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 CO₂ 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.
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 1906 that, under certain 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 bisphosphate (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 ecological terms, considering “supply” and “demand” functions for carbon dioxide. Net photosynthesis is defined as the difference between CO₂ uptake and CO₂ release. 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 may provide other possible 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 significant 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 continuously 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 mole refers to the number of atoms of a molecule (1 mol of light = 6.02 x 10¹⁴ photons, Avogadro’s number). Quanta and energy units for sunlight can be interconverted very 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 x 10⁸ m s⁻¹), h is Planck’s constant (6.63 x 10⁻³⁴ J s⁻¹), and λ is the wavelength of light, usually expressed in nm (1 nm = 1 x 10⁻⁶ 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) that is absorbed, about 15% is reflected or transmitted through a green leaf. Because chlorophyll absorbs very strongly in the blue and red regions of the spectrum (see Figure 7.3), the transmitted and reflected light is vastly enriched in green (Figure 9.3)—hence the green color of vegetation. Of the 85% of 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 light 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 times greater than the direct sunlight impinging on the leaf. In the palisade 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 times greater than the direct sunlight impinging on the leaf.
the leaf absorbed by the same amount of chlorophyll in a solution.

Light channelling 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 (Yee 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 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 one to three layers deep (see Figure 9.3). Some leaves have several layers of columnar cells that stand in parallel columns one to three layers deep (see FIGURE 9.3). These are patches of sunlight that pass through small gaps in the leaf canopy and move across shaded leaves as the sun moves. In a dense forest, sunlight 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 leaf canopy. Rapid responses of the photosynthetic apparatus and the stomata to sunflecks have been of substantial interest to plant physiologists and ecologists (Peary 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) would 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 have mechanisms for taking advantage of sunflecks when they occur. Solar tracking is the ability of leaves to track the sun's trajectory in the sky. Many species, including alfalfa, cotton, soybean, and lupine, have leaves capable of solar tracking.
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 15° until sunset, when the laminae are nearly vertical, facing the west. During the night the leaf takes a horizontal position and reorient itself 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 realign themselves 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 Lactuca (Malvaceae) and other plants sensitive to light, 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 diadephotosis ("bending toward the sun"), used to describe sun-induced leaf movements, we call leaves that maximize light interception by solar tracking diadephotosic. Some solar-tracking plants can also move their leaves so that they are fully exposed to sunlight, thus minimizing heating and water loss. These sun-avoiding leaves are called paradoephotosic. Some plant species have leaves that can display diadephotosic movements when they are well watered and paradoephotosic movements when they experience water stress. By the peak of the growing season, the sun, solar-tracking plants are able to maintain maximum photosynthetic rates throughout the day, including early morning and late afternoon, their 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). Paradoephotosic 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 formed set of biochemically and morphologically 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 to a sunny environment. The lack of acclimation suggests that these plants are adapted to either a sunny or a shady environment. When plants adapted to a sunny environment are transferred to 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 diadephotosic leaves show some light 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 (Araujo et al. 1986). Other shade plants, rather than changing the ratio of PSI to PSII 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 C3 and C4 species. The section continues with descriptions of how leaves respond to excess light.

**Light-response curves reveal photosynthetic properties**

Measuring net CO2 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, CO2 is given off by the plant (see Chapter 11). CO2 uptake is negative in this part of the light-response curve. At greater photon flux levels, photosynthetic CO2 assimilation eventually reaches a point at which photosynthetic CO2 uptake exactly balances CO2 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 ecotypes. 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 20 µmol m–2 s–1, whereas corresponding values for shade plants are 1 to 5 µmol 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 CO2 exchange to zero. Low respiratory rates allow shade plants to acclimate their CO2 uptake rates to the shading environment.

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. Even different light stimulations do not improve the ability to achieve positive CO2 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. Even different light stimulations do not improve the ability to achieve positive CO2 uptake rates at lower values of PAR than sun plants.

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 habits.
photosynthesis: physiological and ecological considerations

But under today's atmospheric conditions quantum yield can vary among plants with differing 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 CO2 or an O2 basis, and as such it can be constant at about 0.05 mole of CO2 per mole of photons. In contrast, if C4 leaves are exposed to low O2 concentrations, the quantum yield for CO2 fixation remains constant at about 0.05 mole of CO2 per mole of photons. This is because the carbon-concentrating mechanism in C4 photosynthesis effectively eliminates CO2 evolution via photorespiration.

Quantum yield also varies with temperature and CO2 concentration because of the 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 C4 plants are higher than those of C3 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 tricarbonyl sugars, have become limiting to photosynthesis.

Above the saturation point, photosynthesis is commonly referred to as CO2-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 µmol m–2 s–1—well below full sunlight (which is about 2000 µmol m–2 s–1). Although individual leaves are rarely able to utilize full sunlight, whole plants usually consist of many leaves that shade each other, 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 sub saturating 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 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).
THE KANTHOPYLL 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 involved in the dissipation of excess light energy in the leaf (see Figure 7.35). 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.)

THE KANTHOPYLL CYCLE IN SUN AND SHADE

Leaves that grow in full sunlight contain a substantially larger xanthophyll pool than do shade leaves, so they have a dis- sipate higher amounts of excess light energy. Nevertheless, the xanthophyll cycle also operates in plants that must dissipate higher amounts of excess light energy. At higher irradiances there is a large difference between the fractions 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.)

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

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. Chloro- plast movement is widespread among algae, mosses, and leaves of higher plants (Haupt and Schweinlein 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, chloro- plast movement is controlled by phytochrome (Haupt and Schweinlein 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).

Absorption of too much light can lead to photo-inhibition

Recall from Chapter 7 that when leaves are exposed to more light than they can utilize (see Figure 9.11), the reaction center of PSI is inactivated and often damaged in a phenomenon called photo-inhibition. The characteristics of photo-inhibition in the intact leaf depend on the amount of light to which the plant is exposed. The two types of photo-inhibition are dynamic photo-inhibition and chronic photo-inhibition (Osmond 1994).

Under moderate excess light, dynamic photo-inhibition is observed. Quantum efficiency decreases, but the maxi- mum photosynthetic rate remains unchanged. Dynamic photo-inhibition 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-
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 (CO2 uptake) and transpiration (H2O loss) share a common pathway: that is, CO2 diffuses into the leaf, and H2O 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 H2O loss to CO2 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 (300–3000 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-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 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 closure 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 C3 leaf or a C4 leaf under ambient CO2 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 C4 species, Atriplex glabrifolia, commonly grows in cool coastal environments, while the C3 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 9.14 Changes over the course of a day in the allocation of photons absorbed from sunlight. 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.)

**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.

**FIGURE 9.16** Changes in photosynthesis as a function of temperature at normal atmospheric CO2 concentrations for a C4 plant grown in its natural cool habitat and a C3 plant growing in its natural hot habitat under current ambient CO2 concentrations. (After Berry and Bjorkman 1980.)
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 CO₂ concentration affects photosynthesis. CO₂ diffuses from the atmosphere into leaves—first through stomata, then through the intercellular air spaces, and ultimately into chloroplasts. In the presence of adequate amounts of light, higher CO₂ concentrations support higher photosynthetic rates. The reverse is also true: Low CO₂ concentrations can limit the amount of photosynthesis in C₃ plants.
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.

Current atmospheric 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 studying carbon dioxide 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 80 to 60% faster when CO2 concentrations are doubled (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 of CO2 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 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 we do not expect to see large gradients in CO2 concentration and temperature when water changes as atmospheric CO2 concentrations continue to rise. Under laboratory conditions, most C3 plants grow 80 to 60% faster when CO2 concentrations are doubled (600–750 ppm), and the growth rate becomes limited by the nutrients available to the plant (Bowes 1993).

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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 CO₂ 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.

**CO₂ imposes limitations on photosynthesis**

For many crops, such as tomatoes, lettuce, cucumbers, and grapes, 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 CO₂ in the intercellular air space (c) within the leaf (see WEB TOPIC 9.4) makes it possible to evaluate limitations to photosynthesis caused by CO₂ supply. At very low intercellular CO₂ concentrations, photosynthesis is strongly limited by the low CO₂.

Increasing intercellular CO₂ to the concentration at which photosynthesis and respiration balance each other defines the CO₂ compensation point, at which the net efflux of CO₂ 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 CO₂ compensation point reflects the balance between photosynthesis and respiration as a function of CO₂ concentration, whereas the light compensation point reflects that balance as a function of photon flux under constant O₂ concentration.

**C₃ PLANTS**

In C₃ plants, increasing atmospheric CO₂ above the compensation point stimulates photosynthesis over a wide concentration range (see Figure 9.21). At low to intermediate CO₂ concentrations, photosynthesis is limited by the carboxylation capacity of rubisco. At high CO₂ 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 CO₂ because carboxylation replaces oxygenation on rubisco (see Chapter 8). By regulating stomatal conductance, most leaves appear to regulate their cᵢ (internal partial pressure for CO₂) 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 CO₂ assimilation as a function intercellular partial pressures of CO₂ tells us how photosynthesis is regulated by CO₂, independent of the functioning of stomata (see Figure 9.21). Inspection of such a plot for C₃ and C₄ plants reveals interesting differences between the two pathways of carbon metabolism:

- In C₃ plants, photosynthetic rates saturate at cᵢ values of about 15 Pa, reflecting the effective carboxylation capacity of rubisco and the capacity to regenerate ribulose 1,5-bisphosphate.

- In C₄ plants, increasing cᵢ values continue to stimulate photosynthesis over a much broader CO₂ range.

- In C₃ plants, the CO₂ compensation point is zero or nearly zero, reflecting their very low levels of photorespiration (see Chapter 8).

- In C₄ plants, the CO₂ compensation point is about 10 Pa, reflecting CO₂ production because of photorespiration (see Chapter 8).

These responses indicate that C₃ plants may benefit more from ongoing increases in today’s atmospheric CO₂ concentrations than C₄ plants would (see Figure 9.18). Because photosynthesis in C₃ plants is CO₂-saturated at low concentrations, C₃ plants have an advantage over C₄ plants in terms of increases in atmospheric CO₂ concentrations.

In fact, the ancestral photosynthetic pathway is C₃ photosynthesis, and C₃ photosynthesis is a derived pathway. During geologic time periods when atmospheric CO₂ concentrations were very much higher than they are today, CO₂ diffusion through stomata into C₃ leaves would have resulted in higher cᵢ values and therefore higher photosynthetic rates. While C₃ photosynthesis is typically CO₂ diffusion limited today, C₃ plants still account for nearly 70% of the world’s primary productivity. The evolution of C₄ photosynthesis is one biochemical adaptation of C₃ plants to a CO₂ limited atmosphere. Our current understanding is that C₃ photosynthesis may have evolved recently, some 10 to 15 million years ago.

**C₄ PLANTS**

If the ancient Earth of more than 50 million years ago had atmospheric CO₂ concentrations that were well above the present-day atmospheric conditions, under what atmospheric conditions might we expect that C₄ photosynthesis would become a major photosynthetic pathway found in the Earth’s ecosystems? Ebeling et al. (1977) suggest that C₄ photosynthesis first became a prominent component of terrestrial ecosystems in the warmest growing regions of the Earth when global CO₂ concentrations decreased below some critical and as yet unknown threshold CO₂ concentration (FIGURE 9.22). That is, the negative impacts of high photorespiration and CO₂ limitation on C₄ photosynthesis would be greatest under warm to hot growing conditions, especially when atmospheric CO₂ is reduced. The C₄-favorable growing areas would have been located in those geographic regions with the warmest temperatures. C₄ plants would have been most favored during periods of Earth’s history when CO₂ levels were lowest. In today’s world, these regions are the tropical grasslands and savannas. There are now extensive data to indicate that C₄ photosynthesis was more prominent during the glacial periods when atmospheric CO₂ levels were below 200 ppm than it is today (see Figure 9.18). Other factors may have contributed to the expansion of C₄ plants, but certainly low atmospheric CO₂ was one important factor favoring their geographic expansion.

Because of the CO₂-concentrating mechanisms in C₄ plants, CO₂ remains available even in the carboxylation sites within C₄ chloroplasts is often saturating for rubisco activity. As a result, plants with C₄ metabolism need less rubisco than C₃ plants to achieve a given rate of photosynthesis, and require less nitrogen to grow (von Caemmerer 2000).

In addition, the CO₂-concentrating mechanism allows the leaf to maintain high photosynthetic rates at lower cᵢ values, which may be necessary for a given rate of photosynthesis. Thus, C₄ plants can use water and nitrogen more efficiently than C₃ plants can. On the other hand, the additional energy cost of the concentrating mechanism (see Chapter 8) makes C₄ plants less efficient in their utilization of light. This is probably one of the reasons that most shade-adapted plants in temperate regions are C₃ 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 C₃ and C₄ plants. CAM plants open their stomata at night and close them during the day, exactly the opposite of the pattern observed in leaves of C₃ and C₄ plants (Figure 9.23). At night, atmospheric CO₂ diffuses into CAM plants where it is combined with phosphoenolpyruvate to form malate, a C₅ compound. By day, malate is released by respiration is refixed into malate. This process, which has been called CAM cycling, 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 CO₂ conditions?

A central question in plant physiology today is how photosynthesis and respiration modified in an environment where CO₂ levels are 400 ppm, 500 ppm, or even...
While 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 C3 photosynthetic pathway are much more responsive than C4 plants under well-watered conditions, with the net photosynthetic rate increasing 20% or more in C3 plants and not at all in C4 plants. Photosynthesis rises because intercellular CO2 levels increase (recall Figure 9.23). At the same time, there is a down-regulation of photosynthetic capacity manifest in reduced activity of the enzymes associated with the dark reactions of photosynthesis (Ainsworth and Rogers 2007).

While CO2 is indeed important for photosynthesis, other factors are important for growth under elevated CO2 (Long et al. 2004, 2006). For example, a common FACE observation is that plant growth becomes quickly constrained by soil moisture and the presence of trace gases, such as ozone, 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 CO2 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 CO2. 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 CO2 levels will affect many plant processes; for instance, leaves tend to keep their stomata more closed under elevated CO2 levels. As a direct consequence of reduced transpiration, leaf temperatures are higher (see Figure 9.24C). Elevated temperatures will feed back on 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 CO2 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 CO2. Understanding these responses is crucial as society looks for increased agricultural outputs to support rising human populations and to provide raw materials for biofuels.

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against the heavier isotope of carbon during photosynthesis, and therefore they have lower δ13C/δ12C ratios than are found in atmospheric CO2.

The δ13C/δ12C isotope composition is measured by use of a mass spectrometer, which yields the following ratio:

\[ \delta = \frac{\text{C}\text{O}_2}{\text{C}\text{O}_2} - 1 \times 1000 \]  

The carbon isotope ratio of plants, δ13C, is quantified on a per mil (‰) basis:

\[ \delta^{13}C = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \]  

where the standard represents the carbon isotopes contained in fossil belemnites from the Pee Dee limestone formation of South Carolina. The δ13C of atmospheric CO2 has a value of −8‰, meaning that there is less 13C in atmospheric CO2 than is found in the carbonate of the belemnite standards.

What are some typical values for carbon isotope ratios of plants? C3 plants have a δ13C value of about −28‰, C4 plants have an average value of −14‰ (Farquhar et al. 1989). Both C3 and C4 plants have less 13C than does CO2 in the atmosphere, which means that leaf tissues discriminate against 13C during the photosynthetic process. Cerling et al. (1997) provided δ13C data for a large number of C3 and C4 plants from around the world (Figure 9.25).

What becomes clear from Figure 9.25 is that there is a wide spread of δ13C values in C3 and C4 plants, with averages of −28‰ and −14‰, respectively. These δ13C variations actually reflect the consequences of small variations in physiological processes associated with changes in stomatal conductance in different environmental conditions. Thus, δ13C values can be used both to distinguish between C3 and C4 photosynthesis and to further reveal details about stomatal conductance for plants grown in different environments (such as the tropics versus deserts).

Differences in carbon isotope ratio are easily detectable with mass spectrometry. A δ13C value of more than ±1‰ in a plant tissue sample indicates that there was a significant difference in the ambient CO2 concentration experienced by the leaf of interest. The δ13C of a plant is determined by its carbon isotope ratio, which is influenced by both leaf carbon isotope ratio and stomatal conductance. Therefore, a plant with a higher δ13C value than its environment will have a positive δ13C value, while a plant with a lower δ13C value than its environment will have a negative δ13C value.

Why are there carbon isotope ratio variations in plants?

What is the physiological basis for 13C depletion in plants relative to CO2 in the atmosphere? It turns out that both the diffusion of CO2 into the leaf and the carboxylation selectivity for 13CO2 play a role.

We can predict the carbon isotope ratio of a C4 leaf as

\[ \delta^{13}C_{\text{leaf}} = \delta^{13}C_{\text{atm}} - (b - a) \]  

where \( \delta^{13}C_{\text{atm}} \) and \( \delta^{13}C_{\text{leaf}} \) are the carbon isotope ratios of the leaf and atmosphere, respectively; \( a \) is the diffusion fraction; \( b \) is the net carboxylation fraction in the leaf, and \( c \) is the ratio of intercellular to ambient CO2 concentrations. CO2 diffuses from air outside of the leaf to the carboxylation sites within leaves in both C3 and C4 plants. We express this diffusion using the term \( a \). Because CO2 is lighter than 13CO2, it diffuses slightly faster toward the carboxylation site, creating an effective diffusion fraction of about 44%. Thus, we would expect leaves to have a more negative δ13C value simply because of this diffusion effect. Yet this factor alone is not sufficient to explain the δ13C values of C3 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 C3 photosynthesis and has an intrinsic discrimination value against 13C of −30‰. By contrast, PEP carboxylase, the primary CO2 fixation enzyme of C4 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 C3 and C4 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 CO2 in the intercellular air spaces of leaves (\( c_i \)). In C3 plants, the potential isotope discrimination by rubisco of about −30‰ is not fully expressed during photosynthesis because the availability of CO2 at the carboxylation site becomes a limiting factor, restricting the discrimination by rubisco. Greater discrimination against 13CO2 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 13C (Ehleringer et al. 1993). When leaves are exposed to water stress, stomata tend to close, reducing \( c_i \) values. As a consequence, C3 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 CO2 value in a leaf. Intercellular CO2 levels are then directly linked with photosynthesis and stomatal constraints. Once stomata close in C3 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 stomatal and water stress. These applications of carbon isotopes to study plant performance in both agricultural and ecological studies (Ehleringer et al. 1993, Bunce and Körner 2008).

One emergent environmental pattern is that, on average, leaf carbon isotope ratio values decrease as precipitation decreases. Figure 9.26 illustrates this pattern in a transect across Australia. Here we see that the δ13C 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 δ13C data, we conclude that intercellular CO2 levels of desert plants are lower than what we would typically see in leaves of rainforest plants. Because of the sequential nature of tree ring formation, δ13C 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 C3 to C4 foods in an animal’s δ13C values in its tissues—bones, hair, teeth; bones, hair, 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 examined sequential δ13C values in segments of tail hair to reconstruct the daily diets of each animal. They observed very predictable seasonal shifts in diets between trees (C3) and grasses (C4) as physiological 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 C4 plant) plays in the diets of North Americans. Another application of δ13C 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 C3 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 δ13C values that are very close to those of C3 plants. In CAM plants that fix CO2 at night via PEP carboxylase, δ13C is expected to be similar to that of C3 plants. However, when some CAM plants are well watered, they can switch to C4 mode by opening their stomata and fixing CO2 during the day via rubisco. Under these conditions the isotope composition shifts toward that of C3 plants. Thus the δ13C values of CAM plants reflect how much carbon is fixed via the C3 pathway versus the C4 pathway.
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 movements 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 photospiration, 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 photospiration 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 290 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 C3 sugars into C4 food products, such as the introduction of sugar cane into honey to increase yield.
9.8 Reconstruction of the Expansion of C4 Taxa
- The 813C 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.
CHAPTER REFERENCES


