we presume that they are adaptive and that they increase the reproductive success of individuals. We can see why desert plants have small leaves with thick cuticles to reduce water loss. The close color matching of grasshoppers to their backgrounds makes sense when one understands that they are eaten by visually hunting predators. Life histories, too, are shaped by natural selection. An organism’s life history represents its solution to the problem of allocating limited time and resources so as to achieve maximum reproductive success.

For decades, ecologists have used observation, mathematical modeling, and experimentation to unravel the causes of variation in life histories among living beings. Songbirds in the Tropics, for example, lay fewer eggs (two or three, on average) than their counterparts at higher latitudes (generally four to ten, depending on the species) (Figure 10.2). Professor David Lack of Oxford first placed
this life history observation in an evolutionary context. Lack recognized that birds could increase their overall reproductive success by increasing the size of their clutches (the set of eggs laid together in a nest), unless something reduced the survival of offspring in large broods. He hypothesized that the ability of adults to gather food for their young was limited and, accordingly, that chicks in large broods, where there were too many mouths to feed relative to the food supply, would be undernourished and survive poorly. Lack further noted that at temperate and arctic latitudes, birds had longer days in which to gather food during summer, when their offspring are reared. Therefore, it made sense that birds at high latitudes could rear more offspring than birds breeding in the Tropics, where day length remains close to 12 hours year-round.

Lack made three important points. First, he stated that because life history traits, such as number of eggs in a clutch, contribute to reproductive success, they also influence evolutionary fitness. Second, he demonstrated that life histories vary consistently with respect to factors in the environment, such as the length of time available for feeding. This finding suggested the possibility that life history traits are molded by natural selection. Third, he proposed a hypothesis that could be subjected to experimental testing. In the case of clutch size, Lack suggested that the number of offspring that parents can rear is limited by their food supply. To test this idea, one could add eggs to nests to create enlarged clutches and broods. According to Lack's hypothesis, parents should be unable to rear added chicks because they cannot gather the additional food required by a larger brood.

This experiment has been conducted many times over the last several decades, generally with the result predicted by Lack. For example, the Swedish ecologist Göran Hogstedt manipulated the clutch sizes of magpies (relatives of crows) by moving eggs between nests. His results showed that magpies lay a clutch that corresponds to the maximum number of offspring that a pair can rear. Either adding or subtracting eggs results in fewer offspring fledged (Figure 10.3), just as Lack had predicted.

### Trade-offs in the allocation of resources provide a basis for understanding life histories

Organisms have limited time, energy, and nutrients at their disposal. Adaptive modifications of form and function either increase the resources available to individuals or allow them to use those resources to their best advantage. Many modifications involve trade-offs, meaning that limited time, energy, or materials devoted to one structure or function cannot be allotted to another. Therefore, each organism is faced with the problem of allocation. Given that time and resources are limited, how can the organism best use them to achieve its maximum possible evolutionary fitness?

Practical solutions to the allocation problem depend on how a change in any given structure or function affects fitness. When modification of a trait influences several components of survival and reproduction, as is often the case, the evolution of that trait can be understood only by considering the entire life strategy. For example, an increase in the number of seeds produced by an oak tree may contribute to fitness by increasing the number of offspring. But such a modification may also reduce the survival of seedlings (if seed size is reduced to make more of them), the survival of adult trees (if resources are shifted from root growth to support increased seed production), or subsequent seed production (if seed production in one year reduces tree growth, and therefore size, in subsequent years).

From an evolutionary point of view, an individual's reason for existence is to produce successful progeny—as many as possible. Reproduction involves choosing among many options: when to begin to breed, how many offspring to have at one time, how much care to bestow upon them. The set of rules and choices influencing an individual's survival and reproduction at each age governs its life history. Each life history has many components, the most important of which are maturity, or age at first
reproduction; parity, or number of episodes of reproduction; fecundity, or number of offspring produced per reproductive episode; and aging (Figure 10.4).

The optimum life history for an individual depends on the particular circumstances of its environment. As we have seen in the last chapter, when an individual's environment varies, it can respond by altering its behavior, its physiology, or even its development. Individuals also can alter their life history traits. Thus, the capacity to respond to variation in the environment is itself an aspect of the life history that is subject to natural selection. Before we discuss life histories in detail, we shall take some time to distinguish between evolutionary adaptations of populations and responses of individuals to the range of environmental conditions they normally encounter. Both are governed by sets of decision rules concerning allocation of time and resources. Individual responses are nongenetic. However, the ways in which individuals can respond to their environments may be under genetic control and subject to evolutionary change by natural selection. Thus, phenotypic plasticity may be considered a part of the life history strategy.

Phenotypic plasticity allows an individual to adapt to environmental change

Virtually all attributes of an individual are affected by environmental conditions and by the response of the individual to those conditions. The observed relationship between the phenotype of an individual and the environment is referred to as a reaction norm (Figure 10.5). Many of the responses discussed in Chapter 9 are examples of reaction norms. The general responsiveness of the phenotype to the surroundings is called phenotypic plasticity.

Some reaction norms are a simple consequence of the influence of the physical environment on life processes. Heat energy accelerates most life processes. Therefore, we should not be surprised that caterpillars of the swallowtail butterfly *Papilio canadensis* grow faster at higher temperatures. The relationship between growth rate and temperature for an individual describes the reaction norm of growth rate with respect to temperature for that individual. However, individuals of the same species from Michigan and from Alaska exhibit different relationships between...
The reaction norm indicates the response to different environments.

**Figure 10.5** A reaction norm is the observed relationship between the phenotype and the environment. The graph shows the reaction norm of a single genotype over a range of environments. Each particular environment (for example, A or B) produces a characteristic phenotype.

growth rate and temperature (**Figure 10.6**). In one experiment, larvae from Alaskan populations grew more rapidly at low temperatures and larvae from Michigan grew more rapidly at high temperatures, as one might have predicted from the typically warmer temperatures in Michigan during the growing season. This finding indicates that reaction norms may be modified by evolution to improve performance under the particular conditions experienced by a population, as shown diagrammatically in **Figure 10.7**.

![Diagram](image)

**Figure 10.6** The reaction norms of different populations may differ. Fourth-instar larvae of the swallowtail butterfly *Papilio canadensis* were obtained from populations in Alaska and Michigan and reared on balsam poplar in the laboratory at temperatures of 12°C and 24°C. After M. P. Ayres and J. M. Sweeney, *Ecol. Monogr.* 64:465–482 (1994).

**Genotype–environment interaction**

As swallowtail growth rates show, the genetic makeup of the individual and the individual’s environment interact to determine its performance. When the reaction norms of two genotypes cross, as they do in the case of the swallowtail butterfly, then individuals with each genotype perform better in one environment and worse in the other. Such a relationship is referred to as a genotype–environment interaction.

![Diagram](image)

**Figure 10.7** Reaction norms may be modified by evolution. Reaction norms may diverge when two populations of the same species exist for long periods under different conditions. Very often an increase in performance under the prevalent conditions is accompanied by a decrease in performance when individuals are exposed to conditions outside the population’s normal range.
interaction because each genotype responds differently to variation in the environment.

Interactions between genetic and environmental factors are the basis for the evolution of specialization. Over time, when two populations are exposed to different ranges of environmental conditions, genotype–environment interactions will cause different genotypes to predominate in each population. The populations will therefore become differentiated and will have different reaction norms, each of which enables individual organisms to perform better in their own environment, as illustrated in Figure 10.7.

**Reciprocal transplant experiments**

Whether differences between populations are due to genetic differences or to phenotypic plasticity often can be revealed by **reciprocal transplant experiments**. Transplant studies compare the observed phenotypes of individuals kept in their native environment with those of individuals transplanted to a different environment (Figure 10.8). Reciprocal transplants involve the switching of individuals between two localities. When phenotypic values of native and transplanted individuals do not vary between the two environments, we may conclude that the traits of interest are genetically determined. That is, the trait values reflect the population from which an individual comes (genotype) rather than where it is living (environment). When trait values reflect where an individual is living (environment) rather than where it comes from (genotype), then the results of the experiment are consistent with phenotypic plasticity. Of course, intermediate results are possible, in which case one might conclude that the reaction norm has been subject to evolutionary modification.

**ECOLOGISTS IN THE FIELD**

Peter Niewiarowski and Willem Roosenberg, then at the University of Pennsylvania, transplanted fence lizards (Sceloporus undulatus) between nutrient-poor pine barrens in New Jersey and nutrient-rich tall-grass prairies in Nebraska. The effect of the switch on the lizards' growth rates revealed both genetic determination and phenotypic plasticity (Figure 10.9). The growth rates of Nebraska lizards, about twice those of New Jersey lizards in their native environments, decreased by half—to the New Jersey level—when Nebraska individuals were transplanted to New Jersey. In contrast, New Jersey lizards did not grow faster in Nebraska.

A simple interpretation of these results is that resources for growth are consistently scarcer in New Jersey than in
Nebraska and that Nebraska lizards transplanted to New Jersey cannot gather resources fast enough to support their natural growth rates. Apparently, New Jersey lizards have a genetically regulated growth rate that is adjusted to a low resource level. That is, they have lost the ability to modify individual growth rates in response to higher resource levels—levels that they probably experience rarely, if ever.

It is fair to ask whether the slower growth of Nebraska lizards under New Jersey conditions is adaptive or merely a consequence of reduced resources and more stressful conditions. If their slower growth was an example of adaptive phenotypic plasticity, it would reduce the negative effects of this environmental change on their fitness. That is, we would expect adaptation to compensate in some beneficial way for a change in environmental conditions. The fence lizard shows that organisms may have little control over their rate of growth under poor conditions. If resources are not available, individuals cannot grow rapidly and achieve large stature. Nonetheless, other aspects of their lives can be modified in response to growth performance.

**MORE ON THE WEB**

Ecotypes and reaction norms. The response of yarrow plants to variation in growing conditions has been studied in a reciprocal transplant experiment.

**Food supply and timing of metamorphosis**

Many types of organisms undergo dramatic changes during the course of their development. Metamorphosis from larval to adult forms and sexual maturation are the most prominent of these changes. The best time to undergo such transitions depends on the presence of resources and natural enemies in the environment, and their timing is made more complicated by variations in rate of growth due to food supply, temperature, and other environmental factors.

Imagine two growth curves resulting from two levels of food supply (Figure 10.10). Let us suppose that under a

**Figure 10.9** The growth rates of fence lizards reveal both genetic determination and phenotypic plasticity. Juvenile eastern fence lizards (*Sceloporus undulatus*) from populations in Nebraska and New Jersey were exchanged in a reciprocal transplant experiment. Arrows indicate the growth responses of the transplanted populations. From data in P. H. Niewiarowski and W. Roosenberg, *Ecology* 74:1992–2002 (1993).

good nutritional regime resulting in rapid growth, an individual matures at a given mass and age. Poorly nourished individuals clearly cannot reach the same mass at a given age and therefore must mature at a different point with respect to size, age, or both. Faced with such environmental variation, an individual can follow one of two pathways, or some intermediate between them. First, the individual may mature when it achieves a certain mass, however long this takes. With poor nourishment, it will take longer to achieve this mass, and maturation will be delayed. Consequently, the individual will be exposed to a longer period of risk prior to reproduction. Alternatively, the individual may mature at a predetermined age. With poor nourishment, this strategy will result in a smaller size at maturity, and perhaps a reduced reproductive rate as an adult. The optimum solution is usually somewhere in between, depending in part on the risk of death as a juvenile (high risk favors earlier maturation at a smaller size) and the slope of the relationship between fecundity and size at maturity (higher values favor delayed maturation at a larger size because the fecundity payoff is greater).

Tadpoles raised under conditions of high and low food availability exhibit different growth rates, as expected. In one experiment, the tadpoles given the poorer diet metamorphosed into adult frogs at a smaller size, but a later age, than those reared with abundant food (Figure 10.11).

This finding supports the theoretical conclusion that the timing of metamorphosis should be sensitive to both age and size: poor nutrition slows the developmental program in frogs, but does not stop it altogether. The relationship between age and size at metamorphosis under different feeding regimes is the reaction norm of metamorphosis with respect to age and size.

**Phenotypic plasticity and contrasting mechanisms of growth and reproduction in animals and plants.** The modular organization of plants allows them to respond to the challenge of herbivory and changes in light and nutrients by differential growth of root and shoot tips.

**Figure 10.11** The relationship between age and size at metamorphosis in frogs grown at high and low food availabilities. The metamorphosis reaction norm lies between constant size and constant age extremes. Symbols represent weights of tadpoles at 40 days and at metamorphosis; these data were used to obtain the growth relationship of each treatment group. After data in J. Travis, Ecology 65:1155–1160 (1984).

Life histories vary along a slow–fast continuum

Life history traits, such as age at maturity, fecundity, and longevity, vary widely among different species and even among different populations of the same species. Two points can be made about this variation. First, life history traits often vary consistently with respect to habitat or conditions in the environment. Seed size, for example, is generally larger among plants of the forest than among plants of grasslands.

Second, variation in one life history trait is often correlated with variation in other traits. For example, the number of independent offspring produced each year is positively correlated with adult annual mortality rate (Figure 10.12). As a result, life history characteristics are generally organized together along a single continuum of values. At one extreme, which we can refer to as the “slow” end of the spectrum, organisms such as elephants, albatrosses, giant tortoises, and oak trees exhibit long life, slow development, delayed maturity, high parental investment, and low reproductive rates. At the fast end of the spectrum are mice, fruit flies, and weedy plants, which exhibit the opposite life history characteristics. The correlation between mortality and fecundity across species must in part reflect the fact that in persistent populations, births and deaths must balance on average. In addition, however, these life history traits may be modified by evolution.

The English plant ecologist J. P. Grime emphasized the relationship between the life history traits of plants and certain conditions of the environment. He envisioned variation in life history traits lying between three extreme apexes, like points of a triangle, and called plants with life histories at these extremes “stress tolerators,” “ruderals” (weeds), and “competitors” (Table 10.1). As their name implies, stress tol-
operators grow under extreme environmental conditions. They grow slowly and conserve resources. Because seeding establishment is difficult in stressful environments, vegetative spread is emphasized. Where conditions for plant growth are more favorable, ruderals and competitors occupy opposite ends of a spectrum of disturbance. Ruderals, which colonize disturbed patches of habitat, exhibit rapid growth, early maturation, high reproductive rates, and easily dispersed seeds. These traits enable them to reproduce quickly and disperse their progeny to other disturbed sites—"growing like weeds"—before being overgrown by superior competitors. Competitors tend to grow to large stature, mature at large sizes, and exhibit long life spans. The competitor life history therefore requires stable conditions for its success.

Larger organisms tend to have longer life spans and lower reproductive rates than smaller organisms. This pattern is partly a function of the physical and physiological consequences of body size and partly results from the different environmental factors affecting large and small organisms.

**Table 10.1** Typical life histories of plants in environments with different selective factors

<table>
<thead>
<tr>
<th>Competitors</th>
<th>Ruderals</th>
<th>Stress tolerators</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbs, shrubs, or trees</td>
<td>Herbs, usually annuals</td>
<td>Lichens, herbs, shrubs, or trees; usually evergreen</td>
</tr>
<tr>
<td>Large, with a fast potential growth rate</td>
<td>High potential growth rate</td>
<td>Potential growth rate slow</td>
</tr>
<tr>
<td>Reproduction at a relatively early age</td>
<td>Reproduction at an early age</td>
<td>Reproduction at a relatively late age</td>
</tr>
<tr>
<td>Small proportion of production to seeds</td>
<td>Large proportion of production to seeds</td>
<td>Small proportion of production to seeds</td>
</tr>
<tr>
<td>Seed bank sometimes, vegetative spread often important</td>
<td>Seed bank and/or highly vagile seeds</td>
<td></td>
</tr>
<tr>
<td>Vegetative spread important</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

A life history represents the best resolution of conflicting demands on the organism

Life history traits are, to a greater or lesser extent, under the control of the individual, but not without constraint. For example, electing to produce larger offspring inevitably results in fewer being produced. Watching more carefully for predators takes time away from feeding, and so while this tactic may increase survival, fewer young may be produced. Each of these choices affects other aspects of an individual's life. Because breeding takes time and resources from other activities and entails risks, investment in offspring generally diminishes the survival of parents. In many cases, rearing offspring drains a parent's resources so much that fewer offspring are produced later.

An optimized life history represents a resolution of conflicts between the competing demands of survival and reproduction to the best advantage of the individual in terms of reproductive success. A critical effort in the study of life histories has been to understand the fitness consequences of changing the allocation of limited time and resources to such competing functions.

**ECOLOGISTS IN THE FIELD**

*The cost of parental investment in the European kestrel*

Although it is widely believed that trade-offs between functions constrain life histories, demonstrating such trade-offs has proved difficult. One useful approach is to manipulate experimentally individual components of the phenotype. As we saw above, adding and subtracting eggs in the nests of birds has, in many cases, revealed an inverse relationship between the number of chicks in a nest and their survival. Consequently, production of offspring is often greatest from clutches of intermediate size. Sometimes, however, having more mouths to feed stimulates parents to increase their effort to hunt for food for their chicks. In this case, an artificially enlarged brood might result in higher reproductive success, but impose a cost on parents in the form of smaller future broods or decreased survival.

Cor Dijkstra, Serge Daan, and their colleagues at the University of Groningen in The Netherlands have conducted extensive studies of the ecology and reproduction of European kestrels. Kestrels are small hawks that search for voles and shrews in open fields, often by hovering high overhead. Thus, kestrel foraging requires a high rate of energy expenditure, but small mammals are so abundant that individual kestrels normally can catch enough prey to feed their brood in a few hours each day. Kestrels lay an average of five eggs. When the broods in a sample of nests were about a week old, the investigators either removed two chicks or added two chicks, creating reduced and enlarged broods as well as unchanged controls. Parents that were provided extra chicks worked harder to feed their enlarged broods, increasing their foraging time and energy expenditure.

The fruits of the increased parental investment were an increase in the number of chicks successfully reared per brood. However, in spite of the increased efforts of their parents, chicks in the enlarged broods were somewhat undernourished, and only 81% survived to fledging, compared with 98% in control and reduced broods. Consequently, the extra parental investment netted the harder-working parents only an extra 0.8 chick per nesting attempt, and this gain may have been diminished by subsequent lower survival of the underweight fledglings. A more telling effect of the increased parental effort was seen in the lower survival of adults with enlarged broods to the next breeding season (Figure 10.13). Clearly, at some level of parental investment, the law of diminishing returns sets in, and further parental effort reduces the possibility of future reproductive success more than it increases the success of the present brood.

**Figure 10.13** Parental investment affects parental survival. The annual survival rate of male and female European kestrels (*Falco tinnunculus*) was affected by the number of chicks they reared. From data in C. Dijkstra et al., *J. Anim. Ecol.* 59:269–289 (1990).
Life histories balance trade-offs between current reproduction and future reproduction

Most issues concerning life histories can be phrased in terms of three questions: When should an individual begin to produce offspring? How often should it breed? How many offspring should it attempt to produce in each breeding episode? The variation among species in these life history traits illustrates the different ways of resolving the fundamental trade-off between fecundity and adult growth and survival—that is, between present and future reproduction.

Age at first reproduction

When should an animal or plant begin to breed? Long-lived organisms typically begin to reproduce at an older age than short-lived ones (Figure 10.14). Why should this be so? At every age, an individual must choose, whether consciously or not, between breeding and abstaining from breeding. Thus, we may understand age at first reproduction in terms of the benefits and costs of breeding at a particular age. The benefits appear as an increase in fecundity at that age. Costs may appear as reduced survival to older ages or reduced fecundity at older ages, or both.

Consider the following hypothetical example. A type of lizard continues to grow only until it reaches sexual maturity. Its fecundity varies in direct proportion to its body size at maturity. Suppose that the number of eggs laid per year increases by ten for each year that an individual delays reproduction. Thus, individuals that begin to breed in their first year produce ten eggs that year and the same number each year thereafter; individuals first breeding in their second year produce twenty eggs per year; and individuals maturing in their third year produce thirty eggs and so on. Comparing the cumulative egg production of early-maturing and late-maturing individuals (Table 10.2) reveals that the age at maturity that maximizes lifetime reproduction varies in direct proportion to the life span. For example, for a lizard with a life span of 3 years, maturing at 2 years results in the greatest lifetime reproduction. When the life span is 7 years, 4 years is the best age to mature.

For organisms that do not grow after their first year (most birds, for example), the decision whether to breed in a particular year after the onset of sexual maturity may reflect a trade-off between current reproduction and survival (which is, of course, related to future reproduction). Nonbreeding individuals avoid the risks of preparations for reproduction, such as courtship, nest building, and migration to breeding areas. Presumably, life experience gained with age also reduces the risks associated with breeding or increases the number of offspring resulting from a certain level of parental investment, or both, and thereby favors delayed reproduction. Among birds, age at maturity varies directly with the annual survival rate of adults, up to about 10 years in certain long-lived seabirds (see Figure 10.14).

**Figure 10.14** Long-lived organisms mature later than short-lived ones. Age at maturity is correlated with annual adult survival rate, which is directly proportional to life span, in a variety of birds. From R. E. Ricklefs, in D. S. Farner (ed.), Breeding Biology of Birds, National Academy of Sciences, Washington, D.C. (1973), pp. 366–455.
Table 10.2  Total eggs produced by individuals in a hypothetical population as a function of life span and age at first reproduction

<table>
<thead>
<tr>
<th>Age at first reproduction (years)</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>10</td>
<td>20</td>
<td>30</td>
<td>40</td>
<td>50</td>
<td>60</td>
<td>70</td>
<td>80</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>20</td>
<td>40</td>
<td>60</td>
<td>80</td>
<td>100</td>
<td>120</td>
<td>140</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>0</td>
<td>30</td>
<td>60</td>
<td>90</td>
<td>120</td>
<td>150</td>
<td>180</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>40</td>
<td>80</td>
<td>120</td>
<td>160</td>
<td>200</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>50</td>
<td>100</td>
<td>150</td>
<td>200</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>60</td>
<td>120</td>
<td>180</td>
</tr>
</tbody>
</table>

*Bold type indicates most productive ages at first reproduction for a given life span.*

Tending to offset the advantages of delayed reproduction are many factors that reduce the expectation of future reproduction. These factors include high predation rates, encroaching senescence at old age, and, for organisms with a life span of a single year or less living in seasonal environments, the end of the reproductive season.

MORE ON THE WEB  *Annual and perennial life histories. Why should some plants grow, reproduce, and die within one season while others persist from year to year?*

### The trade-off between fecundity and survival

When a particular life history attribute affects both current fecundity and future growth or survival, selection would be expected to optimize the trade-off between the two. Intuitively, we would expect high mortality rates for adults to tip the balance in favor of current fecundity. Conversely, when the life span is potentially long, individuals should not increase current fecundity so much as to jeopardize future reproduction. This insight has a simple algebraic proof, which is as follows.

We use a model in which the geometric rate of population growth ($\lambda$) is equal to $S_0B + S$, where $S$ is annual adult survival, $B$ is annual fecundity, and $S_0$ is the survival of offspring to maturity at 1 year of age. Thus, the annual per capita growth rate of the population is the sum of the surviving adults ($S$) and new recruits to the breeding population ($S_0B$). We now partition adult survival into two components, one directly related to reproduction ($S_p$) and the other independent of reproduction ($S$). Thus, the rate of population growth may be expressed as

$$\lambda = S_0B + SS_p$$

Changes in reproductive traits that cause small changes in the values of survival ($\Delta S_p$) and fecundity ($\Delta B$) will influence the rate of population growth ($\Delta \lambda$) as follows:

$$\Delta \lambda = S_0\Delta B + SS_p \Delta S_p$$

When changes that enhance fecundity (make $\Delta B$ positive) also reduce survival (make $\Delta S_p$ negative), as we have seen in the case of the European kestrel, their effects on $\Delta \lambda$ depend on the relative values of $S$ and $S_0$. Indeed, by rearranging the last equation, we can show that a change in life history traits will be favored ($\Delta \lambda > 0$) when

$$\frac{\Delta B}{\Delta S_p} > \frac{S}{S_0}$$

change in fecundity with respect to change in reproductive risk > ratio of adult to prereproductive survival
The trade-off between growth and fecundity

Many plants and invertebrates, as well as some fishes, reptiles, and amphibians, do not have a characteristic adult size. They grow, although often at a continually decreasing rate, throughout their adult lives, a condition referred to as indeterminate growth. Fecundity is directly related to body size in most species with indeterminate growth. Because egg production and growth draw on the same resources of assimilated energy and nutrients, increased fecundity during one year must be weighed against reduced fecundity in subsequent years. Accordingly, a long life expectancy should favor growth over fecundity during each year. For organisms with less chance of living to reproduce in future years, allocating limited resources to growth rather than eggs wastes potential fecundity at a young age.

Table 10.3 Numerical comparisons of the strategies of slow growth/high fecundity and rapid growth/low fecundity in two hypothetical fish

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Slow growth/high fecundity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body weight</td>
<td>10</td>
<td>12</td>
<td>14.4</td>
<td>17.3</td>
<td>20.8</td>
<td>25.0</td>
</tr>
<tr>
<td>Growth increment</td>
<td>2</td>
<td>2.4</td>
<td>2.9</td>
<td>3.5</td>
<td>4.2</td>
<td>5.0</td>
</tr>
<tr>
<td>Weight of eggs</td>
<td>8</td>
<td>9.6</td>
<td>11.5</td>
<td>13.8</td>
<td>16.6</td>
<td>20.0</td>
</tr>
<tr>
<td>Cumulative weight of eggs</td>
<td>8</td>
<td>17.6</td>
<td>29.1</td>
<td>42.9</td>
<td>59.5</td>
<td>79.5</td>
</tr>
<tr>
<td><strong>Rapid growth/low fecundity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body weight</td>
<td>10</td>
<td>15</td>
<td>22.5</td>
<td>33.8</td>
<td>50.7</td>
<td>76.1</td>
</tr>
<tr>
<td>Growth increment</td>
<td>5</td>
<td>7.5</td>
<td>11.3</td>
<td>16.9</td>
<td>25.4</td>
<td>38.1</td>
</tr>
<tr>
<td>Weight of eggs</td>
<td>5</td>
<td>7.5</td>
<td>11.3</td>
<td>16.9</td>
<td>25.4</td>
<td>38.1</td>
</tr>
<tr>
<td>Cumulative weight of eggs</td>
<td>5</td>
<td>12.5</td>
<td>23.8</td>
<td>40.7</td>
<td>66.1</td>
<td>104.2</td>
</tr>
</tbody>
</table>

Note: All weights in grams. Body weight + growth increment = next year's body weight. Cumulative weight of eggs to last year + weight of eggs = cumulative weight of eggs to this year. Growth increment and weight of eggs in each year are equal to the body weight.
growth result in greater overall productivity (cumulative weight of eggs), whereas for fish living longer than 4 years, low fecundity and rapid growth are more productive. Adult mortality, therefore, determines the optimal allocation of resources between growth and reproduction.

Semelparous organisms are those that breed once and then die.

Unlike most fish, which breed repeatedly, some species of salmon grow rapidly for several years, then undertake a single episode of breeding. During this one burst of reproduction, females convert a large portion of their body tissues into eggs, and then die shortly after spawning. Because salmon make such a great effort to migrate upstream to reach their spawning grounds, it may be to their advantage to make the trip just once. After arriving at their breeding areas, they should then produce as many eggs as possible, even if this supreme reproductive effort results in the wastage of most body tissues and ensures death. This pattern is called programed death because it is a direct consequence of adaptation to maximize reproductive success.

The salmon life history pattern is sometimes called "big-bang" reproduction, but is more properly referred to as semelparity. This term comes from the Latin senel ("once") and pario ("to bear"); the opposite of semelparity is iteroparity, from iero ("to repeat"). Semelparity is not the same as annual reproduction. For one thing, annuals may have more than one episode of reproduction, or prolonged continuous reproduction, within a season; for another, like perennials, semelparous individuals must survive at least one nonbreeding season—and usually many—before maturing sexually, reproducing, and then dying. Semelparity is rare among long-lived animals and plants.

The best-known cases of semelparous reproduction in plants occur in agaves and bamboos, two distinctly different groups, although this life history pattern has been reported even for some tropical forest trees. Most bamboos are tropical or warm temperate zone plants that form dense stands in disturbed habitats. Reproduction in bamboos does not appear to require substantial preparation or resources, as might be needed to grow a heavy flowering stalk. But there are probably few opportunities for successful seed germination. Once established, a bamboo plant increases by asexual reproduction (vegetative growth), continually sending up new stalks until the habitat in which it germinated is fairly packed with bamboo. Only then, when vegetative growth becomes severely limited, do the plants benefit from producing seeds, which can colonize new disturbed sites. In many species of bamboo, breeding is highly synchronous over large areas, after which the future of the entire population rests with the crop of seeds. Synchronous breeding may facilitate fertilization in this wind-pollinated plant group, or perhaps overwhelm seed predators, which cannot consume such a large crop of seeds.

The environments and habits of agaves occupy the opposite end of the spectrum from those of bamboos. Most species of agaves live in arid climates with sparse and erratic rainfall. Each agave plant grows vegetatively as a rosette of leaves produced from a single meristem over several years (the number of years varies from species to species). The plant then sends up a gigantic flowering stalk. Physiological studies have shown that the growth of the flowering stalk is too rapid to be fully supported by photosynthesis or uptake of water by the roots. As a consequence, the nutrients and water necessary for stalk growth are drawn from the leaves, which die soon after the seeds are produced (Figure 10.16).

Agaves frequently grow side by side with yuccas, a closely related group of plants that have a similar growth pattern

Figure 10.16 Agaves are semelparous plants. The Parry agave (Agave parryi) of Arizona grows as a rosette of thick, fleshy leaves for many years. Then it rapidly sends up its flowering stalk and sets fruit, after which the rosette dies. Photo by Toni Bean/DRK Photo.
form but which are iteroparous. Yuccas typically are branched and have many terminal rosettes of leaves. The root systems of agaves and yuccas also differ markedly. Yucca roots descend deeply to tap persistent sources of groundwater; agaves have shallow, fibrous roots that catch water percolating through the surface layers of desert soils after rain showers, but are left high and dry during drought periods. Thus, the semelparous agaves may experience greater variation in moisture availability from year to year than the iteroparous yuccas.

Several explanations have been proposed for the occurrence of semelparous and iteroparous reproduction in plants. First, variable environments might favor iteroparity, which would reduce the variation in lifetime reproductive success by spreading reproduction over both good and bad years. This tactic is referred to as bet hedging. However, this hypothesis can be rejected because semelparous plants tend to occur in more variable (usually drier) environments than their iteroparous relatives. On the other hand, variable environments might favor semelparity when a plant can time its reproduction to occur during a very favorable year. Storing resources for the big event makes sense, just as not holding back resources for an uncertain episode of future reproduction also makes sense. Carpe diem: seize the day. Semelparity is particularly favored when adult survival is relatively low and the interval between good years is long. Finally, attraction of pollinators to massive floral displays might favor plants that put all their effort into one reproductive episode. The few ob-

![Figure 10.17](image) The semelparous plant *Lobelia telekii* is found on the slopes of Mount Kenya. The giant inflorescences in the foreground are *L. telekii*, while the stalked rosette plants in the background are *L. keniensis*. Courtesy of Truman P. Young.

servations on this point are mildly supportive. For example, in the semelparous rosette plant *Lobelia telekii*, which grows high on the slopes of Mount Kenya in Africa (Figure 10.17), a doubling of inflorescence size was seen to result in a fourfold increase in seed production.

Comparison of *Lobelia telekii* with its iteroparous relative *L. keniensis* (Table 10.4), like the comparison between

<table>
<thead>
<tr>
<th>Trait</th>
<th>Lobelia telekii</th>
<th>Lobelia keniensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life history</td>
<td>Semelparous</td>
<td>Iteroparous</td>
</tr>
<tr>
<td>Habitat</td>
<td>Dry rocky slopes</td>
<td>Moist valley bottoms</td>
</tr>
<tr>
<td>Growth form</td>
<td>Unbranched</td>
<td>Branched</td>
</tr>
<tr>
<td>Reproductive output</td>
<td>Larger inflorescences, more seeds</td>
<td>Smaller inflorescences, fewer seeds</td>
</tr>
<tr>
<td>Variation in inflorescence size</td>
<td>Highly variable, increases with soil moisture</td>
<td>Relatively invariable, independent of soil moisture</td>
</tr>
<tr>
<td>Demography</td>
<td>Virtually no adult survivorship</td>
<td>Populations in drier sites have lower adult survivorship and less frequent reproduction</td>
</tr>
<tr>
<td>Variation in number of seeds per pod</td>
<td>Strongly positively correlated with inflorescence size</td>
<td>Independent of inflorescence size, positively correlated with number of rosettes</td>
</tr>
<tr>
<td>Effects of pollinators</td>
<td>Increased seed quality, but not seed quantity</td>
<td>Increased seed quality, but not seed quantity</td>
</tr>
</tbody>
</table>

agaves and yuccas, suggests that semelparity is associated with dry habitats that are highly variable in both space and time. Presumably, infrequent conditions that are highly favorable for the establishment and growth of seedlings trigger the massive flowering episodes in these plants. In summary, semelparity appears to arise either when preparation for reproduction is extremely costly, as it is for species that undertake long migrations to breeding grounds, or when the payoff for reproduction is highly variable but favorable conditions are predictable from environmental cues.

**Senescence is a decline in physiological function with increasing age**

Although few long-lived organisms exhibit programmed death associated with reproduction, most do experience a gradual increase in mortality and a decline in fecundity resulting from the deterioration of physiological function. This phenomenon is known as senescence, and humans are no exception to the general pattern seen in virtually all animals. Most physiological functions in humans decrease in a roughly linear fashion between the ages of 30 and 85 years, by 15–20% for rates of nerve conduction and basal metabolism, 55–60% for volume of blood circulated through the kidneys, and 60–65% for maximum breathing capacity. Birth defects in offspring and infertility generally occur with increasing prevalence in women after 30 years of age, and fertility decreases dramatically in males after 60 years. Reproductive decline and death in old age do not result from abrupt physiological changes. Rather, they follow upon a gradual decrease in physiological function. This decline includes the function of the immune system and other repair mechanisms, and with their decline, the incidence of deaths from tumors and cardiovascular disease rises (*Figure 10.18*).

Why does senescence exist, when survival and reproduction presumably confer advantages on an individual at any age? Perhaps physiological decline is just a fact of life and evolution can do nothing about it. Senescence may simply reflect the accumulation of molecular defects that fail to be repaired, just as an automobile eventually wears out and has to be junked, ionizing radiation and highly reactive forms of oxygen break chemical bonds; macromolecules become cross-linked; DNA accumulates mutations. However, this wear and tear cannot be the entire explanation for patterns of aging because maximum longevity varies widely even among species of similar size and physiology. For example, many small insectivorous bats achieve ages in captivity of 10–20 years, whereas mice of similar size rarely live beyond 3–5 years. In addition, cellular mechanisms for repairing damaged DNA and protein molecules appear to be better developed in long-lived animals than in their short-lived relatives. These observations suggest that, while senescence may be inevitable, rates of senescence are under the influence of natural selection and evolutionary modification. For instance, prolonging the maximum potential life span by postponing senescence may exact costs in terms of reduced reproduction at younger ages. If repair processes require time and resources, and if mortality is so high that an individual has little chance of living to old age, it may be more productive for the individual to allocate resources to reproduction early in life and let the body fall apart with age.

Even in the absence of senescence, accidental causes of death result in fewer and fewer individuals remaining alive at older ages. Consequently, progressive physiological deterioration and loss of reproductive capacity have little effect on average lifetime reproduction because most adults in a population never achieve old age. By this reasoning, selection on changes in survival or fecundity in old age is weak. Thus, selection should tend to favor improvements in reproductive success at young ages over those later in life. Because this effect is greater in populations with low adult survival rates than in populations with high

Figure 10.19 The strength of selection varies with mortality rates. The strength of selection on changes in mortality and fecundity at a particular age is related to the proportion of individuals in the population alive at that age, which depends largely on rates of mortality caused by extrinsic factors earlier in life.

Figure 10.20 Populations with higher extrinsic mortality rates age faster. The relationship between senescence and extrinsic mortality rate is shown for a number of populations of birds and mammals. Senescence is measured as the rate of increase in mortality with age. From R. E. Ricklefs, Am. Nat. 152:24–44 (1998).

Summary

1. Life history traits include maturity (age at first reproduction), parity (number of episodes of reproduction), fecundity (number of offspring produced per reproduction episode), and aging. The values of these traits can be interpreted as solutions to the problem of allocating limited time and resources among various structures, physiological functions, and behaviors.

2. Most phenotypic traits of individuals are sensitive to variations in the environment. This response of form and function to the environment is referred to as phenotypic plasticity, and the quantitative relationship between phenotypic values and environmental variables is called the reaction norm.

3. Phenotypic plasticity itself is under genetic control. Differences in the sensitivities of individuals with different genotypes to variation in the environment are referred to as genotype–environment interactions. Such interactions can be revealed by reciprocal transplant experiments, in which individuals with the same genotypes are allowed to develop in each of several different environments.
When the performance of a genotype is superior to others over some range of environmental conditions, genotype–environment interactions can lead to specialization.

4. Life history traits often vary consistently with respect to the environment. Variation in one life history trait is often correlated with variation in others. Delayed reproduction, long life, and low reproductive rates are frequently associated with one another.

5. Plant ecologists have recognized clusters of life history attributes, including relative allocation of resources to reproduction and size of seeds. One such scheme includes three life history strategies associated with ruderal, stressful, and highly competitive environments.

6. Larger organisms tend to have longer life spans and lower reproductive rates.

7. Many theories concerning life history variation among species, including correlations among life history traits, are based on the principle that limited time and resources are allocated among competing functions in such a way as to maximize lifetime reproductive success.

8. Delayed reproduction is favored when life span is relatively long and when immature individuals benefit from increased growth or accumulation of experience by having greater fecundity later in life.

9. High extrinsic adult mortality rates favor increased reproductive effort, or investment in offspring, at the expense of adult survival and future reproduction.

10. When reproduction requires costly preparation, selection may favor a single all-consuming reproductive event followed by death, as in salmon. This pattern of reproduction, called semelparity, is the converse of iteroparity, or repeated reproduction.

11. Senescence, the progressive deterioration of physiological function with age, causes declines in fecundity and probability of survival. Senescence is caused by the wear and tear and the detrimental biochemical changes brought about just by living. Senescence is also subject to evolutionary modification.

12. Owing to accidental deaths, few individuals in most natural populations survive to old age. As a result, the strength of selection diminishes on traits expressed at progressively later ages. Individuals in populations subjected to higher extrinsic mortality rates age faster.

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**PRACTICING ECOLOGY**

**CHECK YOUR KNOWLEDGE**

Life History Surprises

Experiments are usually designed to test a certain hypothesis, and not all experiments turn out as expected. When the results contradict the hypothesis, one must reject the hypothesis. On the bright side, this can lead to the creation of new hypotheses and further experimentation. David Lack observed that both bird clutch size and day length are greater at high latitudes compared to the equator, leading him to hypothesize that parent birds rear only as many young birds as they can feed during the day. One way to test this hypothesis is to manipulate clutch size by providing more mouths to feed. In many cases such experiments show that parent birds are unable to nourish the larger brood adequately and that adding eggs or chicks to a nest reduces the reproductive success of the parents.

As mentioned earlier in this chapter, Göran Hogstedt conducted brood size manipulation experiments in magpies. He found that the most productive clutch size corresponded to the size of the clutch laid by the female bird. Adding eggs to the nest or removing eggs always reduced the reproductive success, independent of the actual numbers of eggs present. In certain other cases, however, the most productive natural clutch size is larger than the most common clutch size observed within a population (Figure 10.21).

Other studies have failed to demonstrate expected trade-offs between life history traits. David Reznick, of the University of California, Riverside, and colleagues have studied life history traits of guppies. They prevented females from mating with males. If we assume that growth and reproduction compete for resources, the experimental females (the nonmated ones) should have grown larger than control females that were mated with males. In fact, there was little difference in female reproductive tissue mass when mated and nonmated females were compared. Indeed, mated females simply ate more food to gain the energy necessary to produce the mass of eggs.

**CHECK YOUR KNOWLEDGE**

1. Using Figure 10.21, determine which clutch size has the highest survival rate. What is the approximate survival rate for the most common clutch size?

2. How can you explain the pattern depicted in Figure 10.21 from an evolutionary standpoint?

4. How is life history different from natural history?

**Suggested Readings**


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**Figure 10.21** The frequencies of clutch sizes (blue bars, left-hand scale) among clutches of the great tit (*Parus major*) near Oxford, England, between 1968 and 1982, and number of young per clutch surviving at least to the next season (orange bars, right-hand scale) as a function of clutch size. Note that the most common clutch size is not the most productive. From M. S. Boyce and C. M. Perrins, *Evolution* 68:142–153.
Adaptation results from natural selection on traits that affect evolutionary fitness.

The phenotype is the expression of the genotype in the form and function of the individual organism.

Each type of organism has an activity space defined by conditions of the environment.

Organisms can select microhabitats.

Acclimation is a reversible change in structure in response to environmental change.

Developmental responses are irreversible changes in response to persistent variation in the environment.

Migration, storage, and dormancy enable organisms to survive extreme conditions.

Animals forage in a manner that maximizes their fitness.

The Mojave Desert of southern California has a climate with little rain, searing summer heat, and chilling winter cold. These conditions are so forbidding that, except for a few struggling plants, the desert appears nearly devoid of life for most of the year. But the desert’s silence is occasionally broken during the milder days of winter by swarms of insects and other creatures that appear on the surface or fly above it for a few hours, and then disappear as mysteriously as they came. One of the more conspicuous of these creatures is the giant red velvet mite (Figure 9.1).

Several decades ago, biologists Lloyd Tevis and Irwin Newell began a study of the behavior of the giant red velvet mite in relation to the physical conditions of its environment. They found that the mites spend most of the year in burrows dug in the sand. The particular conditions that favor the emergence of mites occur infrequently in the Mojave Desert. During four years of observation, adults appeared aboveground only ten times, always during the cooler months of December, January, or February, when they can tolerate the temperatures on the desert’s surface. An individual mite appeared only once each year. Tevis and Newell could predict from their observations that an emergence would occur on the first sunny day after a rain of more than 8 millimeters, provided that air temperatures were moderate. On the day of a major emergence, the mites came out of their burrows between 9:00 and 10:00 AM, and by late morning one could find thousands of mites scurrying across the desert sands in all directions. At midday, between 11:30 and 12:30, the mites dug back into the sand, not to emerge again until the following year.
During its 2- to 3-hour stay above ground each year, each mite must perform two important functions: feeding and mating. The mites feed on termites, which appear on the same day the mites emerge, flying in large swarms over the desert sand, their own emergence presumably triggered by the same physical cues that urge the mites to leave their burrows. Because mites cannot fly, they can feed only after the termites have dropped to the ground and shed their wings, but before they have burrowed into the sand to form new colonies. If a mite feeds successfully during this narrow window of opportunity, it soon mates and prepares to re-enter the sand itself.

About midday, after the mites have fed and mated, they congregate in troughs on the windward sides of sand dunes, where surface temperature and the size of the sand particles are "just right" (less than half a millimeter in diameter). Here they re-enter the sand almost simultaneously. The mites continue digging their new burrows until the coolness of the late winter afternoon slows their activity. Burrowing continues on subsequent days when the sand becomes warm enough, until the burrows are completed. During the rest of the year, the adult mite spends its time moving up and down in its burrow to follow the movement of its preferred temperature zone as the surface of the sand heats and cools each day (Figure 9.2).

**Figure 9.1** The giant red velvet mite lives in a stressful desert environment. An adult mite is shown on the surface of the ground close to its burrow, within which it spends all but a few hours of its life. Photo by P. Ward/Bruce Coleman.

![Temperature vs. Depth in Soil Graph]

**Figure 9.2** The giant red velvet mite must adjust to changing environmental conditions. The vertical migration of a mite in its burrow follows changes in soil temperature throughout the course of a typical summer day.
The red velvet mite's world is extremely variable in time and space. Rain comes sporadically. Desert temperatures vary between day and night extremes almost as much as between summer and winter. The mite's world is so forbidding that an individual can be active only in a small portion of its environment, or for only a very limited amount of time. Indeed, all organisms—except, perhaps, for those living at great depths in the seas and in the farthest reaches of caves—must cope with a varied and constantly changing environment. Organisms that can adjust to these changes have the best possible chance of surviving and producing offspring for the next generation.

Each response of an organism to a change in its environment affects the number of descendants it leaves in future populations. Individuals that make the "wrong" response are more likely to die or fail to reproduce than those that respond appropriately. Of course, what is "right" or "wrong" depends on the qualities of the organism and its particular ecological circumstances. For example, whether a sparrow should store fat during times of food abundance depends on whether it is likely to need energy reserves in the near future for a long-distance migration, or as insurance to carry it through a spell of bad weather. In the absence of such need, extra fat is disadvantageous because it reduces speed and maneuverability and increases risk of predation.

In the course of this chapter, we shall learn how different kinds of environmental variation demand different adaptations of individuals. Some kinds of variation occur over space, in which case an organism can make choices about where to live. Other kinds of variation occur over time and are unavoidable; each individual, or its lineage, must be able to survive all the extremes of the environment to persist. Because most of the traits organisms possess have evolved in response to the particular environments in which they live, we shall begin our discussion of adaptation to life in varied and varying environments with a brief explanation of some important aspects of evolution.

### Adaptation results from natural selection on traits that affect evolutionary fitness

Each individual in a sexually reproducing population is endowed with a unique genetic constitution, or genotype, made up of a combination of genes from its mother and its father. Such genetic variability within a population has many consequences, the most important of which for the study of ecology is evolution by natural selection. The term evolution pertains to any change in the genetic makeup of a population. When genetic factors cause differences in fecundity and survival among individuals, evolutionary change comes about through natural selection. Individuals whose attributes enable them to achieve higher rates of reproduction leave more descendants, and therefore the genes responsible for these attributes increase in the population. The reproductive success of an individual is referred to as its evolutionary fitness.

Consider how these principles apply in the following example of evolutionary change in a California citrus pest. Early in the twentieth century, certain species of scale insects were serious pests in citrus orchards in southern California. An effective means of controlling scale populations was to fumigate orchards with cyanide gas. However, after several years of such treatment, the gas killed fewer of the insects, and before long the scale regained its pest status. Researchers determined that scale insects had evolved a genetically based resistance to cyanide poisoning. Furthermore, when they surveyed orchards in areas that had never been fumigated, they found that small numbers of individuals possessed an innate resistance to cyanide. Thus, despite their initial successes, fumigation programs in the end had favored reproduction by cyanide-resistant individuals, whose progeny then increased to epidemic proportions (Figure 9.3). The citrus scale story illustrates the three main ingredients of evolution by natural selection: (1) variation among individuals, (2) inheritance of that variation (the genetic basis of evolution), and (3) differences in reproductive success, or fitness, related to genetic variation.

Most evolutionary biologists believe that the diversification of living beings over the long history of life has been guided primarily by natural selection. It is important to understand, however, that natural selection is not an external force that urges organisms toward some predetermined goal, in the sense that humans artificially "select" cows to achieve a higher rate of milk production in their herds. Quite the opposite. Selection occurs because of differences in reproductive success among individuals endowed with different form or function in a particular environment. The process that creates selection is ecological—namely, the interaction of individuals with their environment, including its physical conditions, food resources, predators, and so on. A cold winter wind doesn't care whether a bird is well insulated by its plumage. Whether a rabbit runs fast or not is irrelevant to evolution. All that matters is whether fast rabbits leave more offspring, perhaps because they are more likely to escape foxes. One presumes that a fox would prefer to chase slow rabbits, but, alas, by catching slow ones, it ends up favoring reproduction by faster ones.
The phenotype is the expression of the genotype in the form and function of the individual organism

Each individual's genotype includes all of its genes. The outward expression of its genotype, called the phenotype, is its structure and function. Thus, a genotype is a set of genetic instructions, and a phenotype is the rendering, or expression, of a genotype in the form of an organism. Of course, the environment also influences this rendering. To put it another way, the genotype is to the phenotype as blueprints are to the structure of a building. In this analogy, the effects of environmental influences are like details in a blueprint that are left up to the discretion of the building contractor, which may hinge, for example, on unpredictable changes in the availability of certain construction materials.

Most genes code for a particular protein, which may be used as part of an organism's structure or may function as an enzyme or hormone. Different forms of a particular gene are referred to as alleles. In many cases, alleles create perceptible and measurable differences in an organism's phenotype. For example, blue-eyed and brown-eyed humans have different alleles of a single gene, which controls one of the pigment systems that determines eye color. Many genetic disorders, such as sickle-cell anemia, Tay-Sachs disease, cystic fibrosis, and albinism, as well as tendencies to develop certain cancers and Alzheimer's disease, are caused by defective alleles of individual genes.

Every individual has two copies of each gene, one inherited from its mother and one from its father (exceptions include sex-linked genes and organisms that reproduce without the sexual union of gametes). An individual that has two different alleles of a particular gene is said to be heterozygous for that gene. When both copies of a gene are the same, that individual is homozygous. When an individual is heterozygous, the two different alleles may produce an intermediate phenotype, or one may mask the expression of the other. In the latter case, one allele is said to be dominant and the other recessive. When heterozygotes have an intermediate phenotype, the alleles are said to be codominant. Most harmful alleles are recessive, and the normal gene product of the dominant allele masks the defective function of their gene products in heterozygous individuals.

While all phenotypic traits have a genetic basis, they are also influenced by variations in the environment, either through the effects of environmental conditions on individuals (as in the effect of food supply on growth and development) or through the responses of individuals to variation in their environments. Such environmentally induced variation in the phenotype is referred to as phenotypic plasticity. The capacity of an individual to exhibit different responses to its environment may itself be an evolved trait. That is, the way in which the individual responds to environmental variation is also subject to evolution by natural selection. We shall look at phenotypic plasticity in more detail in the next chapter, but let us keep in mind the difference between these plastic responses by individuals and evolutionary responses by populations as we consider the relationship of organisms to their environments.
Each type of organism has an activity space defined by conditions of the environment

Each organism functions best within a limited range of conditions, which we may refer to as its activity space. This concept applies to all aspects of an individual’s life, whether it is literally active or not: here we may think of “activity” as synonymous with “performance.” For some environmental factors, the activity of individual organisms tends to be highest within a relatively narrow range (Figure 9.4). Activity might be measured as rate of photosynthesis, survival, or swimming speed, all of which influence an individual’s reproductive success in some way. The environmental factor might be temperature, soil acidity, nutritional quality of food items, or structure of the foraging substrate. Away from the optimum conditions, activity decreases, and consequently so does the individual’s probability of surviving and ability to produce offspring. Close to the optimum conditions, reproductive success is high enough to maintain a population. Under marginal conditions, an individual might be able to maintain itself indefinitely, but not replace itself in future populations. Extreme conditions are unsuitable for individual maintenance, and an individual can venture into such conditions only for short periods.

Organisms can select microhabitats

Plants have relatively little choice as to where they live, even though, as we have seen, roots can “forage” for high concentrations of soil minerals, growing shoots can seek out light gaps, and wind, water, and animal dispersers may distribute plant seeds nonrandomly through the environment. Unlike plants, most animals have freedom to move about the environment and choose a habitat in which to live. Nonetheless, even within a habitat, there are distinct differences in temperature, moisture, salinity, and other factors. Parts of the environment that can be distinguished by their conditions are referred to as microhabitats or microenvironments. In deserts, for example, the shaded ground under a shrub is often cooler and moister than surrounding areas exposed to direct sunlight, although clearly these conditions vary through the course of the daily cycle and with the seasons.

Responses of animals to the changing array of microhabitats in their environments can be illustrated by the diurnal behavioral cycles of lizards. Although lizards do not regulate their body temperatures by generating heat metabolically, they do take advantage of solar radiation and warm surfaces to maintain their temperatures within a suitable range during the day. Thus, it is not surprising that lizards respond to the temperatures of different microhabitats. At night, external sources of heat disappear, and the lizard’s body temperature gradually drops to that of the surrounding air.

The desert iguana (Dipsosaurus dorsalis) of the southwestern United States lives in a severe environment. Shade temperatures can reach 45°C in summer and plunge below freezing in winter. Desert iguanas have a preferred body temperature range of 39°C–43°C. During mid-July, the thermal environment changes rapidly between day and night extremes. Desert iguanas can move about the desert surface in search of food and remain within their preferred range for only about 45 minutes in mid-morning and a similar period in the early evening (Figure 9.5). During the remainder of the day, they seek the shade of plants or the coolness of their burrows, where temperatures rarely exceed their preferred range. At night,
The desert iguana regulates its body temperature by basking in the sun…

or retreating to deep shade or its burrow.

The time spent in each location varies at different times of the year. January through March the iguana stays in its burrow...

but in July it moves between the three locations over the course of the day.

Movements from location to location...

reflect the temperature range required for activity...

which is directly related to air and surface temperatures.

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ECOLOGISTS IN THE FIELD

Temperature and microhabitat selection by the cactus wren

Unlike the desert iguana, the cactus wren (Figure 9.6), an insectivorous bird that lives in deserts of the southwestern United States and northern Mexico, maintains a constant body temperature. However, because the wren has no source of free water, it must avoid gaining too much heat from its environment. Otherwise, it would have to dissipate excess body heat by the cooling effect of evaporation from its respiratory tract (see Chapter 2).
Thus, the wren’s activity space, like that of the desert iguana, reflects changes in environmental conditions throughout the day and season.

Observations made by Robert E. Rickles and F. Reed Hainsworth in deserts near Tucson, Arizona, showed that cactus wrens seek favorable microhabitats within which to feed as the thermal environment changes throughout the day. During cool early mornings, wrens forage throughout most of the environment, searching for food among foliage and on the ground. As the day brings warmer temperatures, wrens select cooler parts of their habitat, particularly the shade of small trees and large shrubs, always managing to avoid feeding where the temperature exceeds 35°C (Figure 9.7). When the minimum temperature in the environment rises above 35°C, at which point birds must use evaporative cooling to maintain their body temperatures even when inactive, the wrens stop feeding and perch quietly in deep shade.

Although an adult cactus wren can move without restraint to any part of its habitat, its nest is fixed in place: wren chicks cannot move among microhabitats until they are old enough to leave the nest. The microenvironment of the nest must therefore be within the tolerance range of chicks at all times. Cactus wrens appear to achieve this both by choosing particular nest sites and by orienting their nests in particular directions. Cactus wrens build untidy, enclosed nests—bulky, somewhat haphazardly constructed balls of grass—with side entrances. Once a nest is built, of course, its position and orientation cannot be changed. For a month and a half, from the first egg until the young fly off, the nest must provide a suitable environment day and night in hot and cool weather.

During the long breeding period (March through September) in southern Arizona, cactus wrens usually rear several broods of young. Early in spring, they build their nests so that the entrances face away from the direction of the cold winds; during the hot summer months, they orient their nests to face prevailing afternoon breezes, which circulate air through the nest chamber and facilitate heat loss (Figure 9.8). This strategy makes a difference! Nests ori-

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**Figure 9.6** The cactus wren (*Campylorhynchus brunneicapillus*) is a conspicuous resident of deserts in the southwestern United States and northern Mexico. Photo by Craig K. Lorenz/Photo Researchers.

**Figure 9.7** Temperature affects microhabitat use by cactus wrens. Microhabitat use is shown over the course of a day in late spring. Microhabitats vary in degree of thermal stress between exposed ground (a) and the deep shade of trees (e). From R. E. Rickles and F. R. Hainsworth, *Ecology* 49:227–233 (1968). Photo by R. E. Rickles.
Adaptation to Life in Varying Environments

15–20 kph at 20°C in March

In cool weather, nest entrances face away from the cooling wind.

Wind direction

Early nests

Late nests

15–20 kph at 35°C in June

In hot weather, nest entrances face the cooling wind.

Figure 9.8 The orientation of cactus wren nest entrances changes during the breeding season. Lengths of bars represent relative numbers of nests with each orientation. After R. E. Ricklefs and F. R. Hainsworth, Condor 71:52–57 (1969).

orientation is a strategy restricted to seasonal and other persistent variations in conditions. Acclimation is reversible, and allows organisms to follow the ups and downs of their environments. As long as the environmental change is persistent, it is a good strategy. However, increased tolerance of one extreme often brings reduced tolerance of the other.

By producing enzymes and other molecules having different temperature optima, a cold-blooded (poikilothermic) animal can adjust its activity space in response to prevailing environmental conditions. The relationship between the swimming speed of goldfish and water temperature shows both the advantages and the limitations of acclimation. Goldfish swim most rapidly when acclimated to 25°C and placed in water between 25°C and 30°C, conditions that closely resemble those of their natural habitat (Figure 9.9). Lowering the acclimation temperature to 5°C increases the swimming speed at 15°C, but reduces it at 25°C.

An organism’s capacity for acclimation often reflects the range of conditions experienced in its natural environment. Larea divaricata (creosote bush) inhabits interior deserts in western North America and maintains photosynthetic activity during the cool winters as well as the hot summers. Measurements of the rate of photosynthesis in this plant show a shift in the temperature optimum characteristic of thermal acclimation. Specifically, photosynthetic rate reaches the same level in plants grown at 20°C and 45°C, but plants grown at 20°C do not perform as well at 45°C as plants acclimated to that temperature. The basis for this acclimation seems to be changes in the viscosity of membranes directly related to photosynthetic pathways.

Where the environment normally is relatively constant, we would not expect organisms to have evolved the ability to respond strongly to environmental variation or to tolerate conditions that differ from the norm. Evolution favors

Acclimation is a reversible change in structure in response to environmental change

Growing thicker fur in winter, producing smaller leaves during the dry season, increasing the number of red cells in the blood at high altitude, and producing enzymes with different temperature optima or lipids that remain fluid at different temperatures are all forms of acclimation. Acclimation may be thought of as a shift in the range of physiological tolerances of the individual. Because these changes involve modifications of the body’s structure and metabolic machinery, they require days to weeks. Thus, acclima-

Figure 9.9 Acclimation can shift an organism’s activity space in response to environmental conditions. Swimming speed as a function of temperature is shown for goldfish acclimated to 5°C and to 25°C. After F. E. J. Fry and J. S. Hart. J. Fish. Res. Bd. Can. 7:169–174 (1948).
economical designs, and we presume that the capacity to respond to environmental change imposes a cost for the organism. That these mechanisms have been dispensed with when plants experience only narrow ranges of temperatures is shown by the photosynthetic rates of two other plants from western North America. *Atriplex glabriuscula* is a species of saltbush native to cool coastal regions of California, where temperatures during the growing season rarely exceed 20°C. Unlike *Larrea*, *Atriplex* does not increase its photosynthetic rate at high temperatures when acclimated to 40°C, although it may respond in other ways. However, whatever physiological changes that do occur during acclimation to high temperature cause saltbush plants to perform less well at lower temperatures (Figure 9.10). In contrast, the thermophilic (heat-loving) species *Tidestromia oblongifolia* cannot acclimate to cool temperatures. Photosynthesis is reduced uniformly over a wide range of leaf temperatures from 16°C to 40°C when plants are maintained for long periods in cool temperatures. The responses of *Atriplex* to growing under hot temperatures and of *Tidestromia* to growing under cool temperatures appear to be generalized stress responses that allow individuals to survive under extreme conditions, rather than mechanisms that effectively broaden their activity spaces.

**Developmental responses are irreversible changes in response to persistent variation in the environment**

Light intensity, among many other factors, influences the course of development in plants. Loblolly pine seedlings grown in shade have smaller root systems and more foliage than seedlings grown in full sunlight. Because a shaded environment taxes a plant's water economy less, shade-grown seedlings can allocate more of their production to stem and needles; sun-grown seedlings develop more extensive root systems to obtain sufficient water. The larger proportion of foliage in a shade-grown seedling results in a higher rate of photosynthesis per unit of plant mass under given light conditions, particularly under low light intensities (Figure 9.11). These growth responses of pine seedlings show how plants allocate their production in such a way as to optimize their fitness in their environment.


**Figure 9.11** Plants show developmental responses to light intensity. Distribution of dry matter and rates of photosynthesis are shown for loblolly pine (*Pinus taeda*) seedlings grown under shade and in full sunlight. After F. H. Bormann, in D. V. Thimann (ed.), *The Physiology of Forest Trees*, Ronald Press, New York (1968), pp. 197–215.
way as to acquire more of the resource that most limits their growth.

Another striking example of a developmental response is the coloration of several species of locusts and grasshoppers. It is important for the color of such insects to match the color of their backgrounds if they are to avoid detection by predators that use sight to locate prey. In tropical habitats with seasonal precipitation, the onset of the wet season stimulates the growth of lush, green vegetation. During the early part of the dry season this vegetation browns and dies, often exposing red-brown earth. As the seasonal drought intensifies, natural fires and those set by humans blacken the ground over vast areas. Consequently, there is a regular seasonal progression of color from green to brown to black and back to green again. Where this happens, many species of grasshoppers match the background coloration of the environment in which they develop (Figure 9.12).

The epidermis of the African grasshopper *Gastrimargus africanus* has a pigment system that permits any given area of skin to be either green or brown; both colors may occur on a single animal, but not in the same area of the body. The green and brown colors represent small biochemical variations on a single pigment molecule. In combination with brown, additional pigments may produce colors ranging from yellow through orange and red to black. Furthermore, black pigment (melanin) may be deposited in the cuticle that covers the epidermis. Between developmental stages a grasshopper sheds its epidermis, discarding its pattern of camouflage-like coloration. A new layer of epidermis develops underneath, and thus a young grasshopper can change its color with each molt if the background color of its environment has changed in the meantime. Coloration in *Gastrimargus* responds to environmental conditions that are correlated with the color of its background, particularly quality and intensity of light, which are perceived by the eye and transmitted to the epidermis by hormones produced in the brain.

Developmental responses generally do not reverse themselves; once fixed during development, they remain unchanged for the rest of an individual’s life (or particular developmental stage). Because of their long response times and irreversibility, developmental responses cannot accommodate short-term environmental changes. As a rule, therefore, only plants and animals in environments with persistent variation in the conditions experienced by different individuals exhibit developmental responses. Such organisms include plant species, such as loblolly pines, whose seeds may settle in many different kinds of habitats. In such cases, spatial rather than temporal heterogeneity in the environment may create the kind of persistent environmental variation that favors developmental responses. Observed developmental responses generally match environmental change rather well, because individuals that respond inappropriately do not survive to produce descendants.

**MORE ON THE WEB** Rate of phenotypic response. The mechanisms that organisms use to respond to the environment, as shown by the example of wing-length polymorphism in water striders, must match the pattern of environmental change.

**Migration, storage, and dormancy enable organisms to survive extreme conditions**

In many parts of the world, extremes of temperature, drought, darkness, and other adverse conditions are so severe that individuals cannot change enough to maintain their normal activities, or if they could, the change would not be worth the cost. Under such conditions, organisms resort to a number of extreme responses. These responses include migration, moving to another region where conditions are more suitable; storage, relying on resources accumulated under more favorable conditions; and dormancy, becoming inactive.
Migration

Many animals, particularly those that fly or swim, undertake extensive migrations. Arctic terns probably hold the record for long-distance migration. Individuals make yearly round trips of 30,000 km between their North Atlantic breeding grounds and Antarctic wintering grounds (where it is the local summer). Each fall hundreds of species of land birds leave temperate and arctic North America, Europe, and Asia for the south in anticipation of cold winter weather and dwindling supplies of their invertebrate food. Populations of monarch butterflies migrate between wintering areas in the southern United States and Mexico to summer breeding areas far to the north into southern Canada. In East Africa, many large ungulates, such as wildebeests, migrate long distances, following the geographic pattern of seasonal rainfall and fresh vegetation (Figure 9.13).

Some migratory movements occur in response to occasional failure or depletion of local food supplies, which forces individuals to move out of an area in search of new feeding places. Such movements are perhaps best known from outbreaks of migratory locusts. These migrations occur when locusts leave areas of high local density where food has been depleted. They can reach immense proportions and cause extensive crop damage over wide areas (Figure 9.14). Irruptive behavior in locusts is a developmental response to population density. When locusts occur in sparse populations, they become solitary and sedentary as adults. In dense populations, however, frequent contact with other locusts stimulates young individuals to develop gregarious, highly mobile behavior, which can develop into a mass migration.

Storage

Where environmental changes plunge organisms from feast into famine and migration is not a possibility, storage of resources acquired during periods of abundance for use in times of scarcity may be a way to cope. During infrequent rainy periods, desert cacti swell with water stored in their succulent stems. Plants growing on infertile soils absorb, in times of abundance, more nutrients than they require, and use them when soil nutrients are depleted. In habitats that frequently burn—such as the chaparral of southern California—perennial plants store food reserves in fire-resistant root crowns, which sprout and send up new shoots shortly after a fire has passed (Figure 9.15).

Many temperate and arctic animals accumulate fat during mild weather in winter as a reserve of energy for periods when snow and ice make food sources inaccessible. The problem with fat reserves is that heavier animals are often slower and less agile, and therefore are more likely to
be caught by predators. One way to avoid this problem is to store food before consuming it. Some winter-active mammals (beavers, squirrels, and pikas) and birds (corn woodpeckers and jays, for example) cache food supplies underground or under the bark of trees for later retrieval. Often these hoards are immense and may sustain individuals for long periods.

Dormancy

Environments sometimes become so cold, dry, or nutrient-depleted that animals and plants can no longer function normally. In such circumstances, some species that are not capable of migration enter physiologically dormant states. Many tropical and subtropical trees shed their leaves during seasonal periods of drought; many temperate and arctic trees shed theirs in the fall before the onset of winter frost and long nights. Many mammals, such as ground squirrels, hibernate (spend winter in a dormant state) because they cannot find food in winter, not because they are physiologically unable to cope with the harsh physical environment.

In most species, environmental conditions requiring dormancy are anticipated by a series of physiological changes in the individual (for example, production of antifreezes, dehydration, and fat storage) that prepare it for a partial or complete shutdown of activity. Before winter, some insects enter a resting state known as diapause, in which water is chemically bound or reduced in quantity to prevent freezing and metabolism drops so low that it is barely detectable. Drought-resistant insects that enter a summer diapause dehydrate themselves and tolerate the desiccated condition of their bodies, or secrete an impermeable outer covering to prevent drying. Plant seeds and spores of bacteria and fungi exhibit similar dormancy mechanisms. Indeed, there are many cases of seeds stored in burial chambers or recovered in other archeological settings that have sprouted after hundreds of years of dormancy. By whatever mechanism it
occurs, dormancy reduces exchange between organisms and their environments, enabling animals and plants to "ride out" unfavorable conditions.

**Stimuli for change**

What stimulus indicates to birds wintering in the Tropics that spring is approaching in northern forests? What urges salmon to leave the sea and migrate upstream to their spawning grounds? How do aquatic invertebrates in the Arctic sense that if they delay entering diapause, a quick freeze may catch them unprepared for winter?

In 1938, J. R. Baker made an important distinction between two kinds of cues that trigger these changes. **Proximate factors** are cues, such as day length, by which organisms can assess the state of the environment but that do not directly affect its well-being. **Ultimate factors** are features of the environment, such as food supplies, that bear directly on the well-being of the organism. Virtually all plants and animals sense **photoperiod** (the length of the day) as a proximate factor that indicates season, and many can distinguish periods of lengthening and shortening days. Different populations of a single species may differ strikingly in their responses to photoperiod in different locations, reflecting different relationships of environmental changes to day length. Under controlled cycles of light and dark, southern populations (at 30°N) of side oats grama grass flower in autumn, when day length is 13 hours, whereas more northerly populations (at 47°N) flower in summer, only when the light period exceeds 16 hours each day. In Michigan, at 45°N, populations of small freshwater crustaceans known as water fleas (**Daphnia**) form diapausing broods at photoperiods of 12 hours (mid-September) or less. In Alaska, at 71°N, related species enter diapause when the light period decreases to fewer than 20 hours per day, which happens in mid-August. Warm temperatures and low population densities tend to shorten the day length that triggers diapause (and hence delay the inception of diapause in autumn), suggesting that these factors portend more favorable environmental conditions for **Daphnia**.

**Animals forage in a manner that maximizes their fitness**

Because animals live in varied and variable environments, they are constantly forced to make decisions about how to behave. Many of these decisions concern food: where to forage, how long to feed in a certain patch of habitat, which types of foods to eat, and so on. Theories of **optimal foraging** seek to explain these decisions in terms of the likely costs and benefits of each possible behavior. Animals are expected to select the behavior that gives the greatest benefit. Cost can be measured in terms of time and energy expended, but the benefit is best judged in terms of evolutionary fitness. However, it is often difficult to measure the consequence of a particular behavioral choice for an individual's survival and reproductive success. Consequently, ecologists usually measure benefit in terms of factors that are likely to be correlated with fitness, such as amount of food gathered per unit of time. We shall examine a number of behavioral decisions from the standpoint of such costs and benefits. Each of these cases features some aspect of variation in time or space.

**Central place foraging**

When birds feed their offspring in a nest, the chicks are tied to a single location, while the parents are free to search for food at a distance. This situation is referred to as **central place foraging**. The greater the foraging range, the greater the amount of food that is potentially available to the parent. But traveling a longer distance also increases the time, energy costs, and risks of travel. Is there some best distance from the nest at which a parent should forage, and how much food should the parent bring to its brood with each trip? That is, how much time should the parent spend gathering food before it returns to its nest?

Studies on the foraging behavior of European starlings allowed investigators to approach these questions from an economic standpoint. During the summer season, starlings typically forage on lawns or pastures for leatherjackets, which are the larvae of tipulid flies (crane flies). Starlings feed by thrusting their bills into the soft turf and spreading the mandibles to expose prey. When they are gathering food for their young, they hold captured leatherjackets at the base of the bill. You can imagine that the more leatherjackets a starling has in its bill, the more difficult it is to capture the next one. For this reason, the time between captures increases as more prey are caught (Figure 9.16). That is, as a predator captures more prey, the rate of capture decreases, and the total number of prey increases less steeply. Indeed, a starling cannot continue to feed efficiently with eight leatherjackets in its bill.

Now, from the standpoint of feeding its offspring, the rate at which a parent delivers food to its young is the number of prey caught divided by the length of the for-
the rate at which it delivers food to its chicks by spending an intermediate amount of time in the feeding area during each trip and bringing back something less than the maximum possible amount of food (Figure 9.17). Imagine yourself in a grocery store where you have to buy as much food as you can in an hour and you have to carry your items by hand. How frequently would you take your items to the cashier? Carrying one item at a time clearly is silly, particularly if there is a long line waiting to be checked out (analogous to a long foraging distance). Trying to carry more than you can handle well, and having to spend time picking up dropped items off the floor and rearranging them, also seem uneconomical. As in the case of the starling with a bill full of leatherjackets, the "law of diminishing returns" sets in. The best strategy is somewhere in the middle. The optimum load varies in direct relation to the traveling time, or more generally, to any fixed cost per trip.

Spatially partitioned foraging by oceanic seabirds. Albatrosses and other seabirds may intersperse long and short foraging trips to gather food alternately for themselves and their chicks.
ECOLOGISTS IN THE FIELD

Optimal foraging by starlings

To what extent do organisms actually forage optimally? Figure 9.17 is theory. In reality, we have all seen some inefficient shoppers in our local grocery stores. How good are starlings as economists?

This question was addressed in a clever experiment by behavioral ecologist Alex Kacelnik of Oxford University. Instead of letting starlings feed on their natural prey, he trained them to visit feeding tables at which mealworms could be provided through a plastic tube at precisely timed intervals. A starling would arrive at the table, eat the first mealworm, and then wait for the next one to be delivered. Kacelnik adjusted the timing so that each successive mealworm would arrive at a progressively longer interval, mimicking the longer intervals at which a starling would catch leathery jackets as its beak became full. Kacelnik then placed feeding tables at different distances from nests and observed how many mealworms a starling would wait for at different travel times. As expected, starlings increased their load size as travel time increased (Figure 9.18). Kacelnik concluded that starlings are good economists, at least when it comes to gathering food.

As predicted, starlings deliver larger loads of food when the food source is more distant.

Risk-sensitive foraging

The value of a feeding area depends not only on the rate at which an individual can gather food, but also on the relative safety of the place. Every activity carries a risk of mortality. For many animals, predation is the most significant mortality risk, and the presence of a predator, or even the perceived threat of predation, can reduce the value of an otherwise good foraging place. The extra food is simply not worth the increased risk of becoming food. The predation factor has been incorporated into foraging theory in studies of risk-sensitive foraging.

ECOLOGISTS IN THE FIELD

Experiments with risk-sensitive foraging

James F. Gilliam and Douglas F. Fraser demonstrated the principle of risk-sensitive foraging elegantly in a simple experiment with fish. They constructed cages having two compartments and placed these directly in an experimental stream. The subjects were small minnows (juvenile creek chubs), and the predators in the system were adult creek chubs. The minnows were provided with tubifex worms buried in mud placed in small trays in the compartments. A refuge area that permitted passage of the minnows, but not the adult chubs, connected the two compartments.

In the experiment, minnows were presented with a low density of food (0.17 worms per cm²) and only one predator in one compartment, and a higher density of food but two or three predators in the other compartment. The design of the experiment was to increase the amount of food in the more dangerous part of the cage to determine at what point the minnows would expose themselves to greater risk in order to obtain more food. Chub minnows were very sensitive to predation risk. When the more dangerous side of the cage had two adult chubs, minnows switched to foraging there only after prey density was increased to more than 0.33 worms per cm², or twice the level in the less risky side of the cage (Figure 9.19). When there were three predators, the food level had to be more than four times that on the safer side to entice the minnows to switch.

MORE ON THE WEB Variable food supplies and risk-sensitive foraging. Would you choose a predictable supply of a lower-quality food or a more variable food supply with a higher average reward?

Prey choice

Foraging decisions also include choices concerning particular prey items. An actively foraging individual, such as an insectivorous bird flitting among the foliage of trees, encounters in sequence a variety of potential foods of different types. Each type of food has an intrinsic value based on its nutrient and energy content, difficulty of handling, and potential danger from toxins. The cost of selecting a
Diet mixing

One reason that some foragers consume a varied diet is that one or a few food items might not provide all necessary nutrients, but these might be present in other food items. Different food types are complementary when each contains a required nutrient missing in the other. Humans, for example, can subsist on a diet of rice and beans, but not on either of these alone, because rice and beans each contain essential amino acids missing in the other. The principle of complementarity also applies when foods contain small amounts of different toxins that individually would be dangerous in large doses, but are relatively harmless in the smaller doses ingested with a mixed diet.

The benefits of diet mixing were demonstrated by Elizabeth Bernays and her colleagues at the University of Arizona using nymphs (immature stages) of the grasshopper *Schistocerca americana*. Grasshopper nymphs grew faster when fed a mixture of kale, cotton, and basil than when they were offered any one of these food plants alone (Figure 9.20). The effect was even more pronounced on lower-quality, natural food plants, such as mesquite and mulberry: nymphs with mixed diets grew almost twice as fast as those feeding on either one of these plant species alone. Similar results were obtained on artificial diets that were low in either protein or carbohydrates, both of which are required for proper growth. Grasshoppers on mixed diets grew more rapidly than those provided either of the lower-quality foods alone.

Experiments with birds feeding on fruits in the fall in the Morton Arboretum, Chicago, also demonstrated diet mixing. Fruits of two species of shrubs were presented together on artificial “bushes” against a natural background of either one or the other shrub species—that is, with many...
shrubs of the background species in the immediate vicinity—and fruit consumption was then recorded. The results support the hypothesis of complementarity in that birds selected the fruit that contrasted with the background fruit supply. For example, rough-leaved dogwood (Cornus drummondii) and pokeweed (Phytolacca americana) are similarly sized (7.4 and 8.9 mm) fruits with high lipid/low sugar and low lipid/high sugar contents, respectively. In a paired choice test, in an area with abundant natural dogwood, 3.2% of dogwood and 29% of pokeweed fruits were consumed; in an area with abundant natural pokeweed, 97% of dogwood and 71% of pokeweed fruits were consumed. In other words, the birds showed a preference for the less abundant alternative.

Summary

1. Most of the traits of organisms have evolved in response to their environments, including variation in environmental conditions and resources. For this reason, an understanding of evolution is essential to interpreting adaptations to varying environments.

2. Evolution by natural selection occurs when genetic factors influence survival and reproductive success. The genetic characteristics of those individuals that achieve the highest reproductive success increase in the population with time.

3. The genotype includes all the genetic factors that determine the structure and functioning (which together constitute the phenotype) of an individual. Many genetic factors have unique, measurable effects on the phenotype.

4. Individual organisms can respond to changes in their environments by altering their behavior, physiology, or morphology. Such changes are referred to as phenotypic plasticity.

5. Organisms have characteristic activity spaces defined by the conditions within which they can live and reproduce.

6. The availability of suitable activity space for an individual depends on the range of conditions and resources in the environment at any given time.

7. Animals select microhabitats whose physical conditions fall within their activity space.

8. Acclimation involves reversible changes in structure (for example, fur thickness) or biochemical pathways (changes in the amounts of different enzymes). Such changes require longer periods (usually days or weeks) than behavioral or metabolic changes. Acclimation plays a prominent role in responses of long-lived organisms to seasonal change.

9. Developmental responses express the interaction between an organism and its environment during its growth. Different environmental conditions lead to different characteristic, irreversible structures and appearances.

10. When conditions exceed the range of tolerance, organisms may migrate elsewhere, rely on materials stored during periods of abundance, or enter inactive states.

11. In many cases, the individual must anticipate environmental changes in order to respond successfully. Organisms rely on proximate cues, such as day length, to predict changes in ultimate factors, such as food supply, that directly affect their well-being.

12. Food supplies vary spatially, temporally, and with respect to the quality of prey items. Thus, animals must make choices about when, where, and how to feed that maximize their reproductive success.

13. Central place foragers, which must deliver food to a fixed place, such as a nest with young, balance the costs and risks of travel against the size of the area within which they can forage.

14. The quality of a feeding area is affected by the risk of predation on a foraging individual. Many animals avoid feeding in high-risk areas even though food may be plentiful. This strategy is referred to as risk-sensitive foraging.

15. Some foragers consume a mixed diet to obtain an appropriate balance of required nutrients or to reduce levels of toxic substances in their diets. Diet mixing is especially common among animals that feed on plants.

PRACTICING ECOLOGY

CHECK YOUR KNOWLEDGE

Tolerance of Variable Environments

We started this chapter by discussing how organisms cope with climate variability in the Mojave Desert. Indeed, this desert is hot in the summer. But it also can be cold in the winter, when air temperatures regularly fall below 0°C. Thermal extremes, which can limit the distributions of plants and animals, often occur in brief episodes, such as heat waves and cold snaps, and are not so apparent in annual averages. However, this kind of short-term variability can severely decrease the capacity of organisms to survive and reproduce. Consequently, extreme conditions help explain the
geographic distributions of many species. For example, the northern limit of the creosote bush *Larrea tridentata* matches the southern extent of minimum temperatures down to -18°C in the Mojave Desert. Creosote bush, particularly seedlings, cannot tolerate colder winter temperatures.

Besides accommodating temperature extremes, plants will have to adapt to variations in the environment caused by increasing atmospheric carbon dioxide. Burning fossil fuels and cutting forests will alter the global climate, perhaps substantially. The resulting increases in air and soil temperatures and changes in soil water and nutrient content are expected to have dramatic implications for the productivity and distribution of terrestrial vegetation in both natural and managed ecosystems. For example, as winter temperatures increase, the distributions of plants such as creosote bush will likely shift northward and to higher elevations. Plants also respond directly to elevated CO₂. Elevated atmospheric CO₂ increases photosynthetic efficiency, but this effect often decreases upon long-term exposure. In certain ecosystems, exposure to elevated CO₂ can also cause a reduction in leaf water loss. Plants in arid lands, such as the Mojave Desert, may benefit from this water saving more than those in other biomes.

Recent studies by Stan Smith, James Coleman, Robert Novak, and Jeffrey Seemann at the Nevada Desert FACE Facility have focused on the ability of plants to tolerate stressful conditions. "FACE" is an acronym for "Free Air Carbon Enrichment," a procedure in which large quantities of carbon dioxide gas are released directly to the atmosphere at ground level over small areas. Thus plants can be exposed to elevated CO₂ in natural environments. This method avoids complicating factors caused by exposing plants inside greenhouses, which alter the climate in unrealistic ways. One of the studies from this project has compared the ability of *Yucca brevifolia* (the Joshua Tree), *Yucca schidigera* (the Mojave Yucca), and *Yucca whipplei* to withstand high-temperature extremes under predicted CO₂ concentrations of the future. In this and other studies, elevated CO₂ has been shown to have a direct impact on the responses of plants to environmental variability.

**CHECK YOUR KNOWLEDGE**

1. Why is it important to understand the responses of desert organisms to their physical environment?

2. Refer to Figure 9.21. Which of the *Yucca* species exhibits the greatest effect due to elevated CO₂? What is the effect of elevated CO₂ on the magnitude of photosynthesis?

3. How do the three different *Yucca* species vary in their responses to elevated CO₂ and high-temperature events?

4. Go to the Weather page of the Nevada Desert FACE Facility from *Practicing Ecology on the Web* at [http://www.whfreeman.com/ricklefs](http://www.whfreeman.com/ricklefs) and examine the temperature and precipitation records measured at this site. By how much do they vary from summer to winter? And from year to year? What does this require of plants and animals in terms of evolution of adaptations to climatic variability?

![Figure 9.21](image-url) Curves for three species of *Yucca* exposed to either ambient or elevated CO₂ in a glasshouse, prior to the temperature increase. Red symbols and lines are from ambient plants, while blue symbols dotted lines are from elevated plants. From T. E. Huxman, et al., *Plant, Cell and Environment* 21:1275–1283.
Suggested Readings


Pathways of Elements in the Ecosystem

Energy transformation and element cycling are intimately linked.

Ecosystems may be modeled as a series of linked compartments.

Water provides a physical model of element cycling in the ecosystem.

The carbon cycle is closely tied to the flux of energy through the biosphere.

Nitrogen assumes many oxidation states in its cycling through ecosystems.

The phosphorus cycle is uncomplicated chemically.

Sulfur exists in many oxidized and reduced forms.

Microorganisms assume diverse roles in element cycles.

Should you be worried about the change in carbon dioxide concentration in the earth’s atmosphere? Combustion of fossil fuels and burning of forests to clear land for agriculture has increased the atmospheric concentration of CO₂ from 280 to 360 parts per million during the past century. Most of the change has been produced in recent decades, and projections show this trend increasing. The projected increases could bring about dramatic changes in climate through global warming, perhaps on the order of what we experience during extreme El Niño events. Such a scenario may disrupt agriculture and displace some of the human population. But major worries also include a rise in sea level due to melting ice caps and expansion of the surface waters of the oceans as they warm. These changes could flood vast coastal areas, causing economic disaster and rearranging human geography.

Yet the earth has witnessed far greater changes in atmospheric carbon dioxide concentrations in the past. Before the Industrial Revolution, CO₂ concentrations probably were as low as they have ever been in the geologic history of the earth. There is an important difference, however, between the present and the past. CO₂ levels are changing much more rapidly than they ever have before. Carbon and other chemical elements cycle continually through the ecosystem. The routes they take are determined by the particular chemical transformations in which each element participates. Organisms—including humans—move elements through their cycles within the ecosystem whenever they carry out energy transformations. This chapter shows how physical, chemical, and biological processes result in the cycling of elements within ecosystems. We shall see that many aspects of element cycling make sense only when one understands that chemical transformations and energy transformations go hand in hand.
Chemical elements, unlike energy, remain within the ecosystem, where they continually cycle between organisms and the physical environment. Materials used to form biological compounds originate in rocks of the earth's crust or in the earth's atmosphere, but within the ecosystem they are reused over and over by plants, animals, and microbes before being lost in sediments, streams, and groundwater or escaping to the atmosphere as gases. Though all the energy assimilated by green plants is "new" energy received from outside the ecosystem, most nutritive materials taken up by plants have been used before. Ammonia absorbed from the soil by roots might have been leached out of decaying leaves on the forest floor that same day. The carbon dioxide assimilated by a green plant might have been produced recently by animal, plant, or microbial respiration.

Energy transformation and element cycling are intimately linked

Organisms help to move elements through their cycles within the ecosystem whenever they make the chemical transformations needed to carry out their life processes. Transformations that incorporate inorganic forms of elements into the molecules of plants, animals, and microbes are referred to as assimilatory processes. One example of an assimilatory transformation of an element is photosynthesis, in which plants use energy to change an inorganic form of carbon (carbon dioxide) into the organic form of carbon found in carbohydrates. In the overall cycling of carbon, photosynthesis is balanced by respiration, a complementary dissimilatory process that involves the transformation of organic carbon back to an inorganic form, accompanied by release of energy.

Not all transformations of elements in the ecosystem are biologically mediated, nor do all involve the net assimilation or release of useful quantities of energy. Many chemical reactions take place in the air, soil, and water. Some of these, such as the weathering of bedrock, release certain elements (potassium, phosphorus, and silicon, for example) from compounds in rock and make them available to the ecosystem. Lightning storms produce small amounts of reduced nitrogen (ammonia, NH₃) from molecular nitrogen (N₂) and water vapor (H₂O) in the atmosphere, which plants and microbes can assimilate. Such reactions may have been involved in the origin of life itself. Other physical and chemical processes, such as sedimentation of calcium carbonate in the oceans, remove elements from circulation and incorporate them into rocks in the earth's crust, where they may remain untouched for eons.

Most biological energy transformations are associated with the biochemical oxidation and reduction of carbon, oxygen, nitrogen, and sulfur. As we saw in Chapter 2, an atom is oxidized when it gives up electrons, and it is reduced when it accepts electrons. In a sense, the electrons carry with them a portion of the energy content of an atom. In biological transformations, an energy-releasing oxidation is paired with an energy-requiring reduction, and energy shifts from the reactants in one transformation to the products in the other (Figure 7.1). Such coupled transformations are possible only when the oxidation side releases at least as much energy as the reduction side requires. The energy changes associated with various transformations vary widely depending on the compounds involved and the number of electrons exchanged. It is in the nature of the physical world that the energies of the two transformations rarely match. Energy supplied by an oxidation reaction in excess of that required by a coupled reduction reaction cannot be used, and is lost in the form of heat. These imbalances account for the thermodynamic inefficiency of life processes.

A typical coupling of transformations might involve the oxidation of carbon in a carbohydrate (glucose, for example), which releases energy, and the reduction of nitrate-nitrogen to amino-nitrogen (which forms the building blocks of proteins), which requires energy. This, like many biochemical transformations, ties an energy-releasing transformation to the assimilation of an element—nitrogen, in this case—required for growth and reproduction. In animals, such biochemical transformations are also used to maintain the cellular environment and to effect movement. Some of these transformations involve many

![Figure 7.1](image) The coupling of energy-releasing and energy-requiring transformations is the basis of energy flow in ecosystems.
intermediate steps of the type shown in Figure 7.1, linked
together into a biochemical pathway (Figure 7.2). Plants
accomplish the initial input of energy into the ecosystem
by an assimilatory reduction of carbon in which light,
rather than a coupled dissimilatory process, serves as the
source of energy. A portion of that energy escapes biologi-
cal systems with each subsequent transformation. The
cycling of elements between the living and nonliving parts
of the ecosystem is thus connected to energy flow by the
coupling of the dissimilatory part of one cycle to the assim-
ilatory part of another.

**Ecosystems may be modeled as a series of linked compartments**

With each biochemical transformation, one or more ele-
ments are changed from one form to another. Each form of
an element within an ecosystem may be thought of as a
separate compartment, like a room of a house, into and out
of which atoms move as physical and biological processes
transform them. The entire ecosystem may be thought of as
a set of compartments among which elements are cycled
(Figure 7.3). For example, photosynthesis moves carbon
from the inorganic carbon compartment to that containing
organic forms of carbon (assimilation); respiration returns it
to the inorganic compartment (dissimilation). Such comp-
artment models of ecosystems can be organized hier-
archically, having subcompartments within compartments.

The inorganic carbon compartment includes carbon dio-
xide both in the atmosphere and dissolved in water, carbon-
ate and bicarbonate ions dissolved in water, and calcium
carbonate, mostly as a precipitate in the water column
and in sediments. The organic carbon compartment also
has many subcompartments: autotrophs, animals, micro-
organisms, and detritus. As organisms feed on others, they
move carbon among these subcompartments.

The movement of elements within and between com-
partments often involves energy. Photosynthesis adds
energy to carbon, which we may think of as lifting the ele-
ment to the second floor of a house. In descending the res-
piration "staircase," carbon releases this stored chemical
energy, which an organism can then use for other purposes.

Elements cycle rapidly among some compartments of
ecosystems and much more slowly among others. The
movement of an element between living organisms and
inorganic forms occurs over periods ranging from a few
minutes to the life spans of organisms or their subsequent
existence as organic detritus. We saw in the last chapter that
some organic matter in some terrestrial environments has
an average residence time on the order of centuries. Both
organic and inorganic forms of elements occasionally leave
rapid circulation within ecosystems for compartments that
are not readily accessible to transforming agents. For exam-
ple, coal, oil, and peat contain vast quantities of organic car-
bon that has been removed from circulation in ecosystems,
often for many millions of years. Inorganic carbon is re-
moved from circulation in aquatic ecosystems by precipi-
tation of calcium carbonate, which forms thick layers of
marine sediments that may eventually turn to limestone. These forms of carbon are returned to the rapidly cycling compartments of the ecosystem only by the slow geologic processes of volcanism, uplift, and erosion.

**Water provides a physical model of element cycling in the ecosystem**

Water is involved chemically in photosynthesis, but it is evaporation, transpiration, and precipitation that drive most movement of water through terrestrial ecosystems (Figure 7.4). These physical processes nonetheless couple the movement of water to transformations of energy. Thus, the global hydrologic cycle illustrates many basic features of the cycles of elements.

Light energy absorbed by water performs the work of evaporation. Water vapor has a potential energy, which is the energy of separation of individual water molecules from each other. When atmospheric water vapor condenses to form clouds, water molecules aggregate, and the potential energy in water vapor is released as heat, which eventually escapes the earth as long-wave radiation. From a thermodynamic standpoint, evaporation and condensation resemble photosynthesis and respiration.

Water in the biosphere totals about 1.4 billion cubic kilometers, or $1,400,000 \times 10^{18}$ g. It's hard to get a feeling for such a large number. $10^{18}$ g of water is a billion times a billion, or a quadrillion, grams. Each cubic meter contains $10^6$ g, or 1,000 kg (a metric ton, T) of water, and so $10^{18}$ g is a trillion ($10^{12}$) metric tons—that is, a teraton (TT). Numbers on the order of $10^{18}$ generally are reserved for astronomy and the federal budget, but we'll use
Figure 7.4: The global water cycle.

More than 97% of the water in the biosphere resides in the oceans. Other reservoirs of water include ice caps and glaciers (29,000 TT), underground aquifers (8,000 TT), lakes and rivers (100 TT), soil moisture (100 TT), water vapor in the atmosphere (13 TT), and all the water in living organisms (1 TT). Each of these may be regarded as a separate compartment in a compartment model of water in the biosphere.

Over land surfaces, precipitation (111 TT per yr, which is 22% of the global total) exceeds evaporation and transpiration (71 TT per yr; 16% of the global total). Over the oceans, evaporation exceeds precipitation by a similar amount. Much of the water that evaporates from the surface of the oceans is carried by winds to the continents, where it is captured as precipitation by the land. This net flow of atmospheric water vapor from ocean to land (40 TT per yr) is balanced by runoff from the land by way of rivers back into ocean basins.

Evaporation determines how fast water moves through the biosphere. The absorption of radiant energy by liquid water to create water vapor couples an energy source to the hydrologic cycle. We can calculate the energy that drives the global hydrologic cycle by multiplying the total weight of water evaporated (456 TT per yr) by the energy required to evaporate 1 g of water (2.24 kJ). The product, approximately 10^21 J per yr (about 32 billion megawatts), represents about one-fourth of the total energy of the sun’s radiation striking the earth. Condensation of water vapor to form precipitation releases the same amount of energy as heat. Evaporation and precipitation are closely linked because the atmosphere has a limited capacity to hold water vapor; any increase in the evaporation of water into the atmosphere creates an excess of vapor and causes an equal increase in precipitation.
The amount of water vapor in the atmosphere at any one time corresponds to an average of about 2.5 cm of water spread evenly over the surface of the earth. An average of 65 cm of rain or snow falls each year (the water flux), which is 26 times the average amount of water vapor. Thus the steady-state content of water in the atmosphere—the atmospheric compartment—replaces itself 26 times each year on average. (Conversely, water has an average residence time in the atmosphere of 1/26 of a year, or 2 weeks.) Soils, rivers, lakes, and oceans contain more than 100,000 times as much water as exists in the atmosphere. Fluxes through both compartments are the same, however, because evaporation balances precipitation. Thus the average residence time of water in its liquid form at the earth’s surface (about 2,800 years) is about 100,000 times longer than its residence time in the atmosphere.

The carbon cycle is closely tied to the flux of energy through the biosphere

The carbon cycle resembles the hydrologic cycle in that energy from the sun provides its driving force. The carbon cycle is much more complex, however, owing to the various chemical reactions of carbon. Three classes of processes cause carbon to cycle through aquatic and terrestrial ecosystems (Figure 7.5): (1) assimilatory and dissimilatory reactions of carbon, primarily in photosynthesis and respiration, (2) exchange of carbon dioxide between the atmosphere and the oceans, and (3) sedimentation of carbonates.

Figure 7.5 The global carbon cycle. The sizes of compartments and transfers between compartments are in billions of metric tons (10^12 g), or gigatons (GT), and GT per year. After T. Fenchel and T. H. Blackburn, Bacteria and Mineral Cycling, Academic Press, New York (1979); W. D. Grant and P. E. Long, Environmental Microbiology, Wiley, New York (1981).
Photosynthesis and respiration

Photosynthesis and respiration are the major energy-transforming reactions of life. Approximately 85 billion metric tons (85 × 10^{15} g) of carbon enter into such reactions worldwide each year. (We will refer to a billion metric tons as a gigaton, using the symbol GT). During photosynthesis, carbon gains electrons and is reduced (Figure 7.6). This gain of electrons is accompanied by a gain in chemical energy. An equivalent amount of energy is released by respiration, which results in a loss of electrons and a loss of chemical energy.

Although it is difficult to estimate the total carbon in organic matter within the biosphere, it probably adds up to something like 2,650 GT, including both living organisms and organic detritus and sediments. Thus, considering that 85 GT of carbon are assimilated by photosynthesis each year, the average residence time of carbon in biological molecules is approximately 2,650 GT divided by 85 GT per yr, which equals 31 years.

Ocean–atmosphere exchange

The second class of carbon cycling processes involves the physical exchange of carbon dioxide between the atmosphere and oceans, lakes, and streams. Carbon dioxide dissolves readily in water; indeed, the oceans contain about 50 times as much CO\textsubscript{2} as the atmosphere. Exchange across the air–water boundary links the carbon cycles of terrestrial and aquatic ecosystems. In fact, the ocean is an important sink for the carbon dioxide produced by the burning of fossil fuels. As the CO\textsubscript{2} content of the atmosphere increases, the rate of solution of CO\textsubscript{2} in the ocean increases, thereby reducing the rate of increase of CO\textsubscript{2} in the atmosphere below what it would be in the absence of air–water interchange.

Of the total carbon in the atmosphere in the form of carbon dioxide (640 GT), approximately 35 GT is assimilated by land plants, and 84 GT dissolves in the ocean and other surface waters, each year. Respiration and the escape of dissolved carbon dioxide from water to the atmosphere replace these amounts. Overall, the average residence time of carbon in the atmosphere is about 5 years. Because of this short residence time, the amount of carbon dioxide in the atmosphere is very sensitive to the rate of CO\textsubscript{2} production, increasing very nearly in parallel with the burning of fossil fuels. By 1990, combustion of fossil fuels contributed about 6 GT of carbon annually, equivalent to almost 1% of the total atmospheric carbon dioxide and a sixth of the total assimilation of carbon by land plants.

Precipitation of carbonates

The third class of carbon cycling processes occurs only in aquatic systems. It involves the dissolution of carbonate compounds in water and their precipitation (deposition) as sediments, particularly limestone and dolomite. On a global scale, dissolution and precipitation approximately balance each other, although certain conditions favoring precipitation have led to the deposition of extensive layers of calcium carbonate sediments in the past. Dissolution and deposition in aquatic systems occur about 100 times more slowly than assimilation and dissimilation by biological processes.
Figure 7.7 Most of the earth's carbon is in sedimentary rocks. These sedimentary deposits of limestone in the mountains of southern Texas represent calcium carbonate precipitated out of solution in the shallow seas that once covered the area. Photo by Gerald & Buff Corsi/Visuals Unlimited.

Igneous systems. Thus, the exchange between sediments and the water column is relatively unimportant to the short-term cycling of carbon in the ecosystem. Locally and over long periods, however, it can assume much greater importance; in fact, most of the ecosystem's carbon is locked up in sedimentary rocks (Figure 7.7).

As we saw in Chapter 2, when carbon dioxide dissolves in water, it forms carbonic acid,

\[ \text{CO}_2 + \text{H}_2\text{O} \rightarrow \text{H}_2\text{CO}_3 \]

which readily dissociates into hydrogen, bicarbonate, and carbonate ions:

\[ \text{H}_2\text{CO}_3 \rightarrow \text{H}^+ + \text{HCO}_3^- \rightarrow 2\text{H}^+ + \text{CO}_3^{2-} \]

Calcium, when present, also equilibrates with the carbonate ions to form calcium carbonate:

\[ \text{Ca}^{2+} + \text{CO}_3^{2-} \rightarrow \text{CaCO}_3 \]

Calcium carbonate has low solubility under most conditions, and readily precipitates out of the water column to form sediments. This sedimentation effectively removes carbon from aquatic ecosystems, but the rate of removal is less than 1% of the annual cycling of carbon in these ecosystems, and this amount is added back by input from rivers, which are naturally somewhat acid and tend to dissolve limestone (carbonate) sediments.

Dissolution and dissociation may be affected locally by the activities of organisms. In the marine system, under approximately neutral pH conditions, carbonate and bicarbonate are in chemical equilibrium:

\[ \text{CaCO}_3 \text{ (insoluble)} + \text{H}_2\text{O} + \text{CO}_2 \rightleftharpoons \text{Ca}^{2+} + 2\text{HCO}_3^- \text{ (soluble)} \]

Uptake of \( \text{CO}_2 \) for photosynthesis by aquatic algae and plants shifts the equilibrium to the left, resulting in the formation and precipitation of calcium carbonate. Many algae excrete this calcium carbonate to the surrounding water, but reef-building algae and coralline algae incorporate it into their hard body structures (Figure 7.8). In the system as a whole, when photosynthesis exceeds respiration (as it does during algal blooms), calcium tends to precipitate out of the system.

Changes in the carbon cycle over time

Geologists can estimate the amounts of carbon removed from the atmosphere by burial of organic matter and precipitation of carbonates in marine sediments, as well as when these sediments were formed. From this information, they...
can estimate the original concentration of carbon dioxide in the atmosphere and its change over time (Figure 7.9).

These estimates indicate that during the early part of the Paleozoic era, roughly 550–400 million years ago (Mya), the atmosphere held 15 to 20 times more carbon dioxide than at present. This amount decreased precipitately early in the Devonian period, nearly 400 Mya, dipping to nearly its present levels by 300 Mya. This decline was initiated by a sharp increase in the rate of weathering of terrestrial environments following the development of forests on land. The deposition of the vast accumulations of organic sediments that made up most of the earth’s coal beds. Toward the end of the Paleozoic era, at about 250 Mya, CO₂ concentration in the atmosphere again increased, to nearly five times its present level, remained high for approximately 100 million years through the early Mesozoic, and has been declining steadily ever since.

The early Paleozoic and early Mesozoic eras were truly greenhouse times. Average temperatures throughout the earth were hot, and tropical life flourished even at high latitudes. Declining CO₂ in the Devonian set the stage for cooler climates and extensive glaciations at the end of the Mesozoic era, much like those the earth has experienced during the past million years. The current increase in atmospheric CO₂, troubling as it is, will not return the earth to the hothouse conditions of former times, at least not any time soon. Most of the “geologic” carbon taken from the earth’s primitive atmosphere is bound up in limestone sediments. This carbon is returned to the atmosphere very slowly as limestone is subducted below the edges of continental plates, carbonates are turned to carbon dioxide under intense heat and pressure deep in the earth, and carbon dioxide is finally outgassed in volcanic eruptions.

ECOLOGISTS IN THE FIELD

What caused the precipitate decline in atmospheric carbon dioxide during the Devonian?

Why did concentrations of carbon dioxide in the atmosphere decline precipitately over a period of 50 million years during the Devonian period (409–363 Mya)? How can we infer events in the biosphere that occurred so long ago? Were ecological changes in ancient ecosystems involved? Geologist Gregory Retallack of the University of Oregon used several lines of evidence to provide a plausible explanation for this change. Retallack studied fossilized soils (paleosols) formed during the Devonian period in what is now Antarctica. (At that time, the climate there was warm, and vegetation flourished.) By comparing paleosols with modern soils, it is possible to interpret many processes occurring in soils in the past and their consequences for the biosphere.

The beginning of the Devonian was marked by two striking changes (Figure 7.10). One was a change in soil chemistry, indicated by a marked increase in clay content. The other was a dramatic increase in the density and depth of plant roots. The middle of the Devonian witnessed a striking increase in the diameter of trunks, stems, roots, and rhizomes of plants, indicating the development of the first forests on earth. These changes were followed at the end of the Devonian and beginning of the Carboniferous by the appearance of thick peat deposits, which later turned into coal.

The level of atmospheric CO₂ itself may be estimated by the ratio of ¹³C to ¹²C carbon isotopes in soil carbonates. Carbon dioxide in soil comes both from atmospheric sources directly and by respiration of soil organisms. The ¹³C/¹²C ratio indicates the relative amounts of atmospheric carbon compared with respired CO₂. With some assumptions about the production of CO₂ in soil, one can estimate the concentration of CO₂ in the atmosphere.

Why did the earth lose its greenhouse atmosphere during the Devonian? Retallack surmised that the increase in terrestrial vegetation, particularly the penetration of soil by fine roots, would have dramatically increased the rate of weathering of soil, thus increasing its clay content. Roots and
dous amounts of calcium and magnesium to be washed out of soil wherever terrestrial vegetation had developed. As solubilized calcium and magnesium ions entered the oceans, they formed insoluble compounds with the abundant bicarbonate ions there and precipitated out of the water as sediments. As bicarbonate was withdrawn from the oceans, it was replaced by carbon dioxide diffusing in from the atmosphere. Thus, as vegetation promoted weathering, new sedimentary rock was formed, partly from constituents of old continental crust and partly from the missing atmospheric carbon dioxide.

Nitrogen assumes many oxidation states in its cycling through ecosystems

The ultimate source of nitrogen for life is molecular nitrogen (N$_2$) in the atmosphere. This form of nitrogen dissolves to some extent in water, but is absent from native rock. Lightning discharges convert some molecular nitrogen to forms, such as ammonia, that plants can use, but most enters the biological pathways of the nitrogen cycle (Figure 7.11) through its assimilation by certain microorganisms in a process referred to as nitrogen fixation. Although this pathway (N$_2$ $\rightarrow$ NH$_3$) constitutes only a small fraction of the earth's annual nitrogen flux, most biologically cycled nitrogen can be traced back to nitrogen fixation. Once in the biological realm, nitrogen follows pathways more complicated than those of carbon because more oxidized and reduced forms are possible for nitrogen atoms.

Ammonification

Let's begin with the reduced (organic) nitrogen found in proteins. Plants obtain nitrogen from the soil, either as ammonia or as nitrate, which they must then reduce to an organic form. From this point, the first step in the nitrogen cycle is ammonification. Ammonification involves the breaking down of proteins into their component amino acids by hydrolysis and the oxidation of the carbon in those amino acids. This results in the production of ammonia (NH$_3$). Ammonification is carried out by all organisms. Although carbon is oxidized, releasing energy, the nitrogen atom itself is not oxidized, and so its energy potential does not change during ammonification.

Nitrification and denitrification

Nitrification involves the oxidation of nitrogen, first from ammonia to nitrite (NO$_2^-$), then from nitrite to nitrate.
Figure 7.11 Schematic diagram of transformations of compounds in the nitrogen cycle.
The most reduced state of the nitrogen atom has the highest chemical energy potential.
(NO$_3^-$), during which nitrogen atoms are stripped of six, and then two more, of their electrons. These oxidation steps release much of the potential chemical energy of organic nitrogen. Each step is carried out only by specialized bacteria: NH$_3$ → NO$_2^-$ by *Nitrosomonas* in the soil and by *Nitroscoccus* in marine systems; NO$_2^-$ → NO$_3^-$ by *Nitrobacter* in the soil and *Nitrooccus* in the oceans. The overall pathway for nitrification is thus

\[ \text{NH}_3 \rightarrow \text{NO}_2^- \rightarrow \text{NO}_3^- . \]

Because both nitrification steps are oxidations, they can occur only in the presence of a powerful oxidizing agent, such as molecular oxygen, that can act as an electron acceptor. However, in waterlogged, anaerobic soils and sediments and in oxygen-depleted bottom waters, nitrate and nitrite are more oxidized than the surrounding environment, and they themselves can act as electron acceptors (oxidizers). Under these conditions, reduction reactions are thermodynamically favorable, and nitrogen may be reduced to nitric oxide (NO):

\[ \text{NO}_3^- \rightarrow \text{NO}_2^- \rightarrow \text{NO} . \]

This reaction, called denitrification, is accomplished by bacteria such as *Pseudomonas denitrificans*. Denitrification is important for breaking down organic matter in oxygen-depleted soils and sediments, but it also results in the loss of nitrogen from soils because some nitric oxide escapes as a gas. Additional chemical reactions under anaerobic, reducing conditions in soils and water can produce molecular nitrogen,

\[ \text{NO} \rightarrow \text{N}_2\text{O} \rightarrow \text{N}_2 , \]

with the consequent loss of nitrogen from general biological circulation.

Denitrification may be a major cause of low availability of nitrogen in marine systems. When organic remains of plants and animals sink to the depths of the oceans, their oxidation by bacteria in deep waters and bottom sediments often is accomplished anaerobically using nitrate as an oxidizer. This results in the conversion of nitrate and nitrite to the dissolved gases NO and N$_2$, which cannot be used by algae.

**Nitrogen fixation**

The loss of readily available nitrogen to ecosystems by denitrification is offset by nitrogen fixation. This assimilatory reduction of nitrogen is accomplished by bacteria such as *Azotobacter*, which is a free-living species; *Rhizobium*, which occurs in symbiotic association with the roots of some legumes (members of the pea family) and other plants (Figure 7.12); and cyanobacteria. The enzyme responsible for nitrogen fixation by these microorganisms—

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**Figure 7.12** Some bacteria carry out nitrogen fixation. The nodules on the roots of soybeans (left) harbor symbiotic nitrogen-fixing bacteria, as shown in red in the false-color transmission electron micrograph (right). Photo (a) courtesy of Thomas R. Sinclair; photo (b) by Dr. Jeremy Burgess/Science Photo Library/Photo Researchers.
nitrogenase—is inactivated by oxygen and works efficiently only under extremely low oxygen concentrations. This explains why Azotobacter bacteria, living freely in the soil, exhibit only a small fraction of the nitrogen-fixing capacity of Rhizobium bacteria, which are sequestered in the relatively anoxic cores of root nodules. In these nodules, root cells infected by Rhizobium form membrane-bounded structures called symbiosomes, within which the bacteria are maintained. Oxygen within a symbiosome is maintained at a very low level so as not to interfere with the activity of nitrogenase. This level of oxygen would limit respiration of plant root cells severely, but is suitable for respiration by Rhizobium. Although symbiosomes contain little free oxygen, they do have an abundant supply bound to a special kind of hemoglobin. This so-called leghemooglobin has a high affinity for oxygen and therefore keeps the concentration of free oxygen very low while providing a continuous supply for respiration.

Nitrogen fixation proceeds by reducing nitrogen and therefore requires energy, though no more than the conversion of an equivalent amount of nitrate to ammonia by plants. The reduction of one atom of molecular nitrogen to ammonia requires approximately the amount of energy released by the oxidation of an atom of organic carbon to carbon dioxide. Nitrogen-fixing microorganisms obtain the energy and reducing power they need to reduce N\textsubscript{2} to NH\textsubscript{3} by oxidizing sugars or other organic compounds. Free-living bacteria must obtain these resources by metabolizing organic detritus in the soil, sediments, or water column. More abundant supplies of energy are available to the Rhizobium bacteria that enter into symbiotic relationships with plants, which provide them with malate, a four-carbon carbohydrate produced as an end product of glycolysis.

On a global scale, nitrogen fixation approximately balances the production of N\textsubscript{2} by denitrification. These fluxes amount to about 2% of the total cycling of nitrogen through the ecosystem. On a local scale, nitrogen fixation can assume much greater importance, especially in nitrogen-poor habitats. When land is first exposed to colonization by plants—as, for example, are areas left bare by receding glaciers or newly formed lava flows—species with nitrogen-fixing capabilities dominate the colonizing vegetation.

The phosphorus cycle is uncomplicated chemically

Ecologists have studied the role of phosphorus in ecosystems intensively because organisms require this element at a relatively high level (though only about one-tenth that of nitrogen). Phosphorus is a major constituent of nucleic acids, cell membranes, energy transfer systems, bones, and teeth. Phosphorus is thought to limit plant productivity in many aquatic habitats. Influxes of phosphorus into rivers and lakes in the form of sewage and runoff from fertilized agricultural lands can artificially stimulate production in aquatic habitats, which can upset natural ecosystem balances and alter the quality of aquatic habitats. Pollution by phosphorus-containing detergents was a major contributor to this problem until phosphorus-free alternative detergents were developed.

The phosphorus cycle (Figure 7.13) has fewer steps than the nitrogen cycle because, except in a very few microbial transformations, phosphorus does not undergo oxidation-reduction reactions in its cycling through the ecosystem. Plants assimilate phosphorus as phosphate ions (PO\textsubscript{4}\textsuperscript{3-}) directly from soil or water and incorporate it directly into various organic compounds. Animals eliminate excess phosphorus in their diets by excreting phosphate salts in urine; phosphatizing bacteria also convert phosphorus in detritus to phosphate ions. Phosphorus does not enter the atmosphere in any form other than dust, so the phosphorus cycle involves only soil and aquatic compartments of the ecosystem.

Acidity greatly affects the availability of phosphorus to plants. In acidic soils, phosphorus binds tightly to clay particles and forms relatively insoluble compounds with iron and aluminum. In basic soils, it forms other insoluble compounds—for example, with calcium. When both calcium and iron or aluminum are present under aerobic conditions, the highest concentration of dissolved phosphate—that is, the greatest availability of phosphorus—occurs at a pH of between 6 and 7.

In well-oxygenated aquatic systems, phosphorus readily forms insoluble compounds with iron or calcium and precipitates out of the water column. Thus, marine and freshwater sediments act as a phosphorus sink, continually removing precipitated phosphorus from rapid circulation in the ecosystem. Phosphorus compounds readily dissolve and enter the water column only in oxygen-depleted aquatic sediments and bottom waters. Under such conditions, iron tends to form soluble sulfides rather than insoluble phosphate compounds.
importance of sulfur in the ecosystem goes far beyond this role. Like nitrogen, sulfur exists in many reduced and oxidized forms, and so it follows complex chemical pathways and affects the cycling of other elements (Figure 7.14).

The most oxidized form of sulfur is sulfate ($\text{SO}_4^{2-}$); the most reduced forms are hydrogen sulfide ($\text{H}_2\text{S}$) and organic forms of sulfur, such as those found in amino acids. Under aerobic conditions, energy-requiring assimilatory sulfur reduction by organisms ($\text{SO}_4^{2-} \rightarrow \text{organic S}$) balances the oxidation of organic sulfur back to sulfate, which occurs either directly or with sulfite ($\text{SO}_3^{2-}$) as an intermediate step. This oxidation occurs when animals excrete excess dietary organic sulfur and when microorganisms decompose plant and animal detritus.

Under anaerobic conditions, such as those in waterlogged sediments, sulfate, like nitrate, may function as an oxidizer. In such reducing environments, the bacteria *Desulfovibrio* and *Desulfomonas* can use energetically favorable sulfate reduction to oxidize organic carbon. The coupling of these reactions makes some energy available to the organisms. The reduced sulfur may then be used by photosynthetic bacteria to assimilate carbon by pathways analogous to photosynthesis in green plants. In these reactions, sulfur takes the place of the oxygen atom in water as an electron donor. As a result, elemental sulfur (S) accumulates unless the sediments are exposed to aeration or oxygenated water, at which point sulfur may be further oxidized by aerobic chemosynthetic bacteria, such as *Thiobacillus*, to sulfite and sulfate.

The fate of reduced sulfur produced under anaerobic conditions depends on the availability of positive ions. Frequently, hydrogen sulfide ($\text{H}_2\text{S}$) forms; it escapes from shallow sediments and mucky soils as a gas having the characteristic smell of rotten eggs. Anaerobic conditions
Figure 7.14 Schematic diagram of transformations of compounds in the sulfur cycle.

generally favor the reduction of ferric iron (Fe$^{3+}$) to ferrous iron (Fe$^{2+}$), which can combine with sulfide ions to form iron sulfide (FeS). For this reason, sulfides are commonly associated with coal and oil deposits. When these materials are exposed to the atmosphere in mine wastes or burned for energy, the reduced sulfur oxidizes (with the help of Thiobacillus bacteria in mine wastes) to sulfate. This oxidized sulfur combines with water to produce sulfuric acid (H$_2$SO$_4$), which leads to acid rain and acid mine drainage (Figure 7.15).
Microorganisms assume diverse roles in element cycles

As you may have noticed, many of the transformations discussed in this chapter are accomplished mainly or entirely by bacteria. In fact, were it not for the activities of such microorganisms, many element cycles would be altered drastically and the productivity of the ecosystem much reduced. For example, without the capacity of some microbes to use nitrogen, sulfur, and iron as electron acceptors, little decomposition would occur in anaerobic organic sediments, and their resulting accumulation would reduce the amount of inorganic carbon in the ecosystem. Without nitrogen-fixing bacteria, denitrification under anaerobic conditions would slowly deplete ecosystems of available nitrogen and reduce biological productivity proportionally.

Many of the transformations carried out by microorganisms, such as metabolism of sugars and other organic molecules, are accomplished in similar ways by plants and animals. The bacteria and cyanobacteria are distinguished physiologically by the ability of many species to metabolize substrates under anaerobic conditions and to use substrates other than organic carbon as energy sources.

Every organism needs, above all, a source of carbon for building organic structures and a source of energy to fuel the life processes. As pointed out earlier in this book, we can distinguish organisms in terms of their sources of carbon. Heterotrophs obtain carbon in reduced (organic) form by consuming other organisms or organic detritus. All animals and fungi, and many bacteria, are heterotrophs. Autotrophs assimilate carbon as carbon dioxide and expend energy to reduce it to an organic form. Photoautotrophs use sunlight as their source of energy for this reaction (photosynthesis). All green plants and algae are photoautotrophs, as are cyanobacteria, which use H₂O as an electron donor (reducing agent) and are aerobie; and purple and green bacteria, which have light-absorbing pigments different from those of green plants, use H₂S or organic compounds as electron donors, and are anaerobic.

Chemoautotrophs all use CO₂ as a carbon source, but they obtain energy for its reduction by the aerobic oxidation of inorganic substrates: methane (for example, Methanospirillum and Methylomonas); hydrogen (Hydrogenomonas and Micrococcus); ammonia (the nitrifying bacteria Nitrosomonas and Nitrobacter); nitrite (the nitrifying bacteria Nitrobacter and Nitrooccus); hydrogen sulfide, sulfur, and sulfite (Thiobacillus); or ferrous iron salts (Ferrobacillus and Gallionella). Chemoautotrophs are almost exclusively bacteria, which apparently are the only organisms that can become specialized biochemically as to make efficient use of inorganic substrates in this way and efficiently dispose of the waste products of chemoautotrophic metabolism.

The special role of microorganisms in ecosystem function is illustrated nicely by the highly productive communities of marine organisms that develop around deepsea hydrothermal vents (Figure 7.16). Scientists from the Woods Hole Oceanographic Institution in Massachusetts first discovered these miniature ecosystems in deep water off the Galápagos archipelago in 1977. Vent communities have since been found to be widely distributed in the ocean basins of the world. The most conspicuous members of the community are giant white-shelled clams and tube worms (pogonophorans) that grow to 3 meters long, but numerous crustaceans, anelids, mollusks, and fish also cluster at great densities around hydrothermal vents. The high productivity of vent communities contrasts strikingly with the desertlike appearance of the surrounding ocean floor.

How do these communities obtain energy? These deepsea vents occur well below the level of light penetration, and so there can be no photosynthesis. As you might suspect, the productivity of the vent communities is based on the unique qualities of the water issuing from the vents themselves. This water is hot and loaded with a reduced form of sulfur, hydrogen sulfide (H₂S). Where vent water and seawater mix, conditions are ideal for chemoautotrophic
Summary

1. Unlike energy, nutrients are retained within ecosystems, where they are cycled between physical and biotic components. The paths that elements follow through ecosystems depend on chemical and biological transformations, which themselves depend on the chemistry of each element, the physical and chemical conditions of the environment, and the ways in which each element is used by various organisms.

2. Movement of energy through ecosystems parallels the paths of several elements, particularly carbon, whose transformations either require or release energy.

3. Energy transformations in biological systems occur primarily in the course of oxidation-reduction reactions. An oxidizer is a substance that readily accepts electrons; a reducer is one that readily donates electrons. Upon being reduced, an atom gains energy along with the electrons it accepts; upon being oxidized, an atom releases energy along with the electrons it gives up.

4. The cycling of each element may be thought of as movement between compartments of ecosystems. The major compartments are living organisms, organic detritus, immediately available inorganic forms, and unavailable organic and inorganic forms, for the most part locked away in sediments.

5. The water cycle, or hydrologic cycle, provides a physical analogy for element cycling in ecosystems. Energy is required to evaporate water because molecules of water vapor have a higher energy content than molecules of liquid water. This energy is released as heat when water vapor condenses in the atmosphere to produce precipitation.

6. All organisms require organic carbon as the primary substance of life. Organic carbon is also the major source of energy for most animals and microorganisms. Carbon shuttles between organic forms and the inorganic compartments of ecosystems by way of photosynthesis and respiration.

7. The carbon cycle involves nonbiological processes such as the dissolution of carbon dioxide in surface waters. Dissolved carbon dioxide enters into a chemical equilibrium with bicarbonate and carbonate ions, which, in the presence of calcium, tend to precipitate and form sediments. Thick accumulations of these marine sediments can become limestone rock.

8. Nitrogen has many reduced and oxidized forms and consequently follows many pathways through ecosys-
tems. Quantitatively, most nitrogen follows the cycle leading from nitrate through organic nitrogen (following assimilation by plants), ammonia, nitrite (following nitrification by bacteria), and then back to nitrate (following further nitrification). The last two steps are accomplished by certain bacteria in the presence of oxygen.

9. Under anaerobic conditions in soils and sediments, certain bacteria can use nitrate in place of oxygen as an oxidizing agent (denitrification): in this process, nitrate leads to nitrite and (eventually) to molecular nitrogen (N₂). This loss of nitrogen from general biological cycling is balanced by nitrogen fixation by some microorganisms.

10. Plants assimilate phosphorus in the form of phosphate ions (PO₄³⁻). The availability of phosphorus varies with the acidity and oxidation level of the soil or water. The energy potential of the phosphorus atom does not change during its cycling through ecosystems.

11. Sulfur is an important element in anaerobic habitats, where it may serve as an oxidizer in the form of sulfate ions (SO₄²⁻) or as a reducing agent (for photoautotrophic bacteria) in the forms of elemental sulfur and sulfide.

12. Many elemental transformations, particularly under anaerobic conditions, are accomplished by biochemically specialized microorganisms. These organisms therefore play important roles in the cycling of elements through the ecosystem.

**PRACTICING ECOLOGY**

**CHECK YOUR KNOWLEDGE**

**Methanogenesis**

Understanding oxidation and reduction reactions can help to clarify many aspects of element cycling in ecosystems. Each reduction reaction is coupled to an oxidation reaction; thus they are referred to together as a reduction-oxidation (redox) reaction. For the chemical reactions that lead to nutrient transformations in ecosystems, oxidation generally involves oxygen because it readily accepts electrons from other atoms. In contrast, the reduction reaction that is coupled to oxidation usually involves organic forms of carbon because carbon atoms are good at donating electrons during redox reactions.

In some kinds of habitats, such as waterlogged sediments in swamps or marshes, oxygen is not available to serve as a terminal electron acceptor for respiration. Certain kinds of bacteria that live in such sediments (Archae-bacteria) have evolved the ability to use organic carbon to oxidize organic carbon when oxygen is not available. They utilize organic carbon in the form of methanol or acetate as a substrate. Organic carbon acts as an electron acceptor to produce methane (CH₄) and as an electron donor to result in the production of carbon dioxide. The overall reaction is:

\[ 4\text{CH}_3\text{OH} \rightarrow 3\text{CH}_4 + \text{CO}_2 + 2\text{H}_2\text{O} \]

The resulting methane is released from the surface of the water and results in the phenomenon known as “swamp gas.”

The factors that control methane production have received considerable research attention in late. Methane is an important greenhouse gas that is contributing to the increased absorption of infrared radiation in the atmosphere and global warming. In fact, the heating effectiveness of one molecule of methane is about 25 times that of one carbon dioxide molecule. Moreover, methane production is increasing due to growing numbers of cattle and land conversion to rice paddies (both cattle and the sediments of rice paddies contain methanogenic bacteria). Several factors facilitate the production and release of methane from waterlogged sediments. For example, Grünfeld and Brix (1999) showed that methanogenesis and emission from water is affected by differences in the composition of the sediments, the depth of the water level below the sediments, and the presence of plants that emerge above the water (Table 7.1).

<table>
<thead>
<tr>
<th>Table 7.1</th>
<th>Estimated methane (CH₄) production rate and CH₄ oxidation from treatments that differ in plant cover and water level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emergent vegetation</td>
<td>+</td>
</tr>
<tr>
<td>Water level</td>
<td>Low</td>
</tr>
<tr>
<td>Methanogenesis (mmol per m² per day)</td>
<td>41</td>
</tr>
<tr>
<td>CH₄ emission (mean) (mmol per m² per day)</td>
<td>22</td>
</tr>
<tr>
<td>CH₄ oxidation (% of methanogenesis)</td>
<td>46</td>
</tr>
</tbody>
</table>
CHECK YOUR KNOWLEDGE

1. Of the elements that cycle from the surface of the earth to the atmosphere and back, which is the most important for organisms?

2. From the results presented by Grünfeld and Brix, what is the effect of vegetation cover on methane production, oxidation, and emission?

3. How might a changing climate affect methane production and emission in light of the results presented by Grünfeld and Brix?

MORE ON THE WEB

4. Read the article "Ruminant Livestock and the Global Environment" from the EPA through Practicing Ecology on the Web at http://www.wwf-free-man.com/rickerts. Why is the cow-calf sector of the beef industry the largest emitter of methane within U.S. livestock industries? How can livestock producers reduce the amount of greenhouse gas emissions coming from their cows?

Suggested Readings


Energy in the Ecosystem

Alfred J. Lotka developed the first thermodynamic concept of the ecosystem.

Primary production is the assimilation of energy and production of organic matter by photosynthesis.

Only 5% to 20% of energy passes between trophic levels.

Energy moves through ecosystems at different rates.

Ecosystem energetics summarizes the movement of energy through the ecosystem.

We humans consume a large proportion of the earth's production. The total production of dry plant biomass over the surface of the earth amounts to 224 billion tons per year. Of this, approximately 59% is produced in terrestrial ecosystems. Of that terrestrial production, an astonishing 35% to 40% is used by humans, either directly as food and fiber crops or indirectly as feed for animals. The oceans, traditionally a source of food for people living near the coast, are now becoming a major source of food for much of the world's population. By the early 1980s, the global fish catch amounted to 75 million tons per year, and this has since increased substantially.

How much of the production of algae in the oceans is required to sustain the fisheries on which humans depend? How much of the total algal production is represented in the 75 million tons of fish and other seafood we harvest each year? How much more food can we expect to harvest from the oceans? Two marine ecologists, D. Pauly and V. Christensen, who were working at the International Center for Living Aquatic Resources Management in the Philippines, sought to answer these questions from their understanding of energy flow in natural ecosystems.

Pauly and Christensen assumed that for each step in the chain of feeding relationships that leads from microscopic algae to the fish we eat, about 90% of consumed energy is used to maintain the consumer. This means that only 10% is converted through growth and reproduction to biomass, and thus potential food for other organisms. From studies of the diets of marine organisms, Pauly and Christensen estimated the number of feeding steps leading from algae to fish. These varied from averages of about 1.5 for coastal and reef ecosystems to 3 for the open ocean. Knowing the number of feeding steps and assuming an energy transfer efficiency of 10% per step, they used a simple calculation to convert harvested fish into amounts of algae.
needed to sustain them. Such calculations showed that for inshore fisheries, which produce most of the fish consumed by humans, the algal growth required to sustain the harvested fish amounted to 24% to 35% of the total production of the ecosystem. Because much of the production in these systems consists of species not eaten by humans, our harvesting may be approaching its upper limit. Only in the open ocean, which is much more difficult for humans to exploit, do we usurp a small fraction (about 2%) of the total production.

During the early part of the twentieth century, several new concepts emerged that led the study of ecology in novel directions. One of these was the realization that feeding relationships link organisms into a single functional entity. Foremost among the proponents of this new ecological viewpoint during the 1920s was the English ecologist Charles Elton. Elton argued that organisms living in the same place not only had similar tolerances of physical factors in the environment, but also interacted with one another, most importantly in a system of feeding relationships that he called a food web. Of course, every organism must feed in some manner to gain nourishment, and each may be fed upon by some other organism. However, regarding these feeding relationships as an ecological unit was a novel idea early in the twentieth century.

A decade later, the English plant ecologist A. G. Tansley took Elton’s idea an important step further by considering animals and plants, together with the physical factors of their surroundings, as ecological systems. Tansley called this concept the ecosystem, and regarded it as the fundamental unit of ecological organization. Tansley envisioned the biological and physical parts of nature together, unified by the dependence of animals and plants on their physical surroundings and by their contributions to maintaining the conditions and composition of the physical world.

Alfred J. Lotka developed the first thermodynamic concept of the ecosystem

Working independently of the ecologists of his day, Alfred J. Lotka, a chemist by training, was the first to consider populations and communities as energy-transforming systems. He suggested that each system can be described in principle by a set of equations that represent exchanges of matter and energy among its components. Such exchanges include the assimilation of carbon dioxide into organic carbon compounds by plants, the consumption of plants by herbivores, and the consumption of animals by carnivores.

Lotka believed that the size of a system and the rates of energy and material transformations within it obeyed certain thermodynamic principles that govern all energy transformations. Just as heavy machines and fast machines require more fuel to operate than lighter and slower ones, and inefficient machines require more fuel than efficient ones, the energy transformations of ecosystems grow in direct proportion to their size (roughly, the total mass of their constituent organisms), productivity (rate of transformations), and efficiency. The earth itself is a giant thermodynamic machine in which the circulation of winds and ocean currents and the evaporation of water are driven by the energy in sunlight. Part of that energy is assimilated by the photosynthesis of plants, and this energy ultimately fuels all biological systems.

Lotka’s ideas were not widely appreciated by ecologists of his time. His mathematical representations were difficult and unfamiliar, and he did little to promote his ideas. The concept of the ecosystem as an energy-transforming system was brought to the attention of many ecologists for the first time in 1942 by Raymond Lindeman, a young aquatic ecologist at the University of Minnesota. Lindeman’s framework for understanding ecological systems on the basis of thermodynamic principles made a deep impression. He adopted Tansley’s notion of the ecosystem as the fundamental unit in ecology and Elton’s concept of the food web, including inorganic nutrients at the base, as the most useful expressions of ecosystem structure.

The sequence of feeding relationships by which energy passes through the ecosystem is referred to as a food chain. A food chain has many links—plant, herbivore, and carnivore, for example—which Lindeman referred to as trophic levels. (The Greek root of the word trophic means “food.”) Furthermore, Lindeman visualized a pyramid of energy within the ecosystem, with less energy reaching each successively higher trophic level (Figure 6.1). Lindeman argued that energy is lost at each level because of the work performed by organisms at that level and because of the inefficiency of biological energy transformations. Thus, plants gather only a portion of the light energy available from the sun. Herbivores harvest even less of that light energy because plants use a portion of the energy they assimilate to maintain themselves, and that energy is not available to herbivores as plant biomass. The same may be said of the consumers of herbivores, and of each successively higher level of the food chain.

By the 1950s, the ecosystem concept had fully pervaded ecological thinking and had spawned a new branch of ecology, called ecosystem ecology, in which
the cycling of matter and the associated passage of energy through an ecosystem provided a basis for characterizing that system's structure and function. Energy and the masses of elements, such as carbon, provided a common "currency" that ecologists could use to compare the structure and functioning of different ecosystems in terms of the energy and matter residing in, and transferred among, the plants, animals, microbes, and abiotic components of the ecosystem. Measurements of energy assimilation and energetic efficiencies became the tools for exploring this new thermodynamic concept of the ecosystem.

With this new conceptual framework, ecologists began to measure energy flow and the cycling of nutrients. One of the strongest proponents of this approach has been Eugene P. Odum of the University of Georgia, whose text *Fundamentals of Ecology*, first published in 1953, influenced a generation of ecologists. Odum depicted ecosystems as energy flow diagrams (Figure 6.2a). For any one trophic level, such a diagram features a box representing the biomass (or its energy equivalent) of all the organisms making up that trophic level at any given time. For example, a box might represent all the plants or all the herbivores in a particular ecosystem. Superimposed on this box are pathways representing the flow of energy through that trophic level. These diagrams simplified nature, but nonetheless conveyed the important principle that energy passes from one

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**Figure 6.1** An ecological pyramid of energy. The breadth of each bar represents the net productivity of a trophic level in the ecosystem. For this particular system, ecological efficiencies are 20%, 19%, and 10% between trophic levels, but these values vary widely in different communities.

**Figure 6.2** E. P. Odum's "universal" model of ecological energy flow. (a) A single trophic level. (b) Representation of a food chain. The net production of one trophic level becomes the ingested energy of the next higher level.
link in the food chain to the next, diminished by respiration and the shunting of unused foodstuffs to detritus-based food chains. Odum depicted feeding relationships as two or more energy flow diagrams linked into food chains, as shown in Figure 6.2b.

Unlike energy, which enters ecosystems as light and leaves as heat, nutrients are regenerated and retained within the system. Odum extended his model to include this cycling of elements. He showed that matter cycles within the ecosystem, being taken up in inorganic forms by plants and converted to biomass and eventually returned to inorganic forms by the process of decomposition. The most obvious recycling of material in this manner is the production of carbon dioxide by respiration and its uptake by plants during photosynthesis. However, each element is eventually returned to an inorganic form in its cycle through the ecosystem. In ecosystem energetics, studies of the cycling of elements have assumed equal standing with studies of the flow of energy. Amounts of elements and their movement among ecosystem components provide a convenient index to the flow of energy, which is difficult to measure directly. For instance, because light energy is transferred to the chemical energy content of organic molecules during photosynthesis, tracking of the movement of biological forms of carbon can be used to follow the movement of energy through the ecosystem.

A second reason for the importance of nutrient cycling in ecosystem ecology is the fact that, in many circumstances, the quantities of certain nutrients regulate the production of biomass by plants, which is the material and energetic base of the entire ecosystem. For example, availability of water, rather than sunlight or minerals in the soil, limits the productivity of desert plants. In contrast, the open oceans are deserts by virtue of their scarce nutrients, particularly nitrogen. Understanding how elements cycle among components of the ecosystem is crucial to understanding the regulation of ecosystem structure and function.

**Primary production is the assimilation of energy and production of organic matter by photosynthesis**

Plants, algae, and some bacteria capture light energy and transform it into the energy of chemical bonds in carbohydrates. This process is referred to as primary production, and its rate is quantified as primary productivity. As we have seen, photosynthesis chemically unites two common inorganic compounds, carbon dioxide ($\text{CO}_2$) and water ($\text{H}_2\text{O}$), to form the sugar glucose ($\text{C}_6\text{H}_{12}\text{O}_6$) with the release of oxygen ($\text{O}_2$). The overall chemical balance of the photosynthetic reaction is

$$6\text{CO}_2 + 6\text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2.$$  

Photosynthesis transforms carbon from an oxidized (low-energy) state in CO$_2$ to a reduced (high-energy) state in carbohydrates. Because work is performed on the carbon atoms to increase their energy level, photosynthesis requires energy. This energy is provided by visible light. In quantitative terms, for each gram of carbon assimilated, a plant transfers 39 kilojoules (kJ) of energy from sunlight to the chemical energy of carbon in carbohydrates.

The pigments that capture the energy of light for photosynthesis actually absorb only a small fraction of the total incident solar radiation. In addition, because of inefficiencies in many biochemical steps of photosynthesis, plants assimilate no more than a third (and usually much less) of the light energy absorbed by those photosynthetic pigments. The rest is lost as heat.

Photosynthesis supplies the carbohydrates and energy that a plant needs to build tissues and grow. Rearranged and joined together, glucose molecules become fats, starches, oils, and cellulose. Glucose and other organic compounds (starches and oils, for example) may be transported throughout the plant or stored as a source of energy for future needs. Combined with nitrogen, phosphorus, sulfur, and magnesium, simple carbohydrates derived from glucose produce an array of proteins, nucleic acids, and pigments. Plants cannot grow unless they have all these basic building materials. For example, the photosynthetic pigment chlorophyll contains an atom of magnesium, and so even when all other necessary elements are present in abundance, a plant lacking sufficient magnesium cannot produce chlorophyll, and thus cannot engage in photosynthesis.

Plants and other photosynthetic autotrophs form the base of all food chains, and therefore they are referred to as the **primary producers** of the ecosystem. Ecologists are interested in the rate of primary production because this determines the total energy available to the ecosystem. The total energy assimilated by photosynthesis is referred to as gross primary production. Plants use some of this energy to support the synthesis of biological compounds and to maintain themselves, and so their biomass contains substantially less energy than the total assimilated (Figure 6.3). The energy accumulated in plants, and which is therefore available to consumers, is referred to as **net primary production**. The difference between gross and net primary production is the energy of respiration, which is the amount used by plants for maintenance and biosynthesis.
ECOLOGISTS IN THE FIELD

Primary production can be measured by gas exchange or the growth of plants

Plant production involves fluxes of carbon dioxide, oxygen, minerals, and water and the accumulation of biomass (Figure 6.4). In principle, the rates of any of these flows could provide an index to the rate of primary production. It is worth discussing the measurement of primary production in some detail, as this will provide a better understanding of the processes involved in production and of the difference between gross and net production.

The unit of production is energy per unit of area per unit of time. For comparing production, ecologists often use kilojoules per square meter per year (kJ per m² per yr) or watts per square meter (W per m²). Production need not be measured only in terms of energy, however. Net production can be quantified conveniently as grams of carbon assimilated, dry weight of plant tissues, or their energy equivalents. Ecologists use such indices interchangeably because they are highly correlated. The energy equivalent of an organic compound depends primarily on its carbon content. Organic compounds contain approximately 39 kJ of metabolizable energy per gram of carbon, with some energy added or subtracted during various biochemical transformations.

In terrestrial ecosystems, ecologists often estimate net production by the amount of plant biomass produced in a year. In areas of seasonal growth, annual production may be estimated by cutting, drying, and weighing plants at the end of the growing season. Clearly, such harvesting methods measure net, rather than gross, production. Root growth is often ignored because roots are difficult to remove from most soils; thus harvesting measures annual aboveground net productivity (AANP), the most common basis for comparing terrestrial communities. Production of small plants or individual leaves is most often quantified directly by carbon dioxide uptake. Because the atmosphere contains so little carbon dioxide (0.03%), plants can measurably reduce its concentration in an enclosed chamber within a short period. This change in CO₂ concentration can provide a direct estimate of photosynthetic rate. A convenient application of this method is to enclose leaves (or whole herbaceous plants or branches of trees) in a clear chamber (light must penetrate for photosynthesis) and measure the change in the concentration of CO₂ in air passed through the chamber. The technology for doing this is now so advanced that rates of carbon dioxide uptake can be measured on a few square centimeters of leaf under natural conditions in a matter of seconds. The change in CO₂ concentration per gram of dry weight or per square centimeter of leaf surface area is then extrapolated to the

![Figure 6.4](image)

**IN**
- CO₂ (CO₂ uptake measured by decrease in closed chamber or by uptake of carbon-14 labeled CO₂)
- O₂ (in aquatic ecosystems, change in concentrations measured in closed chambers-light and dark bottle method)
- H₂O (not directly related to rate of photosynthesis)
- Water and minerals (difficult to measure and not directly related to rate of photosynthesis)
- Carbohydrate (harvest methods used to measure net production)

**OUT**

![Figure 6.5](image)
entire tree or forest. When a plant is exposed to light, carbon dioxide flux includes both assimilation (uptake) and respiration (output), and thus measures net production. Respiration can be measured separately by carbon dioxide production in the absence of light. Gross production can then be estimated by adding respiration to the net production (Figure 6.5).

The radioactive isotope carbon-14 ($^{14}$C) provides a useful variation on this method of measuring productivity. When a known amount of $^{14}$C-labeled carbon dioxide is added to an airtight chamber, plants assimilate the radioactive carbon atoms roughly in proportion to their occurrence in the air inside the chamber. Thus, the rate of carbon fixation can be calculated by dividing the amount of $^{14}$C in the plants by the proportion of $^{14}$C in the chamber at the beginning of the experiment. For example, if a plant takes up 10 mg of $^{14}$C in an hour, and $^{14}$C constitutes 5% of the carbon in the chamber, we can conclude that the plant assimilates carbon at a rate of about 200 mg per h (10 divided by 0.05).

In aquatic systems, harvesting provides a convenient method for estimating the primary production of large photosynthetic organisms, such as kelps, but this technique is not practical for small organisms, such as phytoplankton. Because of the high concentrations of bicarbonate in most waters, measuring changes in carbon dioxide in aquatic systems is not practical either. However, because oxygen dissolves so poorly in water, one can measure small changes in oxygen concentration in most aquatic systems. Remember that photosynthesis produces molecular oxygen ($O_2$) as a by-product. To estimate primary production, samples of water containing phytoplankton are suspended in pairs of sealed bottles at desired depths beneath the surface of the body of water. One bottle (the 'light bottle') is clear and allows sunlight to enter; the other (the 'dark bottle') is opaque (Figure 6.6). In the light bottle, photosynthesis and respiration occur together, and part of the oxygen produced by the first process is consumed by the second. In the dark bottle, respiration consumes oxygen without its being replenished by photosynthesis. Thus, gross production can be estimated by adding the change in oxygen concentration in the dark bottle (respiration alone) to that in the light bottle (photosynthesis and respiration). In unproductive waters, such as those of deep lakes and the open ocean, changes in oxygen concentration are too slow to measure easily. In such situations, the uptake of $^{14}$C by plants and algae provides a more sensitive measure of carbon assimilation.

**Light and temperature influence rates of photosynthesis**

Primary production is sensitive to variations in light and temperature. For plants growing in full sunlight, light levels usually exceed the saturation point of their photosynthetic pigments (see Figure 3.10); therefore the photosynthetic rate of such plants generally is not restricted by light availability. For plants growing in shade or at depth in aquatic systems, however, the rate of photosynthesis often is limited by light. In addition, any particular leaf does not al-
ways operate at its maximum possible photosynthetic rate. Cloud cover, shading by other leaves, plant leaves, and low levels of light early and late in the day reduce the photosynthetic rate below its maximum.

Photosynthetic efficiency is the percentage of the energy in sunlight that is converted to net primary production during the growing season. This measure provides a useful index to rates of primary production under natural conditions. Where water and nutrients do not limit plant production severely, the photosynthetic efficiency of an ecosystem as a whole varies between 1% and 2%. What happens to the remaining 98–99% of the light energy? Leaves and other surfaces reflect anywhere from 25% to 75% of it. Molecules other than photosynthetic pigments absorb most of the remainder, which is converted to heat and either radiated or conducted across the leaf surface or dissipated by the evaporation of water from the leaf (transpiration).

Like the rates of most other physiological processes, the rate of photosynthesis generally increases with temperature, at least up to a point. The optimum temperature for photosynthesis varies with the prevailing temperature of the environment—from about 16°C in many temperate species to as high as 38°C in tropical species. Net production depends on the rate of respiration as well as on the rate of photosynthesis, and respiration generally increases with increasing leaf temperature as well. Thus, net production, and therefore net assimilation of CO₂, and may actually decrease with increased temperature.

Water limits primary production in many terrestrial habitats

As we saw in Chapter 3, the tiny openings (stomata) in leaves through which carbon dioxide and oxygen are exchanged with the atmosphere also allow water to leave the leaf by transpiration. When the soil moisture approaches a plant's wilting point, the stomates close to reduce water loss. This prevents uptake of CO₂, and photosynthesis slows to a standstill. Consequently, the rate of photosynthesis depends on the availability of soil moisture, a plant's ability to tolerate water loss, and the influence of air temperature and solar radiation on the rate of transpiration.

Agronomists quantify the drought resistance of crop plants in terms of transpiration efficiency, also called water use efficiency, which is the number of grams of dry matter produced (net production) per kilogram of water transpired. In most plants, transpiration efficiencies are less than 2 g of production per kilogram of water, but they may be as high as 4 g per kilogram in drought-tolerant crops. Because transpiration efficiency varies little among a wide variety of plant species, production can be directly related to water availability in the environment, as we saw in the case of maize crops in Zimbabwe (see Figure 4.16). However, much of the precipitation received by an area is never taken up by plants. Ground water, surface water (streams), and evaporation from the soil account for the remainder of the water budget. For example, in perennial grassland in southern Arizona, production varies in direct proportion to precipitation during the summer growing season, but at a rate of only about 200 kilograms of dry matter per hectare for each 10 cm of precipitation. Ten centimeters of rainfall is equivalent to a million kilograms of water per hectare. Thus, the water use efficiency of the grassland biome as a whole is only 0.2 g per kilogram, about one-tenth that based on transpired water. This finding indicates that only about 10% of the precipitation is taken up and transpired by plants in this habitat. Most of the rain comes in extremely heavy thundershowers during the summer months, and most of the water quickly runs off the land.

Nutrients stimulate plant production in both terrestrial and aquatic ecosystems

Fertilizers stimulate plant growth in most environments. When nitrogen and phosphorus fertilizers were applied singly and in combination to chaparral habitat in southern California, most species responded with increased production to additions of nitrogen, but not phosphorus (Figure 6.7). This result suggests that production in most chaparral species is limited by the availability of nitrogen. However, the growth of California lilac bushes (Ceanothus greggin), which harbor nitrogen-fixing bacteria in their root systems, responded to the addition of phosphorus, but not to nitrogen. The production of annual plants (forbs and grasses) in the same environment increased when nitrogen was applied, but was depressed somewhat by the application of phosphorus alone. When equal amounts of nitrogen and phosphorus were applied together, however, production soared. Evidently, the annual plants could take advantage of increased phosphorus only in the presence of high levels of nitrogen.

Nutrients limit primary production most strongly in aquatic environments, particularly in the open ocean, where the scarcity of dissolved minerals reduces production far below terrestrial levels. Even in shallow coastal waters, where vertical mixing, upwelling currents, and run-off from the land maintain nutrients at high concentrations, the addition of fertilizers (as often occurs inadvertently through pollution) may greatly enhance aquatic production, upsetting the natural balance of aquatic ecosystems.
Primary production varies among ecosystems

The favorable combination of intense sunlight, warm temperature, abundant rainfall, and ample nutrients in parts of the humid Tropics results in the highest terrestrial productivity on earth. In temperate and arctic ecosystems, low winter temperatures and long winter nights curtail production. Within a particular latitude belt, where light does not vary appreciably from one locality to the next, net production is related directly to temperature and annual precipitation. Above a certain threshold of water availability, net production increases by 0.4 g of dry matter per kilogram of water in hot deserts and by 1.1 g per kilogram in short-grass prairies and cold deserts. Thus, a given amount of water supports almost three times as much plant production in the cooler climates as in the hotter climates within a given latitudinal belt.

Global patterns of net primary production are summarized in Figure 6.8. The production of terrestrial vegetation is highest in the humid Tropics and lowest in tundra and desert habitats. Swamp and marsh ecosystems, which occupy the interface between terrestrial and aquatic habitats, can produce as much biomass annually as tropical forests because of the continuous availability of water and the rapid regeneration of nutrients in mucky sediments surrounding plant roots.

In the open ocean, scarcity of mineral nutrients limits productivity to a tenth that of temperate forests, or even less. Upwelling zones (where nutrients reach the surface from deeper waters) and continental shelf areas (where bottom sediments in shallow water rapidly exchange nutrients with surface waters) support greater production. In estuaries, coral reefs, and coastal algal beds, production approaches levels observed in terrestrial habitats. Primary production in freshwater environments is considerably higher than that in the open oceans, achieving the highest levels in rivers, shallow lakes, and ponds and the lowest levels in clear streams and deep lakes.

Only 5% to 20% of energy passes between trophic levels

Primary production by plants, algae, and some bacteria forms the base of ecological food chains. Animals, fungi, and most microorganisms obtain their energy and most of their nutrients from plants or animals, or the dead remains of either. These organisms, therefore, have dual roles as food producers and food consumers. These roles give the ecosystem a trophic structure that is determined by food webs through which energy flows and nutrients cycle. The
food chain shown in Figure 6.1, from grass to rabbit to fox to hawk, traces one particular path that energy may follow through the trophic structure. As we have seen, biochemical transformations dissipate much of the energy of gross primary production before it can be consumed by organisms feeding at the next higher trophic level. With each step in the food chain, 80–95% of energy is lost. All the grass in Africa piled together would dwarf a mound of all the grasshoppers, gazelles, zebras, wildebeests, and other animals that eat grass. That mound of herbivores, in turn, would overwhelm the pitiful heap of all the lions, hyenas, and other carnivores that feed on them.

As Raymond Lindeman first pointed out in 1942, the amount of energy reaching each trophic level depends on the net primary production at the base of the food chain and on the efficiencies of energy transfers at each higher trophic level. Of the light energy assimilated by photosynthesis, plants use between 15% and 70% for maintenance, thereby making that portion unavailable to consumers. Herbivores and carnivores are more active than plants, and expend correspondingly more of their assimilated energy on maintenance. As a result, the production of each trophic level is typically only 5% to 20% that of the level below it.

Ecologists refer to the percentage of energy transferred from one trophic level to the next as ecological efficiency or food chain efficiency. To understand why ecological efficiencies are only 5–20%, we must examine how organisms make use of the energy they consume.

Regardless of the source of its food, an organism uses the energy from that food to maintain itself, to fuel its activities, and to grow and reproduce. Once ingested, the energy in food follows a variety of paths through the organism. To begin with, many components of food are not easily digested: hair, feathers, insect exoskeletons, cartilage, and bone in animal foods, and cellulose and lignin in plant foods (Figure 6.9). These substances may be defecated or regurgitated, and the energy they contain is referred to as egested energy. What an organism digests and absorbs constitutes its assimilated energy. The portion of this assimilated energy used to meet metabolic needs, most of which escapes the organism as heat, makes up the respired energy. Animals excrete another, usually smaller, portion of the assimilated energy in the form of nitrogen-containing organic wastes (primarily ammonia, urea, or uric acid), produced when the diet contains an excess of nitrogen; this is called excreted energy. Assimilated energy

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The most active animals have the lowest net production efficiencies

Each organism grows and produces offspring. The biomass it adds in this manner represents the organism’s production, and is also potentially food for other organisms. The ratio of the energy contained in this production to the total assimilated energy is referred to as net production efficiency, and is usually expressed as a percentage. Active, warm-blooded animals exhibit low net production efficiencies: those of birds are less than 1% and those of small mammals with high reproductive rates range up to 6% (Figure 6.10). These organisms use most of their assimilated energy to maintain salt balance, circulate blood, produce heat for thermoregulation, and move. In contrast, sedentary, cold-blooded animals, particularly aquatic species, channel as much as 75% of their assimilated energy into growth and reproduction.

Production efficiency can be based on total energy ingested rather than on energy assimilated. In this case, it is referred to as gross production efficiency, which is the product of assimilation efficiency and net production efficiency. Thus,

\[
\text{gross production efficiency} = \left( \frac{\text{assimilation}}{\text{ingestion}} \right) \times \left( \frac{\text{production}}{\text{assimilation}} \right) \times 100
\]

\[
= \left( \frac{\text{production}}{\text{ingestion}} \right) \times 100.
\]
Gross production efficiency represents the overall energetic efficiency of biomass production within a trophic level. Gross production efficiencies of warm-blooded terrestrial animals rarely exceed 5%, and those of some birds and large mammals fall below 1%. For insects, these efficiencies lie within the range of 5% to 15%, and for some aquatic animals they exceed 30%.

Production efficiency in plants

The concept of production efficiency differs somewhat between plants and animals because plants do not digest and assimilate food. For plants, net production efficiency is defined as the ratio of net production to gross production. Net production efficiency varies between 30% and 85% in plants, depending on environment and growth form. Rapidly growing plants in temperate zones—whether trees, old-field herbs, crop species, or aquatic plants—have uniformly high net production efficiencies, typically between 75% and 85%. Similar types of vegetation in the Tropics exhibit lower net production efficiencies (40–60%). As we might expect because of the higher temperature, respiration increases relative to photosynthesis in tropical latitudes.

Detritus food chains

Terrestrial plants, especially woody species, allocate much of their production to structures that are difficult to ingest, let alone digest. As a result, even though herbivores have specialized adaptations to extract energy from plants, they still tend to have low assimilation efficiencies. Consequently, most of the production of terrestrial plants is consumed as detritus—dead remains of plants and undigestible excreta of herbivores—by organisms specialized to attack wood, leaf litter, and fibrous plant egesta. This partitioning between herbivory and detritus feeding establishes two parallel food chains in terrestrial communities (Figure 6.11). The first originates when relatively large animals feed on leafy vegetation, fruits, and seeds; the second originates when relatively small animals and microorganisms consume detritus in the litter and soil. These separate food chains sometimes mingle considerably at higher trophic levels, but the energy of detritus tends to move into the food chain much more slowly than the energy assimilated by herbivores.

The relative importance of herbivore-based and detritivore-based food chains varies greatly among communities. Herbivores predominate in plankton communities,
detritivores in terrestrial communities. The proportion of net production that enters each of these food chains depends on the relative allocation of plant tissue between structural and supportive functions, on one hand, and growth and photosynthetic functions, on the other. A variety of studies have shown that herbivores consume 1.5–2.5% of the net primary production in temperate deciduous forests, 12% of that in old-field habitats, and 60–99% of that in plankton communities.

**Exploitation efficiency**

Because most biological production is consumed by one organism or another, little energy accumulates in any one trophic level. Rather, a balance is achieved between the production of biomass at one level and its consumption at another, so that the trophic structure of an ecosystem remains relatively constant. Viewed in this way, the ecological efficiency of a particular link in the food chain is equivalent to gross production efficiency. Under some conditions, however, production and consumption are not balanced, and energy may accumulate in an ecosystem, whether as organic matter in soil or as organic sediments in aquatic ecosystems. In such a case, we may say that exploitation efficiency—that is, the proportion of production on one trophic level that is consumed by organisms on the next higher level—is less than 100%. In this case, the overall ecological efficiency of the ecosystem is discounted by the exploitation efficiency:

\[
\text{ecological efficiency} = \text{exploitation efficiency} \times \text{gross production efficiency.}
\]

**Energy moves through ecosystems at different rates**

Ecological efficiencies describe what proportion of the energy assimilated by plants eventually reaches each higher trophic level of an ecosystem. The rate of transfer of energy between trophic levels or, inversely, its residence time in each trophic level, provides a second index to the energy dynamics of an ecosystem. For a given rate of production, the residence time of energy and the storage of energy in living biomass and detritus are directly related: the longer the residence time, the greater the accumulation of energy (Figure 6.12).

---

*Figure 6.12 Copepods and other zooplankton cycle the energy and nutrients in their algal food very rapidly. Photo (a) by M. I. Walker/Science Source/Photo Researchers; photo (b) by Roland Birke/Photo Researchers.*
The average residence time of energy at a particular trophic level equals the energy stored divided by the rate at which energy is converted into biomass:

\[
\text{residence time (yr)} = \frac{\text{energy stored in biomass (kJ per m}^2\text{)}}{\text{net productivity (kJ per m}^2\text{ per yr})}
\]

We may also calculate the residence time defined by this equation in terms of mass rather than energy, in which case it expresses the **biomass accumulation ratio**. Accordingly,

\[
\text{biomass accumulation ratio (yr)} = \frac{\text{biomass (kg per m}^2\text{)}}{\text{rate of biomass production (kg per m}^2\text{ per yr)}}
\]

Plants in humid tropical forests produce dry matter at an average rate of 1.8 kg per m\(^2\) per yr and have an average living biomass of 42 kg per m\(^2\). Inserting these values into the above equation, we obtain 23 years (42/1.8) for the average residence time of biomass in plants. Biomass accumulation ratios for primary producers may average from more than 20 years in forested terrestrial environments to less than 20 days in aquatic phytoplankton-based communities (\textit{\textbf{Figure 6.13}}). In all ecosystems, however, some energy remains for a long time, and some disappears quickly. For example, leaf eaters and root feeders consume much of the energy assimilated by forest trees during the year of its production, some of it within days of assimilation by the plant. Energy accumulated in the cellulose and lignin in the trunks of trees, on the other hand, may not be recycled for centuries.

\textit{\textbf{Figure 6.13}} underestimates the average residence time of energy in energy-containing organic matter because it does not include the accumulation of dead organic matter in leaf litter. The residence time of energy in accumulated litter can be determined by an equation analogous to that for the biomass accumulation ratio:

\[
\text{residence time (yr)} = \frac{\text{litter accumulation (g per m}^2\text{)}}{\text{rate of litter fall (g per m}^2\text{ per yr)}}
\]

For forested ecosystems, this value varies from 3 months in the humid Tropics to 1–2 years in dry and montane tropical habitats, 4–16 years in the southeastern United States, and more than 100 years in temperate mountains and boreal regions. Warm temperatures and the abundance of moisture in lowland tropical regions create optimal conditions for rapid decomposition of litter.
Ecosystem energetics summarizes the movement of energy through the ecosystem.

The flux of energy and the efficiency of its transfer describe certain aspects of the structure of an ecosystem: number of trophic levels, relative importance of detritus feeding and herbivory, steady-state values for biomass and accumulated detritus, and turnover rates of organic matter. The importance of these measures to understanding ecosystem function was argued by Lindeman, who constructed the first energy budget for an entire biological community—that of Cedar Bog Lake in Minnesota (Figure 6.14). The proliferation of energy flow studies during the 1950s and 1960s clearly reflected energy’s acceptance as a universal currency, a common denominator to which all populations and their acts of consumption could be reduced.

The overall energy budget of an ecosystem reflects a balance between income and expenditure, just as in a bank account. The ecosystem gains energy through the photosynthetic assimilation of light by autotrophs and through the transport of organic matter into the system from external sources. Organic material produced outside the system are referred to as allochthonous inputs (from the Greek *a-* “of the earth,” and *allo,* “other”); (Figure 6.15). Photosynthesis that occurs within the system is referred to as autochthonous production. In Root Spring, near Concord, Massachusetts, the herbivores assimilated energy at a rate of 0.31 W per m², but the net productivity of aquatic plants and algae was only 0.09 W per m²; the balance was transported into the spring in the form of leaves from nearby vegetation. In general, autochthonous production predominates in large rivers, lakes, and most marine ecosystems; allochthonous imports make up the largest part of energy flux in small streams and springs under the closed canopies of forests. Life in caves and the abyssal depths of the oceans, to which no light penetrates, subsists entirely on energy transported in from outside.

Lindeman constructed the Cedar Bog Lake energy budget from measurements of the harvestable net production at each of three trophic levels—plants and algae, herbivores, and carnivores—and from laboratory determinations of respiration and assimilation efficiencies. Lindeman’s findings were somewhat surprising in that the herbivores consumed only 20% of net primary production, and the carnivores consumed only 33% of the net production of the herbivores. These are extremely low exploitation efficiencies. The majority of plant and herbivore biomass that was not consumed ended up as organic sediments at the bottom of the lake.

Even with this sedimentation, the Cedar Bog Lake ecosystem achieved a 12% overall ecological efficiency of energy transfer between trophic levels. After comparing similar analyses of other aquatic communities, ecologist D. G. Kozlovski concluded that (1) assimilation efficiency increases at higher trophic levels; (2) net and gross production efficiencies decrease at higher trophic levels; and (3) ecological efficiency averages about 10%. A simple, and rather surprising, consequence of this 10% rule of thumb for ecological efficiencies is that only 1% of the total energy assimilated by plants and algae ends up as production on the third trophic level. Very little energy is available to support consumers at even higher trophic levels. Thus, as shown in Figure 6.1, the pyramid of energy narrows very quickly as one climbs from one trophic level to the next. For humans, who already command a large proportion of the total primary production of the earth for their own use, this means that food supplies can be increased primarily by eating lower on the food chain—that is, eating more plant products and fewer animal products.

Summary

1. An ecosystem is the entire complex of organisms and the physical environments they inhabit. It is also a giant thermodynamic machine that dissipates energy continu-
1 Figure 6.15 Some energy comes from allochthonous inputs. A small stream running through a forest receives much of its energy from detritus produced by trees. Photo by Mark Gamba/The Stock Market.

Usually in the form of heat. This energy initially enters the biological realm of the ecosystem via photosynthesis and plant production, which provide energy for animals and nonphotosynthetic microorganisms.

2. Charles Elton described biological communities in terms of feeding relationships, which he emphasized as a dominant organizing principle in community structure.

3. A. G. Tansley coined the term ecosystem to include the organisms and all the abiotic factors in a habitat.

4. Alfred J. Lotka provided a thermodynamic perspective on ecosystem function, showing that the movements and transformations of mass and energy conform to thermodynamic laws.

5. Raymond Lindeman, in 1942, popularized the idea of the ecosystem as an energy-transforming system.

6. The study of ecosystem energetics dominated ecology during the 1950s and 1960s, due largely to the influence of Eugene P. Odum, who championed energy as a common currency for describing ecosystem structure and function.

7. Gross primary production is the total energy assimilated by photosynthesis. Net primary production is the energy accumulated in plant biomass; hence it is gross primary production minus respiration.

8. Primary production can be measured by one or some combination of methods, such as harvesting, gas exchange (carbon dioxide in terrestrial habitats, oxygen in aquatic habitats), or assimilation of radioactive carbon (14C).

9. Photosynthetic efficiency (gross production divided by total incident light energy) during daylight periods in the growing season is 1–2% in most habitats.
PRACTICING ECOLOGY

CHECK YOUR KNOWLEDGE

How Long Are Food Chains?

The generalization that 10% of energy is passed from one trophic level to another is not a fixed law of ecological energetics. Because of a variety of complicating factors, the energy transferred from one level to another can be greater or less than 10%. Indeed, Pauly and Christensen (1995) summarized the energy transfer rate for 40 studies of trophic energy transfer in aquatic or marine communities, and found that the values varied from 2% to 24%. Ecological efficiencies are often lower in terrestrial compared to aquatic ecosystems. From this information, one might be led to ask how long the longest food chain in an ecosystem is.

If we can determine three pieces of information about ecosystem energetics, some simple calculations can shed light on how high a single population of consumers can feed on the energy available within the ecosystem. The required information includes: (1) the net primary production (NPP), which is the basic amount of energy that is available to be transferred to higher trophic levels; (2) the energy needed by a population of consumers (E); and (3) the average ecological efficiency for energy transfer from level to level within a food chain (Eff). A small portion of the energy may actually go through several trophic-level transfers, but it is important to note that these small amounts of energy are not sufficient to support the large predators that usually occupy the top of food chains.

For an ecosystem with some number of trophic levels \( n \), where plants are at level 1, the amount of energy available to a consumer at level \( n \) is denoted \( E(n) \). The energy available is determined by multiplying the net primary productivity by the ecological efficiencies leading up to level \( n \):

\[
E(n) = \text{NPP} / \text{Eff}^{n-1}.
\]

In this equation, \( \text{Eff} \) is the geometric mean of the efficiencies of energy transfer between each trophic level. Rearranging the equation, it is possible to solve for \( n \):

\[
n = 1 + \frac{\log [E(n)/\text{NPP}]}{\log (\text{Eff})}.
\]

CHECK YOUR KNOWLEDGE

1. Why is it important to understand the length of food chains?

2. What can food chains tell us about the cycling of energy and materials in an ecosystem?
Table 6.1 Rough estimates of food chain data from various field studies

<table>
<thead>
<tr>
<th>Community</th>
<th>Net primary production (kcal/m²/yr)</th>
<th>Consumer ingestion (kcal/m²/yr)</th>
<th>Ecological efficiency (%)</th>
<th>Number of trophic levels (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open ocean</td>
<td>500</td>
<td>0.1</td>
<td>25</td>
<td>7.1</td>
</tr>
<tr>
<td>Coastal marine</td>
<td>8,000</td>
<td>10.0</td>
<td>20</td>
<td>5.1</td>
</tr>
<tr>
<td>Temperate grassland</td>
<td>2,000</td>
<td>1.0</td>
<td>10</td>
<td>4.3</td>
</tr>
<tr>
<td>Tropical forest</td>
<td>8,000</td>
<td>10.0</td>
<td>5</td>
<td>3.2</td>
</tr>
</tbody>
</table>

Values are approximations based on many studies.

3. From the estimates presented in Table 6.1, what factor contributes most to variations in food chain length among ecosystems?

4. From the material in this and previous chapters, what biological factors account for variation in the factor you chose as your answer to Question 3?

5. Read the article from World Watch Magazine on Practicing Ecology on the Web at http://www.whfreeman.com/ricklefs about fishing down the food chain. What effects do you think overfishing will have on nutrient cycling and energy balance in the ocean?

Suggested Readings


Biological Communities: The Biome Concept

Climate is the major determinant of plant distribution.

Variations in topography and soils influence local distributions of plants.

Form and function are adapted to match the environment.

Climate defines the boundaries of terrestrial biomes.

Walter climate diagrams distinguish the major terrestrial biomes.

Temperate climate zones have average annual temperatures between 5°C and 20°C.

Boreal and polar climate zones have average temperatures below 5°C.

Equatorial and tropical climate zones have average temperatures exceeding 20°C.

The biome concept must be modified for aquatic systems.

Imagine that you are on safari on an East African savanna and one of your group shouts, 'Look over there, a cactus tree!' With your training in botany, you know immediately that this can't be so, because the cactus family (Cactaceae) is restricted to the New World. Yet the plant looks just like cacti you have seen in similar environments in Mexico (Figure 5.1). Closer inspection of the flowers shows that the African plant is a cactus look-alike, a member of the spurge family (Euphorbiaceae).

Your friend was fooled by a common phenomenon in biology, that of convergence. Convergence is the process by which unrelated organisms evolve a resemblance to each other in response to common environmental conditions. The leafless, thick, fleshy branches of the cactus and the cactus-like euphorb evolved as adaptations to reduce water loss in semiarid environments. The two plants look alike because they evolved in response to the same conditions, although they descended from different-looking ancestors. Natural selection and evolution are oblivious to the ancestry of a particular organism as long as it is capable of an adaptive response to a particular condition of the environment.

The principle of convergence explains why we can recognize an association between the forms of organisms and their particular environments anywhere in the world. Tropical rain forest trees have the same general attributes of form no matter where they are found or to which evolutionary lineage they belong. Trees that live in mangrove communities in the Tropics all have thick, leathery leaves, and many have root systems that project above the surface of the waterlogged sediments on which they grow. Several species of mangrove trees share a trait found nowhere else among plants—viviparity, or the germination and growth of seedlings before they are shed from the parent plant (Figure 5.2). Mangrove seedlings disperse by floating in salt water, and their ability to tolerate these conditions and become established on tidal mudflats is greatly enhanced by viviparity. Thus, although different species of
mangroves have evolved from many different lineages of terrestrial plants, they share certain traits because of convergent evolution adapting them to the stressful conditions of their environment.

Climate, topography, and soil—and parallel influences in aquatic environments—determine the changing character of plant and animal life over the surface of the earth. Although no two locations harbor exactly the same assemblage of species, we can group biological communities in categories based on their dominant plant forms, which give communities their overall character. These categories are referred to as biomes. The biome concept is a system of classifying biological communities and ecosystems based on similarities in their vegetational characteristics. Thus, biomes provide convenient reference points for comparing ecological processes in various kinds of communities and ecosystems.

The important terrestrial biomes of North America, for example, are tundra, boreal forest, temperate seasonal forest, temperate rain forest, shrubland, grassland, and subtropical desert. To the south in Mexico and Central America, the important biomes are tropical rain forest, tropical deciduous forest, and tropical savanna. As one would

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**Figure 5.1** Unrelated organisms can evolve similar structures in response to common environmental conditions. (a) A tree-forming cactus near Oaxaca, Mexico, and (b) an East African euphorb tree have converged in response to dry climate. Photos by R. E. Ricklefs.

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**Figure 5.2** Some traits are shared among many species in a particular environment. The seeds of the red mangrove *Rhizophora mangle* germinate while still attached to the tree (a), so that the developing seedling can become established rapidly (b). This pattern of viviparity occurs in many mangrove plants, but is unknown in other environments. Photos by R. E. Ricklefs.
expect, the geographic distributions of these biomes correspond closely to the major climate zones of North America. Although each biome is immediately recognizable by its distinctive vegetation, it is important to realize that different systems of classification make coarser or finer distinctions among biomes, and that the characteristics of one biome usually intergrade gradually into the next. The biome concept is nonetheless a useful tool that enables ecologists to work together to understand the structure and functioning of large ecological systems.

That biomes can be distinguished at all results from the simple fact that no single type of plant can endure the whole range of conditions at the surface of the earth. If plants had such broad tolerances of physical conditions, then the earth would be covered by a single biome. To the contrary, trees, for example, cannot grow under the dry conditions that shrubs and grasses can tolerate, simply because the physical structure, or growth form, of trees creates a high demand for water. The grassland biome exists because grasses and nongrass herbs (called forbs) can survive the cold winters typical, for example, of the Great Plains of the United States, the steppes of Russia, and the pampas of Argentina.

This matching of growth form and environment allows us to make generalizations about the distributions of life forms and the extents of biomes. If that were the whole of it, however, the study of ecology could simply focus on the biological relationships of individual organisms to their physical environments, and everything else in ecology would emanate from that point. We must remind ourselves that life is not so simple. In addition to physical conditions of the environment, two other kinds of factors influence the distributions of species and growth forms. The first of these is the myriad interactions between species—competition, predation, and mutualism—that determine whether a species or growth form can persist in a particular place. For example, grasses grow perfectly well in eastern North America, as we see along roadides and on abandoned agricultural lands, but trees are the dominant growth form there, and in the absence of disturbance, they exclude grasses, which cannot grow and reproduce under the deep shade of trees.

The second kind of factor is that of chance and history. The present biomes have developed over long periods, during which the distributions of landmasses, ocean basins, and climate zones have changed continually. Most species fail to occupy some perfectly suitable environments simply because they have not had the opportunity to get to all ends of the earth. This fact is amply illustrated by the successful introduction by humans of such species as European starlings and Monterey pines to parts of the world that had suitable environmental conditions but which were far outside the restricted natural distributions of these species.

In addition, evolution has proceeded along independent lines in different parts of the world, leading in some cases to unique biomes. Australia has been isolated from other continents for the past 40–50 million years, which accounts both for its unusual flora and fauna and for the absence of many of the kinds of plants and animals familiar to northerners. Because of its unique history, areas of Australia that have a climate like California’s could support the shrub vegetation—referred to as chaparral—or oak savanna found there, but instead are clothed with tall eucalyptus woodland. Similarities between chaparral and eucalyptus forest include drought and fire resistance, but the predominant plant growth forms in these areas of Australia and California differ, primarily because of historical accidents. We shall consider these biological and historical factors later in this book. As we shall see in the present chapter, the physical environment ultimately determines the character and distribution of the major biomes.

Climate is the major determinant of plant distribution

Species ranges are often limited by physical conditions of the environment. In terrestrial environments, temperature and moisture are the most important variables. The distributions of several species of maples in eastern North America show how these factors operate. Sugar maple, a common forest tree in the northeastern United States and southern Canada, is limited by cold winter temperatures to the north, by hot summer temperatures to the south, and by summer drought to the west (Figure 5.3). Attempts to grow sugar maples outside their normal range have shown that they cannot tolerate average monthly summer temperatures above about 24°C or winter temperatures below about −18°C. The western limit of the sugar maple, determined by dryness, coincides with the western limit of forest in eastern North America. Because temperature and rainfall interact to control the availability of moisture, sugar maples require less annual precipitation at the northern edge of their range (about 50 cm) than at the southern edge (about 100 cm). To the east, the range of the sugar maple stops abruptly at the Atlantic Ocean.

The distributions of the sugar maple and other tree-sized maple species—black, red, and silver—reflect differences in their ecological tolerances, or the range of conditions within which each species can survive (Figure 5.4). Where their geographic ranges overlap, the maples exhibit distinct preferences for certain local environmental conditions created by differences in soil and topography. Black maple frequently occurs in the same areas as the closely
Variations in topography and soils influence local distributions of plants

The distributions of plants reveal the effects of many factors, which vary over different scales of distance. You saw in Chapter 4 that topography may cause local variation in climate within small areas, and that geology may cause variation in soil characteristics at even finer scales. Characteristics of soil that influence the distributions of plants are referred to as edaphic factors. These factors vary most in mountainous regions, and ecologists frequently turn to the varied habitats of mountains to study plant distribution.

Along the coast of northern California, mountains create conditions that support a variety of plant communities, ranging from coastal chaparral to tall needle-leaved (coniferous) forests of Douglas fir and redwood. When localities are ranked on scales of available moisture, the distribution of each plant species among the localities reveals a distinct optimum—the type of site in which it does best (Figure 5.5). The coast redwood dominates the central portion of the moisture gradient and frequently forms pure stands. Cedar, Douglas fir, and madrone—a broad-leaved evergreen species with small, thick leaves—occur at the drier end of the moisture gradient. Big-leaf maple—a deciduous species—occupies the wetter end, along with the broad-leaved, evergreen California bay tree.

MORE ON THE WEB: Edaphic specialization. Why are some species of plants restricted to particular soil types?

Figure 5.3 The distributions of species are limited by the physical conditions of the environment. The red area shows the range of sugar maple in eastern North America. After H. A. Fowells, Silvis of Forest Trees of the United States, U.S. Department of Agriculture, Washington, D.C. (1965).

Related sugar maple, but usually on drier, better-drained soils higher in calcium content (and therefore less acidic). Silver maple occurs widely in the eastern United States, but especially on the moist, well-drained soils of the Ohio and Mississippi river basins. Red maple grows best either under wet, swampy conditions or on dry, poorly developed soils—that is, under extreme conditions that limit the growth of the other species.

Figure 5.4 Related species may differ in their ecological tolerances. The red areas show the ranges of black, red, and silver maples in eastern North America. The range of the sugar maple is outlined on each map to show the area of overlap. After H. A. Fowells, Silvis of Forest Trees of the United States, U.S. Department of Agriculture, Washington, D.C. (1965).
Form and function are adapted to match the environment

The adaptations of an organism cannot easily be separated from the environment in which it lives. Insect larvae from stagnant aquatic environments in ditches and sloughs can survive longer without oxygen than related species from well-aerated streams and rivers; species of marine snails that occur high in the intertidal zone, where they are frequently exposed to air, tolerate desiccation better than do species from lower levels. These are examples of specializations, or adaptations that suit organisms to particular ranges of environmental conditions. Species may be broad or narrow in their range of specialization. Those that have a relatively narrow range of tolerance are called specialists; those that have a wide range of tolerance are called generalists. Compare the leaves of deciduous forest trees growing in mesic environments with those of desert species. The former are typically broad and thin, providing a large surface area for light absorption. Desert trees have small, finely divided leaves (Figure 5.6)—or sometimes none at all. (Cacti rely

Figure 5.6 The leaves of desert plants are adapted to hot, dry conditions. These three species from the Sonoran Desert in Arizona all have adaptations that help them cope with desert conditions. Photos by R. E. Ricklefs.
### Table 5.1 Characteristics of chaparral and coastal sage vegetation in southern California

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Chaparral</th>
<th>Coastal sage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roots</td>
<td>Deep</td>
<td>Shallow</td>
</tr>
<tr>
<td>Leaves</td>
<td>Evergreen</td>
<td>Summer deciduous</td>
</tr>
<tr>
<td>Average leaf duration (months)</td>
<td>12</td>
<td>6.0</td>
</tr>
<tr>
<td>Average leaf size (cm²)</td>
<td>12.6</td>
<td>4.5</td>
</tr>
<tr>
<td>Leaf weight (g dry weight per dm²)*</td>
<td>1.8</td>
<td>1.0</td>
</tr>
<tr>
<td>Maximum transpiration (g H²O per dm²-per h)</td>
<td>0.34</td>
<td>0.94</td>
</tr>
<tr>
<td>Maximum photosynthetic rate (mg C per dm² per h)</td>
<td>3.9</td>
<td>8.3</td>
</tr>
<tr>
<td>Relative annual CO₂ fixation</td>
<td>49.8</td>
<td>46.8</td>
</tr>
</tbody>
</table>

*dm = decimeter (10 cm).

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Entirely on their stems for photosynthesis; their leaves are modified into thorns for protection.) Leaves heat up in the desert sun. Structures lose heat by convection most rapidly at their edges, where wind currents disrupt insulating boundary layers of still air. The more edges, the cooler the leaf, and the lower the water loss per unit of photosynthetic area. Small leaf size means that a large proportion of each leaf is close to its edge.

Coastal sage and chaparral plants in southern California have divergent forms and lifestyles due to the different levels of water stress in their respective environments (Table 5.1). Chaparral habitat ranges over higher elevations than that of the coastal sage and thus is cooler and moister. Both plant types are exposed to prolonged summer drought, but the soils present greater water stress in the sage habitat. Coastal sage plants typically have shallow roots and small, delicate leaves (Figure 5.7). It is not surprising, therefore, that most coastal sage species shed their leaves during the summer drought period. Chaparral species have deep roots that often extend through tiny cracks and fissures far into the bedrock; their thick evergreen leaves have a waxy outer covering that reduces water loss. Sage and chaparral plants are differently specialized. Black sage is active only during the rainy season of winter and early spring. Its leaves are designed for high rates of photosynthesis and high rates of growth, but they are dropped, and the plant becomes dormant, as soon as water becomes scarce in the soil. Black sage is thus specialized for the transient moisture of the Mediterranean climate winter. Chaparral and other chaparral species make use of the more limited water that lies deeper in the soil, but persists longer through the year.

However, they fail to cash in on the winter water bonanza in the upper layers of the soil the way that coastal sage species do.

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**Figure 5.7** The adaptations of plants match their environments. Profiles of the root systems of chamise (*Adenostoma fasciculatum*), a chaparral species (left), and black sage (*Salvia mellifera*), a member of the coastal sage community (right), show their differing adaptations to different levels of water stress. After H. Hellmers et al, *Ecology* 36:667–678 (1955).
MORE ON THE WEB: Living together on different resources. Where chaparral and coastal sage species grow together near the overlapping edges of their ranges, they exploit different parts of the environment.

Certain kinds of plants make the environment more favorable for themselves. As we saw in the last chapter, the tough needles of pine, spruce, and fir trees produce abundant organic acids when they decompose. This acid leaches minerals from the soil under podsolizing conditions and makes the soils even poorer than they were. The needle-leaved trees tolerate these conditions better than deciduous trees. Thus, the different effects of these two types of vegetation on soil conditions reinforce the boundary between deciduous and needle-leaved forest.

These examples drive home the important point that growth form is closely related to the physical conditions of the environment. With respect to terrestrial plants, larger growth forms are often competitively superior because they shade smaller growth forms, but they also require moister soils. Thus, we should not be surprised that the availability of water is the predominating factor determining the character and distribution of terrestrial biomes. Because heat influences moisture stress and moisture availability, temperature and precipitation together are the important determinants of the boundaries of biomes.

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**Climate defines the boundaries of terrestrial biomes**

One of the most widely adopted climate classification schemes is the climate zone system developed by the German ecologist Heinrich Walter. This system, which has nine major divisions, is based on the annual course of temperature and precipitation. The important attributes of climate and the characteristic vegetation in each of these zones are presented in Figure 5.8. The values of temperature and precipitation used to define climate zones correspond to conditions of moisture and cold stress that are particularly important determinants of plant form. For example, within the Tropics, the tropical climate zone is distinguished from the equatorial climate zone by the occurrence of water stress.

<table>
<thead>
<tr>
<th>Biome name</th>
<th>Climate zone</th>
<th>Vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical rain forest</td>
<td>Equatorial: Always moist and lacking temperature seasonality</td>
<td>Evergreen tropical rain forest</td>
</tr>
<tr>
<td>Tropical seasonal forest, savanna</td>
<td>Tropical: Summer rainy season and &quot;winter&quot; dry season</td>
<td>Seasonal forest, scrub, or savanna</td>
</tr>
<tr>
<td>Subtropical desert</td>
<td>Subtropical (hot deserts): Highly seasonal, arid climate</td>
<td>Desert vegetation with considerable exposed surface</td>
</tr>
<tr>
<td>Woodland/shrubland</td>
<td>Mediterranean: Winter rainy season and summer drought</td>
<td>Scrubophyllous (drought-adapted), frost-sensitive shrublands and woodlands</td>
</tr>
<tr>
<td>Temperate rain forest</td>
<td>Warm temperate: Occasional frost, often with summer rainfall maximum</td>
<td>Temperate evergreen forest, somewhat frost-sensitive</td>
</tr>
<tr>
<td>Temperate seasonal forest</td>
<td>Temperate: Occasional frost, often with summer rainfall maximum</td>
<td>Frost-resistant, deciduous, temperate forest</td>
</tr>
<tr>
<td>Temperate grassland/desert</td>
<td>Temperate: Moderate climate with winter freezing</td>
<td>Grasslands and temperate deserts</td>
</tr>
<tr>
<td>Boreal forest</td>
<td>Boreal: Cold temperate with cool summers and long winters</td>
<td>Evergreen, frost-hardy needle-leaved forest (taiga)</td>
</tr>
<tr>
<td>Tundra</td>
<td>Polar: Very short, cool summers and long, very cold winters</td>
<td>Low, evergreen vegetation, without trees, growing over permanently frozen soils</td>
</tr>
</tbody>
</table>

| Figure 5.8 | Heinrich Walter classified the climate zones of the world according to the annual course of temperature and precipitation. Biome names for these zones under Whittaker's classification scheme are shown in the left-hand column. |
during a pronounced dry season. Subtropical climate zones are perpetually water-stressed. The typical vegetation of these three climate zones is evergreen rain forest, deciduous forest or savanna, and desert scrub, respectively. We will look at Walter's climate zones in more detail below.

Cornell University ecologist Robert H. Whittaker took a somewhat different approach to the relationship between terrestrial biomes and climatic variables. Whittaker defined biomes by their vegetation structure, and then devised a simple climate diagram on which he plotted the approximate boundaries of the major biomes with respect to average temperature and precipitation (Figure 5.9). The result is similar to Walter's scheme. Plotted on Whittaker's diagram, most locations on earth fall within a triangular area whose three corners represent warm-moist, warm-dry, and cool-dry climates. Cold regions with high rainfall are rare because water does not evaporate rapidly at low temperatures and because the atmosphere in cold regions holds little water vapor.

At tropical and subtropical latitudes, where mean temperatures range between 20°C and 30°C, vegetation ranges from rain forest, which is wet throughout the year and generally receives more than 250 cm (about 100 inches) of rain annually (Walter’s equatorial climate zone), to desert, which generally receives less than 50 cm of rain (Walter’s subtropical climate zone). Intermediate climates support seasonal forests (150–250 cm rainfall), in which some or all trees lose their leaves during the dry season, or scrub and savannas (50–150 cm rainfall).

Plant communities at temperate latitudes follow the pattern of tropical communities with respect to rainfall, having four vegetation types: rain forest, seasonal forest, woodland/shrubland, and grassland/desert. At high latitudes, however, precipitation varies so little from one locality to another that vegetation types are poorly differentiated by climate. Where mean annual temperatures are below −5°C, all plant communities may be lumped into one type: tundra.

Toward the drier end of the precipitation spectrum within each temperature range, fire plays a distinct role in shaping plant communities. The influence of fire is greatest where moisture availability is intermediate and highly seasonal. Deserts and moist forests burn infrequently; deserts rarely accumulate enough plant debris to fuel a fire, and moist forests rarely dry out enough to be highly flammable.

Figure 5.9 Whittaker's biomes are delineated according to average temperature and precipitation. Main diagram: Whittaker plotted the boundaries of observed vegetation types with respect to average temperature and precipitation. In climates intermediate between those of forest and desert biomes, fire, soil, and climatic seasonality determine whether woodland, grassland, or shrubland develops. Inset: Average annual temperature and precipitation for a sample of localities more or less evenly distributed over the land area of the earth. Most of the points fall within a triangular region that includes the full range of climates, excluding those of high mountains. From R. H. Whittaker, Communities and Ecosystems, 2d ed., Macmillan, New York (1975).
Grassland and shrub biomes have the combination of abundant fuel and seasonal drought that make fire a frequent visitor. In these biomes, fire is a dominating factor to which all community members must be adapted and, indeed, for which many are specialized: some species require fire for germination of their seeds and growth of their seedlings. In many areas of African savanna and North American prairie, frequent fires kill the seedlings of trees and prevent the encroachment of forests, which could be sustained by the local precipitation if it were not for fire. Burning favors perennial grasses and forbs with extensive root systems that can survive underground. After an area has burned over, grass and forb roots sprout fresh shoots and quickly establish new vegetation above the surface of the soil. In the absence of frequent fires, tree seedlings become established and eventually shade out savanna and prairie vegetation.

As in all classification systems, exceptions appear, and boundaries between biomes are fuzzy. Moreover, not all plant growth forms correspond with climate in the same way; as mentioned earlier, Australian eucalyptus trees form forests under climatic conditions that support only shrubland or grassland on other continents. Finally, plant communities reflect factors other than temperature and rainfall. Topography, soils, fire, seasonal variations in climate, and herbivory all leave their mark. The overview of the major terrestrial biomes at the end of this chapter emphasizes the distinguishing features of the physical environment and how these are reflected in the form of the dominant plants.

More on the Web

Biomes and animal forms. Why are biome definitions based on the predominant life forms of plants, rather than referring to their animal inhabitants?

More on the Web

Characterizing climate. Integrated descriptions of climate emphasize the interaction of temperature and availability of water.

Walter climate diagrams distinguish the major terrestrial biomes

Temperature and precipitation interact to determine conditions and resources available for plant growth. It is not surprising, then, that the distributions of the major biomes of the earth follow patterns of temperature and precipitation. Because of this close relationship, it is important to describe climate in a manner that reflects the availability of water, taking into consideration changes in temperature and precipitation through the year.

Heinrich Walter developed a climate diagram that conveys seasonal periods of water deficit and abundance and therefore permits ecologically meaningful comparisons of climates between localities (Figure 5.10). The Walter climate diagram portrays average monthly temperature and precipitation throughout the course of a year. The vertical scales of temperature and precipitation are adjusted so that when precipitation is higher than temperature on the diagram, water is plentiful, and plant production is limited primarily by temperature. Conversely, when temperature is higher than precipitation, plant production is limited by availability of water. Walter’s scales equate 20 mm of monthly precipitation with 10°C in temperature. Thus, as a rule of thumb, at an average temperature of 20°C, 40 mm of monthly precipitation provides sufficient moisture for plant growth. We’ll use Walter climate diagrams to compare the biomes characterized below.

Climate diagrams for locations in each of Walter’s climate zones are shown in Figure 5.11. The seasonal distributions of wet and dry periods differ among climate

As a rule of thumb, about 20 mm of monthly precipitation for each 10°C in temperature provides sufficient moisture for plant growth. This occurs wherever the precipitation line (blue) is above the temperature line (orange) on this graph.

These months of above-freezing temperatures are the effective growing season for plants.

Figure 5.10 Walter climate diagrams allow ecologically meaningful comparisons between localities. These diagrams portray the annual progression of monthly mean temperature (left-hand scale) and precipitation (right-hand scale).
Figure 5.11 Each climate zone has a typical seasonal pattern of temperature and precipitation. Climate diagrams for representative locations in each of the nine major terrestrial climate zones are shown. The dashed blue line at the top of the graphs for climate zones I and V indicates monthly precipitation exceeding 100 mm all year long. From H. Walter and S.-W. Breckle, Ecological Systems of the Geobiosphere, I, Ecological Principles in Global Perspective, Springer-Verlag, Berlin (1983).
Figure 5.12 Different localities within the same climate zone have similar climate patterns. Climate diagrams of three localities within each of three terrestrial climate zones show consistency within zones. The biomes found at all three localities within each zone are the same. From H. Walter and S.-W. Breckle, Ecological Systems of the Geobiosphere, Ecological Principles in Global Perspective, Springer-Verlag, Berlin (1985).
zones at lower latitudes. Equatorial climates (climate zone I) like that at Andagoya, Colombia, are aseasonal; that is, they are warm and wet throughout the year. Subtropical climates (III), such as that of Chiclayo, Peru, are warm and dry throughout the year. Tropical climates (II, Brasilia, Brazil) are characterized by summer rains, and Mediterranean climates (IV, Lisbon, Portugal) by winter rains. The climate of Sitka, Alaska (warm temperate, VI), is wet and mild throughout the year and supports an evergreen forest type of vegetation.

Seasonality of temperature is a major factor in climate zones VI–IX, which occur at middle and high latitudes. Precipitation is typically low, but because of the low temperatures, moisture is generally not limiting during the short summer growing season. Continental climates (VII, Salt Lake City, Utah) are typically dry throughout the year and become warm enough in summer to develop significant water stress. Such areas, which include much of the Great Basin of the western United States, support shrubby desert vegetation.

In striking contrast to the variation in patterns of temperature and precipitation between climate zones, different localities within the same climate zone have similar climates, regardless of their geographic location (Figure 5.12). For example, the tropical climates of Brasilia (Brazil), Salisbury (Zimbabwe), and Darwin (Australia) all share the even year-round warm temperatures and summer rainfall typical of climate zone II. And each of these areas supports deciduous forest vegetation grading into savanna where precipitation is particularly low. The similar patterns of climate within each climate zone support characteristic vegetation that defines the biome type and makes it easy for us to recognize the general attributes of ecosystems in any region.

The worldwide distribution of biome types follows patterns of temperature and precipitation over the earth (Figure 5.13). We shall consider the biomes and general ecological characteristics of each of the major climate zones in the series of vignettes that follow. Because most readers of this book live in the so-called temperate zone, it is a good place to start.

![Figure 5.13 Global distribution of the major biomes.](image-url)
Temperate climate zones have average annual temperatures between 5°C and 20°C

Temperate climates are characterized by average annual temperatures in the range of 5°C–20°C at low elevations. Such climates are distributed approximately between 30°N and 45°N in North America and between 40°N and 60°N in Europe, which is warmed by the Gulf Stream current. Frost is an important factor throughout the temperate zone, perhaps even a defining one. Within the temperate zone, biomes are differentiated primarily by total amounts and seasonal patterns of precipitation, although the length of the frost-free season, which is referred to as the growing season, and the severity of frost also are important.

**Figure 5.14** Major features of the temperate seasonal forest biome. Photos by R. E. Ricklefs.
acid and moderately leached, and are brown in color owing to abundant organic humus. Deciduous trees are the dominant plant growth form. The vegetation often includes a layer of smaller trees and shrubs beneath the dominant trees, as well as herbaceous plants on the forest floor, many of which complete their growth and flower early in spring, before the trees have fully leafed out.

Warmer and drier parts of the temperate seasonal forest biome, especially where soils are sandy and nutrient-poor, tend to develop needle-leaved forests, dominated by pines. The most important of these formations in North America are the pine forests of the coastal plains of the Atlantic and Gulf states of the United States; pine forests also occur at higher elevations in the western United States. Because of the warm climate in the southeastern United States, soils are usually lateritic and have low nutrient levels. The low availability of nutrients and water favors evergreen, needle-leaved trees, which resist desiccation and give up nutrients slowly because they retain their needles for several years. Because soils tend to be dry, fires are frequent, and most species are able to resist fire damage.

**Temperate rain forest biome (climate zone V)**

In warm temperate climates near the coast in the northwestern North America, and also in southern Chile, New Zealand, and Tasmania, mild winters, heavy winter rains, and summer fog create conditions that presently support extremely tall evergreen forests (Figure 5.15). In North America these forests are dominated toward the south by coast redwood and toward the north by Douglas fir. Trees are typically 60–70 m high and may grow to over 100 m. It is not well understood why these sites are dominated by needle-leaved trees, but the fossil record shows that these plant formations are very old and that they are remnants

![Biome: Temperate rain forest](image)

![Sitka, Alaska](image)

**Figure 5.15** Major features of the temperate rain forest biome. Photo (a) by Photosphere Images/PictureQuest; photo (b) by Tom & Pat Leeson Photo Researchers.
of forests that were vastly more extensive during the Mesozoic era, as recently as 70 million years ago. In contrast to that of rain forests in the Tropics, the diversity of temperate rain forests typically is very low.

**Temperate grassland/desert biome**

(climate zone VII)

In North America, grasslands develop within continental climate zones, where the rainfall ranges between 30 and 85 cm per year ([Figure 5.16]). Summers are hot and wet; winters are cold. The growing season increases from north to south from about 120 to 300 days. These grassland biomes are often called prairies. Extensive grasslands are also found in central Asia, where they are called steppes. Because precipitation is low, organic detritus does not decompose rapidly, and the soils are rich in organic matter. Because of their low acidity, prairie soils, which belong to the mollisol group, are not heavily leached and tend also to be rich in nutrients. The vegetation is dominated by grasses, which grow to over 2 m in the moister parts of the grassland biome and to less than 0.2 m in more arid regions. There are also abundant non-grass forbs. Fire is a dominant influence in grasslands, particularly where the habitat dries out during the late summer. Most grassland species have fire-resistant underground stems, or rhizomes, from which shoots resprout, or they have fire-resistant seeds.

Where precipitation ranges between 25 and 50 cm per year, and winters are cold and summers are hot, grasslands grade into deserts. The temperate desert biome covers most of the Great Basin of the western United States. In the northern part of the region, sagebrush (Artemisia) is the dominant plant, whereas toward the south and on somewhat moister soils, widely spaced juniper and pinon trees predominate, forming open woodlands of less than 10 m stature with sparse coverings of grass. In these temperate deserts, the evaporation and transpiration potential of the habitat exceeds precipitation during most of the
year, so soils are dry and little water percolates through them to form streams and rivers. The soils tend to accumulate, at depths to which water usually penetrates, calcium carbonate leached from the surface layers. Fires occur infrequently in temperate deserts because the habitat produces little fuel. However, because of the low productivity of the plant community, grazing can exert strong pressure on vegetation and may even favor the persistence of shrubs, which are not good forage. Indeed, many dry grasslands in the western United States and elsewhere in the world have been converted to deserts by overgrazing.

Woodland/shrubland biome (climate zone IV)

The Mediterranean climate zone is distributed at 30°–40° north and south of the equator—somewhat higher in Europe—on the western sides of continental landmasses where cold-water currents and winds coming off the continents dominate the climate. Mediterranean climates are found in southern Europe and southern California in the Northern Hemisphere and in central Chile, the Cape region of South Africa, and southwestern Australia in the Southern Hemisphere. Mediterranean climates are characterized by mild winter temperatures, winter rain, and summer drought. These climates support thick, evergreen shrubby vegetation, 1–3 m in height, with deep roots and drought-resistant foliage (Figure 5.17). The small, durable leaves of typical Mediterranean-climate plants have earned them the label of **sclerophyllous** (hard-leaved) vegetation. Fires are frequent in woodland/shrubland biomes, and most plants have either fire-resistant seeds or root crowns that respout soon after a fire.

Subtropical desert biome (climate zone III)

What people call deserts varies tremendously. Many people refer to the dry areas of the Great Basin and of central
Asia as deserts—the Gobi Desert is a name familiar to most of us. But the climates of these "deserts" fall within Walter’s continental climate zone, characterized by low precipitation and cold winters. In contrast, subtropical deserts (Figure 5.18) develop at latitudes of 20°–30° north and south of the equator in areas having high atmospheric pressure, very sparse rainfall (less than 25 cm), and generally long growing seasons. Because of the low rainfall, the soils of subtropical deserts (aridosols) are shallow, virtually devoid of organic matter, and neutral in pH. Impermeable hardpans of calcium carbonate often develop at the limits of water penetration—depths of a meter or less. Whereas sagebrush dominates Great Basin (continental climate) deserts, creosote bush takes its place in the subtropical deserts of the Americas. Moister sites support a profusion of succulent cacti, shrubs, and small trees, such as mesquite and paloverde. Most subtropical deserts receive summer rainfall, during which many herbaceous plants sprout from dormant seeds, grow quickly, and reproduce before the soils dry out again. Many of the plants in subtropical deserts are not frost-tolerant. Species diversity is usually much higher than it is in temperate arid lands.

Boreal and polar climate zones have average temperatures below 5°C

Boreal forest biome (climate zone VIII)

Stretching in a broad belt centered at about 50°N in North America and about 60°N in Europe and Asia lies the boreal forest biome, often called taiga (Figure 5.19). The average annual temperature is below 5°C, and winters are severe. Precipitation is in the range of 40–100 cm, and because evaporation is low, soils are moist throughout most of the growing season. The vegetation consists of seemingly endless dense stands of 10–20 m high ever-

![Figure 5.18 Major features of the subtropical desert biome. Photos by R. E. Ricklefs.](image-url)
green needle-leaved trees, mostly spruce and fir. Because of the low temperatures, litter decomposes very slowly and accumulates at the soil surface. The needle-leaf litter produces high levels of organic acids, so the soils are acid, strongly podzolized, and generally of low fertility. Growing seasons are rarely as much as 100 days, and often half that. The vegetation is extremely frost-tolerant, as temperatures may reach −60°C during the winter. Species diversity is very low.

**Tundra biome (climate zone IX)**

To the north of the boreal forest, in the so-called polar climate zone, lies the arctic tundra, a treeless expanse underlain by permanently frozen soil, or permafrost (Figure 5.19). The soils thaw to a depth of 0.5–1 m during the brief summer growing season. Precipitation is generally less and often much less, than 60 cm, but in low-lying areas where drainage is prevented by the permafrost, soils may remain saturated with water throughout most of the growing season. Soils tend to be acid because of their high organic matter content, and they are very low in nutrients. In this nutrient-poor environment, plants hold their foliage for years. Most plants are dwarf, prostrate, woody shrubs, which grow low to the ground to gain protection under the winter blanket of snow and ice. Anything protruding above the surface of the snow is sheared off by blowing ice crystals. For most of the year, the tundra is an exceedingly harsh environment, but during the 24-hour-long summer days, the rush of activity in the tundra biome testifies to the remarkable adaptability of life.

At high elevations within temperate latitudes, and even within the Tropics, one finds vegetation resembling that of the arctic tundra and even including some of the same species, or their close relatives. These areas above the tree line occur most broadly in the Rocky Mountains of North America and, especially, on the Tibetan Plateau of central Asia. In spite of their similarities, alpine and arctic tundra

![Biome: Boreal forest](image)

**Figure 5.19** Major features of the boreal forest biome. Photos by R. E. Ricklefs.
have important points of dissimilarity as well. Areas of alpine tundra generally have warmer and longer growing seasons, higher precipitation, less severe winters, greater productivity, better-drained soils, and higher species diversity than arctic tundra. Still, as in the high-latitude tundra, harsh winter conditions ultimately limit the growth of trees.

Equatorial and tropical climate zones have average temperatures exceeding 20°C

Within 20° of the equator, the temperature varies more throughout the day than average monthly temperatures vary throughout the year. Average temperatures at sea level generally exceed 20°C. Environments within tropical latitudes are distinguished by differences in the seasonal pattern of rainfall. This creates a continuous gradient of vegetation from wet, aseasonal rain forest through seasonal forest, scrub, savanna, and desert. Frost is not a factor in tropical biomes, even at high elevations, and tropical plants and animals generally cannot tolerate freezing.

Tropical rain forest biome (climate zone I)

Climates under which tropical rain forests develop are always warm and receive at least 200 cm of precipitation throughout the year, with not less than 10 cm during any single month. These conditions prevail in three important regions within the Tropics (Figure 5.21). First, the Amazon and Orinoco basins of South America, with additional areas in Central America and along the Atlantic coast of Brazil, constitute the American rain forest. Second, the area from southernmost West Africa and extending eastward through the Congo River basin constitutes the African rain forest. Third, the Indo-Malayan rain forest covers parts of Southeast Asia (Vietnam, Thailand, and the Malay Peninsula), the islands between Asia and Australia, includ-
ing the Philippines, Borneo, and New Guinea, and the Queensland coast of Australia.

The tropical rain forest climate often exhibits two peaks of rainfall centered around the equinoxes, corresponding to the periods when the intertropical convergence lies over the equatorial region. Rain forest soils are typically old and deeply weathered oxisols. Because they are relatively devoid of humus and clay, they take on the reddish color of aluminum and iron oxides and have poor ability to retain nutrients. In spite of the low nutrient status of the soils, rain forest vegetation is dominated by a continuous canopy of tall evergreen trees rising to 30–40 m, with occasional emergent trees, which rise above the canopy to heights of 55 m. Because water stress on emergents is great due to their height and exposure, they are often deciduous, even in an evergreen rain forest. Tropical rain forests have several understory layers beneath the canopy, containing smaller trees, shrubs, and herbs, but these are usually quite sparse because so little light penetrates the canopy. Climbing lianas, or woody vines, and epiphytes, plants that grow on the branches of other plants and are not rooted in soil (also called air plants; see Figure 1.7), are prominent in the forest canopy itself. Species diversity is higher than anywhere else on earth.

Per unit of area, the biological productivity of rain forests exceeds that of any other terrestrial biome, and their standing biomass exceeds that of all other biomes except temperate rain forests. Because of the continuously high temperatures and abundant moisture, plant litter decomposes quickly, and vegetation immediately takes up the released nutrients. This rapid nutrient cycling supports the high productivity of the rain forest, but also makes the rain forest ecosystem extremely vulnerable to disturbance. When tropical rain forests are cut, many of the nutrients are cycled off in logs or go up in smoke. The vulnerable soils erode rapidly and fill the streams with silt. In many cases, the environment degrades rapidly and the landscape becomes unproductive.
Tropical seasonal forest/savanna biomes (climate zone II)

Within the Tropics, but beyond 10° from the equator, tropical climates often exhibit a pronounced dry season, corresponding to winter at higher latitudes. This is Walter’s tropical climate zone. Seasonal forests in the Tropics have a preponderance of deciduous trees that shed their leaves during the season of water stress. Increasingly longer and more severe dry seasons generally result in vegetation with lower stature and more thorns to protect leaves from grazing. Progressive aridity leads to dry forest, thorn forest, and finally true deserts in the rain shadows of mountain ranges or along coasts with cold ocean currents running alongside. As in wetter tropical environments, soils tend to be strongly laterized and poor in nutrients.

Savannas are grasslands with scattered trees, and they spread over large areas of the dry Tropics, especially at high elevations in East Africa. Rainfall is typically 90–150 cm per year, but the driest three or four months receive less than 5 cm each. Fire and grazing undoubtedly play important roles in maintaining the character of the savanna biome, particularly in wetter regions, as grasses can persist better than other forms of vegetation under both influences. Often when grazing and fire are controlled within a savanna habitat, dry forest begins to develop. Vast areas of African savanna owe their character to the influence of human activity, including burning, over many millennia.

The biome concept must be modified for aquatic systems

The biome concept was developed for terrestrial ecosystems, where the growth form of the dominant vegetation

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**Figure 5.22** Major features of the tropical seasonal forest/savanna biome. Photos by R. E. Ricklefs.
reflects climatic conditions. Moreover, terrestrial and aquatic ecologists have generated concepts and descriptive terms for ecological systems independently. As a consequence, aquatic "biomes" do not exist in the sense in which the term is applied to terrestrial systems. Indeed, defining aquatic biomes according to vegetation would be impossible, because the primary producers in many aquatic systems are single-celled algae, which do not form "vegetation" with a characteristic structure. As a result, classifications of aquatic systems have been based primarily on such physical characteristics as salinity, water movement, and depth. The major kinds of aquatic environments are streams, lakes, estuaries, and oceans, and each of these can be subdivided further with respect to many factors. Streams form wherever precipitation exceeds evaporation and excess water drains from the surface of the land. Within small streams, ecologists distinguish areas of riffles, where water runs rapidly over a rocky substrate, and pools, which are deeper stretches of slowly moving water (Figure 5.23). Water is well oxygenated in riffles, whereas pools tend to accumulate silt and organic matter. Production in small streams is often dominated by allochthonous material—organic material, such as leaves, that enters the aquatic system from the outside. Streams are usually bordered by a riparian zone of terrestrial vegetation that is influenced by seasonal flooding and elevated water tables. Streams grow with distance as they join together to form rivers. The larger a river, the more of its production is home-grown, or autochthonous.

A river continuum concept has grown up around the continuous change in environments and ecosystems between the headwaters and the mouth of a fluvial system. As one moves downstream, water is warmer, more slowly flowing, and richer in nutrients; ecosystems are more complex and generally more productive. Fluvial systems, as rivers are called, are also distinguished by the fact that currents continually move material, including animals and plants, downstream. To maintain a fluvial system in a steady state, this so-called downstream drift must be balanced by active movement of animals upstream, by the productivity of the upstream portions of the system, and by input of allochthonous materials.

Lakes form in any kind of depression. For the most part, such bodies of water are the products of recent glaciation, which leaves behind gouged-out basins and blocks of ice buried in glacial deposits, which eventually melt. Lakes are also formed in geologically active regions, such as the Rift Valley of Africa, where vertical shifting of blocks of the earth's crust creates basins within which water accumulates. Broad river valleys, such as those of the Mississippi and Amazon, have oxbow lakes, which are broad bends of the former river, cut off by shifts in the main channel.

![Figure 5.23 Conditions of a stream environment differ in pools and riffles. Photo by Ed Reschke/Peter Arnold.](image)

An entire lake could be considered a biome, but it is usually subdivided into regions, each of which has its own character. The littoral zone is the shallow zone around the edge of a lake or pond within which one finds rooted vegetation, such as water lilies and pickerel weed (Figure 5.24). The open water beyond the littoral zone is the limnetic zone, where primary production is accomplished by floating single-celled algae, or phytoplankton. Lakes may also be subdivided vertically on the basis of light penetration and the formation of thermally stratified layers of water (see Chapter 4). The sediments at the bottoms of lakes and ponds constitute the benthic zone, which provides habitat for burrowing animals and microorganisms.

Estuaries are found at the mouths of rivers, especially where the outflow is partially enclosed by landforms or barrier islands (Figure 5.25). Estuaries are unique because of their mix of fresh and salt water. In addition, the nutrients carried by rivers and the rapid exchange between surface waters and sediments contribute to extremely high biological productivity. Because estuaries tend to be shallow areas within which sediments are deposited, they are often edged by extensive tidal marshes. Indeed, the marshes that surround many estuaries are among the most productive habitats on earth, owing to a combination of high
nutrient levels and freedom from water stress. These marshes contribute abundant additional organic matter to the estuarine ecosystem, which in turn supports abundant populations of estuarine and marine species.

Oceans cover the largest portion of the surface of the earth. Beneath the surface of the water lies an immensely complex realm harboring a great variety of ecological conditions and ecosystems. Variation in marine environments comes from temperature, depth, current, substrate, and, at the edge of the seas, tides.

Many marine ecologists categorize oceanic zones according to depth. The littoral zone (also called the intertidal zone) extends between the highest and lowest tidal levels and so, to a varying extent depending on position within the intertidal range, is exposed periodically to air. The rapid changes in ecological conditions within the littoral zone often create sharp zonation of organisms according to their ability to tolerate the stresses of terrestrial conditions. Beyond the range of the lowest tide level, the neritic zone extends to depths of about 200 m, which corresponds to the edge of the continental shelf. Often the neritic zone is a region of high productivity because the sunlit surface layers of water are not far removed from the regeneration of nutrients in the sedi-
ments below. Strong waves can move suspended materials from depths of 100–200 m to the surface. Beyond the neritic zone, the seafloor drops rapidly to the great depths of the oceanic zone. Here, production usually is strictly limited by low availability of nutrients. The seafloor beneath the oceanic zone constitutes the benthic zone. Both the neritic and the oceanic zones may be subdivided vertically into a superficial photic zone, in which there is sufficient light for photosynthesis, and an aphotic zone without light, in which organisms depend mostly on organic material raining down from above.

Whereas the open ocean has been compared to a desert, coral reefs are like tropical rain forests, both in the richness of their biological production and the diversity of their inhabitants (Figure 5.28). Reef-building corals occur in shallow waters of warm oceans, usually where water temperatures remain above 20°C year-round, and often surround volcanic islands. The high production of the reef is fed by nutrients eroding from the rich volcanic soil and by deep-water currents forced upward by the profile of the island. Corals are doubly productive because photosynthetic algae within their tissues generate the carbohydrate energy base for the coral's phenomenal rates of growth.

The unique qualities that characterize each biome or aquatic ecosystem are manifested in most aspects of ecosystem structure and function. The most direct way to evaluate these attributes is to measure the flux of energy through the ecosystem and the cycling of nutrients within the ecosystem. These aspects of ecological structure and function, and how they differ among the terrestrial biomes and aquatic ecosystems, are the subjects of the next part of this book.
Summary

1. The geographic distributions of plants on continental scales are determined primarily by climate, whereas local distributions within regions may vary according to topography and soils.

2. Climate profoundly affects the evolution of plants and animals, which become specialized to particular conditions of the physical environment. As a consequence, each climatic region has characteristic types of vegetation that differ in growth form, leaf morphology, and seasonality of foliage.

3. Because plant growth form is directly related to climate, we can match major types of vegetation to temperature and precipitation. This relationship emphasizes the way in which temperature and precipitation interact to determine water availability. Major vegetation types can be used to classify ecosystems into categories called biomes. Soil, climatic seasonality, fire, and grazing additionally influence the character of biomes.

4. Two major approaches to the classification of biomes are the climate zone approach of Walter and the vegetation approach exemplified by Whittaker. The first classifies regions on the basis of the climate within which a characteristic type of vegetation normally develops. The second classifies regions according to vegetation, which generally reflects the local climate.

5. Climate zones and biomes are broadly divided into tropical, temperate, boreal, and polar zones according to their latitudes north and south of the equator. Principally temperature, and the adaptations of plants to temperature, distinguish these latitudinal bands. Within these latitudinal zones, the annual level of precipitation and its seasonality further distinguishes biomes.

6. Within temperate climate zones, the major biomes are seasonal forest, rain forest, and grassland/desert. At lower latitudes within temperate regions, are Mediterranean-climate woodlands and shrublands. Subtropical deserts lie between temperate and tropical climate zones.

7. At high latitudes, one encounters boreal forests, usually consisting of needle-leaved trees with persistent foliage and low growth rates on nutrient-poor, acid soils, and tundra, a treeless biome that develops on permanently frozen soils, or permafrost.

8. Tropical climate zones are dominated by evergreen rain forest and seasonal forest, which grades from partly to fully deciduous to thorn forest in drier climates, and sometimes savanna, a grassland with scattered trees that is maintained by fire and grazing pressure.

9. Aquatic systems are not classified as biomes because they lack the equivalent of terrestrial vegetation. One may, however, distinguish streams, lakes, estuaries, and oceans, and each of these systems can be further subdivided on the basis of other factors, such as depth of water.

PRACTICING ECOLOGY

Checking Your Knowledge

Shifting Biome Boundaries

Climate and soil types dictate the geographic distribution of biomes that we observe today. Various lines of evidence indicate that over long periods of time, biomes have occupied different locations around the globe. Changes in the distribution of biomes over time are caused by large-scale processes including continental drift, the uplift of mountains, and natural climatic variations, such as periods of glaciation. It is
important to understand the dynamics of biomes, as subtle changes in their composition may be sensitive indicators of changing ecological conditions.

Where conditions of climate and soil types are changing, the types of plants that occur at that location are likely to change over time. One might expect such changes to be most apparent at the borders or transition zones between biomes (sometimes referred to as ecotones). These borders can be caused by a variety of processes. Ecotones can be abrupt zones of vegetation change over space, such as occurs when temperatures decrease as elevation increases up a mountain. In the midwestern United States, the transition between eastern deciduous forest and shortgrass prairie is determined in part by recurring grass fires that kill young tree seedlings. Ecotones can also be created by human activities. Cutting tropical forests to create cattle pastures leaves an abrupt edge along the forest that can dramatically affect temperature, humidity, light, and wind at the forest-pasture boundary.

Biomes are large-scale categories of ecological communities. As such, it is important to ask how it is possible to detect a change in a biome's distribution. The vegetation type would determine the ease with which a shifting ecotone might be detected. For example, changes at the boundary between desert and grassland might be easier to see compared to the ecotone between tropical rainforest and tropical thorn scrub. The visibility of changes would also depend in part on the scale of observations. In other words, the right combination of time scale and spatial scale would have to be used. Over time, one might examine and re-examine certain locations to determine whether vegetation composition has changed. Jim Hastings and Raymond Turner, of the U.S. Geological Survey in Arizona, have done this using repeat photography. Hastings and Turner started by finding photographs of various locations in the Southwest taken at different time intervals going back to the 1800s. They then went back to the same locations and took new photographs, which they then compared to the older pictures. The results were striking. In some locations, such as in Saguaro National Monument (now Saguaro National Park), the saguaro forests had dramatically declined in density in just a few decades.

Airborne photographs can also be used to analyze vegetation dynamics over large areas. In 1930s the U.S. Army began a campaign of aerial photography to map the nation. At certain times, such photography has been repeated in order to update or increase the accuracy of maps, thereby creating a database of repeat photography. Craig Allen (of the U.S. Geological Survey) and David Breshears (of Los Alamos National Laboratory) used repeat airborne photography to study the changes in the boundary between ponderosa pine forest and piñon-juniper woodland in New Mexico. In theory, the distribution of a community type can increase or decrease by expansion or contraction of its borders. A community might appear to migrate (i.e., move over time and space) by a combination of range expansion on one boundary and contraction at the opposite boundary. Indeed, Allen and Breshears found that the ecotone between ponderosa forest and piñon-juniper woodland shifted by over 2 km in less than five years in response to a regional drought. In particular, ponderosa forest died off at its lower elevation boundary and was replaced by piñon-juniper woodland. There was no change at the upper elevation boundary. The rapid change resulted in fragmented (isolated) portions of ponderosa forest and considerably enhanced rates of soil erosion.

CHECK YOUR KNOWLEDGE

1. How are ecotones similar or different from one pair of biomes to another?

2. Read the data in Figure 5.29. Why do you think that tree diameter increase was greatest at high elevations as compared to medium and lower elevations?

MORE ON THE WEB

3. Read Allen and Breshears’s journal article by linking to Practicing Ecology on the Web at http://www.whfreeman.com/ricklefs. What do Allen and Breshears conclude regarding the importance of

**Figure 5.29** Mean changes in stem diameter during calendar year 1996 for ponderosa pine along an elevation/moisture gradient. Ten trees were measured at each of three sites: 2,010 m elevation ("Low" line) with 41 cm/year precipitation; 2,320 m ("Mid" line) with 51 cm/year, and 2,780 m ("High" line) with 89 cm/year.
vegetation mortality when predicting ecotone shifts over time?

4. Why do you think that biomes are classified according to their vegetational characteristics and not differences in animal form?

Suggested Readings


Variations in the Physical Environment

Global patterns in temperature and precipitation are established by the energy of solar radiation.

Ocean currents redistribute heat and moisture.

Seasonal variation in climate is caused by the movement of the sun's zenith.

Temperature and winds drive seasonal cycles in temperate lakes.

Climate sustains irregular fluctuations.

Topographic and geologic features cause local variation in climate.

Climate and the underlying bedrock determine the diversification of soils.

Few people make important decisions based on the evening weather report. Forecasting weather is notoriously difficult because of the irregular and unpredictable changes in the causes of weather patterns. On a global scale, one of the most dramatic weather conditions is the so-called El Niño, which is associated with periodic changes in air pressure patterns over the central and western Pacific Ocean. The cause of these changes is poorly understood, but their effects have been experienced, for better or worse, by most of the human population. For example, the 1991–92 El Niño event, one of the strongest on record, was accompanied by the worst drought of the twentieth century in Africa, which was followed by poor crop production and widespread starvation. The event also brought extreme dryness to many areas of tropical South America and Australasia. Droughts and hot temperatures in Australia reduced populations of red kangaroos to less than half their pre-El Niño levels. Outside the Tropics and Subtropics, El Niño events tend to increase, rather than decrease, precipitation, boosting the production of natural and agricultural systems, but also causing flooding. The most recent El Niño, in 1997–98, was blamed for 23,000 deaths—mostly from famine—and $35 billion in damages to crops and property worldwide.

Fluctuations in climate, whether local or affecting most of the globe, are one manifestation of variation in the earth's environment. Much of this variation can be traced to changes in incident radiation from the sun or to spatial patterns established by the shapes and positions of the earth's ocean basins, continents, and mountain ranges. On top of these predictable variations, physical and biological processes themselves establish new patterns of variation as the outcome of unpredictable interactions among their components. Ecologists strive to understand both the origin of variation in climate and its consequences for ecological systems.
The physical environment varies widely over the surface of the earth. Conditions of temperature, light, substrate, moisture, salinity, soil nutrients, and other factors have shaped the distributions and adaptations of plants, animals, and microbes. The earth has many distinct climate zones whose extents are broadly determined by the intensity of solar radiation and the redistribution of heat and moisture by wind and water currents. Within climate zones, such geologic factors as topography and composition of bedrock further differentiate the environment on a finer spatial scale. This chapter explores some important patterns of variation in the physical environment that underlie diversity in the biological components of ecosystems.

The surface of the earth, its waters, and the atmosphere above it make up a giant heat-transforming machine. Climatic patterns originate as the earth absorbs the energy in sunlight. As its surface varies from bare rock to forested soil, open ocean, and frozen lake, its ability to absorb sunlight varies as well, thus creating differential heating and cooling. The heat energy absorbed by the earth eventually radiates back into space, after undergoing further transformations that perform the work of evaporating water and driving the circulation of the atmosphere and oceans. All these factors have created a great variety of physical conditions that, in turn, have fostered the diversification of ecosystems.

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**Global patterns in temperature and precipitation are established by the energy of solar radiation**

The earth’s climate tends to be cold and dry toward the poles and hot and wet toward the equator. Although there are many exceptions to this general rule, climate does exhibit broadly defined patterns. The primary cause of global variation in climate is the greater intensity of sunlight at the equator than at higher latitudes. This is a simple consequence of the angle of the sun relative to the surface of the earth at different latitudes (Figure 4.1). The sun warms the atmosphere, oceans, and land most when it lies directly overhead. A beam of sunlight spreads over a greater area when the sun approaches the horizon, and it also travels a longer path through the atmosphere, where much of its energy either is reflected or is absorbed by the atmosphere and reradiated into space as heat. The sun’s highest position each day varies from directly overhead in the Tropics to near the horizon in polar regions; thus the warming effect of the sun diminishes from the equator to the poles.

At higher latitudes, light strikes the earth’s surface at a lower angle, and is spread over a greater area.

![Figure 4.1 The warming effect of the sun is greatest at the equator. The sun is closer to the perpendicular at the equator and shines directly down at the surface of the earth during the middle of the day.](image)

Patterns of change in temperature and precipitation are as important to biological systems as long-term averages. Periodic cycles in climate follow astronomical cycles: the rotation of the earth upon its axis causes daily periodicity; the revolution of the moon around the earth creates lunar cycles in the amplitude of the tides; and the revolution of the earth around the sun brings seasonal change.

The equator is tilted $23\frac{1}{2}^\circ$ with respect to the path the earth follows in its orbit around the sun. Therefore, the Northern Hemisphere receives more solar energy than the Southern Hemisphere during the northern summer, and less during the northern winter (Figure 4.2). The seasonal range in temperature increases with distance from the equator, especially in the Northern Hemisphere, where there is less area of ocean to moderate temperature changes (Figure 4.3). At high latitudes in the Northern Hemisphere, mean monthly temperatures vary by an average of $30^\circ$C, with extremes of more than $50^\circ$C annually. For example, at $60^\circ$N, the average coldest month is $-12^\circ$C and the average warmest month is $16^\circ$C, a difference of $28^\circ$C. Average temperatures of the warmest and coldest months in the Tropics are much higher, and they differ by as little as $2^\circ$C or $3^\circ$C.

The tilt of the earth also results in a seasonal shift in the area near the equator that receives the greatest amount of sunlight. This area lies at the solar equator, which is the parallel of latitude lying directly under the sun’s zenith.
Figure 4.2 The orientation of the earth's axis relative to the sun changes between winter and summer, causing seasonal variation in climate. The position of the solar equator at the summer and winter solstices is indicated.

The solar equator reaches 23½° N on June 21 and 23½° S on December 21.

Hadley cells

Warming air expands, becomes less dense, and tends to rise. As air heats up, its ability to hold water vapor increases, and evaporation quickens. As we saw in Chapter 2, the rate of evaporation from a wet surface nearly doubles with each 10°C rise in temperature. The heat of the sun warms a mass of air in the Tropics, which rises and eventually spreads to the north and south in the upper layers of the atmosphere. This air is replaced from below by surface-level air from subtropical latitudes. The rising tropical air mass cools as it radiates heat back into space. By the time this air has extended to about 30° north and south, its temperature has fallen sufficiently to cause the air to sink. This descending air mass is the Hadley cell.
Warm, moist air rises in the tropics, which results in abundant rainfall.

Cool, dry air descends to the surface at subtropical latitudes, creating desert conditions.

**Figure 4.4** Differential warming of the earth’s surface creates Hadley cells. Warm, moist air rises in the Tropics, and cool, dry air moves toward the Tropics from subtropical latitudes to replace it. The Intertropical Convergence is the latitudinal belt at the solar equator within which surface winds converge from the north and south.

South of the equator, it has become dense enough to sink back to the earth’s surface and spread out to the north and south, thus completing a cycling of air within the atmosphere (**Figure 4.4**). This type of circulation pattern is called a Hadley cell.

One Hadley cell forms around the earth immediately to the north of the equator and another to the south, like a pair of giant waistbands girdling the earth. The sinking air of the tropical Hadley cells drives secondary Hadley cells in temperate regions, which circulate in the opposite direction. The circulation of Hadley cells in temperate latitudes (roughly 30°-60° north and south of the equator) causes air to rise at about 60°N and 60°S, which in turn leads to the formation of polar Hadley cells. All this circulation of air is driven by the differential heating of the atmosphere with respect to latitude. The Hadley cells are linked together by the rising or falling air at the northern and southern edges of the cells. Thus, the movement of air in each Hadley cell helps to drive the circulation of the adjacent cells.

**The Intertropical Convergence and Subtropical High Pressure Belt**

The region within which surface currents of air from the northern and southern Subtropics meet near the equator and begin to rise under the warming influence of the sun is referred to as the Intertropical Convergence. As the moisture-laden tropical air rises and begins to cool within the convergence area, the moisture condenses to form clouds and precipitation. Thus, the Tropics are wet not because there is more water at tropical latitudes than elsewhere, but because water cycles more rapidly through the tropical atmosphere. The heating effect of the sun causes water to evaporate and warmed air masses to rise; the cooling of the air as it rises and expands causes precipitation because cold air has a lower capacity to hold water.

The air mass moving high in the atmosphere to the north and south, away from the Intertropical Convergence, has already lost much of its water to precipitation in the Tropics. Because this air has cooled, it becomes denser and
Ocean currents and mountains create high rainfall in some temperate areas. Despite their prevalent ice and snow, polar regions have little precipitation.

**Figure 4.6** The distribution of the earth’s major deserts and wet areas is established by the major latitudinal climate belts. Wet areas in western North America, Chile, and New Zealand are temperate rain forests. Dry areas at high latitude are polar deserts.

begins to sink. This descending mass of heavy air creates a high atmospheric pressure, and so these regions north and south of the equator are known as the **subtropical high pressure belts**. As the air sinks and begins to warm again at subtropical latitudes, its capacity to evaporate and hold water increases. As it descends to ground level and spreads to the north and south, it draws moisture from the land, creating zones of arid climate centered at latitudes of about 30° north and south of the equator (Figure 4.5). The great deserts of the world—the Arabian, Sahara, Kalahari, and Namib of Africa; the Atacama of South America; the Mojave, Sonoran, and Chihuahuan of North America; and the Australian—all fall within subtropical high pressure belts.

**Surface winds and rain shadows**

The rotation of the earth deflects the surface flows in the Hadley cells because the rotational speed of the earth is higher close to the equator than it is at higher latitudes. Consequently, surface flows are shifted to the west in the Tropics, where air moves away from the equator, and to the east in the middle latitudes, where air moves toward the equator (Figure 4.6). The resulting wind patterns, known as the trade winds and the westerlies, respectively, help to distribute water vapor through the atmosphere.

The positions of continental landmasses exert a secondary effect on the global pattern of precipitation. At any given latitude, rain falls more plentifully in the Southern Hemisphere because oceans and lakes cover a greater proportion of its surface (81% compared with 61% of the Northern Hemisphere). Water evaporates more readily from exposed surfaces of water than from soil and vegetation. For the same reason, the interior of a continent usually experiences less precipitation than its coasts, simply because it lies farther from the major site of water evaporation, the surface of the ocean. Furthermore, coastal (maritime) climates vary less than interior (continental) climates because the heat storage capacity of ocean waters reduces temperature fluctuations. For example, the hottest and coldest
mean monthly temperatures near the Pacific coast of the United States at Portland, Oregon, differ by only 16°C. Farther inland, this range increases to 18°C at Spokane, Washington; 26°C at Helena, Montana; and 33°C at Bismarck, North Dakota.

Global wind patterns interact with other features of the landscape to create precipitation. Mountains force air upward, causing it to cool and lose its moisture as precipitation on the windward side of a mountain range. As the dry air descends the leeward slope and travels across the lowlands beyond, it picks up moisture and creates arid environments called rain shadows (Figure 4.7). The Great Basin deserts of the western United States and the Gobi Desert of Asia lie in the rain shadows of extensive mountain ranges.

Ocean currents redistribute heat and moisture

The physical conditions of the oceans, like those of the atmosphere, are complex. Variation in marine conditions is caused by winds, which propel the major surface currents of the oceans, and by the underlying topography of the ocean basin. In addition, deep currents are established by
differences in the density of ocean water caused by variations in temperature and salinity. In large ocean basins, cold water circulates toward the Tropics along the western coasts of the continents, and warm water circulates toward temperate latitudes along the eastern coasts of the continents (Figure 4.8). The cold Peru Current of the eastern Pacific Ocean, which moves northward from the Antarctic Ocean along the coasts of Chile and Peru, creates cool, dry environments along the west coast of South America, in the rain shadow of the Andes Mountains, all the way to the equator. As a result, the coasts of northern Chile and Peru have some of the driest deserts on earth. Conversely, the warm Gulf Stream, emanating from the Gulf of Mexico, carries a mild climate far to the north into western Europe and the British Isles (see Figure 1.4).

Any upward movement of ocean water is referred to as upwelling. Upwelling occurs wherever surface currents diverge, as in the western tropical Pacific Ocean. As surface currents move apart, they tend to draw water upward from deeper layers. Strong upwelling zones are also established on the western coasts of continents where surface currents move toward the equator. A curious consequence of the rotation of the earth is the deflection of these currents away from the continental margins, which is aided by winds. As this water moves away from the continents, it is replaced by water from greater depths. Because deep water tends to be rich in nutrients, upwelling zones are often regions of high biological productivity. The most famous of these support the rich fisheries of the Benguela Current along the western coast of southern Africa and the Peru Current along the western coast of South America.

Seasonal variation in climate is caused by the movement of the sun’s zenith

Within the Tropics, the seasonal northward and southward movement of the solar equator determines the seasonality of rainfall. The intertropical convergence follows the solar equator, producing a moving belt of rainfall. Therefore,
seasonality of rainfall is most pronounced in broad latitudinal belts lying about 20° north and south of the equator.

Mérida, located on Mexico's Yucatán Peninsula, lies about 20° north of the equator. The intertropical convergence reaches Mérida only during the Northern Hemisphere summer months, which are the rainy season for that region (Figure 4.9). During the winter, the intertropical convergence lies far to the south of Mérida, and the local climate comes under the influence of the subtropical band of high pressure. Rio de Janeiro, at the same latitude as Mérida, but to the south of the equator, has its rainy season during the Northern Hemisphere winter, roughly six months after Mérida. Close to the equator at Bogotá, Colombia, the intertropical convergence passes overhead twice each year at the time of the equinoxes, resulting in two rainy seasons with peak rainfall in April and October. Thus, as the seasons change, tropical regions alternately come under the influence of the intertropical convergence, which brings heavy rains, and subtropical high-pressure belts, which bring clear skies.

Panama lies at 10°N and, like Mérida, it has a dry and windy winter and a humid, rainy summer. Panama's climate is wetter on the northern (Caribbean) side of the isthmus—the direction from which the prevailing trade winds come—than on the southern (Pacific) side; mountains intercept moisture coming from the Caribbean side and produce a rain shadow (Figure 4.10). The Pacific low-
Southern California, at the same latitude, lies to the west of the summer rainfall belt and has a winter-rainfall, summer-drought climate, often referred to as a Mediterranean climate. Named for the Mediterranean region of

- Figure 4.11 Many trees shed their leaves during the dry season, as these trees on the Pacific slope of Panama have done. Photo by R. E. Ricklefs.

- Figure 4.12 Seasonal climatic patterns differ between subtropical localities. (a) The Chihuahuan Desert in central Mexico has a summer rainy season. (b) The Sonoran Desert has a combined climatic pattern, with rainfall in summer and winter. (c) The Pacific coast and the Mojave Desert have a winter rain and summer drought (Mediterranean) climatic pattern.
Europe, which has the same seasonal pattern of temperature and rainfall, Mediterranean climates are also found in western South Africa, Chile, and Western Australia, all lying along the western sides of continents at about the same latitude north or south of the equator.

**Temperature and winds drive seasonal cycles in temperate lakes**

Small temperate zone lakes respond quickly to the changing seasons (Figure 4.13). In winter, a typical lake has an inverted temperature profile; that is, the coldest water (0°C) lies at the surface, just beneath the ice. Because the density of water increases between the freezing point and 4°C, the warmer water within this range sinks, and the temperature increases to as much as 4°C toward the bottom of the lake. In early spring, the sun warms the lake surface gradually. But until the surface temperature exceeds 4°C, the sun-warmed surface water tends to sink into the cooler layers immediately below. This vertical mixing distributes heat throughout the water column from the surface to the bottom, resulting in a uniform temperature profile. Winds cause deep vertical movement of water, or **spring overturn**, in early spring, bringing nutrients to the surface from the bottom sediments and bringing oxygen from the surface to the depths.

Later in spring and in early summer, as the sun rises higher each day and the air above the lake warms, surface layers of water gain heat faster than deeper layers, creating a zone of rapid temperature change at intermediate depth, called the **thermocline**. Once the thermocline is well established, water does not mix across it. Now, the warmer, less dense surface water literally floats on the cooler, denser water below, a condition known as stratification. The depth of the thermocline varies with local winds and with the depth and turbidity of the lake. It may occur anywhere between 5 and 20 m below the surface, lakes less than 5 m deep usually lack stratification.

The thermocline demarcates an upper layer of warm water called the **epilimnion** and a deeper layer of cold
water called the hypolimnion. Most of the primary production of the lake occurs in the epilimnion, where sunlight is most intense. Oxygen produced by photosynthesis supplements oxygen entering the lake at its surface, keeping the epilimnion well aerated and thus suitable for animal life. Plants and algae in the epilimnion, however, often deplete the supply of dissolved mineral nutrients and, in doing so, curtail their own production. The thermocline isolates the hypolimnion from the surface of the lake, so animals and bacteria that remain below the thermocline, where there is little or no photosynthesis, deplete the water of oxygen, creating anaerobic conditions. Thus, during late summer, the productivity of temperate lakes may become severely depressed, as nutrients needed to support plant growth are lacking in surface waters and oxygen needed to support animal life is lacking in the depths.

During the fall, the surface layers of the lake cool more rapidly than the deeper layers, become denser than the underlying water, and begin to sink. This vertical mixing, called fall overturn, persists into late fall, until the temperature at the lake surface drops below 4°C and winter stratification ensues. Fall overturn speeds the movement of oxygen to deep waters and pushes nutrients to the surface. In lakes where the hypolimnion becomes warm by mid-summer, deep vertical mixing may take place in late summer, while temperatures remain favorable for plant growth. The resulting infusion of nutrients into surface waters often causes an explosion in the population of phytoplankton—the fall (autumn) bloom. In deep, cold lakes, vertical mixing does not penetrate to all depths until late fall or early winter, when water temperatures are too cold to support phytoplankton growth.

Climate sustains irregular fluctuations

Most aspects of climate seem unpredictable. Everyone knows that weather is difficult to forecast far in advance. We often remark that a certain year was particularly dry or cold compared with others. The flooding in the Mississippi Valley and the increased intensity of hurricanes along the east coast of the United States in recent years drive home the capriciousness of nature. Such extreme conditions occur infrequently, but they may affect organisms disproportionately. The rich Peruvian fishing industry thrives on the abundant fish in the nutrient-rich waters of the Peru Current, as do some of the world’s largest seabird colonies (Figure 4.14). The Peru Current is a mass of cold water that flows up the western coast of South America and finally veers offshore at Ecuador, toward the Galápagos archipelago. North of this point, warm, tropical inshore waters prevail along the coast. Each year, a warm countercurrent known as El Niño (“little boy” in Spanish, a name referring to the Christ child because this countercurrent appears around Christmas time) moves down the coast toward Peru. In some years, it flows strongy enough and far enough to force the cold Peru Current offshore, taking with it the food supply of millions of birds.

During “normal” years between El Niño “events,” a steady wind blows across the equatorial central Pacific Ocean from an area of high atmospheric pressure centered over Tahiti to an area of low pressure centered over Darwin, Australia. An El Niño event appears to be triggered

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**Figure 4.14** Upwelling currents often support high biological productivity. Like its counterpart Peru Current off the western coast of South America, the Benguela Current off the western coast of South Africa has a zone of upwelling and supports an important fishery. The Cape gannets in this dense nesting colony feed on small fish in the adjacent cold, nutrient-rich waters. Accumulated guano is occasionally scraped off the rocks during the nonbreeding season and used for fertilizer. Photo by R.E. Ricklefs.
El Niño–Southern Oscillation (ENSO) events result in dramatic climatic changes. (a) A map of the changes that occur during ENSO events. (b) ENSO events are marked by large positive anomalies in the ENSO index, which is correlated with sea surface temperature in South American coastal waters. (c) A map of the changes that occur during La Niña events. (a) and (c) from C. Supko, National Geographic Magazine 195:73–95 (1999); (b) courtesy of the NOAA Climate Diagnostics Center.

by a reversal of these pressure areas (the so-called Southern Oscillation) and of the winds that flow between them (Figure 4.15a). As a result, the westward-flowing equatorial currents stop or even reverse, upwelling off the coast of South America weakens or ceases, and warm water—the El Niño current—piles up along the coast of South America. Historical records of atmospheric pressure at Tahiti and Darwin, and of sea surface temperatures on the Peruvian coast, reveal pronounced ENSO (El Niño–Southern Oscillation) events at irregular intervals of 2 to 10 years (Figure 4.15b).

El Niño events are often followed by La Niña, a period of strong trade winds that accentuate normal oceanic and upwelling currents and bring extreme weather of a different sort than El Niño to much of the world (Figure 4.15c). La Niña is characterized by heavy rainfall in many regions of the Tropics, drought in north-temperate regions, and an increase in hurricane activity in the North Atlantic Ocean.

The climatic and oceanographic effects of an ENSO event extend over much of the world, affecting ecosystems in such distant areas as India, South Africa, Brazil, and western Canada. A record ENSO event in 1982–83 disrupted fisheries and destroyed kelp beds in California, caused reproductive failure of seabirds in the central Pacific Ocean, and resulted in widespread mortality of coral in Panama. Precipitation was also dramatically affected in many terrestrial ecosystems. The deserts of northern Chile, normally the driest place on earth, received their first recorded rainfall in over a century.

The 1982–83 ENSO event drew the world's attention to the far-reaching effects of oceanographic and climatic changes in many parts of the world. For example, data from Zimbabwe for the period 1970–1993 show striking variation in yields of maize. As one might expect, these variations in yield were correlated with variations in rainfall, but, more surprisingly, they were also correlated with sea surface temperatures in the eastern tropical Pacific Ocean (Figure 4.16). One can see the far-reaching effects of the 1982–83 and 1991–92 El Niño events in these data.

During the 1991–92 El Niño, rainfall was so high in the Great Basin of the western United States that runoff nearly doubled the volume of water in Great Salt Lake. This reduced the lake's salinity from the usual 100 grams of salt per liter (about 3 times that of seawater) to 50 g per L, which caused marked changes in the ecosystem of the lake. Reduced salinity allowed predaceous corvids bugs to move into shallower parts of the lake. The corvids ate the brine shrimp Artemia, which graze on algae and normally dominate the ecosystem. With brine shrimp numbers reduced, algae increased dramatically, turning the lake into the aquatic equivalent of a lawn.

Some of the most striking effects of El Niño events are evident in the Galápagos archipelago, whose islands straddle the equator some 1,000 km off the west coast of Ecuador. The climate of the Galápagos is strongly influenced by the Peru Current, which brings cold water and periods of extreme dryness to the islands. When the Peru Current fails during El Niño conditions, warm water pervades the archipelago, triggering a drastic deterioration of local coldwater fish stocks and bringing extraordinary amounts of precipitation. Thus, El Niño conditions cause populations of seabirds and sea lions that rely on abundant fish to crash. On land, the heavy rains result in luxuriant growth of vegetation and abundant insects and seeds for the populations of birds and reptiles that rely on these

![Figure 4.16 ENSO events have far-reaching effects.](https://example.com/figure416.png)

Deviations from the long-term average in rainfall and maize production in Zimbabwe are correlated with sea surface temperatures in the eastern equatorial Pacific Ocean. From M. A. Cane, G. Seshel, and R. W. Buckland, Nature 370:204–205 (1994).
foods (Figure 4.17). As we shall see later in the book, this seesawing between scarcity and abundance has important consequences for the population dynamics and evolution of organisms in the Galápagos archipelago.

**ECOLOGISTS IN THE FIELD**

*A half-million-year climate record*

Humans have kept records of climate systematically for about 200 years and sporadically for several hundred years before that. Variation in the thickness of the growth rings in trees extends records of climate in some regions—at least from a tree’s point of view—back to several thousand years. Whether a climatic record encompasses decades, centuries, or millennia, one sees both regular cycles of climate and irregular fluctuations. But what about longer periods? We know from geological evidence that the Northern Hemisphere has undergone multiple glacial cycles during the past million years, and that these cycles reflect broader patterns of global climatic change. Later in this book, we shall consider the evidence linking glacial cycles to changes in biological communities throughout the world. Here we will consider physical evidence of changes in temperature over the past half-million years.

The sediments of the ocean basins consist largely of the calcium carbonate shells of small protists known as foraminifera (Figure 4.18). The shells of these long-dead creatures are tiny permanent thermometers that provide a long-term record of temperature fluctuations. The foraminifera have made this possible by incorporating oxygen in the form of carbonate into their shells. Most of the oxygen in the biosphere has an atomic weight of 16, and is referred to as the form, or isotope, 16O. Oxygen also occurs in an isotope with two additional neutrons, which has an atomic weight of 18. Oxygen-18, or 18O, is relatively rare, making up only 0.2% of the total in the biosphere. The rate of incorporation of the heavier 18O into calcium carbonate shells is influenced by temperature. Thus, the proportion of
Topographic and geologic features cause local variation in climate

Topography and geology can modify the environment on a local scale within regions of otherwise uniform climate. In hilly areas, the slope of the land and its exposure to the sun influence the temperature and moisture content of the soil. Soils on steep slopes drain well, often causing drought stress for plants on the hillside at the same time that water saturates the soils of nearby lowlands. In arid regions, stream bottomlands and seasonally dry riverbeds may support well-developed riparian forests, which accentuate the contrasting bleakness of the surrounding desert. In the Northern Hemisphere, south-facing slopes directly face the sun, whose warmth and drying power limit vegetation to shrubby, drought-resistant xeric forms. The adjacent north-facing slopes remain relatively cool and wet and harbor moisture-requiring mesic vegetation (Figure 4.19).

Air temperature decreases with altitude by about 6°–10°C for each 1,000 m increase in elevation, depending on the region. This decrease in temperature, which is caused by the expansion of air in the lower atmospheric pressures at higher altitudes, is referred to as adiabatic cooling. Climb high enough, even in the Tropics, and you will encounter freezing temperatures and perpetual snow. Where the temperature at sea level averages 30°C, freezing temperatures are reached at about 5,000 m, the approximate altitude of the snow line on tropical mountains.

$^{16}$O in shells decreases by approximately one part per thousand ($\delta^{18}$O) for each 4°C decrease in temperature.

Jerry McManus and his colleagues at the Woods Hole Oceanographic Institute analyzed a 65-meter-long core of sediments taken from the North Atlantic Ocean northwest of Ireland. The record of $\delta^{18}$O values from the sediment core is shown in Figure 4.18. As one might expect, temperatures indicated by the shells of the surface-dwelling foraminiferan Neogloboquadridina pachyderma are several degrees higher than those indicated by the bottom-dwelling Cibicidoides wuellerstorfi. (Sorry, they don’t have common names.) Both species, however, exhibit 100,000-year-long cycles of temperature, corresponding to glacial and interglacial climatic cycles. Temperature changes at the bottom of the ocean parallel those at the surface, confirming that no place on earth escapes variations of climate. Superimposed on the long-term temperature cycles are numerous variations of shorter duration. These correspond to a wide range of global climatic patterns resulting from periodic variations in the distance of the earth from the sun.

Figure 4.18 Variations in marine temperatures are recorded by foraminifera in ocean-floor sediments. Variations in oxygen isotopes in the shells of foraminifera in sediments from the North Atlantic Ocean during the last 500,000 years. The $\delta^{18}$O value becomes more negative the colder the temperature of the water in which the foraminifera lived. The record clearly shows five warm interglacial periods separated by cold glacial periods. From J. F. McManus, D. W. Oppo, and J. L. Cullen, Science 285:971–975 (1999). Inset: Shells of several species of the single-celled protists. Photo by Charles Gellis/Photo Researchers.

Figure 4.19 Topography can modify the environment on a local scale. Exposure influences the vegetation growing on a series of mountain ridges near Aspen, Colorado. The cool and moist north-facing slopes permit the development of spruce forest. Shubby, drought-resistant vegetation grows on the south-facing slopes. Photo by R. E. Ricklefs.
In north-temperate latitudes, a 6°C drop in temperature with each 1,000 m of altitude corresponds to the temperature change encountered over an 800-km increase in latitude. In many respects, the climate and vegetation of high altitudes resemble those of sea-level localities at higher latitudes. But despite their similarities, alpine environments usually vary less from season to season than their low-elevation counterparts at higher latitudes. Temperatures in tropical montane environments remain nearly constant, and some of these areas remain frost-free over the year, which makes it possible for many tropical plants and animals to live in the cool environments found there.

In the mountains of the southwestern United States, changes in plant communities with elevation result in more or less distinct belts of vegetation, which the nineteenth-century naturalist C. H. Merriam referred to as life zones. Merriam's scheme of classification included five broad zones, which he named, from low to high elevation (or from south to north), the Lower Sonoran, Upper Sonoran, Transition, Canadian (or Hudsonian), and Alpine (or Arctic-Alpine) (Figure 4.20). At low elevations, one encounters a cactus and desert shrub association characteristic of the Sonoran Desert of northern Mexico and southern Arizona. In the riparian forests along streambeds, the plants and ani-
Figure 4.20 Vegetation changes at increasing elevation in the mountains of Arizona.
At the lowest elevations (bottom photograph), the Lower Sonoran zone supports mostly
saguaro cactus, small desert trees such as paloverde and mesquite, numerous annual and
perennial herbs, and small succulent cacti. Agave and grasses are conspicuous elements of the
Upper Sonoran zone, and oaks appear toward its upper edge. At higher elevations, large trees
predominate; ponderosa pine in the Transition zone, spruce and fir in the Hudsonian zone.
These gradually give way to bushes, willows, herbs, and lichens in the Alpine zone above the
tree line. Photo by Tom Bean/DRK Photo.

...mals have a distinctly tropical flavor. Many hummingbirds
and flycatchers, ring-tailed cats, jaguars, and peccaries make
their only temperate zone appearances in this area. In the
Alpine zone, 2,600 m higher, one finds a landscape resem-
blying the tundra of northern Canada and Alaska. Thus, by
climbing 2,600 m, one experiences changes in climate and
vegetation that would occur in the course of a journey to
the north of 2,000 km or more at sea level.

Climate and the underlying bedrock determine the
diversification of soils

Climate affects the distributions of plants and animals indi-
crectly through its influence on the development of soil,
which provides the substrate within which plant roots
grow and many animals burrow. The characteristics of soil
determine its ability to hold water and to make available
the minerals required for plant growth. Thus, its variation
provides a key to understanding the distributions of plant
species and the productivity of biological communities.
Soil defies simple definition, but we may describe it as the
layer of chemically and biologically altered material that
overlies rock or other unaltered materials at the surface of
the earth. It includes minerals derived from the parent
rock, modified minerals formed anew within the soil,
organic material contributed by plants, air and water
within the pores of the soil, living roots of plants, microor-
ganisms, and the larger worms and arthropods that make
the soil their home. Where a recent road cut or excavation
exposes soil in cross section, one often notices distinct lay-
ners, which are called horizons (Figure 4.21). A general-
ized, and somewhat simplified, soil profile has four major
divisions, the O, A, B, and C horizons. The A horizon has
two subdivisions, A1 and A2 (Table 4.1). Five factors deter-
mine the characteristics of soils: climate, parent material
(underlying rock), vegetation, local topography, and, to
some extent, age. Soil horizons reveal the decreasing influ-
ence of climatic and biotic factors with increasing depth.

Figure 4.21 Soil profiles may show distinct layers, or
horizons. (a) This profile of a prairie soil from Nebraska is
weathered to a depth of about 3 feet (0.9 m), where the
subsoil contacts the parent material, which consists of
loosely aggregated, calcium-rich, wind-deposited sediments (loess). A1 and A2 horizons are not clearly
distinguished. The B horizon (between the arrows)
contains less organic material. Rainfall in Nebraska is
sufficient to leach readily soluble ions completely from the
soil; hence there are no B layers of redeposition. The
C horizon is light-colored and has been leached of some
of its calcium. (b) A prairie soil from Texas. The A layer is
only about 6 inches thick. The B layer extends down to
the bottom of the dark layer, which represents organic
material redeposited from the A layer above. Considerable
calcium has been redeposited at the base of the B layer
and in the C layer below. Courtesy of the U.S. Department of
Agriculture, Soil Conservation Service.
Table 4.1 Characteristics of the major soil horizons

<table>
<thead>
<tr>
<th>Soil horizon</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>O</td>
<td>Primarily dead organic litter. Most soil organisms inhabit this layer.</td>
</tr>
<tr>
<td>A₁</td>
<td>A layer rich in humus, consisting of partly decomposed organic material mixed with mineral soil.</td>
</tr>
<tr>
<td>A₂</td>
<td>A region of extensive leaching of minerals from the soil. Because minerals are dissolved by water—that is to say, mobilized—in this layer, plant roots are concentrated here.</td>
</tr>
<tr>
<td>B</td>
<td>A region of little organic material, whose chemical composition resembles that of the underlying rock. Clay minerals and oxides of aluminum and iron leached out of the overlying A₂ horizon are sometimes deposited here.</td>
</tr>
<tr>
<td>C</td>
<td>Primarily weakly altered material, similar to the parent rock. Calcium and magnesium carbonates accumulate in this layer, especially in dry regions, sometimes forming hard, impenetrable layers or “pans.”</td>
</tr>
</tbody>
</table>

Soils exist in a dynamic state, changing as they develop on newly exposed rock. And even after soils achieve stable properties, they remain in a constant state of flux. Groundwater removes some substances; other materials enter the soil from vegetation, in precipitation, as dust from above, and from the rock below. Where little rain falls, the parent material decomposes slowly, and plant production adds little organic detritus to the soil. Thus arid regions typically have shallow soils, with bedrock lying close to the surface. Soils may not form at all where decomposed bedrock and detritus erode as rapidly as they form. Soil development also stops short on alluvial deposits, where fresh layers of silt deposited each year by floodwaters bury older material.

At the other extreme, soil formation proceeds rapidly in parts of the humid Tropics, where chemical alteration of parent material may extend to depths of 100 meters. Most soils of temperate zones are intermediate in depth, extending to an average of about 1 meter. The variety of soil types, their characteristics, and their distributions are presented in Table 4.2.

Weathering

Weathering—the physical and chemical alteration of rock material near the earth’s surface—occurs wherever surface water penetrates. The repeated freezing and thawing of

Table 4.2 Soil types, their characteristics, and their distribution

<table>
<thead>
<tr>
<th>KEY</th>
<th>Soil type</th>
<th>Characteristic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alfisols</td>
<td>Moist, moderately weathered mineral soils</td>
<td></td>
</tr>
<tr>
<td>Aridosols</td>
<td>Dry mineral soils with little leaching and accumulations of calcium carbonate</td>
<td></td>
</tr>
<tr>
<td>Entisols</td>
<td>Recent mineral soils lacking development of soil horizons</td>
<td></td>
</tr>
<tr>
<td>Histosols</td>
<td>Organic soils of peat bogs, mucks</td>
<td></td>
</tr>
<tr>
<td>Inceptisols</td>
<td>Young, weakly weathered soils</td>
<td></td>
</tr>
<tr>
<td>Mollisols</td>
<td>Well-developed soils high in organic matter and calcium; very productive</td>
<td></td>
</tr>
<tr>
<td>Oxisols/Andisols</td>
<td>Deeply weathered, lateritic soils of moist tropics (not represented in continental United States)</td>
<td></td>
</tr>
<tr>
<td>Spodosols</td>
<td>Acid, podzolized soils of moist, often cool climates with shallow leached horizon and a deeper layer of deposition</td>
<td></td>
</tr>
<tr>
<td>Ultisols</td>
<td>Highly weathered soils of warm, moist climates with abundant iron oxides</td>
<td></td>
</tr>
<tr>
<td>Vertisols</td>
<td>High content of swelling-type clays developing deep cracks in dry seasons</td>
<td></td>
</tr>
</tbody>
</table>
water in crevices physically breaks rock into smaller pieces and exposes a greater surface area to chemical action. Initial chemical alteration of the rock occurs when water dissolves some of its more soluble minerals, especially sodium chloride (NaCl) and calcium sulfate (CaSO₄). Other materials, such as the oxides of titanium, aluminum, iron, and silicon, dissolve less readily.

The weathering of granite exemplifies some basic processes of soil formation. The minerals responsible for the grainy texture of granite—feldspar, mica, and quartz—consist of various combinations of oxides of aluminum, iron, silicon, magnesium, calcium, and potassium, along with other, less abundant compounds. The key to weathering is the displacement of certain elements in these minerals—notably calcium, magnesium, sodium, and potassium—by hydrogen ions, followed by the reorganization of the remaining oxides into new minerals. This chemical process provides the basic structure of soil.

Feldspar and mica grains consist of aluminosilicates of potassium, magnesium, and iron. Hydrogen ions percolating through granite displace potassium and magnesium ions, and the remaining iron, aluminum, and silicon form new, insoluble materials, particularly clay particles. These particles are important to the water-holding and nutrient-holding capacity of soils. Quartz, a type of silica (SiO₂), is relatively insoluble and therefore remains more or less unaltered in the soil as grains of sand. Different changes in chemical composition as granite weathers from rock to soil in different climate regions show that weathering is most severe under tropical conditions of high temperature and rainfall (Figure 4.22).

Where do the hydrogen ions involved in weathering come from? They derive from two sources. One of these is the carbonic acid that forms when carbon dioxide dissolves in rainwater (see Chapter 2). In regions not affected by acidic pollution, concentrations of hydrogen ions in rainwater produce a pH of about 5. The other source of hydrogen ions is the oxidation of organic material in the soil itself. The metabolism of carbohydrate, for example, produces carbon dioxide, and dissociation of the resulting carbonic acid generates additional hydrogen ions. In the Hubbard Brook Forest of New Hampshire, which is a particularly well studied watershed, these internal processes account for about 30% of the hydrogen ions needed for the weathering of bedrock; the remainder come from precipitation. In the Tropics, however, internal sources of hydrogen ions assume greater importance and may lead to more rapid weathering.

**Podsolization occurs in acid soils**

Under mild, temperate conditions of temperature and precipitation, sand grains and clay particles resist weathering and form stable components of the soil. In acid soils, however, clay particles, which retain nutrients in the soil, break down in the A horizon, and their soluble ions are transported downward and deposited in lower horizons. This process, known as **podsolization**, reduces the fertility of the upper layers of the soil.

Acid soils occur primarily in cold regions where needle-leaved trees dominate the forests. The slow microbial decomposition of plant litter shed by spruce and fir trees produces organic acids. In addition, rainfall usually exceeds evaporation in regions of podsolization. Under these moist conditions, because water continuously moves downward through the soil profile, little clay-forming material is transported upward from the weathered bedrock below.

In North America, podsolization advances farthest under spruce and fir forests in New England and the Great Lakes region and across a wide belt of southern and western Canada. A typical profile of a highly podsolized soil (Figure 4.23) reveals striking bands corresponding to the regions of leaching and redeposition. The topmost layer of
Laterization occurs in warm, wet climates

Soils weather to great depths in the warm, wet climates of many tropical and subtropical regions. One of the most conspicuous features of weathering under these conditions is the breakdown of clay particles, which results in the leaching of silica from the soil, leaving oxides of iron and aluminum to predominate in the soil profile. This process is called laterization, and the iron and aluminum oxides give lateritic soils their characteristic reddish coloration (Figure 4.24). Even though the rapid decomposi-
tion of organic material in tropical soils contributes an abundance of hydrogen ions, these are quickly neutralized by the bases formed by the breakdown of clay minerals; consequently, lateritic soils usually are not acidic. Laterization is enhanced in certain soils that develop on parent material deficient in quartz (SiO₂) but rich in iron and magnesium (basalt, for example); these soils contain little clay to begin with because they lack silicon. Regardless of the parent material, weathering reaches deepest and laterization proceeds farthest on low-lying soils, such as those of the Amazon basin, where highly weathered surface layers are not eroded away and the soil profiles are very old.

One of the consequences of laterization in many parts of the Tropics is that the capacity of the soil to hold nutrients is very poor. Without clay and humus particles to hold mineral nutrients, they are readily leached out of the soil. Where soils are weathered deeply, new minerals formed by the decomposition of the parent material are simply too far from the surface layers of the soil to contribute to soil fertility. Besides, heavy rainfall keeps water moving down through the soil profile, preventing the upward movement of nutrients. In general, the deeper the ultimate sources of nutrients in the unaltered bedrock, the poorer the surface layers. Rich soils do, however, develop in many tropical regions, particularly in mountainous areas where erosion continually removes nutrient-depleted surface layers of soil, and in volcanic areas where the parent material of ash and lava is often rich in such nutrients as potassium.

Soil formation emphasizes the role of the physical environment, particularly climate, geology, and landforms, in creating the tremendous variety of environments for life that exist at the surface of the earth and in its waters. In the next chapter, we shall see how this variety affects the distribution of life forms and the appearance of biological communities.

ECOLOGISTS IN THE FIELD

Which came first, the soil or the forest?

When the glaciers retreated from most of Europe and North America, beginning about 18,000 years before the present (BP), dramatic changes in vegetation and soils moved across the landscape. In central Europe, cold, dry steppes were replaced by coniferous forests and then by deciduous forests that occur throughout the region today. At about the same time as the coniferous–deciduous forest transition, there was a change from strongly podzolized soils to richer brown forest soils. But, as British ecologist Kathy Willis and her colleagues asked, "Which changed first? Did climatic warming result in a transformation from one soil type to another, which in turn resulted in a change in forest composition, or did the vegetation change first and subsequently alter the soil?"

The answer, at least for one area in northeastern Hungary, comes from a core of sediments removed from small, shallow Lake Kis-Mohos Tó. Lake sediments preserve a record of the local conditions over time. Pollen grains become trapped in the sediments (Figure 4.25), as do minerals

![Figure 4.25 Pollen grains from different types of plants have distinctive surface patterns that allow them to be recognized in lake sediments. These scanning electron micrographs depict pollen grains of three subtropical plants from North America: Ipomoea arboreascens, Cebu pentandra, and Agave palmeri, magnified approximately 500 times. Courtesy of Norman Hodgkin.](image-url)
carried in water draining from soils surrounding the lake. The pollen and minerals tell the story of changes in vegetation and soils.

What does the sediment core from Lake Kis-Mohos Tó reveal? First, the pollen record tells us that the local forest changed from coniferous to deciduous in a few centuries. You can see in Figure 4.26 that spruce, pine, and birch, trees typical of boreal forests, abruptly disappeared from the region about 9,500 years BP, and were just as quickly replaced by an oak-hornbeam deciduous forest. Up until this transition, most of the sediment in the lake was inorganic, suggesting that the area was cold and unproductive. Abundant aluminum, potassium, and magnesium in the sediment core suggested rapid breakdown and leaching of clay components of the surrounding soils, typical of a heavily podzolized area. The first indication of change was a release of large amounts of strontium and barium into the lake. Spruce trees preferentially take up these elements from the soil instead of calcium. The strontium and barium are deposited in the spruce needles and then accumulate in the thick layer of litter on the forest floor. Willis and her colleagues interpreted the release of these elements into ground and surface water flowing into Lake Kis-Mohos Tó as resulting from a rapid breakdown of the spruce litter.

What triggered this breakdown? It is difficult to know with certainty, but again the sediment core provides a clue. In the contemporaneous increase in charcoal particles entering the lake. Climate modelers suggest that central Europe experienced a warm, dry period between 10,000 and 9,000 BP. This climate may have promoted natural fires that burned away the litter layers of the coniferous forests. This period also marks the disappearance of spruce from the area. Spruce requires cooler and moister conditions than pines can tolerate. The appearance of charcoal in the sediment core is also associated with a spike of fern spores, which is a sure sign of frequent fires. Ferns colonize burned areas quickly and produce luxuriant growth for a few years after a fire has swept through a forest (Figure 4.27). The fires mark the transition from coniferous to deciduous forest because pines disappear and are replaced by oaks at this time. After broad-leaved deciduous trees became established, large quantities of iron, magnesium, and phosphorus were released into the lake during another brief period. This represents a period of leaching of these elements under the still acid conditions of the forest soils, probably accompanied by a transient reduction in soil fertility. The final phase of the transition is marked by an increase in calcium in the sediment core. Calcium is not particularly abundant in the rock underlying the region, but deciduous trees like oaks preferentially take up calcium from the soil and begin to enrich the calcium content of the top layers of soil through annual leaf fall.

So, which changed first, the soil or the forest? Clearly, the forest retained its acidic, podzolized nature until well after the establishment of deciduous vegetation, so apparently the vegetation change caused the soil change in this case, illustrating the contribution of vegetation to the development of soil. The change in the vegetation itself was evidently sparked, so to speak, by warmer and drier climates, which were less favorable for spruce and fostered fires that created openings in the pine forests. These openings allowed oak and other broad-leaved species to invade.

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**Figure 4.26** Layers of sediments in lakes preserve the history of environmental change in the surrounding watershed. This core from Lake Kis-Mohos Tó in Hungary shows the replacement of needle-leaved forest by broad-leaved deciduous forest and accompanying changes in soils about 10,000 years ago. From K. J. Willis et al., *Ecology* 78(3):740–750 (1997).
Summary

1. Global patterns of temperature and rainfall result from differential input of solar radiation in different regions and from the redistribution of heat energy by winds and ocean currents. Prominent features of terrestrial climates include a band of warm, moist climate over the equator and bands of dry climate at about 30° north and south latitude.

2. Variation in the marine environment is determined on a global scale by the major ocean currents. These currents redistribute heat over the surface of the earth and greatly affect climates on land. Upwelling currents, caused by winds, ocean basin topography, and variations in water density related to temperature and salinity, bring cold, nutrient-rich water to the surface in some areas.

3. Seasonality in terrestrial environments is caused by the annual progression of the solar equator northward and southward and by the latitudinal movement of associated belts of temperature, wind, and precipitation. At high latitudes, the seasons are expressed primarily as annual cycles of temperature; within the Tropics, seasonality of precipitation is more pronounced.

4. Seasonal warming and cooling profoundly change the characteristics of lakes in the temperate zone. During summer, such lakes are stratified, with a warm surface layer (epilimnion) separated from a cold bottom layer (hypolimnion) by a sharp thermocline. In spring and fall, the profile of temperature with depth becomes more uniform, allowing vertical mixing.

5. Irregular and unpredictable variations in climate, such as El Niño-Southern Oscillation events, may cause major changes in temperature and precipitation and disrupt biological communities on a global scale.

6. Topography and geology superimpose local variation in environmental conditions on more general climatic patterns. Mountains intercept rainfall, creating and rain shadows or their lee. Conditions at higher altitudes resemble conditions at higher latitudes.

7. The characteristics of soil reflect the influences of the bedrock below and the climate and vegetation above. Weathering of bedrock results in the breakdown of some of its minerals and their re-formation into clay particles, which mix with organic detritus entering the soil from the surface. These vertically graded processes usually result in distinct soil horizons.

8. In acid (podsolic) soils of cool, moist parts of the temperate zone and in deeply weathered (laterized) tropical soils, clay particles break down and the fertility of the soil is much reduced.

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**PRACTICING ECOLOGY**

**CHECK YOUR KNOWLEDGE**

Variation over Space and Time

As we have discussed throughout this chapter, variations in the physical environment play an important role in ecological interactions that determine the distributions and abundances of organisms. The way in which individual organisms respond to changes in climate is critical to their success in surviving and reproducing. Therefore, it is important to understand how past and present patterns of climatic variability affect plants and animals so that we can predict the probable effects of future changes in the environment.

In regions subject to cold winters, one of the most critical periods of an individual's life is the initiation of activity in the spring. Insects come out of their resting state (diapause), mammals come out of hibernation, seeds germinate, dormant buds break open and trees begin to leaf out, and birds return from their tropical wintering grounds. These responses are cued by a variety of environmental factors, including day length, which indicates time of year and therefore predicts the average conditions to be expected (see Chapter 9). Organisms are also sensitive to factors that vary between years, such as air temperature, snow depth, soil temperature, and soil water content, and they may
adjust the timing of their spring activity accordingly. For example, years with particularly mild winter and spring temperatures usually stimulate earlier plant growth and flowering. Insect herbivores and pollinators usually adjust their activity in parallel by responding to the same cues.

Examples of the relationship between the timing of spring activity and annual variation in climate for a number of European organisms can be found at http://www.student.iwan.nl/~arnold/gpmn.html. Some of these studies have recorded the timing of activity, or phenology, over many decades. The records show variation in phenology over time. A few of the studies show long-term trends in date of flowering, for example, in response to recent warming of the environment.

A recent study in the Rocky Mountains suggests that when different organisms respond to different cues, the phenology of one organism might become unsynchronized with the phenology of others with which it interacts. David Inouye, Billy Barr, Ken Armitage, and Brian Inouye, working at the Rocky Mountain Biological Laboratory (RMBL) at an elevation of about 3,000 m (10,000 feet) in Colorado, examined springtime records of plant emergence, bird migrations from lower elevations, and emergence of marmots from hibernation. They tracked the dates at which these events occurred in relation to date of snowmelt and air temperature from 1975 to 1999. Although temperature, snow cover, and plant phenology varied from year to year, there was no trend in the date of onset of plant growth, in spite of generally increasing temperatures over the period of the study. Increasing winter snowfall, which resulted in later disappearance of the snowpack from mountain meadows, might possibly have offset the effect of increasing temperatures. Indeed, the depth of the snowpack, and the date at which it is fully melted, is tightly linked to the emergence of many plant species.

Temperatures have also been increasing at lower elevations in Colorado; however, there is little snow at lower elevations, and biological activity has shown a trend toward beginning earlier there, just as it has in much of eastern North America and Europe. For organisms that are resident at low elevations, this response to milder winter and spring conditions is appropriate. However, several animals migrate from lowlands to higher elevation in the spring, and if they take their cue from temperatures in their wintering areas, they are likely to show up on their breeding grounds too early. For example, American robins now arrive at RMBL two weeks earlier than they did in 1981, probably cued by warmer conditions at lower elevations, but they are greeted by still heavy snow cover. The changing relationship between spring temperatures and snow cover may also be a problem for hibernating animals, which probably respond to changes in temperature in their burrows. Inouye and colleagues reported that marmots now emerge from hibernation 38 days earlier than they did in the 1970s, more than a month ahead of the growth of most of their food plants. This disparity between the phenological responses of different populations that take their cues from different signals is bound to affect survival and reproductive success, and may even lead to the decline and disappearance of some populations from the area over time. Climatic change brought about by human activity is bound to magnify problems of this kind and cause changes in the species composition of many ecosystems.

CHECK YOUR KNOWLEDGE

1. What was the purpose of the Inouye, Barr, Armitage, and Inouye study?

2. Read Figure 4.28 and determine by how much winter snowfall has changed over the period from 1975 to 1999.

Understanding phenological responses to variation in the physical environment depends initially on using correlations between biological and climatic data to develop hypotheses about the cues that are important for plant and animal responses. It is important to select the appropriate cue for your question of interest, and to evaluate variation on the right spatial and temporal scales.

MORE ON THE WEB

3. Suppose you were assigned the task of comparing the phenology of plant growth and flowering with climatic variations resulting from El Niño events.

![Figure 4.28 Winter snowfall at Rocky Mountain Biological Laboratory (RMBL) 1975–1999. After D. W. Inouye et al., Proceedings of the National Academy of Sciences USA 97: 1630–1633 (2000).](image-url)
A. How would you monitor the phenology of a plant species? Which attribute of plant phenology (e.g., date of the appearance of first leaves, first flower opening date, etc.) would you use to chart the timing of plant development? To find out more about monitoring phenology you might want to visit the Lilac Phenology Network Home Page through www.whfreeman.com/ricklefs.

B. What data would you use to monitor El Niño activity? For some hints, see Figure 4.16 or go to the El Niño page of the National Oceanic and Atmospheric Administration through www.whfreeman.com/ricklefs.

4. You can view the article by Inouye et al. at http://www.pnas.org/cgi/content/full/97/4/1630 or at www.whfreeman.com/ricklefs. Read in the introduction section of the journal article about other studies that suggest climate change is affecting the seasonal timing of animal and plant activity at low altitudes. Why is this important to animals that live at higher altitudes?

Answers are found at www.whfreeman.com/ricklefs.

Suggested Readings


Adaptation to Aquatic and Terrestrial Environments

- Availability of water depends on the physical structure of soil
- Plants obtain water from the soil by the osmotic potential of their root cells
- Forces generated by transpiration help to move water from roots to leaves
- Adaptations to arid environments control loss of water from leaves
- Plants obtain mineral nutrients from soil water
- Photosynthesis varies with levels of light
- Plants modify photosynthesis in environments with high water stress
- Salt balance and water balance go hand in hand
- Animals excrete excess nitrogen in the form of small organic molecules
- Water conservation mechanisms are important in hot environments
- Organisms maintain a constant internal environment
- Large animals deliver oxygen to their tissues through circulatory systems
- Countercurrent circulation increases transfer of heat and substances between fluids
- Each organism functions best under a restricted range of conditions

Sperm whales routinely dive to depths of 500 meters and occasionally as deep as 2 kilometers, staying below the surface for more than an hour. The reason sperm whales and other deep divers take the plunge is clear: They are after food. Fish, squid, krill, and other prey are abundant at these depths. How the whales manage such feats of diving is another story, which demonstrates the extremes to which some organisms have adapted to their environments.

Like all mammals, sperm whales must breathe air. Indeed, all diving mammals, and diving birds as well, are ultimately limited when under water by the need for oxygen to sustain their metabolism. As you would expect, a diver begins its descent with a large supply of oxygen stored in its body. What may come as a surprise, however, is that very little of this oxygen resides in the lungs. The Weddell seal, a native of antarctic waters and an excellent diver (Figure 3.1), carries an average of 87 milliliters of oxygen per kilogram of body mass when it submerges. Only 5% is in the lungs. Two-thirds is bound to hemoglobin in the blood, and the rest is bound to a similar molecule, myoglobin, in the muscles. In contrast, humans have only 20 ml per kg oxygen at the beginning of a dive, a quarter of which is in the lungs and only 15% in the muscles. While under water, deep-diving mammals shut down their metabolism considerably by blocking blood flow to nonvital organs such as the skin, viscera, lungs, kidneys, and muscles (which have their own oxygen supply bound to myoglobin), and keep blood flowing primarily to the brain and heart. Consequently, the temperature of all but a few key organs drops, heart rate slows, and demand for oxygen drops to a minimum.

The adaptations of diving mammals show how the structure and functioning of an organism is adapted to the particular environment it lives in. All organisms are constrained by their physical environments, whether water, light, or nutrients are in short supply or conditions of
organisms are specialized to rather narrow ranges of environmental conditions, particularly those organisms living under extreme conditions. This specialization provides a basis for understanding the ecological distributions of populations and why certain adaptations of morphology and physiology are associated with certain physical conditions.

We shall begin this exploration by considering how plants cope with the limited availability of water in their environment. Plants need water in prodigious quantities because they lose so much by evaporation from their leaves while taking up carbon dioxide from the atmosphere. The ability of plants to obtain water from the soil is determined by the physical properties of soil and of water and by the way differences in solute concentrations cause water to move.

**Availability of water depends on the physical structure of soil**

Most terrestrial plants obtain the water they need from the soil. The amount of water in soil and its availability to plants varies with the physical structure of the soil. Water is sticky. The capacity of water molecules to cling to one another (the basis for surface tension) and to the surfaces of soil particles (a tendency known as capillary attraction) is responsible for the retention of water in soil. The more surface area it has, the more water a soil can hold.

Soils consist of grains of clay, silt, and sand, as well as particles of organic material, in varying proportions. Because the total surface area of particles in a given volume of soil increases as their size decreases, soils with abundant clay (particles less than 0.002 mm in diameter) and silt (0.002–0.05 mm) hold more water than coarse sands (> 0.05 mm), through which water drains quickly (Figure 3.2).

Plant roots easily take up water that clings loosely to soil particles. But close to the surfaces of soil particles, water adheres tightly by more powerful forces of attraction. The strength of these forces is called the water potential of the soil. Because the physical matrix of the soil generates these forces, they are often referred to as the matric potential of the soil. Soil scientists quantify soil water potential in terms of pressure. In the International System of Units (see Appendix A), the unit of pressure is the pascal (Pa) or the megapascal (MPa), where 1 MPa equals 1 million Pa. However, in this book, we shall use the more familiar unit of the atmospheric pressure at the surface of the earth. One atmosphere (1 atm) is equal to 101,325 Pa, or 0.1 MPa. By convention, water potentials
Figure 3.2 Finer-grained soils hold more water. Soils with large grain sizes have large spaces between them that are not filled completely at field capacity.

are expressed as negative values because potentials measure the capacity of one substance to extract water from another. Larger negative values indicate greater water potential. Water moves in the direction of the lower (more negative) water potential—that is, toward the substance with the strongest attraction for water.

Matric potential is greatest at the surface of soil particles and decreases with distance from them. Water held by a matric potential of less than about −0.1 atm drains out of the soil under the pull of gravity and joins the groundwater in the crevices of the bedrock below. This applies to water in the interstices between large soil particles, which is generally more than 0.005 mm from their surfaces. The amount of water held against gravity by water potential more negative than −0.1 atm is called the field capacity of the soil. Imagine a particle of silt with a diameter of 0.01 mm enlarged to the size of this page (×25,000); the film of water held at field capacity by the matric potential would be as thick as half the width of the page.

As soils dry out, the remaining water is held with increasingly stronger force, on average, because a greater proportion of the water lies close to the surfaces of soil particles. Soils having water potentials as great as −100 atm are very dry. Most plants can extract water held with water potentials as great as −15 atm. At more negative water potentials, plants wilt, even though some water still remains in the soil. Thus, ecologists refer to a water potential of −15 atm as the wilting coefficient or wilting point of the soil.

Plants obtain water from the soil by the osmotic potential of their root cells

Water in the environment and in the bodies of organisms has many substances dissolved in it. Dissolved substances, called solutes, influence the diffusion of water molecules. Plants take advantage of the tendency of water to move from regions of low solute concentration (high water concentration) to regions of high solute concentration. Ions and other solutes diffuse through water in the opposite direction—from regions of high concentration to regions of low concentration. This movement of ions and water molecules tends to even out concentrations of solutes within a volume of water. Water also moves readily across most biological membranes. Thus, when a cell maintains a high concentration of ions and other solutes, water tends to move from the surrounding environment into the cell. This process is called osmosis. The force with which a solution attracts water by osmosis is known as its osmotic potential. Like the water potential of soil, osmotic potential is expressed as a pressure; specifically, as the pressure that would be required to keep water from diffusing into the solution (Figure 3.3). It is the osmotic potential in the roots of trees that causes water to enter the roots from the soil against the attraction of soil particles.

If the solute responsible for the osmotic potential of a solution also can diffuse across cell membranes, then its concentration within cells and its concentration in the surrounding water will eventually come into equilibrium. At this point, the osmotic potentials of the cell and its surroundings will be equal, and there will be no net movement of water across the cell membrane. This equalization of osmotic potential can be prevented by two mechanisms. First, a membrane can be semipermeable, meaning that some small molecules and ions can diffuse across it, but larger ones cannot. Many carbohydrates and most proteins are too large to pass through the pores of a cell membrane. Membranes may also transport ions and small molecules actively against a diffusion gradient to maintain their concentrations within the cell. However, this active transport requires expenditure of considerable energy.

The osmotic potential generated by an aqueous solution depends on the concentration of the solute. More specifically, it depends on the number of solute molecules or ions per volume of solution. Thus, a given mass of a
small solute generates greater osmotic potential than the same mass of a larger molecule. You will remember from your introductory chemistry course that the concentration of molecules in solution is expressed in terms of gram molecular weights, or moles, per liter. For example, the sugar glucose (C₆H₁₂O₆) has a molecular weight of 180, and so a 1 molar solution of glucose contains 180 grams of glucose per liter of water.

A molar concentration of a substance in solution creates an osmotic potential of −21 atmospheres. Thus, the water potential of the root hair cells of plants with a wilting point of −15 atm is equivalent to the osmotic potential of an approximately 0.7 molar solution. Plants growing in deserts and salty environments have been shown to increase (make more negative) the water potential of their roots to as much as −60 atm by increasing the concentrations of amino acids, carbohydrates, or organic acids in their root cells. They pay a high metabolic price, however, to maintain such concentrations of dissolved substances.

**Forces generated by transpiration help to move water from roots to leaves**

Osmotic potential draws water from the soil into the cells of plant roots. But how does the water get from the roots to the leaves? Plants conduct water to their leaves through xylem elements, which are the empty remains of xylem cells in the cores of roots and stems, connected end-to-end to form the equivalent of water pipes. For water to flow into these elements, their water potential must be more negative than that in the living cells of roots, into which water enters from the soil. Then, for water to move through the xylem from roots to leaves, the water potential of the leaves must exceed that of the roots enough to draw water upward against the osmotic potential of the root cells, the pull of gravity, and the resistance of the xylem elements.

Leaves generate water potential when water evaporates from leaf cell surfaces into the atmosphere, a process known as transpiration. Dry air at 20°C has a water potential of −1,332 atm. Thus, even with high relative humidity, air has more than enough water potential to pull water through the roots, xylem, and leaves. Transpiration creates a continuous gradient of more negative water potential from the soil to the air.

The water potential that is produced in leaf cells by transpiration has led to the tension–cohesion theory of water movement (Figure 3.4). This theory states that the force required to move water within xylem elements is generated when water moves from the vessels in the vascular tissues of leaves to leaf cells to replace transpiration losses. This force, which represents a water potential as high as −20 to −50 atm, is transmitted all the way to the roots of the plants through the water column in the xylem elements.
of the stem. Thus, water is literally pulled from the roots by the force generated from transpiring leaves. The water potential required to overcome soil water potential and draw water against the force of gravity to the top of a tall tree represents a force equivalent to many atmospheres.

Adaptations to arid environments control loss of water from leaves

For plants that live in dry habitats, where water is limiting, the rate of photosynthesis represents a balance between the need to acquire carbon dioxide and the need to conserve water. Openings at the leaf surfaces, called stomates (Figure 3.5), are the point of entry for CO₂, and also allow water to escape to the atmosphere by transpiration. Plants control water loss by closing their stomates. As leaf water potential decreases, the cells bordering the stomates collapse slightly and close the openings. This prevents further water loss, and also prevents carbon dioxide from entering the leaf.

The loss of water that accompanies the uptake of CO₂ presents a problem for plants in hot climates (see Figure 2.9). And because the vapor pressure of water increases with temperature, heat magnifies the problem of water loss. Heat- and drought-adapted plants have anatomic and physiologic modifications that reduce transpiration across plant surfaces, reduce heat loads, and enable plants to tolerate high temperatures. When plants absorb sunlight, they heat up. Plants can minimize overheating by increasing their surface area for heat dissipation and by protecting
are cool, but less so in hot deserts. Plants may further reduce transpiration by covering their surfaces with a thick, waxy cuticle that is impervious to water and by recessing the stomates in deep pits, often themselves filled with hairs (Figure 3.7).

Plants obtain mineral nutrients from soil water

Plants acquire mineral nutrients—primarily nitrogen, phosphorus, potassium, and calcium—from dissolved ionic forms of these elements in soil water. Their uptake of abundant elements whose ions diffuse rapidly in the soil solution, such as calcium (Ca$^{2+}$) and magnesium (Mg$^{2+}$), is limited primarily by the absorptive capacity of the roots. Plants compensate for low levels of a nutrient in the soil by active transport or by increasing root growth.

In laboratory experiments, barley and beet roots took up phosphorus by diffusion when its concentration in the water surrounding the roots exceeded a critical level, approximately 0.2–0.5 millimolar (mM) (1 millimole equals one-thousandth of a mole), which is slightly higher than the concentration of phosphorus in root tissues. However, at soil concentrations below 0.2–0.5 mM, the rate of phosphorus uptake by diffusion would have been too low to meet the plant's needs, and the roots actively transported phosphorus across their surfaces. Active transport requires the expenditure of energy as the root tissue moves ions against a concentration gradient.

Plants may also respond to a scarcity of soil nutrients by increasing the extent of the root system. When plants increase their root growth, they do so at the expense of their surfaces from direct sunlight with dense hairs and spines (Figure 3.6). Spines and hairs also produce a still boundary layer of air that traps moisture and reduces evaporation. Because thick boundary layers retard heat loss as well, hairs are prevalent in arid environments that


Figure 3.6 Spines and hairs help plants adapt to heat and drought. (a) Cross section and (b) surface view of the leaf of the desert perennial herb Encelia argophylla, which uses this strategy. Courtesy of J. R. Ehleringer. From H. R. Ehleringer, in E. Rodrigues, P. Healy, and I. Mehta (eds.), Biology and Chemistry of Plant Trichomes, Plenum Press, New York (1984), pp. 113–132.
Figure 3.7 Oleander, a drought-resistant plant, reduces water loss by placing its stomates in hair-filled pits on the leaf’s undersurface. The hairs reduce water loss by slowing air movement and trapping water. The photo on the right, showing the pit in detail, is magnified about 400 times. The dark red staining cells in the pit lining are the guard cells surrounding the stomate openings. Photos by Jack M. Bostrack/Visuals Unlimited.

Shoot growth (Figure 3.8). This strategy balances the nutrient requirements of the plant with nutrient availability by reducing the nutrient demand created by the leaves, increasing the absorptive surface area of the root system, and sending roots into new areas of soil from which the plant has not already removed scarce minerals.

Species adapted to nutrient-poor soils may also cope with low nutrient availability by establishing symbiotic relationships with fungi, which enhance mineral absorption, and by growing slowly and retaining leaves for long periods, thereby reducing nutrient demand. Such species typically cannot respond to artificially increased nutrient levels by increasing their growth rates. Instead, their roots absorb more nutrients than the plant requires and store them for subsequent use when the soil nutrient availability declines.

ECOLOGISTS IN THE FIELD

Effects of patchy soil nutrients on plant growth

Like most of the environment, soils are heterogeneous, often at very small scales. The nutrient supply in a small patch of soil depends on recent inputs from decaying wood, fruits, leaves, feces, urine, and bodies of animals as well as disturbances, such as trampling and burrowing, and local depletion of nutrients by plant roots. In one study in a sagebrush steppe habitat near Logan, Utah, pairs of soil samples only 12.5 cm apart varied by a factor as high as 12 in available nitrogen. Samples 3 cm apart varied on average by a factor of almost 3. How do plants respond to so much variation in their immediate environments? Do plants grow better or worse in highly heterogeneous soils than in uniform soils? Do all plants respond in the same way to this variation?
To answer these questions, James Cahill and Brenda Casper, at the University of Pennsylvania in Philadelphia, grew two common herbaceous plants individually in pots having either patchy or uniform distributions of nutrients in the soil. The plants were ragweed (Ambrosia artemesitia) and pokeweed (Phytolacca americana). Nutrients were added to the soil in the form of 75 ml of dried cow manure, which was either mixed uniformly throughout the soil (homogeneous treatment) or concentrated in a 1.5 cm diameter hole approximately 5 cm from the center of the pot (heterogeneous treatment). The plants were watered on a regular basis. After 9 weeks, Cahill and Casper terminated the experiments and determined the dry masses of the root and shoot portions of the plants. Roots were removed from the soil by washing them over a fine sieve. In both species, shoot biomass was greater in the heterogeneous soil than in the homogeneous soil (Figure 3.9). Although the total root biomass did not differ between treatments for either species, both grew higher densities of roots in the cow manure patches in the heterogeneous treatment. Because of the high concentration of nutrients in these patches, the rate of nutrient uptake increased enough to support faster growth above ground.

It was surprising, therefore, that when ragweed and pokeweed were grown together in the same pot, heterogeneous soils did not stimulate greater shoot growth in either species. One explanation is that both plants grew roots into the nutrient patch and divided the nutrients between them, causing nutrient levels in the patch to drop to levels too low to stimulate aboveground growth. These experiments show that plants can respond to variations in nutrient levels in the soil, but they also suggest that fine-scale heterogeneity may not be so important in natural environments, where the root responses of plants quickly exhaust patches of concentrated nutrients. Thus, by seeking out and utilizing nutrient patches, plants tend to increase the uniformity of the soil on a local scale.

Photosynthesis varies with levels of light

The rate of photosynthesis in plants varies in direct proportion to the amount of light under low light intensities. With brighter light, however, the rate of photosynthesis increases more slowly or levels off as intensity increases. The response of photosynthesis to light intensity has two reference points (Figure 3.10). The first, called the compensation point, is the level of light intensity at which photosynthetic assimilation of energy just balances plant respiration. Above the compensation point, the energy balance of the plant is positive; below the compensation point, the energy balance is negative. The second reference point is the saturation point, above which the rate
where RuBP (ribulose bisphosphate) is a five-carbon compound. Because the product of this step is a three-carbon compound, biologists call this pathway C₃ photosynthesis. 3PG then enters what is known as the Calvin–Benson cycle, which regenerates one molecule of RuBP while making one carbon atom available to synthesize glucose. All of these processes occur in the mesophyll cells of the leaves.

The enzyme responsible for the assimilation of carbon, RuBP carboxylase, has a low affinity for carbon dioxide. Consequently, at the low concentration of CO₂ found in the atmosphere and the resulting low concentration in the mesophyll cells, plants assimilate carbon inefficiently. To achieve high rates of carbon assimilation, plants must pack their mesophyll cells with large amounts of RuBP carboxylase—up to 30% of the dry weight of leaf tissue. However, this enzyme also catalyzes the reverse reaction,

$$2 \text{3PG} \rightarrow \text{CO}_2 + \text{RuBP},$$

in the presence of high oxygen and low carbon dioxide concentrations, especially at elevated leaf temperatures. This reaction partially undoes what RuBP carboxylase accomplishes when it assimilates CO₂, making photosynthesis inefficient and self-limiting. Carbon assimilation therefore tends to inhibit itself as levels of CO₂ decline and levels of oxygen produced by photosynthesis increase in the leaves. Plants could lessen this condition by keeping their stomata open—but that, of course, would lead to high water loss.

**C₄ photosynthesis**

Raising the concentration of CO₂ and reducing the concentration of O₂ in the leaf tissue could solve the problem of water loss created by the inefficiency of C₃ photosynthesis. Many plants in hot climates modify C₃ photosynthesis by using a different initial step in the assimilation of carbon dioxide as well as by spatially separating that initial assimilation step from the Calvin–Benson cycle within the leaf. Biologists call this modification C₄ photosynthesis because the assimilation of CO₂ initially results in a four-carbon compound:

$$\text{CO}_2 + \text{PEP} \rightarrow \text{OAA},$$  
$$1 \text{carbon} \quad 3 \text{carbons} \quad 4 \text{carbons}$$

where PEP (phosphoenol pyruvate) contains three carbons and OAA (oxaloacetic acid) contains four. The assimilatory reaction is catalyzed by the enzyme PEP carboxylase, which, unlike RuBP carboxylase, has a high affinity for CO₂. Assimilation occurs in the mesophyll cells.
C₃ PLANT

C₃ cell arrangement

Upper epidermis
Palisade mesophyll cell
Vein
Spongy mesophyll cell
Lower epidermis

Bundle sheath cells lack chloroplasts.

C₄ PLANT

C₄ cell arrangement

Mesophyll cell

Close association permits CO₂ pumping from mesophyll cells to bundle sheath cells for the Calvin-Benson cycle.

Bundle sheath cells have chloroplasts.

C₃ photosynthesis

Mesophyll cell

CO₂

Calvin-Benson cycle

3PG (3-carbon compound)

RUBP (5-carbon compound)

Sugars

The CO₂ is used in the Calvin-Benson cycle when sugars are produced.

C₄ photosynthesis

Mesophyll cell

CO₂ (from air space)

OAA (4-carbon compound)

PEP

Pyruvate (3-carbon compound)

Bundle sheath cell

CO₂

3PG

Sugars

C₄ compounds release CO₂ within the cells.

Crassulacean acid metabolism

Night

CO₂

OAA

PEP

Pyruvate

C₄ compounds

Day

Sugars
The process of photosynthesis is modified in plants in water-stressed habitats. (a) A C₃ plant, the wild dovefoot geranium (Geranium molle); (b) A C₄ plant, cultivated sorghum (Sorghum vulgare); (c) a CAM plant, the Sierra sedum (Sedum obtusatum). Below the photos are idealized cross sections of a leaf, illustrating the locations of chloroplasts (small dark green dots) in each plant type. At the bottom, the major steps of the Calvin–Benson cycle are shown for each plant type. Photo (a) by Bert Kragis/Visuals Unlimited; photo (b) by John Spragens, Jr; photo (c) by John Gerlach/DRK Photo.

of the leaf, but in most C₄ plants, photosynthesis (including the Calvin–Benson cycle) takes place in specialized cells surrounding the leaf veins, called bundle sheath cells (Figure 3.11b). Oxaloacetic acid diffuses into the bundle sheath cells, where it is converted to malic acid, which then breaks down to produce CO₂ and pyruvate, a three-carbon compound. The CO₂ enters the Calvin–Benson cycle, just as it does in C₃ plants. The pyruvate moves back into the mesophyll cells, where enzymes convert it to PEP. This strategy solves the problem of creating high concentrations of CO₂ in leaf tissue. Because the bundle sheath cells are removed from the surface of the leaf, oxygen concentrations also are reduced.

C₄ photosynthesis confers an advantage because CO₂ can be concentrated within the bundle sheath cells to a level that far exceeds its equilibrium established by diffusion from the atmosphere. At this higher concentration, the Calvin–Benson cycle operates more efficiently. Also, because the enzyme PEP carboxylase has a high affinity for CO₂, it can bind CO₂ at a lower concentration in the cell, thereby allowing the plant to open its stomates less and reduce water loss. The disadvantage of C₄ carbon assimilation is that less leaf tissue is devoted to photosynthesis itself, thereby reducing the maximum potential photosynthetic rate. Consequently, C₃ photosynthesis is favored in cool climates with abundant soil water.

Salt balance and water balance go hand in hand

The water balance of aquatic animals is closely tied to the concentrations of salts and other solutes in their body tissues and in the environment. The osmotic potential of seawater is about −12 atmospheres, and that of fresh water is close to zero. The body fluids of vertebrate animals, which have an osmotic potential of about −3 to −5 atm (30–40% of that of seawater), occupy an intermediate position. Thus, the tissues of freshwater fish have higher concentrations of salts than the surrounding water. Such organisms, which are hyperosmotic, tend to gain water from and lose solutes to their surroundings. Marine fish, which have lower concentrations of salts than the surrounding seawater, are referred to as hypo-osmotic. They tend to gain solutes and lose water. Fish solve these osmotic problems by using active transport mechanisms to pump ions in one direction or the other across various body surfaces (skin, kidney tubules, and gills), expending considerable energy in the process.

Ion retention is critical to freshwater organisms

Freshwater fish continuously gain water by osmosis across the surfaces of the mouth and gills, which are the most
permeable of their tissues that are exposed to the surroundings, and in their food (Figure 3.12). To counter this influx, fish eliminate excess water in their urine. If fish did not also selectively retain dissolved ions, however, they would soon become lifeless bags of water. The kidneys of freshwater fish retain salts by actively removing ions from the urine and infusing them back into the bloodstream. In addition, the gills can selectively absorb ions from the surrounding water and release them into the bloodstream.

Water retention is critical to marine organisms

Marine fish are surrounded by water with a salt concentration higher than that of their bodies. As a result, they tend to lose water to the surrounding seawater and must drink seawater to replace it (see Figure 3.12). The salt that comes in with the water and with food, as well as that which diffuses in across body surfaces, must be excreted at great metabolic cost from the gills and kidneys.

Some sharks and rays have found a solution to the problem of water flux. Sharks retain urea, CO(NH₂)₂—a common nitrogenous waste product of metabolism in vertebrates—in the bloodstream instead of excreting it from the body in the urine. The urea raises the osmotic potential of the blood to the level of seawater without any increase in the concentration of sodium and chloride ions (Figure 3.13). Consequently, there is no net movement of water across a shark’s surfaces. This makes it much easier for sharks to regulate the flux of ions such as sodium because they do not have to drink extra salt-laden water to replace water lost by osmosis. The fact that freshwater species of sharks and rays do not accumulate urea in their blood emphasizes the importance of urea for osmoregulation in marine members of this group.

The small copepod Tigrionus takes an approach to water balance similar to that of sharks. Tigrionus lives in pools high in the splash zone along rocky coasts (Figure 3.14). These pools receive seawater infrequently from the splash of high waves, and as the water evaporates, the salt concentration rises to high levels. A heavy rainfall, on the other hand, can rapidly lower the salt concentration in these pools. Ron Burton, at the Scripps Institute of Oceanography, has shown that Tigrionus, like sharks, manages its water balance by changing the osmotic potential of its body fluids. When salt concentration is high, it synthesizes large quantities of certain amino acids such as alanine and proline. These small molecules increase the osmotic potential of the body to match that of the habitat, without the deleterious physiological consequences of high levels of salt. This response to salt stress is costly, however. In a laboratory experiment, individual Tigrionus were switched from 50% seawater to 100% seawater, as might happen when waves at high tide filled a pool previously flushed with rainwater. In response to this change, the respiration rate of the copepods initially declined, owing to the initial
salt stress, and then increased as they synthesized alanine and proline to restore their water balance (Figure 3.15). When salinity was suddenly decreased from 100% of seawater down to 50% of seawater, their respiration rate immediately increased as excess free amino acids were rapidly degraded and metabolized.

Certain environments pose special osmotic problems. Aquatic environments with salt concentrations greater than that of seawater occur in some landlocked basins, particularly in dry regions where evaporation considerably exceeds precipitation. The Great Salt Lake (20% salt, or about six times saltier than normal seawater) in Utah and the Dead Sea (23% salt), lying between Israel and Jordan, are well-known examples of such hypersaline environments. The osmotic potentials of these bodies of water—well in excess of -100 atm—would shrivel most organisms. However, a few aquatic creatures, such as brine shrimp (Artemia), can survive in salt water concentrated to the point of crystallization (300 grams per liter, or 30%). Brine shrimp excrete salt at a prodigious rate, and a high energy cost, to keep the salts in their body fluids less concentrated than those in their surroundings.

Figure 3.14 The tiny copepod Tigriopus lives in splash pools high in the rocky intertidal zone in California. Photo (a) courtesy of Ron Burton; photo (b) by R. E. Ricklefs.
Water balance and salt balance in terrestrial organisms

Terrestrial plants transpire hundreds of grams of water for every gram of dry matter they accumulate in tissue growth, and they inevitably take up salts along with the water that passes into their roots. In saline environments, plants actively pump excess salts back into the soil across their root surfaces, which therefore function as the plant’s “kidneys.” Mangrove plants grow on coastal mudflats that are inundated daily by high tides (Figure 3.16). Not only does this habitat impose a high salt load, but the high osmotic potential of the root environment also makes it difficult for the roots to take up water. To counter this problem, many mangrove plants have high levels of organic solutes, such as the amino acids proline and glycinebetaine and the six-carbon sugar sorbitol, in their roots and leaves to increase their osmotic potential. In addition, they have salt glands that secrete salt by active transport to the exterior surface of the leaves. The roots of many species exclude salts, apparently by means of semipermeable membranes that do not allow the salts to enter. Mangrove plants further reduce salt loads by decreasing the transpiration of water from their leaves.

Because many of these adaptations resemble those of plants from environments where water is scarce, the mangrove habitat has been referred to as an osmotic desert.

Because they are not immersed continuously in fresh water, terrestrial animals have little trouble retaining ions. They acquire the mineral ions they need in the water they drink and the food they eat. Lack of sodium in some areas forces animals to obtain salt directly from such mineral sources as salt licks, but most terrestrial animals obtain more salts in their food than they need. They eliminate the excess salts in their urine.

Where fresh water abounds, animals can drink large quantities of water to flush out salts that would otherwise accumulate in the body. Where water is scarce, however, animals must produce a concentrated urine to conserve water. And so, as one would expect, desert animals have champion kidneys. For example, whereas humans can concentrate most solutes in their urine to about 4 times the level in their blood plasma, the kangaroo rat’s kidneys produce urine with a concentration as high as 14 times that of its blood, and the Australian hopping mouse, another desert-adapted species, produces urine that has 25 times the solute concentration of its blood. Because

![Figure 3.15](image-url) *Tigriopus* alters free amino acid levels and metabolic rate in response to hyperosmotic stress (50% to 100% seawater, left) and hypo-osmotic stress (100% to 50% seawater, right). From E. M. Gooch and R. S. Burton, *Functional Ecology* 3:81–89 (1989).
Figure 5.16 Mangrove plants have adaptations for coping with a high salt load.
(a) The roots of mangrove vegetation are immersed in salt water at high tide. Some species exclude salt from their roots. (b) Specialized glands in the leaves of the button mangrove, Conocarpus erecta, excrete salt, which precipitates on their outer surfaces. Photos by R. E. Ricklefs.

Sodium and chloride ions are part of the mechanism by which the kidney retains water, the kidney is not particularly effective at excreting these ions. Hence, many organisms lacking access to fresh water have specialized salt-secreting organs. Birds and reptiles have "salt glands," which are modified tear glands located in the orbit of the eye and which are capable of secreting a concentrated salt solution. These glands are especially well developed in species that feed on marine organisms and receive high salt loads in their diets.

The following experiment shows the relative importance of the salt gland in ridding the body of excess sodium ions. A gull was given 134 ml of seawater containing 63 millimoles (mmol) of sodium—a concentration of 470 mM. After 3 hours, it had excreted 47.3 mmol of sodium in 56.3 ml of water from the salt gland, at a concentration of 800 mM, nearly twice the concentration of salt in seawater. At the same time, only 4.4 mmol of sodium were excreted by the kidneys, in 75.2 ml of water at an average concentration of 59 mM. Without the salt gland, the gull could not rid itself of salt in its diet without losing too much water.

Animals excrete excess nitrogen in the form of small organic molecules.

Most carnivores, whether they eat crustaceans, fish, insects, or mammals, consume excess nitrogen in their diets. This nitrogen, which is part of the proteins and nucleic acids of their prey, must be eliminated from the body when these compounds are metabolized. Most aquatic animals produce the simple metabolic by-product ammonia (NH₃). Although ammonia is mildly poisonous to tissues, aquatic animals eliminate it rapidly in a copious, dilute urine, or
directly across the body surface, before it reaches a
dangerous concentration within the body. Terrestrial animals
cannot afford to use large quantities of water to excrete
nitrogen. Instead, they produce metabolic by-products that
are less toxic than ammonia and which can therefore accu-
mulate to higher levels in the blood and urine without dan-
ger. In mammals, this waste product is urea ($\text{CO(NH}_2\text{)}_2$),
the same substance that sharks produce and retain to
achieve osmotic balance in marine environments. Because
urea dissolves in water, excreting it requires some urinary
water loss—how much depends on the concentrating
power of the kidneys. Birds and reptiles have carried adap-
tation to terrestrial life one step further: they excrete nitro-
gen in the form of uric acid ($\text{C}_4\text{H}_4\text{N}_4\text{O}_3$), which crystallizes
out of solution and can then be excreted as a highly con-
centrated paste in the urine. Although excreting urea and
uric acid saves water, there is also a cost, which is the
energy lost in the organic carbon used to form these com-
 pounds. For each atom of nitrogen excreted, 0.5 and 1.25
atoms of organic carbon are lost in urea and uric acid
respectively.

Water conservation
mechanisms are important
in hot environments

When air and substrate temperatures approach or exceed
the maximum tolerable body temperature, animals can
dissipate heat only by evaporating water from their skin
and respiratory surfaces. In deserts, the scarcity of water
makes evaporative heat loss a costly mechanism; animals
often must reduce their activity, seek cool microclimates,
or undertake seasonal migrations to cooler regions. Many
desert plants orient their leaves in such a way as to avoid
the direct rays of the sun; others shed their leaves and
become inactive during periods of combined heat and
water stress.

Among mammals, the kangaroo rat is well suited to
life in a nearly waterless environment (Figure 3.17). Its
large intestine resorbs water from waste material so effi-
ciently that it produces virtually dry feces. Kangaroo rats
also recover much of the water that evaporates from their
lungs by condensation in their enlarged nasal passages.
When the kangaroo rat inhales dry air, moisture in its nasal
passages evaporates, cooling the nose and saturating the
inhaled air with water. When moist air is exhaled from the
lungs, much of the water vapor condenses on the cool
nasal surfaces. By alternating condensation with evapora-
tion during breathing, the kangaroo rat reduces its respira-
tory water loss. The cold, moist nose of a dog serves the
same function.

Kangaroo rats avoid the desert's greatest heat by feed-
ing only at night, when it is cooler; during the blistering
heat of the day, kangaroo rats remain comfortably below
ground in their cool, humid burrows. In sharp contrast,
ground squirrels remain active during the day. They also
conserve water by restricting evaporative cooling. As you
would expect, their body temperatures rise when they
forage above ground, exposed to the hot sun. How do
they manage? Before their body temperatures become
dangerously high, they return to their burrows, where they
cool down by conduction and radiation rather than by
evaporation. By shuttling back and forth between their
burrows and the surface, ground squirrels extend their
activity into the heat of the day and pay a relatively small
price in water loss.

Like that of the ground squirrel, the camel's body tem-
perature rises in the heat of the day—by as much as 6°C.
Large body size gives the camel a distinct advantage, how-
ever. Because of its low surface to volume ratio, the camel
heats up so slowly that it can remain in the sun most of
the day. It dumps excess heat at night by conduction and
radiation to the cooler surroundings.
Organisms maintain a constant internal environment

**Homeostasis** is an organism's ability to maintain constant internal conditions in the face of a varying external environment. All organisms exhibit homeostasis to some degree, as we have seen in the case of water and salt balance, although the occurrence and effectiveness of homeostatic mechanisms vary. Regardless of how organisms regulate their internal environments, all homeostatic systems exhibit negative feedback, meaning that when the system deviates from its norm, or desired state, internal response mechanisms act to restore that state. Those of you who use thermostats to control temperature in your homes can readily understand how a negative feedback system works. When the house is cold, a temperature-sensitive switch turns on a heater, which restores the temperature to its desired setting. Homeostatic mechanisms in animals and plants work in much the same way (Figure 3.18).

Most mammals and birds maintain their body temperatures between 36°C and 41°C, even when the temperature of their surroundings may vary from −50°C to +50°C. Such temperature regulation, which is referred to as [homeothermy](https://en.wikipedia.org/wiki/Homeothermy) (the Greek root *homo* means "same"), creates constant temperature (homeothermic) conditions within cells, under which biochemical processes can proceed efficiently. Cold-blooded, or [poikilothermic](https://en.wikipedia.org/wiki/Poikilothermy), organisms, such as frogs and grasshoppers, conform to the external temperature (the Greek root *poikilos* means "varying"). Thus, frogs cannot function at either high or low temperature extremes, so they are active only within a narrow part of the range of environmental conditions over which mammals and birds thrive.

Many so-called cold-blooded organisms, including reptiles, insects, and plants, adjust their heat balance behaviorally simply by moving into or out of shade, by changing their orientation with respect to the sun, or by adjusting their contact with warm substrates. When horned lizards are cold, they lie flat against the ground and gain heat by conduction from the sun-warmed surface. When hot, they decrease their exposure to the surface by standing erect upon their legs. Basking behavior is widespread among reptiles and insects, which can use it effectively to regulate their body temperatures within a narrow range. Indeed, their temperatures may rise considerably above that of surrounding air, well into the range of the "warm-blooded" birds and mammals. Because their source of heat lies outside the body, biologists refer to these animals as [ectotherms](https://en.wikipedia.org/wiki/Ectothermy) (external heat), animals that generate their body heat internally are referred to as [endotherms](https://en.wikipedia.org/wiki/Endothermy) (internal heat).

**Homeostasis is costly**

Sustaining internal conditions that differ significantly from the external environment requires work and energy. Let us consider the costs to birds and mammals of maintaining constant high body temperatures in cold environments. As air temperature decreases, the gradient (difference) between internal and external environments increases. Heat is lost across body surfaces in direct proportion to this gradient. An animal that maintains its body temperature at 40°C loses heat twice as fast at an ambient (surrounding) temperature of 20°C (a gradient of 20°C) as at an ambient temperature of 30°C (a gradient of only 10°C). To maintain a constant body temperature, endothermic organisms replace heat lost to their environment by generating heat metabolically. Thus, the rate of metabolism required to maintain body temperature increases in direct proportion to the difference between body and ambient temperature, all other things being equal.
Limits to homeothermy

An organism's ability to sustain a high body temperature while exposed to extremely low ambient temperatures is limited. Over the short term, the physiological capacity to generate heat limits heat production, and therefore defines the coldest temperature that a homeotherm can withstand. Over the long term, a homeotherm is limited by its ability to gather food or metabolize nutrients to satisfy the energy requirements of generating heat. The maximum rate at which an organism can perform work, even during the most strenuous exercise, generally does not exceed ten to fifteen times its minimum, or basal, level of metabolism. Such high rates of metabolism, typical of a bird in flight, are rarely maintained for more than a few minutes or hours at a time. Over the course of a day, few organisms—even migrating birds—expend energy at a rate exceeding four or five times the basal metabolic rate.

When the environment becomes so cold that heat loss exceeds an organism's physiological capacity to produce heat, body temperature begins to drop, a condition that is fatal to most homeotherms. The lowest environmental temperatures that homeotherms can survive for long periods often depend on their ability to gather food, rather than on their ability to assimilate and metabolize the energy in food. At low temperatures, animals may starve rather than freeze to death when they metabolize food energy to maintain body temperature more rapidly than they can gather food.

Partial homeostasis

All birds and mammals generate heat metabolically to regulate body temperature, but many cold-blooded species also become endothermic or partially endothermic at times. Pythons, for example, maintain high body temperatures while incubating eggs. Some large fishes, such as the tuna, maintain temperatures up to 40°C in the center of their metabolically active muscles; swordfish employ special metabolic heaters, derived from muscle tissue, to keep their brains warm. Large moths and bees often require a preflight warm-up period during which the flight muscles shiver to generate heat. Even some plants, notably philodendron and skunk cabbage, use metabolic heat production to raise the temperature of their floral structures. In this case, the high temperatures volatilize chemicals used to attract insect pollinators.

Because they are small, hummingbirds have a large exposed surface area relative to their mass, and consequently lose heat rapidly relative to the amount of tissue that is available to produce it. As a result, hummingbirds must sustain very high metabolic rates to maintain their at-rest body temperatures near 40°C. Species living in cool climates would starve overnight if they did not enter torpor, a voluntary, reversible condition of lowered body temperature and inactivity. The West Indian hummingbird, *Eulampis jugularis*, drops its body temperature to between 18°C and 20°C when resting at night. It does not cease to regulate its body temperature; it merely changes the setting on its thermostat to reduce the difference between ambient and body temperature, and thereby reduces the energy expenditure needed to maintain its temperature at the regulated set point (Figure 3.19).

Large animals deliver oxygen to their tissues through circulatory systems

Most animals release the chemical energy contained in organic compounds primarily by respiration. Because oxygen plays such an important role in this process, low availability of oxygen can restrict metabolic activity. Oxygen availability is a particular problem in aquatic habitats, where its solubility is low and its diffusion is slow. Even ter-
restrial organisms, which breathe an atmosphere containing abundant oxygen, must get oxygen through an aqueous medium to all the tissues of the body.

Active organisms require an abundant supply of oxygen for cell respiration. Diffusion can satisfy the oxygen needs of tiny aquatic organisms, but the centers of organisms larger than about 2 mm in diameter are too far from the external environment for diffusion to ensure a rapid supply of oxygen. Tissue metabolism consumes diffusing oxygen before it has gone much farther than a millimeter. Insects have solved this problem with systems of branching pipes (tracheae) that carry air directly to the tissues (Figure 3.20). Other animals have blood circulatory systems to distribute oxygen from the respiratory surfaces to the body.

Complex protein molecules such as hemoglobin and hemocyanin, to which oxygen molecules readily attach, increase the oxygen-carrying capacity of the blood of most animals. While blood plasma can carry only a small amount of oxygen in solution (about 1% by volume), whole blood can transport up to 50 times more oxygen bound to these oxygen-carrying molecules. In most animals utilizing hemoglobin, including all vertebrates, this protein is packed densely into red blood cells, whose color is that of hemoglobin. When oxygen binds to hemoglobin—four molecules of oxygen can bind to each molecule of hemoglobin—it comes out of solution in the blood plasma, making room for the diffusion of more oxygen into the blood from the lungs or gills. In the body tissues, where oxygen concentrations are low, the binding process reverses, and oxygen is released (Figure 3.21).

These adaptations for procuring oxygen illustrate a set of solutions to the problems that organisms confront at the

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**Figure 3.20** Insects get oxygen to their body tissues through the tracheal system, a system of branching pipes through which air can move. Scanning electron micrograph courtesy of Thomas Eisner, Cornell University.

**Figure 3.21** Most circulatory systems have oxygen-binding proteins. The binding of oxygen by hemoglobin in the red blood cells lowers the concentration of dissolved oxygen in the blood plasma and speeds the diffusion of oxygen from the lungs into the bloodstream. In the body's tissues, where the concentration of oxygen is low, the process is reversed, and oxygen is offloaded from hemoglobin and diffuses toward regions of high metabolic rate.
interface between themselves and their environments. The hemoglobin molecule, which must bind oxygen efficiently in the lungs but release it easily in the tissues, demonstrates that adaptation often requires compromise. No hemoglobin molecule designed only for maximum efficiency of oxygen binding could also release oxygen easily where it was needed, and vice versa. Therefore, the hemoglobin molecules that have evolved represent a compromise between these two functions.

**Countercurrent circulation increases transfer of heat and substances between fluids**

Solute diffusion from regions of high concentration to regions of low concentration. With time, this movement equalizes concentrations, and the net movement of solutes stops. Heat is conducted from hotter to cooler substances. Eventually temperatures equalize, and net movement of heat comes to a standstill. Thus, diffusion reduces the efficiency of gas exchange and the transport of ions in excretory organs, and conduction works against the retention of heat within the body. How do organisms counteract these problems?

Such problems have been solved in many cases by a simple and effective arrangement of vessels carrying moving fluids called **countercurrent circulation**. This mechanism is illustrated by the structure of fish gills, which causes water and blood to flow in opposite directions ([Figure 3.22](#)). In a countercurrent system, blood moving in one direction continually encounters water flowing past in the opposite direction. This water has progressively greater oxygen concentrations because it has traveled a progressively shorter distance along the gill lamella. This arrangement maintains a large gradient of oxygen concent-

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**Figure 3.22** A fish's gill is designed to promote countercurrent circulation of blood and water. The gill consists of several gill arches, each of which carries two rows of filaments. The filaments have thin lamellae (leaflike structures) oriented parallel to the flow of water through the gill. Within the lamellae, blood flows in the direction opposite to the movement of water past the surface, establishing a countercurrent circulation. From D. J. Randall, *Am. Zool.* 8:179–189 (1968).
traition between the blood plasma and the surrounding water, so that the oxygen from the water diffuses readily into the blood. With this mechanism, the oxygen concentration in the blood can approach the concentration in the surrounding water.

The countercurrent circulation principle appears frequently in adaptations that increase the flux of heat or materials between fluids. Among terrestrial organisms, birds have a unique lung structure that, unlike that of the lungs of mammals, results in a one-way flow of air opposite to the flow of blood. This adaptation allows birds, with lungs whose weight and volume are small, to achieve the high rates of oxygen delivery required by their active lives. The extremities of some birds and mammals have countercurrent blood circulation to reduce loss of heat to the surrounding environment. Because the legs and feet of most birds do not have feathers, they would be major avenues of heat loss in cold regions were they not held at a lower temperature than the rest of the body (Figure 3.23). Gulls conserve heat by using countercurrent heat exchange in their legs. Warm blood in arteries leading to the feet cools as it passes close to veins that return cold blood to the body. In this way, heat is transferred from arterial to venous blood and transported back into the body rather than lost to the environment. Tuna use the same principle to retain heat in the active swimming muscles close to the body core, a strategy that allows them to swim very fast and pursue smaller fish as prey even in cold oceans.

Each organism functions best under a restricted range of conditions

Each organism generally has a narrow range of environmental conditions to which it is best suited, which define its optimum. The optimum is subject to natural selection, which acts on variations in the properties of enzymes and lipids, the structures of cells and tissues, and the form of the body to enable the organism to function well under the particular conditions of its environment.

Adaptation to different environmental conditions often involves shifts in the optima of biochemical processes. For example, several enzymes of the halophilic (salt-loving) bacterium Halobacterium salinarium exhibit peaks of activity at higher salt concentrations than the same enzymes of species adapted to low salt concentrations (Figure 3.24).

However, although the optimum salt concentration for H. salinarium is very high, not all of its individual enzymes have high salt optima. The structures of some enzymes make it impossible for them to function well at high salt concentrations, and the organism just has to make do.

Organisms sometimes accommodate predictable changes in environmental conditions by having more than one form of an enzyme or structural molecule, each of which functions best within a different range of conditions. The rainbow trout, for example, experiences low temperatures in its native habitat during winter, when water temperatures may drop close to the freezing point, and much higher temperatures in summer. These seasonal changes in temperature are predictable, and the trout responds by producing different forms of many enzymes in winter and summer. One of these enzymes is acetylcholinesterase, which plays an important role in degrading neurotransmitters and ensuring proper functioning of the nervous system. The affinity of this enzyme for its substrate, acetylcholine, is a good measure of enzyme function.
Substrate affinity in the winter form of the enzyme is high between 0°C and 10°C, but drops rapidly at higher temperatures. Substrate affinity of the summer form of the enzyme is low at 10°C, rises to a peak between 15°C and 20°C, and drops slowly at higher temperatures (Figure 3.24). Which form of the enzyme a trout produces at a particular time depends directly on the temperature of the water. When trout are maintained at 2°C, they produce the winter form; at 17°C, they produce only the summer form.

Measurements of enzyme activities are made in the laboratory from extracts of plant and animal tissues. The values obtained in such studies reveal the performance of a single type of molecule under highly controlled conditions. The performance of the whole organism, however, depends on the integration of many biochemical processes that together must be adjusted to conditions that the organism experiences. Comparisons of the function of organisms from different environments make the best test of how well performance matches environment. For example, many fish in the frigid oceans surrounding Antarctica swim actively and consume oxygen at a rate comparable to fish living among tropical coral reefs. Put a tropical fish in cold water, however, and it becomes sluggish and soon dies; conversely,antarctic fish cannot tolerate temperatures warmer than 5°-10°C.

How can fish from cold environments swim as actively as fish from the Tropics? Swimming depends on a series of biochemical transformations, most of which are catalyzed by enzymes. Because most of these transformations occur more rapidly at high temperatures than at low temperatures, cold-adapted organisms must either have more of the substrate for a biochemical reaction, more of the enzyme that catalyzes the reaction, or a qualitative change in the enzyme itself. As we have seen, a particular enzyme obtained from a variety of organisms may exhibit different catalytic properties when tested over ranges of temperature, pH, salt concentration, and substrate abundance (see Figures 3.24 and 3.25).

This picture of metabolic compromise is greatly simplified, of course. Adapting to changes in the environment requires adjustment of whole metabolic pathways, which may involve changes in enzyme structure or concentration or the use of alternative metabolic pathways. Indeed, the examples of adaptation to the physical environment con-
considered in this chapter emphasize the unity of the organism and the interrelatedness of all facets of organism structure and function.

**Summary**

1. The mechanisms by which organisms interact with their physical environments help us to understand why organisms are specialized to narrow ranges of conditions and how adaptations of morphology and physiology are associated with certain conditions.

2. Because water clings tightly to soil surfaces, its availability depends in part on the physical structure of soil. Soils having a high proportion of small clay particles hold water more strongly than do sandy soils. The force by which soil holds water is called the water potential, or matric potential, of the soil. Most plants cannot remove water from soil when the water potential is more negative than −15 atmospheres of pressure. This is referred to as the wilting point of soil.

3. Plants extract water from soils by using solutes to generate high osmotic potentials in their root cells. According to the cohesion–tension theory, water is drawn from the roots to the leaves by the gradient in water potentials generated by transpiration—the evaporation of water from leaf surfaces.

4. Heat- and drought-adapted plants cut down on transpiration by reducing heat loads, using hairs on leaf surfaces to establish boundary layers of humid air, and waterproofing leaf surfaces with waxy cuticles.

5. Plants obtain mineral nutrients from the soil by passive diffusion when nutrients are abundant and by active uptake when they are scarce. When the concentrations of soil nutrients are low, plants can increase their total root surface area at the expense of shoot growth.

6. Photosynthesis varies in proportion to light intensity at low light levels. The level of light below which plant respiration exceeds photosynthesis is called the compensation point. Above the saturation point, usually 10–20% of direct sunlight, photosynthesis levels off.

7. During photosynthesis, most plants assimilate carbon through a reaction (the C₃ pathway) catalyzed by the enzyme RuBP carboxylase. This enzyme has a low affinity for carbon dioxide and brings about oxidation at high temperatures, resulting in a low efficiency of carbon assimilation. Plants adapted to high temperatures interpose a more efficient (C₄) carbon assimilation step, which is spatially separated from the C₃ reactions in the leaf. CAM plants separate carbon assimilation and the Calvin–Benson cycle reactions into nighttime and daytime phases.

8. To maintain salt balance and water balance, freshwater organisms, which are hyperosmotic, retain salts while excreting the water that continuously diffuses into their bodies. Marine organisms, which are hypo-osmotic, actively exclude salts. Some marine organisms increase the level of solutes, such as urea and amino acids, in their body fluids to match the osmotic potential of seawater and thus reduce the movement of water out of their bodies.

9. Terrestrial organisms reduce water loss in part by concentrating salts and nitrogenous waste products in their urine or by excreting them through salt glands.

10. Nitrogenous waste products of protein metabolism are excreted as ammonia by most aquatic organisms, as urea by mammals, and as uric acid by birds and reptiles. Because uric acid crystallizes out of solution, birds and reptiles may excrete it at high concentrations and thereby gain considerable economy of water use.

11. Water stress increases with temperature. In dry environments, evaporative cooling is impractical, and animals must use other strategies to get rid of excess heat, such as seeking cool microclimates during the hottest period of the day.

12. Maintenance of constant internal conditions, called homeostasis, depends on negative feedback responses. Organisms sense changes in their internal environment and respond in such a manner as to return those conditions to a set point.

13. Homeostasis requires energy when a gradient between internal and external conditions must be maintained. For example, endotherms must generate heat metabolically to balance loss of heat to their cooler surroundings.

14. Oxygen diffuses too slowly to reach tissues more than about a millimeter from an organism’s surface. Large animals overcome this problem either by conducting air directly to the tissues via a multibranched tracheal system (as in insects) or by transporting oxygen dissolved in circulating fluids throughout the body. Oxygen-binding proteins, such as hemoglobin, compensate for the low solubility of oxygen in water.

15. The uptake of oxygen by aquatic organisms is greatly facilitated by countercurrent circulation of blood through the gills in a direction opposite to that of water flowing over the gill surfaces. In this way, countercurrent circulation maintains high gradients of oxygen concentration, and the blood can achieve nearly the oxygen concentration of the surrounding water. Countercurrent arrangements are also used to retain heat within the body.
16. Most organisms function best within a narrow range of environmental conditions. These optima may be shifted by evolution to match more closely the environmental conditions within which the organism lives. This is often accomplished by altering the structure and quantity of enzymes responsible for controlling metabolic processes.

17. Overall, adaptation to the physical environment depends on reaching compromises between opposing functions to increase both the individual’s chances of survival and its productivity in a particular environment.

**PRACTICING ECOLOGY**

**CHECK YOUR KNOWLEDGE**

Adaptations and Conservation

Throughout this chapter, we have seen many examples of how plants and animals have evolved to survive and reproduce in a variety of habitats. Deserts are particularly harsh terrestrial environments because of low, sporadic rainfall, high temperatures in summer (and in some deserts, low temperatures at night or in winter), high rates of evaporation, and strong winds. Desert tortoises are among the many animal species that are highly adapted to deserts. They lead solitary lives for most of the year. They spend a portion of the day in underground burrows to prevent overheating in summer and freezing in winter, and to reduce the amount of water they need for cooling. Desert tortoises start to reproduce at 12 to 20 years of age, when they lay about 4 to 6 eggs one or two times per year, depending of course, on the ambient conditions of the desert.

Dr. Ken Nagy of the University of California, Los Angeles, and his colleagues have studied the water and nutrient balances of desert animals, including the desert tortoise *Gopherus agassizii*. Not surprisingly, water is of primary importance for the survival of desert tortoises. When rain does fall in the desert, the tortoises dig depressions in the soil and drink the rain they collect. They can also resorb water from their bladders during dry times. Desert tortoise reproduction is highest in years when there is enough winter rain for annual plants, which are important food resources for tortoises, to grow. Cattle grazing on desert lands are affecting the abundances of annual plants and, therefore, the desert tortoises.

**CHECK YOUR KNOWLEDGE**

1. Why is it important for desert tortoises to conserve their energy?

**MORE ON THE WEB**

2. Go to Ken Nagy’s Web page from Practicing Ecology on the Web at http://www.whfreeman.com/ricklews. How did Nagy and his colleagues measure the amount of water used by desert animals?

Dr. Park Nobel (also of UCLA) and his colleagues have studied the adaptations of desert cacti to the hot, dry conditions of the desert Southwest, and in particular the functions of their spines. Cactus spines are leaves that have been modified over millions of years to serve several purposes, such as protection from herbivory, shading the stem to prevent overheating in summer, and insulating sensitive growth regions to protect them from freezing in winter. The combination of their unusual stem shapes (for water storage), the intricate patterns of their spines, and their bright flowers in red, orange, yellow, pink, and purple make cacti beautiful plants to observe in nature. Indeed, the remarkable appearance of cacti makes their growth and cultivation a popular hobby.

**CHECK YOUR KNOWLEDGE**

3. How are cacti and desert tortoises similar in their adaptations to the desert environment?

4. How do they differ?

**Suggested Readings**


The Physical Environment

Water has many properties favorable for the maintenance of life.

All natural waters contain dissolved substances.

The concentration of hydrogen ions profoundly affects ecological systems.

Carbon and oxygen are intimately involved in biological energy transformations.

The availability of inorganic nutrients influences the abundance of life.

Light is the primary source of energy for the biosphere.

The thermal environment provides several avenues of heat gain and loss.

Organisms must cope with temperature extremes.

Organisms use many physical stimuli to sense the environment.

Those of you who saw the movie *Titanic* will recall the terrible loss of human life caused by freezing in the cold arctic waters. One might wonder how blood and body tissues could freeze solid in perfectly liquid water. The answer is that dissolved substances depress the freezing temperature of water and other liquids. While pure water freezes at 0°C, seawater, which contains about 3.5% dissolved salts, freezes at −1.9°C, or almost 2°C colder. The blood and body tissues of most vertebrates, including humans, contain less than half the salt content of seawater, and thus freeze at a higher temperature than the freezing point of the ocean. This was a terrible problem for victims of the *Titanic* disaster. It is also a problem for fish living in polar seas.

Two questions come to mind: First, why don’t polar fish have high salt levels in their blood and tissues? Second, how can these fish survive at such low temperatures? Polar fish do not use salts to keep their body fluids from freezing because salts interfere with many biochemical processes. Maintaining a low-salt internal environment allows more rapid and efficient metabolism and movement. Instead, antarctic fish have circumvented their resulting susceptibility to freezing by raising their blood and tissue levels of such compounds as glycerol—common drugstore glycerin—which lower the freezing temperature of their body fluids, but do not severely disrupt functioning. As we look at these and similar questions in this chapter, we will see that, although physical properties of the environment and biological materials constrain life, they also provide solutions to many of its problems.
We often speak of the living and the nonliving as opposites. But although we can easily distinguish these two great realms of the natural world, they do not exist in isolation from each other. Life depends on the physical world. Living beings also affect the physical world: soils, the atmosphere, lakes and oceans, and many sedimentary rocks owe their properties in part to the activities of plants and animals.

Although distinct from physical systems, life forms nonetheless function within limits set by physical laws. The physical world provides the context for life, but also constrains its expression. Biological systems must use energy to counteract the physical forces of gravity, heat flow, diffusion, and chemical reaction. A bird in flight constantly expends energy to maintain itself aloft against the pull of gravity. Therefore, life exists out of equilibrium with the physical world.

The ability to act against external physical forces distinguishes the living from the nonliving. A bird in flight supremely expresses this quality, but plants also perform work when they absorb soil minerals into their roots and synthesize the highly complex carbohydrates and proteins that make up their structure. Like internal combustion engines, organisms transform energy to perform work. An automobile engine burns gasoline chemically, and it transmits power from the cylinder to the tires mechanically. When an organism metabolizes carbohydrates to provide the energy to move its appendages, it follows related chemical and mechanical principles.

Above all, unlike physical systems, living organisms have a purposeful existence. Their structures, physiology, and behavior are directed toward procuring energy and resources and producing offspring. Certainly life is constrained by physics and chemistry, just as architecture is constrained by the properties of building materials. However, as in biological systems, the purpose of the design of a building is unrelated to, and transcends, the qualities of bricks and mortar.

In the final analysis, life is a special part of the physical world, but it exists in a state of constant tension with its physical surroundings. Organisms ultimately receive their energy from sunlight and their nutrients from the soil and water, and they must tolerate extremes of temperature, moisture, salinity, and the other physical factors of their surroundings. The heat and dryness of deserts exclude most species, just as the bitter cold of polar regions discourages all but the most hardy. But we need not search so far as such extreme conditions for evidence of the tension between the physical and biological realms. The form and function of all plants and animals have evolved partly in response to conditions prevailing in the physical world.

In this chapter, we shall explore those attributes of the physical environment that are most consequential for life. Because life processes take place in an aqueous environment, and because water makes up the largest part of all organisms, water seems a logical place to start.

Water has many properties favorable for the maintenance of life

Water is abundant over most of the earth’s surface, and within the temperature range usually encountered there, it is liquid. Water also is a powerful solvent. Consequently, water is an excellent medium for the chemical processes of living systems. It is hard to imagine life having any other basis than water. No other common substance at the surface of the earth is liquid, and this property is necessary for life as we know it. Movement by living organisms depends on the fluidity of water. The high concentrations of molecules necessary for rapid chemical reactions depend on the density of water. Try to imagine life based on a rigid solid or a thin gas.

Thermal properties of water

Water stays liquid over a broad range of temperatures because it resists changes in temperature. In addition, water conducts heat rapidly, which tends to spread heat evenly throughout a body of water. Thus, the temperature of water changes slowly, even when heat is removed or added rapidly, as can happen at the air–water interface or at an organism’s surface. Water also resists change of state between solid (ice), liquid, and gaseous (water vapor) phases. Over 500 times as much energy must be added to evaporate a quantity of water as to raise its temperature by 1°C! Freezing requires the removal of 80 times as much heat as that needed to lower the temperature of the same quantity of water by 1°C. This property helps to keep large bodies of water from freezing solid during winter.

Another curious, but fortunate, thermal property of water is that, whereas most substances become denser at colder temperatures, water becomes less dense as it cools below 4°C. Water also expands and becomes even less dense upon freezing. Consequently, ice floats (Figure 21), which not only makes ice skating possible, but also prevents the bottoms of lakes and oceans from freezing and enables aquatic plants and animals to find refuge there in winter.
plants contain bone, proteins, dissolved salts, and other materials that are denser than salt water and much denser than fresh water. These materials would cause aquatic organisms to sink were it not for a variety of mechanisms that reduce their density or retard their rate of sinking. Many species of fish have a gas-filled swim bladder, a mechanism that takes advantage of the low density of gases. The swim bladder's size can be adjusted to make the density of the body equal to that of the surrounding water. Some large kelps have gas-filled bulbs that float their leaves to the sunlit surface waters (see Figure 1.23).

Many of the microscopic, unicellular algae that float in great numbers in the surface waters of lakes and oceans (phytoplankton) contain droplets of oil that compensate for their natural tendency to sink (Figure 2.2). Most fats and oils have densities between 0.90 and 0.93 grams per cubic centimeter (90–93% of the density of pure water). Accumulated lipids also enhance the buoyancy of fish and aquatic organisms.

Trimmed-down skeletons, reduced musculature, and perhaps even the decreased salt concentrations of their body fluids further lighten the bodies of aquatic organisms. Unlike bony fishes, sharks and rays lack a swim bladder. But they also lack bony skeletons, and the absence of heavy mineral salts in their skeletons partly compensates for the swim bladder’s absence. Calcium carbonate and calcium phosphate, the principal components of mineralized bone, have densities approximately three times that of water. The density of the cartilage skeleton of sharks and rays is much less—close to that of water.

While the high viscosity of water hampers the movement of some marine organisms, others use that property to avoid sinking. Many tiny marine animals have evolved long, filamentous appendages that retard sinking (Figure 2.3).
just as a parachute slows the fall of a body through air. In contrast, fast-moving aquatic animals have evolved streamlined shapes that reduce the drag encountered in moving through a dense and viscous medium. Barracuda and other swift fishes of the open ocean closely approach the shape of a body ideally proportioned for moving quickly through water (Figure 2.4).

All natural waters contain dissolved substances

Water has an impressive capacity to dissolve various substances, making them accessible to living systems and providing a medium within which they can react to form new compounds. Water is a formidable solvent because water molecules are strongly attracted to many solids. Some solid compounds consist of electrically charged atoms or groups of atoms called ions. For example, common table salt, sodium chloride (NaCl), contains positively charged sodium ions (Na+) and negatively charged chlorine ions (Cl-) arranged in close proximity in a crystal lattice. In water, however, the charged sodium and chlorine ions are powerfully attracted by water molecules, which themselves have both positive and negative charges. These forces of attraction are stronger than the forces that hold salt crystals together, with the result that they readily separate into their component ions when surrounded by water molecules—another way of saying that the salt dissolves.

The powerful solvent properties of water are responsible for most of the minerals in streams, rivers, lakes, and oceans. Water vapor in the atmosphere condenses to form clouds and, eventually, precipitation (rain, snow, and so on). At this point, the water is nearly pure, except for dissolved atmospheric gases, principally nitrogen, oxygen, and carbon dioxide. Rainwater acquires some minerals from dust particles and droplets of ocean spray in the atmosphere as it falls, and picks up more as it flows over and under the ground. Surface waters, such as streams and rivers, pick up additional minerals from the substrates through which they flow. The water in most lakes and rivers contains 0.01–0.02% dissolved minerals, which is far less than the average salt concentration of the oceans (3.4% by weight), in which salts and other minerals have accumulated over several billion years.

The minerals dissolved in fresh water and salt water differ in composition as well as in quantity. Seawater abounds in sodium (Na+) and chloride (Cl-) ions and contains significant amounts of magnesium (Mg2+) and sulfate (SO42-) ions. Fresh water contains a greater variety of ions, but calcium (Ca2+), bicarbonate (HCO3-), and sulfate ions tend to predominate. The concentrations of minerals in fresh water reflect the composition of and solubilities of materials in the rock and soil that the water flows through. Limestone consists primarily of calcium carbonate (CaCO3), and waters flowing through regions with limestone bedrock have high concentrations of calcium and bicarbonate ions (Figure 2.5). Granite is composed of minerals that lack calcium and resist dissolution; waters flowing through granitic areas contain few dissolved substances.

The ocean functions like a large still, concentrating minerals as mineral-laden water arrives via streams and rivers and as pure water evaporates from its surface. Here the concentrations of some elements, particularly calcium, reach limits set by the maximum solubility of the compounds they form. In the oceans, calcium readily forms calcium carbonate, which is not very soluble in water. It dissolves only to the extent of 0.014 grams per liter of water, or 14 milligrams per liter (mg per L). Its concentration in the oceans reached this level eons ago, so excess calcium ions washing into the oceans each year precipitate to form limestone sediments (Figure 2.6). At the other extreme, the solubility of sodium compounds, such as sodium chloride (360 g per L) and sodium bicarbonate (69 g per L), is very high, far exceeding the concentration of sodium in seawater (10 g per L). Most of the sodium chloride washing into ocean basins remains dissolved, and so its concentration in seawater has increased greatly over geologic time.
Aquatic life requires many mineral elements. Among the most important of these are nitrogen and phosphorus, which are needed to make amino acids, nucleic acids, and other important biological molecules. Nitrogen enters bodies of fresh water in relative abundance in the runoff from surrounding terrestrial ecosystems. Typical concentrations in fresh water are about 0.40 mg per L, mostly in the form of nitrate (NO₃⁻) and dissolved organic nitrogen compounds, with smaller amounts of ammonium (NH₄⁺).

In contrast, most of the phosphorus in fresh water readily forms chemical complexes with iron and precipitates out of the system, typically leaving about 0.01 mg per L in solution as phosphate (PO₄³⁻). As a result, phosphorus, rather than nitrogen, usually limits plant growth in freshwater systems. The situation is reversed in the oceans, where phosphorus concentrations are typically higher (0.01–0.1 mg per L) than nitrogen concentrations (often less than 0.01 mg per L).

**Figure 2.6** The limestone sediments that form many mountains represent calcium carbonate precipitated out of solution in shallow seas. Photo by Larry Jon Friesen/Saturdate.

**Figure 2.5** Minerals have accumulated in the oceans for eons. The average concentrations of minerals in streams, whether in areas having granitic or limestone bedrock, are much lower than in the oceans. The exception is bicarbonate ion, which has limited solubility in water and precipitates out of the water column in the ocean.

**The concentration of hydrogen ions profoundly affects ecological systems**

Hydrogen ions (H⁺) deserve special mention because they are extremely reactive. In high concentrations, they affect the activities of most enzymes and have other, generally negative consequences for life processes. They also play a crucial role in dissolving minerals from rock and soil.

The concentration of hydrogen ions in a solution is referred to as **acidity**. Acidity is commonly measured on a scale of pH, which is the negative of the common logarithm of hydrogen ion concentration, measured in moles per liter (**Figure 2.7**). In pure water at any given time, a small fraction of the water molecules (H₂O) are dissociated into their hydrogen (H⁺) and hydroxide (OH⁻) ions. The pH of pure water, which is defined as neutral pH, is 7, which means that the concentration of hydrogen ions is 10⁻⁷ (0.0000001) moles per liter, or one ten-millionth of a gram per kilogram of water. In contrast, strong acids,
such as sulfuric acid (H$_2$SO$_4$) and hydrochloric acid (HCl), dissociate almost completely when dissolved in water. At high concentrations, such acids can produce pH values approaching 0—that is, 1 mole of H$^+$ per liter. The acid in your stomach has a pH of 1. Most natural waters contain weak acids, such as carbonic acid (H$_2$CO$_3$) and various organic acids, and tend to have pH values close to neutral. Some natural waters are somewhat basic, or alkaline (pH > 7), having an excess of OH$^-$ over H$^+$. The normal range of pH in natural waters is between 6 and 9, although small ponds and streams in regions with acid rainfall, or which are polluted by sulfuric acid draining out of coal mining wastes, can reach pH values as low as 4.

Hydrogen ions, because of their high reactivity, dissolve minerals from rock and soil. For example, in the presence of hydrogen ions, the calcium carbonate that makes up limestone dissolves readily, according to the chemical equation

$$\text{H}^+ + \text{CaCO}_3 \rightarrow \text{Ca}^{2+} + \text{HCO}_3^-.$$

As you can see, this chemical reaction removes hydrogen ions from the water and thus increases its pH. Consequently, water in limestone areas contains abundant calcium ions, which make it “hard,” and relatively few hydrogen ions, resulting in a somewhat alkaline pH (that is, pH > 7). Where limestone is absent, water contains few calcium ions and is “soft.” Also, carbonic acid (H$_2$CO$_3$), formed when atmospheric CO$_2$ dissolves in water, tends to accumulate, and this lowers the pH of the water. Calcium ions are important to life processes, and their presence in high concentrations is vital to organisms, such as snails, that form shells made of calcium carbonate. Indeed, mollusks are less abundant and diverse in streams and lakes with soft water than in those with hard water. Thus, hydrogen ions are essential for making certain nutrients available for life processes. However, this same capacity of hydrogen ions also helps to dissolve highly toxic heavy metals, such as arsenic, cadmium, and mercury, that are detrimental to life.

Hydrogen ions react strongly with living matter as well as with rock and soil. Most organisms keep the pH of their blood and cells close to a neutral pH. We humans maintain the pH of our blood between 7.3 and 7.5. Some microorganisms are more tolerant of high acidity. For example, some photosynthetic cyanobacteria can function at a pH as low as 4. Other kinds of bacteria tolerate acidity down to almost pH 0, but do so by maintaining their internal pH in the range of 6 to 7 at great metabolic cost.

![Figure 2.7](image)

**Figure 2.7** The pH scale of hydrogen ion concentration extends from 0 (highly acidic) to 15 (highly alkaline).

**Carbon and oxygen are intimately involved in biological energy transformations**

Organisms are composed of carbohydrates, lipids, proteins, and other biological molecules. These compounds contain energy in the form of chemical bonds, primarily between carbon atoms. The energy in these bonds can be released for use by the organism through reactions that break the bonds. In biological systems, one of the most common of these reactions is the oxidation of organic forms of carbon (Figure 2.8). Oxidation decreases the chemical energy potential of the carbon atom, and the released energy can be used for other biochemical work, such as building cell membranes. The opposite of oxidation is

![Figure 2.8](image)

**Figure 2.8** Oxidation and reduction change the chemical state and energy level of carbon.
reduction. The reduction of carbon increases the energy potential of the atom and allows it to react with other carbon atoms or nitrogen atoms to form organic molecules. Of course, the process of reducing carbon itself requires a source of energy.

Animals and most microorganisms obtain carbon that is already reduced in their food. Such organisms are referred to as heterotrophs because they obtain their energy by consuming (hence “troph”) other (hence “hetero”) organisms. Plants, algae, and many bacteria assimilate oxidized forms of carbon, particularly carbon dioxide, which they reduce chemically using other forms of energy. (The term assimilation refers specifically to the incorporation of energy or matter into the tissues of living organisms.) Such organisms are referred to as autotrophs, literally “self-feeders.” Autotrophs derive the energy they need to reduce carbon from sunlight (phototrophs) or, as in the case of some bacteria, from other chemical reduction reactions (chemotrophs), as we shall see in a later chapter.

Photosynthesis and respiration

The ultimate source of carbon for making organic molecules is carbon dioxide (CO₂), which is an inorganic oxidized form of carbon present in the atmosphere and dissolved in water. During photosynthesis, plants reduce the carbon atom in carbon dioxide using energy from light. All organisms, including plants, undo the results of photosynthesis by oxidizing organic carbon back to carbon dioxide; this process is known as respiration. The oxidation of carbon during respiration releases energy, and organisms can harness a portion of this energy to synthesize proteins, maintain cellular ion concentrations, and move; the rest escapes as heat.

Photosynthesis and respiration involve the complementary reduction and oxidation of carbon and oxygen:

$$\text{energy } + 6\text{CO}_2 + 6\text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_12\text{O}_6 + 6\text{O}_2$$

Notice that as carbon is reduced during photosynthesis, oxygen is oxidized from its form in water to its molecular form, O₂. This molecular oxygen is found as a gas in the atmosphere and dissolved in water. In its reduced state, oxygen has an excess of electrons and readily forms water (H₂O) in combination with positively charged hydrogen ions. During respiration, oxygen is reduced to form water, and carbon is oxidized to form carbon dioxide. Because less energy is needed to reduce oxygen than to reduce carbon, the oxidation of carbon releases more energy than the reduction of oxygen requires. Therefore, the coupling of the oxidation of carbon with the reduction of oxygen results in a net release of energy, which the organism can use to perform other work.

The limited availability of inorganic carbon

Plants assimilate more carbon through photosynthesis than they oxidize by way of respiration (otherwise they would not grow), so they require an external source of carbon. The only practical source of nonbiological carbon, CO₂, has an extremely low concentration in the atmosphere (about 0.03%). Carbon dioxide enters plant cells because there is a higher concentration of CO₂ in the atmosphere than there is in the cells, where CO₂ is continually used up by photosynthesis. However, the atmosphere-to-plant difference in the concentration of CO₂ is much, much less than the plant-to-atmosphere difference in the concentration of water vapor, which drives water out of plant cells into the surrounding air. This makes water conservation a problem for terrestrial plants, especially in arid environments. Plants evaporate 500 g of water from their leaves, more or less, for every gram of carbon they assimilate (Figure 2.9).

![Figure 2.9 Gas exchange occurs across the surface of a leaf. Schematic cross section of the lower portion of a leaf, showing the slow diffusion of carbon dioxide into the leaf compared with the evaporation of water from the leaf surface to the surrounding air. The lower epidermis of the leaf is relatively impermeable to water; gas exchange occurs primarily through pores (stomata) on the undersurface of the leaf. Because the plant uses carbon dioxide in photosynthesis, the concentration of that gas remains lower in the leaf than in the surrounding air.](image-url)
Getting enough carbon poses different problems for aquatic plants. The solubility of carbon dioxide in fresh water is about 0.0003 liters per liter of water, which is 0.03% by volume, or about the same as its concentration in the atmosphere. When carbon dioxide dissolves in water, however, most of the molecules form carbonic acid ($H_2CO_3$). Depending on how acid the water is, carbonic acid molecules dissociate into bicarbonate ions ($HCO_3^-$) and carbonate ions ($CO_3^{2-}$). Within the range of acidity that is typical of most fresh and salt water (pH values between 6 and 9), the more common form is bicarbonate, which dissolves readily in water. As bicarbonate forms, carbon dioxide is removed from solution, and more of the gas can then enter into solution from the atmosphere:

$$CO_2 + H_2O \rightarrow H_2CO_3 \rightarrow H^+ + HCO_3^-.$$

This process continues until the concentration of bicarbonate ions is equivalent to 0.03–6.06 liters of carbon dioxide gas per liter of water (3–6%), more than 100 times the concentration of carbon dioxide in air (Figure 2.10). Thus, bicarbonate ions provide a large reservoir of inorganic carbon in aquatic systems.

**Carbon dioxide diffuses slowly through water**

Inorganic carbon is abundant in water, to be sure. But if that carbon doesn’t move rapidly, plants don’t have access to an abundant supply. The rate of diffusion of carbon dioxide through unstirred water is about 10,000 times less than it is in air, and the larger bicarbonate ions diffuse even more slowly. Every surface of an aquatic plant, alga, or microbe has a **boundary layer** of unstirred water, which may range from as little as 10 micrometers ($\mu$m) for single-celled algae in turbulent waters to 500 $\mu$m (0.5 mm) for a large aquatic plant in stagnant water (Figure 2.11). Thus, in spite of the high concentration of bicarbonate ions in the water surrounding these organisms, photosynthesis may nonetheless be limited by a diffusion barrier of still water at the surface of the organism.

Both carbon dioxide and bicarbonate ions enter the cells of aquatic plants. Once inside the cells, bicarbonate ions can be used directly as a source of carbon for...
photosynthesis, although at only 10–40% of the efficiency of utilizing carbon dioxide. As carbon dioxide itself is taken up during photosynthesis, and thereby depleted within cells, bicarbonate ions associate once more with hydrogen ions to produce more carbon dioxide:

\[ H^+ + HCO_3^- \rightarrow CO_2 + H_2O \]

(Figure 2.12). Bicarbonate ions and carbon dioxide exist in a chemical equilibrium, which represents the balance achieved between \( H^+ \) and \( HCO_3^- \), on one hand, and \( CO_2 \) and \( H_2O \) on the other.

**Oxygen is scarce in water**

The low solubility of oxygen in water often limits the metabolism of animals in aquatic habitats. This limitation is compounded by the vastly lower rate of diffusion of oxygen in water than in air. Compared with its concentration of 0.21 liters per liter (21% by volume) in the atmosphere, the solubility of oxygen in water reaches a maximum (at 0°C in fresh water) of 0.01 liters per liter (1%). Furthermore, below the limit of light penetration in deep bodies of water and in waterlogged sediments and soils, no oxygen is produced by photosynthesis. Therefore, as animals and microbes use oxygen to metabolize organic materials, such habitats may become severely depleted of dissolved oxygen. Habitats, such as deeper layers of water in lakes and mucky sediments of marshes, that are devoid of oxygen are referred to as **anaerobic** or **anoxic** habitats. Such conditions pose problems for terrestrial plants, whose roots need oxygen for respiration. Many plants that live in waterlogged habitats have special vascular tissues that conduct air directly from the atmosphere to the roots. The roots of cypress trees and many mangroves grow vertical extensions that project above the anoxic soil and conduct oxygen directly from the atmosphere to the roots (Figure 2.15).

(Figure 2.12) Bicarbonate ion is a source of carbon dioxide in aquatic systems. When aquatic plants and algae deplete carbon dioxide in their immediate vicinity, it is replenished from the pool of bicarbonate ions. (a) The equilibrium between bicarbonate and dissolved carbon dioxide in water. (b) When plants and algae remove carbon dioxide from the water during photosynthesis, the reduced \( CO_2 \) concentration causes bicarbonate to release additional \( CO_2 \) into solution (\( H^+ + HCO_3^- \rightarrow H_2O + CO_2 \)).

**The availability of inorganic nutrients influences the abundance of life**

Organisms are composed of a variety of chemical elements. After hydrogen, carbon, and oxygen, which are the elements in carbohydrates, those required in greatest quantity are nitrogen, phosphorus, sulfur, potassium, calcium, magnesium, and iron. The functions of these elements in biological systems are outlined in Table 2.1. Certain organisms need other elements in abundance as well. For example, diatoms construct their glassy shells of silicates (Figure 2.14); tunicates, which are sessile marine inverte-
brates, accumulate vanadium in high concentrations, possibly as a defense against predators; nitrogen-fixing bacteria require molybdenum as a part of the key enzyme in nitrogen assimilation.

The scarcity (relative to need) of inorganic nutrients often limits plant growth. Plants acquire mineral nutrients—other than oxygen, carbon, and some nitrogen—as ions from water in the soil around their roots. Nitrogen exists in soil as ammonium ($\text{NH}_4^+$) and nitrate ions ($\text{NO}_3^-$), phosphorus as phosphate ions ($\text{PO}_4^{3-}$), calcium and potassium as their elemental ions $\text{Ca}^{2+}$ and $\text{K}^+$, and so on. The availability of these elements varies with their chemical form in the soil and with temperature, acidity, and the presence of other ions. Phosphorus, in particular,
often limits plant production in terrestrial environments; even when it is abundant, most of the compounds it forms in the soil do not dissolve easily. We shall have much more to say about nutrient uptake by plants in later chapters.

Light is the primary source of energy for the biosphere

Green plants, algae, and some bacteria absorb light and assimilate its energy by photosynthesis, but not all the light striking the earth's surface can be used in this way. Rainbows and prisms show that light consists of a spectrum of wavelengths that we perceive as different colors. Actually, visible light represents only a small part of the spectrum of electromagnetic radiation, which extends from gamma rays (the shortest wavelengths) to radio waves (the longest). Wavelengths are usually expressed in nanometers (nm: one-billionth of a meter). The visible portion of the spectrum, which corresponds to the wavelengths of light suitable for photosynthesis, ranges between about 400 nm (violet) and 700 nm (red). This range is called the photosynthetically active region (PAR) of the spectrum. Light of wavelengths shorter than 400 nm makes up the ultraviolet part of the spectrum; light of wavelengths longer than 700 nm is called infrared. Infrared radiation is perceived primarily as heat. The energy intensity of light varies inversely with its wavelength: shorter-wavelength blue light has a higher energy level than longer-wavelength red light.

Ozone and ultraviolet radiation

Starting in the visible portion of the spectrum and moving toward shorter wavelengths, one encounters ultraviolet radiation and high-energy X-rays. Because of its high energy level, ultraviolet light can damage exposed cells and tissues. Fortunately, the earth's atmosphere is completely transparent only to the visible range of the spectrum. As light passes through the atmosphere, most of its ultraviolet components are absorbed, primarily by a molecular form of oxygen known as ozone (O₃) that occurs in the upper atmosphere. The atmosphere thus shields life at the earth's surface from the most damaging wavelengths of light (Figure 2.15).

Certain pollutants in the atmosphere, particularly the chlorofluorocarbons (CFCs) formerly used as refrigerants and as propellants in aerosol cans, chemically destroy ozone in the upper atmosphere. This degradation has produced "ozone holes"—areas of low ozone concentration in the upper atmosphere—over some parts of the earth, particularly at high latitudes. Consequently, the danger of tis-
sue damage from ultraviolet radiation has increased for humans and most likely for other forms of life. Concern over the increasing size of ozone holes has led to strict controls over the manufacture and release into the atmosphere of substances such as CFCs.

**Infrared light and the greenhouse effect**

Toward the other end of the spectrum from ultraviolet light, one passes through the infrared region to extremely long-wavelength, low-energy radiation such as radio waves. The presence of water vapor, carbon dioxide, methane, and other gases in the atmosphere makes it relatively opaque to infrared light. These gases absorb much of the infrared portion of sunlight, and this absorbed energy contributes to the warming of air. More importantly, because of its infrared opacity, the atmosphere also absorbs radiation from the surface of the earth. Most of the energy in the visible portion of the solar spectrum that reaches the earth's surface is absorbed by vegetation, soil, and surface waters and converted to heat energy. This heat is then radiated from the warmed surface of the earth back toward space as low-intensity infrared radiation. Much of this radiation is absorbed by the atmosphere, which thereby acts as a blanket covering the earth and keeping its surface warm. Because this warming effect resembles the manner in which glass keeps a greenhouse warm, it is called the **greenhouse effect** (Figure 2.16). Eventually, this absorbed energy reaches the upper levels of the atmosphere and is lost to space, but at a much slower rate than would occur in the absence of the infrared-opaque components of air—the so-called greenhouse gases. Overall, the greenhouse effect greatly benefits life by maintaining temperatures on earth within a favorable range. However, our addition of carbon dioxide to the atmosphere by clearing forests and burning fossil fuels has intensified the greenhouse effect, and the surface of the earth is becoming warmer.

**The absorption spectra of plants**

Vision and the photochemical conversion of light energy to chemical energy by photosynthetic organisms occur primarily within that portion of the solar spectrum at the earth's surface that contains the greatest amount of energy. The absorption of radiant energy depends on the nature of the absorbing substance. Water only weakly absorbs light in the visible region of the spectrum; therefore, a glass of water appears colorless. Dyes and pigments strongly absorb some wavelengths in the visible region, reflecting or transmitting light of the color that identifies them. Leaves contain several kinds of pigments, particularly chlorophyll (green) and carotenoids (yellow), that absorb light and
Chlorophyll absorbs mostly in the violet and red wavelengths. What is not absorbed—green and yellow—is reflected back, which is why photosynthetic plants look green.

The transparency of a glass of water is deceptive. Although it appears colorless in small quantities, water absorbs or scatters enough light to limit the depth of the sunlit zone of the sea. In pure seawater, the energy content of light in the visible part of the spectrum diminishes to 50% of the surface value at a depth of 10 meters, and it drops to less than 7% within 100 meters. Moreover, water absorbs longer wavelengths more strongly than shorter ones; most of the infrared radiation disappears within the topmost meter of water. Short wavelengths (violet and blue) tend to scatter when they strike water molecules, so they too fail to penetrate deeply. Because of the absorption and scattering of light by water, green light predominates with increasing depth.

The photosynthetic pigments of aquatic algae parallel this spectral shift. Algae near the surface of the oceans, such as the green sea lettuce (Ulva), which grows in shallow water along rocky coasts, have pigments resembling those of terrestrial plants and best absorb blue and red light and reflect green light. The deep-water red alga Porphyra has additional pigments that enable it to use green light more effectively in photosynthesis (Figure 2.18).

The absorption of light by water limits the depth at which aquatic photosynthetic organisms can exist. The narrow zone close to the surface where there is sufficient light for photosynthesis is called the euphotic zone. The lower limit of the euphotic zone, where the assimilation of

Figure 2.17 Two groups of photosynthetic pigments—chlorophylls and carotenoids—absorb different wavelengths of light. After R. Emerson and C. M. Lewis, J. Gen. Physiol. 25: 579–595 (1942).

harness its energy (Figure 2.17). Carotenoids, which give carrots their orange color, absorb primarily blue and green light and reflect light in the yellow and orange regions of the spectrum. Chlorophyll absorbs red and violet light while reflecting green and blue.

Figure 2.18 Relative rates of photosynthesis by the green alga Ulva and the red alga Porphyra (right) differ as a function of the color of light. After F. T. Haxo and L. R. Blinks, J. Gen. Physiol. 33:389–422 (1950). Photo by Larry Jon Friesen/Saturdaze.
energy by photosynthesis just balances the release of energy by respiration, may lie 100 meters below the surface in some exceptionally clear lakes and oceans, but this is a rare condition. In productive waters with dense phytoplankton, or in waters turbid with suspended silt particles, the euphotic zone may be as shallow as 1 meter.

**Light intensity**

Ecologists measure the intensity of light as the energy content of the light from the photosynthetically active region of the spectrum striking a unit of surface area per unit of time. Light intensity is sometimes referred to as radiant flux, which is commonly expressed as watts per square meter (W m$^{-2}$). The watt, which is the familiar unit used to rate the power consumption of light bulbs and appliances, is equal to one joule of energy per second.

A flat surface above the atmosphere of the earth directly facing the sun would receive approximately 1,400 W per m$^2$. This intensity of solar radiation—the energy reaching the outer limit of the atmosphere—is called the solar constant. In reality, the average intensity of light at any area on the surface of the earth is far less. Nighttime periods without light, the low incidence of light early and late in the day and at high latitudes, absorption of light by the atmosphere, and reflection of light by clouds all diminish light intensity at the earth’s surface.

Most of the solar radiation absorbed by water, soil, plants, and animals is converted to heat. Each object and each organism on earth continually exchanges heat with its surroundings. When the temperature of the environment exceeds that of an organism, the organism gains heat and becomes warmer. When the environment is cooler, the organism loses heat to the environment and cools. An individual organism’s heat budget includes several avenues of heat gain and heat loss (Figure 2.19).

**Radiation** is the absorption or emission of electromagnetic energy. Sources of radiation in the environment include the sun, the sky (scattered light), and the landscape (which radiates heat it has absorbed from the sun). How rapidly an object loses energy by radiation depends on the temperature of the radiating surface. The relationship is nonintuitive in that radiation increases with the fourth power of absolute temperature (K). (Absolute zero, that is, 0 degrees Kelvin—0 K—is equal to −273°C.) Accordingly, a small mammal with a skin temperature of 37°C (310 K) radiates heat 30% more rapidly than a lizard of similar size with a skin temperature of 17°C (290 K). At night, objects

![Figure 2.19 There are many pathways of heat exchange between a plant and its environment.](image-url)

that have warmed in the sunlight radiate their stored heat to colder parts of the environment and, eventually, to space. The bodies of organisms, especially warm-blooded birds and mammals, often are the "brightest" objects emitting infrared radiation in the night (Figure 2.20). Because we are so much hotter than the black void of space (which has a temperature close to 0 K), we radiate tremendous quantities of energy to the clear night sky. We can also receive radiation from water vapor in the atmosphere and from vegetation, which balances some of our nighttime radiation loss. That is why, at a given temperature, one feels warmer at night in a humid environment, particularly when clouds obscure the right sky, than in a dry environment.

Conduction is the transfer of the kinetic energy of heat between substances in contact with one another. Thus, a vacuum, which lacks all substance, conducts no heat. Water, because it is so much denser than air, conducts heat more than 20 times faster than air. The rate at which heat passes between an organism and its surroundings depends on the insulating value of the organism's surface (its resistance to heat transfer), its surface area, and the temperature difference between the organism and its surroundings. An organism can either gain or lose heat by conduction, depending on its temperature relative to that of the environment. That is why lizards often lie flat on hot rocks, warming their bodies by conduction.

Convection is the movement of heat in liquids and gases of different temperatures, particularly over surfaces across which heat is transferred by conduction. Air conducts heat poorly. In still air, a boundary layer of air forms over a surface, just as a boundary layer of still water forms over the surfaces of aquatic plants. A warm organism tends to warm its boundary layer to the temperature of its own body, effectively insulating itself against heat loss. A current of air flowing past a surface tends to disrupt the boundary layer and to increase the rate of heat exchange by conduction (Figure 2.21). This convection of heat away from the body surface is the basis of the "wind chill factor" we hear about in winter on the evening weather report. On a cold day, air movement makes you feel as cold as you would on an even colder windless day. For example, a wind blowing 32 km per hour at an air temperature of −7°C has the cooling power of still air at −23°C.

Evaporation also affects the movement of heat. The evaporation of 1 g of water from the body surface removes 2.43 kilojoules (kJ) of heat when the temperature of the surface is 30°C. As plants and animals exchange gases with the environment, some water evaporates from their exposed surfaces. In plants, the evaporation of water from the surface of a leaf is referred to as transpiration. The rate of heat loss from a surface by evaporation and transpiration depends on the permeability of the surface to water, the relative temperatures of the surface and the air, and the vapor pressure of the atmosphere. Vapor pressure is a measure of the capacity of the atmosphere to hold water. Vapor pressure is expressed in atmospheres (the pressure of the atmosphere at the surface of the earth), and represents the fractional weight of water vapor in saturated air. At 30°C, the vapor pressure of water is 0.042 atm, meaning that the air can hold 4.2% water by weight. At 20°C, the vapor pressure of water is only 0.023 atm. Thus, the water-holding capacity of air varies with its temperature, nearly doubling over each 10°C increase in temperature. Consequently, when the temperature of air saturated with water drops from 30°C to 20°C, its capacity to hold water decreases from 4.2 to 2.3%, and the difference—almost 2%—condenses to form clouds or precipitation.

Like heat, moisture can be trapped in the boundary layer of air that forms above surfaces. Convection tends to disrupt boundary layers and therefore increases evapora-
tive heat loss as well as conductive heat loss. Because warm air can hold more water than cold air, it has greater potential for evaporating water. In hot climates, water evaporating from the skin and respiratory surfaces cools many animals. For warm-blooded animals in cold climates, evaporation can become a problem as cold inhaled air containing little water warms when it encounters the body and respiratory surfaces, thereby speeding evaporation. We see evidence of such water loss on winter days when water evaporated from the warm surfaces of our lungs condenses as our breath mingles with the cold atmosphere.

All of the gains and losses of heat by an organism constitute its heat budget. The heat budget of an organism can be expressed by a simple equation that relates the rate of change in its heat content to the rates of gains and losses through radiation, conduction, convection, and evaporation, plus the internal heat it generates by metabolizing foods:

\[
\text{change in heat content} = \text{metabolism} - \text{evaporation} \\
\pm \text{radiation} \pm \text{conduction} \pm \text{convection}.
\]

Because radiation, conduction, and convection can either add to or remove heat from the organism, a plus/minus (±) sign precedes these terms. When gains and losses are perfectly balanced, the change in heat content is zero.

Because evaporation and metabolism influence body heat, the heat budget is connected to the organism's budgets of water, food, and salts, as illustrated in Figure 2.22. Food is the source of metabolically produced heat, and it also contains water and salts. Evaporative heat loss requires a source of free water, which can be obtained by drinking (where water is available) and produced by the metabolism of organic compounds (as we saw in the chemical formula for respiration above). For example, the metabolism of a gram of fat produces 1.07 grams of water.

**ECOLOGISTS IN THE FIELD**

*Keeping cool on tropical islands*

Organisms that live in the open in tropical climates gain a tremendous amount of heat by radiation from the sun and by conduction and convection from the hot environment in which they live. In many circumstances, this heat can be gotten rid of by evaporation of water from body surfaces. Humans certainly sweat when they are hot. Many animals also lose heat by evaporation of water from the respiratory surfaces of the lungs. Where water is scarce, however, evaporation is not an option, and animals generally find ways of avoiding intense sunlight. So here is an interesting puzzle: Several species of seabirds nest on bare sand on small coral atolls in the Tropics, such as Tern Island in the northwestern Hawaiian Islands. These birds are exposed to punishing levels of solar radiation during the middle of the day. In this harsh environment, the sooty tern nests on the surface of the sand in full sunlight (Figure 2.23), while another species of similar size and coloration, the wedge-tailed shearwater, builds its nests in deep burrows beneath the surface of the sand.

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**Figure 2.22** The heat, water, energy, and salt budgets of organisms are coupled by diet, evaporative water loss, and excretion.

**Figure 2.23** A sooty tern can tolerate a hot environment because its food contains abundant water for evaporation cooling. This bird is sitting on its egg in the hot sun on Christmas Island, located on the equator in the central Pacific Ocean. Photo by R. E. Ricklefs.
Seabird biologist Paul Sievert wondered why the two species place their nests so differently. The conventional wisdom had been that shearwaters nest in burrows to avoid predators such as frigatebirds, which, ever watchful, swoop down to snatch unattended eggs and chicks. By chance, however, the density of shearwaters on Tern Island was so great, and the sand so hard to dig through, that many shearwaters nested on the surface out of desperation. These birds had very low nesting success because they were forced to abandon their eggs under the intense solar radiation. If the eggs weren’t lost to frigatebirds, they heated up in the sun, and the developing embryos died. Sievert found that if he shaded surface nests with plywood A-frames, the shearwaters were able to reproduce successfully because the adults could remain on their eggs throughout the middle of the day (Figure 2.24).

This simple experiment demonstrated the importance of the thermal environment for shearwaters, but it did not explain how sooty terns could nest on the surface in the same environment in full sun. The key to this puzzle lies in the diets and feeding regimes of the two bird species. Sooty terns feed on fish and squid obtained in areas close to their nesting sites. The male and female sooty terns alternate incubation duty, and neither one stays at the nest for more than a day or two at a time. Shearwaters have a diet similar to that of terns, but they feed hundreds of kilometers from their nesting sites. They digest most of what they eat while foraging at sea, and convert the surplus energy to fat deposits to use during their weeklong spells tending the egg. Thus, sooty terns come back to their nests from the sea with a stomach full of water-laden food, which provides a reservoir of free water for evaporative heat loss. Shearwaters have plenty of fat for a prolonged fast, but fat contains little water, and even the water produced by fat metabolism is insufficient to dissipate the heat load absorbed under full sunlight. So why don’t shearwaters drink the abundant seawater all about them? Seawater contains so much salt that they would lose, through their kidneys and salt-secreting glands, as much water as they consumed. Water, water, everywhere, nor any drop to drink!

Organisms must cope with temperature extremes

Unlike birds and mammals, most organisms do not regulate their body temperatures, which vary in parallel with the temperature of their surroundings. Most life processes occur only within the range of temperature at which water is liquid: 0°C–100°C at the earth’s surface. Relatively few plants and animals can survive body temperatures above 45°C, which defines the upper limit of the physiological

**Figure 2.24** Hatching success of wedge-tailed shearwaters is highly dependent on the thermal environment. Individuals protected from the sun in burrows or provided with artificial shade have higher success than do those nesting in the open. Data courtesy of Paul Sievert.
range for most eukaryotic organisms. Clearly, temperature influences life processes. How do organisms cope with temperatures outside the physiological range?

**Tolerance of heat**

Much of the influence of temperature on life processes results from the way in which heat affects organic molecules. Heat imparts a high kinetic energy to living systems, and causes biological molecules to move and change shape at a high rate. By increasing the rate of movement of molecules, heat also accelerates chemical reactions. The rates of most biological processes increase between two and four times for each 10°C rise in temperature throughout the physiological range (Figure 2.25). Higher temperatures mean that organisms can develop more rapidly, swim, run, and fly faster, and digest and assimilate more food. Thus, increasing temperature has a positive effect on biological productivity. But high temperatures also have a depressing effect on life processes. Proteins and other biological molecules become less stable at higher temperatures and may not function properly or retain their structure.

Proteins are long chains of amino acids joined together. The functioning of any particular protein depends on the complicated folding of the amino acid chain. The shape of the protein is maintained by forces of attraction between certain types of amino acids strategically placed in the sequence of the chain. The molecular motion caused by heat tends to open up, or denature, the structure of proteins. Existence at high temperatures requires that proteins and other biological structures have strong forces of attraction within and between molecules to resist being literally shaken apart. The proteins of thermophilic ("heat-loving") bacteria have higher proportions of amino acids that form strong bonds among one another than do those of other, heat-intolerant organisms. Consequently, some photosynthetic cyanobacteria tolerate temperatures as high as 75°C, and some archaebacteria can live in hot springs at temperatures up to 110°C.

Temperature affects other biological compounds as well. The physical properties of fats and oils, which are major components of cell membranes and constitute the energy reserves of animals, depend on temperature. When cold, fats become stiff (picture in your mind the fat on a piece of meat taken from the refrigerator); when warm, they become fluid.

**Tolerance of freezing**

Temperatures on the earth’s surface rarely exceed 50°C except in hot springs and at the soil surface in hot deserts. However, temperatures below the freezing point of water occur commonly, particularly on the land and in small ponds, which may freeze solid during winter. When living cells freeze, the crystal structure of ice disrupts most life processes and may damage delicate cell structures, eventually causing death. Many organisms successfully cope with freezing temperatures, either by maintaining their body temperatures above the freezing point of water or by activating chemical mechanisms that enable them to resist freezing or tolerate its effects.

Dissolved substances that interfere with the formation of ice can depress the freezing point of water below 0°C. Plants and animals take advantage of this physical property to lower the freezing point of their body fluids. As we saw above, salt decreases the freezing point of water. But protein structure and function are also disrupted by high salt concentrations, and so using salts for this purpose is physiologically impractical. Instead, the body fluids of many marine organisms contain high concentrations of dissolved glycerol, which is a three-carbon alcohol that is used to form the backbone of triglyceride fats. A 10% glycerol solution lowers the freezing point of water by about 2.3°C without severely affecting biochemical processes. Glyco-proteins, the class of proteins that contain one or more carbohydrates, also may be used to lower the freezing temperature. Such antifreeze-like compounds in their tissues allow fish in antarctic regions to remain active in seawater that is colder than the normal freezing point of the blood of fish inhabiting temperate or tropical seas.
Terrestrial invertebrates also use the anti-freeze approach, and their body fluids may contain up to 30% glycerol, in extreme cases, as winter approaches. Supercooling provides a second physical solution to the problem of freezing. Under certain circumstances, fluids can cool below the freezing point without ice crystals developing. Ice generally forms around some object, called a seed, which can be a small ice crystal or other particle. In the absence of seeds, pure water may cool more than 20°C below its melting point without freezing. Supercooling has been recorded to −8°C in reptiles and to −18°C in invertebrates. Glycoproteins in the blood of these cold-adapted animals impede ice formation by coating developing crystals, which would otherwise act as seeds.

As you can see, many types of organisms use a variety of physical mechanisms to cope with physical stresses in the environment, emphasizing the general principle that organisms are physical systems, albeit very special ones. This point is further emphasized by the ways in which organisms use physical principles to sense their environments.

Organisms use many physical stimuli to sense the environment

To function in a complex and changing environment, organisms must be able to sense environmental change, detect and locate objects, and navigate the landscape. A predator must find its food before it can eat it. Salmon must recognize the proper river at the end of their spawning migration. Plants must sense the changing seasons to flower at the right time. The senses an organism uses generally match the types of physical stimuli available in the environment and the ways in which the organism relates to it (plants, for example, don't need the acute vision that some predators have).

Sensing electromagnetic radiation

That so many organisms rely on vision to sense the environment is not surprising, considering the high energy levels available in the visible portion of the spectrum and the fact that light travels in a straight line, allowing accurate location and resolution of objects. We ourselves primarily use vision to locate food, particularly as it is now displayed on the shelves of supermarkets. Yet our visual acuity is rather pathetic compared with that of hawks, and many insects and birds can perceive ultraviolet light, which is invisible to us (Figure 2.27). Insects also can detect rapid movement, such as that of wings beating 300 times per second; we humans cannot distinguish individual movie frames flickering at even 30 times per second. Thus, different organisms use the available visual information to different extents.

Some animals that are active at night, when visible light levels are too low to be used effectively, rely on other kinds of radiation. Among the more unusual sensory organs are the pit organs of the pit vipers, a group of reptiles that includes the rattlesnakes. The pit organs, located on each side of the head in front of the eyes (Figure 2.28), detect the infrared (heat) radiation given off by the warm...
bodies of potential prey (see Figure 2.20). Pit vipers are so sensitive to infrared radiation that they can detect small rodents several feet away in less than a second. Moreover, because the pits are directionally sensitive, these snakes can locate warm objects precisely enough to strike them. Even plants make use of light stimuli to measure the length of the day as a cue for the seasonal changes that regulate flowering or initiate dormancy.

Sensing sound

What we perceive as sounds are pressure waves in air created by movements and impacts of objects, vibrating objects, or even turbulence in air flowing around objects.

Pressure waves are propagated in all directions like ripples on the surface of water. This makes sounds easy to detect but difficult to localize. The energy of pressure waves also decreases with distance from the source, effectively limiting the range of detection. Nonetheless, sound may warn of an approaching predator, regardless of the direction from which it comes. Some nocturnal predators can sense the direction of a sound source by the different times of arrival of sound waves at each ear. When the source of a sound is directly ahead, pulses of sound pressure arrive at each ear simultaneously. When the head is turned relative to a sound’s point of origin, peaks and troughs of pressure reach the ears at different times, partially canceling rather than reinforcing each other. Directional sensitivity of hearing is greatest when the distance between the ears is about the same as the distance between sound waves. High-pitched sounds have shorter wavelengths and therefore are more useful sources of information for smaller animals. In fact, the ranges of sound frequencies that an animal can make and hear both vary inversely with size, just as a bass fiddle produces lower sounds than a smaller violin. Owls have such sensitive and directionally informative hearing that they can locate mice and other prey by the sounds they make as they move through the habitat. Their ability to pinpoint sound is further aided by the asymmetrical shapes of their outer ears, which deaden sound arriving from certain angles relative to sounds received from other directions.

Figure 2.27 Many organisms use signals that are “visible” only in ultraviolet light.
(a) The human eye sees this yellow daisy in reflected light in the range of 400–700 nanometers. (b) Bees see a different pattern in the same flower in light from the ultraviolet portion of the spectrum (300–400 nanometers). The light flecks on the petals are pollen grains. Photos by Leonard Lessin/Photo Researchers.

Figure 2.28 The pit organs of the rattlesnake, located between the eye and the nostril, are used for detection of infrared radiation from potential prey. Courtesy of R. B. Suter.
Bats can use sound to find their way around the environment and locate prey in the absence of environmental sounds, because they produce the sound themselves by means of a biological sonar system. Bats emit very loud, high-pitched pulses of sound—generally above the range of human hearing—and sense the echoes that bounce back from objects in the environment, including such prey as moths in flight. The sound has to be produced in pulses so that the bat can listen for the fainter echoes during the quiet intervals between pulses. As a bat closes in on its prey, it emits pulses more frequently to increase the rate of incoming information. A bat can direct most of the energy in its echolocation sound directly in front of its line of flight, which increases the effective range of the sonar. The bat’s hearing is also highly directional because its large, external ears can channel faint returning echoes to the eardrum (Figure 2.29).

One of the most distinctive uses of sound is the long-distance communication of whales. The high density of water is ideal for propagating sounds, especially those having very low frequencies. Some large whales produce extremely loud, deep sounds close to the lower limit of detection by humans (about 20 cycles per second). These sounds travel hundreds of kilometers and presumably allow widely dispersed groups of whales to communicate with one another. What they talk about isn’t known.

Sensing odors

Smell is the detection of molecules diffusing through air or water. This source of information has properties that differ considerably from those of electromagnetic waves (sight) and pressure waves in air or water (hearing). Odors carried by air and water currents are difficult to localize. However, because odors are persistent, the presence of a substance can be detected long after its source has disappeared. Once an odor is detected, an organism can move upstream in the direction of the current to locate the source of the smelly molecules. This is the basis for a great deal of chemical communication, including the production of volatile mate attractants by many insects and the fragrances that many plants use to attract pollinators. Some predators follow trails of volatile chemicals to locate potential prey or other food sources. Snakes sense chemicals by flicking their tongues against the ground as they move and transferring chemicals that adhere to the tongue to sensitive organs of smell located in the roof of the mouth. The forked tongues of snakes and other reptiles allow them to simultaneously test for odors to the left and to the right to determine the correct direction of travel.

Sensing electric fields

A few aquatic animals have developed the sensory ability to detect electric fields. Some species of electric fish continuously discharge electricity from specialized muscle organs, creating a weak electric field around them. Nearby objects distort the field, and these changes are picked up by receptors on the surface of the fish. As one might expect, the production and sensation of electric fields are most highly developed in fishes that inhabit murky waters where visibility is poor. The long, flat snout of the paddlefish, which lives in silt-laden rivers, is highly sensitive to electrical disturbances produced by small prey organisms (Figure 2.30). Because its snout projects so far in front of its mouth, the paddlefish has time to capture the small zooplankton it detects as they float past. Some species use electric signals to communicate, and the electric ray *Torpedo* employs powerful electric currents (up to 50 volts at several amperes) to defend itself and to kill prey.

![Figure 2.29 The head of a leaf-nose bat is adapted for the production and detection of sonar signals. Courtesy of A. Guillen.](image)
Sensing physical contact

In contrast to the magnificent senses of many organisms, others perceive their surroundings only dimly and rely on chance to bump into things. In rivers where visibility is poor, bottom-dwelling species such as catfish use elongated fins and barbels around the mouth as sensitive touch and taste receptors. Even with long barbels and bristles, the tactile sense has a very short range. Nonetheless, touch can provide a tremendous amount of information not available through other senses because of the textural and structural richness of the environment.

We have barely touched, so to speak, on the ways in which organisms perceive and find their way around their environments. Sensory modalities are limited by the availability of information that can be interpreted to reveal pattern and change in the environment, and that information is a feature of the physical environment. The use of information to sense the environment reminds us once again that organisms, above all, are physical systems and, as such, must obey physical laws and operate within limits set by the physical environment.

4. All natural waters contain dissolved substances picked up in the atmosphere or from soils and rocks through which water flows. In limestone-rich areas, streams and lakes have abundant calcium (Ca$^{2+}$) and bicarbonate (HCO$_3^-$) ions. In the oceans, sodium (Na$^+$), chlorine (Cl$^-$), and sulfate (SO$_4^{2-}$) ions predominate owing to their greater solubility.

5. Acidity refers to the concentration of hydrogen (H$^+$) ions and is expressed as pH. Most natural waters have pH values between 6 (slightly acid) and 9 (slightly alkaline). Some organisms can tolerate high acidity (low pH) in the environment, but they maintain their internal environments between pH 6 and 7, or close to neutral, because high concentrations of the strongly reactive hydrogen ions disrupt biological processes.

6. Biological energy transformations are based largely on the chemistry of carbon and oxygen. Energy assimilated during photosynthesis is chemically reduced from its low-energy state in carbon dioxide to its high-energy state in carbohydrates. In a coupled reaction, oxygen is oxidized from its form in water to molecular oxygen. The energy stored in carbohydrates is released by the oxidation of carbon to carbon dioxide (respiration).

7. Carbon dioxide is scarce in the atmosphere (0.03%), but is more abundantly distributed in aquatic systems, where it forms soluble bicarbonate ions. The availability of carbon dioxide in aquatic systems is limited by the rate of diffusion of the gas through water, especially through still boundary layers of unmixed water that adhere to the surfaces of plants.

8. Oxygen, abundant in the atmosphere, is relatively scarce in water, where its solubility and rate of diffusion are low. Oxygen may be depleted by bacterial respiration of organic matter (producing anoxic conditions) in environments where it cannot be replenished by photosynthesis.

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**Summary**

1. Water is the basic medium of life. It is liquid within the range of temperatures encountered over most of the earth, and it has an immense capacity to dissolve inorganic compounds. These properties, and its abundance at the earth's surface, make water an ideal medium for living systems.

2. Water conducts heat rapidly and resists changes in temperature, and temperatures are therefore relatively evenly distributed throughout bodies of water and organisms.

3. Water is denser than air and provides more buoyancy, but it is also more viscous and therefore impedes movement.
9. Organisms require many elements to build necessary biological structures and maintain life processes. The availability of these elements varies tremendously among environments. The scarcity (relative to need) of nitrogen and phosphorus often limits plant growth.

10. Most of the energy for life ultimately comes from sunlight. Solar radiation varies over a spectrum of wavelengths. Short wavelengths (ultraviolet) are absorbed in the atmosphere by ozone; carbon dioxide and water vapor absorb long wavelengths. Absorption in the atmosphere of infrared light radiated by the earth is known as the greenhouse effect and is responsible for the moderate temperatures at the surface of the earth. Plants extract energy primarily in the high-intensity, short-wavelength portion of the spectrum, which roughly coincides with visible light.

11. Light is attenuated by water. The depth of the euphotic zone, at the bottom of which photosynthesis balances respiration, varies from 100 meters in clear waters to a few tens of centimeters in turbid or polluted water.

12. Radiation, conduction, convection, and evaporation determine the thermal environment of organisms, especially in terrestrial habitats. In still air, organisms are surrounded by boundary layers, which impede exchange of heat and water vapor with the environment. The heat budget of an organism is intimately tied to the metabolism of food and regulation of water and salts.

13. Higher temperatures generally increase the rate of biological processes by a factor of about 2 to 4 for each 10°C. Higher thermal energy also causes proteins and other biological molecules to unfold and lose their function, setting an upper limit to temperature tolerance.

14. Most organisms cannot survive temperatures much greater than 45°C, but thermophilic bacteria grow in hot springs at up to 110°C. They tolerate such temperatures because their proteins are chemically designed to generate strong forces of attraction to hold molecules together.

15. Organisms in cold environments withstand freezing temperatures by metabolically maintaining elevated body temperatures, by lowering the freezing point of their body fluids with glycerol or glycoproteins, or by supercooling their body fluids.

16. The senses of organisms depend on the availability of information in the physical environment. The nature of this information—whether it consists of light waves, sound (pressure) waves, or volatile or dissolved molecules—determines how, and how well, the organism can detect and localize sources of information.

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**PRACTICING ECOLOGY**

**CHECK YOUR KNOWLEDGE**

**The Future Physical Environment**

Organisms exhibit a certain geographic distribution in part because of their adaptations to the physical environment. Temperature, precipitation, mineral nutrients, light intensity, day length, oxygen content, and pH all limit where an organism can live and reproduce successfully. In most cases, the importance of these factors is species-specific; that is, the relative influence of each of these factors differs among species.

Many physical factors in the biosphere are expected to change as a direct or indirect consequence of human activities. One such factor is the concentration of CO₂ in the atmosphere. Scientists are concerned that an increase in atmospheric CO₂ could enhance the greenhouse effect enough to cause rapid global warming. In the late 1950s, Dr. Charles Keeling began recording atmospheric CO₂ concentrations atop Mauna Loa, an extinct volcano, in Hawaii. He wanted to test the hypothesis that CO₂ was increasing as a result of emissions from the burning of fossil fuels and the clearing of forests. At the time Keeling began his study, scientists did not have accurate long-term measurements of atmospheric CO₂. Mauna Loa was an ideal place to conduct the study because Hawaii is remote from concentrated sources of human CO₂ production, and measurements made at high altitude there would provide an estimate of average global effects of CO₂ emissions on the atmosphere.

Keeling observed that the average atmospheric CO₂ concentration was increasing dramatically (Figure 2.31). At the start of his observations in 1958, the CO₂ concentration was about 315 parts per million (ppm; 315 CO₂ molecules per million molecules of air), and had increased to about 352 ppm by 1990. By January 2000, the value had reached 370 ppm. Most scientists agree that it will continue to increase if humans continue to burn fossil fuel and clear forests at current rates.

**CHECK YOUR KNOWLEDGE**

1. Use the data in the essay and in Figure 2.31 to determine the percentage increase in CO₂ concentrations from 1958 to 2000.

2. Visit the Carbon Dioxide Information Analysis Center Web site that reports on Dr. Keeling’s research through Practicing Ecology on the Web at http://www.whfreeman.com/ricklefs. How is the concentration of atmospheric CO₂ measured?
As we have already seen, CO₂ acts as a greenhouse gas. Predictions about how much the earth will warm up as a result of these increases vary considerably (the accuracy of such predictions is expected to increase as computing power increases). Currently, it is expected that the average temperature of the earth will increase between 1.5°C and 3°C (and maybe more) by the year 2050 (assuming that emissions rates stay at 1990s levels). Note that this estimate represents the average temperature over the entire planet, meaning that warming may be greater or less depending on where you are. For example, arctic ecosystems could experience an increase of 5°C.

What does global warming mean for the physical conditions that dictate the geographic distributions of organisms? Certainly, the distributions of many species are expected to shift slowly poleward and toward higher elevations. Dr. Robert L. Peters has predicted that if the climate warms by 3°C, species distributions will shift upward mountainsides by about 500 m (Figure 2.32). Similarly, the northern limits of species ranges are expected to move poleward by about 500 km.

But are these predictions realistic? In natural systems, species will experience fragmentation of their ranges, and the rate at which suitable environments are displaced will determine whether species will be able to shift fast enough to keep up with their preferred ranges. For humans, as agricultural zones shift and as sea levels rise due to melting ice caps there may be catastrophic displacement of populations. We know that the earth has been warm before, much warmer than it is at present or is likely to be in the near future. However, the predicted changes will require that plants and animals alter their interactions at a rate that is 10 to 100 times faster than they have ever had to in response to past climate changes.

Figure 2.31 CO₂ concentrations in the atmosphere have changed over time. These measurements were recorded at Mauna Loa, Hawaii, where the effects of nearby human activities are minimal. CO₂ concentration in the Northern Hemisphere is lower during summer, when plant photosynthesis removes carbon from the atmosphere, and higher during winter, when respiration exceeds plant production. Courtesy of C.D. Keeling and T.P. Whorf, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy (1999).

Figure 2.32 The elevational distributions of species are likely to change in response to climatic warming. (a) Ranges of species A, B, and C before climatic warming. (b) Species A has gone extinct, B has moved to a smaller habitat at a higher elevation, C's habitat has become fragmented onto two portions of the mountain, and D has moved into new habitat at higher elevations. From R.L. Peter, in R.L. Peter and T.E. Lovejoy (eds.), Global Warming and Biological Diversity, Yale University Press, New Haven, CT (1992), pp. 15–30.
CHECK YOUR KNOWLEDGE

3. Why are scientists concerned about rising levels of CO$_2$?

4. The mission of the Environmental Protection Agency is to “protect human health and to safeguard the natural environment — air, water, and land — upon which life depends.” Go to the global warming page of their site through Practicing Ecology on the Web at http://www.whfreeman.com/ricklefs. How do greenhouse gases combine to cause the greenhouse effect?

Suggested Readings


