Chapter 9

Photosynthesis: Physiological and Ecological Considerations

THE CONVERSION OF SOLAR ENERGY to the chemical energy of organic compounds is a complex process that includes electron transport and photosynthetic carbon metabolism (see Chapters 7 and 8). Earlier discussions of the photochemical and biochemical reactions of photosynthesis should not overshadow the fact that, under natural conditions, the photosynthetic process takes place in intact organisms that are continuously responding to internal and external changes. This chapter addresses some of the photosynthetic responses of the intact leaf to its environment. Additional photosynthetic responses to different types of stress are covered in Chapter 25.

The impact of the environment on photosynthesis is of interest to both plant physiologists and agronomists. From a physiological standpoint, we wish to understand how photosynthesis responds to environmental factors such as light, ambient CO_2 concentrations, and temperature. The dependence of photosynthetic processes on environment is also important to agronomists because plant productivity, and hence crop yield, depends strongly on prevailing photosynthetic rates in a dynamic environment.

In studying the environmental dependence of photosynthesis, a central question arises: How many environmental factors can limit photosynthesis at one time? The British plant physiologist F. F. Blackman hypothesized in 1905 that, under any particular conditions, the rate of photosynthesis is limited by the slowest step, the so-called *limiting factor*.

The implication of this hypothesis is that at any given time, photosynthesis can be limited either by light or by CO_2 concentration, but not by both factors. This hypothesis has had a marked influence on the approach used by plant physiologists to study photosynthesis—that is, varying one factor and keeping all other environmental conditions constant.

TABLE 9.1
Some characteristics of limitations to the rate of photosynthesis

	Conditions that lead to this limitation		Response of photosynthesis under this limitation to		
Limiting factor	CO_2	Light	CO_2	O_2	Light
Rubisco activity	Low	High	Strong	Strong	Absent
RuBP regeneration	High	Low	Moderate	Moderate	Strong

In the intact leaf, three major metabolic steps have been identified as important for optimal photosynthetic performance:

1. Rubisco activity

2. Regeneration of ribulose bisphosphate (RuBP)

3. Metabolism of the triose phosphates

The first two steps are the most prevalent under natural conditions. Table 9.1 provides some examples of how light and CO_2 can affect these key metabolic steps. In the following sections, biophysical, biochemical, and environmental aspects of photosynthesis in leaves are discussed in detail.

LIGHT, LEAVES, AND PHOTOSYNTHESIS

Scaling up from the chloroplast (the focus of Chapters 7 and 8) to the leaf adds new levels of complexity to photosynthesis. At the same time, the structural and functional properties of the leaf make possible other levels of regulation.

We will start by examining how leaf anatomy, and movements by chloroplasts and leaves, control the absorption of light for photosynthesis. Then we will describe how chloroplasts and leaves adapt to their light environment and how the photosynthetic response of leaves grown under low light reflects their adaptation to a low-light environment. Leaves also adapt to high light conditions, illustrating that plants are physiologically flexible and that they adapt to their immediate environment.

Both the amount of light and the amount of CO_2 determine the photosynthetic response of leaves. In some situations, photosynthesis is limited by an inadequate supply of light or CO_2. In other situations, absorption of too much light can cause severe problems, and special mechanisms protect the photosynthetic system from excessive light. Multiple levels of control over photosynthesis allow plants to grow successfully in a constantly changing environment and different habitats.

CONCEPTS AND UNITS IN THE MEASUREMENT OF LIGHT

Three light parameters are especially important in the measurement of light: (1) spectral quality, (2) amount, and (3) direction. Spectral quality was discussed in Chapter 7 (see Figures 7.2 and 7.3, and Web Topic 7.1). A discussion of the amount and direction of light reaching the plant requires consideration of the geometry of the part of the plant that receives the light: Is the plant organ flat or cylindrical?

Flat, or planar, light sensors are best suited for flat leaves. The light reaching the plant can be measured as energy, and the amount of energy that falls on a flat sensor of known area per unit time is quantified as **irradiance** (see Table 9.2). Units can be expressed in terms of energy, such as watts per square meter (W m^{-2}). Time (seconds) is contained within the term watt: 1 W = 1 joule (J) s^{-1}.

Light can also be measured as the number of incident **quanta** (singular *quantum*). In this case, units can be expressed in moles per square meter per second (mol m^{-2} s^{-1}), where *moles* refers to the number of photons (1 mol of light = 6.02 × 10^{23} photons, Avogadro's number). This measure is called **photon irradiance**. Quanta and energy units can be interconverted relatively easily, provided that the wavelength of the light, λ, is known. The energy of a photon is related to its wavelength as follows:

$$E = \frac{hc}{\lambda}$$

where c is the speed of light (3 × 10^8 m s^{-1}), h is Planck's constant (6.63 × 10^{-34} J s), and λ is the wavelength

TABLE 9.2
Concepts and units for the quantification of light

	Energy measurements (W m^{-2})	Photon measurements (mol m^{-2}s^{-1})
Flat light sensor	Irradiance	Photon irradiance
	Photosynthetically active radiation (PAR, 400-700 nm, energy units)	PAR (quantum units)
	—	Photosynthetic photon flux density (PPFD)
Spherical light sensor	Fluence rate (energy units)	Fluence rate (quantum units)
	Scalar irradiance	Quantum scalar irradiance

(A)

Light

Equal irradiance values

(B)

Light

Sensor

Sensor

(C)

α

Sensor
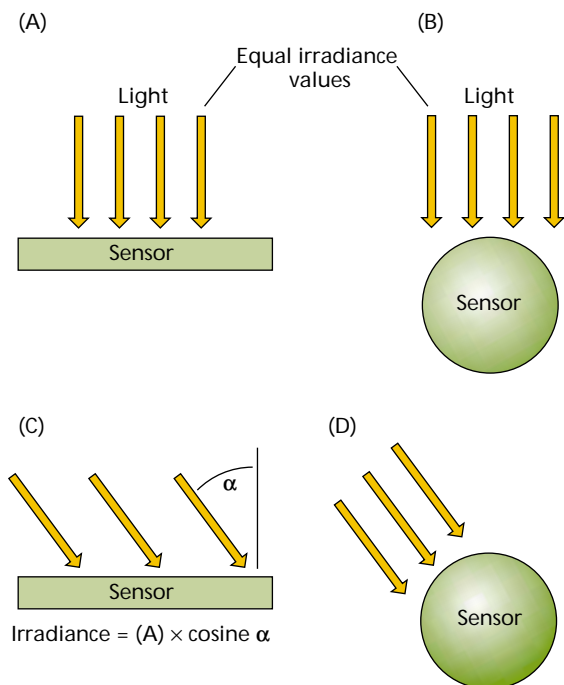
Irradiance = (A) × cosine α

(D)

Sensor

FIGURE 9.1 Flat and spherical light sensors. Equivalent amounts of collimated light strike a flat irradiance-type sensor (A) and a spherical sensor (B) that measure fluence rate. With collimated light, A and B will give the same light readings. When the light direction is changed 45°, the spherical sensor (D) will measure the same quantity as in B. In contrast, the flat irradiance sensor (C) will measure an amount equivalent to the irradiance in A multiplied by the cosine of the angle α in C. (After Björn and Vogelmann 1994.)

of light, usually expressed in nm (1 nm = 10^{-9} m). From this equation it can be shown that a photon at 400 nm has twice the energy of a photon at 800 nm (see Web Topic 9.1).

Now let's turn our attention to the direction of light. Light can strike a flat surface directly from above or obliquely. When light deviates from perpendicular, irradiance is proportional to the cosine of the angle at which the light rays hit the sensor (Figure 9.1).

There are many examples in nature in which the light-intercepting object is not flat (e.g., complex shoots, whole plants, chloroplasts). In addition, in some situations light can come from many directions simultaneously (e.g., direct light from the sun plus the light that is reflected upward from sand, soil, or snow). In these situations it makes more sense to measure light with a spherical sensor that takes measurements omnidirectionally (from all directions).

The term for this omnidirectional measurement is **fluence rate** (see Table 9.2) (Rupert and Letarjet 1978), and this quantity can be expressed in watts per square meter (W m^{-2}) or moles per square meter per second (mol m^{-2} s^{-1}). The units clearly indicate whether light is being measured as energy (W) or as photons (mol).

In contrast to a flat sensor's sensitivity, the sensitivity to light of a spherical sensor is independent of direction (see Figure 9.1). Depending on whether the light is collimated

(rays are parallel) or diffuse (rays travel in random directions), values for fluence rate versus irradiance measured with a flat or a spherical sensor can provide different values (see Figure 9.1) (for a detailed discussion, see Björn and Vogelmann 1994).

Photosynthetically active radiation (**PAR**, 400–700 nm) may also be expressed in terms of energy (W m^{-2}) or quanta (mol m^{-2} s^{-1}) (McCree 1981). Note that PAR is an irradiance-type measurement. In research on photosynthesis, when PAR is expressed on a quantum basis, it is given the special term **photosynthetic photon flux density** (**PPFD**). However, it has been suggested that the term *density* be discontinued because within the International System of Units (SI units, where *SI* stands for *Système International*), *density* can mean area or volume.

In summary, when choosing how to quantify light, it is important to match sensor geometry and spectral response with that of the plant. Flat, cosine-corrected sensors are ideally suited to measure the amount of light that strikes the surface of a leaf; spherical sensors are more appropriate in other situations, such as in studies of a chloroplast suspension or a branch from a tree (see Table 9.2).

How much light is there on a sunny day, and what is the relationship between PAR irradiance and PAR fluence rate? Under direct sunlight, PAR irradiance and fluence rate are both about 2000 μmol m^{-2} s^{-1}, though higher values can be measured at high altitudes. The corresponding value in energy units is about 400 W m^{-2}.

Leaf Anatomy Maximizes Light Absorption

Roughly 1.3 kW m^{-2} of radiant energy from the sun reaches Earth, but only about 5% of this energy can be converted into carbohydrates by a photosynthesizing leaf (Figure 9.2). The reason this percentage is so low is that a major fraction of the incident light is of a wavelength either too short or too long to be absorbed by the photosynthetic pigments (see Figure 7.3). Of the absorbed light energy, a significant fraction is lost as heat, and a smaller amount is lost as fluorescence (see Chapter 7).

Recall from Chapter 7 that radiant energy from the sun consists of many different wavelengths of light. Only photons of wavelengths from 400 to 700 nm are utilized in photosynthesis, and about 85 to 90% of this PAR is absorbed by the leaf; the remainder is either reflected at the leaf surface or transmitted through the leaf (Figure 9.3). Because chlorophyll absorbs very strongly in the blue and the red regions of the spectrum (see Figure 7.3), the transmitted and reflected light are vastly enriched in green—hence the green color of vegetation.

The anatomy of the leaf is highly specialized for light absorption (Terashima and Hikosaka 1995). The outermost cell layer, the epidermis, is typically transparent to visible light, and the individual cells are often convex. Convex epidermal cells can act as lenses and can focus light so that the amount reaching some of the chloroplasts can be many times greater than the amount of ambient light (Vogel-
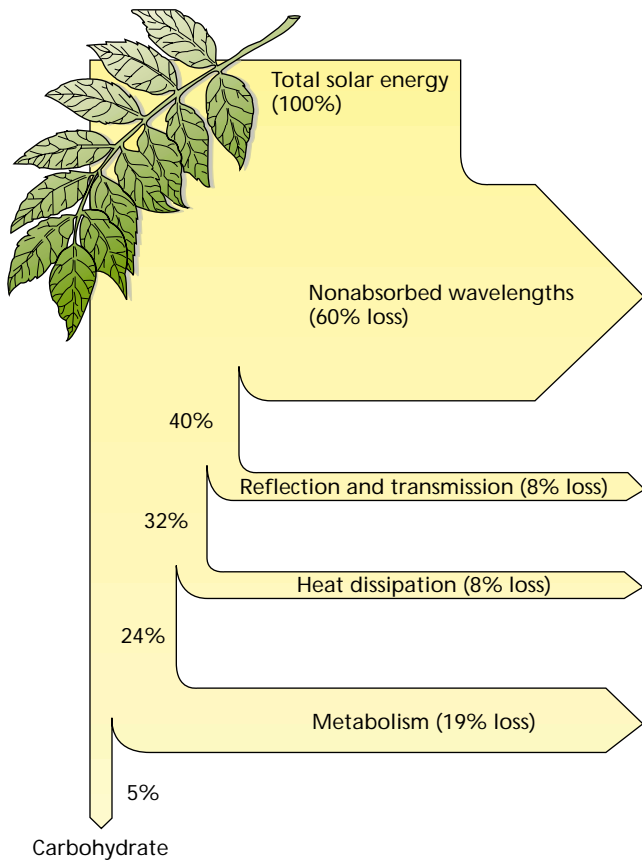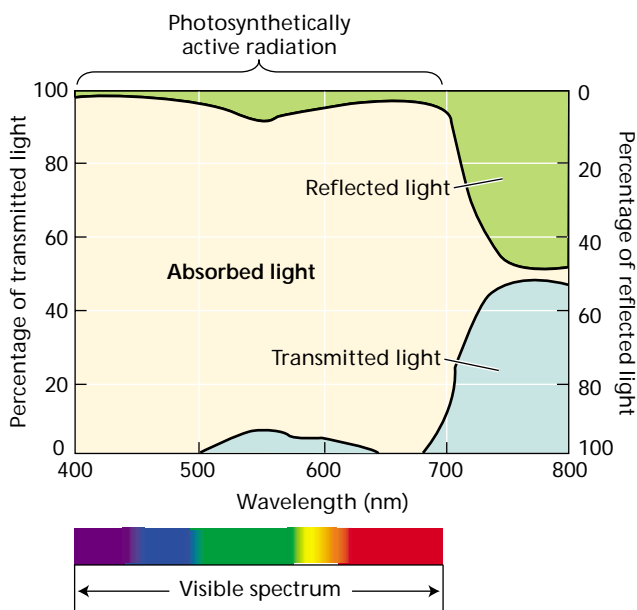
FIGURE 9.2   Conversion of solar energy into carbohydrates by a leaf. Of the total incident energy, only 5% is converted into carbohydrates.

mann et al. 1996). Epidermal focusing is common among herbaceous plants and is especially prominent among tropical plants that grow in the forest understory, where light levels are very low.

Below the epidermis, the top layers of photosynthetic cells are called **palisade cells**; they are shaped like pillars that stand in parallel columns one to three layers deep (Figure 9.4). Some leaves have several layers of columnar palisade cells, and we may wonder how efficient it is for a plant to invest energy in the development of multiple cell layers when the high chlorophyll content of the first layer would appear to allow little transmission of the incident light to the leaf interior. In fact, more light than might be expected penetrates the first layer of palisade cells because of the sieve effect and light channeling.

The **sieve effect** is due to the fact that chlorophyll is not uniformly distributed throughout cells but instead is confined to the chloroplasts. This packaging of chlorophyll results in shading between the chlorophyll molecules and creates gaps between the chloroplasts, where light is not absorbed—hence the reference to a sieve. Because of the sieve effect, the total absorption of light by a given amount of chlorophyll in a palisade cell is less than the light absorbed by the same amount of chlorophyll in a solution.

Light channeling occurs when some of the incident light is propagated through the central vacuole of the palisade cells and through the air spaces between the cells, an arrangement that facilitates the transmission of light into the leaf interior (Vogelmann 1993).

Below the palisade layers is the **spongy mesophyll**, where the cells are very irregular in shape and are surrounded by large air spaces (see Figure 9.4). The large air spaces generate many interfaces between air and water that reflect and refract the light, thereby randomizing its direction of travel. This phenomenon is called *light scattering*.

Light scattering is especially important in leaves because the multiple reflections between cell–air interfaces greatly increase the length of the path over which photons travel, thereby increasing the probability for absorption. In fact, photon path lengths within leaves are commonly four times or more longer than the thickness of the leaf (Richter and Fukshansky 1996). Thus the palisade cell properties that allow light to pass through, and the spongy mesophyll cell properties that are conducive to light scattering, result in more uniform light absorption throughout the leaf.

Some environments, such as deserts, have so much light that it is potentially harmful to leaves. In these environments leaves often have special anatomic features, such as

FIGURE 9.3   Optical properties of a bean leaf. Shown here are the percentages of light absorbed, reflected, and transmitted, as a function of wavelength. The transmitted and reflected green light in the wave band at 500 to 600 nm gives leaves their green color. Note that most of the light above 700 nm is not absorbed by the leaf. (From Smith 1986.)
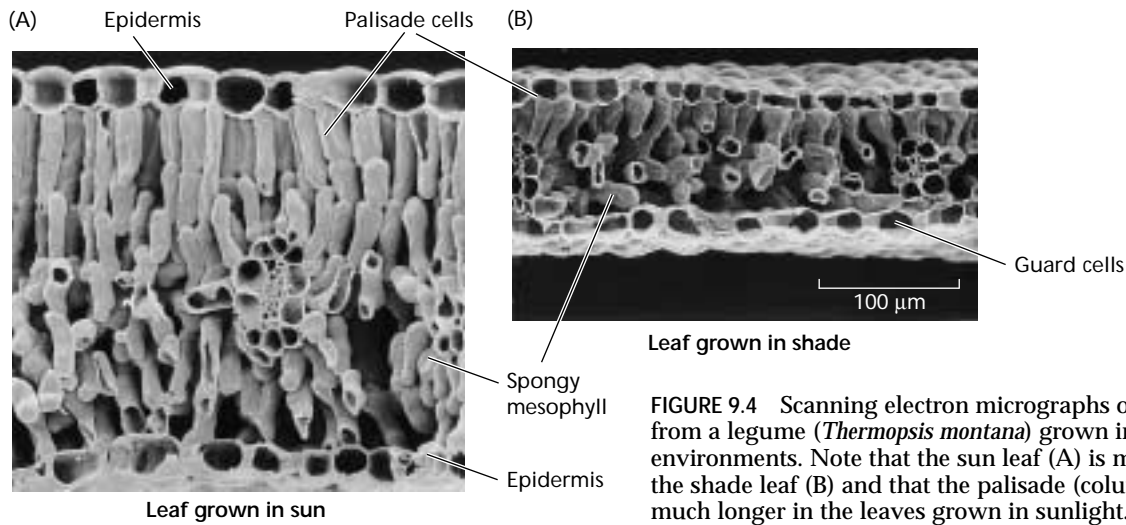
(A)   Epidermis   Palisade cells   (B)

Leaf grown in sun

Guard cells

100 μm

Leaf grown in shade

Spongy
mesophyll

Epidermis

FIGURE 9.4   Scanning electron micrographs of the leaf anatomy from a legume (*Thermopsis montana*) grown in different light environments. Note that the sun leaf (A) is much thicker than the shade leaf (B) and that the palisade (columnlike) cells are much longer in the leaves grown in sunlight. Layers of spongy mesophyll cells can be seen below the palisade cells. (Micrographs courtesy of T. Vogelmann.)

hairs, salt glands, and epicuticular wax that increase the reflection of light from the leaf surface, thereby reducing light absorption (Ehleringer et al. 1976). Such adaptations can decrease light absorption by as much as 40%, minimizing heating and other problems associated with the absorption of too much light.

Chloroplast Movement and Leaf Movement Can Control Light Absorption

Chloroplast movement is widespread among algae, mosses, and leaves of higher plants (Haupt and Scheuerlein 1990). If chloroplast orientation and location are con-trolled, leaves can regulate how much of the incident light is absorbed. Under low light (Figure 9.5B), chloroplasts gather at the cell surfaces parallel to the plane of the leaf so that they are aligned perpendicularly to the incident light—a position that maximizes absorption of light.

Under high light (Figure 9.5C), the chloroplasts move to the cell surfaces that are parallel to the incident light, thus avoiding excess absorption of light. Such chloroplast rearrangement can decrease the amount of light absorbed by the leaf by about 15% (Gorton et al. 1999). Chloroplast movement in leaves is a typical blue-light response (see Chapter 18). Blue light also controls chloroplast orientation
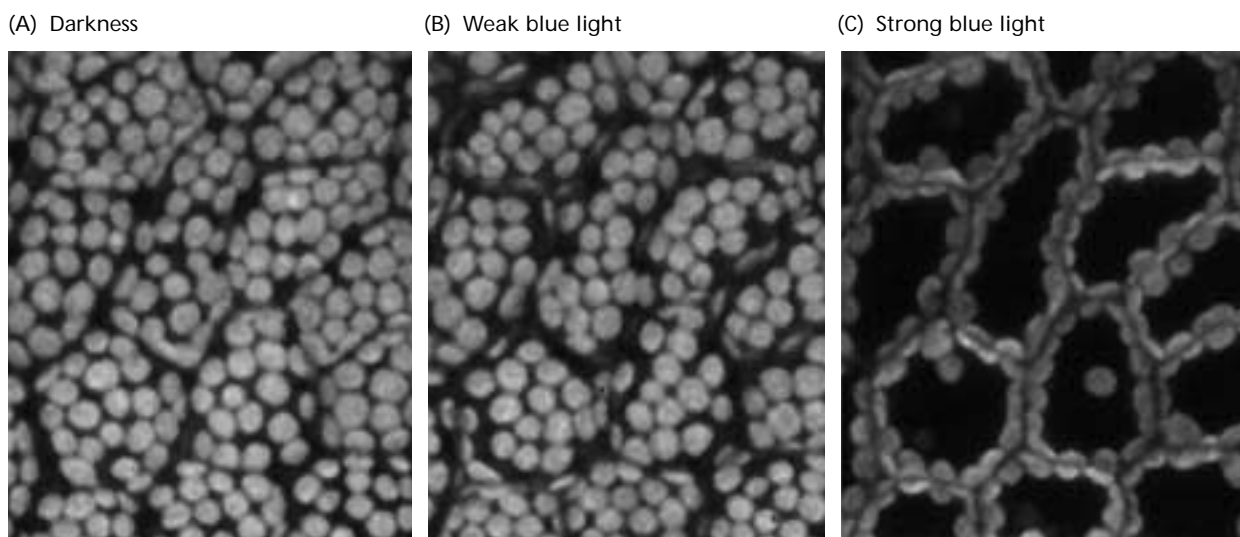
(A) Darkness   (B) Weak blue light   (C) Strong blue light

FIGURE 9.5   Chloroplast distribution in photosynthesizing cells of the duckweed *Lemna*. These surface views show the same cells under three conditions: (A) darkness, (B) weak blue light, and (C) strong blue light. In A and B, chloroplasts are positioned near the upper surface of the cells, where they can absorb maximum amounts of light. When the cells were irradiated with strong blue light (C), the chloroplasts move to the side walls, where they shade each other, thus minimizing the absorption of excess light. (Micrographs courtesy of M. Tlalka and M. D. Fricker.)

in many of the lower plants, but in some algae, chloroplast movement is controlled by phytochrome (Haupt and Scheuerlein 1990). In leaves, chloroplasts move along actin microfilaments in the cytoplasm, and calcium regulates their movement (Tlalka and Fricker 1999).

Leaves have the highest light absorption when the leaf blade, or lamina, is perpendicular to the incident light. Some plants control light absorption by **solar tracking** (Koller 2000); that is, their leaves continuously adjust the orientation of their laminae such that they remain perpendicular to the sun's rays (Figure 9.6). Alfalfa, cotton, soybean, bean, lupine, and some wild species of the mallow family (Malvaceae) are examples of the numerous plant species that are capable of solar tracking.

Solar-tracking leaves keep a nearly vertical position at sunrise, facing the eastern horizon, where the sun will rise. The leaf blades then lock on to the rising sun and follow its movement across the sky with an accuracy of ±15° until sunset, when the laminae are nearly vertical, facing the west, where the sun will set. During the night the leaf takes a horizontal position and reorients just before dawn so that it faces the eastern horizon in anticipation of another sunrise. Leaves track the sun only on clear days, and they stop when a cloud obscures the sun. In the case of intermittent cloud cover, some leaves can reorient as rapidly as 90° per hour and thus can catch up to the new solar position when the sun emerges from behind a cloud (Koller 1990).

Solar tracking is another blue-light response, and the sensing of blue light in solar-tracking leaves occurs in specialized regions. In species of *Lavatera* (Malvaceae), the photosensitive region is located in or near the major leaf veins (Koller 1990). In lupines, (*Lupinus*, Fabaceae), leaves consist of five or more leaflets, and the photosensitive region is located in the basal part of each leaflet lamina.

In many cases, leaf orientation is controlled by a specialized organ called the **pulvinus** (plural *pulvini*), found at the junction between the blade and petiole. The pulvinus contains motor cells that change their osmotic potential and generate mechanical forces that determine laminar orientation. In other plants, leaf orientation is controlled by small mechanical changes along the length of the petiole and by movements of the younger parts of the stem.

Some solar-tracking plants can also move their leaves such that they avoid full exposure to sunlight, thus minimizing heating and water loss. Building on the term **heliotropism** (bending toward the sun), which is often used to describe sun-induced leaf movements, these sun-avoiding leaves are called *paraheliotropic*, and leaves that maximize light interception by solar tracking are called *diaheliotropic*. Some plant species can display diaheliotropic movements when they are well watered and paraheliotropic movements when they experience water stress.

Since full sunlight usually exceeds the amount of light that can be utilized for photosynthesis, what advantage is gained by solar tracking? By keeping leaves perpendicular to the sun, solar-tracking plants maintain maximum photosynthetic rates throughout the day, including early morning and late afternoon. Moreover, air temperature is lower during the early morning and late afternoon, so water stress is lower. Solar tracking therefore gives an advantage to plants that grow in arid regions.

Plants Adapt to Sun and Shade

Some plants have enough developmental plasticity to adapt to a range of light regimes, growing as sun plants in sunny areas and as shade plants in shady habitats. Some shady habitats receive less than 1% of the PAR available in an exposed habitat. Leaves that are adapted to very sunny
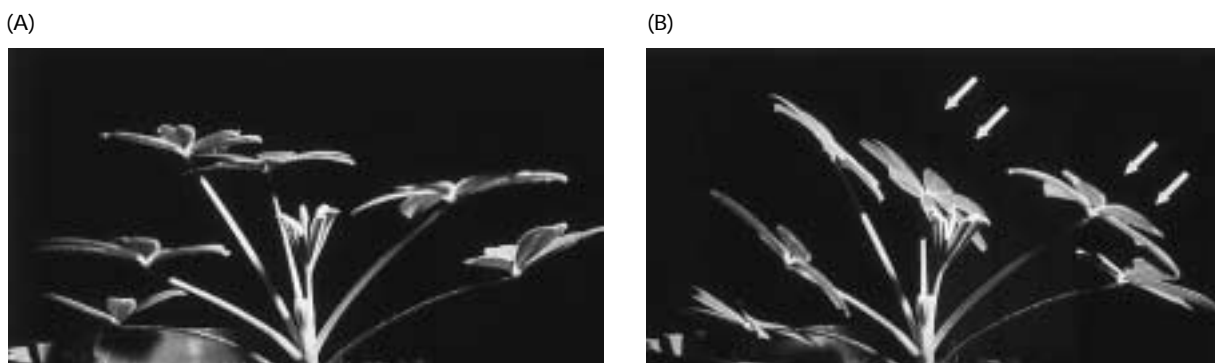
(A)

(B)

FIGURE 9.6   Leaf movement in sun-tracking plants. (A) Initial leaf orientation in the lupine *Lupinus succulentus*. (B) Leaf orientation 4 hours after exposure to oblique light. The direction of the light beam is indicated by the arrows. Movement is generated by asymmetric swelling of a pulvinus, found at the junction between the lamina and the petiole. In natural conditions, the leaves track the sun's trajectory in the sky. (From Vogelmann and Björn 1983, courtesy of T. Vogelmann.)

or very shady environments are often unable to survive in the other type of habitat (see Figure 9.10). Sun and shade leaves have some contrasting characteristics:

- *Shade leaves* have more total chlorophyll per reaction center, have a higher ratio of chlorophyll *b* to chlorophyll *a*, and are usually thinner than sun leaves.

- *Sun leaves* have more rubisco, and a larger pool of xanthophyll cycle components than shade leaves (see Chapter 7).

Contrasting anatomic characteristics can also be found in leaves of the same plant that are exposed to different light regimes. Figure 9.4 shows some anatomic differences between a leaf grown in the sun and a leaf grown in the shade. Sun-grown leaves are thicker and have longer palisade cells than leaves growing in the shade. Even different parts of a single leaf show adaptations to their light microenvironment. Cells in the upper surface of the leaf, which are exposed to the highest prevailing photon flux, have characteristics of cells from leaves grown in full sunlight; cells in the lower surface of the leaf have characteristics of cells found in shade-grown leaves (Terashima 1992).

These morphological and biochemical modifications are associated with specific functions. Far-red light is absorbed primarily by PSI, and altering the ratio of PSI to PSII or changing the light-harvesting antennae associated with the photosystems makes it possible to maintain a better balance of energy flow through the two photosystems (Melis 1996). These adaptations are found in nature; some shade plants show a 3:1 ratio of photosystem II to photosystem I reaction centers, compared with the 2:1 ratio found in sun plants (Anderson 1986). Other shade plants, rather than altering the ratio of PSI to PSII, add more antennae chlorophyll to PSII. These adaptations appear to enhance light absorption and energy transfer in shady environments, where far-red light is more abundant.

Sun and shade plants also differ in their respiration rates, and these differences alter the relationship between respiration and photosynthesis, as we'll see a little later in this chapter.

Plants Compete for Sunlight

Plants normally compete for sunlight. Held upright by stems and trunks, leaves configure a canopy that absorbs light and influences photosynthetic rates and growth beneath them.

Leaves that are shaded by other leaves have much lower photosynthetic rates. Some plants have very thick leaves that transmit little, if any, light. Other plants, such as those of the dandelion (*Taraxacum* sp.), have a rosette growth habit, in which leaves grow radially very close to each other and to the stem, thus preventing the growth of any leaves below them.

Trees represent an outstanding adaptation for light interception. The elaborate branching structure of trees vastly increases the interception of sunlight. Very little PAR pen-
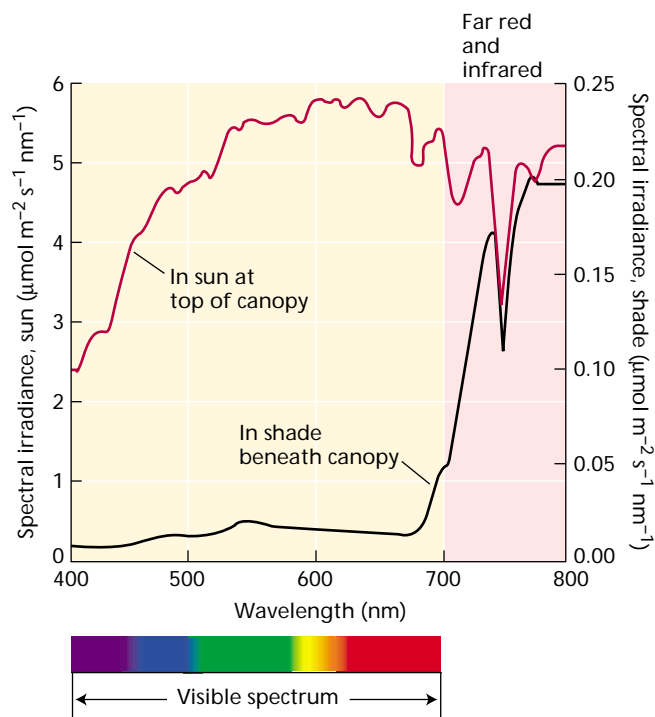

FIGURE 9.7   The spectral distribution of sunlight at the top of a canopy and under the canopy. For unfiltered sunlight, the total irradiance was 1900 µmol m^{-2} s^{-1}; for shade, 17.7 µmol m^{-2} s^{-1}. Most of the photosynthetically active radiation was absorbed by leaves in the canopy. (From Smith 1994.)

etrates the canopy of many forests; almost all of it is absorbed by leaves (Figure 9.7).

Another feature of the shady habitat is **sunflecks**, patches of sunlight that pass through small gaps in the leaf canopy and move across shaded leaves as the sun moves. In a dense forest, sunflecks can change the photon flux impinging on a leaf in the forest floor more than tenfold within seconds. For some of these leaves, a sunfleck contains nearly 50% of the total light energy available during the day, but this critical energy is available for only a few minutes in a very high dose.

Sunflecks also play a role in the carbon metabolism of lower leaves in dense crops that are shaded by the upper leaves of the plant. Rapid responses of both the photosynthetic apparatus and the stomata to sunflecks have been of substantial interest to plant physiologists and ecologists (Pearcy et al. 1997) because they represent unique physiological responses specialized for capturing a short burst of sunlight.

PHOTOSYNTHETIC RESPONSES TO LIGHT BY THE INTACT LEAF

Light is a critical resource for plants that can often limit growth and reproduction. The photosynthetic properties

of the leaf provide valuable information about plant adaptations to their light environment.

In this section we describe typical photosynthetic responses to light as measured in light-response curves. We also consider how an important feature of light-response curves, the light compensation point, explains contrasting physiological properties of sun and shade plants. We then describe quantum yields of photosynthesis in the intact leaf, and the differences in quantum yields between C_3 and C_4 plants. The section closes with descriptions of leaf adaptations to excess light, and the different pathways of heat dissipation in the leaf.

Light-Response Curves Reveal Photosynthetic Properties

Measuring CO_2 fixation in intact leaves at increasing photon flux allows us to construct light-response curves (Figure 9.8) that provide useful information about the photosynthetic properties of leaves. In the dark there is no photosynthetic carbon assimilation, and CO_2 is given off by the plant because of respiration (see Chapter 11). By con-
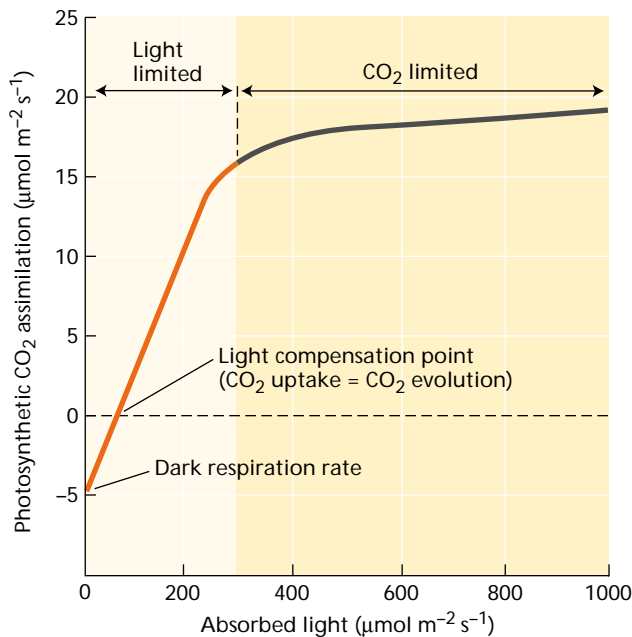
vention, CO_2 assimilation is negative in this part of the light-response curve. As the photon flux increases, photosynthetic CO_2 assimilation increases until it equals CO_2 release by mitochondrial respiration. The point at which CO_2 uptake exactly balances CO_2 release is called the **light compensation point**.

The photon flux at which different leaves reach the light compensation point varies with species and developmental conditions. One of the more interesting differences is found between plants grown in full sunlight and those grown in the shade (Figure 9.9). Light compensation points of sun plants range from 10 to 20 μmol m^{-2} s^{-1}; corresponding values for shade plants are 1 to 5 μmol m^{-2} s^{-1}.

The values for shade plants are lower because respiration rates in shade plants are very low, so little net photosynthesis suffices to bring the net rates of CO_2 exchange to zero. Low respiratory rates seem to represent a basic adaptation that allows shade plants to survive in light-limited environments.

Increasing photon flux above the light compensation point results in a proportional increase in photosynthetic rate (see Figure 9.8), yielding a linear relationship between photon flux and photosynthetic rate. Such a linear rela-
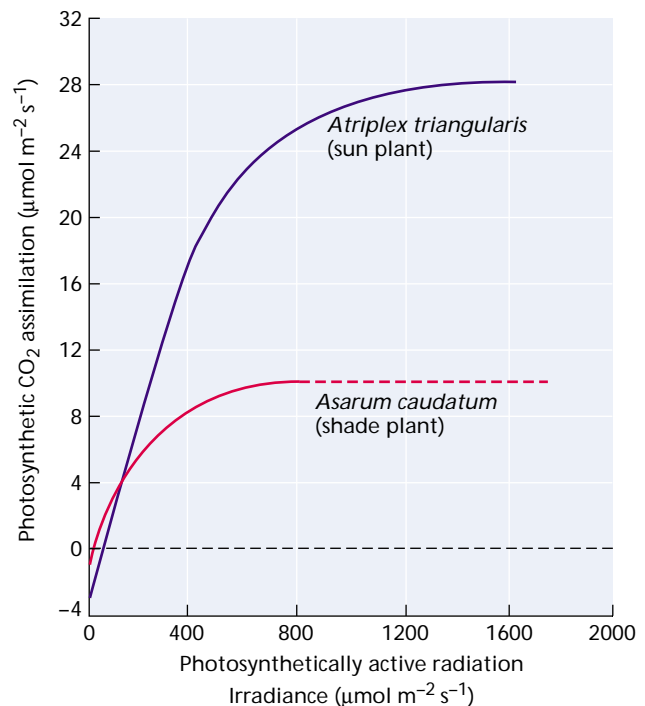

FIGURE 9.8 Response of photosynthesis to light in a C_3 plant. In darkness, respiration causes a net efflux of CO_2 from the plant. The light compensation point is reached when photosynthetic CO_2 assimilation equals the amount of CO_2 evolved by respiration. Increasing light above the light compensation point proportionally increases photosynthesis indicating that photosynthesis is limited by the rate of electron transport, which in turn is limited by the amount of available light. This portion of the curve is referred to as light-limited. Further increases in photosynthesis are eventually limited by the carboxylation capacity of rubisco or the metabolism of triose phosphates. This part of the curve is referred to as CO_2 limited.

FIGURE 9.9 Light–response curves of photosynthetic carbon fixation in sun and shade plants. *Atriplex triangularis* (triangle orache) is a sun plant, and *Asarum caudatum* (a wild ginger) is a shade plant. Typically, shade plants have a low light compensation point and have lower maximal photosynthetic rates than sun plants. The dashed line has been extrapolated from the measured part of the curve. (From Harvey 1979.)

tionship comes about because photosynthesis is *light limited* at those levels of incident light, so more light stimulates more photosynthesis.

In this linear portion of the curve, the slope of the line reveals the **maximum quantum yield** of photosynthesis for the leaf. Recall that quantum yield is the relation between a given light-dependent product (in this case CO_2 assimilation) and the number of absorbed photons (see Equation 7.5).

Quantum yields vary from 0, where none of the light energy is used in photosynthesis, to 1, where all the absorbed light is used. Recall from Chapter 7 that the quantum yield of photochemistry is about 0.95, and the quantum yield of oxygen evolution by isolated chloroplasts is about 0.1 (10 photons per molecule of O_2).

In the intact leaf, measured quantum yields for CO_2 fixation vary between 0.04 and 0.06. Healthy leaves from many species of C_3 plants, kept under low O_2 concentrations that inhibit photorespiration, usually show a quantum yield of 0.1. In normal air, the quantum yield of C_3 plants is lower, typically 0.05.

Quantum yield varies with temperature and CO_2 concentration because of their effect on the ratio of the carboxylase and oxygenase reactions of rubisco (see Chapter 8). Below 30°C, quantum yields of C_3 plants are generally higher than those of C_4 plants; above 30°C, the situation is usually reversed (see Figure 9.23). Despite their different growth habitats, sun and shade plants show similar quantum yields.

At higher photon fluxes, the photosynthetic response to light starts to level off (see Figure 9.8) and reaches *saturation*. Once the saturation point is reached, further increases in photon flux no longer affect photosynthetic rates, indicating that factors other than incident light, such as electron transport rate, rubisco activity, or the metabolism of triose phosphates, have become limiting to photosynthesis.

After the saturation point, photosynthesis is commonly referred to as *CO₂ limited*, reflecting the inability of the Calvin cycle enzymes to keep pace with the absorbed light energy. Light saturation levels for shade plants are substantially lower than those for sun plants (see Figure 9.9). These levels usually reflect the maximal photon flux to which the leaf was exposed during growth (Figure 9.10).

The light-response curve of most leaves saturates between 500 and 1000 μmol m^{-2} s^{-1}, photon fluxes well below full sunlight (which is about 2000 μmol m^{-2} s^{-1}). Although individual leaves are rarely able to utilize full sunlight, whole plants usually consist of many leaves that shade each other. For example, only a small fraction of a tree's leaves are exposed to full sun at any given time of the day. The rest of the leaves receive subsaturating photon fluxes in the form of small patches of light that pass through gaps in the leaf canopy or in the form of light transmitted through other leaves. Because the photosynthetic response of the intact plant is the sum of the photosynthetic activity of all the leaves, only rarely is photosynthesis saturated at the level of the whole plant.
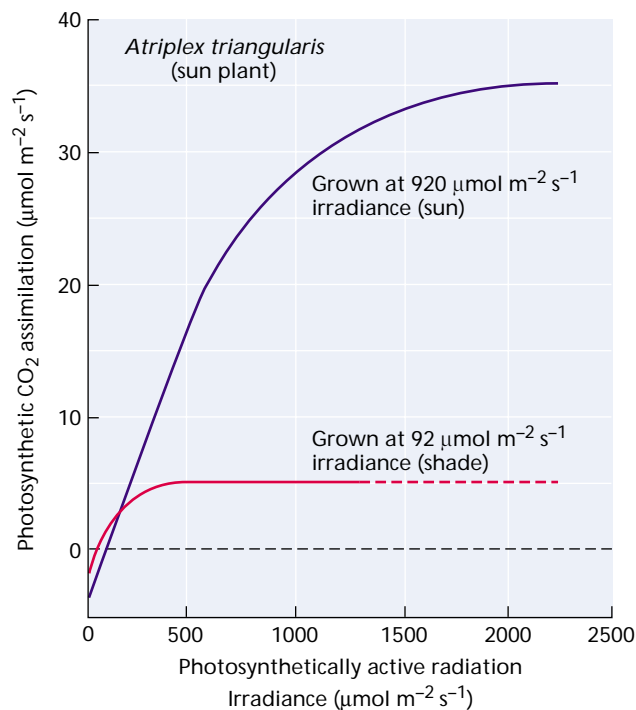

FIGURE 9.10   Light–response of photosynthesis of a sun plant gown under sun or shade conditions. The upper curve represents an *Atriplex triangularis* leaf grown at an irradiance ten times higher than that of the lower curve. In the leaf grown at the lower light levels, photosynthesis saturates at a substantially lower irradiance, indicating that the photosynthetic properties of a leaf depend on its growing conditions. The dashed line has been extrapolated from the measured part of the curve. (From Björkman 1981.)

Light-response curves of individual trees and of the forest canopy show that photosynthetic rate increases with photon flux and photosynthesis usually does not saturate, even in full sunlight (Figure 9.11). Along these lines, crop productivity is related to the total amount of light received during the growing season, and given enough water and nutrients, the more light a crop receives, the higher the biomass (Ort and Baker 1988).

Leaves Must Dissipate Excess Light Energy

When exposed to excess light, leaves must dissipate the surplus absorbed light energy so that it does not harm the photosynthetic apparatus (Figure 9.12). There are several routes for energy dissipation involving *nonphotochemical quenching* (see Chapter 7), which is the quenching of chlorophyll fluorescence by mechanisms other than photochemistry. The most important example involves the transfer of absorbed light energy away from electron transport toward heat production. Although the molecular mechanisms are not yet fully understood, the xanthophyll cycle appears to be an important avenue for dissipation of excess light energy (see Web Essay 9.1).
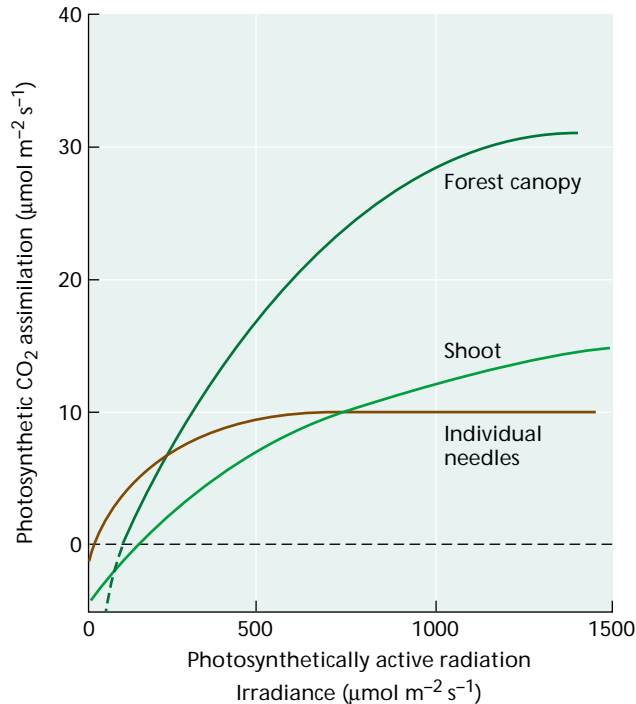
FIGURE 9.11   Changes in photosynthesis (expressed on a per-square-meter basis) in individual needles, a complex shoot, and a forest canopy of Sitka spruce (*Picea sitchensis*) as a function of irradiance. Complex shoots consist of groupings of needles that often shade each other, similar to the situation in a canopy where branches often shade other branches. As a result of shading, much higher irradiance levels are needed to saturate photosynthesis. The dashed line has been extrapolated from the measured part of the curve. (From Jarvis and Leverenz 1983.)

The xanthophyll cycle.   Recall from Chapter 7 that the xanthophyll cycle, which comprises the three carotenoids violaxanthin, antheraxanthin, and zeaxanthin, is involved in the dissipation of excess light energy in the leaf (see Figure 7.36). Under high light, violaxanthin is converted to antheraxanthin and then to zeaxanthin. Note that the two aromatic rings of violaxanthin have a bound oxygen atom in them, antheraxanthin has one, and zeaxanthin has none (again, see Figure 7.36). Experiments have shown that zeaxanthin is the most effective of the three xanthophylls in heat

FIGURE 9.12   Excess light energy in relation to a light–response curve of photosynthetic evolution. The broken line shows theoretical oxygen evolution in the absence of any rate limitation to photosynthesis. At levels of photon flux up to 150 μmol m^{-2} s^{-1}, a shade plant is able to utilize the absorbed light. Above 150 μmol m^{-2} s^{-1}, however, photosynthesis saturates, and an increasingly larger amount of the absorbed light energy must be dissipated. At higher irradiances there is a large difference between the fraction of light used by photosynthesis versus that which must be dissipated (excess light energy). The differences are much higher in a shade plant than in a sun plant. (After Osmond 1994.)

dissipation, and antheraxanthin is only half as effective. Whereas the levels of antheraxanthin remain relatively constant throughout the day, the zeaxanthin content increases at high irradiances and decreases at low irradiances.

In leaves growing under full sunlight, zeaxanthin and antheraxanthin can make up 60% of the total xanthophyll cycle pool at maximal irradiance levels attained at midday (Figure 9.13). In these conditions a substantial amount of excess light energy absorbed by the thylakoid membranes can be dissipated as heat, thus preventing damage to the photosynthetic machinery of the chloroplast (see Chapter 7). The fraction of light energy that is dissipated depends on irradiance, species, growth conditions, nutrient status, and ambient temperature (Demmig-Adams and Adams 1996).

The xanthophyll cycle in sun and shade leaves. Leaves that grow in full sunlight contain a substantially larger xanthophyll pool than shade leaves, so they can dissipate higher amounts of excess light energy. Nevertheless, the xanthophyll cycle also operates in plants that grow in the low light of the forest understory, where they are only occasionally exposed to high light when sunlight passes through gaps in the overlying leaf canopy, forming sunflecks (which were described earlier in the chapter). Exposure to one sunfleck results in the conversion of much of the violaxanthin in the leaf to zeaxanthin. In contrast to typical leaves, in which violaxanthin levels increase again when irradiances drop, the zeaxanthin formed in shade leaves of the forest understory is retained and protects the leaf against exposure to subsequent sunflecks.

The xanthophyll cycle is also found in species such as conifers, the leaves of which remain green during winter, when photosynthetic rates are very low yet light absorption remains high. Contrary to the diurnal cycling of the xanthophyll pool observed in the summer, zeaxanthin lev-
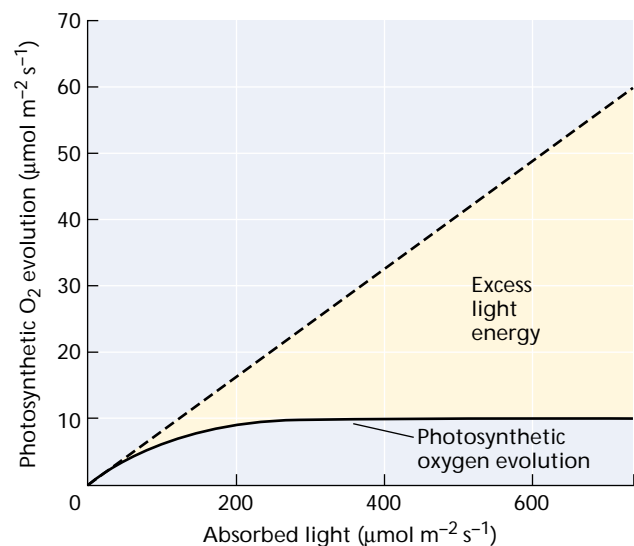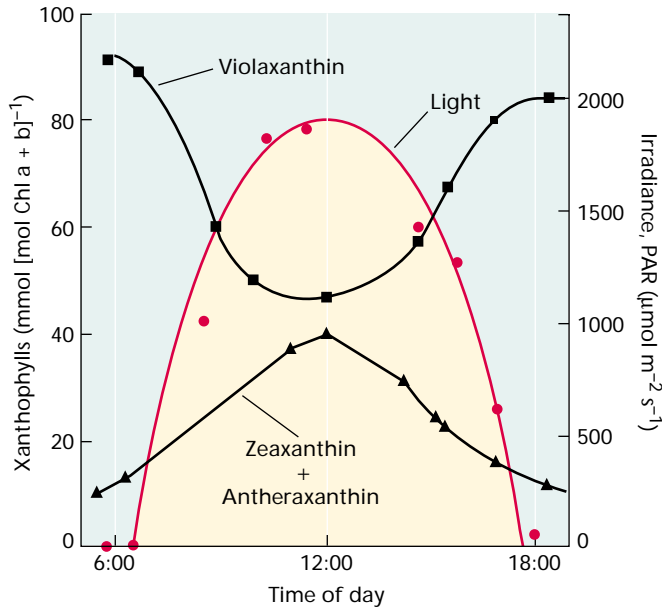
FIGURE 9.13   Diurnal changes in xanthophyll content as a function of irradiance in sunflower (*Helianthus annuus*). As the amount of light incident to a leaf increases, a greater proportion of violaxanthin is converted to antheraxanthin and zeaxanthin, thereby dissipating excess excitation energy and protecting the photosynthetic apparatus. (After Demmig-Adams and Adams 1996.)

els remain high all day during the winter. Presumably this mechanism maximizes dissipation of light energy, thereby protecting the leaves against photooxidation during winter (Adams et al. 2001).

In addition to protecting the photosynthetic system against high light, the xanthophyll cycle may help protect against high temperatures. Chloroplasts are more tolerant of heat when they accumulate zeaxanthin (Havaux et al. 1996). Thus, plants may employ more than one biochemical mechanism to guard against the deleterious effect of excess heat.

Leaves Must Dissipate Vast Quantities of Heat

The heat load on a leaf exposed to full sunlight is very high. In fact, a leaf with an effective thickness of water of 300 μm would warm up by 100°C every minute if all available solar energy were absorbed and no heat were lost. However, this enormous heat load is dissipated by the emission of long-wave radiation, by sensible (i.e., perceptible) heat loss, and by evaporative (or latent) heat loss (Figure 9.14):

- Air circulation around the leaf removes heat from the leaf surfaces if the temperature of the leaf is higher than that of the air; this phenomenon is called **sensible heat loss**.

- **Evaporative heat loss** occurs because the evaporation of water requires energy. Thus as water evaporates

from a leaf, it withdraws heat from the leaf and cools it. The human body is cooled by the same principle, through perspiration.

Sensible heat loss and evaporative heat loss are the most important processes in the regulation of leaf temperature, and the ratio of the two is called the **Bowen ratio** (Campbell 1977):

$$\text{Bowen ratio} = \frac{\text{Sensible heat loss}}{\text{Evaporative heat loss}}$$

In well-watered crops, transpiration (see Chapter 4), and hence water evaporation from the leaf, is high, so the Bowen ratio is low (see Web Topic 9.2). On the other hand, when evaporative cooling is limited, the Bowen ratio is large. For example, in some cacti, stomata closure prevents evaporative cooling; all the heat is dissipated by sensible heat loss, and the Bowen ratio is infinite.

Plants with very high Bowen ratios conserve water but have to endure very high leaf temperatures in order to maintain a sufficient temperature gradient between the leaf and the air. Slow growth is usually correlated with these adaptations.

Isoprene Synthesis Helps Leaves Cope with Heat

We have seen how the xanthophyll cycle can protect against high light, but how do chloroplasts cope with the
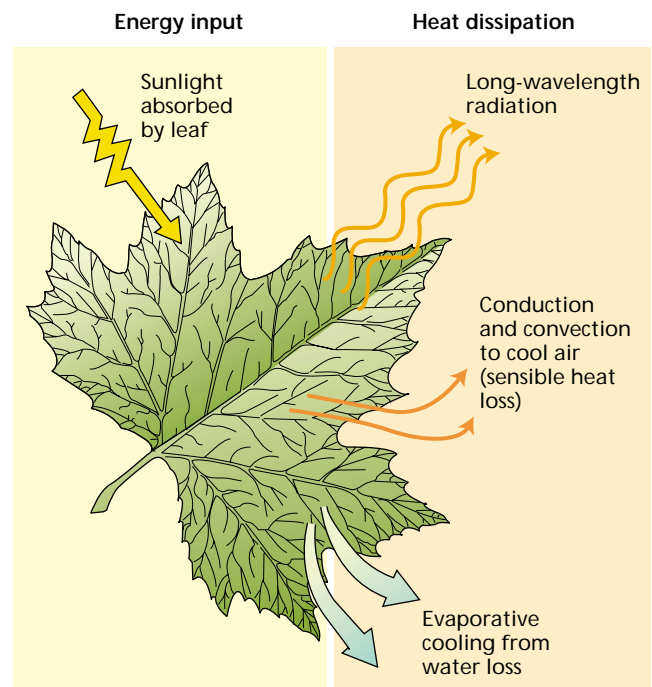

FIGURE 9.14   The absorption and dissipation of energy from sunlight by the leaf. The imposed heat load must be dissipated in order to avoid damage to the leaf. The heat load is dissipated by emission of long-wavelength radiation, by sensible heat loss to the air surrounding the leaf, and by the evaporative cooling caused by transpiration.

high leaf temperatures that usually accompany high light? Isoprene synthesis appears to confer stability to photosynthetic membranes at high light and temperatures. Many plants, including American oak (*Quercus* sp.), aspen (*Populus* sp.), and kudzu (*Pueraria lobata*) emit gaseous five-carbon molecules such as isoprene (2-methyl-1,3-butadiene; see Chapter 13).

On a global scale, these emissions amount to 5×10^{14} g released to the atmosphere each year. These gaseous hydrocarbons are responsible for the pine scent (α- and β-pinene) in coniferous forests and can form a blue haze above forests on hot days. Because isoprene and related hydrocarbons play an important role in atmospheric chemistry, they have attracted much attention from atmospheric scientists.

Isoprene emission from leaves can constitute a significant fraction of the carbon assimilated in photosynthesis. For example, up to 2% of the carbon fixed by photosynthesis in aspen and oak leaves at 30°C is released as isoprene (Sharkey 1996). Sun leaves synthesize more isoprene than shade leaves, and synthesis is proportional to leaf temperature and water stress.

Evidence that isoprene confers stability to photosynthetic membranes under high temperatures comes from three types of experimental results:

1. Whereas preventing isoprene emission with an inhibitor increases susceptibility to damage by heat, adding isoprene to plants that do not produce isoprene confers heat stability (Sharkey et al. 2001).

2. Mutant plants unable to emit isoprene are more easily damaged by high temperatures than are wild-type plants (Sharkey and Singsaas 1995).

3. Isoprene is rapidly synthesized enzymatically in response to elevated leaf temperatures.

Absorption of Too Much Light Can Lead to Photoinhibition

Recall from Chapter 7 that when leaves are exposed to more light than they can utilize (see Figure 9.12), the reaction center of PSII is inactivated and damaged, in a phenomenon called **photoinhibition**. The characteristics of photoinhibition in the intact leaf depend on the amount of light to which the plant is exposed (Figure 9.15), and two types of photoinhibition are identified: dynamic photoinhibition and chronic photoinhibition (Osmond 1994).

Under moderate excess light, **dynamic photoinhibition** is observed. Quantum efficiency decreases (contrast the slopes of the curves in Figure 9.15), but the maximum photosynthetic rate remains unchanged. Dynamic photoinhibition is caused by the diversion of absorbed light energy toward heat dissipation—hence the decrease in quantum efficiency. This decrease is often temporary, and quantum efficiency can return to its initial higher value when photon flux decreases below saturation levels.
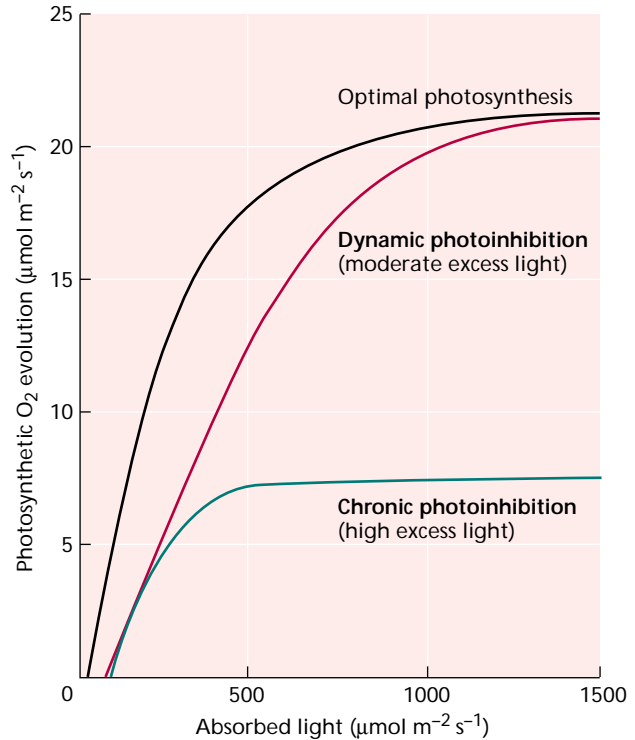

FIGURE 9.15   Changes in the light–response curves of photosynthesis caused by photoinhibition. Exposure to moderate levels of excess light can decrease quantum efficiency (reduced slope of curve) without reducing maximum photosynthetic rate, a condition called dynamic photoinhibition. Exposure to high levels of excess light leads to chronic photoinhibition, where damage to the chloroplast decreases both quantum efficiency and maximum photosynthetic rate. (After Osmond 1994.)

Chronic photoinhibition results from exposure to high levels of excess light that damage the photosynthetic system and decrease both quantum efficiency and maximum photosynthetic rate (see Figure 9.15). Chronic photoinhibition is associated with damage and replacement of the D1 protein from the reaction center of PSII (see Chapter 7). In contrast to dynamic photoinhibition, these effects are relatively long-lasting, persisting for weeks or months.

Early researchers of photoinhibition interpreted all decreases in quantum efficiency as damage to the photosynthetic apparatus. It is now recognized that short-term decreases in quantum efficiency seem to reflect protective mechanisms (see Chapter 7), whereas chronic photoinhibition represents actual damage to the chloroplast resulting from excess light, or a failure of the protective mechanisms.

How significant is photoinhibition in nature? Dynamic photoinhibition appears to occur normally at midday, when leaves are exposed to maximum amounts of light and there is a corresponding reduction in carbon fixation. Photoinhibition is more pronounced at low temperatures, and it becomes chronic under more extreme climatic conditions.

Studies of natural willow populations, and crops of *Brassica napus* (oilseed rape) and *Zea mays* (maize), have shown that the cumulative effects of a daily depression in photosynthetic rates caused by photoinhibition decrease biomass by 10% at the end of the growing season (Long et al. 1994). This may not seem a particularly large effect, but it could be significant in natural plant populations competing for limited resources—conditions under which any reduction in carbon allocated to reproduction can adversely affect reproductive success and survival.

PHOTOSYNTHETIC RESPONSES TO CARBON DIOXIDE

We have discussed how plant growth and leaf anatomy are influenced by light. Now we turn our attention to how CO_2 concentration affects photosynthesis. CO_2 diffuses from the atmosphere into leaves—first through stomata, then through the intercellular air spaces, and ultimately into cells and chloroplasts. In the presence of adequate amounts of light, higher CO_2 concentrations support higher photosynthetic rates. The reverse is also true; that is, low CO_2 concentration can limit the amount of photosynthesis.

In this section we will discuss the concentration of atmospheric CO_2 in recent history, and its availability for carbon-fixing processes. Then we'll consider the limitations that CO_2 places on photosynthesis and the impact of the CO_2-concentrating mechanisms of C_4 plants.

Atmospheric CO_2 Concentration Keeps Rising

Carbon dioxide is a trace gas in the atmosphere, presently accounting for about 0.037%, or 370 parts per million (ppm), of air. The partial pressure of ambient CO_2 (C_a) varies with atmospheric pressure and is approximately 36 pascals (Pa) at sea level (see Web Topic 9.3). Water vapor usually accounts for up to 2% of the atmosphere and O_2 for about 20%. The bulk of the atmosphere, nearly 80%, is nitrogen.

The current atmospheric concentration of CO_2 is almost twice the concentration that has prevailed during most of the last 160,00 years, as measured from air bubbles trapped in glacial ice in Antarctica (Figure 9.16A). Except for the last 200 years, CO_2 concentrations during the recent geological past have been low, fluctuating between 180 and 260 ppm. These low concentrations were typical of times extending back to the Cretaceous, when Earth was much warmer and the CO_2 concentration may have been as high as 1200 to 2800 ppm (Ehleringer et al. 1991).

The current CO_2 concentration of the atmosphere is increasing by about 1 ppm each year, primarily because of the burning of fossil fuels (see Figure 9.16C). Since 1958, when systematic measurements of CO_2 began at Mauna Loa, Hawaii, atmospheric CO_2 concentrations have increased by more than 17% (Keeling et al. 1995), and by 2020 the atmospheric CO_2 concentration could reach 600 ppm.
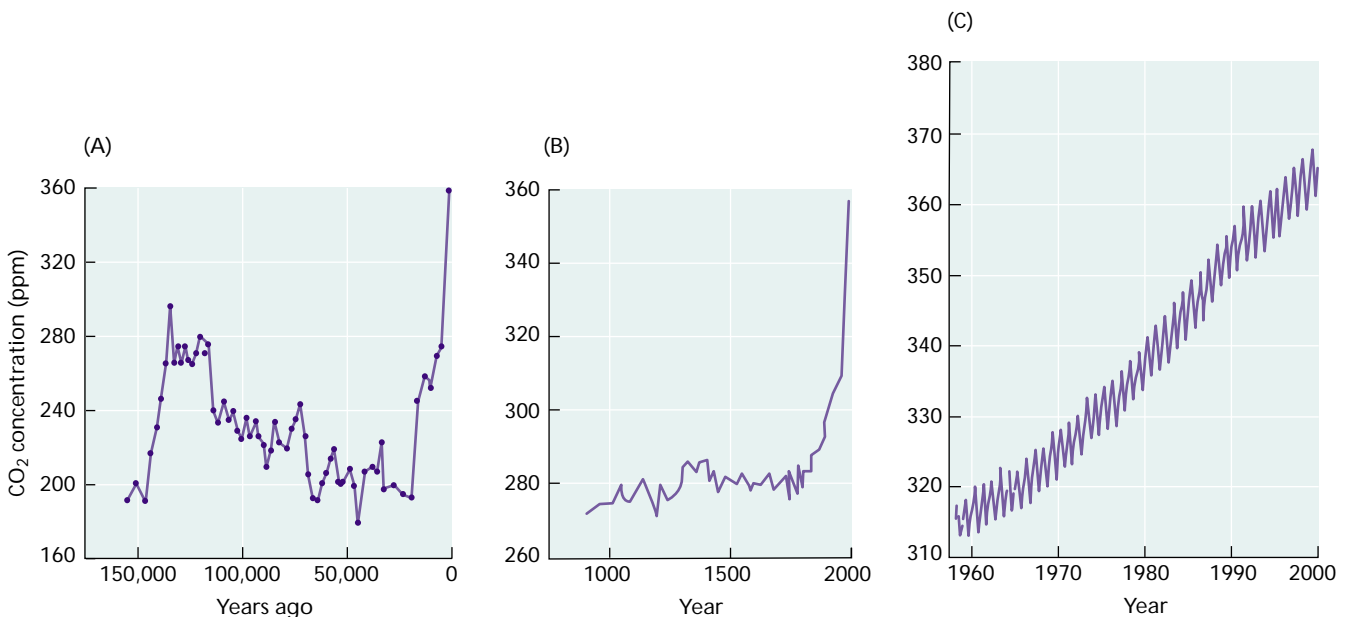

FIGURE 9.16 Concentration of atmospheric CO_2 from the present to 160,000 years ago. (A) Past atmospheric CO_2 concentrations, determined from bubbles trapped in glacial ice in Antarctica, were much lower than current levels. (B) In the last 1000 years, the rise in CO_2 concentration coincides with the Industrial Revolution and the increased burning of fossil fuels. (C) Current atmospheric concentrations of CO_2 measured at Mauna Loa, Hawaii, continue to rise. The wavy nature of the trace is caused by change in atmospheric CO_2 concentrations associated with the growth of agricultural crops. Each year the highest CO_2 concentration is observed in May, just before the Northern Hemisphere growing season, and the lowest concentration is observed in October. (After Barnola et al. 1994, Keeling and Whorf 1994, Neftel et al. 1994, and Keeling et al. 1995.)

The greenhouse effect.   The consequences of this increase in atmospheric CO_2 are under intense scrutiny by scientists and government agencies, particularly because of predictions that the **greenhouse effect** is altering the world's climate. The term *greenhouse effect* refers to the resulting warming of Earth's climate, which is caused by the trapping of long-wavelength radiation by the atmosphere.

A greenhouse roof transmits visible light, which is absorbed by plants and other surfaces inside the greenhouse. The absorbed light energy is converted to heat, and part of it is re-emitted as long-wavelength radiation. Because glass transmits long-wavelength radiation very poorly, this radiation cannot leave the greenhouse through the glass roof, and the greenhouse heats up.

Certain gases in the atmosphere, particularly CO_2 and methane, play the same role as the glass roof in a greenhouse. The increased CO_2 concentration and temperature associated with the greenhouse effect can influence photosynthesis. At current atmospheric CO_2 concentrations, photosynthesis in C_3 plants is CO_2 limited (as we will discuss later in the chapter), but this situation could change as atmospheric CO_2 concentrations continue to rise. Under laboratory conditions, most C_3 plants grow 30 to 60% faster when CO_2 concentration is doubled (to 600–700 ppm), and the growth rate changes depend on nutrient status (Bowes 1993). In some plants the enhanced growth is only temporary.

For many crops, such as tomatoes, lettuce, cucumbers, and roses growing in greenhouses under optimal nutrition, carbon dioxide enrichment in the greenhouse environment results in increased productivity. The photosynthetic performance of C_3 plants under elevated CO_2 is enhanced because photorespiration decreases (see Chapter 8).

Diffusion of CO_2 to the Chloroplast Is Essential to Photosynthesis

For photosynthesis to occur, carbon dioxide must diffuse from the atmosphere into the leaf and into the carboxylation site of rubisco. Because diffusion rates depend on concentration gradients (see Chapters 3 and 6), appropriate gradients are needed to ensure adequate diffusion of CO_2 from the leaf surface to the chloroplast.

The cuticle that covers the leaf is nearly impermeable to CO_2, so the main port of entry of CO_2 into the leaf is the stomatal pore. CO_2 diffuses through the pore into the substomatal cavity and into the intercellular air spaces between the mesophyll cells. This portion of the diffusion path of CO_2 into the chloroplast is a gaseous phase. The remainder of the diffusion path to the chloroplast is a liquid phase, which begins at the water layer that wets the walls of the mesophyll cells and continues through the plasma membrane, the cytosol, and the chloroplast. (For the properties of CO_2 in solution, see Web Topic 8.3.)

Each portion of this diffusion pathway imposes a resistance to CO_2 diffusion, so the supply of CO_2 for photosynthesis meets a series of different points of resistance (Figure 9.17). An evaluation of the magnitude of each point of
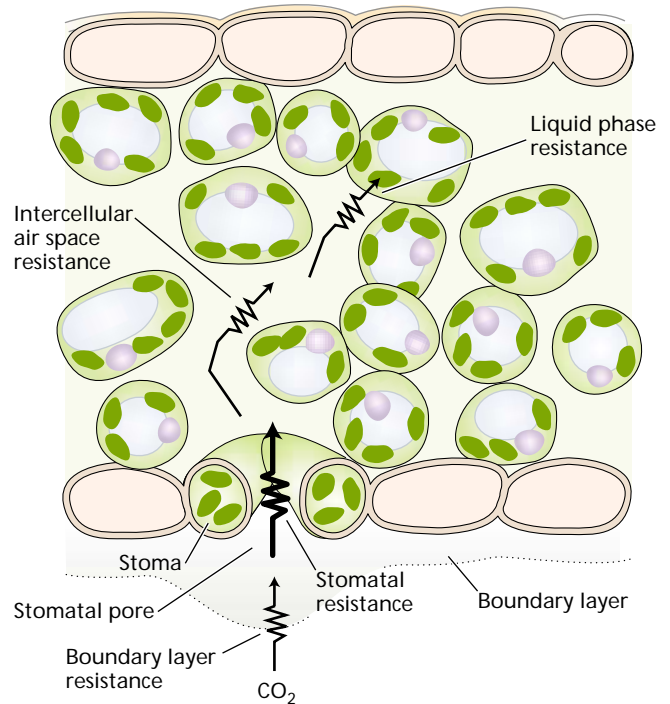

FIGURE 9.17   Points of resistance to the diffusion of CO_2 from outside the leaf to the chloroplasts. The stomatal pore is the major point of resistance to CO_2 diffusion.

resistance is helpful for understanding CO_2 limitations to photosynthesis.

Carbon dioxide enters the intercellular air spaces of the leaf through the stomatal pores. From the air spaces it dissolves in the water of wet cell walls and diffuses into the cell and chloroplast. The same path is traveled in the reverse direction by H_2O.

The sharing of this pathway by CO_2 and water presents the plant with a functional dilemma. In air of high relative humidity, the diffusion gradient that drives water loss is about 50 times larger than the gradient that drives CO_2 uptake. In drier air, this gradient can be even larger. Therefore, a decrease in stomatal resistance through the opening of stomata facilitates higher CO_2 uptake but is unavoidably accompanied by substantial water loss.

Recall from Chapter 4 that the gas phase of CO_2 diffusion into the leaf can be divided into three components—the boundary layer, the stomata, and the intercellular spaces of the leaf—each of which imposes a resistance to CO_2 diffusion (see Figure 9.17).

The boundary layer consists of relatively unstirred air at the leaf surface, and its resistance to diffusion is called the **boundary layer resistance**. The magnitude of the boundary layer resistance decreases with leaf size and wind speed. The boundary layer resistance to water and CO_2 diffusion is physically related to the boundary layer resistance to sensible heat loss discussed earlier.

Smaller leaves have a lower boundary layer resistance to CO_2 and water diffusion, and to sensible heat loss. Leaves

of desert plants are usually small, facilitating sensible heat loss. The large leaves often found in the humid Tropics can have large boundary layer resistances, but these leaves can dissipate the radiation heat load by evaporative cooling because of the high transpiration rates made possible by the abundant water supply in these habitats.

After diffusing through the boundary layer, CO_2 enters the leaf through the stomatal pores, which impose the next type of resistance in the diffusion pathway, the **stomatal resistance**. Under most conditions in nature, in which the air around a leaf is seldom completely still, the boundary layer resistance is much smaller than the stomatal resistance, and the main limitation to CO_2 diffusion is imposed by the stomatal resistance.

There is also a resistance to CO_2 diffusion in the air spaces that separate the substomatal cavity from the walls of the mesophyll cells, called the **intercellular air space resistance**. This resistance is also usually small—causing a drop of 0.5 Pa or less in partial pressure of CO_2, compared with the 36 Pa outside the leaf.

The resistance to CO_2 diffusion of the liquid phase—the **liquid phase resistance**, also called **mesophyll resistance**—encompasses diffusion from the intercellular leaf spaces to the carboxylation sites in the chloroplast. This point of resistance to CO_2 diffusion has been calculated as approximately one-tenth of the combined boundary layer resistance and stomatal resistance when the stomata are fully open. This low resistance value can be attributed in part to the large surface area of mesophyll cells exposed to the intercellular air spaces, which can be as much as 10 to 30 times the projected leaf area (Syvertsen et al. 1995). In addition, the localization of chloroplasts near the cell periphery minimizes the distance that CO_2 diffuses to carboxylation sites within the chloroplast.

The positioning of chloroplasts and the relatively large percentage of intercellular air space (about 20–40%) are special anatomic features that facilitate the internal diffusion and uptake of CO_2 by leaves (Evans 1999). Because the stomatal pores usually impose the largest resistance to CO_2 uptake and water loss in the diffusion pathway, this regulation provides the plant with an effective way to control gas exchange between the leaf and the atmosphere. In experimental measurements of gas exchange from leaves, the boundary layer resistance and the intercellular air space resistance are usually ignored, and the stomatal resistance is used as the single parameter describing the gas phase resistance to CO_2 (see Web Topic 9.4).

Patterns of Light Absorption Generate Gradients of CO_2 Fixation within the Leaf

We have discussed how leaf anatomy is specialized for capturing light and how it also facilitates the internal diffusion of CO_2, but where in the leaf do maximum rates of photosynthesis occur? In most leaves, light is preferentially absorbed at the upper surface, whereas CO_2 enters through the lower surface. Given that light and CO_2 enter from opposing sides of the leaf, does photosynthesis occur uni-

formly within the leaf tissues, or is there a gradient in photosynthesis across the leaf? The photosynthetic properties of a leaf are determined by the following:

- Profiles of light absorption across the mesophyll
- Photosynthetic capacity of those tissues
- Internal CO_2 supply

For most leaves, internal CO_2 diffusion is rapid, so limitations on photosynthetic performance within the leaf are imposed by factors other than CO_2 supply. When white light enters the upper surface of a leaf, blue and red photons are preferentially absorbed by chloroplasts near the irradiated surface (Figure 9.18), owing to the strong absorption bands of chlorophyll in the blue and red regions of the spectrum (see Figure 7.5). Green light, on the other hand, penetrates deeper into the leaf. Compared to blue and red,
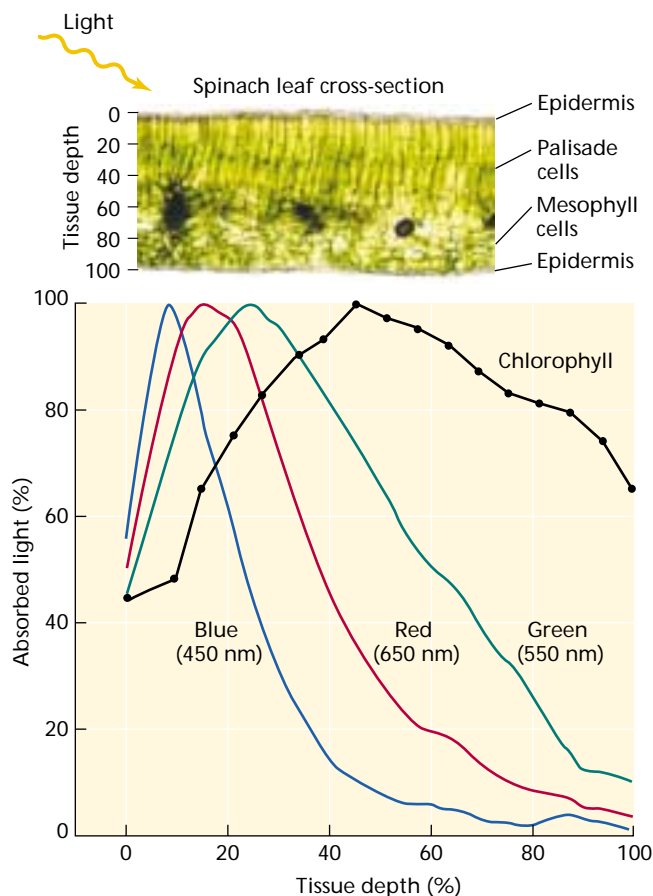

FIGURE 9.18   Distribution of absorbed light in spinach sun leaves. Irradiation with blue, green or red light results in different profiles of absorbed light in the leaf. The micrograph above the graph shows a cross-section of a spinach leaf, with rows of palisade cells occupying nearly half of the leaf thickness. The shapes of the curves are in part a result of the unequal distribution of chlorophyll within leaf tissues. (From Nishio et al. 1993 and Vogelmann and Han 2000; micrograph courtesy of T. Vogelmann.)

chlorophyll absorbs poorly in the green (again, see Figure 7.5), yet green light is very effective in supplying energy for photosynthesis in the tissues within the leaf depleted from blue and red photons.

The capacity of the leaf tissue for photosynthetic CO_2 assimilation depends to a large extent on its rubisco content. In spinach and the faba bean (*Vicia faba*), rubisco content starts out low at the top of the leaf, increases toward the middle, and then decreases again toward the bottom. As a result, the distribution of carbon fixation within the leaf is bell shaped (Figure 9.19). The spongy mesophyll (see Figure 9.4) fixes about 40% of the total carbon in spinach. The functional significance of the rubisco distribution and the profiles of carbon assimilation within leaves is not yet known, although it is likely that photosynthesis profiles vary in leaves with different anatomy and in leaves adapted to different environments.

CO_2 Imposes Limitations on Photosynthesis

Expressing photosynthetic rate as a function of the partial pressure of CO_2 in the intercellular air space (C_i) within the leaf (see Web Topic 9.4) makes it possible to evaluate limitations to photosynthesis imposed by CO_2 supply. At very low intercellular CO_2 concentrations, photosynthesis is strongly limited by the low CO_2, while respiratory rates are unaffected. As a result, there is a negative balance between

CO_2 fixed by photosynthesis and CO_2 produced by respiration, and a net efflux of CO_2 from the plant.

Increasing intercellular CO_2 to the concentration at which these two processes balance each other defines the **CO_2 compensation point**, at which the net efflux of CO_2 from the plant is zero (Figure 9.20A). This concept is analogous to that of the light compensation point discussed earlier in the chapter: *The CO_2 compensation point reflects the balance between photosynthesis and respiration as a function of CO_2 concentration, and the light compensation point reflects that balance as a function of photon flux.*

In C_3 plants, increasing CO_2 above the compensation point stimulates photosynthesis over a wide concentration

(A)

(B)
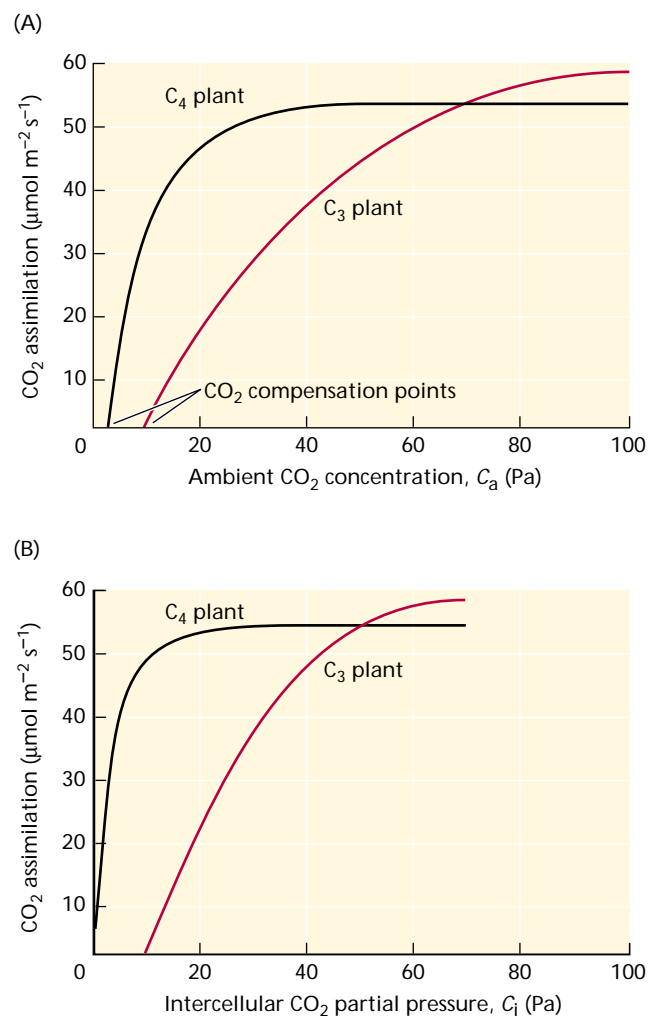
FIGURE 9.20   Changes in photosynthesis as a function of ambient intercellular CO_2 concentrations in *Tidestromia oblongifolia* (Arizona honeysweet), a C_4 plant, and *Larrea divaricata* (creosote bush), a C_3 plant. Photosynthetic rate is plotted against (A) partial pressure of CO_2 in ambient air and (B) calculated intercellular partial pressure of CO_2 inside the leaf (see Equation 5 in Web Topic 9.4). The partial pressure at which CO_2 assimilation is zero defines the CO_2 compensation point. (From Berry and Downton 1982.)
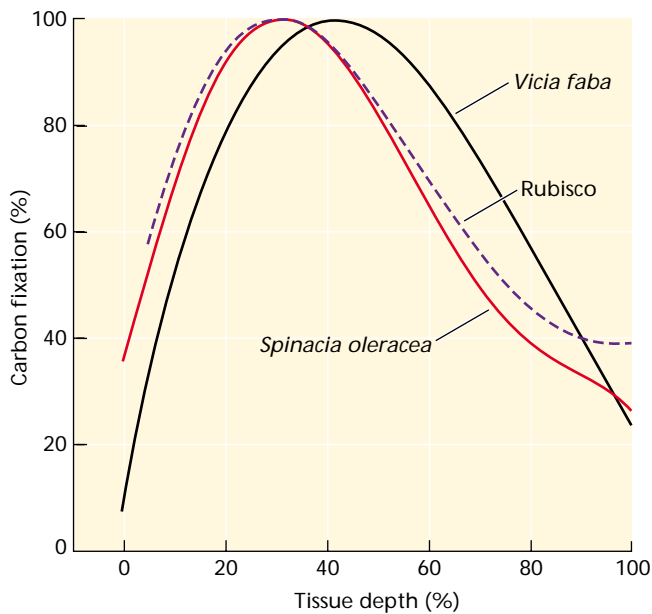
FIGURE 9.19   Distribution of rubisco and carbon fixation within leaves. Carbon fixation (solid line) within spinach leaves closely follows the internal distribution of rubisco (dashed line). Carbon fixation profiles are similar between *Vicia* and spinach. (From Nishio et al. 1993 and Jeje and Zimmermann 1983.)

range (see Figure 9.20A). At low to intermediate CO_2 concentrations, photosynthesis is limited by the carboxylation capacity of rubisco. At high CO_2 concentrations, photosynthesis is limited by the capacity of Calvin cycle to regenerate the acceptor molecule ribulose-1,5-bisphosphate, which depends on electron transport rates. By regulating stomatal conductance, most leaves appear to regulate their C_i (internal partial pressure for CO_2) such that it is intermediate between limitations imposed by carboxylation capacity and the capacity to regenerate ribulose-1,5-bisphosphate.

A plot of CO_2 assimilation as a function intercellular partial pressures of CO_2 tells us how photosynthesis is regulated by CO_2, independent of the functioning of stomata (Figure 9.20B). Inspection of such a plot for C_3 and C_4 plants reveals interesting differences between the two types of carbon metabolism:

- In *C_4 plants*, photosynthetic rates saturate at C_i values of about 15 Pa, reflecting the effective CO_2-concentrating mechanisms operating in these plants (see Chapter 8).

- In *C_3 plants*, increasing C_i levels continue to stimulate photosynthesis over a much broader range.

These results indicate that C_3 plants may benefit more from ongoing increases in atmospheric CO_2 concentrations (see Figure 9.16). In contrast, photosynthesis in C_4 plants is CO_2 saturated at low concentrations, and as a result C_4 plants do not benefit from increases in atmospheric CO_2 concentrations. Figure 9.20 also shows that plants with C_4 metabolism have a CO_2 compensation point of zero or nearly zero, reflecting their very low levels of photorespiration (see Chapter 8). This difference between C_3 and C_4 plants is not seen when the experiments are conducted at low oxygen concentrations because oxygenation is also suppressed in C_3 plants.

CO_2-Concentrating Mechanisms Affect Photosynthetic Responses of Leaves

Because of the operating CO_2-concentrating mechanisms in C_4 plants, CO_2 concentration at the carboxylation sites within C_4 chloroplasts is often saturating for rubisco activity. As a result, plants with C_4 metabolism need less rubisco than C_3 plants need to achieve a given rate of photosynthesis, and require less nitrogen to grow (von Caemmerer 2000).

In addition, the CO_2-concentrating mechanism allows the leaf to maintain high photosynthetic rates at lower C_i values, which require lower rates of stomatal conductance for a given rate of photosynthesis. Thus, C_4 plants can use water and nitrogen more efficiently than C_3 plants can. On the other hand, the additional energy cost of the concentrating mechanism (see Chapter 8) makes C_4 plants less efficient in their utilization of light. This is probably one of the reasons that most shade-adapted plants are C_3 plants.

Many cacti and other succulent plants with CAM metabolism open their stomata at night and close them

during the day (Figure 9.21). The CO_2 taken up during the night is fixed into malate (see Chapter 8). Because air temperatures are much lower at night than during the day, water loss is low and a significant amount of water is saved relative to the amount of CO_2 fixed.

The main constraint on CAM metabolism is that the capacity to store malic acid is limited, and this limitation restricts the amount of CO_2 uptake. However, many CAM plants can fix CO_2 via the Calvin cycle at the end of the day, when temperature gradients are less extreme.

Cladodes (flattened stems) of cacti can survive after detachment from the plant for several months without
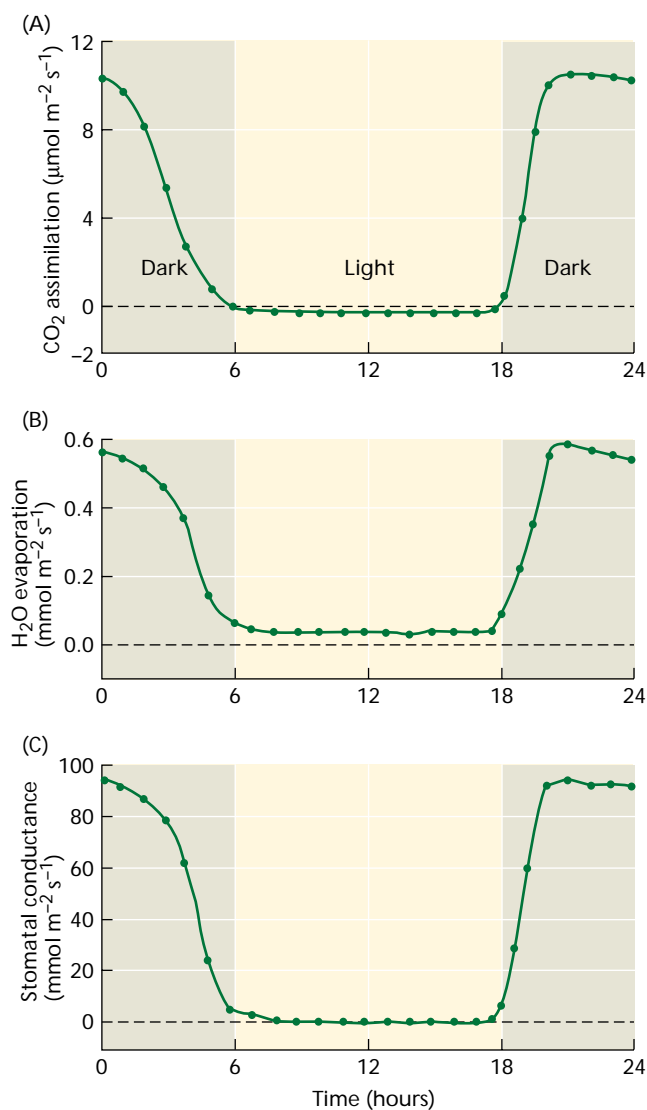

FIGURE 9.21 Photosynthetic carbon assimilation, evaporation, and stomatal conductance of a CAM plant, the cactus *Opuntia ficus-indica*, during a 24-hour period. The whole plant was kept in a gas exchange chamber in the laboratory. The dark period is indicated by shaded areas. In contrast to plants with C_3 or C_4 metabolism, CAM plants open their stomata and fix CO_2 at night. (From Gibson and Nobel 1986.)

water. Their stomata are closed all the time, and the CO_2 released by respiration is refixed into malate. This process, which has been called *CAM idling*, allows the plant to survive for prolonged periods of time while losing remarkably little water.

Discrimination of Carbon Isotopes Reveals Different Photosynthetic Pathways

Atmospheric CO_2 contains the naturally occurring carbon isotopes ^{12}C, ^{13}C, and ^{14}C in the proportions 98.9%, 1.1%, and 10^{-10}%, respectively. $^{14}CO_2$ is present in such small quantities that it has no physiological relevance, but $^{13}CO_2$ is different. The chemical properties of $^{13}CO_2$ are identical to those of $^{12}CO_2$, but because of the slight difference in mass (2.3%), most plants assimilate less $^{13}CO_2$ than $^{12}CO_2$. In other words, plants discriminate against the heavier isotope of carbon, and they have smaller ratios of ^{13}C to ^{12}C than are found in atmospheric CO_2. How effective are plants at distinguishing between the two carbon isotopes? Although discrimination against ^{13}C is subtle, the isotope composition of plants reveals a wealth of information.

Carbon isotope composition is measured by use of a mass spectrometer, which yields the following ratio:

$$R = \frac{^{13}CO_2}{^{12}CO_2} \qquad (9.1)$$

The **isotope composition** of plants, $\delta^{13}C$, is quantified on a per mil (–‰) basis:

$$\delta^{13}C \, ^0/_{00} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \qquad (9.2)$$

where the standard represents the carbon isotopes contained in a fossil belemnite from the Pee Dee limestone formation of South Carolina. The $\delta^{13}C$ of atmospheric CO_2 has a value of –8 ‰, meaning that there is less ^{13}C in the atmospheric CO_2 than is found in the carbonate of the belemnite standard. What are some typical values for carbon isotope ratios of plants? C_3 plants have a $\delta^{13}C$ of about –28 ‰; C_4 plants have an average value of –14 ‰ (Farquhar et al. 1989). Both C_3 and C_4 plants have less ^{13}C than the isotope standard, which means that there has been a discrimination against ^{13}C during the photosynthetic process.

Because the per mil calculation involves multiplying by 1000, the actual isotope discrimination is small. Nonetheless, differences in carbon isotope discrimination are easily detectable with mass spectrometers. For example, measuring the $\delta^{13}C$ of table sugar (sucrose) makes it possible to determine if the sucrose came from sugar beet (a C_3 plant) or sugarcane (a C_4 plant).

What is the physiological basis for ^{13}C depletion in plants? One reason in both C_3 and C_4 plants is diffusion. CO_2 diffuses from air outside of the leaf to the carboxylation sites within leaves. Because $^{12}CO_2$ is lighter than $^{13}CO_2$, it diffuses slightly faster toward the carboxylation site, creating an effective diffusion discrimination of –4.4 ‰. How-

ever, the largest isotope discrimination step is the carboxylation reaction catalyzed by rubisco (Farquhar et al. 1989).

Rubisco has an intrinsic discrimination value against ^{13}C of –30 ‰. By contrast, PEP carboxylase, the primary CO_2 fixation enzyme of C_4 plants, has a much smaller isotope discrimination effect (about –2 to –6 ‰). Thus the inherent difference between the discrimination effects of the two carboxylating enzymes causes the different isotope compositions observed in C_3 and C_4 plants (Farquhar et al. 1989).

Other physiological characteristics of plants affect isotope composition. One factor is the partial pressure of CO_2 in the intercellular air spaces of leaves (C_i). In C_3 plants the potential discrimination by rubisco of –30 ‰ is not fully expressed because the availability of CO_2 at the carboxylation site becomes a limiting factor restricting the discrimination by rubisco. More discrimination occurs when C_i is high, as when stomata are open. Open stomata also facilitate water loss. Thus, lower water use efficiency is correlated with greater discrimination against ^{13}C (Farquhar et al. 1989).

Fossil fuels have a $\delta^{13}C$ of about –26 ‰ because the carbon in these deposits came from organisms that had a C_3 carbon fixation pathway. Furthermore, measuring $\delta^{13}C$ in fossil, carbonate-containing soils and fossil teeth makes it possible to determine that C_4 photosynthesis developed and became prevalent relatively recently (see Web Topic 9.5).

CAM plants can have $\delta^{13}C$ values that are intermediate between those of C_3 and C_4 plants. In CAM plants that fix CO_2 at night via PEP carboxylase, $\delta^{13}C$ is similar to that of C_4 plants. However, when some CAM plants are well watered, they switch to C_3 mode by opening their stomata and fixing CO_2 during the day via rubisco. Under these conditions the isotope composition shifts more toward that of C_3 plants. Thus the $^{13}C/^{12}C$ values of CAM plants reflect how much carbon is fixed via the C_3 pathway versus the C_4 pathway (see Web Topic 9.5).

Plants also fractionate other isotopes, such as $^{18}O/^{16}O$ and $^{15}N/^{14}N$, and the various patterns of isotope enrichment or depletion can be used as indicators of particular metabolic pathways or features.

PHOTOSYNTHETIC RESPONSES TO TEMPERATURE

When photosynthetic rate is plotted as a function of temperature, the curve has a characteristic bell shape (Figure 9.22). The ascending arm of the curve represents a temperature-dependent stimulation of photosynthesis up to an optimum; the descending arm is associated with deleterious effects, some of which are reversible while others are not.

Temperature affects all biochemical reactions of photosynthesis, so it is not surprising that the responses to temperature are complex. We can gain insight into the underlying mechanisms by comparing photosynthetic rates in air at normal and at high CO_2 concentrations. At high CO_2 (see Figure 9.22A), there is an ample supply of CO_2 at the car-
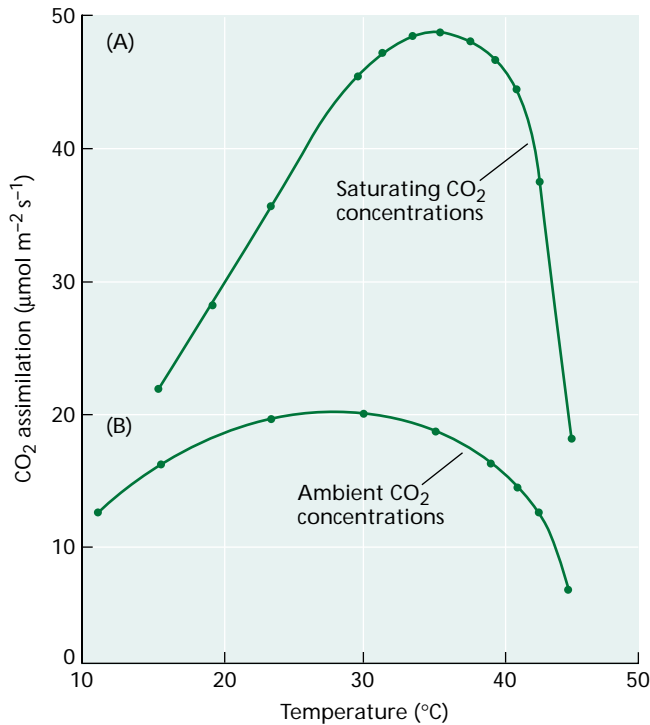
FIGURE 9.22 Changes in photosynthesis as a function of temperature at CO_2 concentrations that saturate photosynthetic CO_2 assimilation (A) and at normal atmospheric CO_2 concentrations (B). Photosynthesis depends strongly on temperature at saturating CO_2 concentrations. Note the significantly higher photosynthetic rates at saturating CO_2 concentrations. (Redrawn from Berry and Björkman 1980.)

1987). When triose phosphates are exported from the chloroplast to the cytosol, an equimolar amount of inorganic phosphate is taken up via translocators in the chloroplast membrane.

If the rate of triose phosphate utilization in the cytosol decreases, phosphate uptake into the chloroplast is inhibited and photosynthesis becomes phosphate limited (Geiger and Servaites 1994). Starch synthesis and sucrose synthesis decrease rapidly with temperature, reducing the demand for triose phosphates and causing the phosphate limitation observed at low temperatures.

The highest photosynthetic rates seen in temperature responses represent the so-called *optimal temperature response*. When these temperatures are exceeded, photosynthetic rates decrease again. It has been argued that this optimal temperature is the point at which the capacities of the various steps of photosynthesis are optimally balanced, with some of the steps becoming limiting as the temperature decreases or increases.

Optimal temperatures have strong genetic and physiological components. Plants of different species growing in habitats with different temperatures have different optimal temperatures for photosynthesis, and plants of the same
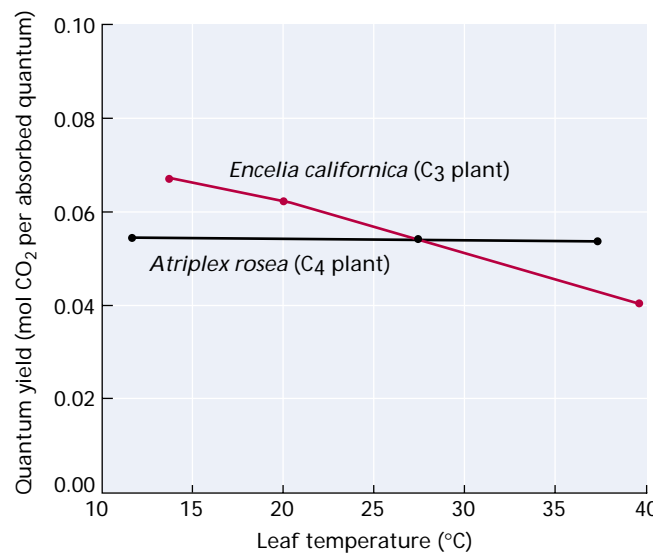
boxylation sites, and the rate of photosynthesis is limited primarily by biochemical reactions connected with electron transport (see Chapter 7). In these conditions, temperature changes have large effects on fixation rates.

At ambient CO_2 concentrations (see Figure 9.22B), photosynthesis is limited by the activity of rubisco, and the response reflects two conflicting processes: an increase in carboxylation rate with temperature and a decrease in the affinity of rubisco for CO_2 as the temperature rises (see Chapter 8). These opposing effects dampen the temperature response of photosynthesis at ambient CO_2 concentrations.

Respiration rates also increase as a function of temperature, and the interaction between photorespiration and photosynthesis becomes apparent in temperature responses. Figure 9.23 shows changes in quantum yield as a function of temperature in a C_3 plant and in a C_4 plant. In the C_4 plant the quantum yield remains constant with temperature, reflecting typical low rates of photorespiration. In the C_3 plant the quantum yield decreases with temperature, reflecting a stimulation of photorespiration by temperature and an ensuing higher energy demand per net CO_2 fixed.

At low temperatures, photosynthesis is often limited by phosphate availability at the chloroplast (Sage and Sharkey

FIGURE 9.23 The quantum yield of photosynthetic carbon fixation in a C_3 plant and in a C_4 plant as a function of leaf temperature. In normal air, photorespiration increases with temperature in C_3 plants, and the energy cost of net CO_2 fixation increases accordingly. This higher energy cost is expressed in lower quantum yields at higher temperatures. Because of the CO_2 concentrating mechanisms of C_4 plants, photorespiration is low in these plants, and the quantum yield does not show a temperature dependence. Note that at lower temperatures the quantum yield of C_3 plants is higher than that of C_4 plants, indicating that photosynthesis in C_3 plants is more efficient at lower temperatures. (From Ehleringer and Björkman 1977.)

species, grown at different temperatures and then tested for their photosynthetic responses, show temperature optima that correlate with the temperature at which they were grown. Plants growing at low temperatures maintain higher photosynthetic rates at low temperatures than plants grown at high temperatures.

These changes in photosynthetic properties in response to temperature play an important role in plant adaptations to different environments. Plants are remarkably plastic in their adaptations to temperature. In the lower temperature range, plants growing in alpine areas are capable of net CO_2 uptake at temperatures close to 0°C; at the other extreme, plants living in Death Valley, California, have optimal rates of photosynthesis at temperatures approaching 50°C.

SUMMARY

Photosynthetic activity in the intact leaf is an integral process that depends on many biochemical reactions. Different environmental factors can limit photosynthetic rates.

Leaf anatomy is highly specialized for light absorption, and the properties of palisade and mesophyll cells ensure uniform light absorption throughout the leaf. In addition to the anatomic features of the leaf, chloroplast movements within cells and solar tracking by the leaf blade help maximize light absorption. Light transmitted through upper leaves is absorbed by leaves growing beneath them.

Many properties of the photosynthetic apparatus change as a function of the available light, including the light compensation point, which is higher in sun leaves than in shade leaves. The linear portion of the light-response curve for photosynthesis provides a measure of the quantum yield of photosynthesis in the intact leaf. In temperate areas, quantum yields of C_3 plants are generally higher than those of C_4 plants.

Sunlight imposes a substantial heat load on the leaf, which is dissipated back into the air by long-wavelength radiation, by sensible heat loss, or by evaporative heat loss. Increasing CO_2 concentrations in the atmosphere are increasing the heat load on the biosphere. This process could cause damaging changes in the world's climate, but it could also reduce the CO_2 limitations on photosynthesis. At high photon flux, photosynthesis in most plants is CO_2 limited, but the limitation is substantially lower in C_4 and CAM plants because of their CO_2-concentrating mechanisms.

Diffusion of CO_2 into the leaf is constrained by a series of different points of resistance. The largest resistance is usually that imposed by the stomata, so modulation of stomatal apertures provides the plant with an effective means of controlling water loss and CO_2 uptake. Both stomatal and nonstomatal factors affect CO_2 limitations on photosynthesis.

Temperature responses of photosynthesis reflect the temperature sensitivity of the biochemical reactions of photosynthesis and are most pronounced at high CO_2 concen-

trations. Because of the role of photorespiration, the quantum yield is strongly dependent on temperature in C_3 plants but is nearly independent of temperature in C_4 plants.

Leaves growing in cold climates can maintain higher photosynthetic rates at low temperatures than leaves growing in warmer climates. Leaves grown at high temperatures perform better at high temperatures than leaves grown at low temperatures do. Functional changes in the photosynthetic apparatus in response to prevailing temperatures in their environment have an important effect on the capacity of plants to live in diverse habitats.

Web Material

Web Topics

9.1 Working with Light

Amount, direction, and spectral quality are important parameters for the measurement of light.

9.2 Heat Dissipation from Leaves: The Bowen Ratio

Sensible heat loss and evaporative heat loss are the most important processes in the regulation of leaf temperature.

9.3 Working with Gases

This web topic explains how to work with mole fractions and other physical parameters of gases.

9.4 Calculating Important Parameters in Leaf Gas Exchange

Gas exchange methods allow us to measure photosynthesis and stomatal conductance in the intact leaf.

9.5 Isotope Discrimination

The carbon isotope composition of plants reveals a wealth of information.

Web Essay

9.1 The Xanthophyll Cycle

Molecular and biophysical studies are revealing the role of the xanthophyll cycle on the photoprotection of leaves.

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