

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 26.

The impact of the environment on photosynthesis is of interest to plant physiologists, ecologists, and agronomists. From a physiological standpoint, we wish to understand the direct responses of photosynthesis to environmental factors such as light, ambient CO_2 concentrations, and temperature, as well as the indirect responses (mediated through the effects of stomatal control) to environmental factors such as humidity and soil moisture. The dependence of photosynthetic processes on environmental conditions is also important to agronomists because plant productivity, and hence crop yield, depend strongly on prevailing photosynthetic rates in a dynamic environment. To the ecologist, the fact that photosynthetic rates and capacities vary among different environments is of great interest in terms of adaptation and evolution.

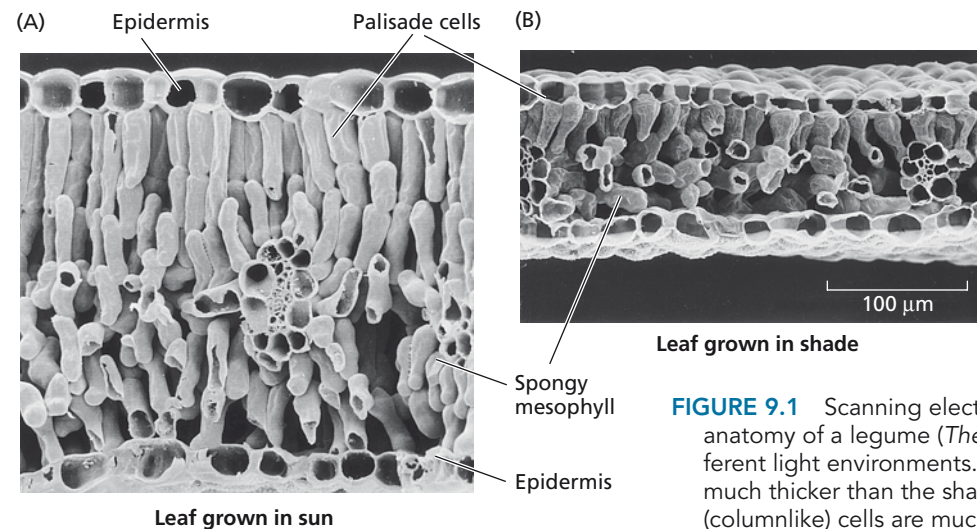


FIGURE 9.1 Scanning electron micrographs of the leaf anatomy of a legume (*Thermopsis montana*) grown in different light environments. Note that the sun leaf (A) is much thicker than the shade leaf (B) and that the palisade (columnlike) cells are much longer in the leaves grown in sunlight. Layers of spongy mesophyll cells can be seen below the palisade cells. (Courtesy of T. Vogelmann.)

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 in the process, 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 CO₂ concentration, for instance, 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. In the intact leaf, three major metabolic properties have been identified as important for optimal photosynthetic performance:

- Rubisco activity
- Regeneration of ribulose biphosphate (RuBP)
- Metabolism of the triose phosphates

Farquhar and Sharkey (1982) added a fundamentally new perspective to our understanding of photosynthesis by pointing out that we should think of the controls on the overall rates of net photosynthetic rate in leaves in economic terms, considering “supply” and “demand” functions for carbon dioxide. Net photosynthesis is defined as net CO₂ uptake.

The biochemical activities referred to above take place in the palisade cells and spongy mesophyll of the leaf (**FIGURE 9.1**). These activities describe the “demand” by photosynthetic metabolism in the cells for CO₂ as a substrate. However, the actual rate of CO₂ “supply” to these cells is controlled by stomatal guard cells located on the epidermal portions of the leaf. These supply and demand functions associated with photosynthesis take place in different cells. It is the coordinated actions of “demand” by photosynthetic

cells and “supply” by guard cells that determine the leaf photosynthetic rate as measured by net CO₂ uptake.

In the following sections, we will focus on how naturally occurring variations in light and temperature influence photosynthesis in leaves and how leaves in turn adjust or acclimate to variations in light and temperature. In addition, we will explore how atmospheric carbon dioxide influences photosynthesis, an especially important consideration in a world where CO₂ concentrations are rapidly increasing as humans continue to burn fossil fuels for energy uses.

Photosynthesis Is the Primary Function of Leaves

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 leaf orientation control the absorption of light for photosynthesis. Then we will describe how chloroplasts and leaves acclimate to their light environment. We will see that the photosynthetic response of leaves grown under different light conditions also reflects the capacity of a plant to grow under different light environments. However, there are also limits in the extent to which photosynthesis in a species can acclimate to very different light environments.

It will become clear that under different environmental conditions, the rate of photosynthesis is limited by different factors. For example, in some situations photosynthesis is limited by an inadequate supply of light or CO₂. In

other situations, absorption of too much light would cause severe problems if special mechanisms did not protect the photosynthetic system from excessive light. While plants have multiple levels of control over photosynthesis that allow them to grow successfully in constantly changing environments, there are ultimately limits to what is possible in terms of acclimation to sun and shade, high and low temperatures, and degrees of water stress.

Think of the different ways in which leaves are exposed to different spectra and quantities of light that result in photosynthesis. Plants grown outdoors are exposed to sunlight, and the spectrum of that sunlight will depend on whether it is measured in full sunlight or under the shade of a canopy. Plants grown indoors may receive either incandescent or fluorescent lighting, each of which is different from sunlight. To account for these differences in spectral quality and quantity, we need uniformity in how we measure and express the light that impacts photosynthesis.

The light reaching the plant is a flux and that flux can be measured in either energy or photon units. **Irradiance** is the amount of energy that falls on a flat sensor of known area per unit time, expressed in watts per square meter (W m⁻²). (Recall that time [seconds] is contained within the term watt: 1 W = 1 joule [J] s⁻¹.) **Photon irradiance** is the number of incident **quanta** (singular *quantum*) striking the leaf, 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 × 10²³ photons, Avogadro’s number). Quanta and energy units for sunlight 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 × 10⁸ m s⁻¹), h is Planck’s constant (6.63 × 10⁻³⁴ J s), and λ is the wavelength 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**).

Photosynthetically active radiation (PAR, 400–700 nm) may also be expressed in terms of energy (W m⁻²) but is more commonly expressed as quanta (mol m⁻² s⁻¹). Note that PAR is an irradiance-type measurement. In research on photosynthesis, PAR is expressed on a quantum basis.

Incoming sunlight can strike a flat leaf surface at a variety of angles depending on the time of day and the orientation of the leaf. When sunlight deviates from directly over the leaf (perpendicular), irradiance is proportional to the cosine of the angle at which the light rays hit the sensor or leaf (**FIGURE 9.2**).

How much light is there on a sunny day? Under direct sunlight, PAR irradiance is about 2000 μmol m⁻² s⁻¹ (900 W m⁻²) at the top of a dense forest canopy, but may be only

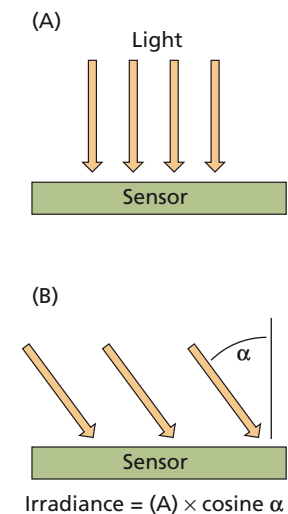


FIGURE 9.2 Incident sunlight relative to leaf angle. The maximum incident sunlight on a leaf will occur when the incoming sunlight is perpendicular to the leaf lamina (A). When the incoming sunlight is at any other angle (B), the incident light levels will be reduced by the cosine of the angle between the sunlight and the leaf lamina.

10 μmol m⁻² s⁻¹ (4.5 W m⁻²) at the bottom of the canopy because of absorption of PAR by the leaves overhead.

Leaf anatomy maximizes light absorption

While roughly 1.3 kW m⁻² of radiant energy from the sun reaches Earth, less than 5% of this energy is ultimately converted into carbohydrates by a photosynthesizing leaf. The reason this percentage is so low is that about half 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 photosynthetically active radiation (PAR, 400–700 nm) that is absorbed, about 15% is reflected or transmitted through a green leaf. 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 (**FIGURE 9.3**)—hence the green color of vegetation. Of the 85% the PAR absorbed by a green leaf, a significant fraction of the absorbed light is lost as heat and a smaller amount is lost as fluorescence (see Chapter 7), resulting in less than 5% of the incident energy being converted into the energy stored within a carbohydrate.

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 focus light so that the intensity reaching some of the chloroplasts can be many

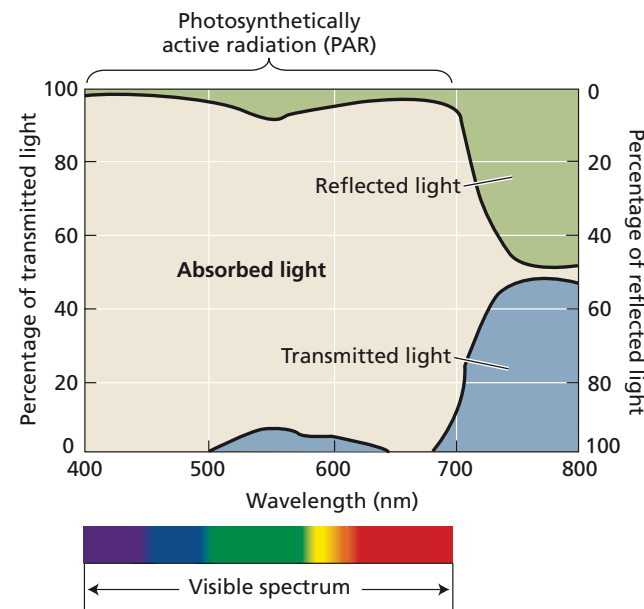


FIGURE 9.3 Optical properties of a bean leaf. Shown here are the percentages of light absorbed, reflected, and transmitted, as a function of wavelength. The transmitted and reflected green light in the wave band at 500 to 600 nm gives leaves their green color. Note that most of the light above 700 nm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

times greater than the intensity of ambient light. 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 (see Figure 9.1). 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*. To increase the efficiency of photosynthetic structures within palisade cells, chloroplasts have high surface-to-volume ratios (Evans et al. 2009).

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 vacuoles 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 9.1). 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 **interface 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 longer than the thickness of the leaf. 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 anatomical features, such as 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 solar energy.

Plants compete for sunlight

Plants normally compete for sunlight. Held upright by stems and trunks, their leaves configure a canopy that absorbs light and influences photosynthetic rates and growth beneath them. Leaves that are shaded by other leaves experience lower light levels and different light quality than the leaves above them and have much lower photosynthetic rates.

Trees with their leaves high above the ground surface represent an outstanding adaptation for light interception. The elaborate branching structure of trees vastly increases the interception of sunlight. Very little PAR penetrates to the bottom of forest canopies; almost all of it is absorbed by leaves (FIGURE 9.4). At the other end of the growth spectrum are plants such as dandelion (*Taraxacum* sp.), which have a rosette growth habit in which leaves grow radially very close to each other on a very short stem, thus preventing the growth of any leaves below them.

In many shady habitats **sunflecks** are a common environmental feature. These are patches of sunlight that pass

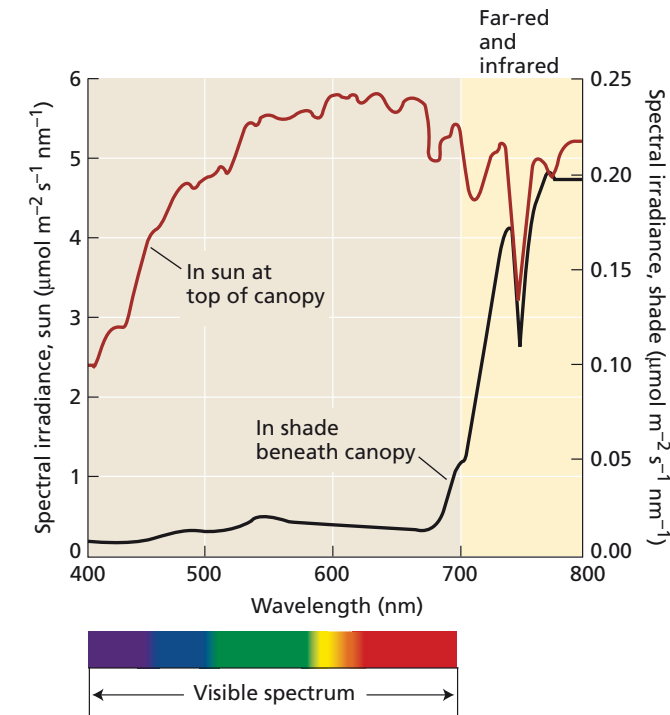


FIGURE 9.4 The spectral distribution of sunlight at the top of a canopy and under the canopy. For unfiltered sunlight, the total irradiance was $1900 \mu\text{mol m}^{-2} \text{s}^{-1}$; for shade, $17.7 \mu\text{mol m}^{-2} \text{s}^{-1}$. Most of the photosynthetically active radiation was absorbed by leaves in the canopy. (After Smith 1994.)

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 incident on a leaf on the forest floor more than tenfold within seconds. This critical energy is available for only a few minutes now and then in a very high dose. For some leaves low in the canopy,

the photons in sunflecks contain nearly 50% of the total light energy available during the day; such leaves often have mechanisms for taking advantage of sunflecks when they occur.

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 by both the photosynthetic apparatus and the stomata to sunflecks have been of substantial interest to plant physiologists and ecologists (Percy et al. 2005), because they represent specialized physiological mechanisms for the capture of short bursts of sunlight.

Leaf angle and leaf movement can control light absorption

How do leaves influence the light levels within a canopy? The angle of the leaf relative to the sun will determine the amount of sunlight incident upon it in a manner identical to that shown in Figure 9.2. If the sun is directly overhead, a horizontal leaf (such as the flat sensor in Figure 9.2A) will receive much more sunlight than a leaf at a steeper angle. Under natural conditions, leaves exposed to full sunlight at the top of the canopy tend to have steep leaf angles so that less than the maximum amount of sunlight is incident on the leaf blade; this allows more sunlight to penetrate into the canopy. It is common to see the angle of leaves within a canopy decrease (become more horizontal) with increasing depth in the canopy.

Leaves absorb the most light when the leaf blade, or lamina, is perpendicular to the incident light. Some plants control light absorption by **solar tracking** (Ehleringer and Forseth 1980); that is, their leaves continuously adjust the orientation of their laminae such that they remain perpendicular to the sun's rays (FIGURE 9.5). Many species, including alfalfa, cotton, soybean, bean, and lupine, have leaves capable of solar tracking.

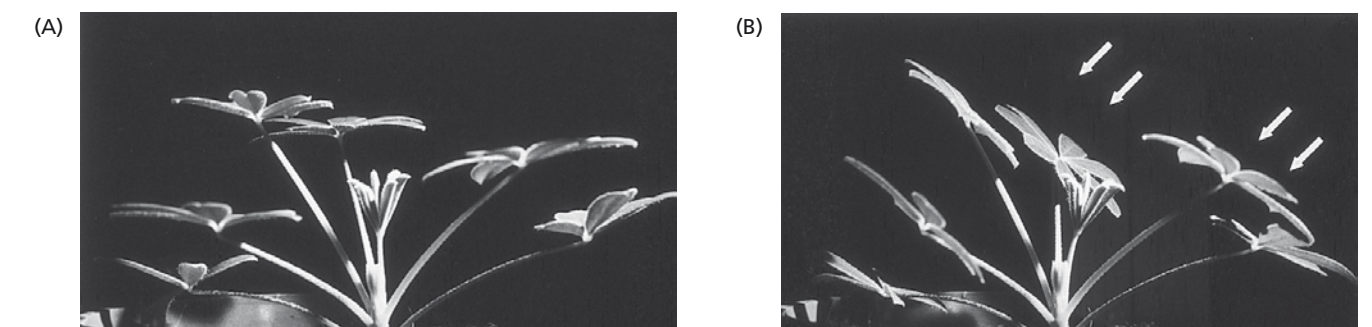


FIGURE 9.5 Leaf movement in sun-tracking plants. (A) Initial leaf orientation in the lupine *Lupinus succulentus*. (B) Leaf orientation 4 hours after exposure to oblique light. The direction of the light beam is indicated by the arrows. Movement is generated by asym-

metric 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.)

Solar-tracking leaves present a nearly vertical position at sunrise, facing the eastern horizon. The leaf blades then begin to track the rising sun, following its movement across the sky with an accuracy of $\pm 15^\circ$ until sunset, when the laminae are nearly vertical, facing the west. 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 moving 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 2000).

Solar tracking is a blue-light response (see Chapter 18), and the sensing of blue light in solar-tracking leaves occurs in specialized regions of the leaf or stem. In species of *Lavatera* (Malvaceae), the photosensitive region is located in or near the major leaf veins (Koller 2000), but in many cases, leaf orientation is controlled by a specialized organ called the **pulvinus** (plural *pulvini*), found at the junction between the blade and the petiole. In lupines (*Lupinus*, Fabaceae), for example, leaves consist of five or more leaflets, and the photosensitive region is in a pulvinus located at the basal part of each leaflet lamina (see Figure 9.5). 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 (Ehleringer and Forseth 1980).

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

By keeping leaves perpendicular to the sun, solar-tracking plants are able to maintain maximum photosynthetic rates throughout the day, including early morning and late afternoon. Air temperature is generally lower during the early morning and late afternoon, so water stress is lower at these times. Solar tracking therefore gives an advantage to rain-fed crop plants with short growing periods, such as pinto beans.

Diaheliotropic solar tracking appears to be a feature common to wild plants that are short-lived and must complete their life cycle before the onset of drought (Ehleringer and Forseth 1980). Paraheliotropic leaves are able to regulate the amount of sunlight incident on the leaf to a nearly constant value. Although the amount of incident sunlight is often only one-half to two-thirds of full sunlight, these

levels may be advantageous under conditions of water stress or excessive solar radiation.

Plants acclimate and adapt to sun and shade environments

Some plants have enough developmental plasticity to respond to a range of light regimes, growing as sun plants in sunny areas and as shade plants in shady habitats. We call this **acclimation**, a growth process in which each newly produced leaf has a set of biochemical and morphological characteristics suited to the particular environment in which it unfolds. The ability to acclimate is important, given that shady habitats can receive less than 20% of the PAR available in an exposed habitat, and deep shade habitats receive less than 1% of the PAR at the top of the canopy.

In some plant species, individual leaves that develop under very sunny or very shady environments are often unable to persist when transferred to the other type of habitat (see Figure 9.4). In such cases, the mature leaf will abscise and a new leaf will develop that is better suited for the new environment. You may notice this if you take a plant that developed indoors and transfer it outdoors; after some time, if it’s the right type of plant, it develops a new set of leaves better suited to high sunlight. However, some species of plants are not able to acclimate when transferred from a sunny to a shady environment. The lack of acclimation suggests that these plants are **adapted** to either a sunny or a shady environment. When plants adapted to deep shade conditions are transferred into full sunlight, the leaves experience chronic photoinhibition and leaf bleaching, and the plants eventually die. Photoinhibition will be discussed later in this chapter.

Sun and shade leaves have contrasting biochemical 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 9.1 shows some anatomic differences between a leaf grown in the sun and a leaf grown in the shade. Most notably, sun-grown leaves are thicker and have longer palisade cells than leaves grown in the shade. Even different parts of a single leaf show adaptations to their light microenvironment (Terashima 1992).

Morphological and biochemical modifications are associated with specific functions found in response to variability in the amounts of sunlight in a plant’s habitat. For

example, far-red light, which is absorbed primarily by PSI, is proportionally more abundant in shady habitats than in sunny ones.

The adaptive response of some shade plants is to produce 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 PSII to PSI reaction centers, add more antenna chlorophyll to PSII to increase absorption by this photosystem and better balance the flow of energy through PSII and PSI. These changes appear to enhance light absorption and energy transfer in shady environments.

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

Photosynthetic Responses to Light by the Intact Leaf

Light is a critical resource for plants that can limit growth and reproduction if too little or too much is received. The relationship between radiation and the photosynthetic properties of the leaf provides valuable information about plant adaptations to the light environment. In this section we describe typical photosynthetic responses to light as measured in light-response curves. We also consider how important features of a light-response curve can help explain contrasting physiological properties between sun and shade plants, and between C_3 and C_4 species. The section continues with descriptions of how leaves respond to excess light.

Light-response curves reveal photosynthetic properties

Measuring net CO_2 fixation in intact leaves across varying levels of absorbed light allows us to construct light-response curves (FIGURE 9.6) that provide useful information about the photosynthetic properties of leaves. In the dark there is no photosynthetic carbon assimilation, but, because mitochondrial respiration continues, CO_2 is given off by the plant (see Chapter 11). CO_2 uptake is negative in this part of the light-response curve. At greater photon flux levels, photosynthetic CO_2 assimilation eventually reaches a point at which photosynthetic CO_2 uptake exactly balances CO_2 release. This is called the **light compensation point**.

The photon flux at which different leaves reach the light compensation point can vary among species and developmental conditions. One of the more interesting differences is found between plants that normally grow in full sunlight and those that grow in the shade (FIGURE 9.7). Light compensation points of sun plants range from 10 to

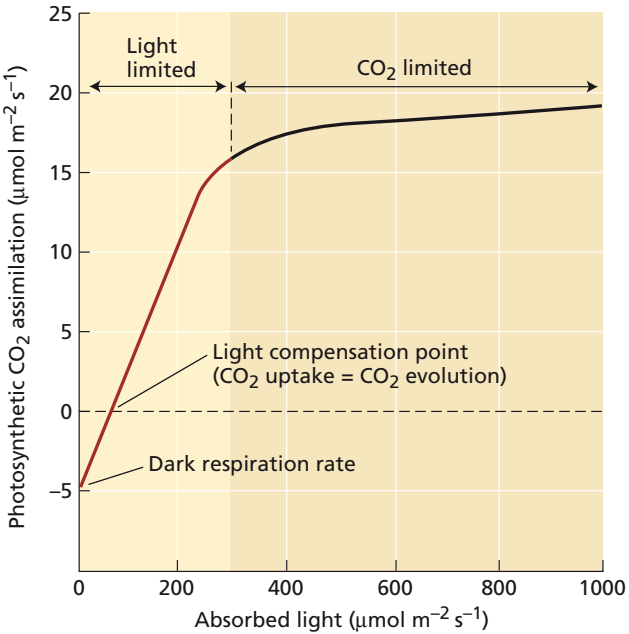


FIGURE 9.6 Response of photosynthesis to light in a C_3 plant. In darkness, respiration causes a net efflux of CO_2 from the plant. The light compensation point is reached when photosynthetic CO_2 assimilation equals the amount of CO_2 evolved by respiration. Increasing light above the light compensation 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.

20 $\mu mol\ m^{-2}\ s^{-1}$, whereas corresponding values for shade plants are 1 to 5 $\mu mol\ m^{-2}\ s^{-1}$.

Why are light compensation points lower for shade plants? For the most part, this is because respiration rates in shade plants are very low; therefore only a little photosynthesis is necessary to bring the net rates of CO_2 exchange to zero. Low respiratory rates allow shade plants to survive in light-limited environments through their ability to achieve positive CO_2 uptake rates at lower values of PAR than sun plants.

The linear relationship between photon flux and photosynthetic rate persists at light levels above the light compensation point (see Figure 9.6). Throughout this linear portion of the light response curve, photosynthesis is light-limited; more light stimulates proportionately more photosynthesis. The slope of this linear portion of the curve reveals the **maximum quantum yield** of photosynthesis for the leaf. Leaves of sun and shade plants show very similar quantum yields despite their different growth habi-

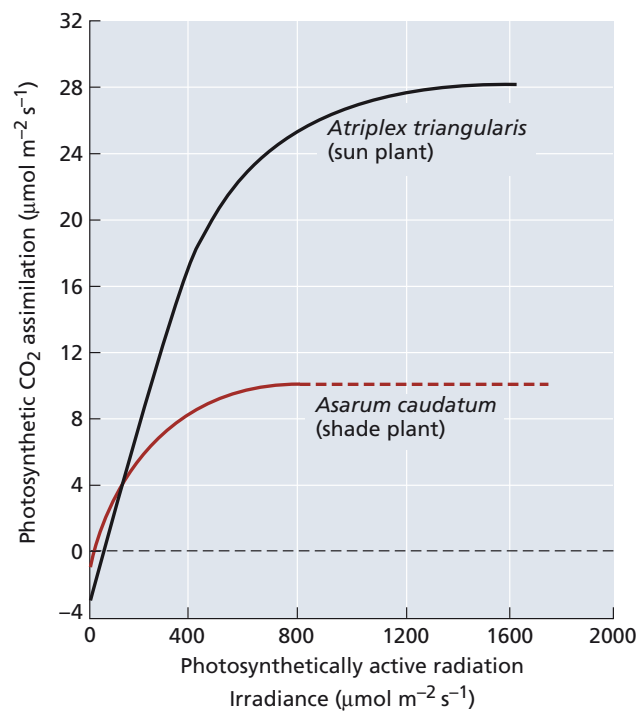


FIGURE 9.7 Light-response curves of photosynthetic carbon fixation in sun and shade plants. *Atriplex triangularis* is a sun plant, and *Asarum caudatum* (a wild ginger) is a shade plant. Typically, shade plants have low light compensation points and have lower maximal photosynthetic rates than sun plants. The dashed red line has been extrapolated from the measured part of the curve. (After Harvey 1979.)

tats. This is because the basic biochemical processes that determine quantum yield are the same for these two types of plants. But quantum yield can vary among plants with different photosynthetic pathways.

Recall that quantum yield is the ratio of a given light-dependent product to the number of absorbed photons (see Equation 7.5). Photosynthetic quantum yield can be expressed on either a CO_2 or an O_2 basis, and as explained in Chapter 7, the quantum yield of photochemistry is about 0.95. However, the photosynthetic quantum yield of an integrated process such as photosynthesis is lower than the theoretical yield when measured in chloroplasts (organelles) or whole leaves. In fact, based on the biochemistry discussed in Chapter 8, we expect the maximum quantum yield for photosynthesis to be 0.125 for C_3 plants (one CO_2 molecule fixed per eight photons absorbed). But under today's atmospheric conditions (390 ppm CO_2 , 21% O_2), the quantum yields for CO_2 of C_3 and C_4 leaves vary between 0.04 and 0.06 mole of CO_2 per mole of photons.

In C_3 plants the reduction from the theoretical maximum is caused primarily by energy loss through photorespiration. In C_4 plants the reduction is caused by the

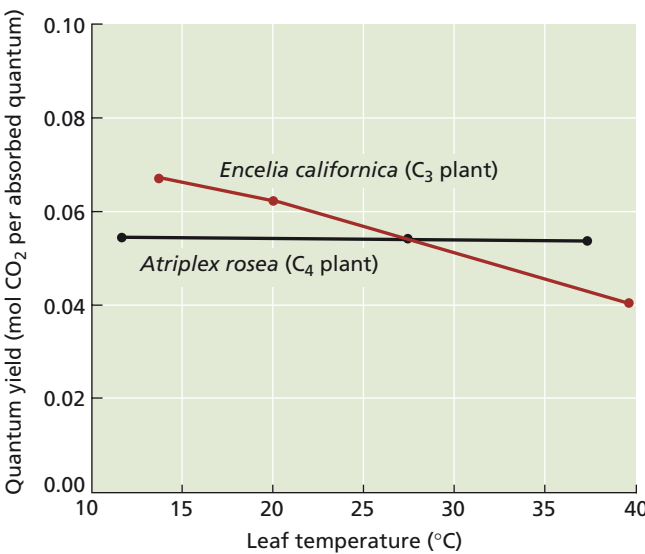


FIGURE 9.8 The quantum yield of photosynthetic carbon fixation in a C_3 plant and a C_4 plant as a function of leaf temperature. In today's atmosphere, photorespiration increases with temperature in C_3 plants, and the energy cost of net CO_2 fixation increases accordingly. This higher energy cost is 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 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. (After Ehleringer and Björkman 1977.)

additional energy requirements of the CO_2 -concentrating mechanism. If C_3 leaves are exposed to low O_2 concentrations, photorespiration is minimized and the quantum yield increases to about 0.09 mole of CO_2 per mole of photons. In contrast, if C_4 leaves are exposed to low O_2 concentrations, the quantum yields for CO_2 fixation remain constant at about 0.05 mole of CO_2 per mole of photons. This is because the carbon-concentrating mechanism in C_4 photosynthesis effectively eliminates CO_2 evolution via photorespiration.

Quantum yield also varies with temperature and CO_2 concentration because of their effect on the ratio of the carboxylase to oxygenase reactions of rubisco (see Chapter 8). Below 30°C in today's environment, quantum yields of C_3 plants are higher than those of C_4 plants; above 30°C , the situation is reversed (Figure 9.8).

At higher photon fluxes, the photosynthetic response to light starts to level off (Figure 9.9) and eventually reaches saturation. Light levels beyond the saturation point 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.

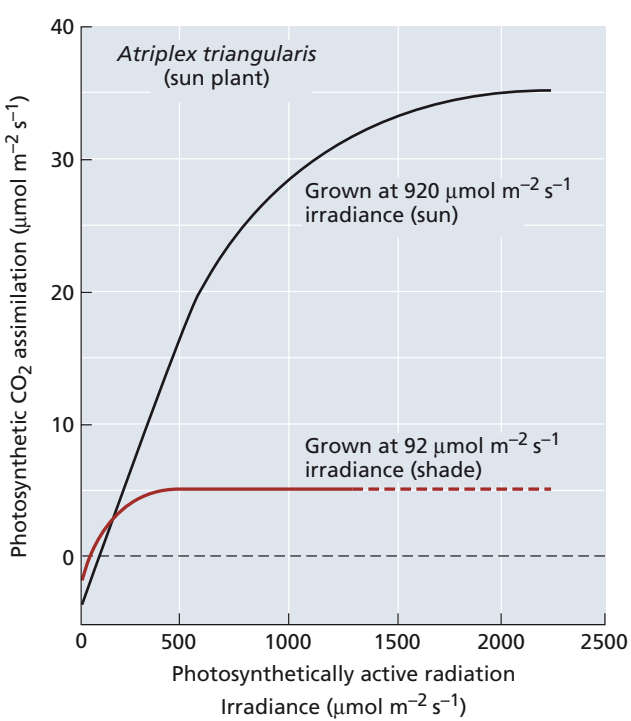


FIGURE 9.9 Light-response of photosynthesis of a sun plant grown under sun or shade conditions. The upper curve represents an *A. triangularis* leaf grown at an irradiance ten times higher than that of the lower curve. In the leaf grown at the lower light levels, photosynthesis saturates at a substantially lower irradiance, indicating that the photosynthetic properties of a leaf depend on its growing conditions. The dashed red line has been extrapolated from the measured part of the curve. (After Björkman 1981.)

Above the saturation point, photosynthesis is commonly referred to as CO_2 -limited (see Figure 9.6), reflecting the inability of the Calvin–Benson cycle enzymes to keep pace with the production of ATP and NADPH from the light-dependent reactions. Light saturation levels for shade plants are substantially lower than those for sun plants. These levels usually reflect the maximum photon flux to which the leaf was exposed during growth.

The light-response curve of most leaves saturates between 500 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ —well below full sunlight (which is about 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Although individual leaves are rarely able to utilize full sunlight, whole plants usually consist of many leaves that shade each other, so only a small fraction of a plant'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 light-saturated at the level

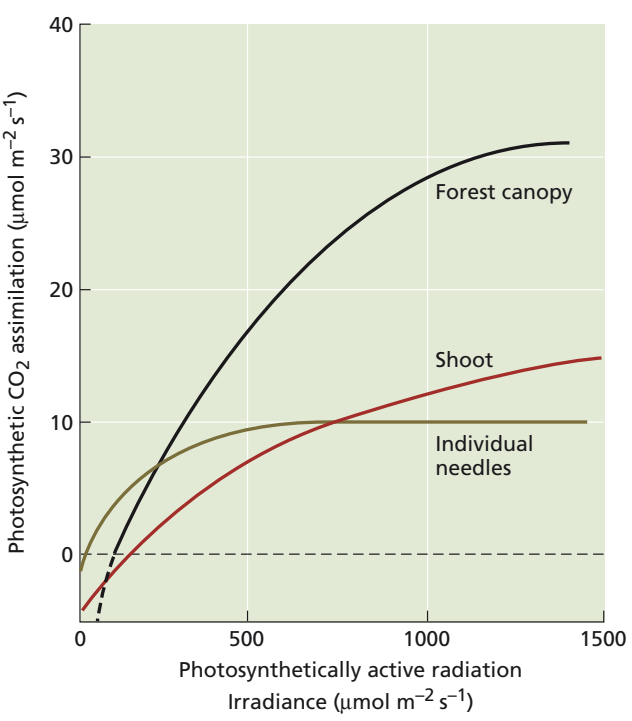


FIGURE 9.10 Changes in photosynthesis (expressed on a per-square-meter basis) in individual needles, a complex shoot, and a forest canopy of Sitka spruce (*Picea sitchensis*) as a function of irradiance. Complex shoots consist of groupings of needles that often shade each other, similar to the situation 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 portion of the forest canopy trace has been extrapolated from the measured part of the curve. (After Jarvis and Leverenz 1983.)

of the whole plant (Figure 9.10). 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 9.11). There are several routes for energy dissipation that involve *nonphotochemical quenching* (see Chapter 7), 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).

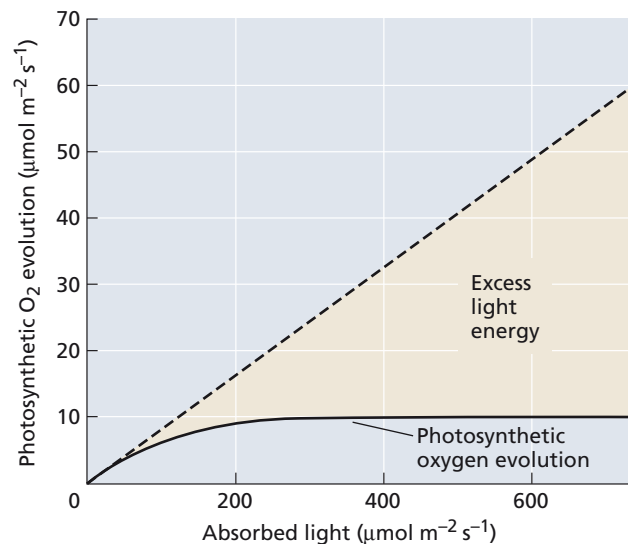


FIGURE 9.11 Excess light energy in relation to a light-response curve of photosynthetic oxygen evolution. The broken line shows theoretical oxygen evolution in the absence of any rate limitation to photosynthesis. At levels of photon flux up to $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, a shade plant is able to utilize the absorbed light. Above $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, 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 greater in a shade plant than in a sun plant. (After Osmond 1994.)

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 7.35). Under high light, violaxanthin is converted to antheraxanthin and then to zeaxanthin. Note that in violaxanthin, both of the aromatic rings have a bound oxygen atom. In antheraxanthin only one of the two rings has a bound oxygen, and in zeaxanthin neither does. Experiments have shown that zeaxanthin is the most effective of the three xanthophylls in heat 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 9.12). 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

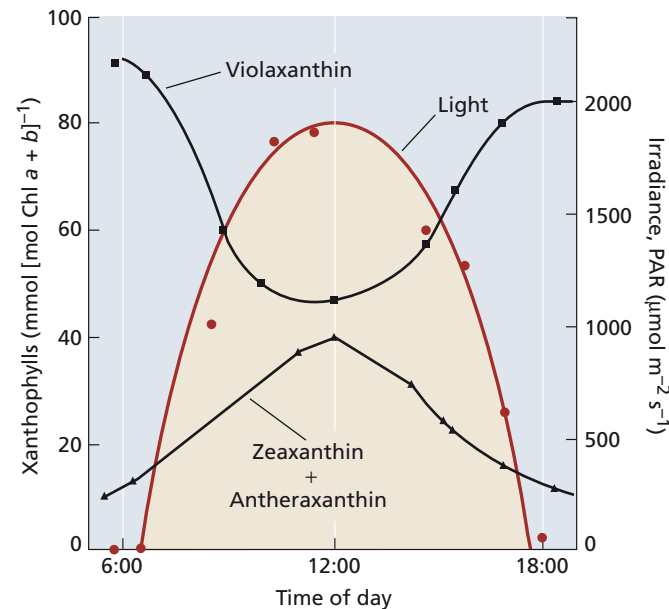


FIGURE 9.12 Diurnal changes in xanthophyll content as a function of irradiance in sunflower (*Helianthus annuus*). As the amount of light incident to a leaf increases, a greater proportion of violaxanthin is converted to antheraxanthin and zeaxanthin, thereby dissipating excess excitation energy and protecting the photosynthetic apparatus. (After Demmig-Adams and Adams 1996.)

on irradiance, species, growth conditions, nutrient status, and ambient temperature (Demmig-Adams et al. 2006).

THE XANTHOPHYLL CYCLE IN SUN AND SHADE Leaves that grow in full sunlight contain a substantially larger xanthophyll pool than do 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 (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 from damage due 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 levels 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).

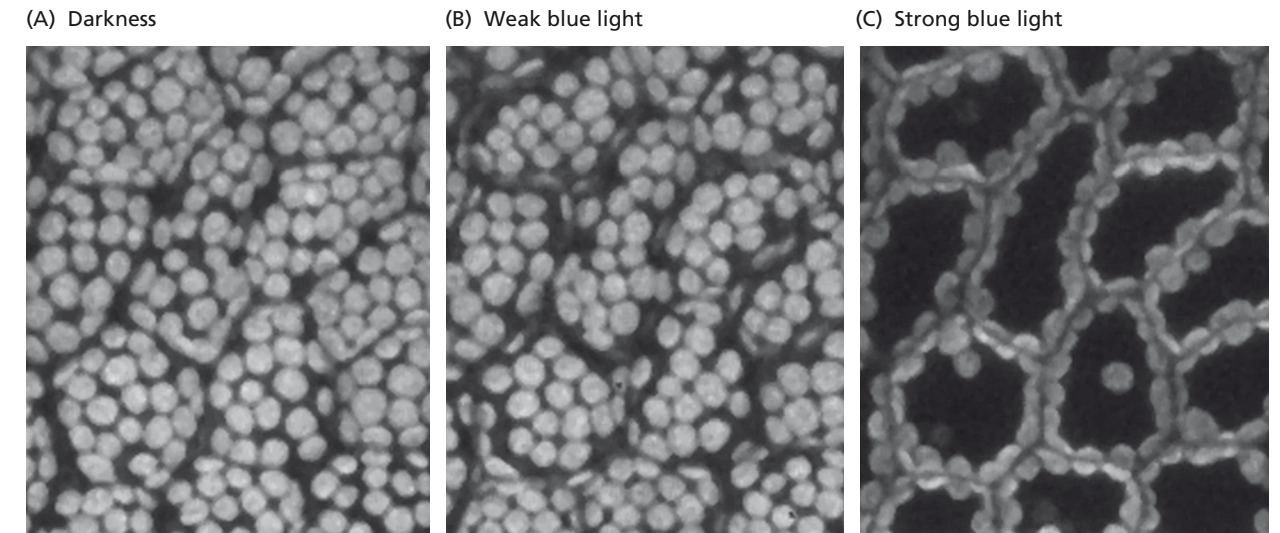


FIGURE 9.13 Chloroplast distribution in photosynthesizing cells of the duckweed *Lemna*. These surface views show the same cells under three conditions: (A) darkness, (B) weak blue light, and (C) strong blue light. In A and B, chloroplasts are positioned near the upper surface of the cells, where they can absorb maximum amounts of light. When the cells are 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. (Courtesy of M. Tlalka and M. D. Fricker.)

CHLOROPLAST MOVEMENTS An alternative means of reducing excess light energy is to move the chloroplasts so that they are no longer exposed to high light. Chloroplast movement is widespread among algae, mosses, and leaves of higher plants (Haupt and Scheuerlein 1990; von Braun and Schleiff 2007). If chloroplast orientation and location are controlled, leaves can regulate how much of the incident light is absorbed. In the dark or under low light (FIGURE 9.13A, B), 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 9.13C), 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 in many of the lower plants, but in some algae, chloroplast movement is controlled by phytochrome (Haupt and Scheuerlein 1990; von Braun and Schleiff 2007). In leaves, chloroplasts move along actin microfilaments in the cytoplasm, and calcium regulates their movement (Tlalka and Fricker 1999).

LEAF MOVEMENTS Plants have evolved responses that reduce the excess light load on leaves during high sunlight periods, especially when transpiration and its cooling effects are reduced because of water stress. These responses often involve changes in the leaf orientation relative to the incoming sunlight. For example, paraheliotropic leaves of both alfalfa and lupine track the sun but at the same time can reduce incident light levels by folding leaflets together so that the leaf laminae become nearly parallel to the sun's rays. These movements are accomplished by changes in the turgor pressure of bulliform cells in the petiole. Another common response is wilting, as seen in many sunflowers, whereby a leaf droops to a vertical orientation, again effectively reducing the incident heat load and reducing transpiration and incident light levels.

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 9.11), the reaction center of PSII is inactivated and often 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. The two types of photoinhibition are dynamic photoinhibition and chronic photoinhibition (Osmond 1994).

Under moderate excess light, **dynamic photoinhibition** is observed. Quantum efficiency decreases, 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 lev-

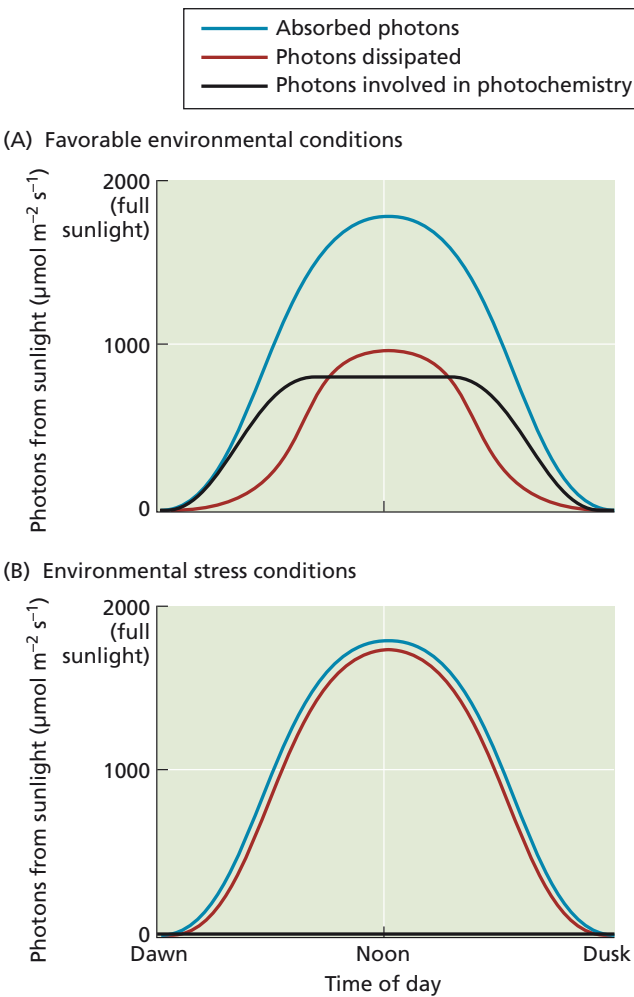


FIGURE 9.14 Changes over the course of a day in the allocation of photons absorbed by sunlight. Shown here are contrasts in how the photons striking a leaf are either involved in photochemistry or thermally dissipated as excess energy by the leaves under favorable (upper panel) and stress (lower panel) conditions. (After Demmig-Adams and Adams 2000.)

els. **FIGURE 9.14** shows how the allocation of photons from sunlight is used for photosynthetic reactions versus being thermally dissipated as excess energy over the course of a day under favorable and stress environmental conditions.

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. This would happen if the stress condition in Figure 9.14 persisted for an extended period of time. 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 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.

Photosynthetic Responses to Temperature

Photosynthesis (CO_2 uptake) and transpiration (H_2O loss) share a common pathway. That is, CO_2 diffuses into the leaf, and H_2O diffuses out, through the stomatal opening regulated by the guard cells. While these are independent processes, vast quantities of water are lost during photosynthetic periods, with the molar ratio of H_2O loss to CO_2 uptake often reaching 250 to 500. This high water loss rate also removes heat from leaves through evaporative cooling, keeping them relatively cool under full sunlight conditions. Since photosynthesis is a temperature-dependent process, it is important to remember this linkage between two processes influenced by the degree of stomatal opening. As we will see, stomatal opening influences both leaf temperature and the extent of transpiration water loss.

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 300 μm of primarily water would warm up to a very high temperature if all available solar energy were absorbed and no heat were lost. However, this does not occur, because leaves absorb only about 50% of the total solar energy (300–3,000 nm), with most of the absorption occurring in the visible portion of the spectrum (see Figure 9.3). Yet the amount of the sun's energy absorbed by leaves is still enormous, and this heat load is dissipated by the emission of long-wave radiation (at about 10,000 nm), by sensible (i.e., perceptible) heat loss, and by evaporative (or latent) heat loss (**FIGURE 9.15**):

- **Radiative heat loss:** All objects emit radiation in proportion to their temperature. However, the maximum wavelength is inversely proportional to its temperature, and leaf temperatures are low enough that the wavelengths emitted are not visible to the human eye.

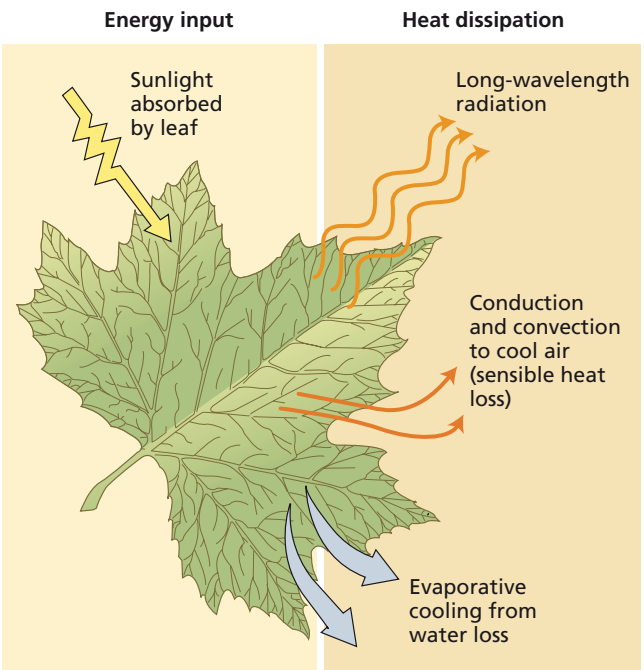


FIGURE 9.15 The absorption and dissipation of energy from sunlight by the leaf. The imposed heat load must be dissipated in order to avoid damage to the leaf. The heat load is dissipated by emission of long-wavelength radiation, by sensible heat loss to the air surrounding the leaf, and by the evaporative cooling caused by transpiration.

- **Sensible heat loss:** If the temperature of the leaf is higher than that of the air circulating around the leaf, the heat is convected (transferred) from the leaf to the air.
- **Latent heat loss:** Because the evaporation of water requires energy, when water evaporates from a leaf (transpiration), it withdraws large amounts of 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 fluxes is called the **Bowen ratio** (Campbell and Norman 1996):

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

In well-watered crops, transpiration (see Chapter 4), and hence water evaporation from the leaf, are high, so the Bowen ratio is low (see **WEB TOPIC 9.2**). Conversely, when evaporative cooling is limited, the Bowen ratio is large. For example, in a water-stressed crop, partial stomatal clo-

sure reduces evaporative cooling and the Bowen ratio is increased. The amount of evaporative heat loss (and thus the Bowen ratio) is influenced by the degree to which stomata remain open.

Plants with very high Bowen ratios conserve water, but also endure very high leaf temperatures. However, the high temperature difference between the leaf and the air does increase the amount of sensible heat loss. Reduced growth is usually correlated with high Bowen ratios, because a high Bowen ratio is indicative of at least partial stomatal closure.

Photosynthesis is temperature sensitive

When photosynthetic rates are plotted as a function of temperature for either a C_3 leaf or a C_4 leaf under ambient CO_2 concentrations, the curve has a characteristic bell shape (**FIGURE 9.16**). Here we see two contrasting responses, in part reflecting the temperature optima expected when each species is grown under its natural temperature conditions. In this case, the C_3 species, *Atriplex glabriuscula*, commonly grows in cool coastal environments, while the C_4 plant, *Tidestromia oblongifolia*, was grown under its natural hot desert conditions. The ascending arm of the curve represents a temperature-dependent stimulation of enzymatic activities; the flat top portion of the curve represents a temperature range over which temperature is optimum for photosynthesis; the descending arm is associated with temperature-sensitive deleterious effects, some of which are reversible while others are not.

Temperature affects all biochemical reactions of photosynthesis as well as membrane integrity in chloroplasts,

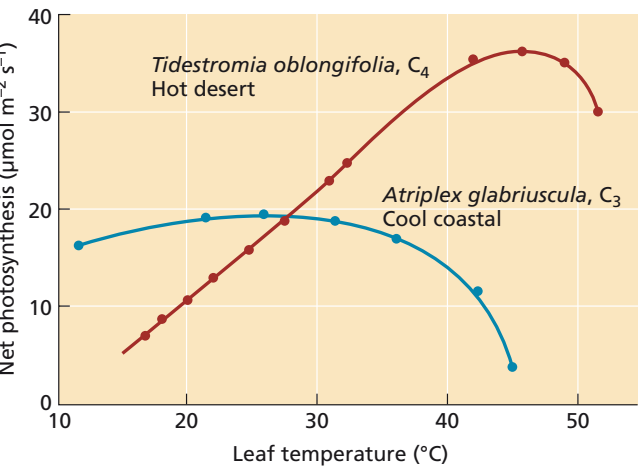


FIGURE 9.16 Changes in photosynthesis as a function of temperature at normal atmospheric CO_2 concentrations for a C_3 plant grown in its natural cool habitat and a C_4 plant growing in its natural hot habitat under current ambient CO_2 concentrations. (After Berry and Björkman 1980.)

so it is not surprising that the responses to temperature are complex. At ambient CO_2 concentrations (see Figure 9.16), photosynthesis is limited by the activity of rubisco, and the response to temperature reflects two conflicting processes: an increase in carboxylation rate and a decrease in the affinity of rubisco for CO_2 as the temperature rises (see Chapter 8). There is evidence that rubisco activity decreases at high temperatures because of temperature effects on rubisco activase (see Chapter 8). These opposing effects dampen the temperature response of photosynthesis at ambient CO_2 concentrations.

By contrast, when photosynthetic rate is plotted as a function of temperature in a leaf with C_4 photosynthesis, the curves are bell-shaped in both cases (see Figure 9.16), since the leaf interior is CO_2 -saturated (as was discussed in Chapter 8). This is one of the reasons that leaves of C_4 plants tend to have a higher photosynthetic temperature optimum than do leaves of C_3 plants when grown under common conditions.

At low temperatures, photosynthesis can also be limited by factors such as phosphate availability in the chloroplast (Sage and Sharkey 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 decreasing temperature, reducing the demand for triose phosphates and causing the phosphate limitation observed at low temperatures.

There is an optimal temperature for photosynthesis

The highest photosynthetic rates seen in response to increasing temperature represent the **optimal temperature response**. When the optimal temperature for a given plant is 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. What factors are associated with the decline in photosynthesis beyond the temperature optimum? Respiration rates increase as a function of temperature, but they are not the primary reason for the sharp decrease in net photosynthesis at high temperatures. Rather, membrane-bound electron transport processes become unstable at high temperatures, cutting off the supply of reducing power and leading to a sharp overall decrease in photosynthesis.

Optimal temperatures have strong genetic (adaptation) and environmental (acclimation) components. Plants of different species growing in habitats with different temperatures have different optimal temperatures for photo-

synthesis, and plants of the same 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 rates 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 .

Figure 9.8 shows changes in quantum yield for photosynthesis as a function of temperature in a C_3 plant and in a C_4 plant. In the C_4 plant the quantum yield or light-use efficiency 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. While quantum yield effects are most expressed under light-limited conditions, a similar pattern is reflected in photorespiration rates under high light as a function of temperature.

The combination of reduced quantum yield and increased photorespiration leads to expected differences in the photosynthetic capacities of C_3 and C_4 plants in habitats with different temperatures. The predicted relative rates of primary productivity of C_3 and C_4 grasses along a latitudinal transect in the Great Plains of North America from southern Texas in the USA to Manitoba in Canada (Ehleringer 1978) are shown in **FIGURE 9.17**. This decline in C_4 relative to C_3 productivity moving northward very closely parallels the declining abundance of plants with these pathways in the Great Plains: C_4 species are more common below 40°N , and C_3 species dominate above 45°N (see Figure 9.17 and **WEB TOPIC 9.3**).

Photosynthetic Responses to Carbon Dioxide

We have discussed how light and temperature influence plant growth and leaf anatomy. 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: Low CO_2 concentrations can limit the amount of photosynthesis in C_3 plants.

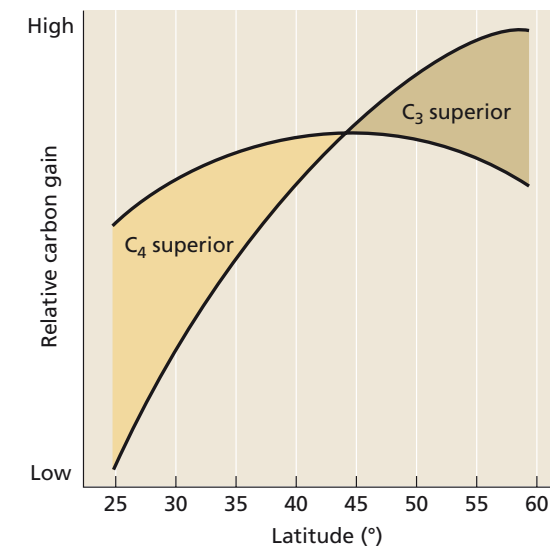


FIGURE 9.17 The relative rates of photosynthetic carbon gain predicted for identical C_3 and C_4 grass canopies as a function of latitude across the Great Plains of North America. (After Ehleringer 1978.)

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

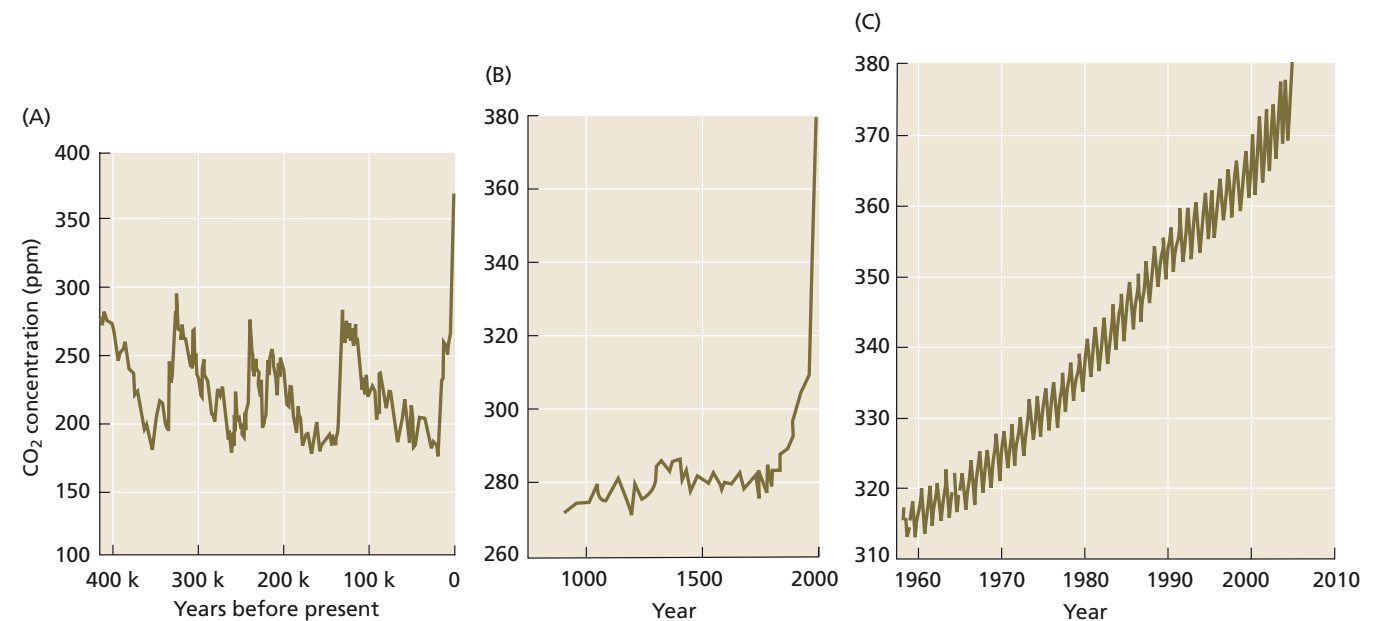
Carbon dioxide is a trace gas in the atmosphere, presently accounting for about 0.039%, or 390 parts per million (ppm), of air. The partial pressure of ambient CO_2 (c_a) varies with

atmospheric pressure and is approximately 39 pascals (Pa) at sea level (see **WEB TOPIC 9.4**). Water vapor usually accounts for up to 2% of the atmosphere and O_2 for about 21%. The bulk of the atmosphere—77%—is nitrogen.

The current atmospheric concentration of CO_2 is almost twice the concentration that has prevailed during most of the last 420,000 years, as measured from air bubbles trapped in glacial ice in Antarctica (**FIGURE 9.18A, B**). Today's atmospheric CO_2 is likely higher than any that Earth has experienced in the last 2 million years. Except for the last 200 years, atmospheric CO_2 concentrations during the recent geologic past are thought to have been low; thus, the plants in the world today evolved in a low- CO_2 world.

The available evidence indicates that CO_2 concentrations greater than 1,000 ppm have not existed on Earth since the warm Cretaceous, over 70 million years ago. Thus, until the dawn of the Industrial Revolution, the geo-

FIGURE 9.18 Concentration of atmospheric CO_2 from 420,000 years ago to the present. (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 seasonal changes in relative balance between photosynthesis and respiration rates. 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.)



logic trend over the past 50 to 70 million years was one of decreasing atmospheric CO₂ concentrations (**WEB TOPIC 9.5**). What we would like to know is just how the recently elevated atmospheric CO₂ level affects photosynthesis and respiration processes, and how higher levels will affect these processes in the future.

Currently, the CO₂ concentration of the atmosphere is increasing by about 1 to 3 ppm each year, primarily because of the burning of fossil fuels such as coal, oil, and natural gas (**FIGURE 9.18C**). Since 1958, when C. David Keeling began systematic measurements of CO₂ in the clean air at Mauna Loa, Hawaii, atmospheric CO₂ concentrations have increased by more than 20% (Keeling et al. 2005). By 2100 the atmospheric CO₂ concentration could reach 600 to 750 ppm unless fossil fuel emissions are controlled (see **WEB TOPIC 9.6**).

THE GREENHOUSE EFFECT The consequences of this increase in atmospheric CO₂ 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 warming of Earth's climate that 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. Some of the absorbed light energy is converted to heat, and some 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 CO₂ and methane, play a role similar to that of the glass roof in a greenhouse. The increased CO₂ concentration and temperature associated with the greenhouse effect can influence photosynthesis. At current atmospheric CO₂ concentrations, photosynthesis in C₃ plants is CO₂ limited (as we will discuss later in the chapter), but this situation could change as atmospheric CO₂ concentrations continue to rise. Under laboratory conditions, most C₃ plants grow 30 to 60% faster when CO₂ concentration is doubled (to 600–750 ppm), and the growth rate becomes limited by the nutrients available to the plant (Bowes 1993).

CO₂ diffusion 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 in leaves (see Chapters 3 and 6), appropriate gradients are needed to ensure adequate diffusion of CO₂ from the leaf surface to the chloroplast.

The cuticle that covers the leaf is nearly impermeable to CO₂, so the main port of entry of CO₂ into the leaf is the

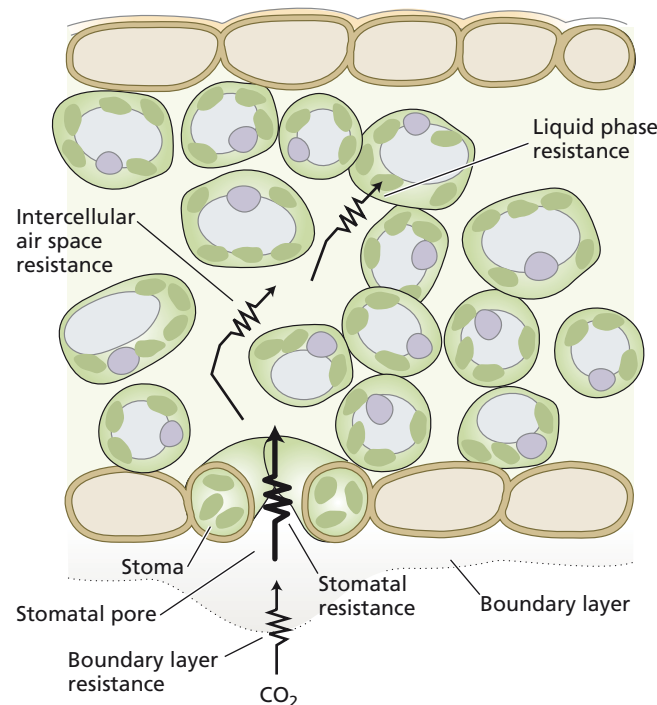


FIGURE 9.19 Points of resistance to the diffusion of CO₂ from outside the leaf to the chloroplasts. The stomatal pore is the major point of resistance to CO₂ diffusion.

stomatal pore. The same path is traveled in the reverse direction by H₂O. CO₂ 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 CO₂ 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 CO₂ in solution, see **WEB TOPIC 9.6**.)

The sharing of the stomatal entry pathway by CO₂ 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 CO₂ uptake. In drier air, this difference can be even larger. Therefore, a decrease in stomatal resistance through the opening of stomata facilitates higher CO₂ uptake but is unavoidably accompanied by substantial water loss.

Each portion of this diffusion pathway imposes a resistance to CO₂ diffusion, so the supply of CO₂ for photosynthesis meets a series of different points of resistance. The gas phase of CO₂ diffusion into the leaf can be divided into three components—the boundary layer, the stoma, and the intercellular spaces of the leaf—each of which imposes a resistance to CO₂ diffusion (**FIGURE 9.19**). An evaluation of the magnitude of each point of resistance is helpful for understanding CO₂ limitations to photosynthesis.

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 bound-

ary layer resistance decreases with leaf size and wind speed. The boundary layer resistance to water and CO₂ diffusion is physically related to the boundary layer resistance to sensible heat loss discussed earlier.

Smaller leaves have a lower boundary layer resistance to CO₂ 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 shade of the humid tropics can have large boundary layer resistances, but these leaves can dissipate the radiation heat load by evaporative cooling made possible by the abundant water supply in these habitats.

After diffusing through the boundary layer, CO₂ enters the leaf through the stomatal pores, which impose the next type of resistance in the diffusion pathway, **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 CO₂ diffusion is imposed by the stomatal resistance.

There is also a resistance to CO₂ 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 usually small, causing a drop of 0.5 Pa or less in partial pressure of CO₂ from the 38 Pa outside the leaf.

The resistance to CO₂ diffusion of the liquid phase in C₃ leaves—the **liquid phase resistance**, also called **mesophyll resistance**—encompasses diffusion from the intercellular leaf spaces to the carboxylation sites in the chloroplast. Since localization of chloroplasts near the cell periphery minimizes the distance that CO₂ must diffuse through liquid to reach carboxylation sites within the chloroplast, the resistance to CO₂ diffusion is thought to be approximately one-tenth of the combined boundary layer resistance and stomatal resistance when the stomata are fully open. However, recent research has suggested that mesophyll resistance can be higher.

Because the stomatal pores usually impose the largest resistance to CO₂ uptake and water loss in the diffusion pathway, this single point of 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 often ignored, and the stomatal resistance is used as the single parameter describing the gas phase resistance to CO₂ (see **WEB TOPIC 9.4**).

Patterns of light absorption generate gradients of CO₂ fixation

We have discussed how leaf anatomy is specialized for capturing light and how it also facilitates the internal dif-

fusion of CO₂, but where inside an individual leaf do maximum rates of photosynthesis occur? In most leaves, light is preferentially absorbed at the upper surface, whereas CO₂ enters through the lower surface. Given that light and CO₂ enter from opposing sides of the leaf, does photosynthesis occur uniformly within the leaf tissues, or is there a gradient in photosynthesis across the leaf?

For most leaves, once CO₂ has diffused through the stomata, internal CO₂ diffusion is rapid, so limitations on photosynthetic performance within the leaf are imposed by factors other than internal CO₂ 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 9.20**), owing to the strong absorption bands of chlorophyll in the blue and red regions of the spectrum (see Figure 7.3). Green light, on the other hand, penetrates deeper into the leaf. Chlorophyll absorbs green

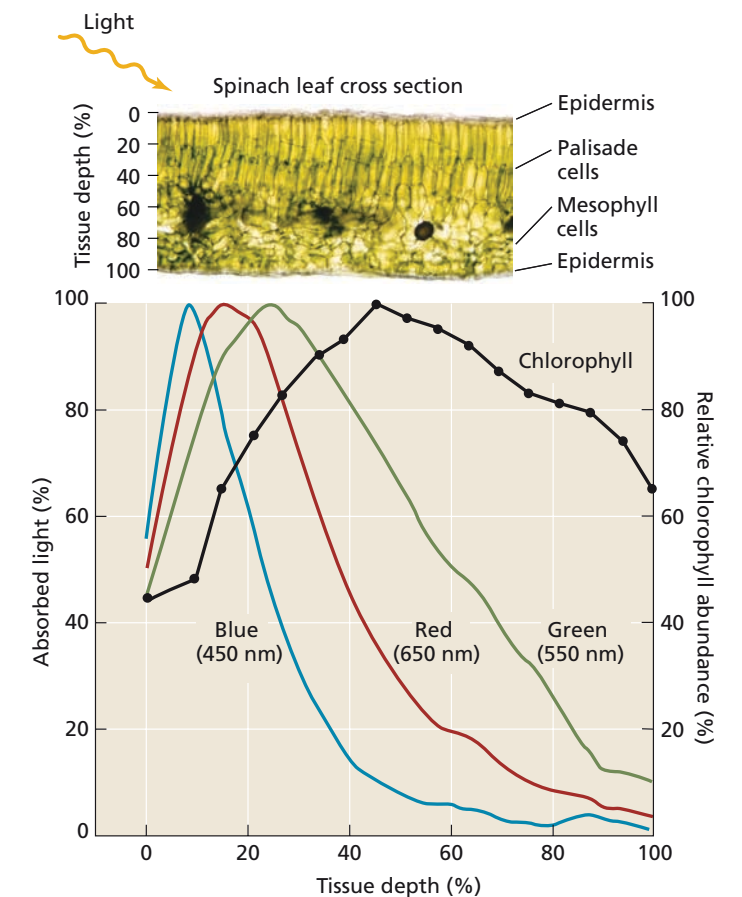


FIGURE 9.20 Distribution of absorbed light in spinach sun leaves. Irradiation with blue, green, or red light results in different profiles of absorbed light in the leaf. The micrograph above the graph shows a cross section of a spinach leaf, with rows of palisade cells occupying nearly half of the leaf thickness. The shapes of the curves are in part a result of the unequal distribution of chlorophyll within the leaf tissues. (After Nishio et al. 1993 and Vogelmann and Han 2000; micrograph courtesy of T. Vogelmann.)

light poorly (again, see Figure 7.3), yet green light is very effective in supplying energy for photosynthesis in the tissues within the leaf depleted of 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 (*Spinacea oleracea*) and fava bean (*Vicia faba*), rubisco content is low at the top of the leaf, increases toward the middle, and decreases again toward the bottom, similar to the distribution of chlorophyll in a leaf, as shown in Figure 9.20. Like the distribution of chlorophyll, the distribution of photosynthetic carbon fixation within the leaf has a bell-shaped curve.

CO_2 imposes limitations on photosynthesis

For many crops, such as tomatoes, lettuce, cucumbers, and roses growing in greenhouses under optimal water and nutrition, the carbon dioxide enrichment in the greenhouse environment above natural atmospheric levels results in increased productivity. 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 .

Increasing intercellular CO_2 to the concentration at which photosynthesis and respiration balance each other defines the **CO_2 compensation point**, at which the net efflux of CO_2 from the leaf is zero (**FIGURE 9.21**). 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, whereas the light compensation point reflects that balance as a function of photon flux under constant O_2 concentration.*

C_3 PLANTS In C_3 plants, increasing atmospheric CO_2 above the compensation point stimulates photosynthesis over a wide concentration range (see Figure 9.21). At low to intermediate CO_2 concentrations, photosynthesis is limited by the carboxylation capacity of rubisco. At high CO_2 concentrations, photosynthesis becomes limited by the capacity of the Calvin–Benson cycle to regenerate the acceptor molecule ribulose 1,5-bisphosphate, which depends on electron transport rates. However, photosynthesis continues to increase with increasing CO_2 because carboxylation replaces oxygenation on rubisco (see Chapter 8). By regulating stomatal conductance, most leaves appear to regulate their c_i (internal partial pressure for CO_2) so that it is at an intermediate concentration between the limits 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

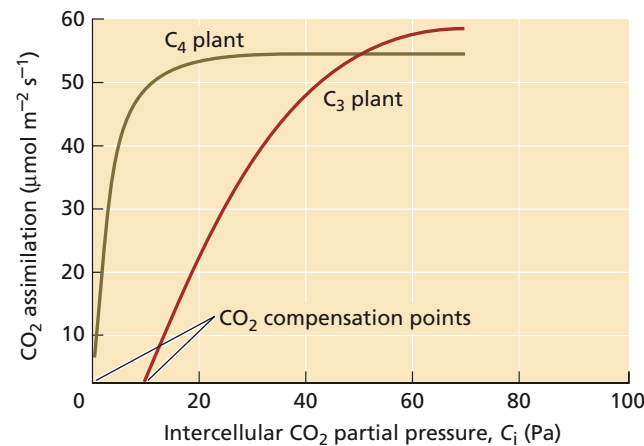


FIGURE 9.21 Changes in photosynthesis as a function of intercellular CO_2 concentrations in Arizona honeysweet (*Tidestromia oblongifolia*), a C_4 plant, and creosote bush (*Larrea divaricata*), a C_3 plant. Photosynthetic rate is plotted against calculated intercellular partial pressure of CO_2 inside the leaf (see Equation 5 in **WEB TOPIC 8.4**). The partial pressure at which CO_2 assimilation is zero defines the CO_2 compensation point. (After Berry and Downton 1982.)

regulated by CO_2 , independent of the functioning of stomata (see Figure 9.21). Inspection of such a plot for C_3 and C_4 plants reveals interesting differences between the two pathways 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 CO_2 range.
- In C_4 plants, the CO_2 compensation point is zero or nearly zero, reflecting their very low levels of photorespiration (see Chapter 8).
- In C_3 plants, the CO_2 compensation point is about 10 Pa, reflecting CO_2 production because of photorespiration (see Chapter 8).

These responses indicate that C_3 plants may benefit more from ongoing increases in today's atmospheric CO_2 concentrations (see Figure 9.18). Because photosynthesis in C_4 plants is CO_2 -saturated at low concentrations, C_4 plants do not benefit much from increases in atmospheric CO_2 concentrations.

In fact, the ancestral photosynthetic pathway is C_3 photosynthesis, and C_4 photosynthesis is a derived pathway. During geologic time periods when atmospheric CO_2 concentrations were very much higher than they are today, CO_2 diffusion through stomata into C_3 leaves would have resulted in higher c_i values and therefore higher photo-

synthetic rates. While C_3 photosynthesis is typically CO_2 -diffusion limited today, C_3 plants still account for nearly 70% of the world's primary productivity. The evolution of C_4 photosynthesis is one biochemical adaptation to a CO_2 -limited atmosphere. Our current understanding is that C_4 photosynthesis may have evolved recently, some 10 to 15 million years ago.

C_4 PLANTS If the ancient Earth of more than 50 million years ago had atmospheric CO_2 concentrations that were well above current atmospheric conditions, under what atmospheric conditions might we expect that C_4 photosynthesis should become a major photosynthetic pathway found in the Earth's ecosystems? Ehleringer et al. (1997) suggest that C_4 photosynthesis first became a prominent component of terrestrial ecosystems in the warmest growing regions of the Earth when global CO_2 concentrations decreased below some critical and as yet unknown threshold CO_2 concentration (**FIGURE 9.22**). That is, the negative impacts of high photorespiration and CO_2 limitation on C_3 photosynthesis would be greatest under warm to hot growing conditions, especially when atmospheric CO_2 is reduced. The C_4 -favorable growing areas would have been located in those geographic regions with the warmest temperatures. C_4 plants would have been most favored during periods of Earth's history when CO_2 levels were lowest. In today's world, these regions are the subtropical grasslands and savannas. There are now extensive data to indicate that C_4 photosynthesis was more prominent during the glacial periods when atmospheric CO_2 levels were below 200 ppm than it is today (see Figure 9.18). Other factors may have contributed to the expansion of C_4 plants, but

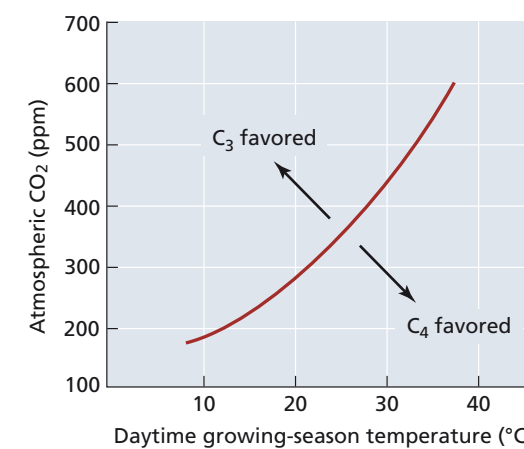


FIGURE 9.22 The combination of atmospheric carbon dioxide levels and daytime growing season temperatures that are predicted to favor C_3 versus C_4 grasses. At any point in time, the Earth is at a single atmospheric carbon dioxide concentration, resulting in the expectation that C_4 plants would be most common in habitats with the warmest growing seasons. (After Ehleringer et al. 1997.)

certainly low atmospheric CO_2 was one important factor favoring their geographic expansion.

Because of the 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 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 in temperate regions are C_3 plants.

CAM PLANTS Plants with crassulacean acid metabolism (CAM), including many cacti, orchids, bromeliads, and other succulents, have stomatal activity patterns that contrast with those found in C_3 and C_4 plants. CAM plants open their stomata at night and close them during the day, exactly the opposite of the pattern observed in leaves of C_3 and C_4 plants (**FIGURE 9.23**). At night, atmospheric CO_2 diffuses into CAM plants where it is combined with phosphoenolpyruvate and fixed into malate (see Chapter 8).

The ratio of water loss to CO_2 uptake is much lower in CAM plants than it is in either C_3 or C_4 plants. This is because stomata are primarily open only at night, when lower temperatures and higher humidity contribute to a lower transpiration rate.

The main photosynthetic constraint on CAM metabolism is that the capacity to store malic acid is limited, and this limitation restricts the total amount of CO_2 uptake. However, some CAM plants are able to enhance total photosynthesis during wet conditions by fixing CO_2 via the Calvin–Benson cycle at the end of the day, when temperature gradients are less extreme. In water-limited conditions, stomata open only at night.

Cladodes (flattened stems) of cacti can survive after detachment from the plant for several months without 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*, also allows the intact plant to survive for prolonged drought periods while losing remarkably little water.

How will photosynthesis and respiration change in the future under elevated CO_2 conditions?

A central question in plant physiology today is: How are photosynthesis and respiration modified in an environment where CO_2 levels are 400 ppm, 500 ppm, or even

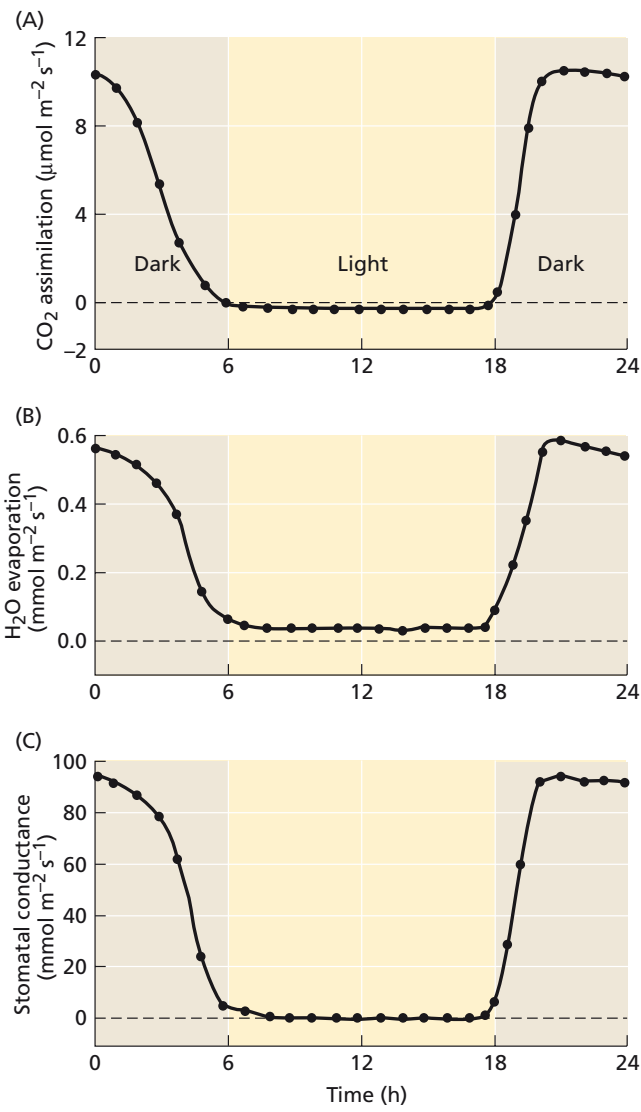


FIGURE 9.23 Photosynthetic carbon assimilation, evaporation, and stomatal conductance of a CAM plant, the cactus *Opuntia ficus-indica*, during a 24-hour period. The whole plant was kept in a gas exchange chamber in the laboratory. The shaded areas indicate the dark periods. Three parameters were measured over the study period: (A) photosynthetic rate, (B) water loss, and (C) stomatal conductance. In contrast to plants with C_3 or C_4 metabolism, CAM plants open their stomata and fix CO_2 at night. (After Gibson and Nobel 1986.)

While these long-term FACE experiments are still underway, they are already providing key new insights into how plants will respond in the future. One key observation is that plants with the C_3 photosynthetic pathway are much more responsive than C_4 plants under well-watered conditions, with the net photosynthetic rate increasing 20% or more in C_3 plants and not at all in C_4 plants. Photosynthesis rises because intercellular CO_2 levels increase (recall Figure 9.21). At the same time, there is a down-regulation of photosynthetic capacity manifested in reduced activity of the enzymes associated with the dark reactions of photosynthesis (Ainsworth and Rogers 2007).

While CO_2 is indeed important for photosynthesis, other factors are important for growth under elevated CO_2 (Long et al. 2004, 2006). For example, a common FACE observation is that plant growth becomes quickly constrained by nutrient availability. A second, surprising observation is that soil moisture and the presence of trace gases, such as ozone, can reduce the net photosynthetic response below the maximum values predicted from initial greenhouse studies of a decade ago. Warmer and drier conditions are also predicted to occur as a result of increased CO_2 in the atmosphere. Important progress will be made in the near future through the study of how fertilized and irrigated crops compare to plants in natural ecosystems in their response to elevated CO_2 . Understanding these responses is crucial as society looks for increased agricultural outputs to support rising human populations and to provide raw materials for biofuels.

Elevated CO_2 levels will affect many plant processes; for instance, leaves tend to keep their stomata more closed under elevated CO_2 levels. As a direct consequence of reduced transpiration, leaf temperatures are higher (see Figure 9.24C). Elevated temperatures will feed back on basic mitochondrial respiration and on the respiration of soil microbes and fungi. This is indeed an exciting and promising area of current research. From FACE studies, it is becoming increasingly clear that an acclimation process occurs under higher CO_2 levels in which respiration rates are different than they would be under today's atmospheric conditions, but not as high as would have been predicted without the down-regulation acclimation response (Long et al. 2004, 2006).

higher? This question is particularly relevant as humans continue to add CO_2 derived from fossil fuel combustion to the world's atmosphere. To study this question, scientists need to be able to create realistic models of future environments. A promising approach to the study of plant physiology and ecology in environments with elevated CO_2 levels has been the use of *Free Air CO_2 Enrichment* (FACE) experiments.

For FACE experiments, entire fields of plants or natural ecosystems are enclosed in rings of tubes that add CO_2 to the air to create the high- CO_2 environment we might expect 25–50 years from now. **FIGURE 9.24** shows FACE experiments in different major vegetation types. Figure 9.24A shows experiments being conducted in Wisconsin, where mixed and unmixed stands of aspen trees are growing in an elevated CO_2 environment. Figure 9.24B shows FACE experiments being conducted in a soybean field in Illinois.



FIGURE 9.24 Free Air CO_2 Enrichment (FACE) experiments are used to study how plants and ecosystems will respond to future CO_2 levels. Shown here are FACE experiments in stands of deciduous trees (A) and in a soybean field (B). (C) Under elevated CO_2 levels, leaf stomata are more closed, resulting in higher leaf temperatures as shown by the infrared image of a soybean canopy. (A courtesy of David F. Karnosky; B courtesy of USDA; C from Long et al. 2006.)

Identifying Different Photosynthetic Pathways

We can learn more about the different photosynthetic pathways in plants by measuring the chemical composition of plant tissues. We do this using measurements of the abundances of stable isotopes in plants (Dawson et al. 2002). In particular, the stable isotopes of carbon atoms in a leaf contain useful information about photosynthesis. Recall that isotopes are simply different forms of an element. In the different isotopes of an element, the number of protons remains constant, since that defines the element, but the number of neutrons varies. Isotopes can be stable or radioactive.

Stable isotopes of an element remain constant in abundance, unchanged over time. In contrast, radioactive

isotopes of an element decay to form different elements over time. The two stable isotopes of carbon are ^{12}C and ^{13}C , differing in composition only by the addition of an additional neutron in ^{13}C . ^{11}C and ^{14}C are radioactive isotopes of carbon that are frequently used in biological tracer experiments.

How do we measure the stable carbon isotopes of plants?

Atmospheric CO_2 contains the naturally occurring stable carbon isotopes ^{12}C and ^{13}C in the proportions 98.9% and 1.1%, respectively. $^{14}\text{CO}_2$ is radioactive and is present in small quantities ($10^{-10}\%$). The chemical properties of $^{13}\text{CO}_2$ are identical to those of $^{12}\text{CO}_2$, but plants assimilate less $^{13}\text{CO}_2$ than $^{12}\text{CO}_2$. In other words, leaves discriminate

against the heavier isotope of carbon during photosynthesis, and therefore they have lower $^{13}\text{C}/^{12}\text{C}$ ratios than are found in atmospheric CO_2 .

The $^{13}\text{C}/^{12}\text{C}$ isotope composition is measured by use of a mass spectrometer, which yields the following ratio:

$$R = \frac{^{13}\text{CO}_2}{^{12}\text{CO}_2} \quad (9.1)$$

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

$$\delta^{13}\text{C} \text{ ‰} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (9.2)$$

where the standard represents the carbon isotopes contained in a fossil belemnite from the Pee Dee limestone formation of South Carolina. The $\delta^{13}\text{C}$ of atmospheric CO_2 has a value of -8‰ , meaning that there is less ^{13}C in 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 $\delta^{13}\text{C}$ value 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 does CO_2 in the atmosphere, which means that leaf tissues discriminate against ^{13}C during the photosynthetic process. Cerling et al. (1997) provided $\delta^{13}\text{C}$ data for a large number of C_3 and C_4 plants from around the world (FIGURE 9.25).

What becomes clear from Figure 9.25 is that there is a wide spread of $\delta^{13}\text{C}$ values in C_3 and C_4 plants, with averages of -28‰ and -14‰ , respectively. These $\delta^{13}\text{C}$ variations actually reflect the consequences of small variations in physiology associated with changes in stomatal conductance in different environmental conditions. Thus, $\delta^{13}\text{C}$ values can be used both to distinguish between C_3 and C_4 photosynthesis and to further reveal details about stomatal conditions for plants grown in different environments (such as the tropics versus deserts).

Differences in carbon isotope ratio are easily detectable with mass spectrometers that allow for very precise measurements of the abundance of ^{12}C and ^{13}C in either different molecules or different tissues. Many of our foods, such as wheat (*Triticum aestivum*), rice (*Oryza sativa*), potatoes (*Solanum tuberosum*), and beans (*Phaseolus* spp.) are products of C_3 plants. Yet many of our most productive crops are C_4 plants such as corn (maize; *Zea mays*), sugarcane (*Saccharum officinarum*), and sorghum (*Sorghum bicolor*). Carbohydrates extracted from all of these foods may be chemically identical, but they are C_3 – C_4 distinguishable on the basis of their $\delta^{13}\text{C}$ values. For example, measuring the $\delta^{13}\text{C}$ values of table sugar (sucrose) makes it possible to determine if the sucrose came from sugar beet (*Beta vulgaris*; a C_3 plant) or sugarcane (a C_4 plant) (see WEB TOPIC 9.7).

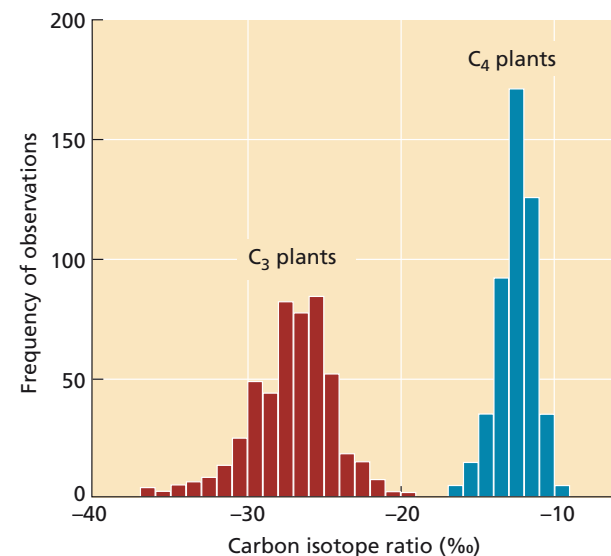


FIGURE 9.25 Frequency histograms for the observed carbon isotope ratios in C_3 and C_4 taxa from around the world. (After Cerling et al. 1997.)

Why are there carbon isotope ratio variations in plants?

What is the physiological basis for ^{13}C depletion in plants relative to CO_2 in the atmosphere? It turns out that both the diffusion of CO_2 into the leaf and the carboxylation selectivity for $^{12}\text{CO}_2$ play a role.

We can predict the carbon isotope ratio of a C_3 leaf as

$$\delta^{13}\text{C}_L = \delta^{13}\text{C}_A - a - (b-a)(c_i/c_a) \quad (9.3)$$

where $\delta^{13}\text{C}_L$ and $\delta^{13}\text{C}_A$ are the carbon isotope ratios of the leaf and atmosphere, respectively; a is the diffusion fraction; b is the net carboxylase fraction in the leaf; and c_i/c_a is the ratio of intercellular to ambient CO_2 concentrations.

CO_2 diffuses from air outside of the leaf to the carboxylation sites within leaves in both C_3 and C_4 plants. We express this diffusion using the term a . Because $^{12}\text{CO}_2$ is lighter than $^{13}\text{CO}_2$, it diffuses slightly faster toward the carboxylation site, creating an effective diffusion fractionation factor of -4.4‰ . Thus, we would expect leaves to have a more negative $\delta^{13}\text{C}$ value simply because of this diffusion effect. Yet this factor alone is not sufficient to explain the $\delta^{13}\text{C}$ values of C_3 plants as shown in Figure 9.25.

The initial carboxylation event is a determining factor in the carbon isotope ratio of plants. Rubisco represents the first carboxylation reaction in C_3 photosynthesis and 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‰ . Thus, the inherent difference between the two carboxylating enzymes contributes to the

different isotope ratio differences observed in C_3 and C_4 plants (Farquhar et al. 1989). We use b to describe the net carboxylation effect.

Other physiological characteristics of plants affect its carbon isotope ratio. One primary factor is the partial pressure of CO_2 in the intercellular air spaces of leaves (c_i). In C_3 plants the potential isotope discrimination by rubisco of -30‰ is not fully expressed during photosynthesis because the availability of CO_2 at the carboxylation site becomes a limiting factor restricting the discrimination by rubisco. Greater discrimination against $^{13}\text{CO}_2$ occurs when c_i is high, as when stomata are open. Yet open stomata also facilitate water loss. Thus, lower ratios of photosynthesis to transpiration are correlated with greater discrimination against ^{13}C (Ehleringer et al. 1993). When leaves are exposed to water stress, stomata tend to close, reducing c_i values. As a consequence, C_3 plants grown under water stress conditions tend to have more positive carbon isotope ratios.

The application of carbon isotope ratios in plants has become very productive, because equation 9.3 provides a strong link between the carbon isotope ratio measurement and the intercellular CO_2 value in a leaf. Intercellular CO_2 levels are then directly linked with aspects of photosynthesis and stomatal constraints. As stomata close in C_3 plants or as water stress increases, we find that the leaf carbon isotope ratio increases. The carbon isotope ratio measurement then becomes a direct proxy to estimate several aspects of shorter-term water stress. These applications include using carbon isotopes to study plant performance in both agricultural and ecological studies (Ehleringer et al. 1993; Bowling et al. 2008).

One emergent environmental pattern is that, on average, leaf carbon isotope ratio values decrease as precipitation increases under natural conditions. FIGURE 9.26 illustrates this pattern in a transect across Australia. Here we see that the $\delta^{13}\text{C}$ values are highest in the arid regions of Australia and become progressively lower in values along a precipitation gradient from desert to tropical rainforest ecosystems. Applying equation 9.3 to interpret these $\delta^{13}\text{C}$ data, we conclude that intercellular CO_2 levels of leaves of desert plants are lower than what we typically see in leaves of rainforest plants. Because of the sequential nature of tree ring formation, $\delta^{13}\text{C}$ observations in tree rings can help to separate the long-term effects of reduced water availability on plants (e.g., desert versus rainforest habitats) from short-term effects (e.g., seasonal drought cycles).

Carbon isotope ratio analyses are commonly used today to determine the dietary patterns of humans and other animals. The proportion of C_3 to C_4 foods in an animal's diet is recorded in its tissues—teeth, bones, muscles, and hair. Cerling and colleagues (2009) described an interesting application of carbon isotope ratio analysis to the eating habits of a family of wild African elephants. They

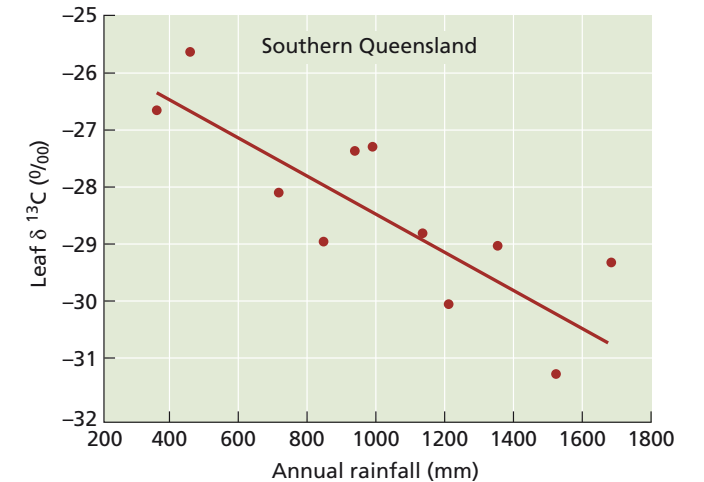


FIGURE 9.26 Vegetation changes occur along rainfall gradients in Australia. Here we see that changes in carbon isotope ratios of vegetation appear to be strongly related to precipitation amounts in a region, suggesting that decreased moisture levels influence c_i values and therefore carbon isotope ratios in C_3 species along a geographical gradient in Australia taxa. (After Stewart et al. 1995.)

examined sequential $\delta^{13}\text{C}$ values in segments of tail hair to reconstruct the daily diets of each animal. They observed very predictable seasonal shifts in shifts between trees (C_3) and grasses (C_4) as resource availability changes with rainfall patterns. Carbon isotope ratio analyses can be expanded to include consideration of human diets. One broad-scale observation is that the carbon isotope ratios of North Americans are higher than those observed in Europeans, indicating the prominent role that corn (a C_4 plant) plays in the diets of North Americans. Another application is measuring $\delta^{13}\text{C}$ in fossil, carbonate-containing soils and fossil teeth. From such observations it is possible to reconstruct the photosynthetic pathways of plants in the ancient past. These approaches have been used to determine that C_4 photosynthesis developed and became prevalent about 6 million years ago and to reconstruct the diets of ancient and modern animals (see WEB TOPIC 9.8).

CAM plants can have $\delta^{13}\text{C}$ values that are very close to those of C_4 plants. In CAM plants that fix CO_2 at night via PEP carboxylase, $\delta^{13}\text{C}$ is expected to be similar to that of C_4 plants. However, when some CAM plants are well watered, they can 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 toward that of C_3 plants. Thus the $\delta^{13}\text{C}$ values of CAM plants reflect how much carbon is fixed via the C_3 pathway versus the C_4 pathway.

SUMMARY

In considering optimal photosynthetic performance, both the limiting factor hypothesis and an “economic perspective” emphasizing CO₂ “supply” and “demand” have guided research.

Photosynthesis Is the Primary Function of Leaves

- Leaf anatomy is highly specialized for light absorption (Figure 9.1).
- Irradiance the amount of energy or photons that falls on a flat sensor of known area per unit time (Figure 9.2).
- About 5% of the solar energy reaching Earth is converted into carbohydrates by photosynthesis. Much absorbed light is lost as heat and fluorescence (Figure 9.3).
- In dense forests, almost all PAR is absorbed by leaves (Figure 9.4).
- Within a canopy, leaves maximize light absorption by solar tracking and chloroplast movements (Figure 9.5).
- Some plants respond to a range of light regimes. However, sun and shade leaves have contrasting biochemical characteristics.
- Some shade plants alter the ratios of photosystems I and II, while others add antenna chlorophyll to PSII.

Photosynthetic Response to Light by the Intact Leaf

- Light response curves show the irradiance where photosynthesis is limited by light or by CO₂ (Figure 9.6). The slope of the linear portion of the light-response curve measures the quantum yield.
- Light compensation points for shade plants are lower than for sun plants because respiration rates in shade plants are very low (Figure 9.7).
- Below 30°C the quantum yield of C₃ plants is higher than that of C₄ plants; above 30°C, the situation is reversed (Figure 9.8).
- Beyond the saturation point, factors other than incident light, such as electron transport, rubisco activity, or triose metabolism, limit photosynthesis (Figure 9.9). Rarely is an entire plant light saturated (Figure 9.10).
- The xanthophyll cycle dissipates excess absorbed light energy to avoid damaging the photosynthetic apparatus (Figures 9.11, 9.12); chloroplast move-ments also limit excess light absorption (Figure 9.13).
- Dynamic photoinhibition temporarily diverts excess light absorption to heat but maintains maximal photosynthetic rate (Figure 9.14).

Photosynthetic Responses to Temperature

- Plants are remarkably plastic in their adaptations to temperature. Optimal photosynthetic temperatures have strong genetic (adaptation) and environmental (acclimation) components.
- Leaf absorption of light energy generates a heat load that must be dissipated (Figure 9.15).
- The temperature sensitivity curves identify (a) a temperature range where enzymatic events are stimulated, (b) a range for optimal photosynthesis, and (c) a range where destructive events occur (Figure 9.16).
- Due to photorespiration, the quantum yield is strongly dependent on temperature in C₃ plants but is nearly independent of temperature in C₄ plants.
- Reduced quantum yield and increased photorespiration leads to differences in the photosynthetic capacities of C₃ and C₄ plants at different latitudes (Figure 9.17).

Photosynthetic Responses to Carbon Dioxide

- Atmospheric CO₂ levels have been increasing since the Industrial Revolution due to human use of fossil fuels (Figure 9.18).
- Concentration gradients drive the diffusion of CO₂ from the atmosphere to rubisco, using both gaseous and liquid routes (Figure 9.19).
- Within the leaf depleted of blue and red photons, green light penetrates deeper into the leaf and effectively supplies energy for photosynthesis (Figure 9.20).
- In the greenhouse, enrichment of CO₂ above natural atmospheric levels results in increased productivity (Figure 9.21).
- C₄ photosynthesis may have become prominent in warmest regions when global CO₂ concentrations fell below a threshold value (Figure 9.22).
- Opening at night and closing during the day, the stomatal activity of CAM plants contrasts with those found in C₃ and C₄ plants (Figure 9.23).
- Free Air CO₂ Enrichment (FACE) experiments suggest that C₃ plants are more responsive to elevated CO₂ than are C₄ plants (Figure 9.24).

Identifying Different Photosynthetic Pathways

- The carbon isotope ratios of leaves can be used to distinguish photosynthetic pathway differences among different plant species.

SUMMARY continued

- Both C₃ and C₄ plants have less ¹³C than does CO₂ in the atmosphere, indicating that leaf tissues discriminate against ¹³C during photosynthesis (Figure 9.25).
- As stomata close in C₃ plants or as water stress increases, the leaf carbon isotope ratio increases and becomes a direct estimate of several aspects of shorter-term water stress (Figure 9.26).

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 The Geographic Distributions of C₃ and C₄ Plants
The geographic distribution of C₃ and C₄ plants corresponds closely with growing season temperature in today’s world.

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 Prehistoric Changes in Atmospheric CO₂**
Over the past 800,000 years, atmospheric CO₂ levels changed between 180 ppm (glacial periods) and 280 ppm (interglacial periods) as Earth moved between ice ages.

9.6 Projected Future Increases in Atmospheric CO₂
Atmospheric CO₂ reached 379 ppm in 2005 and is expected to reach 400 ppm by 2015.

9.7 Using Carbon Isotopes to Detect Adulteration in Foods
Carbon isotopes are frequently used to detect the substitution of C₄ sugars into C₃ food products, such as the introduction of sugar cane into honey to increase yield.

9.8 Reconstruction of the Expansion of C₄ Taxa
The δ¹³C of animal teeth faithfully record the carbon isotope ratios of food sources and can be used to reconstruct the abundances of C₃ and C₄ plants eaten by mammalian grazers.

Web Essay

- 9.1 The Xanthophyll Cycle**
Molecular and biophysical studies are revealing the role of the xanthophyll cycle in the photoprotection of leaves.

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