8.06

Biogeochemistry of Terrestrial Net Primary Production

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8.06.1 INTRODUCTION

Net primary production (NPP) is the amount of carbon and energy that enters ecosystems. It provides the energy that drives all biotic processes, including the trophic webs that sustain animal populations and the activity of decomposer organisms that recycle the nutrients required to support primary production. NPP not only sets the baseline for the functioning of all ecosystem components but also is the best summary variable of ecosystem processes, being the result of numerous interactions among elements, organisms, and environment. This dual role makes NPP the key integrative process in ecosystems (McNaughton *et al.*, 1989) and thus a critical component in our understanding of ecosystem responses to the many changes that are occurring in the global environment. In this chapter, we explain the mechanisms that control NPP, including the environmental constraints on plant growth and the ways in which plants adjust to and alter these constraints.

8.06.2 GENERAL CONSTRAINTS ON NPP

8.06.2.1 What is NPP?

NPP is the net carbon gain by vegetation over a particular time period—typically a year. It is the balance between the carbon gained by photosynthesis and the carbon released by plant respiration. NPP includes the new biomass produced by plants, the soluble organic compounds that diffuse or are secreted by roots into the soil (root 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).

"Measured" NPP is more of an index of net primary production than a true value. Most field measurements of NPP document only the new plant biomass produced and therefore probably underestimate the true NPP by at least 30% (Table 1). There are many sources of error to this estimate. Some biomass above and below ground 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. 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 (i.e., a portion of carbon lost from plants), rather than a component of carbon gain. Volatile emissions are also rarely measured, but are generally a small fraction (<5%) of NPP and thus are probably not a major source of error (Guenther *et al.*, 1995; Lerdau, 1991). For some purposes, these errors may not be too important. A frequent objective of measuring NPP, for example, is to estimate the rate of biomass accumulation. Root exudates, transfers to symbionts, losses to herbivores, and volatile emissions are lost from plants and therefore do not contribute directly to biomass accumulation. Consequently, failure to measure these components of NPP does not bias estimates of biomass accumulation rates. However, these losses of NPP from plants fuel other ecosystem processes such as nitrogen fixation, herbivory, decomposition, and nutrient turnover, so they are important components of the overall carbon dynamics of ecosystems and strongly influence the rates of and interactions among element cycles.

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 total ecosystem NPP actually measure components of 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

Table 1 Major components of NPP and typical relative magnitudes[a].

Components of NPP	*% 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	10–30
Losses to herbivores and mortality	1–40
Volatile emissions	0–5

[a] Seldom, if ever, have all of these components been measured in a single study (Chapin *et al.*, 2002).

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 care must be used when comparing data on NPP or biomass among studies. These limitations suggest that the large number of NPP estimates that are available globally may not be a valid indication of our understanding of the process.

8.06.2.2 The General Biochemistry of NPP

NPP is the carbon gained by photosynthesis after taking into account the respiratory costs associated with growth and maintenance. Thus, the basic recipe for NPP is simply a function of the resources required for photosynthesis (light, CO_2, nutrients, water), coupled with the environmental factors that influence the rate at which these ingredients are assembled. NPP requires the proper balance of resources and is constrained by the resource in least abundance, relative to plant demand. Increasing the availability of the most limiting resource will increase NPP up to the point that another resource becomes limiting. Because NPP ultimately depends on a *balance* of resources, one of the simplest approaches to understanding controls over NPP is a stoichiometric approach. In marine systems, it has been established that the cytoplasm of primary producers has a certain ratio of elements (the Redfield ratio) that supports optimal metabolism (Redfield, 1958). Similar ratios are observed in terrestrial vegetation, with land plants having an average C : N : S : P of 790 : 7.6 : 3.1 : 1 (Bolin *et al.*, 1983). Departures from this ratio of plant nutrients can be used as an indicator of nutrient limitation (Koerselman and Mueleman, 1996). We will discuss the specific stoichiometry of terrestrial NPP later in this chapter, but for now, we will base these discussions on the premise that plants need a balance of these photosynthetic ingredients, and NPP is limited by the resources that are in lowest supply relative to plant demand.

The relative importance of the resources and environmental conditions that limit NPP vary by scale and ecosystem. At the global scale, total NPP varies 14-fold among mature stands of the major terrestrial biomes (Table 2). This variation correlates strongly with climate. In ecosystems where moisture is favorable, NPP increases exponentially with temperature. Where temperature is favorable, NPP increases to a maximum in tropical rainforests with moderately high precipitation (2–3 m annual precipitation) and declines at extremely high precipitation, due to anaerobic conditions and/or depletion of soil minerals by rapid weathering (Schuur, in press) (Figure 1). The global pattern of NPP reflects patterns of precipitation more strongly than patterns of temperature (Foley *et al.*, 1996; Gower, 2002; Kucharik *et al.*, 2000; New *et al.*, 1999) (Figure 2) because most of the terrestrial surface receives an order of magnitude less precipitation than is optimal for NPP.

Much of the variation in NPP simply reflects the length of the growing season. NPP that is averaged over the time that plants actively produce new biomass varies only fourfold among biomes (Table 2). When NPP is normalized by both growing-season length and the quantity of leaf area available to fix carbon, there is no consistent relationship between NPP and climate (Chapin *et al.*, 2002). Biome differences in NPP per unit leaf area and time probably reflect uncertainty in

Table 2 Productivity per day and per unit leaf area.

Biome	*Total NPP* ($g\ m^{-2}\ yr^{-1}$)[a]	*Season length*[b] (days)	*Daily NPP per ground area* ($g\ m^{-2}\ d^{-1}$)	*Total LAI*[c] ($m^2\ m^{-2}$)	*Daily NPP per leaf area* ($g\ m^{-2}\ d^{-1}$)
Tropical forests	2,500	365	6.8	6.0	1.14
Temperate forests	1,550	250	6.2	6.0	1.03
Boreal forests	380	150	2.5	3.5	0.72
Mediterranean shrublands	1,000	200	5.0	2.0	2.50
Tropical savannas and grasslands	1,080	200	5.4	5.0	1.08
Temperate grasslands	750	150	5.0	3.5	1.43
Deserts	250	100	2.5	1.0	2.50
Arctic tundra	180	100	1.8	1.0	1.80
Crops	610	200	3.1	4.0	0.76
Range of values	14-fold	3.7-fold	3.8-fold	6-fold	3.3-fold

[a] NPP is expressed in units of dry mass (Saugier *et al.*, 2001). [b] Estimated. [c] Data from Gower (2002).

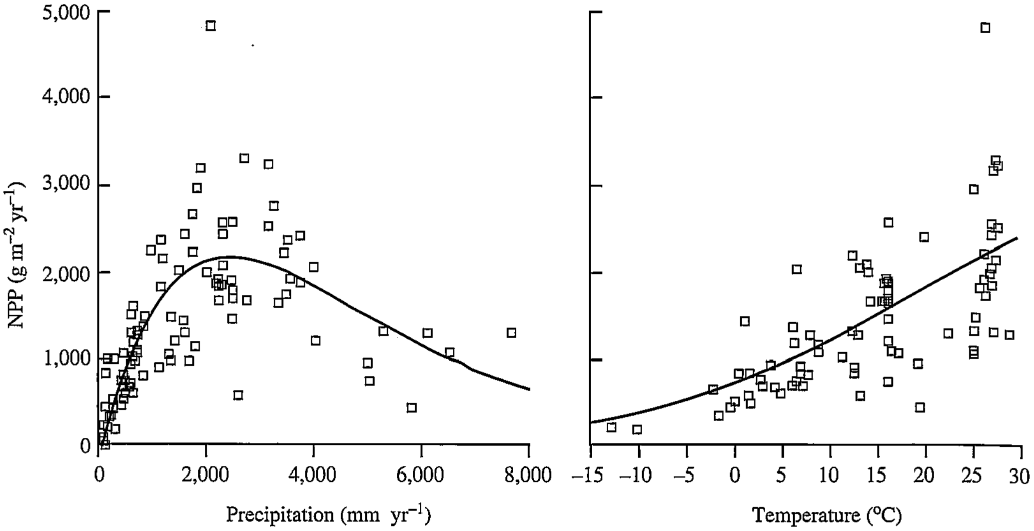


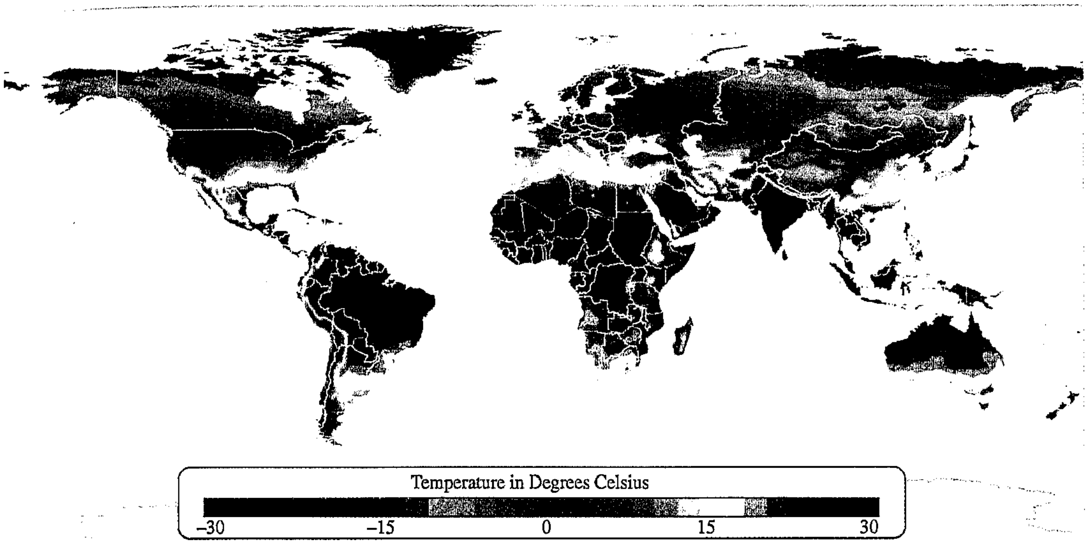
Figure 1 Correlation of NPP (in units of biomass) with temperature and precipitation (Schuur, 2003) (reproduced by permission of Springer from *Principles of Terrestrial Ecosystem Ecology*, **2002**).

the data at least as much as any underlying climatic influence. The climatic controls over NPP of mature stands can therefore be viewed as a combination of the climatic constraints on the length of growing season and the capacity of vegetation to produce and maintain leaf area. Fine root length may be just as important as leaf area in governing the productive potential of vegetation (Craine *et al.*, 2001), but fewer comparative data are available for roots.

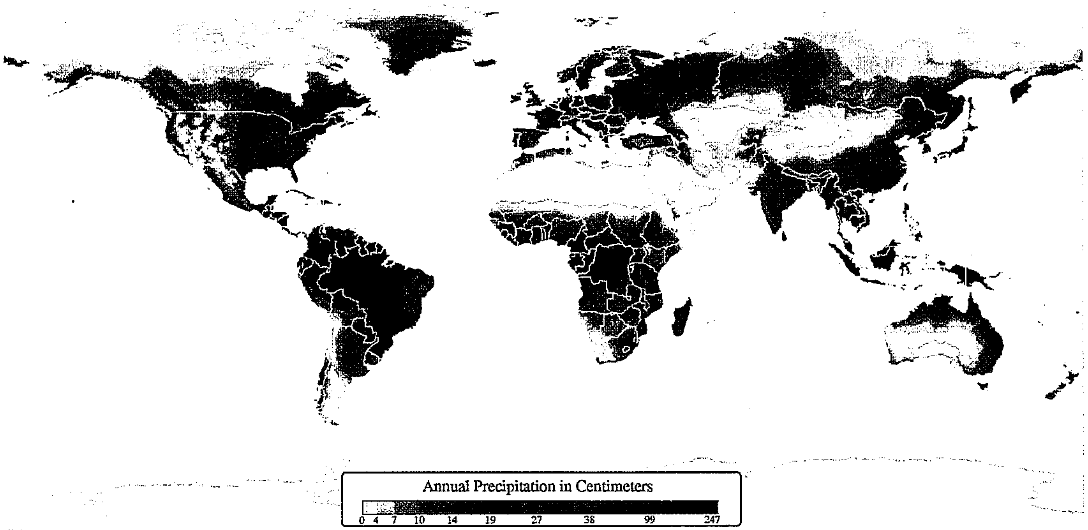
At a global scale, water is the most limiting resource to NPP, and nutrient limitation becomes an important limiting factor at more local scales. Broad global patterns of nutrient limitation exist, with phosphorus being the most commonly limiting nutrient to NPP in wet tropical systems, and nitrogen being limiting in most temperate systems. Beyond these broad patterns, it is necessary to consider environmental conditions, resource availability, and their interactions to understand the constraints on NPP at different scales. To do this, we must first consider the overall constraints of *potential* NPP within an ecosystem (state factors), and then within these constraints, to determine the interactions that occur within ecosystems to determine the conditions that directly influence NPP (interactive controls).

Dokuchaev (1879) and Jenny (1941) proposed that five independent state factors (climate, parent material, topography, time, and potential biota) govern the properties of soils and ecosystems (Amundson and Jenny, 1997). These state factors represent the overall constraints on NPP within an ecosystem. On broad geographic scales, climate is the state factor that most strongly influences ecosystem structure and functioning and determines the global patterns of NPP (Figure 2). Within this broad climatic context, parent material influences the types of soils that develop and the availability of some nutrients, both of which explain much of the regional variation in ecosystem processes. Limestone, granite, and marine sands support radically different patterns of biogeochemistry within a climate zone. Patterns of ecosystem development over time lead to shifts in the relative availability of different nutrients, causing long-term changes in an ecosystem's potential NPP. Topography influences both microclimate and soil development at a local scale, causing additional fine-scale variation in biogeochemical processes. If NPP were determined by a fixed stoichiometry of resources in all terrestrial plants, these first four state factors would be sufficient to predict overall potential patterns of NPP. Functional types of plants differ dramatically, however, in their potentials for growth under different limiting conditions. Potential biota governs the types and diversity of organisms that actually occupy a site. The resulting species composition then determines the observed response of NPP to other state factors because plant species differ in their stoichiometry of NPP.

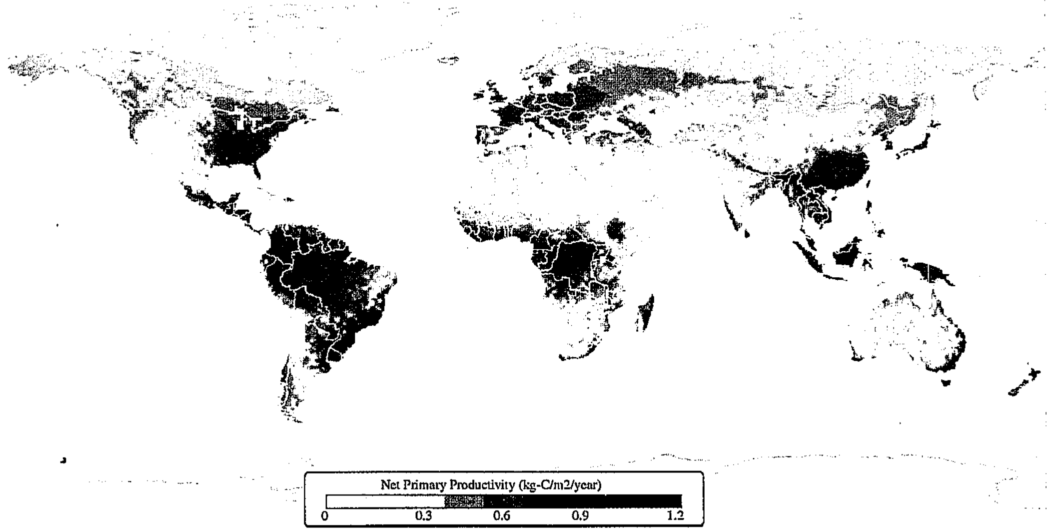
Figure 2 Global patterns of mean annual temperature and precipitation (New *et al.*, 1999) and of modeled NPP (Foley *et al.*, 1996; Kucharik *et al.*, 2000) (reproduced by permission of Atlas of the Biosphere http://atlas.sage.wisc.edu).


Temperature in Degrees Celsius
−30
−15
0
15
30

(a)


Annual Precipitation in Centimeters
0
4
7
10
14
19
27
38
99
247

(b)


Net Primary Productivity (kg-C/m2/year)
0
0.3
0.6
0.9
1.2

(c)

Together these state factors set the potential patterns of NPP and provide a basis for predicting local and global patterns of NPP and other ecosystem processes.

Within the constraints set by state factors, biogeochemical processes are strongly influenced by a web of interactions among organisms and the physical and chemical environment. Interactive controls are factors that both *control* and *are controlled by* ecosystem characteristics (Chapin *et al.*, 1996; Field *et al.*, 1992). These interactive controls include the functional types of organisms that occupy the ecosystem; the resources (e.g., water, nutrients, oxygen) that are used by organisms to grow and reproduce; modulators (e.g., temperature and pH) that influence the activity of organisms but are not consumed by them; disturbance regime; and human activities. These interactive controls respond dynamically to any external change in state factors and to any change in other interactive controls. The composition of a plant community, for example, is influenced both by the global changes in climate and regional biota (state factors) and by nitrogen deposition, livestock density, fire suppression, and timber harvest (interactive controls). Many of the resulting changes in the characteristics of a plant community cause further changes in other interactive controls, including the ecosystem goods and services that benefit society. The control of ecosystem processes by the dynamic interplay among changes in interactive controls is particularly important in a globally changing environment. For this reason, we emphasize the *interactions* between organisms and their environment in describing the biogeochemical controls over NPP.

To revisit our general recipe for NPP, environmental factors influence the rate at which light, CO_2, nutrients and water are combined to form NPP. Any of these environmental factors or resources may constrain NPP, and it is ultimately a proper balance of these factors that is required for plant production. However, the importance of interacting controls in determining ecosystem processes demonstrates that NPP is not a simple function of the ratio of resources available and the environmental conditions. This simple stoichiometric approach would be valid only if plants responded passively to, and had no effect on, their environment. Plants, however, play an active role in their response to, and mediation of, resources and their environment. Within the constraints of their environment, they actively mediate the resource availability and environmental conditions that constrain NPP. Ultimately, biogeochemical cycling is driven by the interactions between organisms and their physical and chemical environment. NPP is therefore sensitive to changes in many factors, and similar levels of NPP can be reached in multiple ways. In this chapter, we begin by discussing resource limitations of photosynthesis and the ways in which plants maximize NPP under different limiting conditions at the leaf, plant, and stand levels. We then discuss how plants not only adjust to limiting conditions, but also modify these conditions to minimize the limitations.

8.06.3 LIMITATIONS TO LEAF-LEVEL CARBON GAIN

8.06.3.1 The Basic Recipe for Carbon Gain

Photosynthesis is the process by which plants use light energy to reduce carbon dioxide (CO_2) to sugars, which are subsequently converted to a variety of organic compounds that constitute ~95% of plant dry mass. Controls over photosynthesis are thus a key regulator of the stoichiometry of NPP. In this section, we describe the environmental factors that control photosynthesis and therefore the carbon inputs to vegetation. Photosynthesis requires a balance of CO_2, H_2O, light, and nutrients. The simplest way to describe limitation of photosynthesis is that, when one of these factors has low availability relative to the ratio of required resources, this is a limiting factor. When any single factor limits photosynthesis, plants exhibit a variety of adjustments that extend the range of conditions under which photosynthesis can occur. As other factors become limiting, plants exhibit trade-offs that modify the relative requirements for different raw materials for plant growth and therefore alter the stoichiometry of NPP.

This principal of adjustments and trade-offs is illustrated by changes in photosynthesis that occur in response to variations in raw materials (light and CO_2). Light is captured by chlorophyll and other photosynthetic pigments. CO_2 enters the leaf through stomata, which are pores in the leaf surface whose aperture is regulated by the plant. When stomatal pores are open to allow CO_2 to diffuse into the leaf (high stomatal conductance), water evaporates from moist cell surfaces inside the leaf and diffuses out through the stomata to the atmosphere, creating a demand for additional water to be absorbed from the soil. Nitrogen-containing photosynthetic enzymes then use chemical energy captured by photosynthetic pigments to reduce CO_2 to sugars. Together these interacting processes dictate that photosynthesis must be sensitive to the availability of at least light, CO_2, water, and nitrogen.

Plants are not exposed to the resources necessary for photosynthesis in optimal proportions, but under a wide variety of circumstances, plants adjust the components of photosynthesis so all these components are about equally limiting to photosynthesis (Farquhar and Sharkey, 1982). Plants make this adjustment by altering the size of stomatal openings, which alters the rate of diffusion of CO_2 and water vapor, or by changing the concentrations of light-harvesting pigments or photosynthetic enzymes, which alters the nitrogen requirement for carrying out the biochemistry of photosynthesis.

The general principle of colimitation 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.

8.06.3.2 Light Limitation

When light is the only factor limiting photosynthesis, net photosynthesis increases linearly with increasing light. The slope of this line (the quantum yield of photosynthesis) is a measure of the efficiency with which plants use absorbed light to produce sugars. The quantum yield is similar among all C_3 plants at low light in the absence of environmental stress. In other words, all C_3 plants have a relatively constant photosynthetic light-use efficiency ($\sim 6\%$) of converting absorbed visible light into chemical energy under low-light conditions. At high irradiance, photosynthesis becomes light saturated, i.e., it no longer responds to changes in light supply, due to the finite capacity of the light-harvesting reactions to capture light. As a result, light energy is converted less efficiently into sugars at high light. As described later, leaves at the top of a plant canopy and species that characteristically occur in high-light habitats saturate at higher light intensities than do leaves and plants characteristic of low-light environments.

In response to short-term environmental variation, individual leaves minimize light limitation by adjusting stomatal conductance and photosynthetic capacity to maximize carbon gain in different light environments (Chazdon and Field, 1987; Chazdon and Pearcy, 1991; Pearcy, 1988; Pearcy, 1990). 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 the hypothesis of colimitation of photosynthesis by biochemistry and diffusion. It allows plants to conserve water under low light and to maximize carbon uptake at high light, thus regulating the trade-off between carbon gain and water loss.

Over longer timescales (days to months) plants acclimate to variations in light availability by producing leaves with different photosynthetic properties. Sun leaves at the top of the canopy have more cell layers, are thicker, and therefore have greater photosynthetic capacity per unit leaf area than do shade leaves (Terashima and Hikosaka, 1995; Walters and Reich, 1999). The respiration rate of a tissue depends on its protein content, as described later, 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 more positive carbon balance (photosynthesis minus respiration) under low light than do sun leaves. The changes in photosynthetic properties as a result of genetic adaptation are similar to patterns observed with acclimation. Species that are adapted to high light and are intolerant of shade typically have a higher photosynthetic capacity per unit mass or area and higher respiration rate than do shade-tolerant species, even in the shade (Walters and Reich, 1999). The net effect of acclimation or adaptation to variation in light availability is to extend the range of light availability over which vegetation maintains a relatively constant light-use efficiency, i.e., a relatively constant relationship between absorbed photosynthetically active radiation and net photosynthesis (Chapin *et al.*, 2002).

8.06.3.3 CO_2 Limitation

When CO_2 is the only factor limiting photosynthesis, net photosynthesis increases linearly with increasing CO_2 concentration, until other factors limit photosynthesis, at which point the curve saturates, much as described for the photosynthetic response to light. Most plants operate at the upper end of the linear portion of the CO_2–response curve, where CO_2 and biochemical processes are about equally limiting to photosynthesis (Farquhar and Sharkey, 1982).

The free atmosphere is so well mixed that its CO_2 concentration varies globally by only 4%. Consequently, spatial variation in CO_2 concentration does not explain much of the global variation in photosynthetic rate (Field, 1991). Nonetheless, the continued worldwide increases in atmospheric CO_2 concentration could cause a general increase in carbon gain by ecosystems. A doubling of the CO_2 concentration to which leaves are exposed, for example, leads to a 30–50% increase in photosynthetic rate over the short term (Curtis and Wang, 1998). The long-term enhancement of photosynthesis by addition of CO_2 is, however, uncertain. Herbaceous plants and deciduous trees (but not conifers) sometimes acclimate to increased CO_2 concentration by reducing photosynthetic capacity and stomatal conductance (Ellsworth, 1999; Mooney *et al.*, 1999). This reduces the nitrogen and water required to fix a given amount of carbon, as expected from the hypothesis of colimitation of photosynthesis by biochemistry and diffusion. In other cases acclimation has no effect on photosynthetic rate and stomatal conductance (Curtis and Wang, 1998). The downregulation of CO_2 uptake in response to elevated CO_2 causes photosynthesis to respond less strongly to elevated CO_2 than we might expect from a simple extrapolation of a CO_2-response curve of photosynthesis.

Over the long term, indirect effects of elevated CO_2 often have an important influence on trade-offs between CO_2 uptake and requirements for water and nitrogen. In dry environments, for example, the reduced stomatal conductance caused by elevated CO_2 leads to a decline in transpiration, which reduces evapotranspiration and increases soil moisture, which can affect nitrogen mineralization (Curtis *et al.*, 1996; Díaz *et al.*, 1993; Hungate *et al.*, 1997). Elevated CO_2 often has a greater effect on plant growth through changes in moisture and nutrient supply than through a direct stimulation of photosynthesis by elevated CO_2 (Hungate *et al.*, 1997; Owensby *et al.*, 1993). Given that the atmospheric CO_2 concentration has increased 30% (by 90 parts per million by volume; ppmv) since the beginning of the Industrial Revolution, it is important to understand and predict these indirect effects of elevated CO_2 on carbon gain by ecosystems.

8.06.3.4 Nitrogen Limitation

Photosynthetic capacity, i.e., the photosynthetic rate per unit leaf mass measured under favorable conditions of light, moisture, and temperature, increases linearly with leaf nitrogen concentration over almost the entire range of nitrogen concentrations found in natural ecosystems (Evans, 1989; Field and Mooney, 1986; Poorter, 1990; Reich *et al.*, 1999, 1992, 1997). This relationship exists because photosynthetic enzymes account for a large proportion of the nitrogen in leaves. Only at extremely high nitrogen concentrations or under conditions where other factors limit photosynthesis is there an accumulation of nitrate and other forms of nitrogen unrelated to photosynthetic capacity (Bloom *et al.*, 1985). 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 turnover. Many species differ in their 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. Environmental stresses that cause plants to produce leaves with a low leaf nitrogen concentration result in low photosynthetic capacity. 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 (Field and Mooney, 1986; Reich *et al.*, 1999, 1997). Thus, as with adjustment to variation in light availability, plants adjust to variation in nitrogen supply by the same physiological mechanism within species (acclimation) as between species (adaptation), in this case by increasing the concentration of photosynthetic enzymes and pigments.

Plants with a high photosynthetic capacity have a high stomatal conductance, in the absence of environmental stress (Reich *et al.*, 1999, 1997). This enables plants with a high photosynthetic capacity to gain carbon rapidly, at the cost of high rates of water loss. Conversely, species with a low photosynthetic capacity conserve water as a result of their lower stomatal conductance. This illustrates the trade-off between water and nitrogen in response to variation in nitrogen supply. As described later, water stress induces the same trade-off. Plants acclimated and adapted to low water availability have a low stomatal conductance to conserve water and a low tissue nitrogen concentration, which reduces photosynthetic capacity. The net effect of these trade-offs is to maintain colimitation of photosynthesis by diffusive and biochemical processes.

There appears to be an unavoidable trade-off between traits that maximize photosynthetic rate and traits that maximize leaf longevity (Reich *et al.*, 1999, 1997). Many plant species that grow in low-nutrient environments produce long-lived leaves because there are insufficient nutrients to support rapid leaf turnover (Chapin, 1980). Shade-tolerant species also produce longer-lived leaves than do shade-intolerant species (Walters and Reich, 1999). 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 (Chabot and Hicks, 1982; Gulmon and Mooney, 1986; Reich *et al.*, 1997). To survive, long-lived leaves must have sufficient structural rigidity to withstand drought and/or 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 (Chapin, 1993; Lambers and Poorter, 1992). 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 compounds that deter herbivores, but also contribute to tissue mass and a low specific leaf area (Coley *et al.*, 1985; Gulmon and Mooney, 1986). Many woody plants in dry environments also produce long-lived leaves. For the same reasons, these leaves typically have a low specific leaf area and a low photosynthetic capacity (Reich *et al.*, 1999).

The broad relationship among species with respect to photosynthetic rate and leaf life span is similar in all biomes; a 10-fold decrease in leaf life span gives rise to about a fivefold increase in photosynthetic capacity (Reich *et al.*, 1999). Species with long-lived leaves, low photosynthetic capacity, and low stomatal conductance are common in all low-resource environments, including those that are dry, infertile, or shaded.

Plants in productive environments, in contrast, 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 sufficient light is available. These leaves have a high specific leaf area, 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 but render plants more vulnerable to environmental stresses such as drought (Schulze and Chapin, 1987). Many early successional habitats, such as recently abandoned agricultural fields or post-fire sites, have sufficient light, water, and nutrients to support high growth rates and are characterized by species with short-lived leaves, high tissue nitrogen concentration, high specific leaf area, and high photosynthetic rates. Even in late succession, environments with high water and nutrient availability are characterized by species with relatively high nitrogen concentrations and photosynthetic rates. Plants in these habitats can grow quickly to replace leaves removed by herbivores or to fill canopy gaps produced by death of branches or individuals.

The changes in tissue nitrogen, and therefore in the C : N ratio of tissues, that occur in response to variation in nitrogen supply constitute an important change in element stoichiometry. This occurs through changes in the ratio of cytoplasm to cell wall and changes in compounds such as tannins and nitrate that are stored in vacuoles. Aquatic phytoplankton have no cell walls and limited capacity for storing compounds in vacuoles and therefore exhibit a much smaller range of variation in C : N ratio than do terrestrial plants (Elser *et al.*, 2000). This variation in stoichiometry enables plants to maximize carbon gain under favorable conditions and maximize efficiency of using other resources to fix carbon, when these resources are limiting to plant growth.

In summary, plants produce leaves with a continuum of photosynthetic characteristics, ranging from short-lived thin 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 specific leaf area (leaf area per unit leaf mass) is often used in ecosystem comparisons as an easily measured index of photosynthetic capacity.

8.06.3.5 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 increases leaf temperature and water vapor concentration inside the leaf, leading to greater water loss by transpiration. 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. 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. This decline in stomatal conductance reduces photosynthetic rate and the efficiency of using light to fix carbon below levels found in unstressed plants.

Plants that are acclimated and adapted to dry conditions reduce their photosynthetic capacity and leaf nitrogen content toward a level that matches the low stomatal conductance that is necessary to conserve water in these environments (Wright *et al.*, 2001). A high photosynthetic capacity provides little benefit if the plant must maintain a low stomatal conductance to conserve water. Conversely, low nitrogen availability or other factors that constrain leaf nitrogen concentration result in leaves with low stomatal conductance. This strong correlation between photosynthetic capacity and stomatal conductance maintains the balance between photosynthetic capacity and CO_2 supply, i.e., the colimitation of photosynthesis by diffusional and biochemical processes. In addition to their low photosynthetic capacity and low 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 (Ehleringer and Mooney, 1978; Forseth and Ehleringer, 1983). 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 altering photosynthetic capacity per unit leaf area. By altering their coarse-scale allocation to biomass (leaves versus roots), plants maintain photosynthetic capacity and associated variation in stomatal conductance within a range in which normal physiological regulation can continue to occur.

Water-use efficiency of photosynthesis is defined as the carbon gain per unit of water lost. Water use 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. 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 resistances 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 because of 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 water-use efficiency. Plants in dry environments also enhance water-use efficiency 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).

8.06.3.6 Summary of Leaf-level Carbon Gain

The individual leaves of plants exhibit a similar response to photosynthetic limitation by any single environmental factor, whether it is CO_2, light, nitrogen, or water. Photosynthesis initially increases linearly in response to increases in the limiting factor, until some point at which other environmental factors become limiting. Because photosynthetic capacity is geared to match the typical availability of resources that the leaf experiences, there is a limit to which photosynthesis can instantaneously respond to changes in availability of a single limiting factor. Over a longer time period, plants acclimate (physiological adjustment), change their distribution (changes in community composition), or adapt (genetic adjustment). In general, both acclimation and adaptation to low availability of an environmental resource occur by the same physiological mechanism. These adjustments extend the range of environmental conditions over which carbon gain occurs in ecosystems. Many of these adjustments involve changes in photosynthetic capacity, which entail changes in C:N ratio. This variation in element stoichiometry enables plants to maximize carbon gain under favorable environmental conditions. Under unfavorable conditions the increased C:N ratio associated with reduced photosynthetic capacity maximizes the efficiency of using other resources to gain carbon, primarily by prolonging leaf longevity and by shifting allocation to production of other tissues such as wood or roots that have lower tissue nitrogen concentrations than leaves.

8.06.4 STAND-LEVEL CARBON GAIN

8.06.4.1 Scaling of Carbon Gain

Gross primary production (GPP) is the sum of the net photosynthesis by all leaves measured at the ecosystem scale. Modeling studies and field measurements suggest that most conclusions derived from leaf-level measurements of net photosynthesis also apply to GPP. In most closed-canopy ecosystems, photosynthetic capacity decreases exponentially through the canopy in parallel with the exponential decline in irradiance (Field, 1983; Hirose and Werger, 1987). This matching of photosynthetic capacity to light availability maintains the colimitation 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, as a result of at least three processes:

(i) Sun leaves at the top of the canopy develop more cell layers than shade leaves and therefore contain more nitrogen per unit leaf area (Terashima and Hikosaka, 1995).

(ii) New leaves are produced primarily at the top of the canopy, causing nitrogen to be transported to the top of the canopy (Field, 1983; Hirose and Werger, 1987).

(iii) Leaves at the bottom of the canopy senesce when they become shaded to the point that they no longer maintain a positive carbon balance, i.e., they consume more energy in respiration than they produce in photosynthesis.

Much of the nitrogen resorbed from these senescing leaves is transported to the top of the canopy to support the production of young leaves with high photosynthetic capacity. 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 in which 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 is abundant throughout the canopy. In these canopies, light availability, nitrogen concentrations, and photosynthetic rates are more uniformly distributed through the canopy.

Canopy-scale relationships between light and nitrogen appear to occur even in multispecies communities (Hirose *et al.*, 1995; Hikosaka and Hirose, 2001). 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 multispecies 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 (Hikosaka and Hirose, 2001; Hirose and Werger, 1994). This specialization and competition among individuals probably contributes to the vertical scaling of nitrogen and photosynthesis that is observed in multispecies stands.

Vertical gradients in other environmental variables reinforce the maximization of carbon gain near the top of the canopy. In addition to irradiance, the canopy modifies wind speed, temperature, relative humidity, and CO_2 concentration. The most important of these effects is the exponential decrease in wind speed from the free atmosphere to the ground surface. This vertical reduction in wind speed is most pronounced in smooth canopies, characteristic of crops or grasslands, whereas rough canopies, characteristic of many forests, create more friction and turbulence that increases the vertical mixing of air within the canopy (McNaughton and Jarvis, 1991). 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. 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. 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 (Landsberg and Gower, 1997). Although multiple environmental gradients within the canopy have complex effects on photosynthesis, they probably enhance photosynthesis near the top of canopies in ecosystems with sufficient water and nutrients to develop dense canopies.

Canopy properties extend the range of light availability over which the light-use efficiency of the canopy remains constant. The light-response curve of canopy photosynthesis, measured in closed canopies (total leaf area index (LAI)—the leaf area per unit ground area—is larger than ~3), saturates at higher irradiance than does photosynthesis by a single leaf (Jarvis and Leverenz, 1983). The canopy increases the efficiency of converting light energy into fixed carbon for several reasons. The more vertical orientation of leaves at the top of the canopy reduces the likelihood that they become light-saturated and increases light penetration deeper into the canopy. The clumped distribution of leaves in shoots, branches, and crowns also increases light penetration into the canopy, particularly in conifer canopies in which needles are clumped around stems. This could explain why conifer forests frequently support a higher LAI than deciduous forests. The light compensation point also decreases from the top to the bottom of the canopy, so lower leaves maintain a positive carbon balance, despite the relatively low light availability. In crop canopies, where water and nutrients are highly available, the linear relationship between canopy carbon exchange and irradiance (i.e., constant light-use efficiency) extends up to irradiance typical of full sunlight. In other words, there is no evidence of light saturation, and light-use efficiency remains constant over the full range of natural light intensities (Figure 3) (Ruimy *et al.*, 1996). In most natural canopies, however, canopy photosynthesis becomes light-saturated at high irradiance.

8.06.4.2 Scaling of Controls over GPP

As described in the previous section, stand-level photosynthesis (GPP) responds to limiting

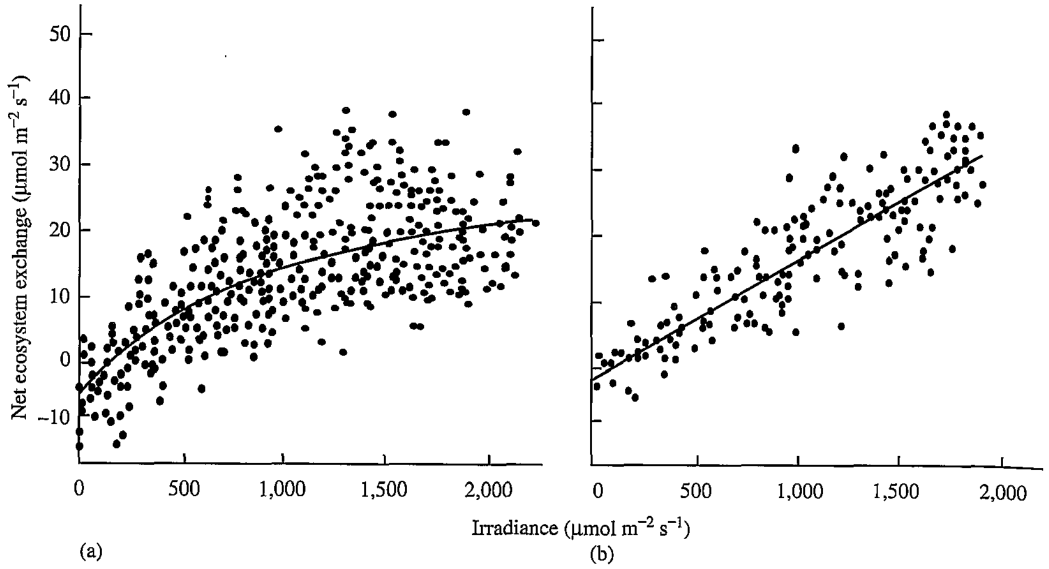


Figure 3 Effect of vegetation and irradiance on net ecosystem exchange in (a) forests and (b) crops (reproduced by permission of Academic Press from *Adv. Ecol. Res.*, **1996**, *26*, 1–68).

factors in a way that qualitatively matches the responses of individual leaves. This occurs because the leaves at the top of the canopy are exposed to the highest irradiance and have primary access to plant nitrogen. In addition, these leaves experience the highest wind speed and therefore have a thin boundary layer, so the gradients in CO_2 concentration, water vapor concentration, and temperature between the leaf and the air are similar to patterns measured on individual leaves.

The major differences between leaf-level and stand-level responses of photosynthesis to environmental constraints relate to differences in leaf area and its control. LAI is both a cause and a consequence of ecosystem differences in NPP. It is governed primarily by the availability of soil resources (water and nutrients) and by the time for recovery from past disturbances and other processes (e.g., herbivory) that remove leaves from vegetation.

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 ~70% of the ice-free terrestrial surface has relatively open canopies (Graetz, 1991) (Figure 4). GPP correlates closely with leaf area below a total LAI of ~8 (projected LAI of 4) (Schulze *et al.*, 1994), suggesting that leaf area is a critical determinant of GPP on most of Earth's terrestrial surface. GPP saturates with increasing LAI in dense canopies, because the leaves in the middle and bottom of the canopy contribute relatively little to GPP. The availability of soil resources, especially water and nutrient supply, is

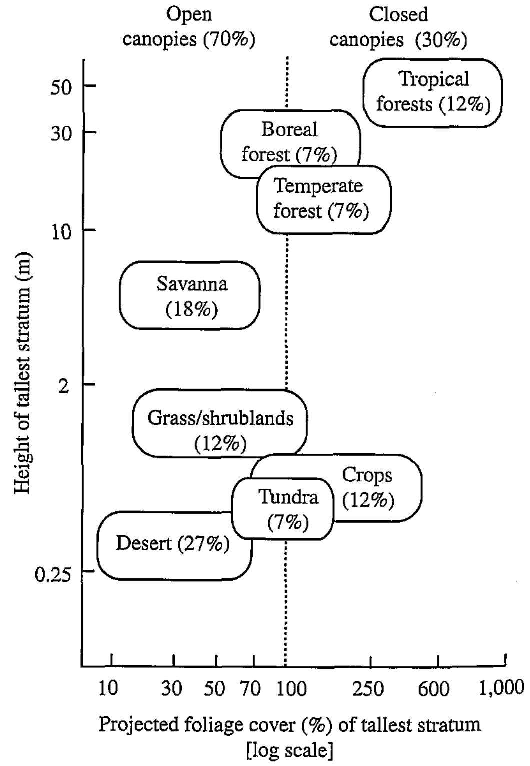


Figure 4 Projected foliage cover and canopy height of the major biomes. Typical values for that biome and the percentage of the terrestrial surface that it occupies are shown. The vertical line shows 100% canopy cover (reproduced by permission of Kluwer from *Climatic Change*, **1991**, *18*, 147–173).

a critical determinant of LAI for two reasons: (i) Plants in high-resource environments produce a large amount of leaf biomass; and (ii) leaves produced in these environments have a high SLA, i.e., a large leaf area per unit of leaf biomass. As discussed earlier, a high specific leaf area maximizes light capture and therefore carbon gain per unit of leaf biomass (Lambers and Poorter, 1992; Reich *et al.*, 1997). In low-resource environments, plants produce fewer leaves, and these leaves have a lower specific leaf area. Ecosystems in these environments have a low LAI and therefore a low GPP.

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 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.

8.06.5 RESPIRATION

All controls on NPP that we have discussed so far have focused on production side, but NPP is also a function of carbon loss through respiration. The environmental controls over plant respiration are quite similar to the controls over GPP because respiration, like photosynthesis, is tightly linked to environmental factors that regulate plant activity. The mechanistic basis for this relationship can be understood by separating plant respiration into three functional components: growth respiration, maintenance respiration, and the respiratory cost of ion uptake.

The carbon expended in plant growth consists of the carbon incorporated into new tissue plus the respiration required to produce the ATPs necessary to carry out this synthesis (Penning de Vries, 1975). This carbon cost can be calculated from the chemical composition of tissues and an estimate from biochemical pathways of the carbon required to synthesize each class of chemical compound (Chapin, 1989; Merino *et al.*, 1982; Penning de Vries, 1975; Williams *et al.*, 1987). Although there is a threefold range in the carbon cost of synthesis among the major classes of chemical compounds in plants, the carbon cost per gram of tissue is surprisingly similar across species, tissue types, and ecosystems (Chapin, 1989; Poorter, 1994). All plant parts contain some expensive constituents. For example, metabolically active tissues, such as leaves, have high concentrations of proteins, tannins, and lipids (primarily lipophilic substances such as terpenes that defend protein-rich tissues from herbivores and pathogens) (Bryant and Kuropat, 1980; Coley *et al.*, 1985), whereas structural tissue is rich in lignin. Similar chemical correlations are observed within a tissue type across species or growing conditions. Leaves of rapidly growing species with high protein concentration, for example, 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. Given that the carbon cost of growth is nearly constant, we expect that growth respiration should be a relatively constant fraction of NPP. Gas exchange and modeling studies support this hypothesis: growth respiration is ~25% of the carbon incorporated into new tissues (Waring and Running, 1998). In summary, the rates of growth and therefore of growth respiration measured at the ecosystem scale (g C m^{-2} d^{-1}) increase when temperature and moisture favor growth, but growth respiration is always a nearly constant fraction of NPP, regardless of environmental conditions.

Ion transport across membranes may account for 25–50% of root respiration (Bloom, 1986; Lambers *et al.*, 1996, 1998). This large requirement for respiratory energy is not well quantified in field studies but may correlate with NPP because the quantity of nutrients absorbed is greatest in productive environments. Several factors cause this cost of ion uptake to differ among ecosystems. The respiratory cost of nitrogen uptake 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 plant species and ecosystems, depending on whether the nitrate is reduced in the leaves, where it may be supported by excess reducing power from the light reaction, or in the roots, where it depends on carbohydrates transported to roots. In general, we expect respiration associated with ion uptake to correlate with the total quantity of ions absorbed and therefore to show a positive relationship with NPP. However, there are few data available to evaluate this hypothesis.

All live cells, even those that are not actively growing, require energy to maintain ion gradients across cell membranes and to replace proteins, membranes, and other constituents. Maintenance respiration provides the ATP for these maintenance and repair functions. Laboratory experiments suggest that ~85% of maintenance respiration is associated with the turnover of proteins (~6% 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; Ryan and Waring, 1992; van der Werf *et al.*, 1992). We therefore expect maintenance respiration to be greatest in ecosystems with high tissue nitrogen concentrations and/or a large plant biomass and thus 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 uptake (Lambers *et al.*, 1998). These proportions may vary with environment and plant growth rate and are difficult to estimate precisely.

Maintenance respiration depends on environment as well as tissue chemistry. It increases with temperature because proteins and membrane lipids turn over more rapidly at high temperatures. Drought also imposes short-term metabolic costs associated with synthesis of osmotically active organic solutes. 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, following 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.

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 *et al.*, 1971; Billings and Mooney, 1968; Mooney and Billings, 1961). The net result of these counteracting temperature effects is that plants from different thermal environments have similar respiration rates, when measured at their mean habitat temperature (Semikhatova, 2000).

In summary, studies of the basic components of respiration associated with growth, ion uptake, and maintenance suggest that total plant respiration should be a relatively constant fraction of GPP. These predictions are consistent with the results of model simulations of plant carbon balance. These modeling studies indicate that total plant respiration is about half (48–60%) of GPP, when a wide range of ecosystems is compared (Landsberg and Gower, 1997; Ryan *et al.*, 1994). Variation in maintenance respiration is the most likely cause for variability in the efficiency of converting GPP into NPP. There are too few detailed studies of ecosystem carbon balance to know how variable this efficiency is among seasons, years, and ecosystems.

8.06.6 PHOTOSYNTHESIS, RESPIRATION, AND NPP: WHO IS IN CHARGE?

Knowing that NPP is the balance of carbon gained by photosynthesis and the carbon lost by respiration does not tell us which is the cause and which is the effect. Do the conditions governing photosynthesis dictate the amount of carbon that is available to support growth or do conditions influencing growth rate determine the potential for photosynthesis? On short timescales (seconds to days), environmental controls over photosynthesis (e.g., light and water availability) strongly influence photosynthetic carbon gain. Leaf carbohydrate concentrations increase during the day and decline at night, allowing plants to maintain a relatively constant supply of carbohydrates to nonphotosynthetic 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.

On weekly to annual timescales, however, plants adjust leaf area and photosynthetic capacity, so carbon gain matches the soil resources that are available to support growth. 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, 1991b). 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. Plants 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 (Chapin, 1991b; Davies and Zhang, 1991; Gollan *et al.*, 1985). 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 uptake (Chapin, 1991b; Lambers *et al.*, 1998). The resulting changes in growth and nutrition determine the LAI and photosynthetic capacity, which, as we have seen, largely account for ecosystem differences in carbon input (Gower *et al.*, 1999).

8.06.7 ALLOCATION OF NPP

In general, plants allocate production preferentially to those plant parts that are necessary to acquire the resources that most strongly limit growth. 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 (Garnier, 1991). 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 uptake by altering root morphology or by increasing root biomass, root longevity, nitrogen uptake rate per unit root, or extent of mycorrhizal colonization. Changes in allocation and root morphology have a particularly strong impact on nutrient uptake. It is the integrated activity (mass × acquisition rate per unit mass × 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. 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 (Gower *et al.*, 1999; Saugier *et al.*, 2001).

The balance between NPP and biomass loss determines the annual increment in plant biomass. Plants retain only part of the biomass that they produce. Some biomass loss is physiologically regulated by the plant—e.g., the senescence of leaves and roots. Senescence occurs throughout the growing season in grasslands and during autumn or at the beginning of the dry season in many trees. Other losses occur with varying frequency and predictability and are less directly controlled by the plant, such as the losses to herbivores and pathogens, wind throw, and fire. The plant also influences these tissue loss rates through the physiological and chemical properties of the tissues it produces. Still other biomass transfers to dead organic matter result from mortality of individual plants. Given the substantial, although incomplete, physiological control over tissue loss, why do plants dispose of the biomass in which they have 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 must have 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 sufficient 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 when resources decline in abundance.

8.06.8 NUTRIENT USE

Given the importance of nutrients in controlling NPP, it is important to understand the relationship between nutrient supply and NPP. Plants respond to increased supply of a limiting nutrient in laboratory experiments primarily by increasing plant growth, giving a linear relationship between rate of nutrient accumulation and plant growth rate (Ingestad and Ågren, 1988). Plants also respond to increased nutrient supply in the field primarily through increased NPP, with proportionately less increase in tissue nutrient concentration. Tissue nutrient concentrations increase substantially only when other factors begin to limit plant growth. The sorting of species by habitat also contributes to the responsiveness of nutrient uptake and NPP to variations in nutrient supply observed across habitats. Species such as trees that use large quantities of nutrients dominate sites with high nutrient supply rates, whereas infertile habitats are dominated by species with lower capacities for nutrient absorption and growth. Despite these physiological and species adjustments, tissue nutrient concentrations in the field generally increase with an increase in nutrient supply.

Nutrient-use efficiency is greatest where production is nutrient-limited. Differences among plants in tissue nutrient concentration provide insight into the quantity of biomass that an ecosystem can produce per unit of nutrient. Nutrient-use efficiency is the ratio of nutrients to biomass lost in litterfall (i.e., the inverse of nutrient concentration in plant litter)

(Vitousek, 1982). This ratio is highest in unproductive sites, suggesting that plants are more efficient in producing biomass per unit of nutrient acquired and lost, when nutrients are in short supply. Several factors contribute to this pattern (Chapin, 1980). First, tissue nutrient concentration tends to decline as soil fertility declines, as described earlier. Individual plants that are nutrient-limited also produce tissues more slowly and retain these tissues for a longer period of time, resulting in an increase in average tissue age. Older tissues have low nutrient concentrations, causing a further decline in concentration (i.e., increased nutrient-use efficiency). Finally, the dominance of infertile soils by species with long-lived leaves that have low nutrient concentrations further contributes to the high nutrient-use efficiency of ecosystems on infertile soils.

There are at least two ways in which a plant might maximize biomass gained per unit of nutrient (Berendse and Aerts, 1987): through (i) a high nutrient productivity (a_n), i.e., a high instantaneous rate of carbon uptake per unit nutrient or (ii) a long residence time (t_r), i.e., the average time that the nutrient remains in the plant:

$$\mathrm{NUE} = a_n \times t_r$$

Species characteristic of infertile soils have a long residence time of nutrients but a low nutrient productivity (Chapin, 1980; Lambers and Poorter, 1992), suggesting that the high nutrient-use efficiency in unproductive sites results primarily from traits that reduce nutrient loss rather than traits promoting a high instantaneous rate of biomass gain per unit of nutrient. Shading also reduces tissue loss more strongly than it reduces the rate of carbon gain (Walters and Reich, 1999).

There is an innate physiological trade-off between nutrient residence time and nutrient productivity. This occurs because the traits that allow plants to retain nutrients reduce their capacity to grow rapidly (Chapin, 1980; Lambers and Poorter, 1992). Plants with a high nutrient productivity grow rapidly and have high photosynthetic rates, which are associated with thin leaves, a high specific leaf area, and a high tissue nitrogen concentration. Conversely, a long nutrient residence time is achieved primarily through slow rates of replacement of leaves and roots. Leaves that survive a long time have more structural cells to withstand unfavorable conditions and higher concentrations of lignin and other secondary metabolites that deter pathogens and herbivores. Together these traits result in dense leaves with low tissue nutrient concentrations and therefore low photosynthetic rates per gram of biomass. The high nutrient-use efficiency of plants on infertile soils therefore reflects their capacity to retain tissues for a long time rather than a capacity to use nutrients more effectively in photosynthesis.

The trade-off between nutrient-use efficiency and rate of resource capture explains the diversity of plant types along resource gradients. Low-resource environments are dominated by species that conserve nutrients through low rates of tissue turnover, high nutrient-use efficiency, and the physical and chemical properties necessary for tissues to persist for a long time. These stress-tolerant plants outcompete plants that are less effective at nutrient retention in environments that are dry, infertile, or shaded (Chapin, 1980; Walters and Field, 1987). A high nutrient-use efficiency and associated traits constrain the capacity of plants to capture carbon and nutrients. In high-resource environments species with high rates of resource capture, rapid growth rates, rapid tissue turnover, and consequently low nutrient-use efficiency therefore outcompete plants with high nutrient-use efficiency. In other words, neither a rapid growth rate nor a high nutrient-use efficiency is universally advantageous, because there are inherent physiological trade-offs between these traits. The relative benefit to the plant of efficiency versus rapid growth depends on environment.

8.06.9 BALANCING NUTRIENT LIMITATIONS

8.06.9.1 Nutrient Requirements

Thus far, we have focused on the mechanisms by which plants minimize the constraints on NPP by balancing the limitations of water, CO_2, light, and nutrients. Photosynthesis and productivity require a balanced proportion of these resources, and plants can adjust their physiology to maximize NPP across a range of limiting factors. Nutrients need further explanation. Unlike light, CO_2, and water, which are relatively homogenous in quality, the nutrient category includes many chemical elements, each with different functions and controls.

Because each nutrient performs a different function in plants (Table 3), the relative amount of each nutrient required and plant response to limitation by these nutrients vary. Primary macronutrients are the nutrients needed in the largest amounts and are most commonly limiting to plant growth. These include nitrogen, phosphorus and potassium. Secondary macronutrients include calcium, magnesium, and sulfur. These are also required in large quantities but are less frequently limiting to growth. Micronutrients are essential for plant growth but are only needed in small quantities. These include boron, chloride, copper, iron, manganese, molybdenum, and zinc. All macro- and micronutrients are essential for plant

Table 3 Nutrients required by plants and their major functions.

Nutrient	*Role in plants*
Macronutrients[a]	Required by all plants in large quantities
Primary	
Nitrogen (N)	Component of proteins, enzymes, phospholipids, and nucleic acids
Phosphorus (P)	Component of proteins, coenzymes, nucleic acids, oils, phospholipids, sugars, starches Critical in energy transfer (ATP)
Potassium (K)	Component of proteins Role in disease protection, photosynthesis, ion transport, osmotic regulation, enzyme catalyst
Secondary	
Calcium (Ca)	Component of cell walls Regulates structure and permeability of membranes, root growth Enzyme catalyst
Magnesium (Mg)	Component of chlorophyll Activates enzymes
Sulfur (S)	Component of proteins and most enzymes Role in enzyme activation, cold resistance
Micronutrients[b]	Required by all plants in small quantities
Boron (B)	Role in sugar translocation and carbohydrate metabolism
Chloride (Cl)	Role in photosynthetic reactions, osmotic regulation
Copper (Cu)	Component of some enzymes Role as a catalyst
Iron (Fe)	Role in chlorophyll synthesis, enzymes, oxygen transfer
Manganese (Mn)	Activates enzymes Role in chlorophyll formation
Molybdenum (Mo)	Role in N fixation, NO_3 enzymes, Fe adsorption, and translocation
Zinc (Zn)	Activates enzymes, regulates sugar consumption
Beneficial nutrients[c]	Required by certain plant groups, or by plants under specific environmental conditions
Aluminum (Al)	
Cobalt (Co)	
Iodine (I)	
Nickel (Ni)	
Selenium (Se)	
Silicon (Si)	
Sodium (Na)	
Vanadium (V)	

[a] Macronutrients: Primary—usually most limiting because used in largest amounts. Secondary—major nutrients but less often limiting.
[b] Micronutrients: essential for plant growth, but only needed in small quantities. [c] Beneficial nutrients—often aid plant growth, but not essential.

growth and metabolism, and other elements cannot substitute for their function. However, certain functions, such as maintenance of osmotic pressure, can be accomplished by various elements. A fourth class of mineral nutrients, "beneficial nutrients" can enhance plant growth, are required by plants under very specific conditions, or are necessary for very specific groups of plants (Marschner, 1995). For example, aluminum is required by ferns, cobalt by *Fabales* with symbionts, and sodium by *Chenopodiaceae* (Larcher, 1995).

8.06.9.2 Limitations by Different Nutrients

Although all of these mineral nutrients are necessary for plant growth, the particular nutrient that limits plant production may vary in space and time. The primary macronutrients, nitrogen, phosphorus, and potassium, are used by plants in the greatest amounts, and tend to most frequently limit plant production. Nitrogen is the most commonly limiting nutrient to plant growth in terrestrial systems, particularly in the temperate zone (Vitousek and Howarth, 1991). Phosphorus generally limits plant growth in the lowland wet tropics (Tanner *et al.*, 1998), on very old soils (Vitousek and Farrington, 1997), on some Mediterranean soils (Cowling, 1993; Specht and Rundel, 1990), and on glacial and aeolian sandy soils in European heathlands (Aerts and Heil, 1993). Sites that would naturally be nitrogen-limited can become phosphorus-limited under certain conditions. Phosphorus limitation, for example, occurs in areas with high nitrogen deposition (Aerts and Berendse, 1988; Aerts and Bobbink, 1999) and in European fens that have lost substantial phosphorus over time through long-term mowing treatments (Verhoeven and Schmitz, 1991). Vegetation composition can also influence whether a site is limited by nitrogen or phosphorus. In California grasslands, for example, grass-dominated sites are nitrogen-limited, but these same sites can be sulfur- and phosphorus-limited if legumes are present (Jones *et al.*, 1970; Jones and Martin, 1964; Jones *et al.*, 1983). The limitation of nitrogen versus phosphorus also changes over successional time, with soils being nitrogen-limited early in primary succession, then becoming phosphorus-limited with time (Chapin *et al.*, 1994; Vitousek and Farrington, 1997; Walker and Syers, 1976). Calcium, magnesium, and potassium also virtually disappear due to leaching in old soils, but are frequently not limiting to plant growth due to atmospheric inputs (Chadwick *et al.*, 1999). There are, however, instances when these nutrients do limit NPP. Potassium is taken up by plants in larger amounts than any element except for nitrogen (Marschner, 1995). It tends to be limiting in ecosystems with high precipitation and very late in soil development, particularly on sandy soils (Tisdale *et al.*, 1993), but its limitation is relatively infrequent compared to nitrogen and phosphorus. Highly weathered tropical soils with high leaching rates can also be limiting in calcium, although calcium is more frequently found in excess of plant demand (Barber, 1984; Chapin, 1991a; Marschner, 1995). Base cations such as calcium and magnesium have also been found to be limiting in areas with high cation leaching associated with high nitrogen deposition (Aber *et al.*, 1998; Driscoll *et al.*, 2001; Schulze, 1989). Limitation by other essential nutrients is rare, but does occur (e.g., manganese (Goransson, 1994), iron (Goransson, 1993), molybdenum (Tisdale *et al.*, 1993)).

Although certain ecosystems can be characterized as being limited by a particular mineral nutrient, changes in the environment, such as rain storms or pulses of litter inputs, can rapidly alter the relative abundance of nutrients, shifting limitation from one nutrient to another at different times during plant growth. Thus, plants must be flexible in taking up different nutrients.

8.06.9.3 Stoichiometry of NPP

A proper balance of nutrients is required for plant growth. In marine systems, the stoichiometry of primary production is determined by the ratio of elements in the cytoplasm (Redfield ratio) that supports optimal metabolism of phytoplankton (Redfield, 1958). The C : N : P ratio is fairly constant in marine phytoplankton, and this ratio in primary producers constrains the cycling of all elements (Elser *et al.*, 2000). The amount and proportions of nitrogen and phosphorus available determine the amount of carbon fixed by phytoplankton. Limitation by either of these elements constrains any further accumulation of carbon or other nutrients by phytoplankton. The carbon and nutrients in phytoplankton in turn determine the recycling of nutrients and the N : P in the deep sea and upwelling waters, so biotic demand for nitrogen and phosphorus closely match their availability.

In terrestrial systems, similar ratios are observed in vegetation, with a general C : N : S : P of land plants being 790 : 7.6 : 3.1 : 1 (Bolin *et al.*, 1983). Such generalizations have been used to guide fertilizer application in agricultural systems. The widespread use of "fixed formulas" of nutrients, such as Hoaglands solution, in controlled environments is an indicator of the robustness of such a stoichiometric relationship (Ingestad and Ågren, 1988). Departures from such ratios have been used as indicators of nutrient limitation in plants (Jones and Martin, 1964; Koerselman and Mueleman, 1996; Ulrich and Hills, 1973). However, ratios of nutrients in tissues are not necessarily an indicator of nutrient limitation in land plants, because uptake of nutrients in terrestrial vegetation is less constrained by nutrient balances than in marine phytoplankton (Marschner, 1995).

In order to extend the simple stoichiometric control implied by the Redfield ratio to terrestrial systems, the element that most constrains NPP must define the quantities of all elements cycled through vegetation. We have already seen, however, that the nutrient-use efficiency of plants differs among growing conditions and among species. In addition, to be truly comparable to marine systems, the input and recycling of nutrients in dead plant material must also approximately equal the nutrient ratio required for plant growth. Observed dynamics in terrestrial systems are far from this simple formula because of several mechanisms that decouple nutrient and carbon cycles in terrestrial ecosystems. Let us start with a simple contrast to marine systems. The Redfield ratio is based on an optimal cytoplasmic stoichiometry of single-celled organisms. Terrestrial plants are both multicellular and have different tissue types and compounds with dramatically different stoichiometries (Bazzaz, 1997; Lambers *et al.*, 1998). In this chapter, we have already described many situations in which plants shift their relative allocation among tissues in response to a change in environment. Allocation can also differ among species. Thus, even assuming that plants receive an ideal ratio of resources, plant species have inherently different allocation strategies and even different nutrient ratios within the same tissues, leading to substantial variation in the stoichiometry of NPP (Eviner and Chapin, in press). A more dramatic departure from the simple marine stoichiometric model occurs with the recycling of nutrients in terrestrial ecosystems. There are many reasons why the supply of resources does not equal demand, as is hypothesized in marine systems. The tight coupling of nitrogen and phosphorus cycling in marine systems does not occur in terrestrial systems, where nitrogen and phosphorus differ dramatically in the controls over mineralization and availability (McGill and Cole, 1981). In addition, litter inputs have a dramatically different stoichiometry from plant demand due to resorption of nutrients from senescing litter (Aerts and Chapin, 2000). Finally, unlike the well-mixed nutrient return through upwelling in marine systems, nutrient availability in the soil is extremely heterogeneous (Caldwell *et al.*, 1996). So unlike marine systems, terrestrial cycling involves significant storage in plants and soils and slow turnover of nutrients, so the stocks of available nutrients have little relation to the fluxes.

8.06.9.4 Uncoupling Mechanisms

NPP in terrestrial systems is not a simple function of the ratio of available nutrients because there are many ways in which carbon and different nutrients become uncoupled in terrestrial ecosystems (Eviner and Chapin, in press) (Figure 5). In the following sections, we discuss those uncoupling mechanisms that cause NPP in terrestrial ecosystems to depart from a simple stoichiometric model.

8.06.9.4.1 Litterfall and leaching inputs

During the transition from live tissue to litter, the ratios and concentrations of nutrients undergo dramatic changes due to both resorption and leaching (Marschner, 1995) (Aerts and Chapin, 2000) (Figure 5). Plants resorb approximately half of their leaf nitrogen and phosphorus during senescence, with a larger percentage of phosphorus than of nitrogen, tending to be resorbed (Aerts, 1995; Aerts and Chapin, 2000; Chapin and Kedrowski, 1983). In contrast, only ~35% of sulfur is resorbed (Quilchano *et al.*, 2002). Calcium and iron cannot be resorbed because they are immobile in the phloem of plants (Gauch, 1972). During resorption, there is a high potential for cations such as potassium, calcium, magnesium, and sodium to leach from leaves in plant-available forms. In fact, up to 80% of leaf

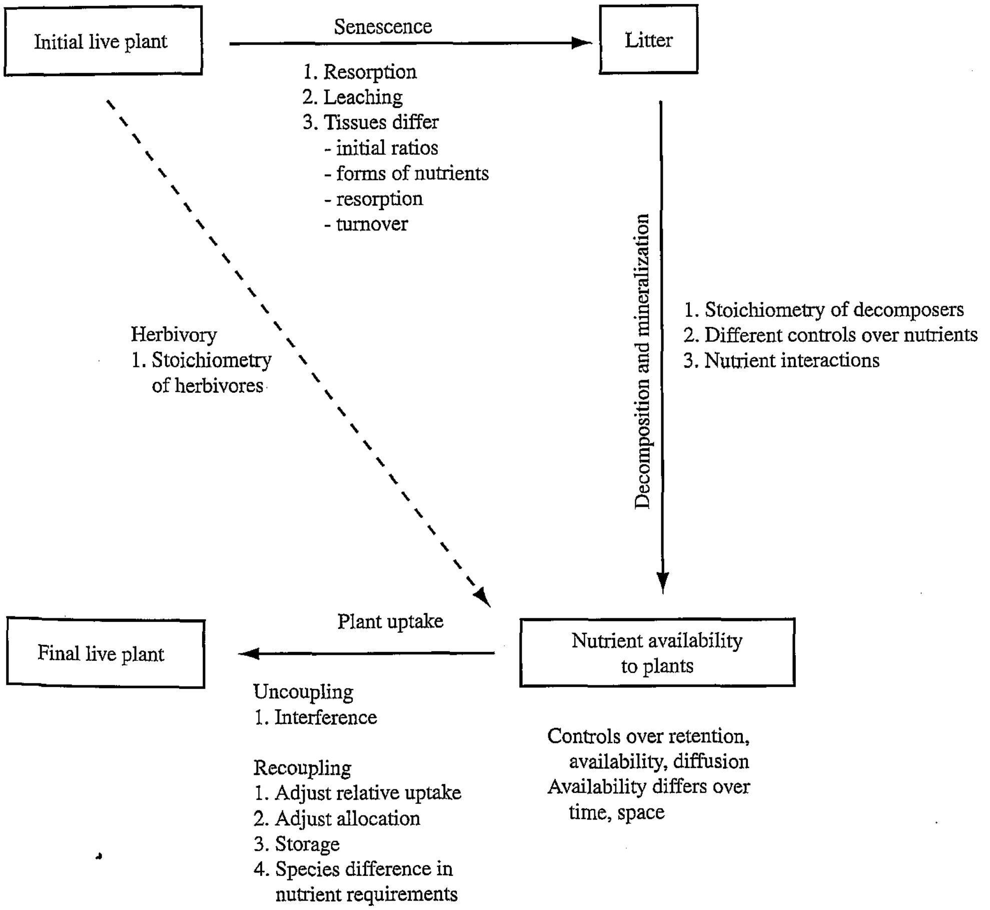


Figure 5 Uncoupling mechanisms that alter rates of cycling of different nutrients relative to the ratios initially present in live plants.

potassium, 50% of leaf calcium, but only ~15% of leaf nitrogen and phosphorus are lost through leaching (Chapin, 1991a). Thus, plant senescence results in a significant decoupling among nutrients returned to the soil in soluble and particulate forms. This causes the stoichiometry of these element inputs from the plants to soil to be extremely different than the ratio required for plant growth. This is very different from the scenario with marine phytoplankton, in which the ratios of nutrients absorbed and lost are similar to the ratios found in plankton (Elser *et al.*, 2000).

Plant species differ in the magnitude of decoupling among nutrients because of differences in allocation to, and turnover of, tissues with different element ratios (Eviner and Chapin, in press). Roots, for example, have low-nutrient-to-carbon ratios, as does wood, which also has a very high concentration of calcium. Roots and leaves, with their high enzyme concentrations, have higher N : P ratios than does wood. The types of nutrient-containing compounds also differ among tissue types (Chapin and Kedrowski, 1983) and can substantially affect recycling rates. The turnover rates of these different tissues differ due to both environmental conditions and plant species identity (Poorter and Villar, 1997). These tissues also differ in their effectiveness in resorption. Leaves resorb about half of their nitrogen and phosphorus; stems have much lower resorption (Aerts and Chapin, 2000), whereas there is no evidence for nutrient resorption from roots (Gordon and Jackson, 2000; Nambiar, 1987).

Disturbances such as hurricanes can result in large inputs of unsenesced plant tissue that contains nutrients in roughly the ratios required to produce living material. However, these inputs occur infrequently and do not govern recycling of nutrients most of the time. Herbivores also harvest plant matter before plant tissues senesce; this is often viewed as a "short circuit" in nutrient recycling. However, because the stoichiometry of herbivores differs from that of plants (Elser and Urabe, 1999), herbivores incorporate nutrients and carbon in different ratios than the plants supply and therefore excrete the nutrients in a ratio that differs from the ideal plant demand. The supply of nutrients recycled by herbivores is also spatially and temporally variable. So unlike marine systems, where phytoplankton sink to the deep ocean, and nutrients are then supplied in upwelling zones in the same nutrient ratio, the inputs of terrestrial litter have their nutrient stoichiometry decoupled from that of live leaves.

8.06.9.4.2 Nutrient mineralization

The release of nutrients from litter is further decoupled through decomposition and mineralization processes, because elements differ in controls over their cycling (McGill and Cole, 1981). From a simple stoichiometric perspective, it is instructive to first consider which organisms are doing the recycling. Soil microbes break down organic matter to meet their energy (C) and nutrient requirements for growth. Because carbon is often limiting to the microbial community and is a common currency for growth and biomass in both plants and microbes, we will express the stoichiometric relationships per unit of C. The average plant has a C:N:S:P of 1,000:9.6:3.9:1.3 (Bolin *et al.*, 1983). Assuming that roughly half of nitrogen and phosphorus (Aerts and Chapin, 2000), and 35% of sulfur (Quilchano *et al.*, 2002) is resorbed from aboveground litter, this would imply an average plant litter ratio of 1,000:4.8:2.5:0.65. Soil bacterial biomass has a ratio of 1,000:100:4.7:23.3, whereas fungi have a ratio of 1,000:62:4.3:5.3 (Bolin *et al.*, 1983). Both groups require ~40% more carbon than the stoichiometric ratios in their biomass would suggest because of the carbon expended in respiration. They also require additional nitrogen for the production of exoenzymes. If the growth efficiency of bacteria and fungi is similar (i.e., the same respiratory carbon requirement for growth), and the nitrogen requirement for exoenzyme production is similar, these stoichiometric ratios suggest that bacteria require nearly twice as much nitrogen and more than four times more phosphorus per unit of growth than do fungi, i.e., bacteria have a higher phosphorus requirement than do fungi.

Because the nutrient demands of soil microbes differ from the ratios of elements available in litter inputs, the decomposition and mineralization processes decouple the cycling of these nutrients from one another, and the nature of this decoupling depends, in part, on the identity of the decomposing organisms (Paul and Clark, 1996). In forests, for example, which are dominated by fungal activity, nitrogen tends to be immobilized by microbes, whereas phosphorus may be more readily mineralized. In bacterially dominated grasslands and agricultural systems, in contrast, there may be greater tendency to immobilize phosphorus and to mineralize or immobilize nitrogen.

The nature of chemical bonds, which bind nutrients to dead organic matter, also influences the patterns of element decoupling that occur during decomposition. Nitrogen and some of the sulfur are bonded directly to the carbon skeleton of organic matter, so nitrogen and sometimes sulfur can be mineralized to plant-available forms as "waste products" of the breakdown of organic compounds during oxidation of carbon for energy (McGill and Cole, 1981; Paul and Clark, 1996). This accounts for the strong relationship between litter C:N and rates of decomposition

(Mafongoya *et al.*, 2000; Mueller *et al.*, 1998) and net nitrogen mineralization (Maithani *et al.*, 1991; Steltzer and Bowman, 1998). Alternatively, if microbes are nitrogen-limited, decomposition may lead to immobilization of nitrogen and mineralization of sulfur. The form of inorganic nitrogen in the soil is governed by a series of redox reactions, which are influenced by soil carbon availability, oxygen, pH, and several other factors.

In contrast to nitrogen, phosphorus is mineralized from dead organic matter by extracellular phosphatases at a rate that is controlled by microbial and plant phosphorus demand, rather than by microbial demand for energy. This occurs because phosphorus is bound to organic matter through ester bonds, which can be broken without disrupting the carbon skeleton. Phosphorus tends to accumulate in microbial biomass, which accounts for 30% of organic phosphorus in the soil (versus 2% of C, 4% of N, and 3% of S) (Jonasson *et al.*, 1999; Paul and Clark, 1996). The size and turnover of this large microbial phosphorus pool is therefore the main biotic control of phosphorus availability to plants. Phosphorus availability to plants is further influenced by its chemical reactions with soil minerals, as discussed in the next section. Unlike nitrogen, phosphorus is not an energy source to microbes and is not involved in redox reactions in the soil.

The control of sulfur release is intermediate between that of nitrogen and phosphorus, because sulfur occurs in organic matter in both carbon-bonded and ester-bonded forms. The mineralization of organic sulfur is therefore responsive to microbial demands for both sulfur and energy. The ester-bonded forms are sulfur-storage compounds produced under conditions of high-sulfur availability. Under sulfur-limiting conditions, plants produce primarily carbon-bonded forms of sulfur, so its mineralization is determined mainly by the carbon demand of microbes (McGill and Cole, 1981). Because ester-bonded sulfur can be mineralized based on microbial sulfur demand, it tends to be a more important source for plant needs under high-sulfur conditions. In summary, controls over sulfur cycling are similar to those of phosphorus cycling under high-sulfur conditions and similar to those of nitrogen cycling under low-sulfur conditions.

Less work has focused on the controls of recycling of other nutrients. Decomposition dynamics are a critical determinant of calcium availability, because calcium is part of cell walls that are difficult to decompose. In contrast, potassium occurs mostly in the cell cytoplasm and is largely lost through leaching, so decomposition dynamics are less important than controls over soil availability in determining plant supply. The importance of decomposition to magnesium and manganese availability is intermediate between calcium and potassium (Chapin *et al.*, 2002).

Although similar environmental factors can limit both NPP and decomposition, these two processes are differentially affected by these constraints, so it is unlikely that the timing and amount of nutrient supply will coincide with plant demand. For example, in some ecosystems, a substantial amount of nutrient mineralization occurs underneath the snow pack and is released in spring thaw before plants actively take up nutrients (Bilbrough *et al.*, 2000; Hobbie and Chapin, 1996). Nutrients are often released from organic matter in pulses associated with the initial stages of decomposition or with wet–dry or freeze–thaw events (Haynes, 1986; Schimel and Clein, 1996; Venterink *et al.*, 2002). Timing of element release also differs among elements. Soluble elements like potassium are immediately available when they enter the soil, whereas the release of nitrogen and calcium depend on microbial demands for energy, and the release of phosphorus depends on microbial phosphorus demands and factors governing microbial turnover.

8.06.9.4.3 Nutrient availability

The ratios at which nutrients are released in their mineral form through decomposition and mineralization does not directly determine the ratio of their availability. Nutrient availability is a function of the presence of nutrients in soil solution, their diffusion rates through soil, and their chemical interactions with soil minerals. Mobile nutrients can be lost from the system through leaching, whereas nitrogen can also be lost through gaseous pathways. Less mobile nutrients, such as phosphorus, can be lost in erosion. Retention mechanisms include microbial immobilization and bonds of varying strength with soil particles and soil organic matter. These retention mechanisms can enhance nutrient availability by minimizing nutrient loss, but also decrease plant access to these nutrients.

As with mineralization dynamics, the factors governing availability of mineralized nutrients differ among nutrients. The two inorganic forms of nitrogen in soil solution behave quite differently. NH_4 diffuses slowly through the soil because its positive charge interacts with the negatively charged soil particles. NO_3 diffuses rapidly, but is also prone to leaching or gaseous loss. Organic nitrogen exhibits a variety of retention mechanisms (Neff *et al.*, 2003). Microbial immobilization of nitrogen can compete with plant nitrogen uptake but can also be important in retaining pulses of nitrogen release, particularly when the pulses do not coincide with periods of plant growth.

Phosphorus availability is determined largely by chemical interactions with soil. Complexes with other elements can remove PO_4 from soil solution. PO_4 precipitates with calcium, aluminum, iron, or manganese, forming insoluble compounds. Charged organic compounds can compete with PO_4 on the binding surface and decrease chelation with metals, increasing PO_4 availability to plants. The microbial phosphorus pool may be the main reservoir of plant-available phosphorus in the soil because it protects phosphorus from chemical reactions with soil minerals (Paul and Clark, 1996). Soil pH can greatly influence phosphorus availability, as well as the availability of manganese, copper, magnesium, and iron. Water-logged soils can limit manganese and zinc availability, and iron availability can decrease with enhanced concentrations of phosphorus, manganese, zinc, or copper (Marschner, 1995).

8.06.9.4.4 *Element interactions*

As discussed above, there are not only different controls on the recycling of these different nutrients, but these elements can also interact to influence one another's dynamics. Nitrogen cycling, for example, is very sensitive to availability of phosphorus and sulfur. Phosphorus and sulfur limit nitrogen fixation (Bromfield, 1975; Jones *et al.*, 1970). Phosphorus also stimulates nitrification and net nitrogen mineralization (Cole and Heil, 1981). Phosphorus availability, in turn, is often enhanced by sulfur, because sulfur can acidify rock phosphorus, and SO_4 leaching enhances leaching of cations that precipitate with phosphorus. Sulfur-releasing enzymes can be inhibited by PO_4 and stimulated or inhibited by nitrogen availability (McGill and Christie, 1983). Inorganic nitrogen additions can increase mineralization of sulfur (Ghani *et al.*, 1992). All of these element interactions modify the ratios of nitrogen, phosphorus, and sulfur availability, causing the degree of coupling of these nutrients to be sensitive to environment.

8.06.9.4.5 *Plant uptake*

Clearly, the ratio of nutrients available to plants does not necessarily correlate with plant needs. For example, soil solutions usually contain lower concentrations of potassium and PO_4 than plants need, and excess calcium and magnesium (reviewed in Larcher, 1995 and Marschner, 1995). This imbalance in nutrient supply can interfere with uptake of limiting nutrients. In general, uptake of cations stimulate anion uptake and vice versa. However, at low external concentrations of nutrients, such as commonly occur in ecosystems, anion and cation uptake are not necessarily coupled. The relative uptake of cations and anions also shifts with pH. In general, cation uptake decreases at low pH, when H^+ concentrations are high relative to mineral cation concentrations, although high concentrations of calcium can mitigate this effect for potassium. In contrast, low pH stimulates or has no effect on anion uptake because of low OH^- concentrations in the soil solution. At high external concentrations, there is nonspecific competition between ions of the same charge. For example potassium can inhibit calcium and magnesium uptake because they have lower transport rates through the plasma membrane. This interference in uptake of certain elements is particularly pronounced when they are supplied in ratios that are unbalanced with respect to plant demand. Plant uptake of nutrients is selective based on the physicochemical characteristics of the elements, and there can be competition for binding sites at the plasma membrane between elements with similar properties. Excess ratios of certain nutrients can inhibit the uptake of others. Ammonium, for example, decreases uptake of potassium, calcium, and magnesium; and high SO_4 decreases molybdenum uptake. High concentrations of magnesium or potassium can inhibit calcium uptake, whereas high calcium levels inhibit potassium uptake. NO_3 and chlorine can inhibit one another, and potassium and calcium can strongly inhibit magnesium uptake. In fact, high fertilization of either of these leads to magnesium deficiency in soils. There are many other negative interactions between elements during uptake. For example, boron is limited by high calcium; iron is limited by high phosphorus, copper, and manganese; and calcium requirement increases with high external concentrations of heavy metals, aluminum, NaCl and at low pH. NO_3 uptake is also inhibited by the presence of NH_4.

Relatively high concentrations of certain nutrients can also increase the uptake of other elements. For example, NH_4 and sodium enhance potassium uptake; magnesium and manganese enhance uptake of one another; calcium enhances potassium uptake; and zinc enhances uptake of both magnesium and manganese (Larcher, 1995). It is clear that the stoichiometry of elements available in soil solution can substantially decouple the stoichiometry of plant uptake from supply.

8.06.9.5 Recoupling Mechanisms

In the previous sections, we showed that many mechanisms can uncouple the stoichiometry of nutrients from their ratios in live plants, so the stoichiometry of available nutrients is very different from demand. If plant growth were dependent on the relative availability of these nutrients at any one time, NPP would be constrained by a shifting balance of nutrients. Conversely, if plants simply took up nutrients in proportion to their availability, the nutrient imbalance within the plant could interfere with its metabolic function, for example through toxicity effects (Marschner, 1995). Over time and space, plants can "recouple" nutrients in ratios needed for growth.

In general, we have seen that plants respond to nutrient limitation by increasing their root : shoot ratio, increasing their nutrient-use efficiency, and by allocating to protective compounds that increase life span. Plants also adjust their physiology to respond to limitations of specific nutrients. Just as water, CO_2, light, and nutrients need to be balanced, plants must also balance the acquisition of different nutrients to grow. Nutrient limitation is strongly determined by the balance of nutrients and cannot necessarily be predicted from the concentration of a single limiting nutrient (Koerselman and Mueleman, 1996; Larcher, 1995). Any nutrient not in balance can limit plant growth as well as plant investment in absorption of these nutrients. There are different controls over the availability of, and plant access to, these different nutrients. For example, enhancing root length is a common response to nutrient limitation, but it does not equally relieve limitation of all nutrients. NO_3 diffuses rapidly in the soil and its uptake will substantially increase with a given increase in root length. In contrast, it takes 6–10 times the root length increase to produce an equivalent increase in PO_4 or NH_4 uptake because the diffusion zones around the roots are much smaller for these nutrients (Marschner, 1995). Mass flow is usually sufficient to supply micronutrients to plants, but macronutrients require additional nutrient movement to the root by diffusion in order to attain the proper balance of these nutrients. Even among the macronutrients, up to 80% of nitrogen can be supplied to crops by mass flow, while only 5% of phosphorus is supplied this way due to lower mobility in the soil (Barber, 1984; Chapin, 1991a; Lambers *et al.*, 1998).

Balancing the supply of these multiple nutrients requires many different strategies. On an individual plant level, plants adjust their relative uptake of these different nutrients through changes in ion transporters in the roots, shifts in enzyme allocation, and by forming associations with mycorrhizal fungi. Active transport is a major mechanism by which plants absorb potentially limiting nutrients. Plants are able to greatly enhance nutrient absorption of a limiting element (Chapin, 1991a; Lee, 1982; Lee and Rudge, 1986, 1987) by increasing the transport proteins specific to that nutrient, while decreasing uptake capacity of other nutrients that do not limit growth (Chapin, 1980; Lambers *et al.*, 1998). This is particularly important for the nutrients that most frequently limit plant growth because NH_4, NO_3, potassium, and SO_4 are transported by different membrane proteins that are individually regulated (Clarkson, 1985). This preferential uptake by increasing specific carriers is seen even among the different forms of nitrogen. NH_4, NO_3 and amino acids are all absorbed by different carriers, and the relative availability of these forms of nitrogen in the soil solution influences the capacity of a plant to absorb these different nitrogen forms.

Plants can also balance their uptake of different nutrients through their production of enzymes and other compounds that help to make specific nutrients more available. Nitrate reductase is required to assimilate NO_3 into plant biomass, and its production is triggered by the presence of NO_3 in soil solution. Phosphorus limitation induces production of root phosphatase enzymes that cleave organically bound PO_4, or siderophores, which solubilize mineral phosphorus by chelating with other minerals that bind to PO_4, such as iron.

Associations with soil microbes such as mycorrhizal fungi can relieve limitation by certain nutrients. Since these fungi dramatically increase the effective surface area of absorption of nutrients, they particularly enhance uptake of nutrients that diffuse slowly in soil, so they greatly enhance uptake of PO_4, and of NH_4–N in soils with low nitrifying potential. Arbuscular mycorrhizae can help to relieve phosphorus limitation, whereas ectomycorrhizae enhance both phosphorus and nitrogen uptake. In fact the presence of arbuscular mycorrhizae can relieve phosphorus limitation, to the extent that ecosystems become nitrogen-limited (Grogan and Chapin, 2000). Associations with plant-growth-promoting rhizobacteria often stimulate growth more under low-nutrient conditions (Belimov *et al.*, 2002).

Although plants have several mechanisms by which they can balance uptake of these multiple nutrients, the supply of these nutrients is rarely in balance, and many of these nutrients are available in short pulses, or mostly at certain times of the year. Plants can balance nutrient availability over time by accumulating each nutrient at times of high availability and storing it to support growth at another time (Chapin *et al.*, 1990). In fact, in many cases, much of the nutrient uptake occurs before plant growth begins (Aerts and Chapin, 2000; Larcher, 1995). Stored nutrients can then be transported to sites of growth to achieve balanced nutrient ratios in growing tissues

(Chapin *et al.*, 1990). Nutrient storage is particularly important for nitrogen, phosphorus, potassium, sulfur, copper, and zinc, but cannot occur for calcium, which is not mobile in the phloem (Nambiar, 1987).

In summary, the many mechanisms by which plants adjust to unbalanced supplies of CO_2, H_2O, nutrients, and light enable plants to maximize NPP in situations where the ratio of supply of essential nutrients is far from balanced.

8.06.10 COMMUNITY-LEVEL ADJUSTMENTS

In the previous sections, we showed that plants can adjust on a leaf and whole-plant level to maintain NPP under limiting conditions. We have also seen that these responses can often be scaled to the stand or community level. For example, allocation of nitrogen to leaves at the top of the canopy occurs both within a plant and within a stand. Changes in community composition are another important mechanism by which vegetation can maximize NPP under limiting conditions. Plants differ in their tolerances of resource and environmental limitations, and the flexibility provided by a diversity of plant species with different traits mirrors the flexibility of traits within an individual plant in its response to limiting conditions. There are many parallels between acclimation of an individual plant and shifts in plant community composition along resource gradients.

A balance of nutrients is critical to support growth of any plant, but the specific proportions of nutrients required can differ among species. For example, species can differ dramatically in the amount of phosphorus they require (Larcher, 1995); dicots contain twice as much calcium as do monocots, and forbs contain more magnesium than do grasses (Lambers *et al.*, 1998). Due to species differences in nutrient requirements, different nutrients can simultaneously limit production, and shifts in community composition can alter the NPP attained at a given nutrient supply. For example, productivity of California grasslands can be enhanced by nitrogen additions, or alternatively, phosphorus and sulfur additions can stimulate legume growth and enhance overall ecosystem productivity beyond the stimulation by nitrogen fertilizer (Jones and Winans, 1967).

Deep-rooted species tap a larger volume of soil than do shallow-rooted species and therefore access more water and nutrients to support production. In California, the deep-rooted *Eucalyptus* trees access a deeper soil profile than do annual grasses, so the forest absorbs more water and nutrients. In dry, nutrient-limited ecosystems, this substantially enhances NPP and nutrient cycling (Robles and Chapin, 1995). Similarly, the introduction of deep-rooted phreatophytes in deserts increases the productivity in watercourses (Berry, 1970). Deep-rooted species can also tap nutrients that are available only at depth. A deep-rooted tundra sedge, for example, is the only species in arctic tussock tundra that accesses nutrients in the groundwater that flows over permafrost. By tapping nutrients at depth, the productivity of this sedge increases 10-fold in sites with abundant groundwater flow, whereas productivity of other species is unaffected by deep resources (Chapin *et al.*, 1988). In the absence of this species, NPP would be greatly reduced. Species with deep roots, and particularly with high fine root biomass in the lower soil profiles, can pump calcium up to the surface layers and enhance overall calcium availability in the system (Andersson, 1991; Dijkstra and Smits, 2002).

Phenological specialization could increase resource capture by increasing the total time available for plants to acquire resources from their environment. This is most evident when coexisting species differ in the timing of their maximal activity. In mixed grasslands, for example, C_4 species are generally active in the warmer, drier part of the growing season than are C_3 species. Consequently C_3 species account for most early-season, and C_4 species account for most late-season production. Similarly, in the Sonoran desert, there is a different suite of annuals that becomes active following winter versus summer rains, and in California grasslands a mixture of early season annuals and late season perennials enhance productivity (Eviner and Chapin, 2001). In all these cases, phenological specialization probably enhances NPP and nitrogen cycling. In mixed-cropping agricultural ecosystems, phenological specialization is more effective in enhancing production than are species differences in rooting depth (Steiner, 1982). The ecosystem consequences of phenological specialization to exploit the extremes of the growing season are less clear. Evergreen forests, for example, have a longer photosynthetic season than deciduous forests, but most carbon gain occurs in midseason in both forest types, when conditions are most favorable (Schulze *et al.*, 1977). Phenological specialization is an area where species effects on ecosystem processes could be important but these effects have been well documented primarily in agricultural ecosystems.

8.06.11 SPECIES EFFECTS ON INTERACTIVE CONTROLS

Plants do much more than simply adjust to the limitations imposed by state factors, they also actively mediate most of the resource and environmental conditions that constrain growth. Some of the most important effects of plant characteristics on NPP operate indirectly through the effects of plants on interactive controls, which are the factors that directly regulate ecosystem processes.

8.06.11.1 Vegetation Effects on Resources

Plant traits that influence the supply of limiting resources (e.g., light, water, and nutrients) have strong feedback effects on NPP. The introduction of a strong nitrogen-fixer into a community that lacks such species can substantially enhance nitrogen availability and cycling. Invasion by the exotic nitrogen-fixing tree, *Myrica faya*, in Hawaii, for example, increased nitrogen inputs, litter nitrogen concentration, and nitrogen availability (Vitousek *et al.*, 1987). A nitrogen-fixing invader is most likely to be successful in ecosystems that are nitrogen-limited, have no strong nitrogen fixers, and have adequate phosphorus, micronutrients, and light (Vitousek and Howarth, 1991).

8.06.11.1.1 Decomposition and nitrogen mineralization

Traits that govern plant growth rate and NPP also determine the microbial processing of carbon and nitrogen in soils. When plant leaves senesce, they resorb approximately half of their nitrogen and phosphorus pool and very little of the initial carbon pool, regardless of the environment in which they grow (Aerts and Chapin, 2000; Chapin and Kedrowski, 1983). The quality of leaf litter, as measured by litter C : N ratio and carbon quality, therefore correlates with corresponding parameters in live leaves. Chemical properties that promote high physiological activity and growth in plants (e.g., high tissue nitrogen concentration) and low lignin content (reflecting less sclerified leaves with a high ratio of cytoplasm to cell wall) also promote rapid decomposition (Hobbie, 1992; Melillo *et al.*, 1982). Litter from species typical of productive environments (e.g., herbs and deciduous species) typically decomposes more rapidly than those from less productive environments (e.g., evergreens) (Cornelissen, 1996; Perez-Harguindeguy *et al.*, 2000).

The quantity of litter input provides the second critical link between NPP and decomposition because NPP governs the quantity of organic matter inputs to decomposers. When biomes are compared at steady state, heterotrophic respiration (i.e., the carbon released by processing of dead plant material by decomposer organisms and animals) is approximately equal to NPP. In other words, net ecosystem production (NEP), the rate of net carbon sequestration, is approximately zero at steady state, regardless of climate or ecosystem type. This indicates that the quantity and quality of organic matter inputs to soils, as determined by plant traits, are the major determinants of decomposition, when ecosystems are compared. Environment exerts important additional controls on decomposition through effects on both NPP (quantity and quality of litter inputs) and the activity of decomposer organisms. Other factors that influence decomposition rate include pH and the composition of the microbial community. Any plant effects on these factors will also influence decomposition.

Litter properties that promote NPP and decomposition also facilitate net nitrogen mineralization. The activity of decomposer organisms, which depends strongly on the carbon quality of substrates and the nitrogen status of microbes (a function of litter nitrogen concentration) are the major effects of plant litter quality on net nitrogen mineralization (Paul and Clark, 1996). Microbes mineralize nitrogen more slowly from litter with high concentrations of lignin or other recalcitrant compounds than from litter with more labile carbon compounds. High-nitrogen litter shows greater net mineralization of nitrogen than does low-nitrogen litter because microbes are seldom nitrogen-limited below a C : N ratio of 25 : 1; the nitrogen in excess of microbial demands for growth is released into the soil, where it becomes available to plants. As with decomposition, traits governing NPP strongly influence the annual net nitrogen mineralization, because productive ecosystems produce large quantities of high-quality litter.

Species differences in litter quality magnify site differences in soil fertility. Differences among plant species in tissue quality strongly influence litter decomposition rates. Litter from low-nutrient-adapted species decomposes slowly because of the negative effects on soil microbes of low concentrations of nitrogen and phosphorus and high concentrations of lignin, tannins, waxes, and other recalcitrant or toxic compounds. This slow decomposition of litter from species characteristic of nutrient-poor sites reinforces the low nutrient availability of these sites (Hobbie, 1992; Wilson and Agnew, 1992). Species from high-resource sites, in contrast, produce rapidly decomposing litter due to its higher nitrogen and phosphorus content and fewer recalcitrant compounds, enhancing rates of nutrient turnover in nutrient-rich sites.

Species differences in labile C inputs from root exudation also influence rates of decomposition and nutrient cycling. Plant carbon inputs to the rhizosphere can increase the size and activity of microbial biomass (Newman, 1985) and have large effects on nitrogen cycling (Flanagan and Van Cleve, 1983; Schimel *et al.*, 1992). More than 70% of the total soil biomass of microbes and grazing fauna are found in the rhizosphere (Ingham *et al.*, 1985). Plant species differ in their effects on the labile carbon pool (Vinton and Burke, 1995). This is one of the key regulators of plant species effects on nitrogen cycling (Wedin and Pastor, 1993), because, beyond the initial flush of labile compounds from litter, litter is unlikely to be the major source of labile carbon. Even though labile carbon is a relatively small component of the total soil carbon pool, species effects on labile carbon are responsible for up to 10-fold differences in nitrogen cycling, with this effect disappearing relatively quickly once plants are removed from the soil (Wedin and Pastor, 1993). Labile carbon inputs provided by growing plants can also accelerate decomposition rates of both recalcitrant litter and soil organic matter (Bottner *et al.*, 1999; Mueller *et al.*, 1998; Sallih and Bottner, 1988).

8.06.11.1.2 Water dynamics

Plant species can also dramatically influence the distribution of available water through space and time. Although there are many examples indicating that the amount of water used by different plants can profoundly influence soil water availability (Gordon and Rice, 1993; Gordon *et al.*, 1989; van Vuuren *et al.*, 1992), there are also examples in which particular species can profoundly alter overall ecosystem dynamics and productivity through their unique capacity to capture water sources that are unavailable to most vegetation. Two such examples are hydraulic lift and collection of fog by vegetation. In some deep-rooted species, soil water is taken up from deep layers of soil, and then is passively released into surface soils at night, when transpiration ceases. These plants supply an appreciable amount of moisture to the surface soil that can enhance the overall productivity of the plant community (Caldwell *et al.*, 1998; Horton and Hart, 1998). Aboveground plant structure may also play a critical role in supplying water to the entire ecosystem. Species with canopies that are tall and have high surface area collect water from fog in many coastal and montane ecosystems (Weathers, 1999). This fog can dramatically enhance water availability for the species responsible for fog collection, but also for the entire ecosystem. Redwood trees in California provide 34% of the annual water input to these systems, primarily at a time of minimal precipitation. This fog water can account for up to 66% of the water use by understory plants and between 13–45% of water use by redwood trees themselves, thus dramatically enhancing the production of this water-limited system (Dawson, 1998).

8.06.11.2 Vegetation Effects on Climate

Species effects on microclimate influence ecosystem processes most strongly in extreme environments. This occurs because ecosystem processes are particularly sensitive to climate in extreme environments (Hobbie, 1995; Wilson and Agnew, 1992). Boreal mosses, for example, form thick mats that insulate the soil from warm summer air temperatures. The resulting low soil temperature retards decomposition, contributing to the slow rates of nutrient cycling that characterize these ecosystems (Van Cleve *et al.*, 1991). Some mosses such as *Sphagnum* effectively retain water, as well as insulating the soil, leading to cold anaerobic soils that reduce decomposition rate and favor peat accumulation. The sequestration of nitrogen and phosphorus in undecomposed peat reduces growth of vascular plants. The shading of soil by plants is an important factor governing soil microclimate in hot environments. Establishment of many desert cactuses, for example, occurs primarily beneath the shade of "nurse plants" (Turner *et al.*, 1966) (Nobel, 1984).

Large-scale shifts in vegetation can even influence regional or global patterns of climate. Conversion of the Amazonian rain forest to pasture, for example, is predicted to result in dramatic reductions in regional precipitation, which could be irreversible since the re-establishment of a tropical forest would be impossible under these drier conditions (Shukla *et al.*, 1990). Similarly, deforestation of the boreal forest can lead to summer cooling and prevent regrowth of trees, whereas spread of the boreal forest due to climatic warming can significantly enhance both regional and global warming (Bonan *et al.*, 1995; Bonan *et al.*, 1992).

8.06.11.3 Species Effects on Disturbance Regime

Plants that alter disturbance regimes change the balance between equilibrium and nonequilibrium processes. Following disturbance, there are substantial changes in most ecological processes, including increased opportunities for colonization by new individuals and often an imbalance between inputs to, and outputs from, ecosystems. Plants that colonize following disturbance, in turn, affect the capacity of the ecosystem to gain carbon and retain nutrients.

Most disturbances produce a pulse of nutrient availability because disturbance-induced changes in environment and litter inputs increase mineralization of dead organic matter and reduce plant biomass and nutrient uptake. Anthropogenic disturbances create a wide range of initial nutrient availabilities. Some disturbances, such as mining, can produce an initial environment that is even less favorable than most primary successional habitats for initiation of succession. Some agricultural lands are abandoned to secondary succession after erosion or (in the tropics) formation of laterite soils, reducing the nutrient-supplying power of soils. Soils from some degraded lands have concentrations of aluminum and other elements that are toxic to many plants.

When initial nutrient availability is high after disturbance, early successional species typically have high relative growth rates, supported by high rates of photosynthesis and nutrient uptake. These species reproduce at an early age and allocate a large proportion of NPP to reproduction. Their strategy is to grow quickly under conditions of high resource supply, and then disperse to new disturbed sites. These early successional species include many weeds that colonize sites disturbed by people. As succession proceeds, there is a gradual shift in dominance to species that have lower resource requirements and grow more slowly. In ecosystems with low initial availability of soil resources, succession proceeds more slowly and follows patterns similar to those in primary succession, with initial colonization by light-seeded species that colonize from outside the disturbed area.

8.06.12 SPECIES INTERACTIONS AND ECOSYSTEM PROCESSES

Plant traits that influence the interactions among species in an ecosystem are among the most profoundly important ways in which plants influence the resources and environmental conditions that control NPP. Interactions such as competition, mutualism, and predation govern the abundance of species in an ecosystem, and therefore the extent to which the traits of a species are represented in the ecosystem. These combinations of species can provide unique functions to ecosystems or increase the efficiency of resource use through niche separation that leads to complementarity of resource use. The effects of species interactions are ubiquitous, but often highly situation-specific and idiosyncratic, so it is difficult to predict *a priori* the full range of ecosystem changes caused by the introduction or loss of a species (Carpenter and Kitchell, 1993). Development of a framework for predicting the effects of species interactions is an emerging challenge that will improve our capacity to predict and mitigate the effects of global changes in species composition and biodiversity (Chapin *et al.*, 2000).

Mutualistic species interactions contribute directly to many essential ecosystem processes, such as nutrient inputs through nitrogen fixation and mycorrhizal associations that govern phosphorus and organic nitrogen uptake by plants (Read, 1991). Other mutualisms, such as pollination and seed dispersal, have indirect effects, influencing the presence or absence of species that may have strong ecosystem effects.

Plant traits that influence herbivory affect virtually all ecosystem processes. In general, plants that characterize low-fertility soils produce chemical defenses that reduce the frequency of herbivory in these habitats; these compounds also retard decomposition, nutrient cycling, and therefore subsequent NPP. In contrast, plants characteristic of high-fertility soils tend to invest preferentially in growth rather than chemical defense (Bryant *et al.*, 1983), and herbivores are an important avenue of carbon and nutrient transfer from plants to soils. In this way, herbivores magnify inherent differences in soil fertility among ecosystems (Chapin, 1993). Herbivory has a major impact on ecosystem processes for several reasons. Herbivores transfer plant tissue to soils before nutrient resorption can occur, so approximately twice as much nitrogen and phosphorus is transferred per unit of plant biomass than would occur through litterfall. Secondly, herbivores preferentially select nutrient-rich tissues, further enhancing nutrient transfer to soils. Finally, animal digestion, especially in homeotherms, uses much of the energy from ingested plant matter to support animal metabolism, resulting in the excretion of nutrients in readily available forms. In these ways, herbivory short-circuits the decomposition process and speeds rates of nutrient cycling (Kielland and Bryant, 1998).

Competitive interactions among plant species obviously influence the relative abundance of species in an ecosystem and therefore the traits that are expressed at an ecosystem scale. The importance of plant combinations is not only through competitive interactions, but also in their ability to coexist. Species with different traits can differ in their resource utilization (in space, time, or the specific form of the resource), leading to an increased use of resources, and thus enhanced NPP (Tilman *et al.*, 1996). However, this can be idiosyncratic, depending on the specific species in the combinations (Hooper, 1998).

8.06.13 SUMMARY

NPP is not a simple function of the resources available at one moment. Although plant growth depends on a balance of resources, these resources are rarely available in the ratios required for growth. Plants, as individuals and communities, can maintain production under limiting conditions. They make many adjustments to maintain the balance of limiting resources imposed by state factors through shifts in physiological traits, or by plant mixtures that enhance access to resources. These adjustments extend the range of environmental conditions over which carbon gain occurs in ecosystems. Many of these adjustments involve changes in photosynthetic capacity, which entail changes in C:N ratio. This variation in element stoichiometry enables plants to maximize carbon gain under favorable environmental conditions. Under unfavorable conditions the increased C:N ratio associated with reduced photosynthetic capacity maximizes the efficiency of using other resources to gain carbon, primarily by prolonging leaf longevity and by shifting allocation to production of other tissues such as wood or roots that have lower tissue nitrogen concentrations than leaves.

Alternatively, plants can enhance the availability of limiting factors through their effects on interactive controls. This can extend the range of habitats that provide adequate resources for plant growth. These multiple processes maximize the NPP that is possible in sites with strongly limiting conditions. There are therefore many ways to achieve a similar level of NPP within any environment.

Clearly, NPP is the product of numerous biogeochemical interactions, environmental conditions, and organisms, making NPP a key summary variable that depends on many ecosystem processes. Because NPP is the basis for sustaining all life on earth, it is critical to understand the mechanisms that determine it. This is particularly true because the biotic and environmental conditions that determine NPP are subject to dramatic changes due to human impacts on ecosystems.

Substantial decreases in NPP are occurring in many ecosystems. Forest decline and dieback are observed in many areas (Huettl, 1993), with particularly large decreases in the northeastern United States, and in 20–25% of European forests (Schulze, 1989). These declines could be due to many interacting factors, including soil acidification, sulfur and nitrogen deposition, ozone pollution, and disease, but the end result of these multiple factors is a decline in NPP. Many arid lands are experiencing desertification, or a permanent loss in productive capacity, due to climate changes and land use practices. With a doubling of atmospheric CO_2, we can expect a further 17% increase in the world area of desert (Schlesinger *et al.*, 1996). The degradation of the productive capacity of terrestrial ecosystems is also widespread through loss of topsoil. Soil erosion is one of the world's most pressing environmental problems, occurring in agricultural lands, managed forests, and natural systems (Pimentel and Kounang, 1998). Each year, six million hectares of land worldwide is lost to production through erosion or salinization (Pimentel *et al.*, 1993). This is a particularly strong trend in agricultural land. In the last forty years, almost one-third of the world's arable land has been lost to production and abandoned as farmland (Pimentel *et al.*, 1995). Eighty percent of the world's agricultural land is undergoing moderate to severe erosion due to both cropping and grazing practices (Pimentel and Kounang, 1998). This has lead to a 15–30% decrease in the productivity of rain-fed agriculture land in the last 25 years, with 8–100% decrease in production at any given site. In the mean time, deforestation is occurring to replace agricultural land at a very large scale. This land is often abandoned once it has lost its productive potential (Pimentel *et al.*, 1995). The world's productive potential is also declining due to the conversion of fertile agricultural lands to suburban and urban land uses. We know from yearly fluctuations in climate that climatic warming can have dramatic effects on NPP (Knapp and Smith, 2001). These projected shifts in climate will impact NPP, but the direction of these changes will likely vary regionally (Watson *et al.*, 1996).

NPP is the basis of life on earth, and such large changes at a global scale not only indicate the presence of significant changes in the earth's biogeochemistry, but also will likely affect many species, and ultimately, human society.

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