

Chapter 9 - Leaves and Plants

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9.1 Introduction

Terrestrial vegetation responds to weather and climate through a variety of physiological, demographic, and ecosystem processes. Physiological processes refer to the uptake and translocation of CO₂, water, and essential nutrients by individual leaves and whole plants. Demographic processes refer to the growth, mortality, and reproduction of plants. These determine population density and community composition. Ecosystem processes refer to the linking of the biotic and abiotic environments through the cycling of carbon, water, and nutrients between vegetation and soil. Together, physiological, demographic, and ecosystem processes determine where plant species grow, how well they grow, and how the composition and structure of vegetation change over time. The physiology of plants and the structure and composition of ecosystems are important determinants of weather and climate.

This chapter and the next two introduce the ecological concepts needed to understand terrestrial ecosystems and their role in the climate system. This chapter focuses on the physiological ecology of leaves and plants (Chabot and Mooney 1985; Kozłowski *et al.* 1991; Larcher 1995; Kramer and Boyer 1995; Bazzaz 1996; Landsberg and Gower 1997). Chapter 10 examines the distribution of populations and communities across landscapes and their organization into ecosystems. Chapter 11 examines how vegetation changes over time in response to stand dynamics, recurring disturbances such as fires, and climate change. The sequencing of material follows the traditional subdisciplines within plant ecology of ecophysiology, population ecology, community ecology, ecosystem ecology, and landscape ecology (Barnes *et al.* 1998; Barbour *et al.* 1999; Smith and Smith 2001).

9.2 Carbon assimilation

Photosynthesis is the process by which light energy is absorbed by green plants and used to produce carbohydrates from carbon dioxide (CO₂) and water (H₂O). The overall chemical reaction is



where n is the number of molecules of CO₂ that combine with water to form the carbohydrate (CH₂O) _{n} , releasing n molecules of oxygen (O₂) to the atmosphere. The compound (CH₂O) _{n} is not real but rather represents the general structure of a carbohydrate. Carbohydrates are sugars, starches and other related

compounds containing carbon combined with hydrogen and oxygen. They are the most abundant organic compounds in nature and provide energy, structural material, and the building blocks for other molecules.

The biochemistry of photosynthesis is much more complicated than represented in this simple equation (Salisbury and Ross 1992; Larcher 1995). It consists of three separate processes: light reactions, which convert light energy into chemical energy; dark reactions, which use this chemical energy to reduce CO₂ to carbohydrates; and diffusion, in which stomata open to allow CO₂ to diffuse into leaves from the surrounding air.

Photosynthesis occurs in the chloroplasts of leaves. These are disk-shaped structures within plant cells that are usually 5-10 μm in diameter. They consist of stroma, a gel-like material containing enzymes to convert CO₂ to carbohydrates during the dark reactions, and thylakoids, which are embedded throughout the stroma and are the site of the light reactions. The membranes of thylakoids contain the chlorophyll and carotenoid pigments essential to photosynthesis. A single leaf mesophyll cell may contain 50 chloroplasts and a square millimeter of leaf area may contain some 500 000 chloroplasts.

9.2.1 Light reactions

The light reactions convert light energy into the chemical energy required for the dark reactions. Absorption of light oxidizes water, providing electrons to create chemical energy and releasing oxygen. The electrons are passed through a series of biochemical reactions to NADP⁺ (oxidized nicotinamide adenine dinucleotide phosphate) where they are temporarily stored in NADPH (reduced nicotinamide adenine dinucleotide phosphate) before being passed to CO₂ to form carbohydrates. In the process of electron transfer, chemical energy in the form of ATP (adenosine triphosphate) is created from adenosine diphosphate (ADP) and inorganic phosphate (e.g., H₂PO₄, which is generically represented as P_i).

The first step in photosynthesis is the absorption of light by pigment molecules contained in chloroplasts. Light energy is transferred in discrete units called photons or quanta. The energy of a photon (E , J photon⁻¹) is related to its wavelength (λ , m) as

$$E = (hc) / \lambda$$

where h is Planck's constant (6.63×10^{-34} J s photon⁻¹) and c is speed of light (3×10^8 m s⁻¹). The energy of a photon of red light with a wavelength of 0.680×10^{-6} m (0.680 μm) is 2.92×10^{-19} joules. One mole of

photons (6.023×10^{23} photons) contains 176 000 joules. For photosynthesis, the number of photons, not the total energy, is important. A photon of light with a blue wavelength (e.g., 0.450 μm) has more energy than a photon of light in the red range of the spectrum, but both have the same effect on photosynthesis. However, plants do not utilize the full spectrum of solar radiation for photosynthesis. Only radiation with wavelengths between 0.4 μm and 0.7 μm , known as photosynthetically active radiation, is used. Sunlight at higher wavelengths (i.e., the near-infrared waveband) is not utilized during photosynthesis. Instead, this radiation is reflected to prevent overheating.

Chlorophyll is the main pigment that makes leaves green, absorbing light primarily in the violet, blue, and red wavelengths while reflecting light in green wavelengths. Another class of pigments involved in photosynthesis is the carotenoids. These are red, orange, and yellow colored pigment molecules. The more abundant chlorophyll masks their color, which is why leaves are green. Chlorophyll and carotenoid pigments are embedded within chloroplasts in units of several hundred pigment molecules called photosystems. Light energy absorbed by a pigment molecule is transferred within the photosystem from one pigment molecule to the next until it reaches a reaction center. This is a special chlorophyll molecule that boosts one of its electrons to a higher energy level when light energy is absorbed. This electron is transferred to an acceptor molecule, initiating a series of biochemical reactions that create reducing power in the form of NADPH and chemical energy in the form of ATP. Plants have two separate groups of photosystems. Photosystem I (PS I) has optimal light absorption at a wavelength of 0.700 μm . Its reaction center is known as the P700 chlorophyll pigment molecule. Photosystem II (PS II) has optimal light absorption at 0.680 μm . Its reaction center is the P680 chlorophyll pigment molecule. Both are cooperatively involved in the light reactions of photosynthesis, using light energy to oxidize water and transfer its two electrons to NADPH.

The light reactions begin when light energy transferred to the P680 reaction center in PS II cause it to lose an electron (Figure 9.1a,b). This electron is transferred to an electron acceptor molecule. The electron-deficient P680 molecule replaces its electron by extracting an electron from water (Figure 9.1c). This splits one water molecule (H_2O) into two protons (2H^+), two electrons ($2e^-$), and oxygen ($\frac{1}{2}\text{O}_2$). The electron from P680 is passed through a series of biochemical reactions to the P700 chlorophyll reaction

center in PS I (Figure 9.1d). The P700 pigment molecule cannot accept an electron unless it has lost one. As with PS II, this occurs when light energy absorbed by surrounding pigment molecules is passed to the reaction center and an electron is boosted to an electron acceptor (Figure 9.1e,f). This electron is then used to reduce NADP^+ to NADPH (Figure 9.1g). Two electrons are required to reduce NADP^+ to NADPH. These are provided when one water molecule is split. The transfer of one electron from water to NADP^+ requires two photons (each photosystem must be excited). Since two electrons are required to reduce NADP^+ to NADPH, four photons are needed to pass two electrons from one water molecule to reduce one NADP^+ molecule. Two NADPH are needed in the dark reactions to reduce one CO_2 molecule. Consequently, eight photons are needed to split two water molecules, which provide the four electrons to produce the two NADPH needed to reduce one CO_2 molecule.

The biochemical reactions that transfer an electron from PS II to PS I also result in the formation of ATP in a process called photophosphorylation. Some of this ATP is created during non-cyclic photophosphorylation when electrons are passed from PS II to PS I (Figure 9.1h). In addition, light absorbed by PS I can initiate electron transport in which an electron is transferred to the electron acceptor and then passed back to P700. In this cyclic photophosphorylation, no water is split and no NADPH is formed but ATP is produced. An additional photon absorbed only by PS I is required for cyclic photophosphorylation, which together with non-cyclic photophosphorylation produces the three ATP molecules required in the dark reactions. The dark reactions can possibly require four ATP molecules, in which case three more photons must be absorbed by PS I only to form an additional ATP molecule. Hence, a total of nine to 12 photons must be absorbed to yield two NADPH and three or four ATP to reduce one molecule of CO_2 during the dark reactions.

9.2.2 Dark reactions

In the dark reactions, NADPH and ATP are used to fix CO_2 into a carbohydrate. Light is not directly involved. In many plants, the first product formed from CO_2 contains three carbon atoms. Hence, this is known as the C_3 photosynthetic pathway. The biochemical reactions that reduce CO_2 to carbohydrates are collectively known as the Calvin cycle and consist of three phases: carboxylation, reduction, and regeneration (Figure 9.2). In the carboxylation phase, the 5-carbon sugar ribulose-1,5-

bisphosphate (RuBP) combines with CO_2 and water to form two 3-carbon compounds known as phosphoglyceric acid (PGA). This reaction is catalyzed by the enzyme ribulose bisphosphate carboxylase-oxygenase (rubisco). In the reduction phase, PGA is reduced to the 3-carbon compound phosphoglyceraldehyde (PGaldehyde) when inorganic phosphate is obtained from ATP and electrons are obtained from NADPH. The ADP and NADP^+ released in these reactions are converted back to ATP and NADPH during the light reactions. Some of the PGaldehyde is used to produce carbohydrates. The remainder is utilized in the regeneration phase, where it combines with additional ATP to regenerate RuBP. Three turns of the cycle fix three CO_2 molecules for a net production of one PGaldehyde. For each CO_2 fixed, two NADPH and three ATP are required.

In some plants such as corn, sugar cane, and most tropical grasses, CO_2 is first fixed into 4-carbon acids (malic and aspartic acids) rather than the 3-carbon PGA. These species are known as C_4 plants. In this pathway, CO_2 combines with phosphoenolpyruvate (PEP) in a reaction catalyzed by the enzyme PEP carboxylase. The resulting 4-carbon compound, oxaloacetate, is then converted to malate or aspartate. These acids are decarboxylated to yield CO_2 and pyruvate. The CO_2 enters the Calvin cycle, reacting with RuBP to form PGA, while the pyruvate reacts with ATP to form more PEP. The C_4 photosynthetic pathway requires a special leaf anatomy because the initial fixing of CO_2 into malate or aspartate occurs in different leaf cells (mesophyll cells) than the Calvin cycle (bundle-sheath cells). It also requires two more ATP in addition to the three already required in the Calvin cycle. These synthesize PEP for continued CO_2 fixation.

At first glance, the C_4 pathway seems inefficient and energetically expensive. In fact, however, C_4 plants are much more efficient at photosynthesis than C_3 plants. In the C_3 pathway, plants lose some of the CO_2 they fix in a light-enhanced process called photorespiration. This occurs because rubisco, which catalyzes CO_2 fixation by RuBP, also catalyzes the oxidation of RuBP by oxygen. This reaction consumes oxygen and releases CO_2 so that the net CO_2 uptake during photosynthesis is reduced by 30% to 50% (Barbour *et al.* 1999, p. 413). The rate of photorespiration depends on the ratio of CO_2 -to- O_2 at the site of the dark reactions. In C_4 plants, the spatial separation of initial CO_2 fixation (mesophyll cells) and the Calvin cycle (bundle-sheath cells) creates a high CO_2 : O_2 ratio at the site of CO_2 fixation into PGA during the Calvin cycle. With relatively little O_2 compared with CO_2 in bundle-sheath cells, RuBP is not oxidized

by oxygen. The C₄ plants, therefore, have little or no photorespiration and consequently have greater net photosynthetic rates than C₃ plants at high light levels and warm temperatures.

Many succulent plants such as cacti, orchids, and bromeliads use a third photosynthetic pathway called crassulacean acid metabolism (CAM). These plants grow in hot, arid regions. In this environment, they cannot open their stomata during the day to obtain CO₂ because they would quickly be desiccated by transpiration. Instead, their stomata open at night, when temperatures are cooler, and CO₂ is fixed by PEP to form malic acid. The malic acid accumulates during the night. During daylight, it is decarboxylated to release CO₂ that is then refixed in the Calvin cycle. Unlike C₄ plants, with their spatial separation of CO₂ fixation by PEP and carbohydrate synthesis during the Calvin cycle, CO₂ fixation and the Calvin cycle take place in the same cell. Instead, night and day temporally separate the two processes.

9.2.3 Stomata

For photosynthesis to occur, CO₂ in the air surrounding a leaf must diffuse into the leaf to the chloroplasts, where it is fixed and converted to carbohydrates. Most leaves have a waxy layer on the surface that restricts gas diffusion. Instead, CO₂ passes through tiny microscopic openings in foliage known as stomata (Figure 9.3). Stomata are typically 10-20 μm in length with a maximum width of about 5 μm (Larcher 1995, p. 81). A leaf may contain 100 to 500 stomata per square millimeter of leaf area with a total pore area of less than 1% of leaf area. Stomatal conductance for CO₂ and water is directly proportional to pore width, with the maximum opening determining the upper limit to the rate of gas exchange. By varying the width of the stomatal pore, plants control gas exchange. Stomata open to allow CO₂ uptake during photosynthesis and close to prevent desiccation during transpiration.

The rate of leaf photosynthesis can be represented as a diffusion process similar to transpiration (Figure 7.5) in which

$$A = \frac{c_a - c_s}{(1.37r_b)P} = \frac{c_s - c_i}{(1.65r_s)P} = \frac{c_a - c_i}{(1.37r_b + 1.65r_s)P}$$

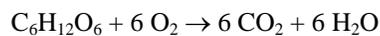
In these equations, c_a , c_s , and c_i are the ambient, leaf surface, and internal CO₂ partial pressures (Pa), respectively, P is atmospheric pressure (Pa), and r_b and r_s are leaf boundary layer and stomatal resistances (i.e., the inverse of conductance) to water vapor diffusion ($\text{s}^2 \mu\text{mol}^{-1} \text{H}_2\text{O}$), respectively. The factors 1.37

and 1.65 are the ratios of the diffusivity of CO₂ to water for leaf boundary layer and stomatal resistances, respectively, and account for the different diffusivity of CO₂ and water. The first equation represents the diffusion of CO₂ from air surrounding a leaf to the leaf surface, which is inversely proportional to leaf boundary layer resistance. The second equation is the diffusion of CO₂ from the leaf surface to inside the leaf, which is inversely proportional to stomatal resistance. The final equation is the combined CO₂ flux from air to inside a leaf.

Stomata open and close in response to a variety of environmental factors (Figure 9.4). Light has a strong influence. Except for CAM plants, stomata open with light and close in darkness. Stomata also close with temperatures warmer and colder than some optimal value. Stomata close to prevent excessive water loss. This occurs in two ways. First, stomatal conductance decreases as leaf water potential decreases. Low leaf water potential occurs when the loss of water by transpiration exceeds the rate of uptake from soil. Stomata close to prevent further desiccation. Second, as the humidity of air decreases, the vapor pressure deficit between the leaf and air increases, creating a high potential for transpiration. Stomata close to prevent excessive desiccation under these conditions.

9.2.4 Net photosynthesis

At the same time as leaves absorb CO₂ during photosynthesis, they release CO₂ in respiration. Respiration is the complement of photosynthesis. It is the process by which organic compounds are oxidized to produce the energy needed to maintain plant functions and grow new plant tissues. For glucose, the overall chemical reaction is



The rate of respiration depends on the biochemical quality of the tissue and increases exponentially with warmer temperatures. This respiration is different from photorespiration, which is driven by fixation of oxygen rather than CO₂ by rubisco, and occurs simultaneously with photosynthesis in leaf cells. The difference between CO₂ uptake during photosynthesis and CO₂ loss during leaf respiration is the net CO₂ uptake by a leaf during photosynthesis.

Figure 9.5 illustrates the effect of leaf respiration on net photosynthesis. At cold temperatures, photosynthesis and respiration are minimal, producing negligible net CO₂ uptake. As temperature increases

above freezing, photosynthetic uptake and respiration loss increase as a result of temperature activation of enzymes. However, uptake exceeds loss for a net CO₂ gain. As temperature increases further, photosynthesis attains a maximum rate and then declines. Greater respiration at warm temperatures contributes to the decline in net photosynthesis. In addition, both photosynthesis and respiration are inhibited by high temperature. As a result, net photosynthesis shows a parabolic response to temperature defined by three cardinal values: the minimum and maximum temperatures at which there is no net CO₂ gain and a range of temperatures over which CO₂ uptake is optimal.

9.2.5 Environmental and physiological controls of photosynthesis

A variety of environmental factors influence net photosynthesis (Figure 9.6). Because of its role in the light reactions, light is an essential factor that limits the rate of photosynthesis. If a leaf absorbs insufficient light, there will not be enough ATP and NADPH to fuel the dark reactions. When the irradiance is below a certain level, typically about 10-40 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, CO₂ uptake during photosynthesis is balanced by CO₂ loss during respiration; net assimilation is zero. Only when light levels are above this light compensation point does a leaf gain carbon. Photosynthetic rates increase with greater irradiance until light saturation, when increased light no longer increases photosynthesis. At these high light levels, the rate of photosynthesis is not limited by light but rather by the amount of CO₂ and rubisco available for the dark reactions.

Temperature affects photosynthesis because sufficient, but not excessive, heat is a prerequisite for biochemical reactions (Figure 9.6). Photosynthesis is restricted to a certain temperature range beyond which biological activity is inhibited. Within this range, photosynthesis increases up to an optimal temperature, beyond which it begins to decrease. The optimum temperature range for most C₃ plants is 15 °C to 30 °C, but the temperature range over which plants can photosynthesize is quite large. Many plants can photosynthesize with temperatures below freezing or in excess of 40 °C (Larcher 1995, p. 109). Desert plants have higher temperature optima than arctic or alpine plants.

The rate of photosynthesis decreases as a leaf becomes desiccated and its foliage water potential decreases (Figure 9.6). When transpiration exceeds root uptake, plants can become desiccated. Cells lose turgor. Leaves wither and become limp. Absorption of soil nutrients and translocation of photosynthetic

products within the plant are inhibited. Because water is so essential, photosynthesis decreases sharply when the leaf water content falls below some minimal value and stomata close. Stomata also close with high vapor pressure deficits to reduce water loss during transpiration (Figure 9.6).

Photosynthetic rates are enhanced by higher concentration of CO₂ in the air (Figure 9.6). In C₃ plants, the additional CO₂ reduces photorespiration by increasing the ratio of CO₂-to-O₂ reacting with rubisco. Similar to light, the rate of photosynthesis increases with higher CO₂ concentrations up to a saturation point, beyond which photosynthesis remains constant. At this point, photosynthesis is not limited by the amount of CO₂ available for fixation but rather by the supply of NADPH and ATP from the light reactions. The rate of photosynthesis decreases markedly with low CO₂ concentrations, when the supply of CO₂ limits photosynthesis. At the CO₂ compensation point, which typically ranges from 30 to 50 parts per million (ppm), the rate of CO₂ uptake during photosynthesis is balanced by CO₂ loss during respiration so that there is no net gain of CO₂ by the leaf. In C₃ plants, there is a strong photosynthetic interaction between light and CO₂. High irradiance increases net photosynthesis more at high CO₂ concentrations than at low concentrations, and CO₂ saturation requires higher CO₂ concentrations at high irradiance than at low light. Conversely, C₄ plants saturate with CO₂ concentrations of about 400 ppm regardless of light. They also have a lower compensation point (about 10 ppm) than C₃ plants.

The rate of photosynthesis increases with increasing amounts of nitrogen in foliage (Figure 9.6). Nitrogen is an essential component of chlorophyll and rubisco. Greater amounts of nitrogen allow for more chlorophyll and rubisco, fueling greater rates of photosynthesis.

These photosynthetic responses to environmental conditions vary greatly among plants. Table 9.1 compares maximum photosynthetic rates under optimal conditions for several plant types. Among herbaceous plants, those utilizing the C₄ pathway generally have the highest maximum photosynthetic rates; CAM plants generally have the lowest rates. Trees, which utilize the C₃ pathway, generally have low rates of maximum photosynthesis. Table 9.2 compares the characteristics of the C₃, C₄, and CAM photosynthetic pathways. One of the major differences is the presence of photorespiration in C₃ plants and absence in C₄ plants. Competition between oxygen and CO₂ for rubisco means that increasing concentration of oxygen in the atmosphere inhibits CO₂ uptake during C₃ photosynthesis and that this inhibition is greater at lower CO₂ concentration. Hence, photosynthesis in C₃ plants is often limited by

ambient CO₂ concentrations while that of C₄ plants is much less limited by CO₂. The lower CO₂ compensation point in C₄ and CAM plants compared with C₃ plants is a result of CO₂ fixation by PEP carboxylase, which has a high affinity for CO₂, and because of the low photorespiration. Plants utilizing the C₄ photosynthetic pathway show little light saturation and at full sunlight can have photosynthetic rates twice that of a C₃ plant. Because of their more efficient use of CO₂, C₄ plants attain similar or greater photosynthetic rates as C₃ plants with less water loss. Hence, they have a higher water use efficiency, defined as the dry matter produced for a given amount of water lost in transpiration. In addition, the optimal temperature for C₄ plants is higher than that of C₃ plants. These features allow C₄ plants to grow well in warm regions with periodic drought such as tropical savanna.

9.2.6 Photosynthesis-transpiration compromise

The physiology of stomata has evolved as a compromise between the two conflicting goals of permitting CO₂ uptake during photosynthesis while restricting water loss during transpiration (Cowan 1977). Stomata are regulated so as to maximize carbon gain and minimize water loss. This is evident from experiments relating stomatal conductance, photosynthesis, and transpiration. Plants grown under a variety of irradiances, nutrient concentrations, ambient CO₂ concentrations, and leaf water potentials show large variation in photosynthetic rate and stomatal conductance, but photosynthesis and stomatal conductance vary in near constant proportion (Wong *et al.* 1979, 1985a,b,c). Photosynthesis and stomatal conductance measurements for jack pine trees illustrate such relationships. Over a wide range of light and foliage water potential, from full illumination to dark and from moist to desiccated, net photosynthesis increases proportionally with increases in stomatal conductance (Figure 9.7). Transpiration also increases with greater conductance. Physiological measurements among a variety of plant communities also show a positive correlation between maximum stomatal conductance and maximum rate of photosynthesis, though the relationship differs between woody and herbaceous plants (Schulze and Hall 1982; Field and Mooney 1986; Körner 1994; Schulze *et al.* 1994) (Figure 9.8). Coherent changes in photosynthetic carbon metabolism and stomatal behavior suggest they change in concert. Stomatal conductance varies to match the photosynthetic capacity of leaves as determined by site conditions and plant physiology so as to minimize the rate of transpiration.

As such, the physiology of stomata and the biophysics of transpiration are linked to the biochemistry of photosynthesis. Collatz *et al.* (1991) describe one approach that links these processes. For C₃ plants, stomatal conductance (g_s , $\mu\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$) is related to net photosynthesis (A_n , $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) as

$$\frac{1}{r_s} = g_s = m \frac{A_n (h_s / 100) P}{c_s} + b$$

where m is a constant, h_s and c_s are the relative humidity (%) and CO₂ partial pressure (Pa) at the leaf surface, respectively, P is atmospheric pressure (Pa), and $b = 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ is a typical minimum leaf conductance. A typical value is $m = 6$ for needleleaf trees and $m = 9$ for other plants. The relative humidity and CO₂ partial pressure at the leaf surface are obtained from resistance networks (Figure 7.5). Collatz *et al.* (1992) describe a similar model for C₄ plants. This approach has been used to model photosynthesis and stomatal conductance in climate models (Bonan 1995a; Denning *et al.* 1995, 1996a,b; Sellers *et al.* 1996a,b, 1997a; Randall *et al.* 1996; Craig *et al.* 1998).

Net photosynthesis is given by a biochemical model of leaf photosynthesis based on the enzyme kinetics of rubisco and the regeneration of RuBP in response to the supply of NADPH and ATP produced in the light reactions (Farquhar *et al.* 1980; Farquhar and von Caemmerer 1982; Farquhar 1989). In this model, photosynthesis is the lesser of these two rates so that

$$A_n = \min(w_c, w_j) - R_d$$

where w_c is the rubisco-limited rate of photosynthesis, w_j is light-limited rate allowed by RuBP regeneration, and R_d is dark respiration (all with units of $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$). The rubisco-limited rate is

$$w_c = \frac{V_{\max} (c_i - \Gamma^*)}{c_i + K_c (1 + O_i / K_o)}$$

and the RuBP regeneration-limited rate is

$$w_j = \frac{J (c_i - \Gamma^*)}{4(c_i + 2\Gamma^*)}$$

where c_i is the partial pressure (Pa) of CO₂ in leaf chloroplast (also known as intercellular CO₂), Γ^* is the CO₂ compensation point (Pa), O_i is the partial pressure (Pa) of oxygen in leaf chloroplast (which is the same as that of ambient air, i.e., 0.209P), and K_c and K_o are Michaelis-Menten constants (Pa) for the

carboxylation and oxygenation of rubisco. Intercellular CO_2 is calculated from the resistance network (Figure 7.5). The parameters Γ_* , K_c , and K_o depend on temperature. Typical values at 25 °C are $\Gamma_* = 2\text{-}4$ Pa, $K_c = 30$ Pa, and $K_o = 30\,000$ Pa. The potential rate of electron transport J ($\mu\text{mol electrons m}^{-2} \text{s}^{-1}$) depends on the amount of photosynthetically active radiation absorbed by a leaf ϕ ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) as the smaller of the two roots of the equation

$$0.7J^2 - (J_{\max} + 0.385\phi)J + 0.385J_{\max}\phi = 0$$

where J_{\max} is the maximum potential rate of electron transport ($\mu\text{mol electrons m}^{-2} \text{s}^{-1}$). The maximum rate of carboxylation V_{\max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$) is proportional to the amount of rubisco in the leaf. The maximum potential rate of electron transport J_{\max} varies in relation to leaf chlorophyll. The parameters V_{\max} and J_{\max} also depend on temperature. Figure 9.9 illustrates these two components of photosynthesis using typical parameter values. At light levels less than about $165 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, photosynthesis is limited by RuBP regeneration (W_j). Higher light levels increase photosynthesis as a result of greater ATP and NADPH production. The initial rate of increase of $0.067 \mu\text{mol CO}_2$ per $\mu\text{mol photon}$ is known as the quantum efficiency. As light increases, photosynthesis becomes limited by rubisco (W_c).

General insights to leaf physiology are readily apparent from these equations. For example, under low irradiance stomatal conductance and transpiration should not be affected by changes in V_{\max} because photosynthesis is limited by the rate of electron transport in the light reactions. At high irradiance, when photosynthesis is limited by rubisco, changes in V_{\max} can alter stomatal conductance. Leaves growing in shaded environments achieve no photosynthetic gain by investing in the energetically expensive rubisco and thus have low V_{\max} . Sunlit leaves have high V_{\max} so as to maximize the rate of photosynthesis.

In addition, there is no need to have extra chlorophyll to trap light if the concentration of rubisco is low. Thus, leaves with low V_{\max} should also have low J_{\max} . Such a relationship has indeed been found in a study of 109 species of C_3 plants (Figure 9.10). These species differ greatly in their biochemical capacity to assimilate CO_2 . Estimates of V_{\max} range from a low of $6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ in trees to a high of $194 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ for some agricultural crops. Desert annuals and perennials have the highest V_{\max} . Monocotyledon crops such as wheat and rice and dicotyledon crops such as cotton, soybean, and tobacco also have high V_{\max} . Temperate needleleaf evergreen trees have the lowest V_{\max} . Values for J_{\max} have a

similar wide range, but there is a positive correlation between V_{\max} and J_{\max} . This reflects an optimal allocation of resources, especially nitrogen, to balance enzymatic (rubisco) and light-harvesting (chlorophyll) capabilities.

9.3 Leaf traits

The preceding discussions of stomatal conductance and photosynthesis suggest leaves have certain characteristics related to photosynthetic capacity. Indeed, numerous studies show a matching of leaf physiology and morphology to environment. In addition, principles of water use efficiency and heat and gas exchange result in an optimal leaf form for a given environment.

9.3.1 Leaf size and shape

The size and shape of leaves is an example of a compromise between leaf energy exchange, leaf temperature, and photosynthesis. Leaves growing in sunny environments are smaller and more deeply lobed than leaves growing in shaded environments. Leafy plants growing in the hot, arid environment of deserts or cold arctic and alpine environments have small leaves. In part, this is related to the influence of leaf dimension on leaf boundary layer resistance and the efficiency with which heat and moisture are transported away from a leaf. For a given wind speed, boundary layer resistance decreases with smaller leaf size or deeper lobes (Figure 7.7). These decrease the surface area of a leaf relative to its perimeter length, allowing for greater heat and moisture transfer. Small leaves provide a thin boundary layer and result in efficient heat transfer. Large leaves have a thick boundary layer and inefficient heat transfer.

Studies that combine the energy budget of a leaf with photosynthesis have determined the optimal leaf size for a given environment (Parkhurst and Loucks 1972; Givnish and Vermeij 1976; Woodward 1993a). Under the assumption that leaf size is determined so as to maximize water use efficiency, large leaves should occur in warm-to-hot climates with low light conditions, such as might be found in the understory of temperate and tropical forests (Parkhurst and Loucks 1972) (Figure 1.3). Small leaves are favored in sunny environments (e.g., the forest overstory) and in cold climates. Another study found large leaves are expected in the humid, shaded environment of the forest understory while small leaves occur in the sunny, dry conditions of the forest overstory (Givnish and Vermeij 1976) (Figure 1.3). In a sunny

environment, large leaf size increases transpiration so that large leaves are favored only in mesic conditions. Conversely, large leaves impede transpiration in a shaded environment; small leaves are favored with increasingly moist conditions.

The effects of energy exchange and stomata on leaf form can be seen in the fossil record. Early vascular plants were leafless or had short cylindrical leaves. Some 40 million years passed between the appearance of the first land plants and the origin of flat leaves that resemble those of modern plants. This may be related to the high atmospheric CO₂ concentrations that prevailed in early stages of terrestrial plant life (Beerling *et al.* 2001). In a CO₂-enriched atmosphere, early plants needed fewer stomata to absorb CO₂ for photosynthesis. However, broad flat leaves with a low density of stomata are prone to overheating. The appearance of broad leaves is associated with a 90% decline in atmospheric CO₂. Plants developed more stomata as atmospheric CO₂ declined, which allowed flat leaves to stay cool. Leaf form may also have led to the extinction of many plant species some 200 million years ago (McElwain *et al.* 1999). An increase in atmospheric CO₂ at this time warmed climate. The temperature of large leaves with entire margins (i.e., no lobes) reached lethal levels in this warm climate. Small or highly lobed leaves had lower temperatures and thus had an advantage over large leaves in warm climates. Indeed, the fossil record shows species with large entire leaves were replaced by species with smaller, more dissected leaves.

These studies suggest a strong relationship between leaf size and shape and environment. The close relationship between the size of leaves, their shape, and their edges (e.g., smooth, serrated, lobed) to temperature and precipitation is one means to reconstruct past climate from fossil leaves (Wolfe 1995; Wilf 1997, 2000; Wolfe *et al.* 1998; Wilf *et al.* 1998).

9.3.2 Coordinated leaf traits

Studies of C₃ plants growing in a wide variety of plant communities and environments and representing a diversity of life forms repeatedly show coordinated relationships among leaf traits such as maximum photosynthetic capacity, maintenance respiration, nitrogen concentration, leaf lifespan, and the ratio of leaf surface area to leaf mass (specific leaf area) (Field and Mooney 1986; Reich *et al.* 1992, 1995a, 1997, 1998a,b; Schulze *et al.* 1994). Central to this is the relationship between maximum photosynthetic capacity and leaf nitrogen content (Field and Mooney 1986; Peterson *et al.* 1999). Figure

9.11 illustrates this relationship for 22 broadleaf deciduous and 9 needleleaf evergreen temperate tree species. Needleleaf evergreen trees have a lower rate of photosynthesis for a similar range of leaf nitrogen than broadleaf deciduous trees. Moreover, the rate at which photosynthetic capacity increases in response to increased leaf nitrogen is less for needleleaf evergreen trees ($1.9 \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1} \text{ N}$) than for broadleaf deciduous trees ($6.4 \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1} \text{ N}$). The physiological basis for this relationship is the role of nitrogen in the enzymes and pigments necessary for photosynthesis.

Subsequent studies have shown that across a diversity of plant communities and environments species with short leaf lifespans generally have high maximum photosynthetic capacity, high leaf nitrogen, and high surface area to mass (thin leaves). For example, the long-lived needles of coniferous trees have a low surface area per unit mass (i.e., are thick) while broadleaf deciduous leaves are thin and have a high surface area per unit mass. Needleleaf evergreen trees have lower maximum photosynthetic capacity and specific leaf area than broadleaf deciduous trees for a common nitrogen content (Figure 9.11). Comparisons among additional plant functional groups show similar distinctions based on type of leaf (broadleaf, needleleaf) and leaf lifespan (deciduous, evergreen). In a study of 257 species, mean leaf traits differ among functional groups (Table 9.3). Forbs have the highest maximum photosynthetic capacity, leaf nitrogen, and specific leaf area. Woody species have lower values of these traits. Within woody species, additional distinction is based on leaf type (needleleaf, broadleaf) and longevity (deciduous or less than one year lifespan, evergreen or greater than one year lifespan). Evergreen species of shrubs, broadleaf trees, and needleleaf trees have lower maximum photosynthetic capacity, leaf nitrogen, and specific leaf area than corresponding deciduous species. The slope of the photosynthesis-nitrogen relationship (i.e., the photosynthetic capacity per unit mass of nitrogen) differs among functional groups. Forbs have the steepest slope; needleleaf evergreen trees have the shallowest slope. Among broadleaf shrubs and trees, short-lived deciduous leaves have a greater slope than long-lived evergreen leaves. Species with long lifespan and low specific leaf area, whether broadleaf or needleleaf, tend to have lower maximum photosynthetic rates per unit leaf nitrogen.

Leaf maintenance respiration is also related to photosynthetic capacity and leaf traits because a high photosynthetic capacity requires a large investment in enzymes and pigments, which have high maintenance respiration costs (Ryan 1991, 1995; Reich *et al.* 1998b). In a study of 69 species from four

functional groups (forbs, broadleaf shrubs, broadleaf trees, needleleaf trees) ranging from alpine tundra to desert to tropical rainforest, leaf respiration rates at 25 °C increase with greater leaf nitrogen and specific leaf area and decrease with increased leaf longevity (Figure 9.12). Respiration and leaf traits differ among functional groups (Table 9.4). Forbs have the highest respiration rate. Needleleaf evergreen trees have the lowest respiration rate. Broadleaf shrubs and trees are intermediate in their traits. Different relationships among functional groups are associated with differences in specific leaf area and leaf lifespan. Functional groups with a high specific leaf area and short leaf lifespan have high respiration rates at any given leaf nitrogen.

Across a wide variety of plant communities, environments, and life forms, maximum photosynthetic capacity and leaf respiration increase with decreasing leaf lifespan, increasing leaf nitrogen, and increasing specific leaf area. Specific leaf area represents the photosynthesizing leaf area produced per unit leaf mass. Species with short-lived leaves generally have high specific leaf area (i.e., low carbon investment per unit leaf area), high leaf nitrogen, high photosynthetic capacity, high maintenance respiration, and high photosynthetic capacity per unit leaf nitrogen. These functional patterns of variation among leaf structure, longevity, nutrition, and metabolism represent co dependent leaf traits that are a tradeoff between high metabolism and persistence. Plants apparently have two types of foliage: thin leaves with high photosynthetic rates and low carbon cost to produce but which are short lived; or thick foliage with low photosynthetic capacity and high carbon cost but which persists for a long time.

9.4 Carbon balance of plants

The carbon balance of a plant is the difference between CO₂ uptake during photosynthesis and CO₂ loss during respiration (Figure 9.13). The photosynthetic uptake of an individual leaf must be summed over all the leaves on a plant, accounting for variations in light, temperature, humidity, foliage nitrogen, and all the other factors controlling photosynthesis. Respiration loss must be summed over all the tissues in a plant.

9.4.1 Canopy photosynthesis

Plant canopies have a vertical gradient of sunlight related to the amount of leaves. The sunlight striking an individual leaf is absorbed, reflected, or transmitted through the leaf (Table 8.2). As the canopy becomes denser with leaves, more solar radiation is absorbed or reflected and less is transmitted deeper into the canopy. With less light, photosynthesis decreases. Figure 9.14 illustrates this for two types of crop plants. Stomatal conductance varies little with height early in the morning when low light levels limit the rate of photosynthesis. Later in the day, stomatal conductance is greater at the top of the canopy than deeper in the canopy where leaves are shaded. The total carbon uptake during photosynthesis requires integration of leaf photosynthesis over the light profile.

The amount of foliage in the canopy is measured by the leaf area index. Leaf area index is the projected area of leaves per unit area of ground. Projected, or one-sided, leaf area is different from total leaf area (Waring and Running 1998, p. 29). For broadleaf trees, total leaf area is twice the projected leaf area (both sides of the leaf are included). For needleleaf trees, total leaf area is typically 2.5 times projected leaf area. A leaf area index of two means there are two square meters of leaf area (one-sided) covering one square meter of ground. A simple model of radiative transfer shows that solar radiation decreases as an exponential function of leaf area index

$$I(z) = I_0 e^{-KL(z)}$$

where I_0 is the solar radiation at the top of the canopy, K is the light extinction coefficient, $L(z)$ is the cumulative leaf area index at height z , and $I(z)$ is the irradiance at height z . The extinction coefficient depends on species, canopy density, and solar zenith angle. The angle at which the solar beam strikes a leaf is particularly important. Greatest radiation per unit surface area is received when the radiation is perpendicular to a surface. At oblique angles, less radiation impinges on a surface. The angle at which solar radiation strikes a leaf depends on solar zenith angle. It also depends on leaf orientation. Some leaves are oriented horizontally while others are vertical. Many leaves are oriented randomly so that there is an equal probability of orientation in any direction. Despite these complexities, a typical value is $K = 0.5$.

Figure 9.15 shows typical vertical profiles of leaves and light within forest canopies. The oak forest has a single overstory between 6.5 m and 3 m. Solar radiation decreases rapidly in the canopy. At a

height of 5.8 m (70 cm into the canopy), the cumulative leaf area index is $1.4 \text{ m}^2 \text{ m}^{-2}$ and irradiance is only 50% of full sunlight. The total leaf area index is $4.6 \text{ m}^2 \text{ m}^{-2}$, so that the forest floor receives only about 10% of full sunlight. The aspen forest has a leaf area index of $7.1 \text{ m}^2 \text{ m}^{-2}$. Leaves are found in both an overstory between 10.5 m and 5.5 m and an understory. Most of the foliage is in the overstory. The understory has a leaf area index of $2.2 \text{ m}^2 \text{ m}^{-2}$. This layer of plants receives only 8.5% of full sunlight. In contrast, leaves above 8.4 m in height receive more than 50% of full sunlight.

The exponential attenuation of light within a canopy represents the average irradiance at any height. This irradiance is the average of two types of leaves: sunlit leaves receiving unattenuated light and shaded leaves receiving only scattered (diffuse) light. One method, then, to integrate photosynthesis over the canopy is to consider the fraction of the canopy that is sunlit and shaded. For a given leaf area index L ($\text{m}^2 \text{ m}^{-2}$), the sunlit leaf area is given by

$$L_{sun} = (1 - e^{-KL}) / K$$

where K is the light extinction coefficient (Sellers 1985; Jones 1992; Campbell and Norman 1998). When the canopy is very dense, only a small portion is sunlit (Figure 9.16). Most of the canopy is shaded and receives only scattered radiation. When the Sun is high in the sky (30° zenith angle), horizontal leaves attenuate the most radiation and have the lowest sunlit leaf area. Vertically oriented leaves have the lowest extinction coefficient and have a greater sunlit leaf area. Maximum sunlit leaf area is only $1 \text{ m}^2 \text{ m}^{-2}$ for horizontal leaves and $1.7 \text{ m}^2 \text{ m}^{-2}$ for randomly oriented leaves. When the Sun is lower in the sky (60° zenith angle), much less of the canopy is sunlit. Maximum sunlit leaf area index is less than $1 \text{ m}^2 \text{ m}^{-2}$ for all leaf orientations.

Leaves growing in shade generally have lower photosynthetic capacities and maximum stomatal conductances than leaves growing in sun. This is a result of different investments in chlorophyll and rubisco. These investments require much nitrogen and are energetically expensive to maintain. Plants that invest too much in photosynthetic capacity will be at a competitive disadvantage if this machinery is underutilized, such as occurs in a shaded understory. Plants that match photosynthetic capacity to local resource availability have an advantage. Based on this reasoning, the vertical profile of leaf nitrogen and photosynthetic capacity through the canopy should be related to the light profile. This concept provides

another means, similar to sunlit and shaded leaves, to integrate photosynthesis and stomatal conductance for a canopy (Sellers *et al.* 1992).

Data collected in the boreal forests of Canada illustrate how light, foliage nitrogen, and photosynthetic capacity within tree canopies are interrelated (Figure 9.17). In jack pine, black spruce, and aspen forests, photosynthetically active radiation decreases exponentially with greater depth from the top of the canopy. Foliage nitrogen decreases with decreasing photosynthetically active radiation. Maximum photosynthetic rates under light-saturated conditions increase with greater foliage nitrogen. Jack pine and black spruce trees differ little in this relationship; aspen trees have a higher photosynthetic capacity for a given nitrogen concentration. These data show that foliage high in the canopy receives more radiation, has greater nitrogen concentration, and has greater photosynthetic capacity than foliage lower in the canopy. Indeed, throughout the canopy there is a linear relationship between the photosynthetic capacity at a given height and the corresponding nitrogen content at the same height, both expressed relative to that at the top of the canopy. Relative photosynthetic capacity decreases exponentially with decreasing photosynthetically active radiation. These relationships between light, foliage nitrogen, and photosynthetic capacity can be used to integrate photosynthetic capacity through the canopy based on the vertical light profile. Similar relationships have been found in other plant communities such as tall grass prairie (Schimel *et al.* 1991).

9.4.2 Whole plant carbon balance

The carbon balance of a plant is the difference between carbon uptake during photosynthesis and carbon loss during respiration (Figure 9.13). Plant respiration is divided into growth respiration, which is independent of temperature, and maintenance respiration, which increases with warmer temperatures (Ryan 1991). Growth respiration is the CO₂ released during the synthesis of new tissues from glucose and minerals. This synthesis involves the incorporation of carbon into organic compounds and the expenditure of metabolic energy to produce the compound. Growth respiration is typically about 25% of photosynthesis. Maintenance respiration is the CO₂ released during the carbohydrate breakdown that provides the energy needed to maintain living cells. Such processes include protein synthesis and replacement, membrane repair, and the maintenance of ionic gradients. Maintenance respiration is an exponential function of temperature and varies with the biochemical composition of organic material.

Foliage and roots have higher respiration rates for the same temperature than woody material (Figure 9.18). The combined whole-plant respiration is typically about 50% of gross photosynthesis (Ryan 1991).

The carbon balance of a plant varies over the course of a year due to seasonal changes in photosynthesis and respiration. This is most obvious in woody plants growing in regions with a distinct growing season (Figure 9.19). In winter, the daily carbon balance is usually negative; there is little or no photosynthetic uptake, but carbon is lost during maintenance respiration. Net carbon uptake, after accounting for respiration losses, occurs during the growing season when photosynthetic uptake exceeds respiration loss. The annual carbon balance—the net production over the course of the year—is obtained by subtracting the wintertime loss from the growing season gain.

9.4.3 Phenology

Phenology is the study of the onset and duration of the different phases of a plant's development during the year. Temperature, moisture, and daylength control the timing of these phases. Temperature is especially important. The rate of chemical reactions increases with warmer temperatures, and nearly all physiological processes involved in plant growth are controlled by temperature. The opening of buds, the growth of leaves, shoots and roots, the onset of flowering, seed ripening, and seed germination are all initiated by specific temperature regimes. These temperature requirements are typically measured in terms of growing degree-days, which is the accumulated daily temperature above some threshold, typically about 5 °C. Measures such as growing degree-days incorporate the accumulated effect of temperature on growth and development. Many developmental processes also have a chilling requirement in which temperatures have to be below some threshold value for a certain period of time before the process can be initiated. This is especially true for budbreak and seed germination, where exposure to low temperatures over several weeks or months is needed to break dormancy. Chilling requirements are expressed as the accumulated daily temperature below some threshold.

The importance of temperature in determining the timing of developmental processes is demonstrated by comparing the phenology of plants growing on different slopes or elevations in mountains. For example, in Austrian mountains with a prominent mid-slope thermal belt, the growing season for beech and maple trees is longest at 800 m elevation, where nighttime temperatures are warmest

(Figure 8.13). For beech, the growing season at the valley bottom is 25 days shorter than at mid-slope. The flowering of spring wildflowers illustrates the stark influence of aspect on temperature and phenology (Figure 9.20). On steep slopes of 100% (45°), the average flowering date is six days earlier on a south-facing slope than the opposing north-facing slope despite being separated by a distance of only 46 m. This difference is related to microclimates. The south-facing slope receives more radiation and is warmer than the north slope. On both slopes, flowering is triggered when the accumulated degree-hours is about 4650 °C-hours, which occurs six days earlier on the south slope than on the north slope.

Length of day is also critical to many developmental processes, triggering the onset of flowering, leaf fall, and winter dormancy in many herbaceous plants, shrubs, and trees. In middle to high latitudes, the length of day varies greatly over the course of a year (Figure 2.19). At latitude 40 °N, the minimum daylength is 9 hours in December; the maximum daylength is 15 hours in June. Further north, the seasonality of daylength is even more pronounced. Photoperiod, the relative duration of light and dark periods during the day, controls the timing of many physiological processes. For example, long-day plants flower in response to days longer than some maximum length; short-day plants flower when days are shorter than some maximum.

To grow in regions with seasonally freezing temperatures, plants must acclimate to the cold or else be subjected to frost and chilling damage. Winter temperatures below -40 °C occur regularly in tundra, boreal forest, and alpine landscapes. In the cold of winter, when temperatures are well below freezing, water in a plant can freeze, destroying plant cells. Woody plants tolerate cold by becoming seasonally dormant. Frost hardy or dormant plants can successfully endure temperatures well below freezing that would severely damage them while actively growing. Short days and exposure to low temperatures initiate dormancy and the development of frost hardiness. Lack of water also promotes dormancy.

In temperate and boreal forests, the most obvious phenology is the seasonal greening and senescence of deciduous trees during the growing season. In spring, as temperatures warm and days become longer, buds break and new leaves emerge. In autumn, short days, long nights, and cool temperatures trigger leaf senescence that prepares deciduous trees for winter dormancy. This seasonal

pattern of growth produces alternating cycles of growth and inactivity and corresponding periods of carbon utilization and storage. In deciduous trees, the carbohydrates stored in the woody tissues and bark of branches, trunks, and roots are used in spring to provide the carbon for emerging leaves (Larcher 1995, p. 147; McLaughlin *et al.* 1980). These reserves are replenished during the growing season, and the surplus photosynthate is stored in branches, trunks, and roots at the end of the growing season. Needleleaf evergreen trees have less pronounced seasonal fluctuations in carbon reserves than deciduous trees. Foliage persists on these trees for several years. If weather is favorable, needleleaf evergreen trees photosynthesize throughout late autumn, winter, and early spring. The existing foliage can supply much of the carbon needed to support new foliage and shoot growth when buds break in spring or early summer. Additional carbon requirements are supplied from reserves held in woody tissues.

The advent of satellite technology has allowed study of leaf phenology at large spatial scales. The Normalized Difference Vegetation Index (NDVI) is a satellite-derived index that is related to leaf biomass and plant productivity. The Sun's radiation is broadly divided into two wavebands: the visible waveband at wavelengths less than 0.7 μm and the near-infrared waveband at wavelengths greater than 0.7 μm . Plants utilize light in these two wavebands differently (Table 8.2). Green leaves typically absorb more than 85% of the solar radiation in the visible waveband that strikes the leaf. This light is used during photosynthesis. Light in the near-infrared waveband is not utilized during photosynthesis and rather than absorbing this radiation, and thus possibly overheating, leaves typically absorb less than 50% of the radiation in the near-infrared waveband. In contrast, other surfaces, especially soil, have smaller spectral differences in solar absorption. The NDVI, with values ranging from -1 to +1, is a measure of the normalized difference in reflection of solar radiation in these two wavebands

$$\text{NDVI} = (r_{\text{nir}} - r_{\text{red}}) / (r_{\text{nir}} + r_{\text{red}})$$

where r_{nir} and r_{red} are reflectances in the near infrared and red wavebands, respectively. Typical values for snow, lakes, and soil range from -0.2 to +0.05. Vegetated surfaces have values ranging from +0.05 to +0.70, with higher values indicating more productive vegetation. The NDVI is related to canopy photosynthetic capacity (Figure 9.17). It has been used to map land cover and productivity, document changes in the length of growing season, and study the response of terrestrial ecosystems to climate variability (Tucker *et al.* 1985, 1986, 1991; Myneni *et al.* 1995, 1997; Braswell *et al.* 1997).

Figure 9.21 and Figure 9.22 (color plates) show seasonal changes in the NDVI, illustrating the timing of leaf emergence, peak leaf area and production, and leaf senescence and dormancy. Low values indicate few leaves and low productivity; high values indicate a dense canopy and high productivity. Arid regions show little greening throughout the year. Tropical rainforests are productive year-round. Elsewhere, there are two distinct patterns to phenology represented by summergreen and raingreen plants (Foley *et al.* 1996; Kaduk and Heimann 1996; White *et al.* 1997; Botta *et al.* 2000; Kucharik *et al.* 2000). Winter deciduous plants in temperate and high latitudes drop leaves with the onset of cold temperature. In spring, as temperature warms and the days become longer, buds on these summergreen plants break open, new foliage emerges, and plants begin to photosynthesize. Peak production typically occurs in July and August, decreasing in autumn as plants again become dormant. In tropical and subtropical latitudes, drought-deciduous plants lose leaves seasonally in relation to low precipitation and drought stress. Leaves emerge on these raingreen plants in response to adequate precipitation.

9.5 Allocation

Plants use the carbon absorbed by leaves during photosynthesis to maintain cellular structures and grow new tissues. Maintenance of existing tissues requires an expenditure of carbon during respiration, which reduces the carbon available for new growth. The net carbon available to a plant, along with the nutrients required for new growth, is then allocated to the growth of leaves, roots, stems, flowers, and seeds and the production of chemicals for protection from insects and herbivores. Collectively, the partitioning of resources to plant parts and functions is known as allocation (Cannell and Dewar 1994; Bazzaz 1996; Barbour *et al.* 1999).

Allocation of available resources is a critical determinant of plant growth and success. For example, high allocation to foliage ensures more leaves to capture light and absorb CO₂ for new growth. However, allocation to foliage is inefficient if there is not enough water or nutrients to support the foliage. Moreover, there usually is a limited amount of resources to spend on growth, maintenance, and reproduction, and allocation to one function is typically at the expense of another function. Hence, plants must allocate resources in a way that balances conflicting needs. Variations among plants in growth rates

are determined as much by differences in allocation and how plants balance resource limitations as by different photosynthetic rates.

9.5.1 Reproduction

Allocation of resources to reproduction illustrates compromises and tradeoffs (Harper 1977; Bazzaz 1996, 1997). Copious seed production increases the probability of descendants in future generations. Dispersal of a heavy blanket of seeds over a wide area ensures that at least some seeds are likely to fall on sites suitable for germination and establishment. However, high seed yield and high growth are not always compatible. Greater reproductive output diverts resources from vegetative growth (Figure 9.23). For example, Douglas fir trees have low stem growth during years of high seed production. The growth of new shoots on California buckeye, a drought-deciduous tree native to California, is dramatically impaired by reproduction. Branches bearing fruit in one year produce 75% smaller new shoots with 79% less leaf area the following year compared with non-flowering branches.

The number and size of seeds represent a compromise between dispersal and food reserves for germination (Grime and Jeffrey 1965; Leishman and Westoby 1994; Saverimuttu and Westoby 1996; Walters and Reich 2000). The size of seeds varies from less than 10^{-6} g for the dust-like seeds of orchids to over 10^4 g for large coconuts (Harper 1977, p. 665). Tree seeds range in size from 10^{-4} g for light, wind-dispersed birch seeds to 0.1-10 g for the large nuts of beech, oak, and chestnut trees. This wide range in seed size represents the outcome of reproductive tradeoffs. Seeds must contain sufficient carbohydrates and nutrients to give embryos support during germination but must be dispersed from the parent and produced in sufficient quantities to ensure a high probability of survival. Seed number and seed size are alternatives in reproductive strategy so that the more seeds produced the smaller their size. Small seeds carry few carbohydrates to support initial growth. The seedling must depend on its own photosynthate at an early stage. However, small seeds can be dispersed in large quantities and spread over large regions by wind, ensuring that some of the seeds fall in a favorable site for germination. In contrast, large, heavy seeds have enough initial reserves to continue growth for extended periods of time and survive in environments with low resource availability. For example, a study of seedling development in nine tree species growing in shade found that seedling height after 12 weeks increased with seed weight while the number of seedlings

that died decreased (Figure 9.24). However, large seeds have a cost. They are produced in less quantity than small seeds, are not as widely dispersed, and because they are highly nutritious are likely to be eaten by wildlife.

9.5.2 Aboveground and belowground growth

The acquisition of resources for growth presents another set of tradeoffs in plants. Foliage is needed to absorb light and CO₂ and construct carbohydrates during photosynthesis. More foliage allows for more light and CO₂ acquisition and, all other factors being equal, more carbon gain. Stems are needed to support this foliage. Trees in particular need large woody trunks and branches to provide mechanical support for their extensive foliage and to store and transport water, nutrients, and carbohydrates. Growth requires water and nutrients, and roots are needed to acquire these resources from soil. Greater investment in aboveground foliage and stem growth comes at the expense of belowground root growth. Conversely, greater allocation to root growth allows for increased acquisition of belowground resources but at the expense of aboveground growth. Hence, resource acquisition is a compromise between aboveground foliage and shoot growth to harvest light and absorb CO₂ and belowground root growth to obtain water and nutrients.

Natural environments are seldom optimal for plant growth. Tall plants shade short neighbors. Soils may be dry or deficient in nutrients. The allocation of resources to build and maintain above- and belowground biomass is not proportioned in fixed ratios. When stressed by lack of light, water, or nutrients, plants change their pattern of resource allocation. Allocation is an integration of plant responses to multiple stresses imposed by nutrient, water, and light availability. One theory of carbon allocation holds that plants adjust their allocation so that all resources equally limit growth (Bloom *et al.* 1985; Chapin 1991; Gleeson and Tilman 1992). Indeed, plants usually respond to altered resource availability by allocating new biomass to the components that acquire the most limiting resource so that resource imbalances are minimized (Table 9.5). Plants in resource-rich environments, where nutrients and water are not limiting, grow best by allocating carbon to leaves. More foliage allows for greater light capture and photosynthesis. Deficiencies in belowground resources such as water and nitrogen result in increased allocation to roots and reduced allocation to foliage. A nitrogen surplus or sufficient water allows for

greater leaf production and reduced need for roots. Hence, irrigation and fertilization can increase foliage growth in forests where these are limiting (Figure 10.15). Cold temperatures favor increased root production because low temperatures reduce the ability of roots to absorb water and nutrients.

9.6 Life history patterns

The optimal allocation of limited resources to growth, maintenance, and reproduction is part of an overall interrelated suite of attributes that have evolved over time through natural selection. These functions and their necessary plant parts all interact to determine fitness – the relative number of descendants in future generations. Natural selection selectively favors those individuals that contribute the most offspring to subsequent generations. However, allocation of carbon and nutrients among the various plant parts usually involves compromises. Different structures are alternatives, and gain in fitness from one may be offset by loss in another. For example, greater allocation to reproduction does not necessarily increase fitness. Less carbon is available for vegetative growth. The plant may not be able to successfully compete with neighbors. Conversely, a plant can increase its fitness by reducing its reproductive effort and investing more in increased growth. Light, water, and nutrients are usurped from neighbors, ensuring the plant survives and leaves descendants.

Natural selection acts to maximize individual fitness by optimizing the form of these compromises, creating a balanced system of resource allocation to plant parts (Bloom *et al.* 1985; Tilman 1988; Chapin 1991; Bazzaz 1996, 1997; Grace 1997). Resources are allocated in a way that maximizes fitness. The allocation of photosynthetic capacity in relation to light profiles and coordinated leaf traits are but two examples of this balance of tradeoffs. More generally, the optimal allocation of resources is reflected in the morphology and life histories of plants, and the outcome of optimal resource allocation is not one specific pattern of allocation, morphology, and life strategy (Harper 1977; Grime 1979; Tilman 1988). Rather, light, water, and nutrients vary spatially and temporally. There are numerous alternative patterns of allocation that allow plants to successfully grow, survive, and reproduce in specific environments. Allocation must be flexible to allow for different patterns in different environments, but is constrained by the overall life history of a species.

A life history is an overall pattern of growth, reproduction, and longevity. A successful life history allows a species to persist through evolutionary time. A successful strategy may be to remain small and allocate resources to a single episode of copious seed dispersal. Plants that reproduce once and then die are called monocarpic or semelparous. They invest a large reproductive effort into a single flowering episode at the expense of future vegetative growth. An equally successful strategy may be to grow slowly, be long lived, and have repeated reproduction during a life cycle, which may extend from several years for herbaceous plants to hundreds of years for trees. Such plants are termed polycarpic or iteroparous.

Life histories are closely matched to environment; the environment determines which life histories are successful. Frequent, recurring disturbances that expose soil for revegetation favors plants that allocate resources to seed production and widespread dispersal. Indeed, monocarpic plants are favored in ephemeral environments with relatively low juvenile mortality and high adult mortality. However, this is a risky strategy when the environment is uncertain. A cold or dry year could destroy an entire cohort of plants, removing their descendants from future generations. In contrast, polycarpic plants are favored where juvenile mortality is high, adult mortality is low, and in uncertain environments so that the risk of a bad year is spread out over several years of reproduction.

9.6.1 Annuals and perennials

The distinction between annual and perennial is one example of alternative morphologies and life histories based on longevity and age of first reproduction. Annual plants complete their life cycle in one year or less, germinating, growing, flowering, and setting seeds in a relatively short period of time. Initially, they allocate resources to foliage and stems. Roots are needed to supply the necessary water and nutrients for growth. Later, as the plant matures, resources are allocated to a single bout of copious seed production and dispersal before they die. *Senecio vulgaris* illustrates the ephemeral life strategy typical of herbaceous annuals (Figure 9.25, top). A period of vegetative growth is followed by seed production culminating in death. Three distinct growth phases are evident. The first phase of growth is marked by development of roots and a leafy rosette. During the second phase, stems grow longer and flowers emerge. The end of this phase is marked by little vegetative growth, peak flower development, and the opening of the first seed heads. In the final stage, seeds mature and leaves and roots begin to die.

Perennial plants take a longer-term allocation strategy, as illustrated by goldenrod (Figure 9.25, bottom). Foliage and stems are maintained throughout the growing season. Moreover, perennials must allocate resources to perennial parts (e.g., buds) and storage (e.g., roots). Consequently, they produce fewer seeds than annuals. But in the subsequent growing season, while annuals start anew from seed, perennials begin growth with an established root system and carbon and nutrient stores. These stores allow more rapid initial growth than plants growing from seeds. This gives perennials an early-season height advantage, whereby they can capture light and shade neighbors.

There are several types of perennials distinguished by differences in position of buds on the plant. Herbaceous perennials have buds at or below the surface. Woody shrubs have buds aboveground on stems and branches. Buds on trees are even higher above ground. The height of buds above ground conveys an advantage to light acquisition. High buds on established shrubs and trees ensure leaves are likely to emerge above neighboring herbaceous plants, depriving them of light. The position of buds is also related to climate (Raunkiaer 1934). Buds close to the ground are sheltered from cold and high winds and are favored in harsh alpine and arctic climates. Buds high in the air are exposed to extremes in temperature, humidity, and wind.

9.6.2 Trees

Trees manage carbon in a way suited to their morphology and long lifespan. Young trees allocate much of their carbon to foliage to acquire carbon and to roots to acquire water and nutrients. As trees grow larger, however, much of their biomass is woody stems and branches; relatively little biomass is foliage (Figure 9.26). The height of trees gives them a competitive advantage over smaller plants; their leaves shade the understory. But the cost is large amounts of carbon expended in the production and maintenance of trunks and branches for mechanical support and other tissues to transport water and nutrients.

Allocation in trees is modulated by allometric constraints that maintain certain dimensional relationships between diameter and foliage, branch, and stem biomass (Figure 9.26). In particular, the structure and anatomy of trees is constrained by the need to transport water to leaves to replace that lost during transpiration and the need to provide mechanical support to foliage. Water flows through specialized structures within wood. However, not all of the woody material in trees conducts water. Large

trees have an interior core of heartwood that provides structural support but which does not conduct water. Only the outer ring of sapwood provides the material to transport water. In angiosperms, vessels are stacked end-to-end in the xylem to form a continuous tube through wood. In gymnosperms, vertically stacked, overlapping tracheids form a pathway for water flow through xylem. Because of its role in water transport, the cross-sectional area of sapwood in a tree is closely related to the amount of foliage (Waring *et al.* 1982). Large leaf area requires a corresponding large area of sapwood to transport water to leaves (Figure 9.27). Hence, there is a functional interdependence between foliage, which fixes carbon and transpires water, and support structures to supply water and nutrients to leaves.

Species that grow in harsh environments support less leaf area for a given sapwood cross-sectional area compared with trees growing in more favorable climates (Table 9.6). For example, Sitka spruce and Douglas fir, which grow in moderate or maritime climates along the Oregon coast, support two to six times as much leaf area for the same sapwood area as do mountain hemlock, ponderosa pine, and western juniper, which grow in harsher inland climates. A study of leaf area and sapwood area in Scots pine growing on a cool, wet site and a warm, dry site illustrates the effect of site conditions on allocation (Figure 9.27). The trees on both sites were grown from the same seed source, minimizing genetic variation between sites, and the stands were of similar age, density, and fertility. The trees growing on the warm, dry site had less leaf area per unit sapwood area compared with the trees on the cool, wet site. Moisture limitation on the warm, dry site allowed for less leaf area per unit sapwood area.

The relationship between sapwood area and leaf area arises because foliage must be supported by a certain area of water-transporting sapwood. If sapwood area falls below the required amount, water transport is limited and foliage suffers water shortage. If there is too much sapwood, resources are allocated to non-essential tissue. This suggests a relationship between climate, soil water-holding capacity, and maximum leaf area index (Grier and Running 1977; Nemani and Running 1989; Woodward 1987a, 1993a). Too much leaf area results in drought as evapotranspiration exceeds precipitation. Too little leaf area results in surplus soil water. Instead, there is an equilibrium between soil water, evapotranspiration, and leaf area whereby trees support a maximum leaf area for which evapotranspiration balances precipitation.

The hydraulics of water movement in trees also affects their height. Height conveys a competitive advantage to tall trees. With increased height relative to neighbors comes greater utilization of light for photosynthesis. But the resource advantage of greater height is tempered by the need to move water from roots to the upper most leaves to replenish water lost in transpiration. Transpiration provides the force that pulls water from soil through roots up the trunk and out of the leaves. The water column from roots to leaves is connected and under tension. Cohesion between water molecules binds them together so that the pull on water exerted at the top of the tree by transpiration extends all the way down the trunk through the roots into the soil. The driving force is the gradient of decreasing (more negative) water potential from soil through the tree to the atmosphere (Figure 5.9). Leaf water potentials (-1 MPa) are typically 10 to 100 times that of moist soil (-0.01 MPa) or roots (-0.1 MPa).

Hydraulic resistance to water flow increases as a tree grows taller and water must travel a longer path. This increased hydraulic resistance likely provides a physical limit to tree height (Friend 1993; Ryan and Yoder 1997). The rate of water transport from roots to leaves is related to the difference in water potential between leaves and roots divided by the hydraulic resistance. A higher tension (more negative water potential) is required to move the same amount of water through a tree with higher resistance. At high tension, air bubbles can form in the water column. These air bubbles interrupt the continuous column of water, hindering replenishment of water in the leaves and inducing stress. The increase in hydraulic resistance with greater height increases water stress in the leaves, closing stomata and reducing carbon gain during photosynthesis.

The large investment in maintenance and support costs of trees requires compromises between growth, maintenance, and reproduction. Among broadleaf deciduous species, the typical age of maturity increases with longevity (Figure 9.28). This suggests a high early investment in growth and support at the expense of reproduction. Growth rates also decline with increased age of longevity. Slow-growing broadleaf deciduous species are nearly three times as long lived as fast-growing species (190 years versus 68 years, on average). This suggests that long-lived trees invest more in maintenance than growth. Similar patterns have been found for needleleaf evergreen trees.

9.6.3 Disturbance and competition

The roles of recurring disturbances and competition for resources (light, water, nutrients) have dominated much of the discussion of life histories among plants. Recurring disturbances such as fires or windthrows create an open environment where new plants are unlikely to be shaded by neighbors. Success favors those species whose seeds fall in such sites, germinate and become established in high light environments, and grow rapidly to dominate the canopy. At the other extreme, closed canopy forests, with little sunlight on the forest floor, favor species that can tolerate shade, grow slowly in the low light of the understory, and wait for a large tree to die and create a gap in the canopy.

This distinction between disturbance and competition is embodied in the classic notion of *r*- and *K*-selected life histories (MacArthur and Wilson 1967; Gadgil and Solbrig 1972). Species that are *r*-selected maintain their abundance in the landscape through high seed production and widespread dispersal. They are short lived, with relatively little allocation to growth and large allocation to reproduction. They have numerous small seeds dispersed over large areas. They are favored in temporally varying environments where recurring disturbance creates potential for rapid colonization of open sites. In contrast, *K*-selected species maintain their abundance at or near the maximum limit for an environment. They are typically long lived and slow growing, allocating a greater proportion of resources to growth and maintenance. This allows them to survive in the intense competition for resources in high-density environments, but provides less energy for reproduction. Their seeds tend to be few and large to provide sufficient resources to germinate and become established in the low light environment of a dense canopy. While the concept of *r*- and *K*-selected species has dominated much of the study of life history patterns, these better represent the endpoints of a continuum of life histories rather than a stark dichotomy. Most plants fall in between these two extremes.

An alternative classification of life history strategies recognizes the importance of resource stressed environments in shaping life histories in addition to competition and disturbance (Figure 9.29). Ruderal plants live in temporary or frequently disturbed environments. They are opportunistic species adapted to disturbance. They are short lived, grow rapidly, and have a large reproductive effort at an early age. Competitor plants live in crowded environments where disturbance is infrequent, stress is low, and competition for resources favors species that compete well with others for limited resources. These plants

utilize resources more efficiently than others, allocate available resources to growth, and are typically long lived, mature later, and have a small reproductive effort. Stress tolerators live in environments with limited resources where plants are physiologically stressed due to lack of water, cold temperatures, low nutrient availability, or low light. These plants persist under conditions of severe resource limitation by growing slowly and allocating resources to maintenance.

The responses of plants to disturbance, competition, and stress produce a variety of life histories intermediate to these three extremes (Figure 9.29). Competitive ruderals are adapted to environments in which stress is low and competition is limited to moderate intensity by recurring disturbances. Stress tolerant competitors are adapted to relatively undisturbed environments with moderate stress. Stress tolerant ruderals are adapted to moderately disturbed, unproductive environments. A final type of plant, C-S-R strategists, is adapted to environments where the level of competition is restricted by moderate stress and recurring disturbances of moderate intensity. Major life forms segregate along these axes of disturbance, competition, and stress. Trees and shrubs are found in environments characterized by low to moderate intensity of disturbance and tolerate a wide range of stress and competition. Annual herbs are characterized by moderate to high intensity of disturbance, low intensity of competition, and low stress. Only perennial herbs and ferns are undifferentiated with respect to disturbance, competition, and stress.

Another useful distinction is between early and late successional species, which differ greatly in their physiology and photosynthetic response to light (Table 9.7). Early successional species are ones that colonize recently disturbed environments. They are exposed to full sunlight and to extremes in humidity, temperature, and wind. In contrast, seedlings of late successional species germinate under a forest canopy and are exposed to less sunlight and less variable microclimates. Seeds of early successional plants require light for germination and can lie dormant for many years in soil, waiting for a disturbance that opens the canopy. Seeds of late successional plants do not require full sunlight for germination and lose viability rapidly. Early successional plants are shade intolerant. They have high rates of photosynthesis at high light intensity and low rates at low light. Light saturation occurs at high light intensity. Late successional plants are shade tolerant and are photosynthetically more efficient at low light intensities than early successional plants. Shade tolerance not only influences leaf physiology, but also is related to longevity. For example,

the typical longevity of shade intolerant species of broadleaf deciduous trees averages 147 years while that of shade tolerant species averages 191 years (Figure 9.28).

9.6.4 Plant functional types

The classification of species into *r*- and *K*-selected plants (MacArthur and Wilson 1967; Gadgil and Solbrig 1972), ruderal, competitor, and stress tolerator plants (Grime 1979), or early and late successional plants (Bazzaz 1979, 1996; Huston and Smith 1987) represent broad classes of plant functional types that reduce the complexity of species diversity in ecological function to a few plant types. Plant functional types are defined by key physiological and life history characteristics that determine vegetation dynamics and response to changing environment (Körner 1993a; T. Smith *et al.* 1993, 1997; Woodward and Cramer 1996). The combination of physiological and morphological traits along with climatic preferences is one basis to define functional types. The distinction between annual or perennial, evergreen or deciduous, and broadleaf or needleleaf is particularly useful because these characteristics are observable from remote sensing and are key ecological properties determining stomatal conductance, photosynthesis, and carbon allocation. Such a classification results in six plant functional types (needleleaf and broadleaf evergreen perennial, needleleaf and broadleaf deciduous perennial, broadleaf annual, grass) based on permanence of aboveground biomass, leaf longevity, and leaf type (Running *et al.* 1995). Simple climate rules can then define thermal- and moisture-related varieties (Nemani and Running 1996; Bonan *et al.* 2001).

Figure 9.30 shows the geographic distribution by latitude of needleleaf, broadleaf, evergreen, and deciduous trees. Needleleaf evergreen trees are most abundant in the boreal forests of Canada, northern Europe, and Russia. They also occur in the montane forests of western United States and to a lesser extent in temperate forests of eastern United States, Europe, and China. Broadleaf evergreen trees dominate tropical forests along the equator. Needleleaf deciduous trees are mostly restricted to the boreal forests of east Siberia, where extreme winter temperatures and desiccation favor a deciduous habit (Gower and Richards 1990). Broadleaf deciduous trees are common throughout temperate forests, savannas, and tropical seasonal forests, where they lose their leaves in response to seasonal cold or drought. The distribution of needleleaf, broadleaf, evergreen, and deciduous trees is related to climate. In particular, the

ability of a species to survive cold winter temperatures greatly influences its biogeography (Woodward 1987a). Chill-sensitive plants are killed by minimum temperatures of 0-10 °C. These are typically broadleaf evergreen. Other broadleaf evergreen trees can tolerate minimum temperatures of –15 °C. Below this threshold, the vegetation is typically broadleaf but winter deciduous. These species are able to tolerate temperatures as low as –40 °C. Needleleaf vegetation, both evergreen and deciduous, can tolerate even colder temperatures.

The distinction between evergreen and deciduous, and more generally the variation among trees in leaf longevity, represents an integrated plant response to environment (Chabot and Hicks 1982; Mooney and Gulmon 1982; Kikuzawa 1991; Reich *et al.* 1995b). Photosynthetic capacity, foliage nitrogen concentration, and specific leaf area decrease with increasing leaf longevity. Evergreen trees have low photosynthetic capacity, low nitrogen concentration in foliage, and low leaf area per unit leaf mass. Their leaves have a high initial carbon cost to construct per unit photosynthesizing leaf area. However, evergreen trees, because they retain foliage throughout the year, can photosynthesize and gain carbon at all times of the year when weather is suitable. Because they retain foliage for several years, the high initial cost to construct foliage is spread out over a long period of time. Over the lifespan of their foliage, evergreen trees can, therefore, recoup the high initial investment to construct foliage despite low photosynthetic capacity. In contrast, deciduous trees shed their leaves annually. The benefit is that leaf shedding reduces transpiration and desiccation during times of the year when cold temperature or seasonal drought restrict photosynthesis. The costs are recurring annual investment of carbon to grow leaves and nutrient loss in litterfall. These costs are minimized by having a high specific leaf area so that the carbon cost to construct photosynthesizing surface area is smaller than in evergreen trees. Moreover, these trees have a high photosynthetic capacity to compensate for the short leaf lifespan.

Deciduous and evergreen leaf habits are also related to defense mechanisms to protect against herbivory. Consumption by herbivores is generally high for leaves with high photosynthetic capacity because of their corresponding high nitrogen concentration. One successful strategy in the face of herbivory is to make foliage unpalatable through structure or chemical defenses. An alternative strategy is to have high photosynthetic rates in short-lived leaves. Evergreen leaves represent an allocation pattern to extend the payback period on the high initial carbon investment to form leaf area, maximize carbon gain

despite low photosynthetic rates, conserve nutrients, and protect against herbivory. Deciduous leaves represent an alternative strategy whereby carbon gain is maximized by high photosynthetic rates in short-lived foliage that is either shed at the end of the growing season or consumed by herbivores.

These different life history patterns result in distinct geographic distributions to evergreen and deciduous trees (Figure 9.30). Evergreen trees have a bimodal geographic distribution. They are abundant at tropical, subtropical, and warm temperate latitudes, less abundant at cold temperate latitudes, and abundant again in subarctic latitudes. Evergreen trees dominate in tropical rainforests where favorable conditions allow for photosynthesis and growth throughout the year. As climate becomes cooler and drier, deciduous trees gain in abundance. Evergreen trees become abundant again on dry, nutrient-poor soils, such as in Southeast United States. Here, efficient nutrient use and the compensating effect of increased leaf lifespan where carbon gain is low give pine trees a competitive advantage over deciduous trees (Monk 1966). Evergreen trees also dominate the forests of the North American Pacific Northwest (Waring and Franklin 1979). In contrast to other temperate forest regions where summers are typically hot and humid and winters cold, the maritime climate of the Pacific Northwest is characterized by mild, wet winters and warm, dry summers. Mild temperatures permit substantial photosynthesis by evergreen trees during the relatively warm, wet autumn and winter months. In contrast, photosynthesis by deciduous trees is restricted to the summer months when leaves have emerged, but during which time soil water is likely to be limiting. The dominance of evergreen trees in subarctic climates is attributed to the cold temperatures, which restrict the growing season and limit mineralization of organically bound nutrients. Nutrient conservation is important. Moreover, the short, cool growing season and long cold winter limits carbon gain. An ability to quickly acquire carbon when conditions are favorable is important.

A physiological and morphological definition of plant functional types must be reconciled with an understanding of plant adaptations to disturbance, which is so critical to understanding vegetation responses to changing environments. Classifications such as *r*- and *K*-selection (MacArthur and Wilson 1967; Gadgil and Solbrig 1972), ruderal, stress tolerant, and competitive (Grime 1979), and early and late succession (Bazzaz 1979, 1996; Huston and Smith 1987) reflect the central role of disturbance in shaping community structure and composition. Other similar classifications include: exploitive and conservative species (Bormann and Likens 1979); gap and non-gap species (Shugart 1984, 1987, 1998); and vital

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attributes such as method of arrival following disturbance, method of persistence during and after disturbance, and ability to establish and grow to maturity (Noble and Slatyer 1980). In many cases, morphological and physiological considerations impose correlated life history traits. For example, early succession plants, in addition to their physiological traits of shade intolerance, high rates of photosynthesis, and high photosynthetic light compensation and saturation points, are also relatively shortlived, fast growing, and have small seeds that are widely dispersed. Indeed, the consistent tradeoff between high investment in photosynthesis and growth versus preferential allocation to storage, defense, and reproduction imposes correlations among vegetative and regenerative traits.

9.7 Tables

Table 9.1. *Maximum net photosynthesis with natural CO₂ availability, saturated light intensity, optimal temperature, and adequate water*

Plant type	CO ₂ uptake ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
<i>Herbaceous</i>	
C ₃	
Grasses	5-15
Crops	20-40
C ₄	30-60
CAM	5-10
<i>Tree</i>	
Tropical broadleaf evergreen	
Sunlit leaves	10-16
Shaded leaves	5-7
Broadleaf deciduous	
Sunlit leaves	10-15
Shaded leaves	3-6
Needleleaf evergreen	3-6
Needleleaf deciduous	8-10

Source: Data from Larcher (1995, pp. 85-86). See also Schulze *et al.* (1994) and Woodward and Smith (1994).

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Table 9.2. *Photosynthetic characteristics of C₃, C₄, and CAM plants*

Characteristic	C ₃ plants	C ₄ plants	CAM plants
Carboxylating enzyme	Rubisco	PEP carboxylase and rubisco	Dark: PEP carboxylase Light: rubisco
First product of photosynthesis	3-carbon acid (PGA)	4-carbon acids (oxaloacetate, malate, aspartate)	Dark: malate Light: PGA
CO ₂ :ATP:NADPH	1:3:2	1:5:2	1:6.5:2
Location of processes	Mesophyll cells	Mesophyll cells then bundle-sheath cells	Mesophyll cells
Stomatal behavior	Open during day, close at night	Open during day, close at night	Close during day, open at night
Photorespiration	High	Low	Low
Photosynthesis inhibited by 21% O ₂	Yes	No	Yes
Photosynthetic capacity	Low to high	High to very high	Medium
Light saturation	Intermediate intensity	No saturation	Intermediate to high intensity
Water use efficiency	1-5 g kg ⁻¹ H ₂ O	3-5 g kg ⁻¹ H ₂ O	6-15 g kg ⁻¹ H ₂ O
Optimum temperature for photosynthesis	15-25 °C	30-45 °C	30-35 °C
CO ₂ compensation point	30-50 ppm	0-10 ppm	0-5 ppm

Source: Data from Larcher (1995, pp. 64, 98, 109, 122), Salisbury and Ross (1992, p. 257), and Barbour *et al.* (1999, pp. 421-422).

Table 9.3. *Maximum photosynthetic capacity, specific leaf area, leaf nitrogen, and slope for photosynthesis-nitrogen relationship for 257 species of forbs, shrubs, broadleaf trees, and needleleaf trees*

Functional group	Photosynthetic capacity ($\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$)	Specific leaf area ($\text{cm}^2 \text{ g}^{-1}$)	Leaf nitrogen (mg N g^{-1})	A_{max} -N slope ($\mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1} \text{ N}$)
Forb	305	197	35.4	9.24
Broadleaf shrub				
Deciduous	157	140	20.8	9.68
Evergreen	62	71	15.8	2.36
Broadleaf tree				
Deciduous	139	137	22.2	4.20
Evergreen	55	89	15.0	1.47
Needleleaf tree				
Deciduous	97	100	19.0	-
Evergreen	28	38	11.6	2.76

Source: Data from Reich *et al.* (1998a).

Table 9.4. *Leaf maintenance respiration at 25 °C, specific leaf area, leaf nitrogen, and leaf lifespan for 69 species of forbs, broadleaf shrubs, broadleaf trees, and needleleaf trees*

Functional group	Respiration (nmol CO ₂ g ⁻¹ s ⁻¹)	Specific leaf area (cm ² g ⁻¹)	Leaf nitrogen (mg N g ⁻¹)	Leaf longevity (months)
Forb	27.3	188	28.2	4.5
Broadleaf shrub	14.4	112	20.9	9.4
Broadleaf tree	11.4	112	19.2	13.3
Needleleaf tree	4.9	48	11.6	43.9

Source: Data from Reich *et al.* (1998b).

Table 9.5. *Changes in carbon allocation in trees in relation to various stresses*

Stress	Root growth	Foliage growth
Shade	Reduced	Increased
Drought	Increased	Reduced
Cold temperature	Increased	Reduced
Nitrogen deficiency	Increased	Reduced
Nitrogen surplus	Reduced	Increased

Source: Adapted from Waring (1991).

Table 9.6. *Ratio of leaf area to sapwood area for tree species growing along a west-to-east transect in Oregon from the coast to the mountains*

Species	Climate	Ratio (m ² cm ⁻²)
Sitka spruce	Maritime	0.44
Douglas fir	Moderate	0.32
Mountain hemlock	Subalpine	0.16
Ponderosa pine	Semi-arid	0.17
Western juniper	Arid	0.07

Source: Data from Waring (1991). See also Waring (1983) and Waring and Schlesinger (1985, p. 31).

Table 9.7. *Physiological and life history characteristics of early and late successional plants*

	Early succession	Late succession
Seeds		
Number	Many	Few
Size	Small	Large
Dispersal	Wind, birds	Gravity, mammals
Dormancy	Long	Short
Germination	Enhanced by light	Not enhanced by light
Photosynthesis		
Light saturation intensity	High	Low
Light compensation point	High	Low
Efficiency at low light	Low	High
Maximum rate	High	Low
Respiration rate	High	Low
Transpiration rate	High	Low
Stomatal resistance	Low	High
Resource acquisition	High	Low
Morphology		
Root-to-shoot ratio	Low	High
Size at maturity	Small	Large
Structural strength	Low	High
Lifespan	Short	Long

Source: Adapted from Bazzaz (1979, 1996) and Huston and Smith (1987).

9.8 Figure Legends

Figure 9.1. Light reactions of photosynthesis showing the various processes that produce the two NADPH and three ATP needed to reduce one CO₂ molecule: absorption of four photons each by PS II and PS I (a, e); transfer of four electrons from PS II to an acceptor molecule (b); oxidation of two water molecules by P680 to obtain four electrons (c); electron transport (d) resulting in non-cyclic photophosphorylation (h) and transfer of four hydrogen to NADP⁺ (j); electron transfer from PS I to an electron acceptor (f); reduction of NADP⁺ (g); and cyclic photophosphorylation (i). Numbers in parentheses show reactions when four ATP molecules are created instead of three.

Figure 9.2. Dark reactions of the C₃ photosynthetic pathway. Three turns of the Calvin cycle are depicted. The symbol [●] indicates the number of carbon atoms contained in the compound.

Figure 9.3. Generalized stomatal gas exchange showing carbon dioxide uptake during photosynthesis and water loss during transpiration. Top: Open stomata. Bottom: Closed stomata.

Figure 9.4. Environmental controls of stomatal conductance for jack pine trees. Stomatal conductance is shown in response to photosynthetic photon flux density (top left), temperature (top right), foliage water potential (bottom left), and vapor pressure deficit (bottom right). Data from Dang *et al.* (1997a,b, 1998). Jarvis (1976) and Collatz *et al.* (1991) provide mathematical models of stomatal conductance.

Figure 9.5. Effect of temperature on photosynthesis and respiration in C₃ plants.

Figure 9.6. Environmental controls of net photosynthesis for jack pine trees. Net photosynthesis is shown in response to photosynthetic photon flux density (top left), temperature (top right), foliage water potential (middle left), vapor pressure deficit (middle right), ambient carbon dioxide concentration (bottom left), and foliage nitrogen (bottom right). Data from Dang *et al.* (1997a,b, 1998).

Figure 9.7. Relationship between photosynthesis, transpiration, and stomatal conductance for jack pine trees. Top: Light response over a range of 0 to 1250 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Bottom: Foliage water potential response over a range of -0.2 to -2.4 MPa. Data from Dang *et al.* (1997a,b, 1998).

Figure 9.8. Relationship between maximum leaf conductance and maximum photosynthesis. Data shown are mean values for 7 types of woody vegetation and 4 types of herbaceous vegetation. The regression equations shown with these data are based on the full dataset of 55 woody plants and 18 herbaceous plants. Data from Körner (1994).

Figure 9.9. Photosynthetic light response curve showing the W_c and W_j rates of photosynthesis. The W_c -limited rate is $8.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The W_j -limited rate increases with light. Actual photosynthesis is the smaller of these two values. The transition from the W_j -limited to W_c -limited rate occurs at about $165 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. From a model by Bonan (1995a).

Figure 9.10. Relationship between maximum rate of carboxylation (V_{max}) and maximum potential rate of electron transport (J_{max}) for 109 C_3 species. Data are shown as averages for broad groups of species. Original data for all 109 species show a similar relationship. Data from Wullschlegel (1993).

Figure 9.11. Coordinated leaf traits for 22 broadleaf deciduous and 9 needleleaf evergreen temperate tree species. Top: Maximum rate of photosynthesis in relation to leaf nitrogen. Middle: Maximum rate of photosynthesis in relation to leaf surface area per unit mass (specific leaf area). Bottom: Leaf nitrogen in relation to specific leaf area. Data from Reich *et al.* (1995a).

Figure 9.12. Relationships of leaf maintenance respiration at $25 \text{ }^\circ\text{C}$ to leaf nitrogen (top), leaf lifespan (middle), and specific leaf area (bottom) for 69 species of forbs, broadleaf shrubs, broadleaf trees, and needleleaf trees. Data from Reich *et al.* (1998b).

Figure 9.13. The carbon balance of a tree. Net carbon is the difference between carbon uptake during photosynthesis and carbon loss during maintenance and growth respiration.

Figure 9.14. Vertical profile of stomatal conductance in crops. Left: Sorghum at 0700, 1200, and 1600 hours. Right: Tobacco at 0830, 1200, and 1830 hours. Adapted from Jarvis and McNaughton (1986).

Figure 9.15. Vertical profile of leaves in forests. The left panels show the actual leaf profile. The right panels show the cumulative leaf profile and irradiance as a percent of that at the top of the canopy. Top: Oak forest. Bottom: Aspen forest with understory. Data from Rauner (1976).

Figure 9.16. Sunlit leaf area index for random, horizontal, and vertical leaves in relation to leaf area index. Top: Solar zenith angle of 30°. Bottom: Solar zenith angle of 60°.

Figure 9.17. Canopy integration of photosynthetic capacity based on relationships among light, foliage nitrogen, and photosynthetic capacity for jack pine, black spruce, and quaking aspen forests. Top left: Photosynthetically active radiation (%PAR), as a percent of full radiation, in relation to depth from the top of the canopy. Top middle: Foliage nitrogen in relation to %PAR. Top right: Leaf photosynthetic capacity in relation to foliage nitrogen. Bottom left: Leaf photosynthetic capacity, as a percent of that in the upper canopy, in relation to leaf nitrogen, as a percent of that in the upper canopy. Bottom middle: Leaf relative photosynthetic capacity in relation to %PAR. Bottom right: Canopy photosynthetic capacity integrated over all leaves in relation to the Normalized Difference Vegetation Index. Data from Dang *et al.* (1997b).

Figure 9.18. Maintenance respiration in relation to temperature for foliage, stem sapwood, and roots. From a terrestrial ecosystem model (Bonan 1993a).

Figure 9.19. Carbon balance (net photosynthesis, shoot respiration, root respiration) of pine seedlings growing near treeline over the course of a year. Adapted from Larcher (1995, p. 133).

Figure 9.20. Average flowering data of nine species of spring wildflowers in an Indiana woodland growing on north- and south-facing slopes separated by 46 m. Top: Topographic setting. Bottom: Cumulative degree-hours above 4.4 °C. Data from Jackson (1966).

Figure 9.21. The Normalized Difference Vegetation Index averaged for January (top) and April (bottom) for 1982 to 1993. Low values indicate low plant production. High values indicate high production. Data

from the NOAA/NASA Pathfinder data product archived at the NASA Goddard Space Flight Center Earth Sciences Distributed Active Archive Center (GSFC DAAC).

Figure 9.22. The Normalized Difference Vegetation Index averaged for July (top) and October (bottom) for 1982 to 1993.

Figure 9.23. Relationship between growth and reproduction. Top: Diameter growth in relation to cone production for Douglas fir. Diameter growth is expressed as a relative growth that removes the effects of age. Adapted from Eis *et al.* (1965). Bottom: Effect of fruit production on the following season's shoot growth for California buckeye. Data from Newell (1991).

Figure 9.24. Relationship between seed weight and seedling growth and survival for nine species of trees grown in shade. Seeds were germinated and then transplanted to grow in shade. Top: Height growth after 12 weeks. Bottom: Number of seedlings that died over the 12 weeks. Adapted from Grime and Jeffrey (1965).

Figure 9.25. Carbon allocation in herbaceous plants. Top: Whole plant allocation for *Senecio vulgaris*, an annual. Adapted from Harper and Ogden (1970). Bottom: Aboveground allocation to foliage, stems, and flowers in a herbaceous perennial (goldenrod, *Solidago*). Adapted from Abrahamson and Gadgil (1973).

Figure 9.26. Relationship between stem diameter and biomass for jack pine, black spruce, and quaking aspen trees growing in Canada. Left: Foliage. Middle: Branch. Right: Stem. Data from Gower *et al.* (1997).

Figure 9.27. Relationship between leaf area and sapwood area for Scots pine trees growing on a cool, wet site and a warm, dry site. Adapted from Mencuccini and Grace (1994).

Figure 9.28. Relationships among growth, maturity, and longevity in 87 species of broadleaf deciduous trees. Left: Typical age of reproduction in relation to typical longevity. Species are separated into shade intolerant and shade tolerant classes. Right: Typical longevity in relation to growth rate. Data are shown for each species and as the average longevity for each growth class. Data from Loehle (1988).

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Figure 9.29. Classification of life history strategies based on relative importance of disturbance, competition, and stress. Top: The three axes of increasing relative competition, disturbance, and stress define seven life histories—competitor (C), ruderal (R), stress tolerator (S), competitive ruderal (C-R), stress tolerant competitor (C-S), stress tolerant ruderal (S-R), and C-S-R strategists. Bottom: Distribution of annual herbs, biennial herbs, and trees and shrubs (left) and lichens, perennial herbs and ferns, and bryophytes (right) with respect to competition, disturbance, and stress. Adapted from Grime (1979, pp. 57, 73).

Figure 9.30. Geographic distribution of trees showing the percent of land area covered by trees in relation to latitude. Top: Needleleaf evergreen and broadleaf evergreen trees. Bottom: Needleleaf deciduous and broadleaf deciduous trees. Derived from DeFries *et al.* (1999, 2000a,b).