

**The balance between carbon inputs through gross primary production (GPP) and carbon losses through plant respiration and tissue turnover govern the carbon balance of plants. This chapter describes the factors that regulate this balance.**

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## Introduction

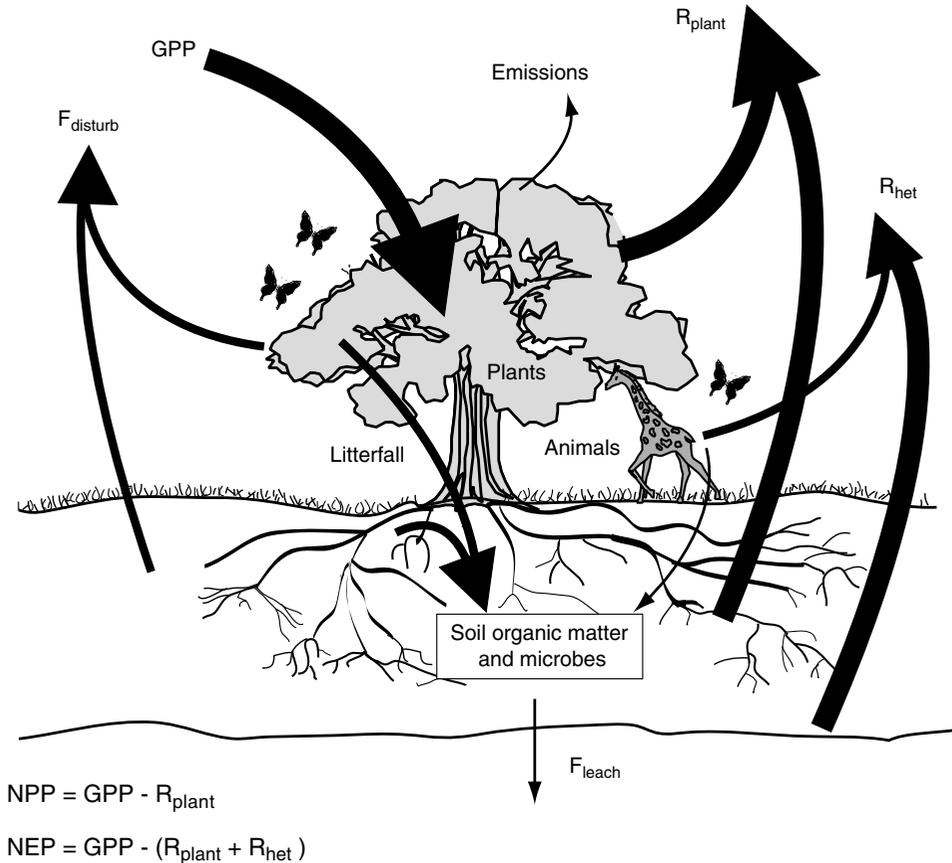
**Plant production determines the amount of energy available to sustain all organisms, including people.** We depend on plant production directly for food and fiber and indirectly because of the critical role of plants in all ecosystem processes. About half of gross primary production (GPP) is respired by plants to provide the energy that supports their growth and maintenance (Schlesinger 1997; Waring and Running 2007). **Net primary production (NPP)** is the net carbon gain by plants and equals the difference between GPP and plant respiration. Plants lose carbon through several pathways besides respiration (Fig. 6.1). These include the death of plants or plant parts (e.g., leaves); the consumption of plants by herbivores; the secretion of water-soluble or volatile organic compounds into the environment; and the targeted transfer of carbon to symbiotically associated microbes (e.g., mycorrhizal fungi and nitrogen-fixing bacteria). Finally, carbon

can be removed from plants by fire, human harvest, and other disturbances.

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## A Focal Issue

**The productivity of the biosphere is concentrated in areas undergoing rapid land-use change.** Tropical wet forests, for example, occupy 12% of terrestrial land area but account for a third of terrestrial primary production (Fig. 6.2). They are being rapidly cleared, much of it by illegal logging (Sampson et al. 2005). Similar high rates of deforestation occurred in the temperate zone centuries earlier and are now returning to forest or being converted to cities (see Chap. 12). Land-use change is equally important at the unproductive end of the spectrum, where lands that are cold and dry (tundra, desert, grasslands, and shrublands) occupy half the terrestrial land area and together contribute about as much productivity as tropical forests. What environmental factors govern the productivity of these changing landscapes? If they are replaced by different vegetation, will they be as productive? The coastal zones of the ocean, which are the marine equivalent of tropical wet forests, are also undergoing rapid changes due to overfishing and nutrient runoff from the land. A clear understanding of factors governing Earth's primary productivity is



**Fig. 6.1** Overview of the major carbon fluxes of an ecosystem. Carbon enters the ecosystem as gross primary production ( $GPP$ ), through photosynthesis by plants. Roots and aboveground portions of plants return about half of this carbon to the atmosphere as plant respiration ( $R_{\text{plant}}$ ). Net primary production ( $NPP$ ) is the difference between carbon gain by  $GPP$  and carbon loss through  $R_{\text{plant}}$ . Most  $NPP$  is transferred to soil organic matter as litterfall, root death, root exudation, and root transfers to symbionts; some  $NPP$  is eaten by animals and sometimes is lost from the ecosystem through disturbance (wildfire or harvest).

Animals also transfer some carbon to soils through excretion and mortality. Most carbon entering the soil is lost through microbial respiration (which, together with animal respiration, is termed heterotrophic respiration:  $R_{\text{het}}$ ). Net ecosystem production ( $NEP$ ) is the balance between  $GPP$  and plant-plus-heterotrophic respiration. Additional carbon is lost from soils through leaching and disturbance. Net ecosystem carbon balance ( $NECB$ ) is the net carbon accumulation by an ecosystem; it equals the carbon inputs from  $GPP$  minus the various avenues of carbon loss (respiration, leaching, disturbance, etc.; see Fig. 7.23)

essential to meet the needs for nature and for human livelihoods in a rapidly changing world.

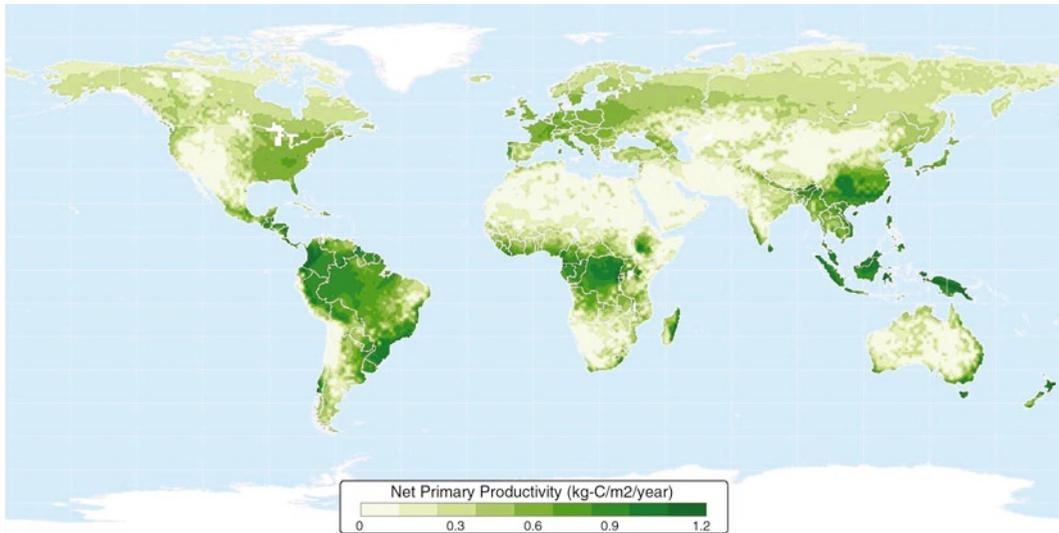
## Plant Respiration

**Respiration provides the energy for a plant to acquire nutrients and to produce and maintain biomass.** Plant respiration is the carbon released by mitochondrial respiration. It is not “wasted” carbon. It serves the essential function

of providing energy for growth and maintenance, just as it does in animals and microbes. We can separate total plant respiration ( $R_{\text{plant}}$ ) into three functional components: growth respiration ( $R_{\text{growth}}$ ), maintenance respiration ( $R_{\text{maint}}$ ), and the respiratory cost of ion absorption ( $R_{\text{ion}}$ ).

$$R_{\text{plant}} = R_{\text{growth}} + R_{\text{maint}} + R_{\text{ion}} \quad (6.1)$$

Each of these respiratory components involves mitochondrial oxidation of carbohydrates to



**Fig. 6.2** The global pattern of net primary productivity (Foley et al. 1996; Kucharik et al. 2000). The patterns of productivity correlate more closely with precipitation than with temperature (see Fig. 2.23), indicating a strong

role of moisture in regulating the productivity of the biosphere. Reproduced from the Atlas of the Biosphere (<http://atlas.sage.wisc.edu>)

**Table 6.1** Concentration and carbon cost of major chemical constituents in a sedge leaf<sup>a</sup>

Component	Concentration (%)	Cost (mg C g <sup>-1</sup> product)	Total cost <sup>b</sup> (mg C g <sup>-1</sup> tissue)
Sugar	11.9	438	52
Nucleic acid	1.2	409	5
Polysaccharide	9.0	467	42
Cellulose	21.6	467	101
Hemicellulose	31.0	467	145
Amino acid	0.9	468	4
Protein	9.7	649	63
Tannin	4.8	767	37
Lignin	4.2	928	39
Lipid	5.7	1,212	69
Total cost			557

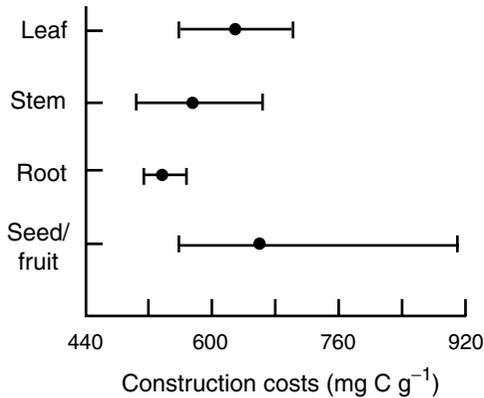
<sup>a</sup>Data from Chapin (1989)

<sup>b</sup>The four most expensive constituents account for 37% of the cost of synthesis but only 24% of the mass of the tissue. The total cost of production (557 mg C g<sup>-1</sup> tissue) is equivalent to 1.23 g carbohydrate per gram of tissue, with 20% of this being respired and 80% incorporated into biomass

produce ATP. They differ only in the *functions* for which ATP is used by the plant. Separation of respiration into these functional components allows us to understand the ecological controls over plant respiration.

**All plants are similar in their efficiency of converting sugars into new biomass.** Growth of new tissue requires biosynthesis of many classes of chemical compounds, including cellulose, proteins,

nucleic acids, and lipids (Table 6.1). The carbon cost of synthesizing each compound includes the carbon that is incorporated into that compound plus the carbon oxidized to CO<sub>2</sub> to provide the ATPs that drive biosynthesis. These carbon costs can be calculated for each class of compound from knowledge of its biosynthetic pathway (Penning de Vries et al. 1974; Amthor 2000). The cost of producing a gram of tissue can then be calculated from the



**Fig. 6.3** Range of construction costs for a survey of leaves ( $n=123$ ), stems ( $n=38$ ), roots ( $n=35$ ), and fruits or seeds ( $n=31$ ). Values are averages with 10th and 90th percentiles in units of  $\text{mg C g}^{-1}$  dry mass. The carbon cost of producing new biomass differs little among plant parts, except for those fruits and seeds that store lipid and have a higher cost of synthesis than do other plant parts. Redrawn from Poorter (1994)

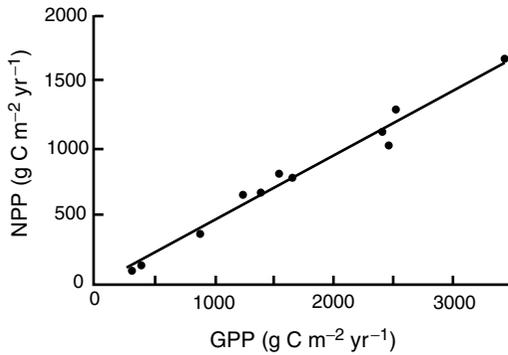
concentration of each class of chemical compound in a tissue and its carbon cost of synthesis.

There is a threefold range in the carbon cost of synthesis of the major classes of chemical compounds found in plants (Table 6.1). The most energetically expensive compounds in plants are proteins, tannins, lignin (vascular land plants only), and lipids. In general, metabolically active tissues, such as leaves, have high concentrations of proteins, tannins, and lipids. The tannins and lipophilic substances such as terpenes serve primarily to defend protein-rich tissues from herbivores and pathogens (see Chap. 10). Structural tissues have high lignin and low protein, tannin, and lipid concentrations. Leaves of rapidly growing species with high protein concentration have higher tannin and lower lignin concentrations than leaves with low protein concentrations. Consequently, most plant tissues contain some expensive constituents, although the nature of these constituents differs among plant parts and species. In fact, the carbon cost of producing plant tissue is surprisingly similar across species, tissue types, and ecosystems (Fig. 6.3; Chapin 1989; Poorter 1994; Villar et al. 2006). These general patterns are observed in both phytoplankton (Hay and Fenical 1988) and terrestrial plants (Chapin 1989).

On average, about 20% of the energy expended in growth is expended as growth respiration, and the remaining 80% is incorporated into new biomass (Table 6.1). The rates of growth and therefore of growth respiration measured at the ecosystem scale ( $\text{g C m}^{-2} \text{ day}^{-1}$ ) increase when temperature and moisture favor growth, but growth respiration is a relatively constant fraction of NPP, regardless of environmental conditions.

**The total respiratory cost of ion absorption probably correlates with NPP.** Ion transport across membranes is energetically expensive and may account for 25–50% of the respiration in roots or phytoplankton cells (Lambers et al. 2008). Several factors cause this cost of ion absorption to differ among ecosystems. The quantity of nutrients absorbed is greatest in productive environments, although the respiratory cost per unit of absorbed nutrients may be greater in unproductive environments (Lambers et al. 2008). The respiratory cost of nitrogen absorption and use depends on the form of nitrogen absorbed because nitrate must be reduced to ammonium (an exceptionally expensive process) before it can be incorporated into proteins or other organic compounds. The cost of nitrate reduction is also variable among terrestrial plant species and ecosystems, depending on whether the nitrate is reduced in roots or leaves (see Chap. 8). In general, we expect  $R_{\text{ion}}$  to correlate with the total quantity of ions absorbed and therefore to show a positive relationship with NPP.

**Maintenance respiration: How variable is the cost of maintaining plant biomass?** All live cells, even those that are not actively growing, require energy to maintain ion gradients across cell membranes and to replace degraded proteins, membranes, and other constituents. Maintenance respiration provides the ATP for these maintenance and repair functions. Laboratory experiments suggest that about 85% of maintenance respiration is associated with the turnover of proteins (about 2–5% turnover per day), explaining why there is a strong correlation between protein concentration and whole-tissue respiration rate in nongrowing tissues (Penning de Vries 1975). We therefore expect maintenance respiration to be greatest in ecosystems with high tissue-nitrogen concentrations or a large plant biomass and thus



**Fig. 6.4** Relationship between GPP and NPP in 11 forests from the U.S., Australia, and New Zealand. These forests were selected from a wide range of moisture and temperature conditions. GPP and NPP were estimated using a model of ecosystem carbon balance. The simulations suggest that all these forests show a similar partitioning of GPP between plant respiration (53%) and NPP (47%), despite large variations in climate. Redrawn from Waring et al. (1998)

to be greatest in productive ecosystems. Simulation models suggest that maintenance respiration may account for about half of total plant respiration; the other half is associated with growth and ion absorption (Lambers et al. 2008).

Maintenance respiration depends on environment as well as tissue chemistry. It increases with temperature because proteins and membrane lipids degrade and must be replaced more rapidly at high temperatures. Drought also imposes short-term metabolic costs associated with synthesis of osmotically active organic solutes (see Chap. 4). These effects of environmental stress on maintenance respiration are the major factors that alter the partitioning between growth and respiration and therefore are the major sources of variability in the efficiency of converting GPP into NPP. Maintenance respiration increases during times of environmental change but, after acclimation, maintenance respiration returns to values close to those predicted from biochemical composition (Semikhatova 2000). Over the long term therefore maintenance respiration may not be strongly affected by environmental stress except in strongly fluctuating environments.

**Plant respiration is a relatively constant proportion of GPP, when ecosystems are compared.** Although the respiration rate of any given

plant increases exponentially with ambient temperature, acclimation and adaptation counterbalance this direct temperature effect on respiration. Plants from hot environments have lower respiration rates at a given temperature than do plants from cold places (Billings and Mooney 1968). The net result of these counteracting temperature effects is that plants from different thermal environments have similar respiration rates, when measured at their average habitat temperature (Semikhatova 2000).

In summary, studies of the basic components of respiration associated with growth, ion absorption, and maintenance suggest that total plant respiration should be a relatively constant fraction of GPP. In phytoplankton, for example, the heat produced by respiration is proportional to biomass (carbon content) across five orders of magnitude in cell mass (Johnson et al. 2009). The predictions are also consistent with more mechanistic modeling of plant carbon balance, which shows that total plant respiration is about half (48–60%) of GPP, when a wide range of ecosystems is compared (Fig. 6.4; Ryan et al. 1994; Landsberg and Gower 1997). In other words, plants have a growth efficiency of about 40–50% – the proportion of GPP that is converted to NPP. Variation in maintenance respiration is the most likely cause for variation in this efficiency. Microbes have a similar growth efficiency (about 40%; see Chap. 9) of producing biomass from their substrates, despite very different mechanisms of acquiring carbon and nitrogen from the environment. This apparent similarity may reflect a common underlying biochemistry of costs of synthesis and maintenance. However, there are too few studies to know how variable this efficiency is among seasons, years, organisms, and ecosystems.

## What Is NPP?

**Net primary production is the net carbon gain by plants.** It is the balance between the carbon gained by GPP and carbon released by plant mitochondrial respiration.

$$NPP = GPP - R_{plant} \quad (6.2)$$

Like GPP, NPP is generally measured at the ecosystem scale, usually over relatively long time intervals, such as a year (g biomass or g C m<sup>-2</sup> year<sup>-1</sup>). NPP includes the new biomass produced by plants, the soluble organic compounds that diffuse or are secreted into the environment (**root or phytoplankton exudation**), the carbon transfers to microbes that are symbiotically associated with roots (e.g., mycorrhizae and nitrogen-fixing bacteria), and the volatile emissions that are lost from leaves to the atmosphere (Clark et al. 2001). Most field measurements of NPP document only the new plant biomass produced and therefore probably underestimate the true NPP by at least 30% (Table 6.2). Root exudates are rapidly taken up and respired by microbes adjacent to roots and are generally measured in field studies as a portion of root respiration. Similarly, pelagic phytoplankton and bacteria often attach to surfaces of organic particles, where bacteria absorb and respire phytoplankton exudates (Mann and Lazier 2006). Volatile emissions are also rarely measured, but are generally a small fraction (<1–5%) of NPP and thus are probably not a major source of error (Guenther et al. 1995). Some biomass dies or is removed by herbivores before it can be measured, so even the new biomass measured in field studies is an underestimate of biomass production. For some purposes, these errors may not be too important. A frequent objective of measuring terrestrial NPP, for example, is to estimate the

rate of biomass increment. Root exudates, transfers to symbionts, losses to herbivores, and volatile emissions are lost from plants and therefore do not directly contribute to biomass increment. Consequently, failure to measure these components of NPP does not bias estimates of biomass accumulation. However, these losses of NPP from plants fuel other ecosystem processes such as herbivory, decomposition, and nutrient turnover and are therefore important components of the overall carbon dynamics of ecosystems and a critical carbon source for microbes (Schlesinger 1997; Mann and Lazier 2006).

Some components of NPP, such as root production, are particularly difficult to measure and have sometimes been assumed to be some constant ratio (e.g., 1:1) of aboveground production (Fahey et al. 1998). Fewer than 10% of the studies that report terrestrial NPP actually measure belowground production (Clark et al. 2001). Estimates of aboveground NPP sometimes include only large plants (e.g., trees in forests) and exclude understory shrubs or mosses, which can account for a substantial proportion of NPP in some ecosystems. Most published summaries of NPP do not state explicitly which components of NPP have been included (or sometimes even whether the units are grams of carbon or grams of biomass). For these reasons, considerable caution must be used when comparing data on NPP or biomass among studies. In general, we know less about the true magnitude of terrestrial NPP than the extensive literature on the topic would suggest.

**Table 6.2** Major components of NPP and representative values of their relative magnitudes

Components of NPP <sup>a</sup>	% of NPP
New plant biomass	40–70
Leaves and reproductive parts (fine litterfall)	10–30
Apical stem growth	0–10
Secondary stem growth	0–30
New roots	30–40
Root secretions	20–40
Root exudates	10–30
Root transfers to mycorrhizae	15–30
Losses to herbivores and mortality	1–40
Volatile emissions	0–5

<sup>a</sup>Seldom, if ever, have all of these components been measured in a single study

## Marine NPP

**The large area of the ocean is offset by their low average productivity per unit area, so the ocean and the land each contribute about half of global NPP.** Although the ocean covers 70% of Earth's surface, the average NPP per unit area is only 20% of that on land (Table 6.3). Aquatic productivity is, however, highly variable, just as on land. The most productive aquatic ecosystems, such as coral reefs, kelp forests, and eutrophic lakes, can be at least as productive as the most productive terrestrial ecosystems (Fig. 6.5). NPP

in the open ocean, which accounts for 90% of the ocean area, however, is similar to that of terrestrial deserts and tundra. Because of its large area, the open ocean accounts for 60% of marine production, with picoplankton accounting for about 90% of this production (Valiela 1995).

**Table 6.3** Characteristics of the ocean and continents<sup>a</sup>

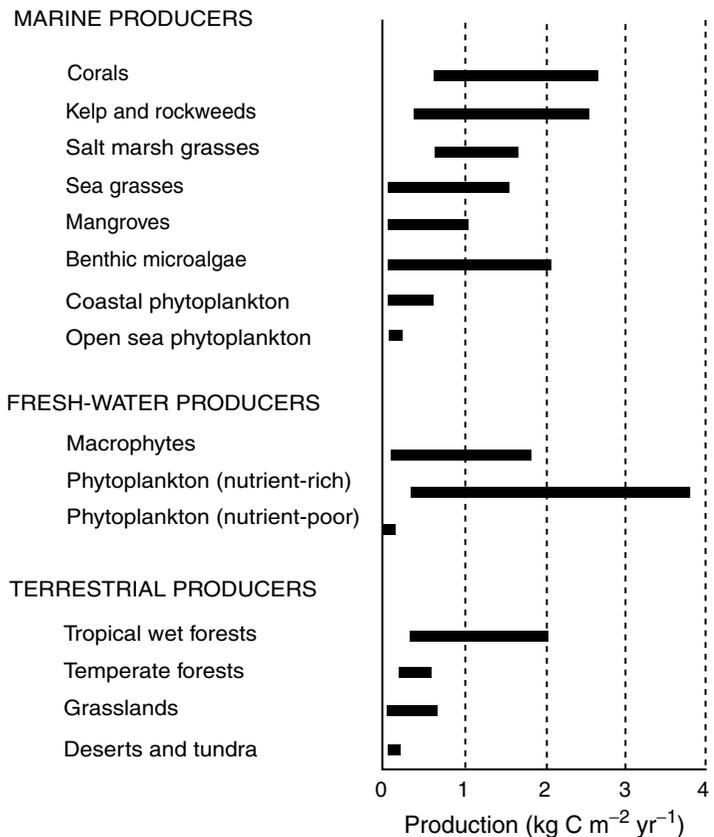
Unit	The ocean	Continents
Surface area (% of Earth)	71	29
Volume of life zone (%)	99.5	0.5
Living biomass ( $10^{12}$ kg C)	2	560
Living biomass ( $10^3$ kg $\text{km}^{-2}$ )	5.6	3,700
Dead organic matter ( $10^6$ kg $\text{km}^{-2}$ )	5.5	10
Net primary production ( $10^3$ kg C $\text{km}^{-2}$ year <sup>-1</sup> )	69	330
Residence time of C in living biomass (year)	0.08	11.2

<sup>a</sup>Data from Cohen (1994)

The small size and lack of non-photosynthetic support structures in marine phytoplankton mean that marine primary producers require relatively little biomass to support a given photosynthetic capacity. The average primary producer biomass per unit area on land, for example, is 660-fold greater than in the ocean, although the average NPP per unit area on land is only fivefold greater than in the ocean (Table 6.3; Cohen 1994). Phytoplankton biomass of the ocean and lakes turns over 20–40 times per year, or even daily under conditions that are favorable for growth, whereas turnover for terrestrial plant biomass generally occurs over years to decades (Valiela 1995).

**Ocean productivity is ultimately limited by the rate of nutrient supply from the land or deep ocean waters.** For this reason, productivity is greater in coastal waters than in the open ocean. Tidal mixing of sediment nutrients into the water

**Fig. 6.5** Comparison of NPP among selected marine, freshwater, and terrestrial ecosystems. Marine and freshwater ecosystems exhibit the same range of NPP that occurs on land, but unproductive marine ecosystems (the open ocean) are much more extensive. Redrawn from Valiela (1995)

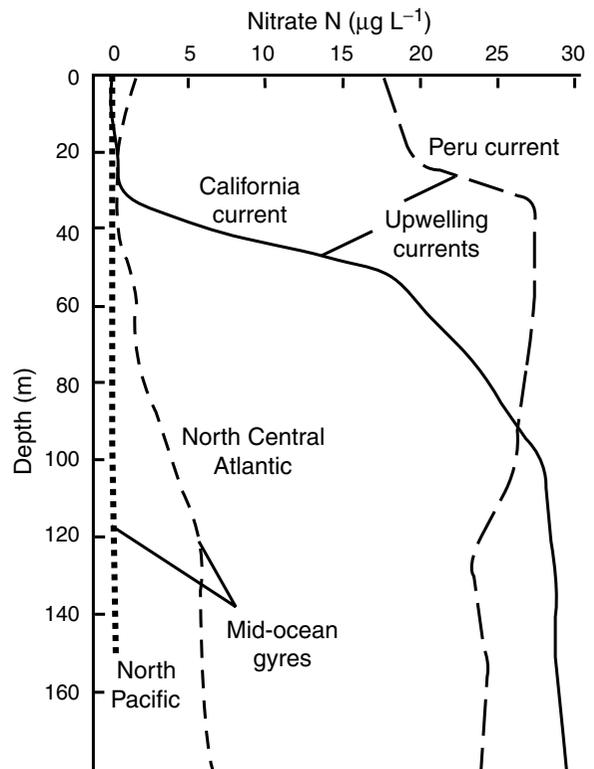


column and oxygenation of the water column contribute to the high productivity of estuaries and intertidal and near-shore marine ecosystems that constitute the **Coastal Boundary Zone Biome** (Nixon 1988; Longhurst 1998). Coral reefs are among the most productive ecosystems on Earth (Fig. 6.5). Frequent tidal flushing supplies nutrients to algae that grow on the surfaces of dead corals. These algae have high turnover rates because fish constantly graze them. The biomass of algae in this ecosystem is therefore small, just like the biomass of phytoplankton in pelagic ecosystems. Human activities have massively increased nutrient inputs to the coastal zone, particularly in estuaries, where rivers deliver nutrients derived from agricultural runoff, sewage, and erosion. This eutrophication disrupts the normal balance between algae, grazers, and decomposers (see Chap. 7; see Fig. 9.1).

In pelagic ecosystems, upwelling near the west coasts of continents provides the greatest rate of nutrient supply. Upwelling supports

some of Earth's major fisheries off Peru, northwest Africa, eastern India, southwest Africa, and the western U.S. (Fig. 6.6; Valiela 1995). In these areas, Coriolis forces cause winds and surface waters to move offshore (see Fig. 2.11). These surface waters are replaced by nutrient-rich waters from depth. Upwelling also occurs in the open ocean where major ocean currents diverge (Mann and Lazier 2006). This occurs, for example, in the Equatorial Pacific, where ocean currents diverge to the north and south and in the Southern Ocean, the North Atlantic, and the North Pacific (Valiela 1995). These regions have relatively high nutrient availability and productivity.

Vertical gradients in water density also influence nutrient transport from subsurface to surface waters. In the **Trades Biome** of the central subtropical ocean basins, high solar input creates a strong vertical temperature gradient with an extremely stable **thermocline**, in which low-density warm water is underlain by high-density cold water (see Chap. 2;



**Fig. 6.6** Depth profiles of nitrate in mid-ocean gyres and upwelling zones of the ocean. Redrawn from Dugdale (1976)

Longhurst 1998). The vertical stability is reinforced by a stable halocline in which high-density saline waters lie beneath less saline surface waters. This stable stratification of water minimizes vertical mixing by waves and ocean currents, so nutrient availability and productivity of the subtropical ocean are extremely low.

As latitude increases, surface ocean temperature declines. This weakens the vertical density gradient, so storm waves and currents are more effective in mixing deep nutrient-rich waters to the surface. The strong westerly winds and storm tracks associated with the polar jet also contribute to effective mixing in the temperate/high-latitude **Westerlies Biome** (Longhurst 1998). Temperate and polar ocean waters are therefore more nutrient rich and productive than are tropical open ocean waters. The upward mixing of nutrients is greatest during winter, when surface waters are coldest, and the vertical stratification is least stable. Winter is also the time of year when strong equator-to-pole heating gradients generate the strongest winds (see Chap. 2). During winter, turbulent mixing disperses the phytoplankton deep within the water column where there is not enough light to support growth. In spring, however, an increase in solar radiation heats the surface waters and reduces the depth of the mixed layer. This concentrates phytoplankton within the euphotic zone, leading to a spring **bloom** of phytoplankton (Mann and Lazier 2006). The bloom ends when nutrients are depleted by production, and most phytoplankton have been consumed by zooplankton grazers. A second bloom sometimes occurs in autumn when a decline in surface stratification increases nutrient mixing into surface waters.

In the **Polar Biome**, surface waters have low salinity because of the large freshwater input from rivers and melting sea ice, leading to a strong stratification of the water column. As the snow-covered sea ice melts, light availability increases, and wind-driven mixing augments upwelling, leading to a summer bloom of productivity (Carmack and Chapman 2003; Mann and Lazier 2006).

The high productivity of high-latitude ocean basins supports rich fisheries, although many of these have been depleted by overfishing (Pauly

et al. 2005). The latitudinal variation in pelagic productivity also explains several other interesting ecological patterns, such as the annual migration of many whales and sea birds between the Antarctic and the Arctic Oceans to capitalize on summer blooms of polar productivity and spring blooms of productivity in the Westerlies Biome. In addition, a high proportion of fish species at high latitudes have an **anadromous** life history, in which they exploit the productive marine environment to support growth during the adult phase and use the relatively predator-free freshwater environment to reproduce. This anadromous life history strategy is increasingly favored as latitude increases because marine productivity increases with increasing latitude, whereas terrestrial productivity declines with increasing latitude (Gross et al. 1988).

In summary, NPP is greatest and least nutrient-limited in the coastal zone. In the open ocean, nutrient limitation is most extreme in zones of greatest surface heating (in the tropics and during summer) because heating reduces the density of surface water, which inhibits the upward mixing of dense, nutrient-rich waters from depth. Conditions that are conducive to deep mixing (strong winds, cold-dense surface waters, tidal mixing, etc.) reduce the magnitude of nutrient limitation to the point that other environmental factors such as light or temperature limit NPP. We discuss the influence of interactions among different nutrients on NPP in Chap. 9.

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## Lake NPP

### **The productivity of unpolluted lakes, like that in the open ocean, is generally nutrient-limited.**

The controls over pelagic productivity of lakes are quite similar to those in the ocean, with nutrient inputs from land and mixing strongly influencing productivity, just as described for NPP of the ocean and GPP of lakes (see Chap. 5). In winter, solar radiation is low at higher latitudes, leading to a shallow euphotic zone. In addition, weak stratification and deep mixing carry phytoplankton below the base of the euphotic zone, leading to low productivity. Light input is further reduced

in those lakes that have snow-covered ice. In spring, the increase in solar radiation deepens the euphotic zone and warms the surface water, leading to a shallower mixing depth and a concentration of phytoplankton within the euphotic zone (Kalff 2002). Favorable light and temperature conditions enable phytoplankton to exploit the nutrients that mix into surface waters over winter, leading to a spring phytoplankton bloom. Just as in the ocean, the bloom ends when phytoplankton have depleted the surface nutrients and grazers reduce phytoplankton biomass. Also, as in the ocean, small phytoplankton (pico- and nanoplankton) dominate pelagic production of lakes under low-nutrient conditions (oligotrophic lakes and mid-summer conditions), and large algal cells dominate under high-nutrient conditions. Small phytoplankton tend to be more readily consumed by zooplankton grazers, so “bottom-up” (nutrient) effects interact with “top-down” (grazing) effects on lake NPP. In general, nutrients appear to explain much of the variation in phytoplankton productivity and biomass among lakes, and temperature influences the rate at which this biomass is attained (Kalff 2002). About 13% of GPP is exuded by phytoplankton into their environment (Kalff 2002). This does not directly contribute to phytoplankton biomass accumulation but may be critical in stimulating decomposition and nutrient mineralization by nearby bacteria (see Chap. 7).

Most lakes differ from the open ocean in supporting substantial benthic primary production. This is true for all small (<1 km<sup>2</sup>) lakes, which account for 43% of total lake area (Downing et al. 2006), and even for many large lakes, which often have a large proportion of their benthic area within the euphotic zone. Benthic production is particularly important in unpolluted clearwater lakes, where it often accounts for half of NPP and an even larger proportion of the energetic base (phytoplankton plus bacteria) that feeds fish production (Vander Zanden et al. 2005, 2006). Many studies of aquatic production overlook benthic production and therefore underestimate the energy available at the base of the food chain (see Chap. 10)

Lakes are generally small aquatic patches in a terrestrial matrix, so they are strongly influenced by nutrient inputs from groundwater and streams (Schindler 1978). The granitic bedrock of the Canadian Shield, from which soils were scraped away by Pleistocene glaciers, for example, have low rates of nutrient input from watersheds to lakes. The strong nutrient limitation of many of these lakes makes them vulnerable to changes in nutrient inputs from agriculture or acid rain (Driscoll et al. 2001). Trout and other top predators in oligotrophic lakes may require decades to reach a large size, whereas this may occur in a few months or years in eutrophic lakes.

The physical properties of lakes also influence the degree of nutrient limitation of NPP. In general, weakly stratified lakes mix nutrients more readily from depth and are therefore less likely to be nutrient-limited. Deep mixing and weak nutrient limitation characterize wind-exposed lakes, large lakes, and tropical lakes with weak vertical temperature gradients and larger nutrient inputs from sediments. Some of the most productive lakes are shallow lowland lakes with naturally high rates of nutrient input (Kalff 2002).

Anthropogenic addition of nutrients to lakes often causes **eutrophication**, a nutrient-induced increase in lake productivity. Eutrophication radically alters ecosystem structure and functioning. Increased phytoplankton biomass reduces water clarity, thereby reducing the depth of the euphotic zone (see Fig. 8.2; Kalff 2002). This in turn reduces the oxygen available at depth. The increased productivity also increases the demand for oxygen to support the decomposition of the large detrital inputs. If mixing is insufficient to provide oxygen at depth, the deeper waters no longer support fish and other oxygen-requiring heterotrophs. This situation is particularly severe in winter, when low temperature limits oxygen production from photosynthesis. In ice-covered lakes, ice and snow reduce light inputs that drive photosynthesis (providing oxygen) and prevent the surface mixing of oxygen into the lake. Lakes in which the entire water column becomes anaerobic during winter do not support fish. Even during summer, the accumulation of algal detritus at times of low surface

mixing can deplete oxygen from the water column, leading to high fish mortality.

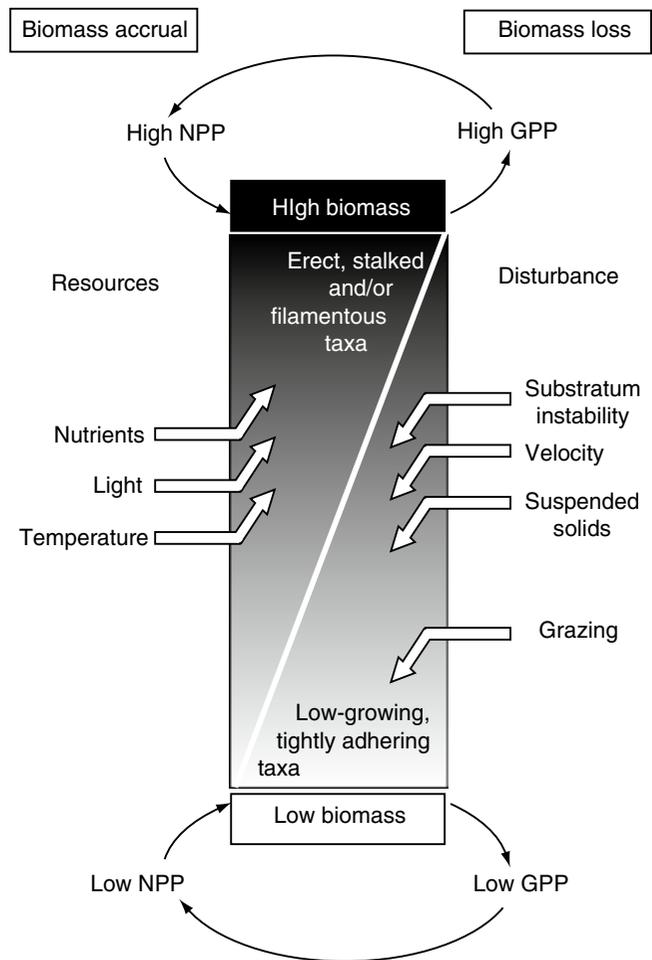
In summary, nutrient limitation of NPP is widespread in lakes and changes seasonally as a result of wind-driven mixing, just as in the ocean.

### Stream and River NPP

**The controls over NPP in streams and rivers vary depending on stream size and environment.** In general, the factors that govern NPP are similar to the controls over stream GPP (see Chap. 5) because of the tight amplifying (positive) feedbacks between photosynthesis and production of new photosynthetic cells in stream and

river ecosystems. Nutrients, light, and warmth enhance GPP and NPP, whereas substrate instability, current velocity, suspended sediments, and grazing reduce plant biomass and therefore GPP and NPP (Fig. 6.7; Biggs 1996). Just as for GPP, NPP in forested headwater streams is about half that in larger open streams (Webster et al. 1995; Mulholland et al. 2001). In many river systems, NPP increases from small headwater streams to larger, more open streams and rivers, just like GPP (see Fig. 5.8). Large rivers are quite variable in NPP (Webster et al. 1995; McTammany et al. 2003; Allan and Castillo 2007), just as described for GPP (see Chap. 5).

The controls over NPP in streams and rivers differ substantially from those in pelagic ecosystems



**Fig. 6.7** Factors controlling the biomass and physical structure of periphyton in streams. Adapted from Biggs (1996)

of the ocean and lakes. In rapidly flowing streams and rivers, light is more often limiting to NPP than in pelagic ecosystems because of shading by streamside vegetation, suspended sediments, or (in slow-moving eutrophic waters) phytoplankton. In addition, flowing water replenishes nutrients at the surface of algal cells more rapidly than in the wind-driven mixing of the ocean and lakes, thereby reducing the degree of nutrient limitation (see Chap. 8). Finally, in slow-moving rivers, where phytoplankton become an important contributor to NPP, downstream export of phytoplankton cells limits the rate of accumulation of photosynthetic biomass and therefore NPP. This contrasts with lakes and the ocean where grazing exerts a more important control over phytoplankton accumulation (Allan and Castillo 2007). In general, the NPP by phytoplankton of slow-moving rivers is much less than in lakes with a similar nutrient and temperature regime.

Temporal and spatial heterogeneity generate tremendous variation in NPP and its controls in stream ecosystems. The biophysical differences between adjacent pools and riffles can be just as extreme as the average differences between lakes and streams. Similarly, most streams and rivers experience periodic floods followed by periods of low flow (or no flow at all). This radically alters both the conditions that influence NPP and the dislodging of primary producer biomass that supports GPP and NPP. These pulse-release properties of streams are much more extreme than the patterns of temporal variation in lakes or the ocean (Kalff 2002; Allan and Castillo 2007).

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## Terrestrial NPP

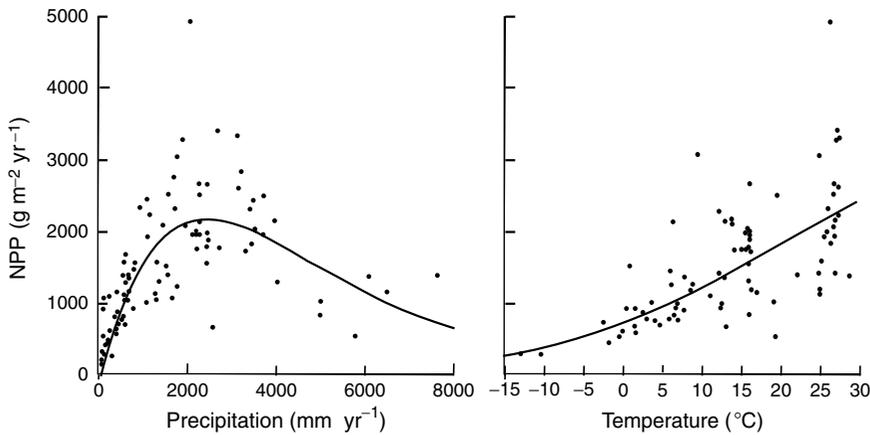
**The nature of environmental regulation of terrestrial NPP differs substantially from that in aquatic ecosystems.** Whereas phytoplankton cells are directly bathed in water and nutrients, terrestrial plants must acquire these resources from a soil medium, where there is no light to power photosynthesis. This complicates the amplifying (positive) feedback between photosynthesis and NPP because much of the new biomass produced by terrestrial plants is roots and support structures

that do not directly enhance the photosynthetic capacity of the plant. In addition, the NPP of terrestrial plants often responds to availability of CO<sub>2</sub> and water, which seldom limit the NPP of aquatic plants. This adds to the number and potential interactions of environmental controls over NPP. Finally, aquatic NPP is the simple balance between photosynthetic carbon gain by all cells during the day and their respiration at night, whereas on land, non-photosynthetic tissues respire both day and night. This complicates the diurnal patterns of carbon use in terrestrial plants.

## Physiological Controls Over NPP

**Photosynthesis, NPP, and respiration: Who is in charge?** NPP is the balance of carbon gained by GPP and the carbon lost by respiration of all plant parts (Fig. 6.1). However, this simple equation (6.2) does not tell us whether the conditions governing photosynthesis dictate the amount of carbon that is available to support growth or whether conditions influencing growth rate determine the magnitude of photosynthesis – in other words whether photosynthesis “pushes” growth or whether growth “pulls” photosynthesis. On short timescales (seconds to days), environmental controls over photosynthesis (e.g., light and water availability) strongly influence photosynthetic carbon gain (photosynthesis “pushes” growth). However, on monthly to annual timescales, plants adjust leaf area and photosynthetic capacity so carbon gain matches the soil resources that are available to support growth (growth “pulls” photosynthesis; see Fig. 5.2). Plant carbohydrate concentrations are usually lowest when environmental conditions favor rapid growth (i.e., carbohydrates are drawn down by growth) and tend to accumulate during periods of drought or nutrient stress or when low temperature constrains NPP (Chapin 1991a). If the products of photosynthesis directly controlled NPP, we would expect high carbohydrate concentrations to coincide with rapid growth or to show no consistent relationship with growth rate.

Results of growth experiments also indicate that growth is not simply a consequence of the controls over photosynthetic carbon gain. Terrestrial plants



**Fig. 6.8** Relationship of aboveground NPP (in units of biomass) with average annual temperature and total annual precipitation. NPP is greatest in warm, moist environments such as tropical wet forests and lowest in cold or dry ecosystems

such as tundra and deserts. In tropical forests, NPP declines at extremely high precipitation ( $>3 \text{ m year}^{-1}$ ), due to indirect effects of excess moisture, such as low soil oxygen and loss of nutrients through leaching. Redrawn from Schuur (2003)

respond to low availability of water, nutrients, or oxygen in their rooting zone by producing hormones that reduce growth rate. The decline in growth subsequently leads to a decline in photosynthesis (Gollan et al. 1985; Chapin 1991a; Davies and Zhang 1991). The general conclusion from these experiments is that plants actively sense the resource supply in their environment and adjust their growth rate accordingly. These changes in growth rate then change the **sink strength** (demand) for carbohydrates and nutrients, leading to changes in photosynthesis and nutrient absorption (Chapin 1991a; Lambers et al. 2008). The resulting changes in growth and nutrition determine the leaf area index (LAI) and photosynthetic capacity, which, as we have seen, largely account for ecosystem differences in carbon input (see Fig. 5.2; Gower et al. 1999).

The feedbacks from sink strength to photosynthesis are not 100% effective. Leaf carbohydrate concentrations increase during the day and decline at night, allowing plants to maintain a relatively constant supply of carbohydrates to non-photosynthetic organs. Similarly, carbohydrate concentrations increase during periods (hours to weeks) of sunny weather and decline under cloudy conditions. Over these short timescales, the conditions affecting photosynthesis are the primary determinants of the carbohydrates available to support growth. The short-term

controls over photosynthesis by environment probably determine the hourly to weekly patterns of NPP, whereas soil resources govern annual carbon gain and NPP and the patterns of variation in NPP across landscapes and biomes.

## Environmental and Species Controls Over NPP

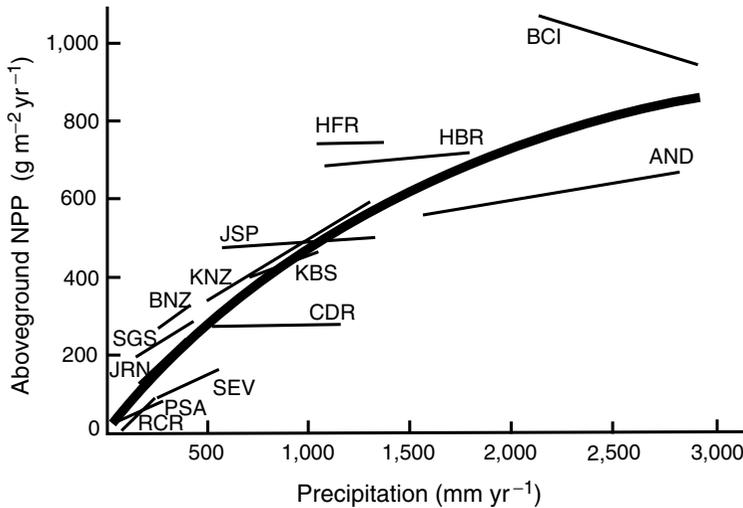
**The climatic controls over NPP are mediated primarily through the availability of below-ground resources.** At a global scale, the largest ecosystem differences in NPP are associated with variation in climate. NPP is greatest in warm, moist environments, where tropical rainforests occur, and is least in climates that are dry (e.g., deserts) or cold (e.g., tundra; Fig. 6.2; see Fig. 2.23). NPP correlates most strongly with precipitation; NPP is highest at about  $2\text{--}3 \text{ m year}^{-1}$  of precipitation (typical of rainforests) and declines at extremely low or high precipitation (Fig. 6.8; Gower 2002; Schuur 2003; Huxman et al. 2004; Luysaert et al. 2007). When dry ecosystems (i.e., deserts) are excluded, NPP also increases exponentially with increasing temperature. The largest differences in NPP reflect biome differences in both climate and vegetation structure. When ecosystems are grouped into biomes, there is a 14-fold range in average NPP (Table 6.4).

**Table 6.4** Net primary production (NPP) of the major biome types based on biomass harvests<sup>a</sup>

Biome	Aboveground NPP (g m <sup>-2</sup> year <sup>-1</sup> )	Belowground NPP (g m <sup>-2</sup> year <sup>-1</sup> )	Belowground NPP (% of total)	Total NPP <sup>b</sup> (g m <sup>-2</sup> year <sup>-1</sup> )
Tropical forests	1,400	1,100	44	2,500
Temperate forests	950	600	39	1,550
Boreal forests	230	150	39	380 (670) <sup>b</sup>
Mediterranean shrublands	500	500	50	1,000
Tropical savannas/grasslands	540	540	50	1,080
Temperate grasslands	250	500	67	750
Deserts	150	100	40	250
Arctic tundra	80	100	57	180
Crops	530	80	13	610

<sup>a</sup>NPP is expressed in units of dry mass. NPP estimated from harvests excludes NPP that is not available to harvest, due to consumption by herbivores, root exudation, transfer to mycorrhizae, and volatile emissions

<sup>b</sup>Data from Saugier et al. (2001). These estimates are generally intermediate among estimates from other NPP compilations (Scurlock and Olson 2002; Zheng et al. 2003), except for boreal forests, where NPP estimates are 75% greater than those of Saugier et al. (2001). Therefore, boreal NPP may be underestimated relative to other biomes



**Fig. 6.9** Relationship of aboveground NPP with total annual precipitation across 14 sites. The thick curved line shows the relationship between average aboveground NPP and average precipitation across all sites. The thin straight lines show the interannual variation in aboveground NPP

and annual precipitation at a given site. Sites include deserts (RCR), grasslands and steppe (PSA, SEV, JRN, SGS, CDR, KNZ, KBS, and JSP), and forests (BNZ, HBR, HFR, AND, and BCI), mostly from Long-Term Ecological Research sites. Redrawn from Huxman et al. (2004)

Do these correlations of NPP with climate reflect simple direct effects of temperature and moisture on plant growth, or are other factors involved?

Comparisons *among ecosystems* show that NPP increases most strongly with increasing precipitation in dry sites (the left-hand end of the curve in Figs. 6.8 and 6.9), suggesting that NPP is most moisture-limited in dry sites. These dry

sites also show greatest sensitivity of NPP to *interannual variation* in rainfall (the slope of the thin straight lines in Fig. 6.9) and to experimental additions of water (Huxman et al. 2004). Within any given site, NPP responds most strongly to experimental addition of water in dry years and to nutrient additions in wet years. Even deserts respond to nutrient addition in wet seasons and

years (Gutierrez and Whitford 1987). In dry sites, NPP responds more strongly to water than to nutrient addition in most years, and in **mesic** (moist) sites, NPP responds more strongly to nutrient addition than to water addition in most years (Huxman et al. 2004). In summary, (1) over the long term, NPP of most ecosystems is limited by multiple belowground resources (both water and nutrients, and sometimes oxygen in very wet sites). (2) The nature of environmental limitation varies among years, being most moisture-limited in dry years, and most nutrient-limited in wet years. (3) Moisture limitation of NPP occurs most often in dry sites, and nutrient limitation occurs most often in mesic sites. Thus a simple characterization of dry sites as water-limited and mesic sites as nutrient-limited is a reasonable first approximation, but it ignores the broader range of environmental limitations that all sites experience from time to time.

The types of plants that occupy an ecosystem also influence its productivity. Any given ecosystem shows a much narrower range of NPP in response to interannual variation in environment (the straight lines in Fig. 6.9) than does the *average* NPP of the full range of sites (the curved line in Fig. 6.9). Thus, a desert or grassland can never be as productive as a mesic forest, no matter how much water and nutrients it receives, because the plants lack the productive potential (capacity to produce leaf area) of large trees. Even among grasslands, the range of variation in NPP from wet to dry years is less for a given site than across all grassland sites (e.g., SGS, CDR, KNZ, JSP in Fig. 6.9) because species that dominate dry grasslands have lower productive potential than do those in mesic grasslands and cannot take full advantage of moist years (Lauenroth and Sala 1992). On the other hand, plants in dry grasslands are better adapted to dry conditions and are less likely to die in response to severe drought (see Chap. 4). Thus, long-term environmental change affects NPP in at least two ways: (1) through direct effects on the balance between water and nutrient limitation, and (2) particularly through changes in species composition and therefore the environmental tolerances and productive potential of the species present in the ecosystem.

What about cold sites, where the climate correlations suggest that NPP should be temperature-limited? In the tundra, NPP increases more in response to added nitrogen than to experimental increases in temperature (Chapin et al. 1995; McKane et al. 1997). Thus, in tundra, the climate–NPP correlation probably reflects temperature effects on nitrogen supply (see Chap. 9) or length of growing season more than a direct temperature effect on NPP. Similarly, NPP in the boreal forest correlates closely with soil temperature, but soil-warming experiments show that this effect is mediated primarily by enhanced decomposition and nitrogen supply (Van Cleve et al. 1990).

In summary, in ecosystems where climate–NPP correlations suggest a strong climatic limitation of NPP, experiments and observations show that this is mediated primarily by climatic effects on belowground resources.

What constrains NPP in warm, moist climates where temperature and moisture appear optimal for growth? Tropical forests typically have higher NPP than other terrestrial biomes (Table 6.4). Among tropical forests, litter production tends to correlate with the supply of nutrients, especially phosphorus (Vitousek 1984), suggesting that NPP in tropical forests may also be limited by the supply of belowground resources. NPP in tropical dry forests is moisture-limited, but in extremely wet climates ( $>3$  m year<sup>-1</sup> of precipitation, Fig. 6.8), NPP declines in response to increasing precipitation, probably due to oxygen limitation to roots and soil microbes and to leaching loss of essential nutrients (Schoor 2003). NPP in tropical forests is therefore probably also limited by the supply of belowground resources, including nutrients and sometimes water (relatively dry forests) or oxygen (relatively wet forests).

In temperate salt marshes, where water and nutrients are abundant, NPP responds directly to increases in CO<sub>2</sub> (Drake et al. 1996), as do crops that are supplied with a high nutrient supply. However, NPP is enhanced by nutrient additions even in the most fertile agricultural systems (Evans 1980), indicating the widespread occurrence of nutrient limitation to NPP (see Fig. 8.1).

In summary, experiments and observations in a wide range of ecosystems provide a relatively

consistent picture. Over the range of conditions that an ecosystem encounters through time, its NPP might be limited by multiple factors. However, the supply of belowground resources is generally among the most important constraints on NPP. The factors determining the supply and acquisition of belowground resources and the productive potential of vegetation are generally the major *direct* controls over NPP and therefore the carbon input to ecosystems.

The importance of belowground resources and species traits in controlling NPP is consistent with our earlier conclusion that GPP is governed more by leaf area and length of the photosynthetic season than by the direct effects of temperature and CO<sub>2</sub> on photosynthesis (see Chap. 5). In fact, modeling studies suggest that NPP is a surprisingly constant fraction (40–52%) of GPP across broad environmental gradients (Fig. 6.4; Landsberg and Gower 1997; Waring and Running 2007). This is consistent with our conclusion that GPP and NPP are controlled by the same factors.

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## Allocation

### Allocation of NPP

**Patterns of biomass allocation minimize resource limitation and maximize resource capture and NPP.** Our discussion of the controls over NPP suggests an interesting paradox: A high leaf area is necessary to maximize NPP, yet the major factors that constrain NPP are belowground resources. The plant is faced with a dilemma of how to distribute biomass between leaves (to maximize carbon gain) and roots (to maximize acquisition of belowground resources). Plants exhibit a consistent pattern of **allocation** – the distribution of growth among plant parts – that maximizes growth in response to the balance between aboveground and belowground resource supply rates (Garnier 1991).

In general, plants allocate production to minimize limitation by any single resource. Plants allocate new biomass preferentially to roots when water or nutrients limit growth. They allocate

new biomass preferentially to shoots when light is limiting (Reynolds and Thornley 1982). Plants can increase acquisition of a resource by producing more biomass of the appropriate tissue, by increasing the activity of each unit of biomass, or by retaining the biomass for a longer time. A plant can, for example, increase carbon gain by increasing leaf area or photosynthetic rate per unit leaf area or by retaining the leaves for a longer time before they are shed. Similarly, a plant can increase nitrogen absorption by altering root morphology or by increasing root biomass, root longevity, nitrogen absorption rate per unit root, or extent of mycorrhizal colonization. Changes in allocation and root morphology have a particularly strong effect on nutrient absorption. It is the integrated activity (mass multiplied by acquisition rate per unit biomass multiplied by time) that must be balanced between shoots and roots to maximize growth and NPP (Garnier 1991). These allocation rules are key features of all simulation models of NPP (Reynolds et al. 1993) and in the differing allocation responses to low water, low nutrients, and low light (Craine 2009).

Observations in ecosystems are generally consistent with allocation theory. Tundra, grasslands, and shrublands, for example, allocate a larger proportion of NPP below ground than do forests (Table 6.4; Gower et al. 1999; Saugier et al. 2001). Crops, with their relatively favorable water and nutrient supplies, show least allocation below ground. More subtle apparent differences in belowground NPP allocation (Table 6.4) should be interpreted cautiously because belowground NPP is difficult to measure and is sensitive to the methods used and to assumptions made about turnover of fine roots.

### Allocation Response to Multiple Resources

**NPP in most ecosystems is limited most strongly by a single resource but also responds to other resources.** If plants were perfectly successful in allocating biomass to acquire the most limiting resource, they would be equally limited by all resources (Bloom et al. 1985; Rastetter and

Shaver 1992). As we have seen, this is seldom the case. NPP in most ecosystems responds most strongly to a particular resource, for example to water in deserts and in arid grasslands and shrublands; to nitrogen in tundra and many boreal and temperate forests; and to phosphorus in many tropical wet and dry forests. Thus, as a first approximation, deserts are water-limited ecosystems, and temperate forests are nitrogen-limited ecosystems. In many ecosystems, however, NPP responds to increased availability of more than one resource. Why does this occur?

The simplest view of environmental limitation is that growth is limited by a single resource at any moment in time. Another resource becomes limiting only when the supply of the first resource increases above the point of limitation (Liebig's **law of the minimum**). At least five processes contribute to the multiple resource limitation observed in many ecosystems: (1) Plants adjust allocation to maximize capture of (and minimize limitation by) the most limiting resource. (2) Changes in the environment (e.g., rainstorms or wet years, pulses of nutrient supply) alter the relative abundance of resources so different factors limit NPP at different times. (3) Plants exhibit mechanisms that increase the supply of the most limiting resource. (4) Organisms retain a larger proportion of some resources (e.g., nutrients) when they are in short supply. (5) Different resources limit different species in an ecosystem, so ecosystem-scale NPP responds to the addition of more than one resource. Each of these processes contributes to the response of ecosystems to multiple resources.

**Plants adjust resource acquisition to maximize capture of (and minimize limitation by) the most limiting resource.** As discussed earlier, plants adjust allocation of new production to roots vs. shoots to minimize limitation by belowground vs. aboveground resources, respectively. Plants also alter allocation within the root system to maximize capture of the most limiting belowground resource (Rastetter and Shaver 1992). For example, in deserts nutrient availability is greatest close to the soil surface, whereas water is generally more consistently available at depth. The amount of nutrient or water that a new root

acquires therefore depends on the depth at which roots are produced. To acquire water, some desert plants produce coarse, deep water-roots that efficiently conduct water but have low rates of nutrient absorption. Other plants produce only shallow roots and remain active only when surface water is available.

The biochemical investment by roots is specific for each nutrient. Nitrogen absorption, for example, requires synthesis of specific enzymes to absorb nitrogen, reduce nitrate, and assimilate reduced nitrogen into amino acids, whereas different enzymes are required to absorb phosphorus (see Chap. 8). This biochemical allocation to absorption of specific nutrients fine-tunes the capacity of plants to absorb those specific nutrients that most strongly limit growth.

**Changes in the environment (e.g., rain storms, pulses of nutrient supply) change the relative abundance of resources so different resources limit NPP at different times.** Most ecosystems experience temporal changes in the factor that most limits NPP because essential resources do not become equally available at the same time. Light, for example, decreases but water increases during rainy periods. Many ecosystems experience a pulse of nutrient availability at the beginning of the growing season, when temperatures may be suboptimal for growth. Because all the major factors that determine NPP change dramatically over several timescales, it would be surprising if there were not corresponding changes in the relative importance of these factors in limiting NPP (Huxman et al. 2004).

Temporal changes in the limitation of NPP are buffered by storage. Plants accumulate carbohydrates or nutrients during times when their availability is high and use their stores to support growth when the supply declines (Chapin et al. 1990). Over seasonal timescales, plants use stored carbohydrates and nutrients to support their burst of spring growth and replenish these stores at other times when photosynthesis and nutrient absorption exceed the demands for growth (see Chap. 8). Other than trees, most plants have very little capacity to store water, relative to their daily water demand and are therefore less buffered against variation in water than in light or nutrients

(Craine 2009). Some desert succulents do, however, have substantial water storage capacity (see Chap. 4). In summary, storage enables plants to acquire resources when they are readily available and use them at times of low supply, thus reducing temporal variation in the identity of the limiting resource.

**In the case of nutrients, plants can increase the supply of the most limiting resource.** Plants that have symbiotic associations with nitrogen-fixing microbes directly promote nitrogen inputs to ecosystems (see Chap. 8). Some ericoid and ectomycorrhizal associates of other plant species break down proteins and transport the resulting amino acids to plants (Read 1991). Some plants enhance the supply of phosphorus through the production of organic chelates that solubilize mineral phosphorus or through the production of phosphatases that cleave organic phosphates in the soil. Plants also exude carbohydrates that enhance mineralization near the root (see Chap. 9). Analogously, plants with fine leaves intercept fog, which increases water inputs to foggy ecosystems (see Chap. 4; Mark and Dickinson 2008).

**Organisms retain a larger proportion of some resources (e.g., nutrients) when these resources are in short supply.** Preferential retention and recycling of growth-limiting nutrients by plants, animals, and microbes retains these nutrients in ecosystems. Those nutrients that are present in excess of the biological requirements of organisms, as when nitrogen deposition saturates the nitrogen demands of vegetation, are more likely to be leached or lost as trace gases to the atmosphere (see Chap. 9; Vitousek and Reiners 1975).

**Species differ in the resources that limit their growth, so ecosystem-scale NPP responds to the addition of more than one resource.** Many species in an ecosystem have slightly different environmental requirements and therefore are limited by different resource combinations. Tundra species in the same ecosystem, for example, differ in their response to temperature, light, and nutrients (Chapin and Shaver 1985), and in some cases to the addition of nitrogen vs. phosphorus. Some desert species respond to summer

rain and others to winter rain. These differences among plant species in the factors that limit or stimulate growth contribute to the coexistence of species in a variable environment (Tilman 1988). This may be particularly important in explaining why species differ in their productivity response to interannual variation in weather and why the productivity of ecosystems varies less among years than does the productivity of any of the component species (Chapin and Shaver 1985). Spatial heterogeneity in the supply of potentially limiting resources also contributes to spatial variation in resource response.

## Diurnal and Seasonal Cycles of Allocation

**Photosynthesis and growth are highly resilient to daily and seasonal variations in the environment.** Daily and seasonal variations in the environment are two of the most predictable perturbations experienced by ecosystems. Many organisms adjust their physiology and behavior based on innate **circadian** (about 24 h) **rhythms** that lead to 24-h cycles. Stomatal conductance and carbon gain, for example, show a circadian rhythm even under constant conditions because stomata have an innate ~24-h cycle of stomatal opening and closing. Plants store starch in the leaves during the day and break it down at night, so the rate of carbohydrate transport to roots is nearly constant over the course of a day (Lambers et al. 2008). Thus belowground processes, such as root exudation and carbon transport to mycorrhizae, are buffered from diurnal variations in photosynthetic carbon gain.

Organisms adjust seasonally in response to changing **photoperiod** (day length). Many temperate plants, for example, exhibit a relatively predictable pattern of **phenology**, the seasonal timing of production and loss of leaves, flowers, fruits, etc. Plant leaves begin to senesce and reduce their rates of photosynthesis when day length or other environmental cues signal the characteristic onset of winter. During physiologically programmed senescence, plants break down many of the compounds in the senescing tissue

and transport about half of the nitrogen and phosphorus and some of the carbon from the senescing tissue to storage organs. This **resorption** minimizes nutrient loss during senescence (see Chap. 8; Chapin and Moilanen 1991). These stores provide resources to support plant growth the next spring, so NPP does not depend entirely on acquisition of new resources at times when no leaves are present. Other ecosystem processes change as either direct consequences of changes in environment (e.g., the decline in decomposition during winter due to lower temperatures) or indirect consequences of changes in other processes (e.g., the pulse of litter input to soil after leaf senescence). Ecosystem processes largely recover after each period of the cycle due to the predictable nature of diurnal and seasonal perturbations and the resilience of most processes to these changes. It is therefore unnecessary to consider explicitly the physiological basis of circadian and photoperiodic controls in order to predict ecosystem processes over longer timescales (see Chap. 12). In contrast to temperate ecosystems, tropical wet forests exhibit a less well-defined seasonality. Individual species often shed their leaves synchronously, but species differ in their timing of senescence, so the ecosystem as a whole shows less pronounced seasonality of production and senescence.

**The seasonality of plant growth depends on the seasonality of leaf area and factors regulating photosynthesis.** Spring growth of plants is initially supported by stored reserves of carbon and nutrients that were acquired in previous years. Leaves quickly become a net source of carbon for the rest of the plant, and growth during the remainder of the growing season is largely supported by the current year's photosynthate. There is often competition among plant parts for allocation of a limited carbohydrate supply early in the growing season, resulting in a seasonal progression of production of different plant parts, for example, with leaves produced first, followed by roots, and then by wood (Kozłowski et al. 1991). Plants species differ, however, in their seasonal allocation calendars. Plants with evergreen leaves may allocate NPP to root growth earlier than would deciduous plants because they already

have a leaf canopy that can provide carbon (Kummerow et al. 1983). Ring-porous temperate trees must first allocate carbon to xylem production in spring to develop a functional water transport system. The water columns in their large-diameter vessels **cavitate** (break) during winter freezing, so xylem vessels remain functional for only a single growing season. This large carbon requirement to rebuild xylem vessels each spring may explain the northern boundary of ring-porous species such as oaks (Zimmermann 1983). Seedlings in dry environments often depend entirely on their cotyledons for photosynthesis during the first weeks of growth and allocate all NPP to root growth to explore for a dependable water supply. The allocation calendar of a plant provides a general seasonal framework for allocation. Fluctuations in environment cause plants to modify this allocation calendar to achieve the appropriate balance of carbon and nutrients.

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## Tissue Turnover

**The balance between NPP and biomass loss determines the annual increment in plant biomass.** Plants retain only part of the biomass they produce. Plants regulate some of this biomass loss, for example the senescence of leaves in autumn. Senescence occurs throughout the growing season in grasslands but occurs as pulses during autumn or at the beginning of the dry season in many ecosystems. Other losses (e.g., to herbivores and pathogens, windthrow, and fire) are more strongly determined by environment, although even these tissue losses are influenced by plant properties such as anti-fungal compounds or fire-resistant bark. Still other biomass transfers to the soil result from mortality of entire plants. Given the substantial, although incomplete, physiological control over tissue loss, why do plants dispose of the biomass in which they invested so much carbon, water, and nutrients to produce?

**Tissue loss is an important mechanism by which plants balance resource requirements with resource supply from the environment.** Plants depend on regular large inputs of carbon,

water, and, to a lesser extent, nutrients to maintain vital processes. For example, once biomass is produced, it requires continued carbon inputs to support maintenance respiration. If the plant (or organ) cannot meet these carbon demands, the plant (or organ) dies. Similarly, if the plant cannot absorb enough water to replace the water that is inevitably lost during photosynthesis, it must shed transpiring organs (leaves) or die. The plant must therefore shed biomass whenever resources decline below some threshold needed for maintenance. Senescence is just as important as production in adjusting to changes in resource supply and is the *only* mechanism by which plants can reduce biomass and maintenance costs when resources decline in availability.

**Senescence** is the programmed breakdown of tissues. The location of senescence is physiologically controlled to eliminate tissues that are least useful to the plant. Grazing of aboveground tissues, for example, causes a decline in root production so that normal rates of root senescence reduce root biomass (Ruess et al. 1998). Similarly, grazing of belowground tissues reduces leaf longevity, which reduces leaf biomass (Detling et al. 1980). Although the controls over senescence and mortality of belowground tissues are poorly understood, these patterns of variation in production and senescence appear to maintain the functional balance between leaves and roots in response to environmental variation (Garnier 1991).

**Growth and senescence together enable individual plants to explore new territory.** Leaf and shoot growth generally occurs at the top of the canopy or in canopy gaps, where light availability is highest. This is balanced by senescence of leaves and stems in less favorable light environments (Bazzaz 1996). This balance between biomass production and loss allows trees and shrubs to grow toward the light. Similarly, roots often proliferate in areas of nutrient enrichment or where there is minimal competition from other roots, and root death is greatest in zones of local water or nutrient depletion (see Chap. 8). This exploration of unoccupied habitat by shoots and roots requires senescence and tissue loss in less favorable microsites to reduce maintenance costs of less productive tissues and to provide the nutrient

capital to produce new tissues. The exploration of new territory through synchronized growth and senescence reduces spatial variability in ecosystems by filling canopy gaps and exploiting nutrient-rich patches of soil.

**Senescence causes tissue loss at times when maintenance costs greatly exceed resource gain.** In seasonally variable environments, there are extended periods of time when temperature or moisture is predictably unfavorable. In these ecosystems, the cost of producing tissues that can withstand the rigors of this unfavorable period and of maintaining tissues when they provide negligible benefit to the plant may exceed the cost of producing new tissues when conditions again become favorable (Chabot and Hicks 1982). Arctic, boreal, and temperate ecosystems, for example, predictably experience seasons that are too cold for plants to acquire resources and grow. There is a pulse of autumn senescence of leaves and roots, often triggered by some combination of photoperiod and low temperature (Ruess et al. 1996). Dry ecosystems experience similar pulses of leaf and root senescence with the onset of drought. Senescence and tissue loss are therefore highly pulsed in most ecosystems and occur just before the period when conditions are least favorable for resource acquisition and growth. These seasonal pulses of senescence account for most tissue loss in highly seasonal environments.

Leaf longevity varies among plant species from a few weeks to several years or decades. In general, plants in high-resource environments produce short-lived leaves with a high specific leaf area (SLA) and a high photosynthetic rate per leaf area, but they have little resistance to environmental stresses. These “disposable leaves” are typically shed when conditions become unfavorable (winter or dry season) and are replaced the next spring. The greater longevity of leaves from low-resource environments reduces the nutrient requirement by plants to maintain leaf area (see Chap. 8). We know much less about the controls over senescence and turnover of roots than of leaves. Roots appear to die when they are attacked by herbivores or pathogens or encounter unfavorable environmental conditions without a programmed pattern of senescence and redistribution of materials to other parts of the plant.

**Senescence enables plants to shed parasites, pathogens, and herbivores.** Because leaves and fine roots represent relatively large packets of nutrients and organic matter, they are constantly under attack by pathogens, parasites, and herbivores. **Phyllosphere fungi**, for example, begin colonizing and growing on leaves shortly after budbreak, initially as parasites and later as part of the decomposer community when the leaf is shed (see Chap. 7). These fungi account for the mottled appearance of many older leaves. Pathogenic root fungi are a major cause of reduced yields in agro-ecosystems and are common in natural ecosystems. Plants have a variety of mechanisms for detecting natural enemies and respond initially through the production of induced chemical defenses (see Chap. 10) and, in the case of severe attack, by shedding tissues.

**Large unpredictable biomass losses occur in most ecosystems.** Windstorms, fires, herbivore outbreaks, and epidemics of pathogens often cause large tissue losses that are unpredictable and occur before any programmed senescence of tissues and associated nutrient resorption. Due to nutrient resorption during senescence, these unpredictable biomass losses incur approximately twice the nutrient loss per gram to the plant as that occurring after senescence (see Chap. 8). They often increase spatial heterogeneity of light and nutrient resources in the ecosystem through patchy pulses of litter input and creation of gaps that range in scale from individual leaves to entire stands. All ecosystems are at some stage in the regrowth after biomass losses occurring at multiple timescales (see Chap. 12).

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## Global Distribution of Biomass and NPP

### Biome Differences in Biomass

**The plant biomass of an ecosystem is the balance between NPP and tissue turnover.** NPP and tissue loss are seldom in perfect balance. NPP tends to exceed tissue loss shortly after disturbance; at other times, tissue loss may exceed NPP (see Chap. 12). Ecosystems that are close to

steady state, however, often show a consistent relationship between plant biomass and climate. Total plant biomass varies 60-fold among Earth's major terrestrial biomes (Table 6.5). Forests have the most biomass. Among forests, average biomass declines 4.5-fold from the tropics to the low-statured boreal forest, where NPP is low and stand-replacing fires often remove biomass. Deserts and tundra have only 1% as much above-ground biomass as do tropical forests. In any biome, disturbance often reduces plant biomass below levels that the climate and soil resources could support. Crops, for example, from which biomass is regularly removed, have a biomass similar to that of tundra or desert, despite more favorable growing conditions. When disturbance frequency declines, for example, through fire prevention in grasslands and savannas, biomass often increases as a result of changes in both production and longevity of leaves and roots. Biomass can also change through invasion of shrubs and trees (see Chap. 12).

Patterns of biomass allocation reflect the factors that most strongly limit plant growth in ecosystems (Table 6.5). About 70–80% of the biomass in forests is above ground because forests characterize sites with relatively abundant supplies of water and nutrients, so light often limits the growth of individual plants. In shrublands, grasslands, and tundra, however, water or nutrients more severely limit production, and the majority of biomass occurs below ground. Crops maintain the smallest proportion of biomass as roots because of their favorable water and nutrient regimes.

Tropical forests account for about half of Earth's total plant biomass, although they occupy only 13% of the ice-free land area; other forests contribute an additional 30% of global biomass (Table 6.6). Non-forested biomes therefore account for less than 20% of total plant biomass, although they occupy 70% of the ice-free land surface. Crops for example, account for only 1% of terrestrial biomass although they occupy more than 10% of the ice-free land area. Thus, most of the terrestrial surface has relatively low biomass (see Fig. 5.24). This observation alone raises concerns about deforestation in the tropics where

**Table 6.5** Biomass distribution of the major terrestrial biomes<sup>a</sup>

Biome	Shoot (g m <sup>-2</sup> )	Root (g m <sup>-2</sup> )	Root (% of total)	Total (g m <sup>-2</sup> )
Tropical forests	30,400	8,400	22	38,800
Temperate forests	21,000	5,700	21	26,700
Boreal forests	6,100	2,200	27	8,300
Mediterranean shrublands	6,000	6,000	50	12,000
Tropical savannas/grasslands	4,000	1,700	30	5,700
Temperate grasslands	250	500	67	750
Deserts	350	350	50	700
Arctic tundra	250	400	62	650
Crops	530	80	13	610

Data from Saugier et al. (2001)

<sup>a</sup>Biomass is expressed in units of dry mass

**Table 6.6** Global extent of terrestrial biomes and their total carbon in plant biomass and NPP<sup>a</sup>

Biome	Area (10 <sup>6</sup> km <sup>2</sup> )	Total plant C pool (Pg C)	Total NPP (Pg C year <sup>-1</sup> )
Tropical forests	17.5	320	20.6
Temperate forests	10.4	130	7.6
Boreal forests	13.7	54	2.4
Mediterranean shrublands	2.8	16	1.3
Tropical savannas/grasslands	27.6	74	14.0
Temperate grasslands	15.0	6	5.3
Deserts	27.7	9	3.3
Arctic tundra	5.6	2	0.5
Crops	13.5	4	3.9
Ice	15.5		
Total	149.3	615	58.9

Calculated from Saugier et al. (2001)

<sup>a</sup>Biomass and NPP are expressed in units of carbon, assuming that plant biomass is 47% carbon (Gower et al. 1999; Sterner and Elser 2002; Zheng et al. 2003)

ecosystem biomass is greatest, independent of the associated species losses.

## Biome Differences in NPP

### The length of the growing season is the major factor explaining biome differences in NPP.

Most ecosystems experience times that are too cold or too dry for significant photosynthesis or plant growth to occur. When NPP of each biome is adjusted for the length of the growing season, all forested ecosystems have similar NPP (about 5 g m<sup>-2</sup> day<sup>-1</sup>), and there is only about a threefold difference in NPP between deserts and tropical forests (Table 6.7). These calculations suggest that the length of the growing season accounts for much of the biome differences in NPP (Bonan

1993; Gower et al. 1999; Körner 1999; Chapin 2003; Kerkhoff et al. 2005). When adjusted for length of growing season, aboveground NPP of the world's biomes shows no relationship to temperature, although deserts and tundra are less productive than forests (Fig. 6.10; Kerkhoff et al. 2005).

**Leaf area accounts for much of the biome differences in carbon gain during the growing season.** Average total LAI varies about sixfold among biomes; the most productive ecosystems generally have the highest LAI (Table 6.7; see Chap. 5). When NPP is adjusted for differences in both length of growing season and leaf area, unproductive ecosystems such as tundra or desert do not differ consistently in NPP from more productive ecosystems (Table 6.7). If anything, the less productive ecosystems may have higher NPP per unit of leaf area and growing-season length

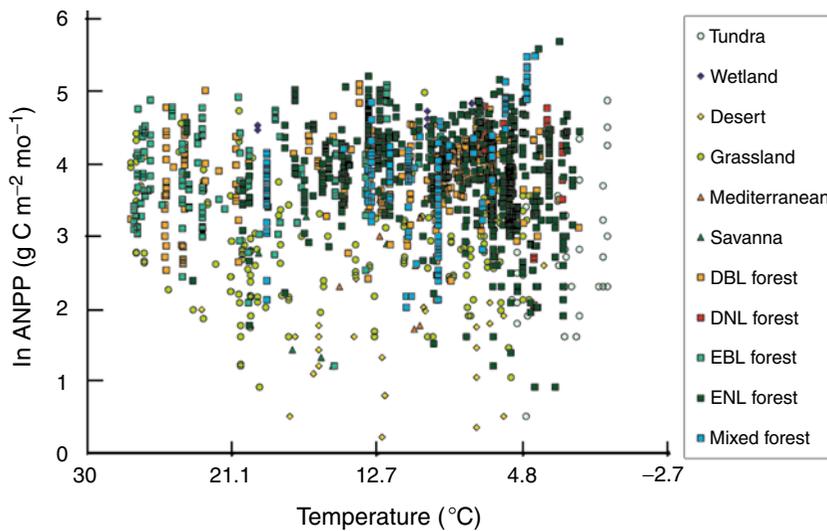
**Table 6.7** Productivity per day and per unit leaf area<sup>a</sup>

Biome	Season length <sup>b</sup> (days)	Daily NPP per ground area (g m <sup>-2</sup> day <sup>-1</sup> )	Total LAI <sup>c</sup> (m <sup>2</sup> m <sup>-2</sup> )	Daily NPP per leaf area (g m <sup>-2</sup> day <sup>-1</sup> )
Tropical forests	365	6.8	6.0	1.14
Temperate forests	250	6.2	6.0	1.03
Boreal forests	150	2.5	3.5	0.72
Mediterranean shrublands	200	5.0	2.0	2.50
Tropical savannas/grasslands	200	5.4	5.0	1.08
Temperate grasslands	150	5.0	3.5	1.43
Deserts	100	2.5	1.0	2.50
Arctic tundra	100	1.8	1.0	1.80
Crops	200	3.1	4.0	0.76

<sup>a</sup> Calculated from Table 6.4. NPP is expressed in units of dry mass

<sup>b</sup> Estimated

<sup>c</sup> Data from Gower (2002)



**Fig. 6.10** Relationship of aboveground NPP per month of growing season (log scale) to the average growing-season temperature (graphed from high to low) for the world’s ecosystems. When adjusted for length of growing

season, aboveground NPP (ANPP) shows no relationship to growing-season temperature. Redrawn from Kerkhoff et al. (2005)

than do crops and forests. On average, plants in most biomes produce 1–3 g total biomass m<sup>-2</sup> leaf day<sup>-1</sup> during the growing season. This is equivalent to a GPP of about 1–3 g carbon m<sup>-2</sup> leaf day<sup>-1</sup> because NPP is about half of GPP, and biomass is about 50% carbon. Apparent differences among biomes in these values reflect substantial uncertainty in the underlying data. At this point, there is little evidence for strong ecological patterns in NPP per unit leaf area and length of growing season.

LAI is both a cause and a consequence of differences in NPP, just as in aquatic ecosystems. LAI is determined largely by the availability of soil resources (mainly water and nutrients). Tropical wet forests, for example, occur in a warm, moist climate that provides adequate water and nutrient release to support a large leaf area. These leaves remain photosynthetically active throughout the year because there are no long periods of unfavorable weather causing massive leaf loss, and plants can tap stores of

deep groundwater during dry months (Woodward 1987). Deserts, in contrast, produce little leaf area because of inadequate precipitation and water storage, and arctic tundra supplies nitrogen too slowly to produce a large leaf area. In both deserts and tundra, the short growing season gives little time for leaf production, and unfavorable conditions between growing seasons limit leaf survival. The resulting low leaf area that generally characterizes these ecosystems is a major factor accounting for their low productivity (Table 6.7).

**Disturbances modify the relationship between climate and NPP.** There is substantial variability in NPP among sites within a biome. Some of this variability reflects variation in state factors such as climate and parent material. However, disturbance also affects NPP substantially, in part through changes in resource supply and LAI. Forest NPP, for example, often declines immediately after disturbance due to loss of LAI and then increases until the canopy closes and the available light is more fully utilized (see Fig. 12.13; Ryan et al. 1997). In later successional forests, NPP declines for a variety of reasons.

About half (50–60%) of the NPP of the biosphere occurs on land; the rest occurs in aquatic ecosystems (see Chap. 14). When summed at the global level, tropical forests account for about a third of Earth's terrestrial NPP; all forests account for about half of terrestrial NPP (Table 6.5). Grasslands and savannas account for an additional third of terrestrial NPP; these ecosystems are much more important in their contribution to terrestrial production than to biomass. Crops contribute to terrestrial NPP in proportion to their areal extent; they account for about 10% of terrestrial production and occupy 10% of the ice-free land surface.

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## Summary

Plant respiration provides the energy to acquire nutrients and to produce and maintain biomass. All plants are similar in their efficiency of converting sugars into biomass. Therefore, ecosystem

differences in plant respiration largely reflect differences in the amount and nitrogen content of biomass produced and, secondarily, in the effects of environmental stress, particularly temperature and moisture, on maintenance respiration. Most ecosystems appear to exhibit a similar efficiency of converting photosynthate (GPP) into NPP; half of the carbon gained through GPP becomes NPP, and the other half returns to the atmosphere as plant respiration.

NPP is the net carbon gained by plants. It includes new plant biomass produced, exudation, carbon transfers to symbionts, and the emission of volatile organic compounds by plants. Differences in NPP among marine and lake ecosystems depend primarily on physical forces that govern nutrient resupply from depth. NPP varies seasonally in these ecosystems in response to changes in light, temperature, and mixing. Light, nutrients, current, and disturbance interact to determine NPP of flowing waters. Differences among terrestrial biomes in NPP correlate with climate at the global scale largely because temperature and precipitation determine the availability of soil resources required to support plant growth. Plants actively sense the availability of these resources and adjust leaf longevity, leaf area, and photosynthesis to match this resource supply. For this reason, NPP is greatest in environments with high availability of belowground resources. After disturbance, leaf area and NPP are often reduced below levels that the environment could potentially support. Plants maximize production by allocating new growth to tissues that acquire the most limiting resources. Constantly shifting patterns of allocation reduce the degree of limitation of NPP by any single resource and make NPP in most ecosystems responsive to more than one resource. Tissue loss is just as important as NPP in explaining changes in plant biomass. Programmed loss of tissues provides a supply of plant nutrients that supports new production. Biomass and NPP are greatest in warm, moist environments and least in environments that are cold or dry. The length of the photosynthetic season and leaf area

are the two strongest determinants of the global patterns in NPP. Most ecosystems have a similar ( $1\text{--}3\text{ g biomass m}^{-2}$  of leaf  $\text{day}^{-1}$ ) daily NPP per unit leaf area.

## Review Questions

1. What controls the partitioning of carbon between growth and respiration? Explain why the efficiency of converting sugars into new biomass is relatively constant.
2. What factors influence the variability in maintenance respiration?
3. Describe how climate influences seasonal variation in NPP of the ocean and lakes through its effects on surface heating and vertical mixing.
4. How do light and nutrients interact to influence NPP in the ocean, lakes, and flowing waters?
5. Describe the multiple ways in which climate affects the NPP of grasslands or tundra.
6. There is generally a close correlation between GPP and NPP. Describe the mechanisms that account for short-term variations in GPP and NPP (e.g., diurnal and seasonal variations).
7. Describe the mechanisms that account for the relationship between GPP and NPP when terrestrial ecosystems from different climatic regimes are compared.
8. How does allocation to roots vs. shoots respond to shade, nutrients, water,  $\text{CO}_2$ , or grazing?
9. How does variation in allocation influence resource limitation, resource capture, and NPP?
10. Why do plants senesce tissues in which they have invested carbon and nutrients rather than retaining tissues until they are removed by disturbance or herbivory?
11. Describe the carbon budget of a terrestrial plant in terms of GPP, respiration, and production. How would you expect each of these parameters to respond to changes in temperature, water, light, and nitrogen?

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