5 Carbon Inputs to Ecosystems

Photosynthesis by plants provides the carbon and energy that drive most biological processes in ecosystems. This chapter describes the controls over carbon input to ecosystems.

Introduction

The energy fixed by photosynthesis directly supports plant growth and produces organic matter that is consumed by animals and soil microbes. The carbon derived from photosynthesis makes up about half of the organic matter on Earth; hydrogen and oxygen account for most of the rest. Human activities have radically modified the rate at which carbon enters the terrestrial biosphere by changing most of the controls over this process. We have increased the quantity of atmospheric CO_2 by 35% to which terrestrial plants are exposed. At regional and global scales, we have altered the availability of water and nutrients, the major soil resources that determine the capacity of plants to use atmospheric CO_2. Finally, through changes in land cover and the introduction and extinction of species, we have changed the regional distribution of the carbon-fixing potential of the terrestrial biosphere. Because of the central role that carbon plays in the climate system (see Chap. 2), the biosphere, and society, it is critical that we understand the factors that regulate its cycling through plants and ecosystems. We address carbon inputs to ecosystems through photosynthesis in this chapter and the carbon losses from plants and ecosystems in Chaps. 6 and 7, respectively. The balance of these processes governs the patterns of carbon accumulation and loss in ecosystems and the carbon distribution between the land, atmosphere, and ocean.

A Focal Issue

Carbon and water exchange through pores (stomata) in the leaf surface governs the efficiency with which increasingly scarce water resources support food production for a growing human population. Open stomata (Fig. 5.1) maximize carbon gain and productivity when water is abundant, but at the cost of substantial water loss. Partial closure of stomata under dry conditions reduces carbon gain but increases the efficiency with which water supports plant growth. What constrains the capacity of the biosphere to gain carbon? Where and in what seasons does most photosynthesis occur? How do plants regulate the balance between carbon gain and water loss? Application of current understanding of the controls over tradeoffs between carbon gain and water loss could reduce the likelihood of a "train wreck" resulting from current trends in increasing food demands and declining availability of freshwater to support agricultural production.

F.S. Chapin, III et al., *Principles of Terrestrial Ecosystem Ecology*,
DOI 10.1007/978-1-4419-9504-9_5,

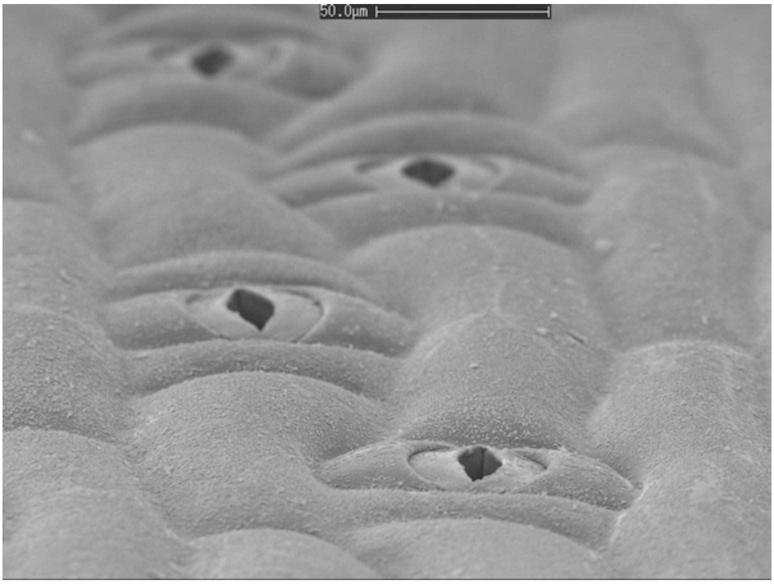

Fig. 5.1 Surface of a *Tradescantia virginiana* leaf with open stomatal pores. Selection for plants that differ in stomatal density and physiological regulation of stomatal opening influences both the maximum rate and the efficiency with which plants use water to gain carbon. Photograph courtesy of Peter Franks

Overview of Carbon Inputs to Ecosystems

Photosynthesis is the process by which most carbon and chemical energy enter ecosystems. The proximate controls over photosynthesis at the cellular or leaf level are the availability of photosynthetic reactants such as light energy and CO_2; temperature, which governs reaction rates; and the availability of nitrogen, which is required to produce photosynthetic enzymes. Photosynthesis at the scale of ecosystems is termed **gross primary production** (GPP). Like photosynthesis by individual cells or leaves, GPP varies diurnally and seasonally in response to variations in light, temperature, and nitrogen supply. *Differences among ecosystems* in annual GPP, however, are determined primarily by the quantity of photosynthetic tissue and the duration of its activity (Fig. 5.2). These, in turn, depend on the availability of soil resources (water and nutrients), climate, and time since disturbance. In this chapter, we explore the mechanisms behind these causal relationships.

Carbon is the main element that plants reduce with energy derived from the sun. Carbon and energy are therefore tightly linked as they enter, move through, and leave ecosystems. Photosynthesis uses light energy (i.e., radiation in the visible portion of the spectrum) to reduce CO_2 and produce carbon-containing organic compounds. This organic carbon and its associated energy are then transferred among components within the ecosystem and are eventually released to the atmosphere by respiration or combustion.

The energy content of organic matter varies among carbon compounds, but for whole tissues, it is relatively constant at about 20 kJ g^{-1} of ash-free dry mass (Golley 1961; Larcher 2003; Fig. 5.3). The carbon concentration of organic matter is also variable but averages about 45% of dry weight in herbaceous tissues and 50% in wood (Gower et al. 1999; Sterner and Elser 2002). Both the carbon and energy contents of organic matter are greatest in materials such as seeds and animal fat that have high lipid content and are lowest in tissues with high concentrations of minerals or organic acids. Because of the relative constancy

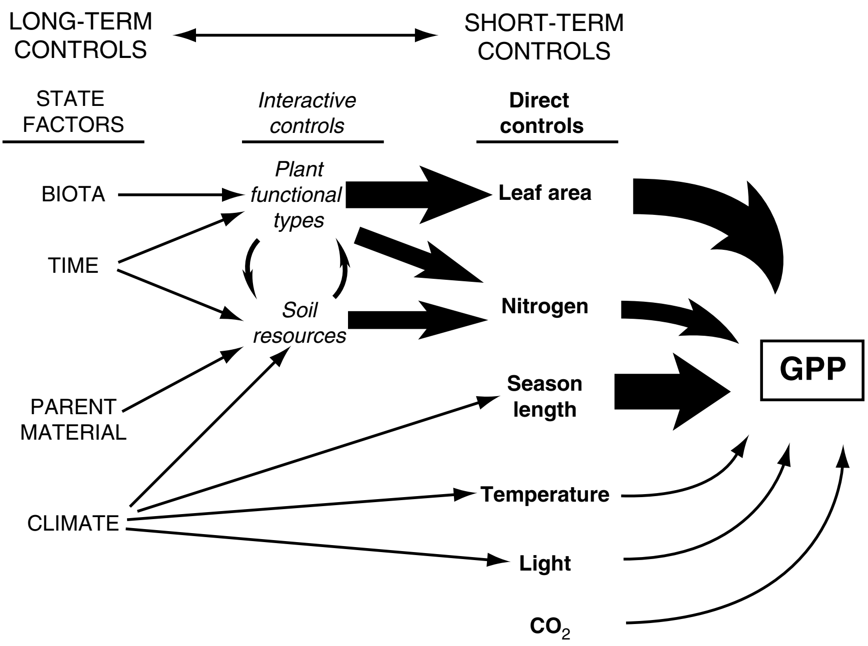

Fig. 5.2 The major factors governing temporal and spatial variation in gross primary production (GPP) in ecosystems. These controls range from proximate controls, which determine the diurnal and seasonal variations in GPP, to the interactive controls and state factors, which are the ultimate causes of ecosystem differences in GPP. Thickness of the *arrows* indicates the strength of the direct and indirect effects. The factors that account for most of the variation among ecosystems in GPP are leaf area and length of the photosynthetic season, which are ultimately determined by the interacting effects of soil resources, climate, vegetation, and disturbance regime

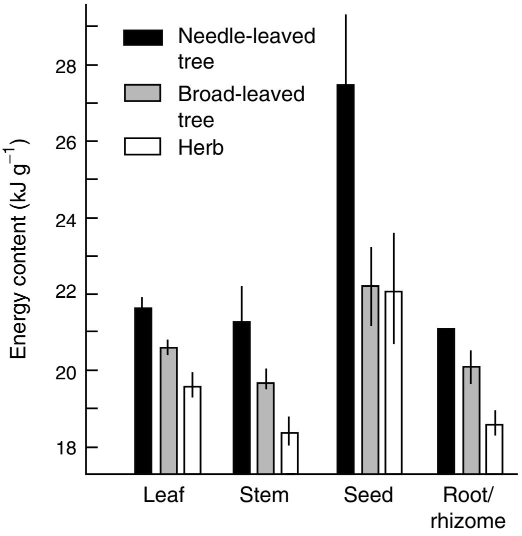

Fig. 5.3 Energy content of major tissues in conifer trees, broad-leaved trees, and broad-leaved herbs. Compounds that contribute to a high energy content include lipids (seeds), terpenes and resins (conifers), proteins (leaves), and lignin (woody tissues). Values are expressed per gram of ash-free dry mass. Data from Larcher (2003)

of the carbon and energy contents of organic matter, carbon, energy, and biomass have been used interchangeably as currencies of the carbon and energy dynamics of ecosystems. The preferred units differ among subfields of ecology, depending on the processes that are of greatest interest or are measured most directly. Production studies, for example, typically focus on biomass, trophic studies on energy, and gas exchange studies on carbon.

Biochemistry of Photosynthesis

The biochemistry of photosynthesis governs the environmental controls over carbon inputs to ecosystems. Photosynthesis involves two major groups of reactions: The **light-harvesting reactions** (or light-*dependent* reactions) transform light energy into temporary forms of chemical energy (ATP and NADPH; Lambers et al. 2008). The

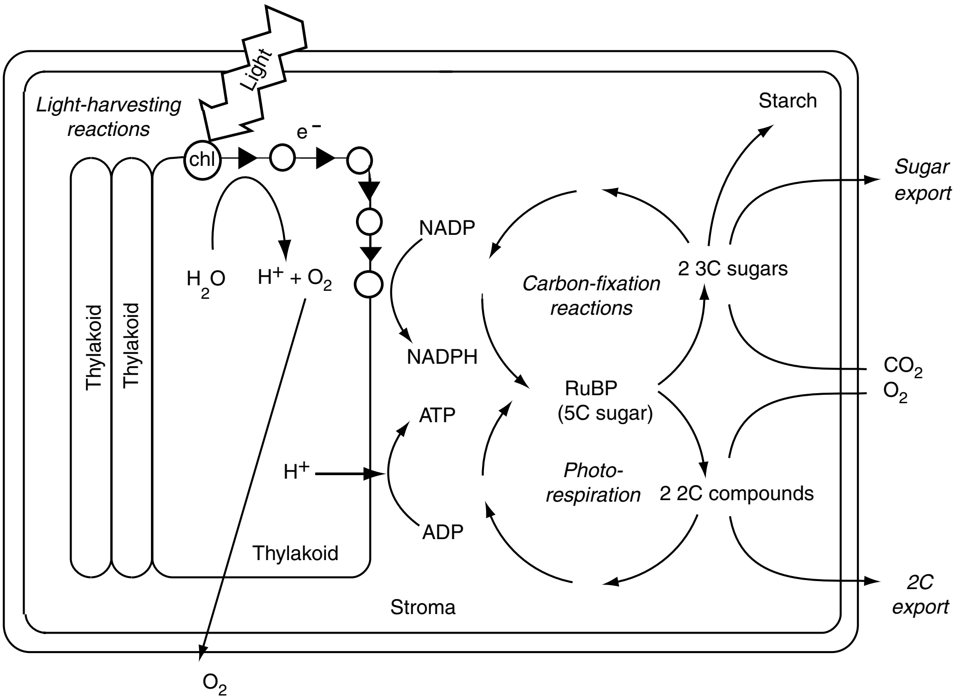

Fig. 5.4 A chloroplast, showing the location of the major photosynthetic reactions. The light-harvesting reactions occur in the **thylakoid** membranes; chlorophyll (chl) absorbs visible light and funnels the energy to reaction centers, where water inside the thylakoid is split to H^+ and O_2, and resulting electrons are passed down an electron-transport chain in the thylakoid membrane, ultimately to NADP, producing NADPH. During this process, protons move across the thylakoid membrane to the **stroma**, and the proton (H^+) gradient drives the synthesis of ATP. ATP and NADPH provide the energy to synthesize ribulose-bisphosphate (RuBP), which reacts either with CO_2 to produce sugars and starch (carbon-fixation reactions of photosynthesis) or with O_2 to produce two-carbon intermediates (photorespiration) and ultimately CO_2. Through either carbon fixation or photorespiration, ADP and NADP are regenerated to become reactants in the production of additional ATP and NADPH. The net effect of photosynthesis is to convert light energy into chemical energy (sugars and starches) that is available to support plant growth and maintenance

carbon-fixation reactions (or light-*independent* reactions, sometimes called the dark reaction) use the products of the light-harvesting reactions to convert CO_2 into sugars, a more permanent form of chemical energy that can be stored, transported, or metabolized. Both groups of reactions occur simultaneously in the light in **chloroplasts**, which are organelles inside photosynthetic cells (Fig. 5.4). In the light-harvesting reactions, **chlorophyll** (a light-absorbing pigment) captures energy from visible light. Absorbed radiation is converted to chemical energy (NADPH and ATP), and oxygen is produced as a waste product. Visible radiation accounts for 40% of incoming solar radiation (see Chap. 2), which places an upper limit on the potential efficiency of photosynthesis in converting solar radiation into chemical energy.

The carbon-fixation reactions of photosynthesis use the chemical energy (ATP and NADPH) from the light-harvesting reactions to reduce CO_2 to sugars. The rate-limiting step in the carbon-fixation reactions is the reaction of a five-carbon sugar (ribulose-bisphosphate [RuBP]) with CO_2 to form two three-carbon organic acids (phosphoglycerate), which are then reduced using ATP and NADPH from the light reactions to form three-carbon sugars (glyceraldehyde 3-phosphate). The initial attachment of CO_2 to a carbon skeleton is catalyzed by the enzyme ribulose-bisphosphate carboxylase-oxygenase (**Rubisco**). The rate of this reaction is generally limited by the products of the light-harvesting reaction and by the concentration of CO_2 in the chloroplast. A surprisingly high concentration of Rubisco is required for carbon fixation. Rubisco accounts for about 25% of the nitrogen in photosynthetic cells, and other photosynthetic enzymes make up an additional 25%. The remaining enzymatic steps in the carbon-fixation reactions use ATP and NADPH from the light-harvesting reactions to convert some molecules of the three-carbon sugar (glyceraldehyde 3-phosphate) to RuBP, thus closing the photosynthetic carbon reduction cycle, and convert the rest to the six-carbon sugar, glucose, that is transported out of the chloroplast (Fig. 5.4). The most notable features of the carbon-fixation reactions are: (1) their large nitrogen requirement for Rubisco and other photosynthetic enzymes; (2) their dependence on the products of the light-harvesting reactions (ATP and NADPH), which in turn depend on **irradiance**, i.e., the light received by the photosynthetic cell; and (3) their frequent limitation by CO_2 delivery to the chloroplast. The basic biochemistry of photosynthesis therefore dictates that this process must be sensitive to light and CO_2 availability over timescales of milliseconds to minutes and sensitive to nitrogen supply over timescales of days to weeks (Fig. 5.2; Evans 1989).

Rubisco is both a **carboxylase**, which initiates the carbon-fixation reactions of photosynthesis, and an **oxygenase**, which catalyzes the reaction between RuBP and oxygen (Fig. 5.4). Early in the evolution of photosynthesis on Earth, oxygen concentrations were very low, and CO_2 concentrations were high, so the oxygenase activity of this enzyme occurred at negligible rates (Sage 2004). The oxygenase initiates a series of steps that break down sugars to CO_2. This process of **photorespiration** immediately respires away 20–40% of the carbon fixed by photosynthesis and regenerates ADP and NADP in the process. Why do plants have such an inefficient system of carbon acquisition, by which they immediately lose a third of the carbon that they acquire through photosynthesis? Photorespiration is best viewed as a carbon recovery process. Photorespiration recycles about 75% of the carbon processed by the oxygenase activity of Rubisco at a cost of two ATPs and one NADPH to produce one CO_2 and one three-carbon acid (phosphoglycerate), which can be recycled back to RuBP. If the plant were to acquire this phosphoglycerate solely through assimilation of three new CO_2 molecules, the cost would be 9 ATP and 6 NADPH. Photorespiration may also act as a safety valve by providing a supply of reactants (ADP and NADP) to the light reaction under conditions in which an inadequate supply of CO_2 limits the rate at which these reactants can be regenerated by carbon-fixation reactions. In the absence of photorespiration, continued light harvesting produces oxygen radicals that destroy photosynthetic pigments.

Plants have additional lines of defense against excessive energy capture that are at least as important as photorespiration. Terrestrial plants and algae in shallow coral reefs, for example, have a **photoprotection** mechanism involving changes in pigments of the **xanthophyll cycle**. When excitation energy in the light-harvesting reactions exceeds the capacity of these reactions to synthesize ATP and NADPH, the xanthophyll pigment is converted to a form that receives this excess absorbed energy from the excited chlorophyll and dissipates it harmlessly as heat (Demming-Adams and Adams 1996). This processing of excess energy under high light prevents **photodestruction** of photosynthetic pigments under these conditions.

The photosynthetic reactions described above are known collectively as **C_3 photosynthesis** because two molecules of the three-carbon acid, phosphoglycerate are the initial products of carbon fixation. *C_3 photosynthesis is the fundamental photosynthetic pathway of all photosynthetic organisms on Earth*, although there are important variations on this theme that we discuss later. Plant chloroplasts, for example, have many similarities to, and probably evolved from, symbiotic bluegreen photosynthetic bacteria. Other carbon-fixation reactions contribute to the photosynthesis of some terrestrial plants (**C_4 photosynthesis** and **Crassulacian Acid Metabolism** or **CAM**). These reactions initially produce a four-carbon acid that is subsequently broken down to release CO_2 that enters the normal C_3 photosynthetic pathway to produce three-carbon sugars. However, the bottom line is that

C_3 photosynthesis is the fundamental mechanism by which carbon enters all ecosystems, so an understanding of its environmental controls provides considerable insight into the carbon dynamics of ecosystems.

Net photosynthesis is the net rate of carbon gain measured at the level of individual cells or leaves. It is the balance between simultaneous CO_2 fixation and respiration of photosynthetic cells in the light (including both photorespiration and mitochondrial respiration). Respiration rate is proportional to protein content, so photosynthetic cells and leaves with a high capacity for photosynthesis (lots of photosynthetic protein), also lose a lot of carbon due to their high respiration rate. The **light compensation point** (irradiance at which photosynthesis just balances respiration) is therefore higher in cells or leaves that have a high photosynthetic capacity. There is therefore a tradeoff between the capacity of plants to photosynthesize at high light (lots of protein and high photosynthetic capacity) and their performance at low light (less protein, lower respiration rate, and positive net photosynthesis at low light availability, i.e., a low light compensation point).

Plants adjust the components of photosynthesis, so the energy trapped by light-harvesting reactions closely matches the energy needed for the CO_2-fixation reactions. As plants produce new cells over days to weeks, protein synthesis is distributed between light-harvesting vs. carbon-fixing enzymes so that capacities for light harvesting and carbon fixation are approximately balanced under the typical light and CO_2 environment of the cell or leaf. Plants increase their investment in *light-harvesting capacity* in low-light environments and their *carbon-fixing capacity* at high light. Total **photosynthetic capacity** reflects the quantity of photosynthetic enzymes, which depends on nitrogen acquisition from their environment. Once a photosynthetic cell is produced, there is limited capacity to adjust the proportions of light-harvesting and carbon-fixing enzymes.

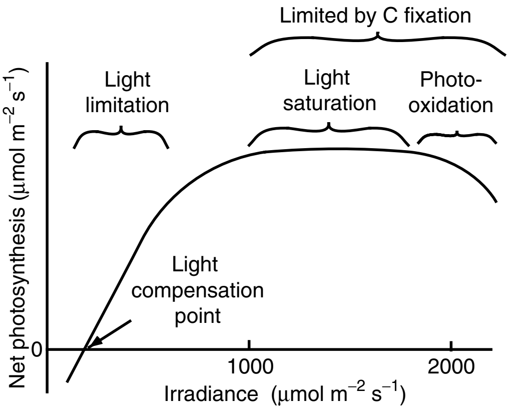

Fig. 5.5 Relationship of net photosynthetic rate to photosynthetically active radiation and the processes that limit photosynthesis at different irradiances. The linear increase in photosynthesis in response to increased light (in the range of light limitation) indicates relatively constant light-use efficiency. The light compensation point is the minimum irradiance at which the leaf shows a net gain of carbon

At low light, where the supply of ATP and NADPH from the light-harvesting reactions limits the rate of carbon fixation, net photosynthesis increases linearly with increasing light (Fig. 5.5). The slope of this line (the **quantum yield** of photosynthesis) is a measure of the efficiency with which photosynthetic cells use absorbed light to produce sugars. Quantum yield is similar (about 1–4% of the incoming light energy) among all C_3 plants (both aquatic and terrestrial) at low light in the absence of environmental stress (Kalff 2002; Lambers et al. 2008). At high irradiance, photosynthesis becomes **light saturated**, i.e., it no longer responds to changes in light supply, due to the finite capacity of light-harvesting reactions to capture light. As a result, light energy is converted less efficiently into sugar energy at high light. **Photosynthetic capacity** (maximum photosynthetic rate measured at light saturation) depends on the quantity of photosynthetic enzymes in the cell and is generally higher in large-celled algal species and rapidly growing terrestrial species that characterize nutrient-rich waters and lands, respectively. Photosynthesis declines at extremely high light, when the xanthophylls cycle photoprotective process in the chloroplast are overwhelmed, due to **photo-oxidation** of photosynthetic enzymes and pigments (Kalff 2002; Mann and Lazier 2006; Lambers et al. 2008).

In the next sections, we describe how environmental controls over photosynthesis operate in aquatic and terrestrial ecosystems. We begin with aquatic systems, where most primary producers are single-celled organisms (phytoplankton), and water seldom limits photosynthesis, thus simplifying the nature of environmental controls over carbon entry to the ecosystem. We then add the additional complexities found in terrestrial ecosystems.

Pelagic Photosynthesis

Light Limitation

Photosynthesis in pelagic (open-water) ecosystems of lakes and the ocean depends on light availability and phytoplankton biomass. Light enters water at the surface of lakes and the ocean and decreases exponentially with depth:

$$I_z = I_o e^{-kz} \tag{5.1}$$

where I is the **irradiance** (the quantity of radiant energy received at a surface per unit time) at depth z (m), I_o is the irradiance at the water surface; and k is the extinction coefficient. Light reduction through the water column results from absorption by water, chlorophyll, dissolved organic substances, and organic or sediment particles. In the clear water of the open-ocean and **oligotrophic** (low-nutrient) lakes, water accounts for most of the energy absorption, and high-energy blue light penetrates to the greatest depth, up to 50–100 m in clear lakes (Kalff 2002) and 200 m in the open ocean (Fig. 5.6; Valiela 1995). In **eutrophic** (high-nutrient) lakes and rivers, chlorophyll absorbs most of the light, which may penetrate only a few meters or less. Tannins absorb most light in tea-colored oligotrophic lakes in acidic low-nutrient landscapes. The depth of light penetration has two important consequences for pelagic ecosystems. First, it determines the depth of the **euphotic zone**, where there is enough light to support phytoplankton growth, i.e., where their photosynthesis exceeds respiration (see Chap. 6). This is often defined arbitrarily as the depth at which light is 1% of that available at the surface, although some phytoplankton photosynthesis occurs at even lower light intensities (Kalff 2002). In small, shallow lakes, which are by far the most numerous, the euphotic zone extends to the lake bottom, and much of the production occurs on the lake bottom, particularly in nutrient-poor settings (Vadeboncoeur et al. 2002; Vander Zanden et al. 2006; Vadeboncoeur et al. 2008). Second, the depth of light penetration in lakes influences stratification because most of the absorbed solar radiation is converted to heat, which reduces water density and promotes stratification (warmer less dense water at the surface). Eutrophic lakes

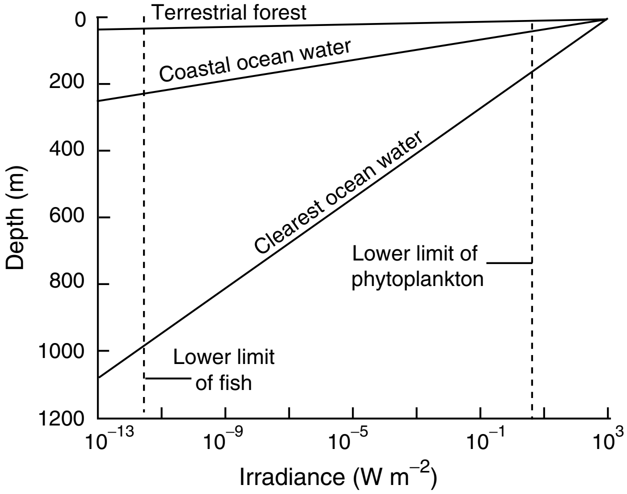

Fig. 5.6 Light availability at different distances beneath the surface of a forest canopy (Chazdon and Fetcher 1984) and the coastal and open ocean (Valiela 1995). Modified from Valiela (1995)

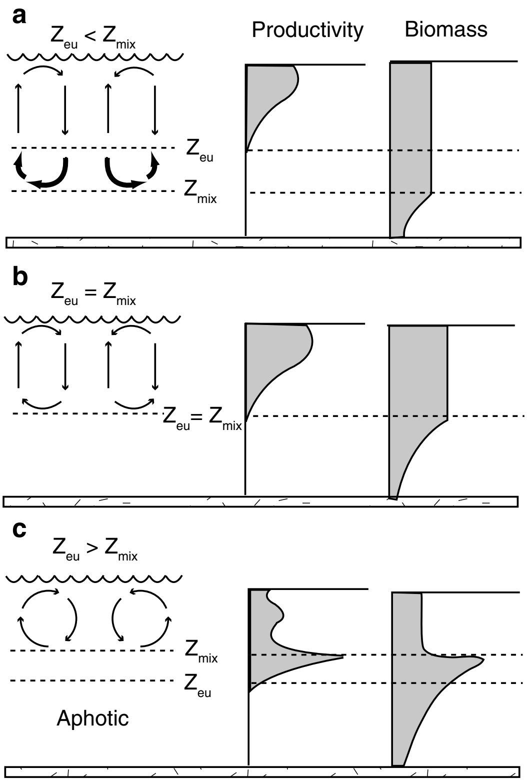

Fig. 5.7 Influence of the relative depths of the euphotic zone (z_{eu}) and mixed layer (z_{mix}) on the vertical distribution of phytoplankton and biomass. Redrawn from Thornton et al. (1990)

with shallow light penetration therefore tend to show greatest stratification and are most resistant to wind-driven mixing.

The distribution of photosynthesis through the water column depends on the depth distribution of phytoplankton and their photosynthetic response to light intensity (Valiela 1995; Kalff 2002). Mixing of the surface water typically occurs more rapidly (e.g., an hour or less) than phytoplankton can produce new cells (about a day; see Fig. 2.21), so turbulent mixing rather than cellular production or death determines the vertical distribution of phytoplankton and therefore the depth distribution of photosynthetic potential in the water column (Fig. 5.7; Thornton et al. 1990). When winds are calm and in sheltered lakes, other factors that influence the vertical distribution of phytoplankton include rates of cell production and mortality and the rates at which algae sink or swim. Large-bodied algae and diatoms with silica skeletons sink more rapidly than other phytoplankton (Kalff 2002; Mann and Lazier 2006).

Phytoplankton are like the terrestrial shade plants that will be described later. Due to their relatively low concentration of photosynthetic enzymes, they have both a low photosynthetic capacity and a low respiration rate. They therefore maintain positive net photosynthesis at the low light levels that characterize most of the water column and the depths at which cells spend most of their lives. Maximum photosynthesis in marine phytoplankton typically occurs at 5–25% of full sun, a few meters below the water surface (Valiela 1995; Mann and Lazier 2006). High light intensities that occur near the water surface on clear days reduce photosynthetic rate, but, due to turbulent mixing, phytoplankton spend relatively little time near the surface. Below the depth of maximum photosynthesis, carbon uptake declines with depth in parallel with the exponential decline in light intensity.

The depth of the euphotic zone is often similar to or less than the mixing depth of surface waters. In this case, there is a relatively uniform depth distribution of phytoplankton biomass, and the depth distribution of photosynthesis can be readily predicted from the light response curve of photosynthesis and the depth profile of light availability (Fig. 5.7b). In strongly stratified or extremely clear lakes, light sometimes penetrates more deeply than the mixed layer. In this case, there is an additional peak in phytoplankton biomass and photosynthesis at the base of the euphotic zone driven by the greater nutrient availability below the mixed layer (Fig. 5.7c). The actual depth distribution of photosynthesis is more complex than these simple rules imply because variability in mixing creates vertical and horizontal patchiness in the distribution of nutrients and phytoplankton.

In the ocean and clear lakes at high latitudes, UV-B may also contribute to low photosynthetic rates in surface waters, raising questions about whether aquatic production may have been reduced by high-latitude increases in UV-B (the “ozone holes” caused by anthropogenic CFCs; see Chap. 1). Colored dissolved organic compounds absorb UV-B radiation, so changes in these dissolved organics will likely mediate any potential UV-B impacts on aquatic ecosystems (Williamson et al. 1996; Kalff 2002). Photosynthesis at the ocean or lake surface appears to be light-limited mainly at high latitudes during winter due to low solar angles, short days, and snow-covered ice. At depth, light limits photosynthesis in all pelagic habitats.

CO_2 Supply

Photosynthesis is less often carbon-limited in aquatic than in terrestrial ecosystems. In marine pelagic ecosystems, for example, only 1% of the carbon in a given water volume is involved in primary production, whereas the nitrogen in this water may cycle through primary production 10–100 times a year (Thurman 1991). One reason for the apparently low responsiveness of pelagic photosynthesis to carbon supply is that inorganic carbon is available in substantial concentrations in several forms, including CO_2, bicarbonate, carbonate, and carbonic acid. When CO_2 dissolves in water, a small part is transformed to carbonic acid, which in turn dissociates to bicarbonate, carbonate, and H^+ ions with a concomitant drop in pH.

$$H_2O + CO_2 \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^- \leftrightarrow 2H^+ + CO_3^{2-} \quad (5.2)$$

As expected from these equilibrium reactions, the predominant forms of inorganic carbon are free CO_2 and carbonic acid at low pH (the equation driven to the left), soluble bicarbonate at about pH 8 (typical of ocean waters), and carbonates at high pH (equation driven to the right). Fossil-fuel emissions to the atmosphere have increased the CO_2 inputs to the ocean, driving (5.2) to the right. The resulting 30% increase in ocean acidity (H^+) tends to dissolve the carbonate shells of marine invertebrates and calcareous phytoplankton (coccolithophores) with potentially profound impacts on the functioning of marine ecosystems (see Chap. 14). Bicarbonate accounts for 90% of the inorganic carbon in most marine waters. Despite the predominance of bicarbonate in the ocean, phytoplankton in pelagic ecosystems use CO_2 as their primary carbon source. As CO_2 is consumed, it is replenished from bicarbonate (5.2). Some marine algae in the littoral zone, such as the macroalga, *Ulva*, also use bicarbonate.

It is still actively debated the extent to which marine productivity will respond directly to increasing atmospheric CO_2. Phytoplankton with low affinity for bicarbonate and most phytoplankton under eutrophic conditions increase photosynthesis and growth in response to added CO_2 (Schippers et al. 2004).

Daily photosynthesis in unpolluted freshwater ecosystems is seldom carbon-limited, just as in the ocean. Groundwater entering freshwater ecosystems is super-saturated with CO_2 derived from root and microbial respiration in terrestrial soils (Kling et al. 1991; Cole et al. 1994). Most streams, rivers, and lakes are net sources of CO_2 to the atmosphere because the CO_2 input from groundwater generally exceeds the capacity of aquatic primary producers to use the CO_2. In addition, aquatic decomposition of both aquatic and terrestrially derived organic carbon generates a large CO_2 source within lakes and rivers (see Chap. 7; Kortelainen et al. 2006; Cole et al. 2007). Eutrophic lakes with their high plankton biomass have a greater demand for CO_2 to support photosynthesis than do oligotrophic systems, but their organic accumulation and high decomposition rate in sediments also contribute a large CO_2 input to the water column from depth. This creates a strong vertical gradient in CO_2 in stratified eutrophic lakes, with CO_2 being absorbed from the atmosphere during the day and returned at night (Carpenter et al. 2001), just as in terrestrial ecosystems. Some freshwater vascular plants such as *Isoetes* use CAM photosynthesis to acquire CO_2 at night and refix it by photosynthesis during the day (Keeley 1990). Other freshwater vascular plants transport CO_2 from the roots to the canopy to supplement CO_2 supplied from the water column.

Nutrient Limitation

Nutrients limit phytoplankton photosynthesis primarily through their effects on the production of new cells. Productivity and photosynthesis are closely linked in all ecosystems through a system of amplifying (positive) feedbacks (see Chap. 6): Photosynthesis provides the carbon and energy to produce new photosynthetic cells, which increases the quantity of photosynthesis that can occur. This feedback is particularly strong in pelagic systems, where most primary production is by phytoplankton through the production of new photosynthetic cells. Nutrients strongly limit productivity in most unpolluted aquatic ecosystems, both freshwater and marine. As nutrient availability increases, the rate of production of new cells increases but each cell maintains a relatively modest concentration of photosynthetic enzymes, which accounts for their low photosynthetic capacity and low light compensation point. In other words, phytoplankton respond to nutrient supply primarily by increasing photosynthetic biomass, not by increasing the photosynthetic capacity of individual cells. This increases the amount of phytoplantkon biomass distributed through the water column but enables each cell to function in the low-light environment in which it spends most of its life (due to its low light compensation point, which is a consequence of its low photosynthetic capacity).

Phytoplankton species differ somewhat in photosynthetic capacity. Large-celled species with a high photosynthetic capacity dominate eutrophic waters, whereas small-celled **nanoplankton** (2–20 μm in diameter) and **picoplankton** (<2 μm in diameter) dominate oligotrophic waters. As described in Chaps. 6 and 9, large-celled species have an advantage in producing biomass rapidly when nutrients are readily available. In contrast, small-celled species, with their higher surface-to-volume ratio, are less limited by nutrient diffusion to the cell surface and are competitively favored in nutrient-poor waters.

Pelagic GPP

Total photosynthesis of pelagic ecosystems integrates the effects of nutrients on phytoplankton biomass and the effects of light and other environmental factors on the photosynthetic activity of individual cells. GPP is the rate of photosynthesis integrated through the water column, typically over time steps of days to a year (e.g., g C m^{-2} of ecosystem yr^{-1}). Ecosystem modeling and remote sensing have played a major role in estimating GPP in aquatic ecosystems. Turbulent mixing maintains a relatively homogeneous distribution of photosynthetic capacity throughout the surface mixed layer (constant photosynthetic capacity and light compensation point), although the efficiency with which chlorophyll traps light adjusts relatively rapidly and is greater at depth than at the surface (Flynn 2003; Mann and Lazier 2006). Because of the relatively homogeneous photosynthetic capacity through the mixed layer, chlorophyll content is a useful indicator of phytoplankton biomass. In the ocean, the vertical distribution of light absorption by chlorophyll can be estimated from satellite-derived color images of the ocean surface using **SeaWiFS** (Sea-viewing Wide Field-of-view Sensor). SeaWiFS estimates the depth profile of radiation absorbed by chlorophyll because different wavelengths of light penetrate to different depths.

As discussed earlier, the shape of photosynthesis-depth curve depends on the intensity and depth of turbulent mixing and the depth of light penetration (Fig. 5.7; Thornton et al. 1990; Kalff 2002; Mann and Lazier 2006). Lakes accumulate carbon when the total photosynthesis integrated through the water column (GPP) exceeds the total respiration. The **compensation depth** is the depth at which GPP equals phytoplankton respiration integrated through the water column. If the mixing depth is below the compensation depth, phytoplankton respiration beneath this depth exceeds photosynthesis, and they lose carbon. In the most productive pelagic ecosystems, such as eutrophic lakes and upwelling systems, the mixing depth is considerably shallower than the compensation depth.

Living on the Edge: Streams and Shorelines

Streams and littoral (shoreline) habitats have properties that depend on both terrestrial and aquatic components. On the terrestrial side, riparian vegetation benefits from a stable water supply and what is often a relatively favorable nutrient environment (see Chap. 13; Naiman et al. 2005). For this reason, salt marshes, freshwater marshes, and emergent vegetation along stable lakeshores often support high rates of photosynthesis and productivity (Valiela 1995). On the aquatic side, shading by emergent vascular plants and terrestrial vegetation largely defines the light environment of headwater streams and stable lake and stream banks, as described later.

Lotic (flowing-water) ecosystems such as streams and rivers have unique properties that distinguish them from both lakes and terrestrial systems. Primary producers of streams include **macrophytes** (large plants) such as vascular plants and mosses, **benthic** (bottom-dwelling) algae, **epiphytic** algae that attach to the surface of vascular plants, moss and macroalgae, and planktonic algae that float in slow-moving waters. The relative contribution of different primary producers to photosynthesis differs among geomorphic zones (erosional, transfer, and depositional) within the river basin and depends on patterns of flow rate, flood frequency, and substrate stability (see Chap. 3). Small headwater streams in the erosional zone of a drainage basin are often shaded by riparian vegetation, have relatively high flows (at least in some seasons), and variable nutrient inputs, depending on the dynamics of adjacent terrestrial ecosystems. Attached algae (**periphyton**), mosses, and liverworts on rocks and stable sediments generally account for most of the photosynthesis in headwater streams (Allan and Castillo 2007). As headwater streams join to form larger rivers, the greater solar input supports more photosynthesis by macrophytes along shallow stable riverbanks and by periphyton on stable riverbeds (Fig. 5.8). During periods of low flow,

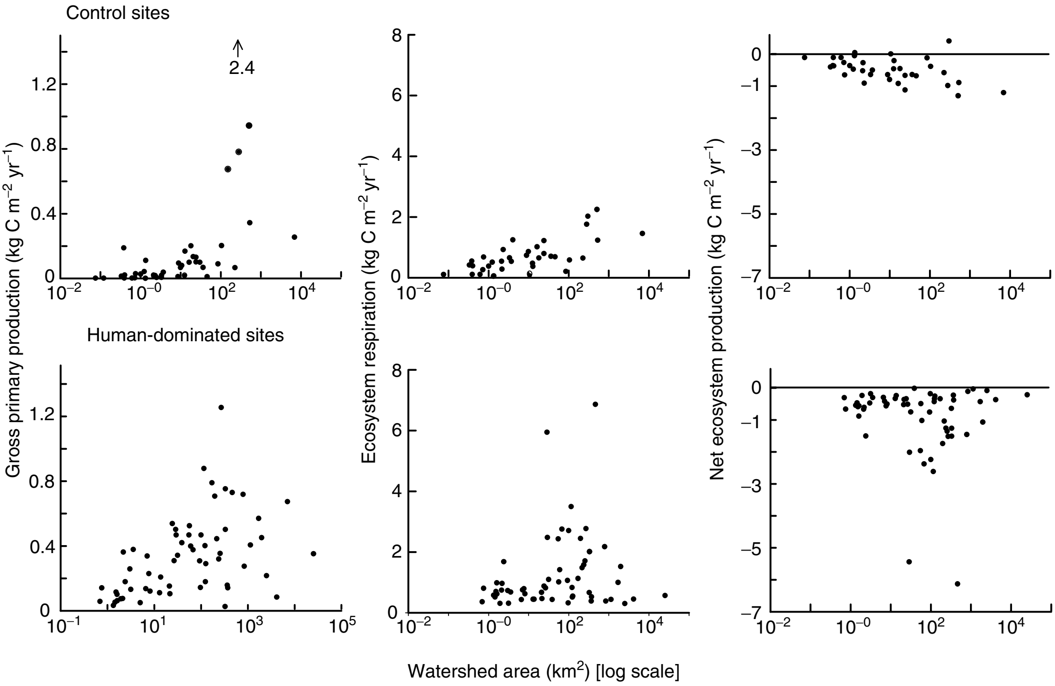

Fig. 5.8 Gross primary production, ecosystem respiration, and net ecosystem production of rivers and streams that differ in watershed area. Redrawn from Finlay 2011

benthic algae such as *Cladophora* can form extensive mats (Power 1992b). Benthic mosses are important in many cold water streams and rivers. In slow-moving rivers polluted by wastewater or agricultural runoff, pelagic algae can dominate if the doubling rate of algae is more rapid than their rate of downstream export (Allan and Castillo 2007). In general, GPP increases with increasing stream size, although it is quite variable, especially in large human-dominated drainage basins (Finlay 2011).

The controls over photosynthesis in streams and rivers vary depending on primary producer type and environment. Benthic algae in forested headwater streams, for example, have relatively low rates of photosynthesis because of low light availability, just as on the adjacent terrestrial forest floor. Removal of riparian trees and shrubs often increases photosynthesis and production in deforested headwater streams (Allan and Castillo 2007). In other cases, nutrients so strongly limit algal growth that algae show relatively little response to added light. In general, nutrients influence benthic photosynthesis primarily through their effect on the rate of production of new photosynthetic cells rather than on the photosynthetic properties of those cells, just as in lakes and the ocean. As discussed later, the high turbulence of flowing waters reduces limitation by nutrient diffusion to algal cells, so nutrient limitation tends to be less pronounced in flowing water than in pelagic ecosystems. Because of the super-saturation of groundwater with CO_2, photosynthesis in the streams that receive this groundwater is seldom CO_2-limited.

Stream macrophytes generally contribute a relatively small proportion of the photosynthetic carbon inputs to flowing-water ecosystems because of the small proportion of the stream surface area that they usually occupy. Mosses tend to dominate in shaded headwater streams, especially when waters are cold, and floating or emergent vascular plants dominate in lowland floodplain rivers and estuaries with slower currents, greater sediment accumulation, and higher light availability.

The phytoplankton present in the water column of slow-moving eutrophic rivers often originate from permanent populations in slow-moving side channels, lakes, reservoirs, or pools and get swept into the river channel. Since the maximum doubling time of most phytoplankton is once or twice per day, there is a strong inverse relationship between discharge and phytoplankton biomass in rivers. River phytoplankton populations can be self-sustaining if the currents are slow enough and nutrients are abundant enough to support rapid production throughout the year. In other cases, the rivers are seasonally seeded with phytoplankton from river-associated lakes and side channels. The roles of light and nutrients in controlling photosynthesis of river phytoplankton are similar to those in lakes. The total photosynthesis (GPP) in a section of river depends not only on the light environment and photosynthetic properties of the plants in that ecosystem but also on algal transport from upstream river segments, as discussed in Chaps. 7 and 9.

Terrestrial Photosynthesis

Photosynthetic Structure of Terrestrial Ecosystems

The physical differences between air and water account for the major photosynthetic differences between terrestrial and aquatic ecosystems. Aquatic algae are bathed in water that physically supports them and brings CO_2 and nutrients directly to photosynthetic cells. Water turbulence continuously mixes planktonic algae to different positions in the vertical light gradient. In contrast, the leaves of terrestrial plants are suspended from elaborate support structures and remain at fixed locations in the canopy. These leaves and their support structures create and respond to the vertical light gradient in terrestrial canopies. Thus, in contrast to phytoplankton, terrestrial leaves have opportunities to adjust photosynthesis to a particular light environment. Photosynthetic cells in the leaves of terrestrial plants are encased in waxy cuticles to minimize water loss, but this impermeable coating also slows CO_2 diffusion to the sites of carbon fixation in chloroplasts. Terrestrial leaves thus face tradeoffs between water loss and

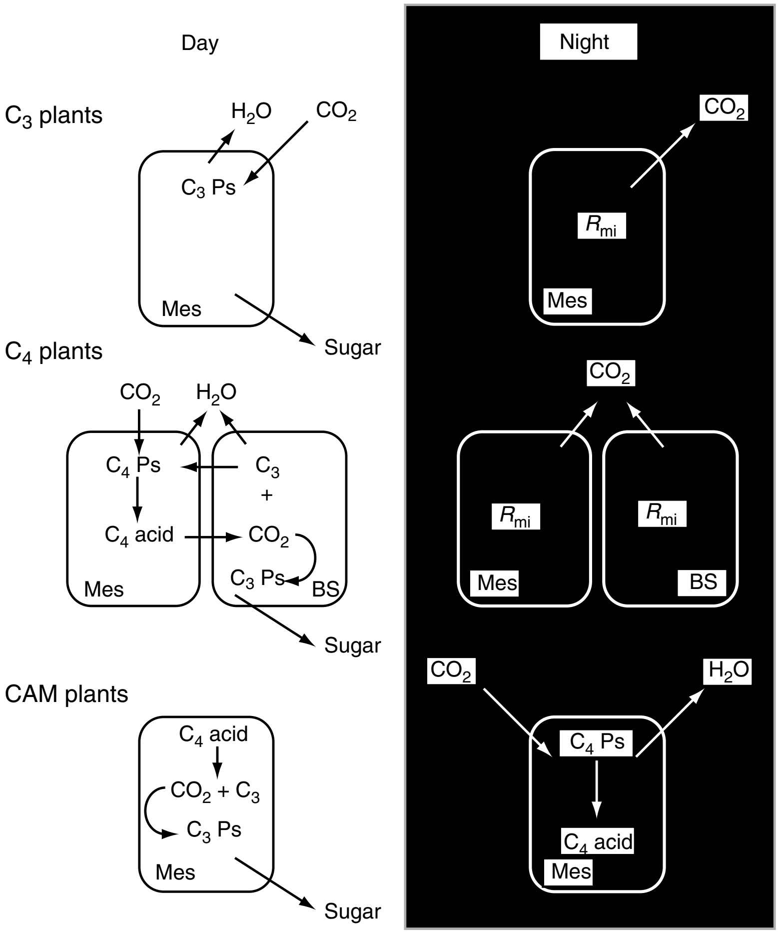

Fig. 5.9 Cellular location and diurnal timing of CO_2 fixation and water exchange in leaves with C_3, C_4, and Crassulacean Acid Metabolism (*CAM*) photosynthetic pathways. In C_3 and CAM plants, all photosynthesis occurs in mesophyll (*Mes*) cells. In C_4 plants, C_4 carbon fixation (*C_4 Ps*) occurs in mesophyll cells and C_3 fixation (*C_3 Ps*) occurs in bundle sheath (*BS*) cells. Mitochondrial respiration (R_{mi}) occurs at night. Exchanges with the atmosphere of CO_2 and water vapor occur during the day in C_3 and C_4 plants and at night in CAM plants

CO_2 absorption that are not an issue in aquatic ecosystems.

In terrestrial plants, the CO_2 used in photosynthesis diffuses along a concentration gradient from the atmosphere outside the leaf to the chloroplast. CO_2 first diffuses across a layer of relatively still air close to the leaf surface (the leaf **boundary layer**) and then through the **stomata** (small pores in the leaf surface), the diameter of which is regulated by the plant (Figs. 5.1, 5.9; Lambers et al. 2008). Once inside the leaf, CO_2 diffuses through air spaces between cells, dissolves in water on the cell surfaces, and diffuses the short distance from the cell surface to the chloroplast. C_3 leaf chloroplasts contain an enzyme, carbonic anhydrase that catalyzes the conversion of bicarbonate to dissolved CO_2, maximizing the concentration of the form of carbon (CO_2) that is fixed by Rubisco. The boundary layer, stomata, and cellular water all influence the overall diffusion of CO_2 from the free air to Rubisco, but stomata are the largest (and most variable) component of this resistance. The thin, flat shape of most leaves and the abundance of air spaces inside leaves maximize the rate of CO_2 diffusion from the bulk air to the chloroplast.

Cell walls inside the leaf are coated with a thin film of water that facilitates the efficient transfer of CO_2 from the air to the interior of cells. This water readily evaporates, and water vapor diffuses out through the stomata across the boundary layer to the atmosphere. The open stomata that are necessary for plants to gain carbon are therefore also an avenue for water loss (see Chap. 4). In other words, terrestrial plants face an inevitable tradeoff between CO_2 absorption (which is necessary to drive photosynthesis) and water loss (which must be replaced by absorption of water from the soil). This tradeoff can be as high as 400 molecules of water lost for each molecule of CO_2 absorbed. Plants regulate CO_2 absorption and water loss by changing the size of stomatal openings, which regulates **stomatal conductance**, the flux of water vapor, or CO_2 per unit driving force (i.e., for a given concentration gradient). When plants reduce stomatal conductance to conserve water, photosynthesis declines, reducing the efficiency with which plants convert light energy to carbohydrates. Plant regulation of CO_2 delivery to the chloroplast is therefore a compromise between maximizing photosynthesis and minimizing water loss and depends on the relative supplies of CO_2, light, and mineral nutrients, as described later. We now describe two photosynthetic pathways that enhance plant performance in warm, high-light environments (C_4 photosynthesis) and dry environments (CAM photosynthesis).

C_4 Photosynthesis

C_4 photosynthesis adds an additional set of carbon-fixation reactions that enable some plants to increase net photosynthesis in warm, high-light environments by reducing photorespiration. About 85% of vascular-plant species fix carbon by the C_3 photosynthetic pathway, in which Rubisco is the primary carboxylating enzyme. The first biochemically stable products of C_3 photosynthesis are three-carbon organic acids. About 3% of the global flora photosynthesizes by the **C_4 photosynthetic pathway** (Sage 2004), contributing about 23% of terrestrial GPP (Still et al. 2003). C_4 species dominate many warm, high-light environments, particularly tropical grasslands and savannas. C_4-dominated ecosystems account for nearly a third of the ice-free terrestrial surface (see Table 6.6) and are therefore quantitatively important in the global carbon cycle. In C_4 photosynthesis, phosphoenolpyruvate (PEP) is first carboxylated by **PEP carboxylase** in mesophyll cells to produce four-carbon organic acids (Fig. 5.9). These organic acids are transported to specialized **bundle sheath cells**, where they are decarboxylated. The CO_2 released from the organic acids then enters the normal C_3 pathway of photosynthesis to produce sugars that are exported from the leaf. There are three ecologically important features of the C_4 photosynthetic pathway:

First, C_4 acids move to the bundle sheath cells, where they are decarboxylated, concentrating CO_2 at the site where Rubisco fixes carbon. This increases the efficiency of carboxylation by Rubisco because it increases the concentration of CO_2 relative to O_2, which would otherwise compete for the active site of the enzyme. Apparent photorespiration measured at the leaf level is low in C_4 plants because most of the RuBP in the bundle sheath chloroplasts reacts with CO_2 rather than with O_2 and because the PEP carboxylase in the mesophyll cells scavenges any photorespired CO_2 that diffuses away from the bundle sheath cells.

Second, PEP carboxylase draws down the concentration of CO_2 inside the leaf to a greater extent than does Rubisco. This increases the CO_2 concentration gradient between the external air and the internal air spaces of the leaf. A C_4 plant can therefore absorb CO_2 with more tightly closed stomata than can a C_3 plant, thus reducing water loss.

Third, the net cost of regenerating the carbon acceptor molecule (PEP) of the C_4 pathway is two ATPs for each CO_2 fixed, a 30% increase in the energy requirement of photosynthesis compared to C_3 plants.

The major advantage of the C_4 photosynthetic pathway is increased carboxylation under conditions that would otherwise favor photorespiration (Sage 2004). Due to their lack of photorespiration, which increases exponentially with rising temperature, C_4 plants maintain higher rates of net photosynthesis at high temperatures than do C_3 plants; this explains the success of C_4 plants in warm environments. C_4 photosynthesis initially evolved with similar frequency in mesic, arid, and saline environments, and today's C_4 plants appear to be no more drought tolerant than C_3 plants (Sage 2004). Nonetheless, the low stomatal conductance of C_4 plants appears to preadapt them to dry conditions, so C_4 genera now occur in a wider range of dry habitats than their C_3 counterparts (Osborne and Freckleton 2009). The main disadvantage of the C_4 pathway is the additional energy cost for each carbon fixed by photosynthesis, which is best met under high-light conditions (Edwards and Smith 2010). The C_4 pathway is therefore most advantageous in warm, high-light conditions, such as tropical grasslands and marshes. The C_4 pathway occurs in 18 plant families and has evolved independently at least 45 times (Sage 2004). C_4 species first became abundant in the late Miocene 6–8 million years ago, probably triggered by a global decline in atmospheric CO_2 concentration (Cerling 1999). C_4 grasslands expanded during glacial periods, when CO_2 concentrations declined, and retracted at the end of glacial periods, when atmospheric CO_2 concentration increased, suggesting that the evolution of C_4 photosynthesis was tightly tied to variations in atmospheric CO_2 concentration. However, there is little geographic variation in atmospheric CO_2 concentration, so the current geographic distribution of C_4 plants appears to be controlled primarily by temperature and light availability, rather than by CO_2 concentration.

C_4 plants have an isotopic signature that allows tracking of their past and present role in ecosystems. C_4 plants incorporate a larger fraction of ^{13}C than do C_3 plants during photosynthesis (Box 5.1) and therefore have a distinct isotopic signature that characterizes any organic matter that originated by this photosynthetic pathway, including animals and soil organic matter. Isotopic measurements are a valuable tool in studying ecological processes in ecosystems where the relative abundance of C_3 and C_4 plants has changed over time (Ehleringer et al. 1993).

Crassulacean Acid Metabolism

Crassulacean acid metabolism (CAM) is a photosynthetic pathway that enables plants to gain carbon under extremely dry conditions. Succulent plant species (e.g., cactuses) in dry environments, including many epiphytes in the canopies of tropical forests, gain carbon through CAM photosynthesis. CAM accounts for a small proportion of terrestrial carbon gain because it is active only under extremely dry conditions. Even in these environments, some CAM plants switch to C_3 photosynthesis when enough water is available.

In CAM photosynthesis, plants close their stomata during the day, when high tissue temperatures and low relative humidity of the external air would otherwise cause large transpirational water loss (Fig. 5.9). At night, they open their stomata, and CO_2 enters the leaf and is fixed by PEP carboxylase. The resulting C_4 acids are stored in vacuoles until the next day when they are decarboxylated, releasing CO_2 to be fixed by normal C_3 photosynthesis. Thus, in CAM plants there is a *temporal* (day-night) separation of C_3 and C_4 CO_2 fixation, whereas in C_4 plants there is a *spatial* separation of C_3 and C_4 CO_2 fixation between bundle sheath and mesophyll cells. CAM photosynthesis is energetically expensive, like C_4 photosynthesis; it therefore occurs primarily in dry, high-light environments such as deserts, shallow rocky soils, and canopies of tropical forests. CAM photosynthesis allows some plants to gain carbon under extremely dry conditions that would otherwise preclude carbon fixation in ecosystems.

CO_2 Limitation

Plants adjust the components of photosynthesis, so physical and biochemical processes colimit carbon fixation. Photosynthesis operates most efficiently when the rate of CO_2 diffusion into the leaf matches the biochemical capacity of the leaf to fix CO_2. Terrestrial plants regulate the components of photosynthesis to approach this balance, as seen from the response of photosynthesis

Box 5.1 Carbon Isotopes

The three isotopic forms of carbon (^{12}C, ^{13}C, and ^{14}C) differ in their number of neutrons but have the same number of protons and electrons. The additional atomic mass causes the heavier isotopes to react more slowly in some reactions, particularly in the carboxylation of CO_2 by Rubisco. Carboxylating enzymes preferentially fix the lightest of these isotopes of carbon (^{12}C). C_3 plants generally have a relatively high CO_2 concentration inside the leaf, due to their high stomatal conductance. Under these circumstances, Rubisco **discriminates** against the heavier isotope ^{13}C, causing $^{13}CO_2$ to accumulate within the airspaces of the leaf. $^{13}CO_2$ therefore diffuses out of the leaf through the stomata along a concentration gradient of $^{13}CO_2$ at the same time that $^{12}CO_2$ is diffusing into the leaf. In C_4 and CAM plants, in contrast, PEP carboxylase has such a high affinity for CO_2 that it reacts with most of the CO_2 that enters the leaf, resulting in relatively little discrimination against $^{13}CO_2$. Consequently, the ^{13}C concentrations of CAM and C_4 plants are much higher (less negative isotopic ratios) than those of C_3 plants (Table 5.1).

This difference in isotopic composition among C_3, C_4, and CAM plants remains in any organic compounds derived from these plants. This makes it possible to calculate the relative proportions of C_3 and C_4 plants in the diet of animals by measuring the ^{13}C content of the animal tissue; this can be done even in fossil bones such as those of early humans. Changes in the isotopic composition of fossil bones are a clear indicator of changes in diet. In situations where vegetation has changed from C_3 to C_4 dominance (or vice versa), the organic matter in plants differs in its isotopic composition from that of the soil (and its previous vegetation). Changes in the carbon isotope composition of soil organic matter over time then provides a tool to estimate the current rates of turnover of soil organic matter that formed beneath the previous vegetation.

Table 5.1 Representative ^{13}C concentrations (‰) of atmospheric CO_2 and selected plant and soil materials

Material	$\partial^{13}C$ (‰)[a]
PeeDee limestone standard	0.0
Atmospheric CO_2	−8
Plant material	
Unstressed C_3 plant	−27
Water-stressed C_3 plant	−25
Unstressed C_4 plant	−13
Water-stressed C_4 plant	−13
CAM plant[b]	−27 to −11
Soil organic matter	
Derived from unstressed C_3 plants	−27
Derived from C_4 or CAM plants	−13

Data from O'Leary (1988) and Ehleringer and Osmond (1989)

[a] The concentrations are expressed relative to an internationally agreed-on standard (PeeDee belemnite):

$$\partial^{13}C_{std} = 1000\left(\frac{R_{sam}}{R_{std}} - 1\right)$$

where $\partial^{13}C$ is the isotope ratio in delta units relative to a standard, and R_{sam} and R_{std} are the isotope abundance ratios of the sample and standard, respectively (Ehleringer and Osmond 1989)

[b] Values of −11 under conditions of CAM photosynthesis; many CAM plants switch to C_3 photosynthesis under favorable moisture regimes, giving an isotopic ratio similar to that of unstressed C_3 plants

to the CO_2 concentration inside the leaf (Fig. 5.10). When the internal CO_2 concentration is low, photosynthesis increases approximately linearly with increasing CO_2 concentration. Under these circumstances, the leaf has more carbon-fixation capacity than it can use, and photosynthesis is limited by the rate of diffusion of CO_2 into the leaf. The plant can increase photosynthesis only by opening stomatal pores. Alternatively, if CO_2 concentration inside the leaf is high, photosynthesis shows little response to variation in CO_2 concentration (the asymptote approached in Fig. 5.10). In this case, photosynthesis is limited by the rate of regeneration of RuBP (the compound

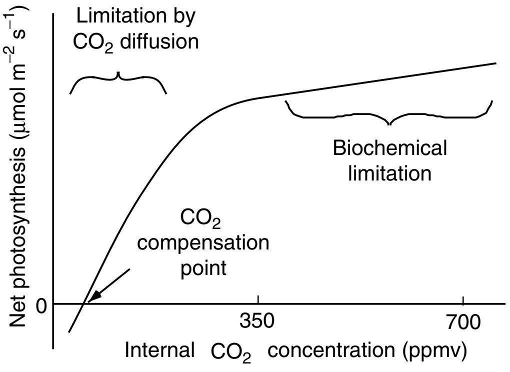

Fig. 5.10 Relationship of the net photosynthetic rate to the CO_2 concentration inside the leaf. Photosynthetic rate is limited by the rate of CO_2 diffusion into the chloroplast in the initial (*left-hand side*) linear portion of the CO_2 response curve and by biochemical processes at higher CO_2 concentrations. The CO_2 compensation point is the minimum CO_2 concentration at which the leaf shows a net gain of carbon

that reacts with CO_2), and changes in stomatal opening have little influence on photosynthesis. At high internal CO_2 concentrations, carboxylation may be limited by: (1) insufficient light (or light-harvesting pigments) to provide energy, (2) insufficient nitrogen invested in photosynthetic enzymes to process the ATP, NADPH, and CO_2 present in the chloroplast, or (3) insufficient phosphate or sugar phosphates to synthesize RuBP.

Under a wide variety of circumstances, terrestrial plants adjust the components of photosynthesis, so CO_2 diffusion and biochemistry are about equally limiting to photosynthesis (Farquhar and Sharkey 1982), causing plants to respond to both CO_2 availability and biochemical limitations (light, nitrogen, or phosphorus). Plants make this adjustment by altering stomatal conductance, which occurs within minutes, or by changing the concentrations of light-harvesting pigments or photosynthetic enzymes, which occurs over days to weeks. The general principle of co-limitation of photosynthesis by biochemistry and diffusion provides the basis for understanding most of the adjustments by individual leaves to minimize the environmental limitations of photosynthesis. Stomatal conductance is regulated, so photosynthesis usually occurs near the break point of the CO_2-response curve (Fig. 5.10; Körner et al. 1979), where CO_2 supply and carbon-fixation capacity are about equally limiting to photosynthesis.

Changes in stomatal conductance by leaves minimize the effects of CO_2 supply on photosynthesis. The free atmosphere is so well mixed that its CO_2 concentration varies globally by only 4% – not enough to cause significant regional variation in photosynthesis. In dense canopies, photosynthesis reduces CO_2 concentration somewhat within the canopy, and soil respiration is a source of CO_2 at the base of the canopy. However, the shade leaves in the lower canopy tend to be light-limited and therefore relatively unresponsive to CO_2 concentration. Consequently, vertical variation in CO_2 concentration within the canopy has relatively little effect on whole-ecosystem photosynthesis (Field 1991).

Although spatial variation in CO_2 concentration does not explain much of the global variation in photosynthetic rate, the 35% increase in atmospheric CO_2 concentration since the beginning of the industrial revolution has caused a general increase in carbon gain by ecosystems (see Chap. 7; Canadell et al. 2007). In both growth-chamber and field studies, a doubling of CO_2 concentration increases photosynthetic rate by 30–50% (Curtis and Wang 1998; Ainsworth and Long 2005). This enhancement of photosynthesis by elevated CO_2 is most pronounced in C_3 plants, especially woody species (Ainsworth and Long 2005). Over time, most plants acclimate to elevated CO_2 by reducing photosynthetic capacity and stomatal conductance, as expected from our hypothesis of co-limitation of photosynthesis by biochemistry and diffusion. This **down-regulation** of CO_2 absorption in response to elevated CO_2 enables plants to sustain carbon uptake, while reducing transpiration rate and their water demand from soils. In this way, elevated CO_2 often stimulates plant growth more strongly by reducing moisture limitation than by its direct effects on photosynthesis. C_4 plants are often just as sensitive to the *indirect* effects of CO_2 as are C_3 plants, so the long-term effects of elevated CO_2 on the competitive balance between C_3 and C_4 plants are difficult to predict (Mooney et al. 1999).

Light Limitation

Physical environment determines light inputs to ecosystems, and leaf area governs the distribution of light within the canopy. Leaves experience large fluctuations (10- to 1,000-fold) in incident light due to changes in sun angle, cloudiness, and the location of **sunflecks** (patches of direct sunlight that penetrate a plant canopy; Fig. 5.11). The vertical distribution of leaf area, however, is the major factor governing the light environment of individual leaves. Light distribution within terrestrial canopies is approximated by an empirical relationship identical to that observed in aquatic ecosystems:

$$I_z = I_o e^{-kLz} \tag{5.3}$$

where I is irradiance at height z (m) beneath the canopy surface, I_o is the irradiance at the top of the canopy, k is the extinction coefficient per unit leaf area, and L is the **leaf area index** (LAI; the projected leaf area per unit of ground area) above the point of measurement. The actual distribution of light through the canopy is more complex and depends on the balance of direct and diffuse radiation. LAI is a key parameter governing ecosystem processes because it determines both the area that is potentially available to absorb light and the degree to which light is attenuated through the canopy. LAI is equivalent to the total upper surface area of all leaves per area of ground (or the projected leaf area in the case of cylindrical needle-like leaves).

LAI varies widely among ecosystems but typically has values of 1–8 m^2 leaf m^{-2} ground for ecosystems with a closed canopy. The **extinction coefficient** is a constant that describes the exponential decrease in irradiance through a canopy. It is low for vertically inclined or small leaves (e.g., 0.3–0.5 for grasses), allowing substantial penetration of direct radiation into the canopy, but high for near-horizontal leaves (0.7–0.8). Clumping of leaves around stems, as in conifers, and variable leaf angles is associated with intermediate values for k. Equation (5.3) indicates that light is distributed unevenly in an ecosystem and that the leaves near the top of the canopy capture most of the available light. Irradiance at the ground surface of a forest, for example, is often only 1–2% of that at the top of the canopy, similar to the light available at the bottom of aquatic euphotic zones (Fig. 5.6).

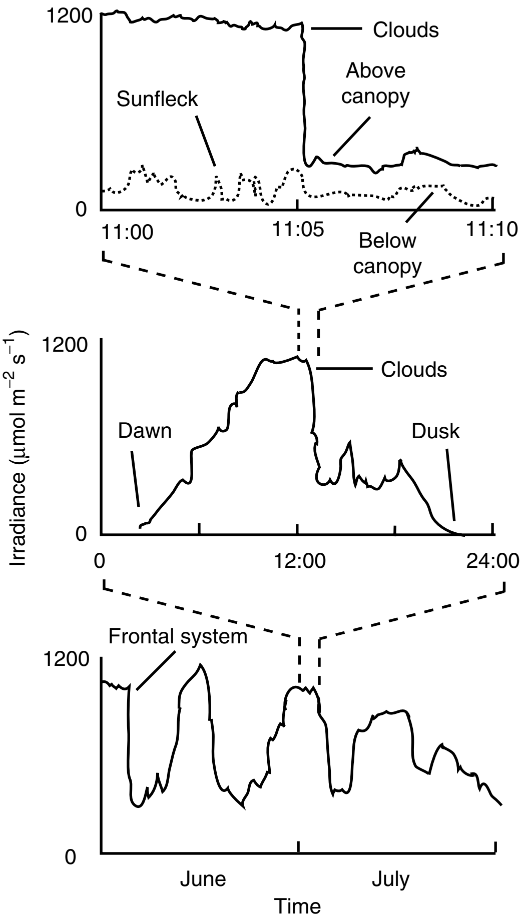

Fig. 5.11 Hypothetical time course of photosynthetically active radiation above and below the canopy of a temperate forest over minutes, hours, and months. Over the course of a few minutes, light at the top of the canopy varies with cloudiness. Beneath the canopy, light also varies due to the presence or absence of sunflecks of direct irradiance, which can last tenths of seconds to minutes. During a day, changes in solar angle and passing clouds cause large changes in light. Convective activity often increases cloudiness in the afternoon. During the growing season, seasonal changes in the solar angle and the passage of frontal systems are the major causes of variation in light. Some times of year have greater frequency of cloudiness than others due to changes in directions of the prevailing winds and the passage of frontal systems

The shape of the light-response curve of photosynthesis in terrestrial plants is identical to that of aquatic algae (Fig. 5.5). Under light-limiting conditions, photosynthesis increases linearly with increasing light availability (constant quantum yield or light-use efficiency). As the light-harvesting capacity of chlorophyll becomes light saturated, photosynthesis reaches its maximum rate (photosynthetic capacity). At extremely high light, photosynthesis may decline due to photo-oxidation of pigments and enzymes, just as in phytoplankton (Fig. 5.5).

In response to fluctuations in light availability over minutes to hours (Fig. 5.11), plants alter stomatal conductance to adjust CO_2 supply to meet the needs of carbon-fixation reactions (Pearcy 1990; Chazdon and Pearcy 1991). Stomatal conductance increases in high light, when CO_2 demand is high, and decreases in low light, when photosynthetic demand for CO_2 is low. These stomatal adjustments result in a relatively constant CO_2 concentration inside the leaf, as expected from our hypothesis of co-limitation of photosynthesis by biochemistry and diffusion. It allows plants to conserve water under low light and to maximize CO_2 absorption at high light.

Over longer time scales (days to months), plants respond to variations in light availability by producing leaves with different photosynthetic properties. This *physiological adjustment by an organism* in response to a change in some environmental parameter is known as **acclimation**. Leaves at the top of the canopy (**sun leaves**) have more cell layers, are thicker, and therefore have a higher photosynthetic capacity per unit leaf area than do **shade leaves** produced under low light (Terashima and Hikosaka 1995; Walters and Reich 1999). The respiration rate of a tissue depends on its protein content (see Chap. 6), so the low photosynthetic capacity and protein content of shade leaves are associated with a lower respiration rate per unit area than in sun leaves. For this reason, shade leaves maintain a positive carbon balance (photosynthesis minus respiration) under lower light levels than do sun leaves (Fig. 5.12).

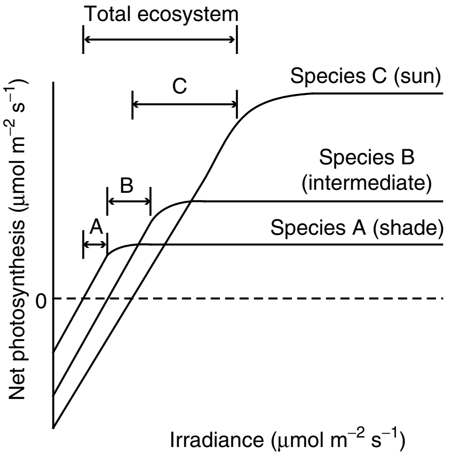

Fig. 5.12 Light response curves of net photosynthesis in plants adapted (or acclimated) to low, intermediate, and high light. *Horizontal arrows* show the range of irradiance over which net photosynthesis is positive and responds linearly to irradiance for each species and for the ecosystem as a whole. Acclimation increases the range of light availability over which net photosynthesis responds linearly to light, i.e., has a constant light-use efficiency

Plants can also produce shade leaves as a result of **adaptation**, the *genetic adjustment by a population* to maximize performance in a particular environment. Species that are *adapted* to high light and intolerant of shade typically have a higher photosynthetic capacity per unit mass or area than do shade-tolerant species, even when growing in the shade (Walters and Reich 1999). The main disadvantage of the high protein and photosynthetic rate typical of shade-intolerant species is that they also have a higher respiration rate, due to their higher protein content. Species that are adapted to low light and are tolerant of shade have a low photosynthetic capacity, but can photosynthesize at lower light levels than shade-intolerant species. In other words, they have a low light compensation point. At the light compensation point, leaf respiration completely offsets photosynthetic carbon gain, resulting in zero net photosynthesis (Fig. 5.5). A mature shaded leaf typically does not import carbon from the rest of the plant, so the leaf senesces and dies if it falls below the light compensation point for a long time. This puts an upper limit on the leaf area that an ecosystem can support, regardless of how favorable the climate and supply of soil resources may be. On average, the leaf-level light compensation point of shade-tolerant species is about half of that of shade-intolerant species (Craine and Reich 2005).

Variations in leaf angle also influence the efficiency with which a plant canopy uses light. At high light, plants produce leaves that are steeply angled, so they absorb less light (see Chap. 4). This is advantageous because it reduces the probability of overheating or photo-oxidation of photosynthetic pigments at the top of the canopy. At the same time, it allows more light to penetrate to lower leaves. Leaves at the bottom of the canopy, on the other hand, are more horizontal in orientation to maximize light capture and are produced in an arrangement that minimizes overlap with other leaves of the plant (Craine 2009).

Do differences in light availability explain the differences among ecosystems in carbon gain? In midsummer, when plants of most ecosystems are photosynthetically active, the daily input of visible light is nearly as great in the Arctic as in the tropics but is spread over more hours and is more diffuse at high latitudes (Billings and Mooney 1968). The greater daily carbon gain in the tropics than at high latitudes is therefore unlikely to be a simple function of the light available to drive photosynthesis. Neither can variation in light availability due to cloudiness explain differences among ecosystems in energy capture. The most productive ecosystems on Earth, the tropical and temperate rainforests, have a high frequency of cloudiness, whereas arid grasslands and deserts, which are less cloudy and receive nearly 10-fold more light annually, are less productive. Seasonal and interannual variations in irradiance can, however, contribute to temporal variation in carbon gain by ecosystems. Aerosols emitted by volcanic eruptions and fires, for example, can reduce solar irradiance and photosynthesis over large areas in particular years. Similarly, photosynthesis (GPP) of the Amazon rainforest is greater in the dry season than under the cloudy conditions of the wet season (Saleska et al. 2007). In summary, light availability strongly influences daily and seasonal patterns of carbon input and the distribution of photosynthesis within the canopy, but it is only a minor factor explaining regional variations in annual carbon inputs to ecosystems (Fig. 5.2).

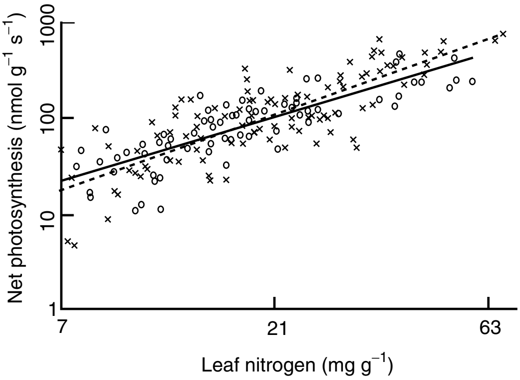

Fig. 5.13 Relationship between leaf-nitrogen concentration and maximum photosynthetic capacity (photosynthetic rate measured under favorable conditions) for plants from Earth's major biomes. *Circles* and the *solid regression line* are for 11 species from 6 biomes using a common methodology. *Crosses* and the *dashed regression line* are data from the literature. Redrawn from Reich et al. (1997)

Nitrogen Limitation and Photosynthetic Capacity

Vascular plant species differ 10 to 50-fold in their photosynthetic capacity. Photosynthetic capacity is the photosynthetic rate per unit leaf mass measured under favorable conditions of light, moisture, and temperature. It is a measure of the carbon-gaining potential *per unit of biomass invested in leaves*. Photosynthetic capacity correlates strongly with leaf nitrogen concentration (Fig. 5.13; Field and Mooney 1986; Reich et al. 1997, 1999; Wright et al. 2004) because photosynthetic enzymes account for a large proportion of the nitrogen in leaves (Fig. 5.2). Many ecological factors can lead to a high leaf-nitrogen concentration and therefore a high photosynthetic capacity. Plants growing in high-nitrogen soils, for example, have higher tissue nitrogen concentrations and photosynthetic rates than do the same species growing on less fertile soils. This acclimation of plants to a high nitrogen supply contributes to the high photosynthetic rates in agricultural fields and other ecosystems with a rapid nitrogen

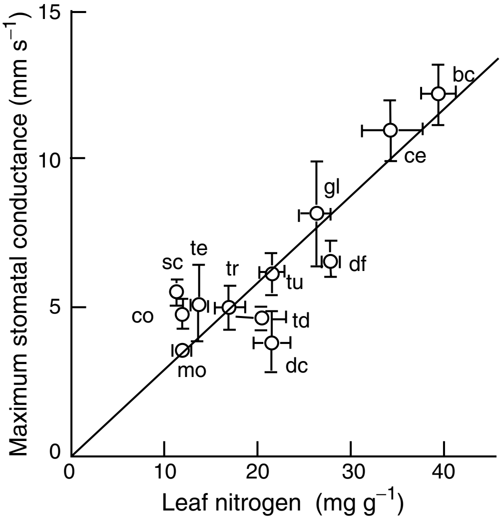

Fig. 5.14 Relationship between leaf-nitrogen concentration and maximum stomatal conductance of plants from Earth's major biomes. Each point and its standard error represent a different biome: bc, broad-leafed crops; ce, cereal crops; co, evergreen conifer forest; dc, deciduous conifer forest; df, tropical dry forest; gl, grassland; mo, monsoonal forest; sc, sclerophyllous shrub; sd, dry savanna; sw, wet savanna; tc, tropical tree crop; td, temperate deciduous broadleaved forest; te, temperate evergreen broadleaved forest; tr, tropical wet forest; tu, herbaceous tundra. Redrawn from Schulze et al. (1994)

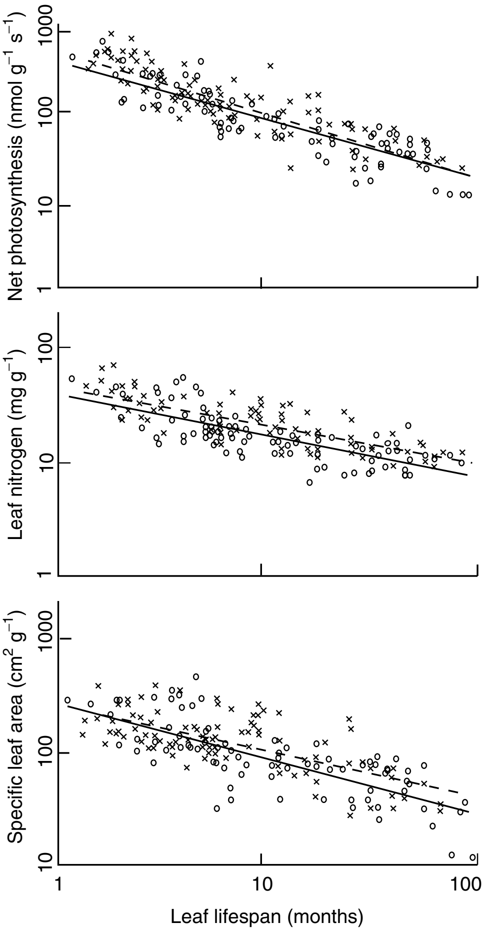

Fig. 5.15 The effect of leaf life span on photosynthetic capacity, leaf-nitrogen concentration, and specific leaf area. Symbols as in Fig. 5.13. Redrawn from Reich et al. (1997)

turnover. Many species differ in their leaf-nitrogen concentration, even when growing in the same soils. Species adapted to productive habitats usually produce leaves that are short-lived and have high tissue-nitrogen concentrations and high photosynthetic rates. Nitrogen-fixing plants also typically have high leaf-nitrogen concentrations and correspondingly high photosynthetic rates. In summary, regardless of the cause of variation in leaf-nitrogen concentration, there is always a strong positive correlation between leaf-nitrogen concentration and photosynthetic capacity (Fig. 5.13; Reich et al. 1997; Wright et al. 2004).

Plants with a high photosynthetic capacity have a high stomatal conductance, in the absence of environmental stress (Fig. 5.14), as expected from our hypothesis of co-limitation of photosynthesis by biochemistry and diffusion. This enables plants with a high photosynthetic capacity to absorb CO_2 rapidly, despite high rates of water loss. Conversely, species with a low photosynthetic capacity conserve water as a result of their lower stomatal conductance.

There appears to be an unavoidable tradeoff between traits that maximize photosynthetic rate and traits that maximize leaf longevity (Fig. 5.15; Reich et al. 1997, 1999; Wright et al. 2004). Many plant species that grow in low-nutrient environments produce long-lived leaves because nutrients are insufficient to support rapid leaf turnover (Chapin 1980; Craine 2009). Shade-tolerant species also produce longer-lived leaves than do shade-intolerant species (Reich et al. 1999; Wright et al. 2004). Long-lived leaves typically have a low leaf-nitrogen concentration and a low photosynthetic capacity; they must therefore photosynthesize for a relatively long time to break even in their lifetime carbon budget (Gulmon and Mooney 1986; Reich et al. 1997). To survive, long-lived leaves must have enough structural rigidity to withstand drought and winter desiccation. These structural requirements cause leaves to be dense, i.e., to have a small surface area per unit of biomass, termed **specific leaf area** (SLA). Long-lived leaves must also be well defended against herbivores and pathogens, if they are to persist. This requires substantial allocation to lignin, tannins, and other non-nitrogenous compounds that deter herbivores, but also contribute to tissue mass and a low SLA.

The broad relationship among species with respect to photosynthetic rate and leaf life span is similar in all biomes; a twofold decrease in leaf life span gives rise to about a fivefold increase in photosynthetic capacity (Reich et al. 1999; Wright et al. 2004).

Plants in productive environments produce short-lived leaves with a high tissue-nitrogen concentration and a high photosynthetic capacity; this allows a large carbon return per unit of biomass invested in leaves, if enough light is available. These leaves have a high SLA, which maximizes the quantity of leaf area displayed and the light captured per unit of leaf mass. The resulting high rates of carbon gain support a high maximum relative growth rate in the absence of environmental stress or competition from other plants (Fig. 5.16; Schulze and Chapin 1987). Many early successional habitats, such as recently abandoned agricultural fields, canopy gaps, or post-fire sites, have enough light, water, and nutrients to support high growth rates and are characterized by species with short-lived leaves, high tissue-nitrogen concentration, high SLA, and high photosynthetic rate (see Chap. 12). Even in late succession, environments with high water and nutrient availability are characterized by canopy species with relatively high nitrogen concentration and photosynthetic rate. Plants in the canopy of these habitats can grow quickly to replace leaves removed by herbivores or to fill canopy gaps produced by death of branches or individuals.

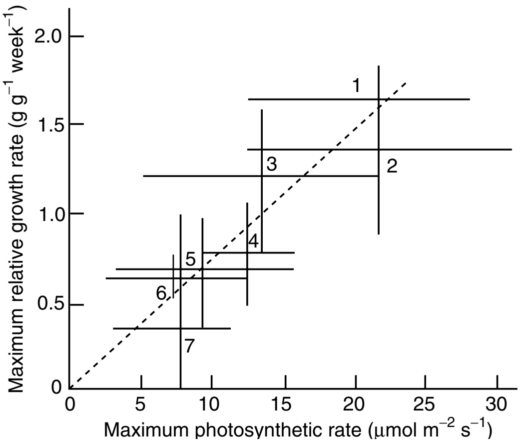

Fig. 5.16 Relationship between maximum photosynthetic rate and maximum relative growth rate for major plant growth forms: (1) agricultural crop species, (2) herbaceous sun species, (3) grasses and sedges, (4) summer deciduous trees, (5) evergreen and deciduous dwarf shrubs, (6) herbaceous shade species and bulbs; (7) evergreen conifers. Redrawn from Schulze and Chapin (1987)

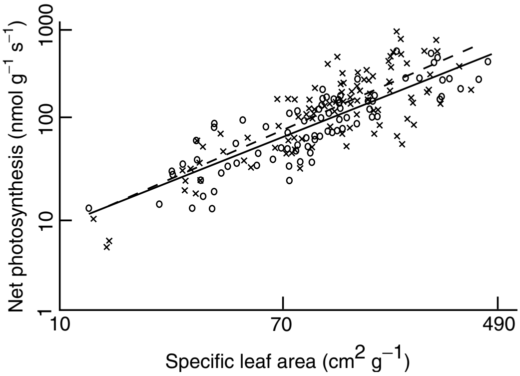

Fig. 5.17 The relationship between specific leaf area (SLA) and photosynthetic capacity. The consistency of this relationship makes it possible to use SLA as an easily measured index of photosynthetic capacity. Symbols as in Fig. 5.13. Redrawn from Reich et al. (1997)

In summary, plants produce leaves with a continuum of photosynthetic characteristics, ranging from short-lived, low-density leaves with a high nitrogen concentration and high photosynthetic rate to long-lived, dense leaves with a low nitrogen concentration and low photosynthetic rate. These correlations among traits are so consistent that SLA is often used in ecosystem comparisons as an easily measured index of photosynthetic capacity (Fig. 5.17).

There is only modest variation in photosynthetic capacity per unit leaf area because leaves with a high photosynthetic capacity per unit leaf biomass also have a high SLA. Photosynthetic capacity or assimilation rate *per unit leaf area* (A_{area}) is a measure of the capacity of leaves to capture a unit of incoming radiation. It is calculated by dividing photosynthetic (assimilation) rate per unit leaf mass (A_{mass}) by SLA.

$$A_{area} = \frac{A_{mass}}{\text{SLA}} \tag{5.4}$$

$$(\text{g cm}^{-2}\,\text{s}^{-1}) = (\text{g g}^{-1}\,\text{s}^{-1}) / (\text{cm}^{2}\,\text{g}^{-1})$$

There is relatively little variation in A_{area} among plants from different ecosystems (Lambers and Poorter 1992). In productive habitats, both mass-based photosynthesis and SLA are high (Fig. 5.15). In unproductive habitats, both of these parameters are low, resulting in modest variation in area-based photosynthetic rate (Lambers and Poorter 1992). To the extent that A_{area} varies among plants, it tends to be higher in species with short-lived leaves (Reich et al. 1997). Mass-based photosynthetic capacity is a good measure of the physiological potential for photosynthesis (the photosynthetic rate per unit of biomass invested in leaves). Area-based photosynthetic capacity is a good measure of the efficiency of these leaves at the ecosystem scale (photosynthetic rate per unit of available light). Variation in soil resources has a much greater effect on the quantity of leaf area produced than on the photosynthetic capacity per unit leaf area.

Water Limitation

Water limitation reduces the capacity of individual leaves to match CO_2 supply with light availability. Water stress is often associated with high light because sunny conditions correlate with low precipitation (low water supply) and with low humidity (high rate of water loss). High light also leads to an increase in leaf temperature and water vapor concentration inside the leaf and therefore greater vapor pressure deficit and water loss by transpiration (see Chap. 4). The high-light conditions in which a plant would be expected to increase stomatal conductance to minimize CO_2 limitations to photosynthesis are therefore often the same conditions in which the resulting transpirational water loss is greatest and most detrimental to the plant. This tradeoff between a response that maximizes carbon gain (stomata open) and one that minimizes water loss (stomata closed) is typical of the physiological compromises faced by plants whose physiology and growth may be limited by more than one environmental resource (Mooney 1972). When water supply is abundant, leaves typically open their stomata in response to high light, despite the associated high rate of water loss. As leaf water stress develops, stomatal conductance declines to reduce water loss (see Fig. 4.17). This decline in stomatal conductance reduces photosynthetic rate and the efficiency of using light to fix carbon (i.e., **light-use efficiency** [LUE]) below levels found in unstressed plants.

Plant acclimation and adaptation to low water is qualitatively different than adaptation to low nutrients (Killingbeck and Whitford 1996; Cunningham et al. 1999; Wright et al. 2001; Craine 2009). Plants in dry habitats typically have thicker leaves, similar leaf-nitrogen concentration, and therefore more nitrogen per unit leaf area than do plants in moist habitats. Dry-site plants also have a low stomatal conductance. This combination of traits enables dry-site plants to maintain higher rates of photosynthesis at a given rate of water loss compared to plants in moist sites (Cunningham et al. 1999; Wright et al. 2001). Dry-site leaves basically service more photosynthetic cells and photosynthetic capacity for a given stomatal conductance.

Plants in dry areas minimize water stress by reducing leaf area (by shedding leaves or producing fewer new leaves). Some drought-adapted plants produce leaves that minimize radiation absorption; their leaves reflect most incoming radiation or are steeply inclined toward the sun (see Chap. 4; Ehleringer and Mooney 1978). High radiation absorption is a *disadvantage* in dry environments because it increases leaf temperature, which increases respiratory carbon loss

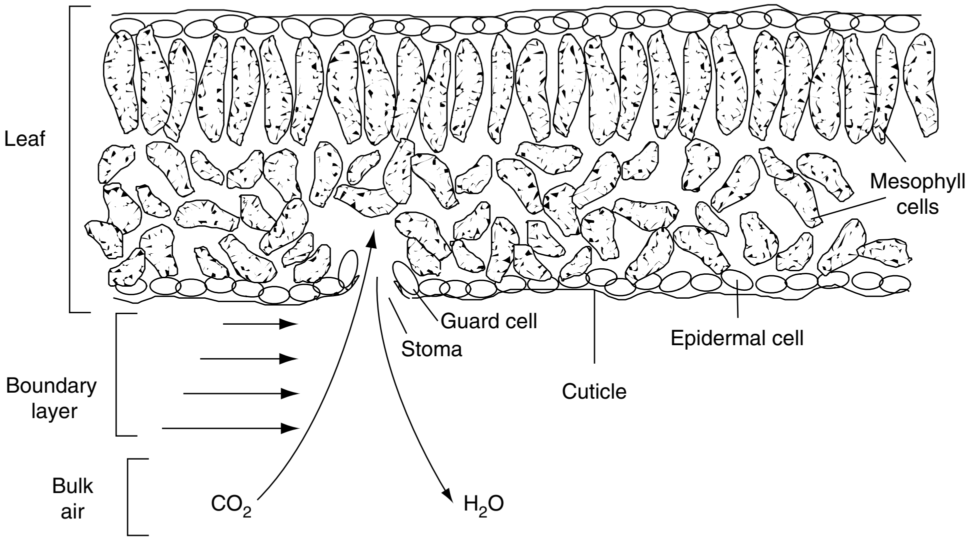

Fig. 5.18 Cross section of a leaf, showing the diffusion pathways of CO_2 and H_2O into and out of the leaf, respectively. Length of the *horizontal arrows* outside the leaf is proportional to wind speeds in the boundary layer

(see Chap. 6) and transpirational water loss (see Chap. 4). Thus plants in dry environments have several mechanisms by which they reduce radiation absorption to conserve water and carbon. The low leaf area, the reflective nature of leaves, and the steep angle of leaves are the main factors accounting for the low absorption of radiation and low carbon inputs in dry environments. In other words, plants adjust to dry environments primarily by altering leaf area and radiation absorption rather than by reducing photosynthetic capacity per unit leaf area.

Water-use efficiency (WUE) of photosynthesis is defined as the carbon gain per unit of water lost. WUE is quite sensitive to the size of stomatal openings because stomatal conductance has slightly different effects on the rates of CO_2 entry and water loss. Water leaving the leaf encounters two resistances to flow: the stomata and the boundary layer of still air on the leaf surface (Fig. 5.18). Resistance to CO_2 diffusion from the bulk air to the site of photosynthesis includes the same stomatal and boundary layer resistances *plus* an additional internal resistance associated with diffusion of CO_2 from the cell surface into the chloroplast and any biochemical limitations associated with carboxylation. Because of this additional resistance to CO_2 movement into the leaf, any change in stomatal conductance has a *proportionately* greater effect on water loss than on carbon gain. In addition, water diffuses more rapidly than does CO_2 because of its smaller molecular mass and the steeper concentration gradient that drives diffusion across the stomata. For all these reasons, as stomata close, water loss declines to a greater extent than does CO_2 absorption. The low stomatal conductance of plants in dry environments results in less photosynthesis per unit of time but greater carbon gain per unit of water loss, i.e., greater WUE. Plants in dry environments also enhance WUE by maintaining a somewhat higher photosynthetic capacity than would be expected for their stomatal conductance, thereby drawing down the internal CO_2 concentration and maximizing the diffusion gradient for CO_2 entering the leaf (Wright et al. 2001). Carbon isotope ratios in plants provide an integrated index of WUE during plant growth because the ^{13}C concentration of newly fixed carbon increases under conditions of low internal CO_2 concentration (Box 5.1; Ehleringer 1993). C_4 and CAM photosynthesis are additional adaptations that augment the WUE of plants, and ultimately ecosystems.

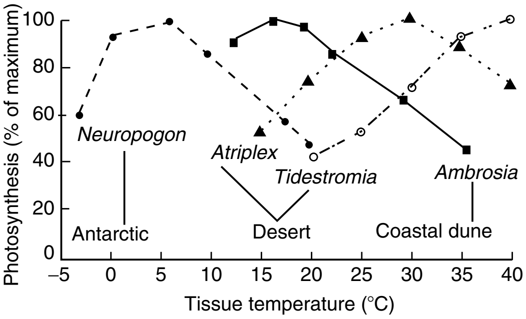

Fig. 5.19 Temperature response of photosynthesis in plants from contrasting temperature regimes. Species include antarctic lichen (*Neuropogon acromelanus*), a cool coastal dune plant (*Ambrosia chamissonis*), an evergreen desert shrub (*Atriplex hymenelytra*), and a summer-active desert perennial (*Tidestromia oblongifolia*). Redrawn from Mooney (1986)

Temperature Effects

Extreme temperatures limit carbon absorption. Photosynthetic rate is typically highest near leaf temperatures commonly experienced on sunny days (Fig. 5.19). Leaf temperature may differ substantially from air temperature due to the cooling effects of transpiration, the effects of leaf surface properties on energy absorption, and the influence of adjacent surfaces on the thermal and radiation environment of the leaf (see Chap. 4). At low temperatures, photosynthesis is limited directly by temperature, as are all chemical reactions. At high temperatures, photosynthesis also declines, due to increased photorespiration and, under extreme conditions, enzyme inactivation and destruction of photosynthetic pigments. Temperature *extremes* often have a greater effect on photosynthesis than does *average* temperature because of damage to photosynthetic machinery (Berry and Björkman 1980; Waring and Running 2007).

Several factors minimize the sensitivity of photosynthesis to temperature. The enzymatically controlled carbon-fixation reactions are typically more sensitive to low temperature than are the biophysically controlled light-harvesting reactions. Carbon-fixation reactions therefore tend to limit photosynthesis at low temperature. Plants adapted to cold climates compensate for this by producing leaves with high concentrations of leaf nitrogen and photosynthetic enzymes, which enable carboxylation to keep pace with the energy supply from the light-harvesting reactions (Berry and Björkman 1980). This explains why arctic and alpine plants typically have high leaf-nitrogen concentrations despite low soil-nitrogen availability (Körner and Larcher 1988). Plants in cold environments also have hairs and other morphological traits that raise leaf temperature above air temperature (Körner 1999). In hot environments with an adequate water supply, plants produce leaves with high photosynthetic rates. The associated high transpiration rate cools the leaf, often reducing leaf temperature below air temperature.

In hot, dry environments, plants close stomata to conserve water, and the cooling effect of transpiration is reduced. Plants in these environments often produce small leaves, which shed heat effectively and maintain temperatures close to air temperature (see Chap. 4). In summary, despite the sensitivity of photosynthesis to short-term variation in temperature, leaf properties minimize the differences in leaf temperature among ecosystems, and plants acclimate and adapt so there is no clear relationship between temperature and average photosynthetic rate of leaves in the field, when ecosystems are compared.

Pollutants

Pollutants reduce carbon gain, primarily by reducing leaf area or photosynthetic capacity. Many pollutants, such as SO_2 and ozone, reduce photosynthesis through their effects on growth and the production of leaf area. Pollutants also directly reduce photosynthesis by entering the stomata and damaging the photosynthetic machinery, thereby reducing photosynthetic capacity (Winner et al. 1985). Plants then reduce stomatal conductance to balance CO_2 absorption with the reduced capacity for carbon fixation. This reduces the entry of pollutants into the leaf, reducing the vulnerability of the leaf to further injury. Plants growing in low-fertility or dry conditions are pre-adapted to pollutant stress because their low stomatal conductance minimizes the quantity of pollutants entering leaves. Pollutants therefore affect these plants less than they affect rapidly growing crops and other plants with high stomatal conductance.

Terrestrial GPP

GPP of terrestrial ecosystems integrates the effects of environmental factors and leaf photosynthetic properties through the canopy. GPP is the sum of the net photosynthesis by all photosynthetic tissue measured at the ecosystem scale. The controls over GPP in terrestrial ecosystems are more complex than in aquatic systems for at least three reasons: (1) Unlike aquatic systems, both the quantity and photosynthetic properties of terrestrial photosynthetic tissues change from the top to the bottom of the canopy. (2) In addition to light and nutrients, which influence photosynthesis in all ecosystems, terrestrial photosynthesis is sensitive to the availability of water and the delivery of CO_2 to photosynthetic cells. (3) The structure of the plant canopy influences the delivery of light and CO_2 to, and the loss of water from, photosynthetic cells. Despite these complexities, recent technological developments allow measurement of fluxes of CO_2 and other compounds at scales of tens to thousands of square meters, making it possible to measure whole-ecosystem carbon fluxes even in large-statured ecosystems like forests (Baldocchi 2003). These measurements, when combined with simulation modeling, permit estimation of GPP and other ecosystem carbon fluxes (see Box 7.2). In this chapter, we focus on ecological controls over GPP and consider its role in the ecosystem carbon balance in Chap. 7.

Canopy Processes

The vertical profile of leaf photosynthetic properties in a canopy maximizes GPP in terrestrial ecosystems. In contrast to pelagic ecosystems, leaves in terrestrial canopies remain fixed in the same vertical location throughout their lives. Their photosynthetic properties are therefore adapted and acclimated to the environment where they are situated. In most closed-canopy ecosystems, for example, photosynthetic capacity of individual leaves decreases exponentially through the canopy in parallel with the exponential decline in irradiance (Eq. (5.3); Hirose and Werger 1987). This is radically different from aquatic ecosystems, where turbulence causes regular mixing of the algal cells in surface waters, and algae at all depths have a low photosynthetic capacity typical of shade plants. The matching of photosynthetic capacity to light availability in terrestrial ecosystems is the response we expect from individual leaves within the canopy because it maintains the co-limitation of photosynthesis by diffusion and biochemical processes in each leaf. The matching of photosynthetic capacity to light availability occurs through the preferential transfer of nitrogen to leaves at the top of the canopy. At least three processes cause this to occur. (1) New leaves are produced primarily at the top of the canopy where light availability is highest, causing nitrogen to be transported to the top of the canopy (Field 1983; Hirose and Werger 1987). (2) Leaves at the bottom of the canopy senesce when they become shaded below their light compensation point. Much of the nitrogen resorbed from these senescing leaves (see Chap. 8) is transported to the top of the canopy to support the production of young leaves with high photosynthetic capacity. (3) Sun leaves at the top of the canopy develop more cell layers than shade leaves and therefore contain more nitrogen per unit leaf area. The accumulation of nitrogen at the top of the canopy is most pronounced in dense canopies, which develop under circumstances of high water and nitrogen availability (Field 1991). In environments where leaf area is limited by water, nitrogen, or time since disturbance, there is less advantage to concentrating nitrogen at the top of the canopy because light availability is high throughout the canopy. In these sparse canopies, light availability, nitrogen concentrations, and photosynthetic rates show a more uniform vertical distribution.

Canopy-scale relationships between light and nitrogen occur even in multi-species communities. In a single individual, there is an obvious selective advantage to optimizing nitrogen distribution within the canopy because this provides the greatest carbon return per unit of nitrogen invested in leaves. We know less about the factors governing carbon gain in multi-species

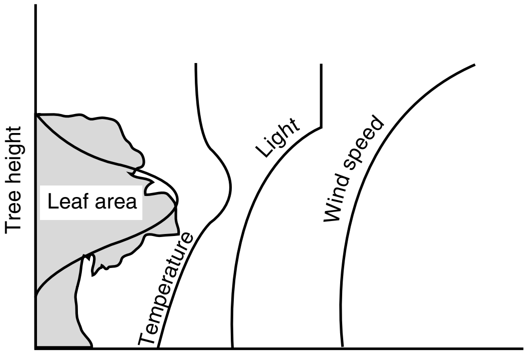

Fig. 5.20 Typical vertical gradients in leaf area, temperature, light, and wind speed in a forest. Temperature is highest in the mid-canopy where most energy is absorbed. Based on Landsberg and Gower (1997)

stands. In such stands, the individuals at the top of the canopy account for most of the photosynthesis and may be able to support greater root biomass to acquire more nitrogen, compared to smaller subcanopy or understory individuals. This specialization and competition among individuals probably contributes to the vertical scaling of nitrogen and photosynthesis observed in multi-species stands (Craine 2009).

Vertical gradients in other environmental variables often reinforce the maximization of carbon gain near the top of the canopy. The canopy modifies not only light availability but also other variables that influence photosynthetic rate, including wind speed, temperature, relative humidity, and CO_2 concentration (Fig. 5.20). The most important of these effects is the decrease in wind speed from the free atmosphere to the ground surface. The friction of air moving across Earth's surface causes wind speed to decrease exponentially from the free atmosphere to the top of the canopy. In other words, Earth's surface creates a boundary layer similar to that which develops around individual leaves (Fig. 5.18). Wind speed continues to decrease from the top of the canopy to the ground surface in ways that depend on canopy structure. Smooth canopies, characteristic of crops or grasslands, show a gradual decrease in wind speed from the top of the canopy to the ground surface, whereas rough canopies, characteristic of many forests, create more friction and turbulence that increases the vertical mixing of air within the canopy (see Chap. 4; McNaughton and Jarvis 1991). For this reason, gas exchange in rough canopies is more tightly **coupled** to conditions in the free atmosphere than in smooth canopies.

Wind speed is important because it reduces the thickness of the boundary layer of still air around each leaf, producing steeper gradients in temperature and in concentrations of CO_2 and water vapor from the leaf surface to the atmosphere. This speeds the diffusion of CO_2 into the leaf and the loss of water from the leaf, enhancing both photosynthesis and transpiration. A reduction in thickness of the leaf boundary layer also brings leaf temperature closer to air temperature. The net effect of wind on photosynthesis is generally positive at moderate wind speeds and adequate moisture supply, enhancing photosynthesis at the top of the canopy, where wind speed is highest. When low soil moisture or a long pathway for water transport from the soil to the top of the canopy reduces water supply to the uppermost leaves, as in tall forests, the uppermost leaves reduce their stomatal conductance, causing the zone of maximum photosynthesis to shift farther down in the canopy. Although multiple environmental gradients within the canopy have complex effects on photosynthesis, they probably enhance photosynthesis near the top of canopies in those ecosystems with enough water and nutrients to develop dense canopies. Variations in light and water availability and leaf-nitrogen concentrations then cause diurnal and seasonal shifts the height of maximum photosynthesis within the canopy.

Canopy properties extend the range of light availability over which the light-use efficiency (LUE) of the canopy remains constant. The light-response curve of canopy photosynthesis, measured in closed canopies ($LAI > \approx 3$), saturates at higher irradiance than does photosynthesis by a single leaf (Fig. 5.21) for several reasons (Jarvis and Leverenz 1983). The more vertical angle of leaves in the upper canopy reduces the probability of their becoming light saturated and increases light penetration into the canopy. The clumped distribution of leaves in shoots, branches, and crowns also increases light penetration into the canopy. Conifer canopies are particularly effective in distributing light through the canopy due to the clumping of needles around stems. This could explain why conifer forests often

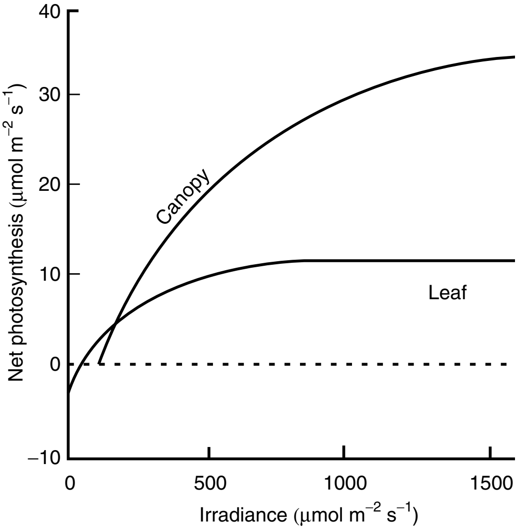

Fig. 5.21 Light response curve of photosynthesis in a single leaf and a forest canopy. Canopies maintain a relatively constant LUE (linear response of photosynthesis to light) over a broader range of light availability than do individual leaves. Redrawn from Ruimy et al. (1995)

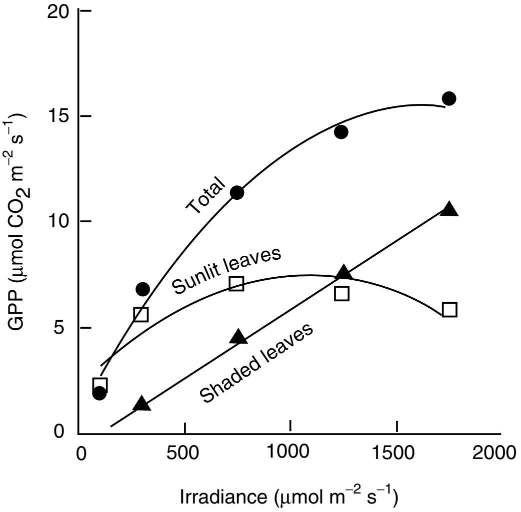

Fig. 5.22 Light response curve of GPP of a deciduous forest, showing the contributions of shaded and sunlit leaves, as calculated by the model CANVEG. Redrawn from Law et al. (2002)

support a higher LAI than deciduous forests. The light compensation point also decreases from the top to the bottom of the canopy (Fig. 5.12), so lower leaves maintain a positive carbon balance, despite their relatively low light availability. In fact, at high light (and correspondingly high temperature and vapor pressure deficit), photosynthesis may decline in the upper canopy, causing shaded leaves to account for most of the total canopy photosynthesis under some circumstances (Fig. 5.22; Law et al. 2002).

In most ecosystems, including all forests that have been measured, GPP approaches a plateau at high light, indicating a decline in LUE at high light (Fig. 5.23; Ruimy et al. 1995; Law et al. 2002; Turner et al. 2003b). This decline in LUE at high light is most pronounced in low-resource environments with sparse canopies, where canopy photosynthetic capacity is low, and all leaves experience a similar light regime (Gower et al. 1999; Baldocchi and Amthor 2001; Turner et al. 2003b). In other words, canopy photosynthetic response to light mirrors a photosynthetic response that is similar to that of all individual leaves. In dense canopies, more leaves are shaded and operate in the linear portion of the light-response curve, increasing LUE of the canopy as a whole (Fig. 5.23; Teskey et al. 1995; Turner et al. 2003b).

Leaf Area

Variation in soil resource supply accounts for much of the spatial variation in leaf area and GPP among ecosystem types. Analysis of satellite imagery shows that about 70% of the ice-free terrestrial surface has relatively open canopies (LAI < 1; Fig. 5.24; Graetz 1991). GPP correlates closely with leaf area below an LAI of about 4 (Schulze et al. 1994), suggesting that leaf area is a critical determinant of GPP on most of Earth's terrestrial surface, just as algal biomass or chlorophyll is a key determinant of pelagic GPP (Fig. 5.1). GPP is less sensitive to LAI in dense canopies because the leaves in the middle and bottom of the canopy contribute relatively little to GPP over the course of a day or year. The availability of soil resources, especially water and nutrient supply, is a critical determinant of LAI for two reasons: (1) Plants in high-resource environments produce a large amount of leaf biomass, and (2) leaves produced in these environments have a high SLA, i.e.,

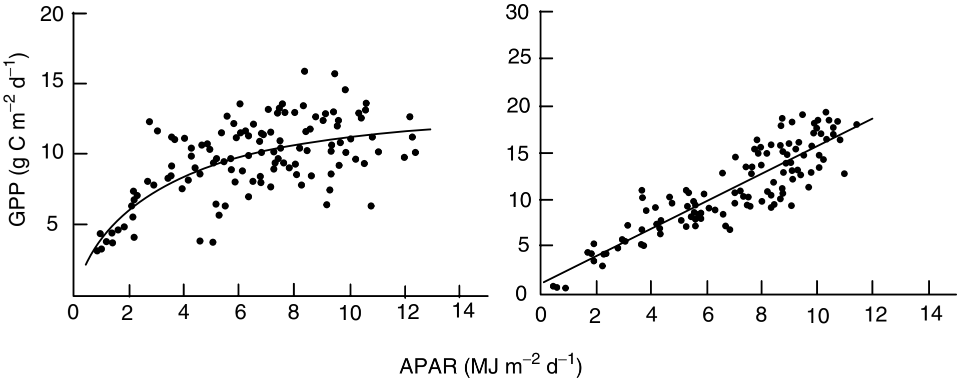

Fig. 5.23 Response of GPP to absorbed photosynthetically active radiation (APAR) in a Massachusetts deciduous forest (*left*) and a Kansas grassland (*right*). The forest maintains a relatively constant light-use efficiency up to 30–50% of full sun, although there is considerable variability. The grassland maintains a constant light-use efficiency over the entire range of naturally occurring irradiance. Redrawn from Turner et al. (2003b)

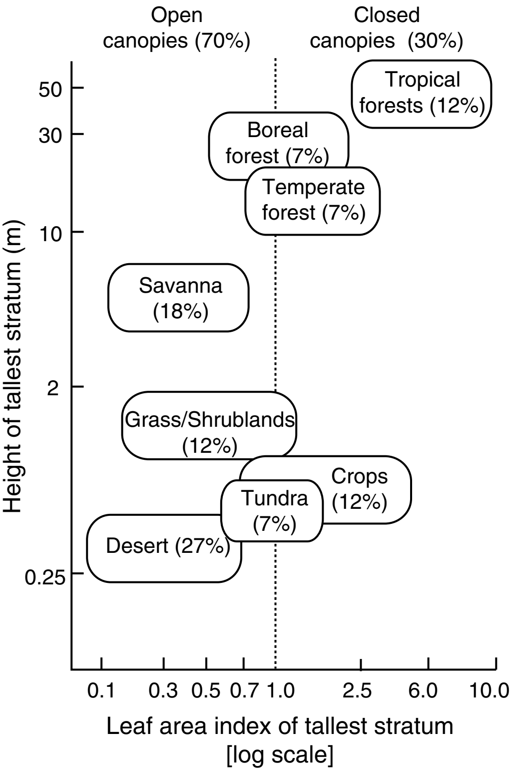

Fig. 5.24 LAI and canopy height of the major biomes. Typical values for that biome and the percentage of the terrestrial surface that it occupies are shown. The vertical line shows 100% canopy cover (LAI = 1). Redrawn from Graetz (1991)

a large leaf area per unit of leaf biomass. As discussed earlier, a high SLA maximizes light capture and therefore carbon gain per unit of leaf biomass (Fig. 5.17; Lambers and Poorter 1992; Reich et al. 1997; Wright et al. 2004).

Disturbances, herbivory, and pathogens reduce leaf area below levels that resources can support. Soil resources and light extinction through the canopy determine the upper limit to the leaf area that an ecosystem can support. However, many factors regularly reduce leaf area below this potential LAI. Drought and freezing are climatic factors that cause plants to shed leaves. Other causes of leaf loss include physical disturbances (e.g., fire and wind) and biotic agents (e.g., herbivores and pathogens). After major disturbances, the remaining plants may be too small, have too few meristems, or lack the productive potential to quickly produce the leaf area that could potentially be supported by the climate and soil resources of a site. For this reason, LAI tends to increase with time after disturbance to an asymptote, then (at least in forests) often declines in late succession (see Chap. 12).

Human activities increasingly affect the leaf area of ecosystems in ways that cannot be predicted from climate. Overgrazing by cattle, sheep, and goats, for example, directly removes leaf area and causes shifts to vegetation types that are less productive and have less leaf area than would otherwise occur in that climate zone (Reynolds and Stafford Smith 2002). Acid rain and other pollutants can also cause leaf loss. Nitrogen deposition can stimulate leaf production above levels that would be predicted from climate and soil type, just as nutrient and water additions to agricultural fields augment LAI and therefore GPP. Because of human activities, LAI cannot be estimated simply from correlations with climate. Fortunately, satellites provide the opportunity to estimate LAI directly, although the technology is still improving. Satellites tend to underestimate the LAI of dense canopies because they cannot "see" all the leaves. LIDAR (Light Detection and Ranging) uses reflection of light pulses (lasers) to detect three-dimensional canopy structure, much like radar, and shows promise in improving remote-sensing estimates of LAI. Fortunately, most of the world's canopies are relatively open, so their LAI can be estimated relatively accurately from satellites. Information about global distribution of LAI is an important input to models that calculate regional patterns of carbon input to terrestrial ecosystems (Running et al. 2004).

Length of the Photosynthetic Season

The length of the photosynthetic season accounts for much of the ecosystem differences in GPP. Most ecosystems experience times that are too cold or too dry for significant photosynthesis to occur. During winter in cold climates and times with negligible soil water in dry climates, plants either die (annuals), lose their leaves (deciduous plants), or become physiologically dormant (some evergreen plants). During these times, there is negligible carbon absorption by the ecosystem, regardless of light availability and CO_2 concentration. In a sense, the non-photosynthetic season is simply a case of extreme environmental stress. At high latitudes and altitudes and in dry ecosystems, this is probably *the* major constraint on carbon inputs to ecosystems (Fig. 5.2; see Chap. 6; Körner 1999). For annuals and deciduous plants, the lack of leaf area is sufficient to explain the absence of photosynthetic carbon gain in the nongrowing season. Lack of water or extremely low temperatures can, however, prevent even evergreen plants from gaining carbon. Some evergreen species partially disassemble their photosynthetic machinery during the nongrowing season. These plants require some time after the return of favorable environmental conditions to reassemble their photosynthetic machinery (Bergh and Linder 1999), so not all early-season irradiance is used efficiently to gain carbon (Xiao et al. 2010). In tropical ecosystems, however, where conditions are more continuously favorable for photosynthesis, leaves maintain their photosynthetic machinery from the time they are fully expanded until they are shed. Models that simulate GPP often define the length of the photosynthetic season in terms of thresholds of minimum temperature or moisture below which plants do not produce leaves or do not photosynthesize (Running et al. 2004).

Environmental controls over GPP during the growing season are similar to those described for net photosynthesis of individual leaves. Soil resources (nutrients and moisture) influence GPP primarily through their effects on photosynthetic potential and leaf area rather than through variations in the efficiency of converting light to carbohydrates (Turner et al. 2003b). Consequently, *ecosystem differences* in GPP depend more strongly on differences in the quantity of light absorbed and length of photosynthetic season than on the efficiency of converting light to carbohydrates (i.e., LUE).

The *seasonal changes* in GPP depend on both the seasonal patterns of leaf area development and loss and the photosynthetic response of individual leaves to variations in light and temperature, which influence LUE. These environmental factors have a particularly strong effect on leaves at the top of the canopy, which account for most GPP. The thinner boundary layer and greater distance for water transport from roots, for example, makes the uppermost leaves particularly sensitive to variation in temperature, soil moisture, and relative humidity.

LUE varies diurnally, being lowest at times of high light. Seasonal patterns of LUE are more complex because they depend not only on light availability but also on seasonal variations in leaf area, canopy nitrogen, and various environmental stresses such as drought and freezing. LUE is highest in high-resource ecosystems such as crops with a high LAI and photosynthetic capacity. LUE is lowest in low-resource ecosystems such as the boreal forest and arid grasslands (Turner et al. 2003b). LUE also declines with increasing temperature (reflecting increases in photorespiration; Lafont et al. 2002; Turner et al. 2003b) and is strongly reduced at extremely low temperatures (Teskey et al. 1995). The detailed patterns and causes of temporal and spatial patterns of LUE and GPP are active research areas that promise to provide important advances in understanding and predicting patterns of carbon inputs to ecosystems (Running et al. 2004; Luyssaert et al. 2007; Waring and Running 2007).

Satellite-Based Estimates of GPP

Satellite-based estimates of absorbed radiation and LUE allow daily mapping of GPP at global scales. An important conclusion of leaf- and canopy-level studies of photosynthesis is that many factors cause convergence of ecosystems toward a relatively similar efficiency of converting absorbed light energy into carbohydrates. (1) All C_3 plants have a similar quantum yield (LUE) at low to moderate irradiance. (2) Penetration of light and vertical variations in photosynthetic properties through a canopy extend the range of irradiance over which LUE remains relatively constant. (3) LUE of a given ecosystem varies primarily in response to light intensity and short-term environmental stresses that reduce stomatal conductance. Over the long term, however, plants respond to environmental stresses by reducing leaf area and the concentrations of photosynthetic pigments and enzymes so photosynthetic capacity matches stomatal conductance. In other words, plants in low-resource environments reduce the amount of light absorbed more strongly than they reduce the efficiency with which absorbed light is converted to carbohydrates. Modeling studies and field measurements suggest that ecosystems differ much more strongly in leaf area and photosynthetic capacity than in LUE (Field 1991; Turner et al. 2003b).

If LUE is indeed similar and shows predictable patterns among ecosystems, GPP can be estimated from satellite measurements of light absorption by ecosystems, and correcting this for known causes of variation in LUE. Leaves at the top of the canopy have a disproportionately large effect on the light that is both absorbed and reflected by the ecosystem. Satellites can measure the incoming and reflected radiation. This similarity in bias between the vertical distribution of absorbed and reflected radiation makes satellites an ideal tool for estimating canopy photosynthesis. The challenge, however, is to estimate the fraction of absorbed radiation that has been absorbed by leaves rather than by soil or other non-photosynthetic surfaces. Vegetation has a different spectrum of absorbed and reflected radiation than does the atmosphere, water, clouds, or bare soil. This occurs because chlorophyll and associated light-harvesting pigments or accessory pigments, which are concentrated at the canopy surface, absorb visible light (VIS) efficiently. The optical properties that result from the cellular structure of leaves, however, make them highly reflective in the near infrared (NIR) range. Ecologists have used these unique properties of vegetation to generate an index of vegetation "greenness": the **normalized difference vegetation index** (**NDVI**).

$$\mathrm{NDVI} = \frac{(\mathrm{NIR} - \mathrm{VIS})}{(\mathrm{NIR} + \mathrm{VIS})} \qquad (5.5)$$

NDVI is approximately equal to the fraction of incoming photosynthetically active radiation (PAR) that is absorbed by vegetation (FPAR):

$$\mathrm{FPAR} \approx \mathrm{NDVI} \approx \mathrm{APAR} / \mathrm{PAR} \qquad (5.6)$$

where APAR is the absorbed photosynthetically active radiation (Running et al. 2004). FPAR can also be measured directly in ecosystems, knowing the irradiance at the top (I_o) and bottom (I_z) of the canopy or the relationship between I_o and leaf area index (LAI, L):

$$\mathrm{FPAR} = 1 - (I_z / I_o) \qquad (5.7)$$

where $I_z = I_o\, e^{-kLz}$, and k is the extinction coefficient (5.3). Sites with a high rate of carbon gain generally have a high NDVI because of their high chlorophyll content (low reflectance of VIS) and high leaf area (high reflectance of NIR). Species differences in leaf structure also influence infrared reflectance (and therefore NDVI). Conifer forests, for example, generally have a lower NDVI than deciduous forests despite their greater leaf area. Consequently, NDVI must be used cautiously when comparing ecosystems dominated by structurally different types of plants (Verbyla 1995). The maximum NDVI measured by satellites is very similar to that measured on the ground (Fig. 5.25). If LUE is known, GPP can be calculated from irradiance (PAR) and FPAR or NDVI:

$$\mathrm{GPP} = \mathrm{LUE} \times \mathrm{FPAR} \times \mathrm{PAR} \approx \mathrm{LUE} \times \mathrm{NDVI} \times \mathrm{PAR} \qquad (5.8)$$

MODIS (Moderate Resolution Imaging Spectroradiometer) sensors carried aboard satellites directly measure reflectance from space, allowing calculation of NDVI. Ecosystem models have estimated LUE for different biomes, under varying conditions of vapor pressure deficit and temperature (Running et al. 2000; White et al. 2000). Using these modeled LUE values (g carbon MJ^{-1}) and observed climate, NDVI and PAR (MJ m^{-2}), daily GPP (g carbon m^{-2}) can now be calculated globally at a 1-km scale (Running et al. 2004). These calculations are based on daily observations of weather, weekly estimates of NDVI, and annual estimates of biome distributions. The methodology for estimating global patterns of GPP is continually being tested and improved. Currently, differences in the scale at which weather observations are made account for much of the discrepancy between GPP estimates from satellites and those measured at specific field sites. Other sources of variation include the controls over GPP that were described in the previous section (Turner et al. 2005; Heinsch et al. 2006). In the conterminous U.S. summer, GPP is highest in fertile moist ecosystems like croplands and deciduous forests and lowest in dry ecosystems like grasslands and forests (Fig. 5.26). Evergreen forests have modest mid-summer GPP but continue photosynthesizing during the winter.

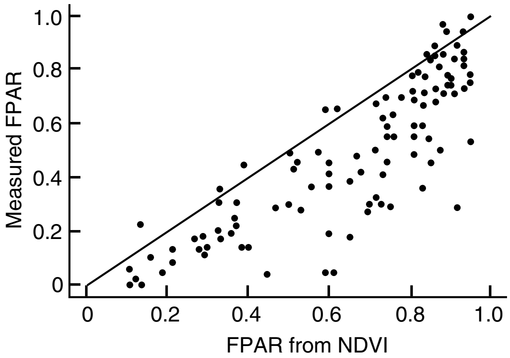

Fig. 5.25 Relationship between FPAR (the fraction of photosynthetically active radiation absorbed by vegetation) estimated from satellite measurements of NDVI (X-axis) and FPAR measured in the field (Y-axis). Data were collected from a wide range of ecosystems, including temperate and tropical grasslands and temperate and boreal conifer forests. Satellites provide an approximate measure of the photosynthetically active radiation absorbed by vegetation and therefore the carbon inputs to ecosystems. Redrawn from Los et al. (2000)

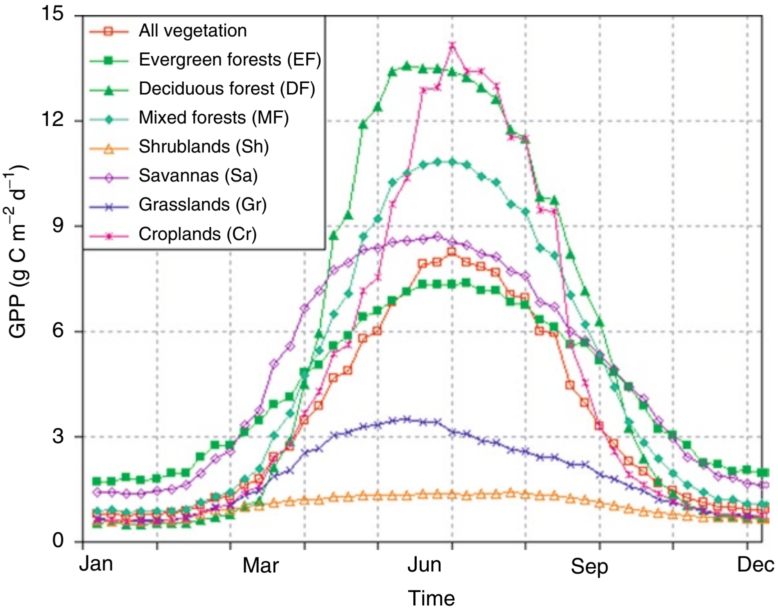

Fig. 5.26 Predicted seasonal pattern of GPP in different biomes of the U.S. averaged from 2001 to 2006, based on a regression model that uses AmeriFlux (a network of ecosystem flux studies) GPP measurements and MODIS satellite imagery. Redrawn from Xiao et al. (2010)

These seasonal and ecosystem differences in GPP are the major factors explaining ecosystem differences in NPP (see Chap. 6) and carbon accumulation (see Chap. 7).

Summary

Most carbon enters terrestrial ecosystems through photosynthesis mediated by primary producers (plants on land and phytoplankton in aquatic ecosystems). The light-harvesting reactions of photosynthesis transform light energy into chemical energy, which is used by the carbon-fixation reactions to convert CO_2 to sugars. The enzymes that carry out these reactions account for about half of the nitrogen in photosynthetic cells.

In pelagic ecosystems, phytoplankton are relatively well mixed throughout the euphotic zone and have photosynthetic properties similar to shade plants. Aquatic GPP depends on the quantity of phytoplankton and the vertical profile of light and other physical factors. Nutrient availability, as affected by stratification and vertical mixing, strongly influences phytoplankton abundance and therefore GPP.

Plants on land adjust the components of photosynthesis so physical and biochemical processes co-limit carbon fixation. At low light, for example, plants reduce the quantity of photosynthetic machinery per unit leaf area by producing thinner leaves. As atmospheric CO_2 concentration increases, plants reduce stomatal conductance. The major environmental factors that explain differences *among* ecosystems in carbon gain are the length of time during which conditions are suitable for photosynthesis and the soil resources (water and nutrients) available to support the production and maintenance of leaf area. Environmental stresses, such as inadequate water supply, extreme temperatures, and pollutants, reduce the efficiency with which plants use light to gain carbon. Plants also respond to these stresses by reducing leaf area and nitrogen content so as to maintain a relatively constant efficiency in the use of light to fix carbon. Consequently, ecosystem differences in photosynthesis at the ecosystem scale (GPP) are determined primarily by leaf area and secondarily by environmental stresses that reduce the efficiency with which these leaves convert light to chemical energy.

Review Questions

1. How do light, CO_2, and nitrogen interact to influence the biochemistry of photosynthesis in C_3 plants? What biochemical adjustments occur when each of these resources declines in availability?
2. Describe the environmental controls over photosynthesis in pelagic ecosystems in terms of the photosynthetic response of individual cells (e.g., light response curve) and ecosystem-scale photosynthesis (GPP).
3. How does each major environmental variable (CO_2, light, nitrogen, water, temperature, pollutants) affect photosynthetic rate in terrestrial plants in the short term? How do plants adjust to changes in each factor over the long term?
4. How does the response of photosynthesis to one environmental variable (e.g., water or nitrogen) affect the response to other environmental variables (e.g., light, CO_2, or pollutants)? Considering these interactions among environmental variables, how might anthropogenic increases in nitrogen inputs affect the response of Earth's ecosystems to rising atmospheric CO_2?
5. How do environmental stresses affect light-use efficiency in the short term? How does vegetation adjust to maximize LUE in stressful environments over the long term?
6. What factors are most important in explaining differences among ecosystems in GPP? Over what timescale does each of these factors have its greatest impact on GPP? Explain your answers.
7. What factors most strongly affect leaf area and photosynthetic capacity of vegetation?
8. How do the factors regulating photosynthesis in a forest canopy differ from those in individual leaves? How do availability of soil resources (water and nutrients) and the structure of the canopy influence the importance of these canopy effects?

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