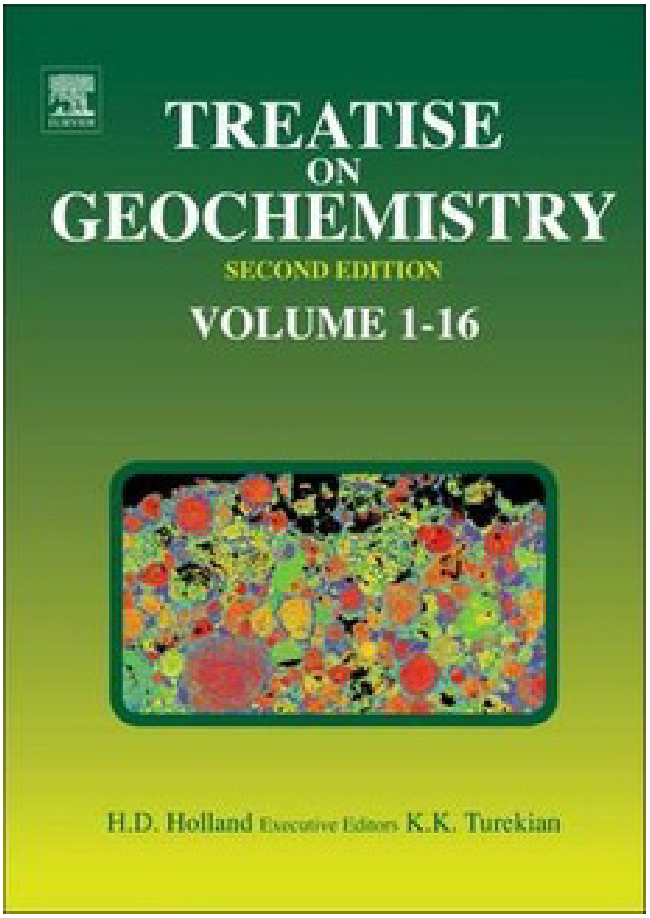

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10.6 Biogeochemical Interactions Governing Terrestrial Net Primary Production

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Glossary

Allocation Proportional distribution of photosynthetic products or newly acquired nutrients among different organs or functions in a plant.

Beneficial nutrients Elements that enhance growth under specific conditions or for specific groups of plants.

Biomass Quantity of living material (e.g., plant biomass).

Biome General class of ecosystems (e.g., tropical rain forest and arctic tundra).

C_3 plants Plants with the C_3 photosynthetic pathway that produce 3-carbon acids as the first product of carbon dioxide (CO_2) fixation reactions.

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C_4 plants Plants with the C_4 photosynthetic pathway that produce 4-carbon acids as the first product of CO_2 fixation reactions.

Conductance Flux per unit driving force (e.g., concentration gradient).

Gross primary production (GPP) Net photosynthesis expressed at the ecosystem scale ($g\ C\ m^{-2}\ year^{-1}$).

Light saturation Range of light availabilities over which the rate of photosynthesis is insensitive to irradiance.

Light-use efficiency (LUE) Ratio of GPP to absorbed photosynthetically active radiation at the leaf or ecosystem scale.

Limitation Reduced rate of a process (e.g., NPP, growth, or photosynthesis) due to inadequate supply of a resource (e.g., nutrient or light) or low temperature. Proximate limitation reflects the immediate response to addition of the resource. Ultimate limitation reflects long-term transformation of the system when the resource is added.

Micronutrients Nutrients that are required in small quantities by organisms.

Mineralization Conversion of carbon and nutrients from organic to inorganic forms due to the breakdown of litter and soil organic matter. Gross mineralization is the total amount of nutrients released via mineralization (regardless of whether they are subsequently immobilized or not). Net mineralization is the *net* accumulation of inorganic nutrients in the soil solution over a given time interval.

Mycorrhizae Symbiotic relationship between plant roots and fungal hyphae, in which the plant acquires nutrients from the fungus in return for carbohydrates that constitute the major carbon source for the fungus.

Net ecosystem production (NEP) Balance between gross primary production and ecosystem respiration (or between net primary production and heterotrophic respiration).

Net photosynthesis Net rate of carbon gain measured at the level of individual cells or leaves. It is the balance between simultaneous CO_2 fixation and respiration of photosynthetic cells in the light (including both photorespiration and mitochondrial respiration).

Net primary production (NPP) Quantity of new plant material produced annually (GPP minus plant respiration); includes new biomass, hydrocarbon emissions, root exudates, and transfers to mycorrhizae.

Nitrogen mineralization Conversion of dissolved organic nitrogen to ammonium.

Nutrients Material resources in addition to carbon, oxygen, and water that are required for life.

Nutrient limitation Limitation of plant growth due to insufficient supply of a nutrient.

Nutrient use efficiency Growth per unit of plant nutrient; ratio of nutrients to biomass lost in litterfall; also calculated as nutrient productivity times residence time.

Photosynthesis A biochemical process that uses light energy to convert CO_2 to sugars. Net photosynthesis is the net carbon input to ecosystems; synonymous at the ecosystem scale with gross primary production.

Photosynthetic capacity Photosynthetic rate per unit leaf mass measured under favorable conditions of light, moisture, and temperature.

Primary production Conversion of CO_2, water, and solar energy into biomass. Gross primary production (GPP) is the net carbon input to ecosystems, that is, net photosynthesis expressed at the ecosystem scale ($g\ C\ m^{-2}\ year^{-1}$). Net primary production is the net carbon accumulation by vegetation (GPP minus plant respiration).

Resorption Withdrawal of nutrients from tissues during their senescence.

Respiration Biochemical process that converts carbohydrates into CO_2 and water, releasing energy that can be used for growth and maintenance.

Rhizosphere Zone of soil that is directly influenced by roots.

Root exudation Diffusion and secretion of organic compounds from roots into the soil.

Root:shoot ratio Ratio of root biomass to shoot biomass.

Siderophore Organic iron-binding chelate produced by plant roots.

Soil resources Water and nutrients available in the soil.

Specific leaf area Ratio of leaf area to leaf mass.

Stoichiometric relationship Ratio between elements, as between carbon and nitrogen.

Stomatal conductance Flux of water vapor or CO_2 per unit driving force between the interior of a leaf and the atmosphere.

10.6.1 Introduction

Net primary production (NPP) is the amount of carbon and energy that enters ecosystems through plants, that is, the balance between net photosynthesis by photosynthetic tissues and plant respiration by all tissues, measured at the ecosystem scale, typically over the course of an annual cycle. It provides the energy that drives all biotic processes, including the trophic webs that sustain animals and human society, and the activity of decomposer organisms that cycle the nutrients required to support primary production. NPP not only sets the baseline for the functioning of all ecosystem components but is also the best summary variable of ecosystem processes, being the result of numerous interactions among elements, organisms, and the environment. This dual role makes NPP the key integrative process in ecosystems (McNaughton et al., 1989) and thus a critical component of our understanding of ecosystem responses to 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.

10.6.2 General Constraints on NPP

10.6.2.1 What is NPP?

NPP is the net carbon gain by plants. It is the balance between the carbon gained by gross primary production (GPP – i.e., net photosynthesis measured at the ecosystem scale) and carbon released by plant mitochondrial respiration, both expressed per unit land area. Like GPP, NPP is generally measured at the ecosystem scale over relatively long time intervals, such as a year (g biomass or g C m^{-2} $year^{-1}$). NPP includes the new biomass produced by plants, the soluble organic compounds that diffuse or are secreted into the environment (root or phytoplankton exudation), the carbon transfers to microbes that are symbiotically associated with roots (e.g., mycorrhizae and nitrogen-fixing bacteria), and the volatile emissions that are lost from leaves to the atmosphere (Clark et al., 2001). Most field measurements of NPP document only the new plant biomass produced and therefore probably underestimate the true NPP by at least 30% (**Table 1**). New biomass production measures typically miss a few components of NPP: (1) root exudates, which are rapidly taken up and respired by microbes adjacent to roots and are generally measured in field studies as a portion of soil respiration, including the respiration of litter and surface organic layers; (2) volatile emissions are rarely measured but are generally a small fraction (<1 to 5%) of NPP and thus probably a modest source of error (Guenther et al., 1995); and (3) biomass that dies or is removed by herbivores before it can be measured. For some purposes, these errors may not be too important. A frequent objective of measuring terrestrial NPP, for example, is to estimate the rate of biomass increment. Root exudates, transfers to symbionts, losses to herbivores, and volatile emissions are lost from plants and therefore do not directly contribute to biomass increment. Consequently, failure to measure these components of NPP does not bias estimates of biomass accumulation. However, these losses of NPP from plants fuel other ecosystem processes such as herbivory, decomposition, and nutrient turnover and are therefore important components of the overall carbon dynamics of ecosystems.

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

Table 1 Major components of NPP and representative values of their relative magnitudes

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

[a] Seldom, if ever, have all of these components been measured in a single study.
Source: Chapin FS III, Matson PA, and Vitousek PM (2011) *Principles of Terrestrial Ecosystem Ecology*, 2nd edn. New York: Springer.

10.6.2.2 Physiological Controls over NPP

NPP is the balance of carbon gained by GPP and the carbon lost by respiration of all plant parts (**Figure 1**). However, this simple relationship does not tell us whether the conditions governing photosynthesis dictate the amount of carbon that is available to support growth or whether conditions influencing growth rate determine the magnitude of photosynthesis. On short timescales (seconds to days), environmental controls over photosynthesis (e.g., light and water availability) strongly influence photosynthetic carbon gain. However, on monthly to annual timescales, plants adjust leaf area and photosynthetic capacity so carbon gain matches the soil resources that are available to support growth. 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. Terrestrial 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 absorption (Chapin, 1991b; Lambers et al., 2008). The resulting changes in growth and nutrition determine the leaf area index (LAI) and photosynthetic capacity, which largely account for ecosystem differences in carbon input (Gower et al., 1999).

The feedbacks from sink strength to photosynthesis are not 100% effective on short timescales. Leaf carbohydrate concentration increases during the day and declines at night, allowing plants to continue to transport carbohydrates to nonphotosynthetic organs at night. Similarly, carbohydrate concentrations increase during short periods (hours to weeks) of sunny weather and decline under cloudy conditions. Over these short timescales, the conditions affecting photosynthesis are the primary determinants of the carbohydrates available to support growth. The short-term controls over photosynthesis by environment probably determine the hourly to weekly

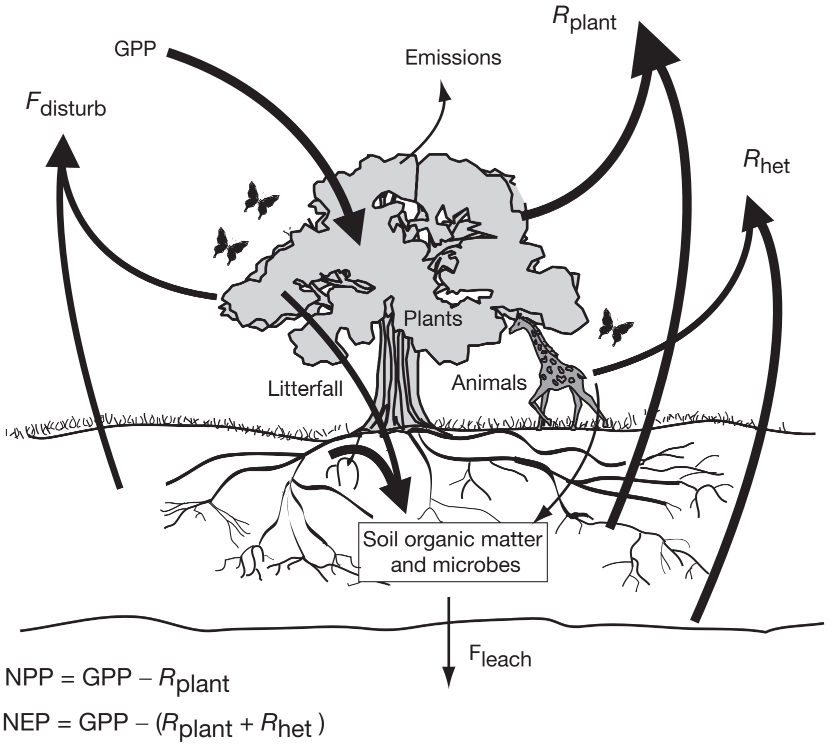

Figure 1 Overview of the major carbon fluxes of an ecosystem. Carbon enters the ecosystem as gross primary production (GPP), through photosynthesis by plants. Roots and aboveground portions of plants return about half of this carbon to the atmosphere as plant respiration (R_{plant}). Net primary production (NPP) is the difference between carbon gain by GPP and carbon loss through R_{plant}. Most NPP is transferred to soil organic matter as litterfall, root death, root exudation, and root transfers to symbionts; some NPP is eaten by animals and sometimes is lost from the ecosystem through disturbance (wildfire or harvest). Animals also transfer some carbon to soils through excretion and mortality. Most carbon entering the soil is lost through microbial respiration (which, together with animal respiration, is termed heterotrophic respiration: R_{het}). Net ecosystem production (NEP) is the balance between GPP and plant and heterotrophic respiration. Additional carbon is lost from soils through leaching and disturbance. Net ecosystem carbon balance (NECB) is the net carbon accumulation by an ecosystem; it equals the carbon inputs from GPP minus the various avenues of carbon loss (respiration, leaching, disturbance, etc.). Reproduced with permission from Chapin FS III, Matson PA, and Vitousek PM (2011) *Principles of Terrestrial Ecosystem Ecology*, 2nd edn. New York: Springer.

patterns of NPP, whereas soil resources govern annual carbon gain and NPP and the patterns of variation in NPP across landscapes and biomes.

10.6.2.3 Environmental Controls over NPP

At the global scale, the largest ecosystem differences in NPP are associated with variation in climate. NPP is greatest in warm moist environments, where tropical rain forests occur, and is least in climates that are dry (e.g., deserts) or cold (e.g., tundra) (**Figure 2**). NPP correlates most strongly with precipitation; NPP is highest at about 2–3 m $year^{-1}$ of precipitation (typical of rainforests) and declines at extremely low or high precipitation (**Figure 3**; Gower, 2002; Huxman et al., 2004; Luyssaert et al., 2007; Schuur, 2003). The decline in NPP in extremely wet climates (>3 m $year^{-1}$ of precipitation) probably reflects oxygen limitation to roots and/or soil microbes and leaching loss of essential nutrients (Schuur, 2003). When dry ecosystems (e.g., deserts) are excluded, NPP also increases exponentially with increasing temperature. The largest differences in NPP reflect differences among biomes (i.e., structurally different types of ecosystems such as forests and grasslands) in both climate and vegetation structure (**Table 2**). Across biomes, there is a 14-fold range in average NPP.

Most ecosystems experience times that are too cold or too dry for significant plant growth to occur. When NPP of each biome (**Table 2**) is adjusted for the length of the growing season, all forested ecosystems have similar NPP (about 5 g m^{-2} day^{-1}), and there is only about a threefold difference in NPP between deserts and tropical forests (**Table 3**). These calculations suggest that the length of the growing season accounts for much of the biome differences in NPP (Bonan, 1993; Chapin, 2003; Gower et al., 1999; Kerkhoff et al., 2005; Körner, 1999). When adjusted for length of the growing season, aboveground NPP of the world's biomes shows no relationship to temperature, although deserts and tundra are less productive than forests (Kerkhoff et al., 2005). This suggests that temperature effects on plant growth do not *directly* determine global patterns of NPP.

Comparisons *within and among ecosystems* show that NPP is limited by multiple factors, and the supply of belowground resources (both water and nutrients, and sometimes oxygen in very wet sites) is generally among the most important constraints on NPP. In ecosystems where climate–NPP correlations suggest a strong climatic limitation of NPP, experiments

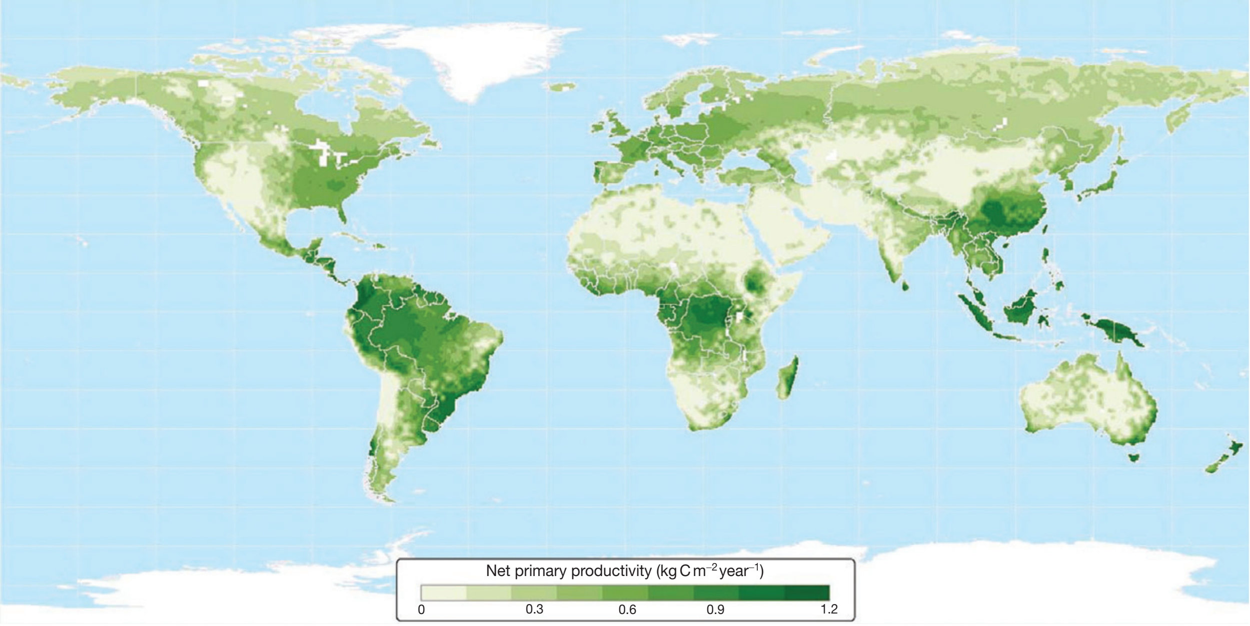

Figure 2 The global pattern of net primary productivity (Foley et al., 1996; Kucharik et al., 2000). The patterns of productivity correlate more closely with precipitation than with temperature, indicating a strong role of moisture in regulating the productivity of the biosphere. Reproduced with permission from the Atlas of the Biosphere (http://atlas.sage.wisc.edu).

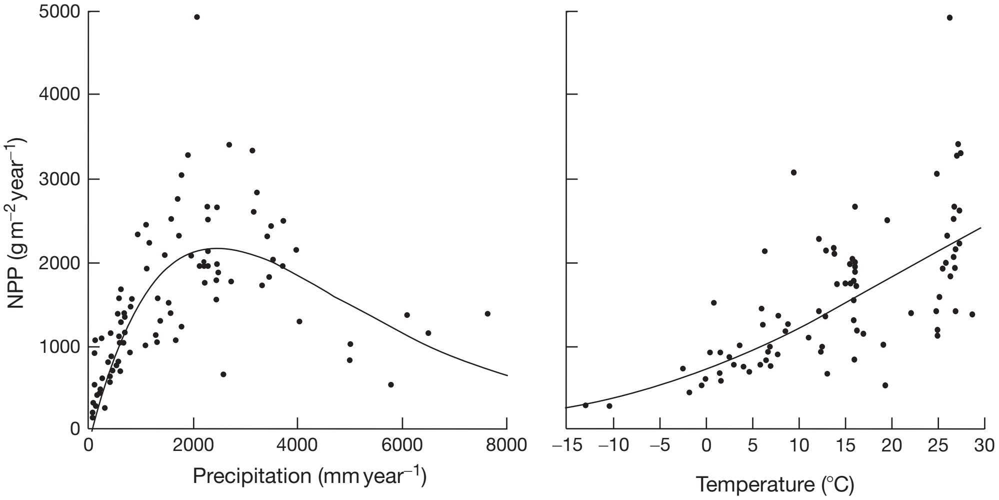

Figure 3 Relationship of aboveground NPP (in units of biomass) with average annual temperature and total annual precipitation. NPP is greatest in warm moist environments such as tropical forests and lowest in cold or dry ecosystems such as tundra and deserts. In tropical forests, NPP declines at extremely high precipitation (>3 m year^{-1}), due to indirect effects of excess moisture, such as low soil oxygen and loss of nutrients through leaching. Redrawn from Schuur EAG (2003) Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. *Ecology* 84: 1165–1170. Reproduced with permission from Chapin FS III, Matson PA, and Vitousek PM (2011) *Principles of Terrestrial Ecosystem Ecology*, 2nd edn. New York: Springer.

and observations show that limitation is mediated primarily by climatic effects on belowground resources. For example, in cold sites such as the tundra, NPP increases more in response to added nitrogen than to experimental increases in temperature (Chapin et al., 1995; McKane et al., 1997), suggesting that the climate–NPP correlation probably reflects temperature effects on nitrogen supply or length of the growing season more than a direct temperature effect on NPP. Similarly, NPP in the boreal forest correlates closely with soil temperature, but soil warming experiments show that this effect is mediated primarily by enhanced decomposition and nitrogen supply (Van Cleve et al., 1990).

Climate can also influence *which* belowground resources are most limiting. NPP is moisture-limited in dry sites, increasing most strongly with increasing precipitation (the left-hand end of the curve in **Figures 3** and **4**). These dry sites also show greatest sensitivity of NPP to *interannual variation* in rainfall (the slope of the straight lines in **Figure 4**) and to experimental

Table 2 Net primary production (NPP) of the major biome types based on biomass harvests[a]

Biome	*Aboveground NPP (g m^{-2} $year^{-1}$)*	*Belowground NPP (g m^{-2} $year^{-1}$)*	*Belowground NPP (% of total)*	*Total NPP*[a] *(g m^{-2} $year^{-1}$)*
Tropical forests	1400	1100	44	2500
Temperate forests	950	600	39	1550
Boreal forests	230	150	39	380 (670)[b]
Mediterranean shrublands	500	500	50	1000
Tropical savannas/grasslands	540	540	50	1080
Temperate grasslands	250	500	67	750
Deserts	150	100	40	250
Arctic tundra	80	100	57	180
Crops	530	80	13	610

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

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

Table 3 Productivity per day and per unit leaf area[a]

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

[a] Data from **Table 1** and Chapin et al. (2011). NPP is expressed in units of dry mass.

[b] Estimated.

[c] Data from Gower (2002).

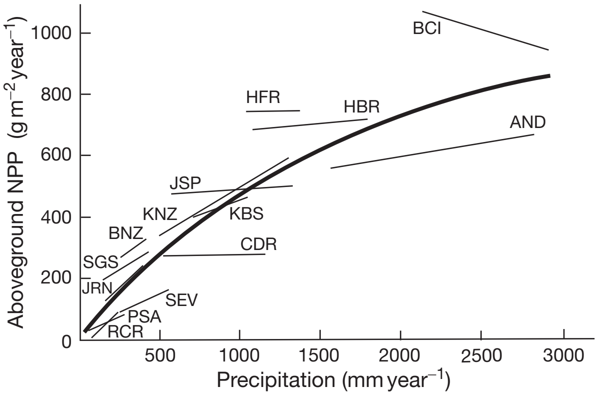

Figure 4 Relationship of aboveground NPP with total annual precipitation across 14 sites. The thick curved line shows the relationship between average aboveground NPP and average precipitation across all sites. The thin straight lines show the interannual variation in aboveground NPP and annual precipitation at a given site. Sites include deserts (RCR), grasslands and steppe (PSA, SEV, JRN, SGS, CDR, KNZ, KBS, and JSP), and forests (BNZ, HBR, HFR, AND, and BCI), mostly from Long-Term Ecological Research sites. Redrawn from Huxman TE, Smith MD, Fay PA, et al. (2004) Convergence across biomes to a common rain-use efficiency. *Nature* 429: 651–654. Reproduced with permission from Chapin FS III, Matson PA, and Vitousek PM (2011) *Principles of Terrestrial Ecosystem Ecology*, 2nd edn. New York: Springer.

additions of water (Huxman et al., 2004). In dry sites, NPP responds more strongly to water than to nutrient addition in most years, but even deserts respond to nutrient addition in wet seasons and years (Gutierrez and Whitford, 1987) and sometimes in both wet and dry years (James et al., 2005). Similarly, in mesic (moist) sites NPP responds more strongly to nutrient addition than to water addition in most years (Huxman et al., 2004). Within any given site, NPP responds most strongly to experimental addition of water in dry years and to nutrient additions in wet years.

When all belowground resources are relatively abundant, NPP responds directly to carbon dioxide (CO_2), the main aboveground resource utilized by plants. In temperate salt marshes, for example, where water and nutrients are abundant, NPP responds directly to increases in CO_2 (Drake et al., 1996), as do crops that are supplied with a large amount of nutrients. Nonetheless, NPP is enhanced by nutrient additions even in the most fertile agricultural systems (Evans, 1980), indicating the widespread occurrence of nutrient limitation to NPP.

In summary, (1) over the long-term, multiple belowground resources (both water and nutrients and sometimes oxygen in very wet sites) limit NPP of most ecosystems. (2) The nature of environmental limitation varies among years, being most moisture-limited in dry years, and most nutrient-limited in wet years. (3) Moisture limitation of NPP occurs most frequently in dry sites, and nutrient limitation occurs most frequently in mesic sites. Thus, a simple characterization of dry sites as water-limited and mesic sites as nutrient-limited is a reasonable first approximation, but it ignores the broader range of environmental limitations that all sites experience from time to time.

10.6.2.4 Species Controls over NPP

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

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

10.6.3 Limitations to Leaf-Level Carbon Gain

10.6.3.1 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 key regulators 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, water, light, and nutrients. The simplest way to describe limitation of photosynthesis is that, when the availability of one of these factors is low relative to others, it is the 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 modify the relative requirements for different raw materials for plant growth and therefore the stoichiometry of NPP.

This principle 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. 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 seldom exposed to an optimal balance of the resources necessary for photosynthesis. However, under a wide variety of circumstances plants adjust the components of photosynthesis so that all these components are about equally limiting (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 imitations of photosynthesis.

10.6.3.2 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. 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), causing plants to respond to both CO_2 availability and biochemical limitations (light, nitrogen, or phosphorus). Plants make this adjustment by altering stomatal conductance, which occurs within minutes, or by changing the concentrations of light-harvesting pigments or photosynthetic enzymes, which occurs over days to weeks.

The free atmosphere is sufficiently well mixed that its CO_2 concentration varies globally by only 4% – not enough to cause significant regional variation in photosynthesis. Nonetheless, the 35% increase in atmospheric CO_2 concentration since the beginning of the industrial revolution has caused a general increase in carbon gain by ecosystems (Canadell et al., 2007). A doubling of CO_2 concentration, for example, increases photosynthetic rate by 30–50% (Ainsworth and Long, 2005; Curtis and Wang, 1998). This enhancement of photosynthesis by elevated CO_2 is most pronounced in C_3 plants, that is, plants using the C_3 photosynthetic pathway, especially woody species (Ainsworth and Long, 2005). Over time, most plants acclimate to elevated CO_2 by reducing photosynthetic capacity and stomatal conductance, as expected from our hypothesis of colimitation of photosynthesis by biochemistry and diffusion. This downregulation of CO_2 absorption in response to elevated CO_2 enables plants to sustain carbon uptake, while reducing transpiration rate and their water demand from soils. In this way, elevated CO_2 often stimulates plant growth more strongly by reducing moisture limitation than by its direct effects on photosynthesis (Hungate et al., 1997; Owensby et al., 1993). C_4 plants, which use the C_4 photosynthetic pathway and are less sensitive to the *direct* effect of CO_2 on photosynthesis, are often just as sensitive to the *indirect* moisture-enhancing effects of CO_2 as are C_3 plants, so the long-term effects of elevated CO_2 on the competitive balance between C_3 and C_4 plants are difficult to predict (Mooney et al., 1999).

10.6.3.3 Light Limitation

When light is the only factor limiting photosynthesis, net photosynthesis increases linearly with increasing light, just as described for CO_2 response under CO_2-limiting conditions. The initial slope of the light response curve (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 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, that is, 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 the 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. Leaves experience large fluctuations (10- to 1000-fold) in incident light due to changes in sun angle, cloudiness, and the location of sunflecks (patches of direct sunlight that penetrate a plant canopy). The vertical distribution of leaf area, however, is the major factor governing the light environment of individual leaves.

In response to fluctuations in light availability over minutes to hours, plants alter stomatal conductance to adjust CO_2 supply to meet the needs of carbon-fixation reactions (Chazdon and Pearcy, 1991; 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 our hypothesis of colimitation of photosynthesis by biochemistry and diffusion. It allows plants to conserve water under low light and to maximize CO_2 absorption at high light.

Over longer timescales (days to months), plants respond to variations in light availability by producing leaves with different photosynthetic properties. Leaves at the top of the canopy (sun leaves) have more cell layers, are thicker, and therefore, have a higher photosynthetic capacity per unit leaf area than do shade leaves produced under low light (Terashima and Hikosaka, 1995; Walters and Reich, 1999). The respiration rate of a tissue depends on its protein content, so the low photosynthetic capacity and protein content of shade leaves are associated with a lower respiration rate per unit area than in sun leaves. For this reason, shade leaves maintain a positive carbon balance (photosynthesis minus respiration) under lower light levels than do sun leaves.

Plants can also produce sun or shade leaves as a result of evolutionary adaptation. Species that are adapted to high light and intolerant of shade typically have a higher photosynthetic capacity per unit mass or area than do shade-tolerant species, even when growing in the shade (Walters and Reich, 1999). The main disadvantage of the high protein and photosynthetic rate typical of shade-intolerant species is that they also have a higher respiration rate, due to their higher protein content. Species that are adapted to low light and are tolerant of shade have a low photosynthetic capacity, but can photosynthesize at lower light levels than shade-intolerant species. In other words, they have a low light compensation point, the light level at which leaf respiration completely offsets photosynthetic carbon gain. On average, the leaf-level light compensation point of shade-tolerant species is about half of that of shade-intolerant species (Craine and Reich, 2005). 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, that is, a relatively constant relationship between absorbed light and net photosynthesis (Chapin et al., 2011).

10.6.3.4 Nitrogen Limitation

Photosynthetic capacity, that is, 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 leaf nitrogen concentration found in natural ecosystems (Field and Mooney, 1986; Reich et al., 1997, 1999; Wright et al., 2004). This occurs because photosynthetic enzymes account for a large proportion of the nitrogen in leaves. 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. In addition, 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. Regardless of the cause of variation in leaf nitrogen concentration, there is always a strong positive correlation between leaf nitrogen concentration and photosynthetic capacity (Reich et al., 1997; Wright et al., 2004).

The changes in tissue nitrogen, and therefore in the C:N ratio of tissues, which occur in response to variation in nitrogen supply constitute an important change in element stoichiometry, as discussed later in the context of nutrient use. 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. This variation in stoichiometry enables plants to maximize carbon gain under favorable conditions and maximize the efficiency of using other resources to fix carbon, when these resources limit plant growth.

Other elements, particularly phosphorus, can also limit photosynthesis, although the impacts are typically less pronounced than those of nitrogen. We address the impact of multiple nutrients on plants in the context of growth in **Section 10.6.9**.

10.6.3.5 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 leads to an increase in leaf temperature and water vapor concentration inside the leaf and therefore greater vapor pressure deficit and water loss by transpiration. 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 the photosynthetic rate and the efficiency of using light to fix carbon (i.e., light-use efficiency, LUE) below levels found in unstressed plants.

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

Plants in dry areas minimize water stress by reducing leaf area (by shedding leaves or producing fewer new leaves). Some drought-adapted plants produce leaves that minimize radiation absorption; their leaves reflect most incoming radiation or are steeply inclined toward the sun (Ehleringer and Mooney, 1978). High radiation absorption is a disadvantage in dry environments because it increases leaf temperature, which increases respiratory carbon loss and transpirational water loss. Thus, there are several mechanisms by which plants in dry environments reduce radiation absorption to conserve water and carbon. The low leaf area, the reflective nature of leaves, and the steep angle of leaves are the main factors accounting for the low absorption of radiation and low carbon inputs in dry environments. In other words, plants adjust to dry environments primarily by altering leaf area and radiation absorption rather than by reducing photosynthetic capacity per unit leaf area.

10.6.4 Stand-Level Carbon Gain

10.6.4.1 Spatial Scaling of GPP

GPP is the sum of the net photosynthesis by all photosynthetic tissue measured at the ecosystem scale. Recent technological developments, such as eddy covariance approaches (Baldocchi, 2003), allow measurement of fluxes of CO_2 and other compounds at scales of tens to thousands of square meters, making it possible to measure whole-ecosystem carbon fluxes even in large-statured ecosystems such as forests. These measurements, when combined with simulation modeling, permit estimation of GPP and other ecosystem carbon fluxes.

The vertical profile of leaf photosynthetic properties in a canopy maximizes GPP in terrestrial ecosystems because the photosynthetic properties of each leaf are generally adapted and acclimated to the environment where they are situated. In most closed-canopy ecosystems, for example, the photosynthetic capacity decreases exponentially through the canopy in parallel with the exponential decline in irradiance (Hirose and Werger, 1987). The matching of photosynthetic capacity to light availability occurs through the preferential transfer of nitrogen to leaves at the top of the canopy. This occurs through at least three processes. (1) 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). (2) Leaves at the bottom of the canopy senesce when they become shaded below their light compensation point. Much of the nitrogen resorbed from these senescing leaves is transported to the top of the canopy to support the production of young leaves with high photosynthetic capacity. (3) Sun leaves at the top of the canopy develop more cell layers than shade leaves and therefore contain more nitrogen per unit leaf area. The accumulation of nitrogen at the top of the canopy is most pronounced in dense canopies, which develop under circumstances of high water and nitrogen availability (Field, 1991). In environments where leaf area is limited by water, nitrogen, or time since disturbance, there is less advantage to concentrating nitrogen at the top of the canopy, because light availability is high throughout the canopy. In these sparse canopies, light availability, nitrogen concentrations, and photosynthetic rates show a more uniform vertical distribution.

Canopy-scale relationships between light and nitrogen occur even in multispecies communities. In such stands, the individuals at the top of the canopy account for most of the photosynthesis and may be able to support greater root biomass to acquire more nitrogen, compared to smaller subcanopy or understory individuals. This specialization and competition among individuals probably contribute to the vertical scaling of nitrogen and photosynthesis observed in multispecies stands (Craine, 2009).

Vertical gradients in other environmental variables often reinforce the maximization of carbon gain near the top of the canopy. The friction of air moving across the earth surface causes wind speed to decrease exponentially from the free atmosphere to the top of the canopy. Wind speed continues to decrease from the top of the canopy to the ground surface in ways that depend on canopy structure. Smooth canopies, characteristic of crops or grasslands, show a gradual decrease in wind speed from the top of the canopy to the ground surface, whereas rough canopies, characteristic of many forests, create more friction and turbulence that increases the vertical mixing of air within the canopy (McNaughton and Jarvis, 1991). For this reason, gas exchange in rough canopies is more tightly coupled to conditions in the free atmosphere than in smooth canopies.

Wind speed is important because it reduces the thickness of the boundary layer of still air around each leaf, producing steeper gradients in temperature and in concentrations of

CO_2 and water vapor from the leaf surface to the atmosphere. This speeds the diffusion of CO_2 into the leaf and the loss of water from the leaf, enhancing both photosynthesis and transpiration. A reduction in thickness of the leaf boundary layer also brings the leaf temperature closer to the air temperature. The net effect of wind on photosynthesis is generally positive at moderate wind speeds and adequate moisture supply, enhancing photosynthesis at the top of the canopy, where wind speed is highest. When low soil moisture or a long pathway for water transport from the soil to the top of the canopy reduces water supply to the uppermost leaves, as in tall forests, the uppermost leaves reduce their stomatal conductance, causing the zone of maximum photosynthesis to shift further down in the canopy. Variations in light and water availability and leaf nitrogen concentrations then cause diurnal and seasonal shifts in the height of maximum photosynthesis within the canopy.

Canopy properties extend the range of light availability over which the LUE of the canopy remains constant. The light response curve of canopy photosynthesis, measured in closed canopies ($LAI > \approx 3$), saturates at higher irradiance than does photosynthesis by a single leaf for several reasons (Jarvis and Leverenz, 1983). The more vertical angle of leaves in the upper canopy reduces the probability of their becoming light-saturated and increases light penetration into the canopy. The clumped distribution of leaves in shoots, branches, and crowns also increases light penetration into the canopy. Conifer canopies are particularly effective in distributing light through the canopy due to the clumping of needles around stems. This could explain why conifer forests 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 their relatively low light availability. In fact, at high light (and correspondingly high temperature and vapor pressure deficit) photosynthesis declines in the upper canopy, and shaded leaves may account for most of the total canopy photosynthesis under these circumstances (Law et al., 2002). In most ecosystems, including all forests that have been measured, GPP approaches a plateau at high light, indicating a decline in LUE at high light (**Figure 5**; Law et al., 2002; Ruimy et al., 1995; Turner et al., 2003). This decline in LUE at high light is most pronounced in low-resource environments with sparse canopies, where canopy photosynthetic capacity is low, and all leaves experience a similar light regime (Baldocchi and Amthor, 2001; Gower et al., 1999; Turner et al., 2003). In other words, canopy photosynthetic response to light mirrors a photosynthetic response seen in individual leaves. In dense canopies, more leaves are shaded and operate in the linear portion of the light response curve, increasing the LUE of the canopy as a whole (**Figure 5**; Teskey et al., 1995; Turner et al., 2003).

Variation in soil resource supply accounts for much of the spatial variation in leaf area and GPP among ecosystem types. About 70% of the ice-free terrestrial surface has relatively open canopies (**Figure 6**; Graetz, 1991). GPP correlates closely with leaf area below an LAI of about 4 (Schulze et al., 1994), suggesting that leaf area is a critical determinant of GPP on most of the Earth's terrestrial surface. GPP is less sensitive to LAI in dense canopies, because the leaves in the middle and the bottom of the canopy contribute relatively little to GPP over the course of a day or a year. The availability of soil resources, especially water and nutrient supply, is a critical determinant of LAI for two reasons: (1) plants in high-resource environments produce a large amount of leaf biomass and (2) leaves produced in these environments have a high specific leaf area (SLA), that is, a large leaf area per unit of leaf biomass. A high SLA maximizes light capture and therefore carbon gain per unit of leaf biomass (Lambers and Poorter, 1992; Reich et al., 1997; Wright et al., 2004).

10.6.4.2 Temporal Scaling of GPP

The length of the photosynthetic season accounts for much of the ecosystem differences in GPP. Most ecosystems experience times that are too cold or too dry for significant photosynthesis to occur. During winter in cold climates and times with negligible soil water in dry climates, plants either die (annuals), lose their leaves (deciduous plants), or become physiologically dormant (some evergreen plants). During these times, there is negligible carbon absorption by the ecosystem, regardless of light availability and CO_2 concentration. At high latitudes and altitudes and in dry ecosystems, this is probably *the* major

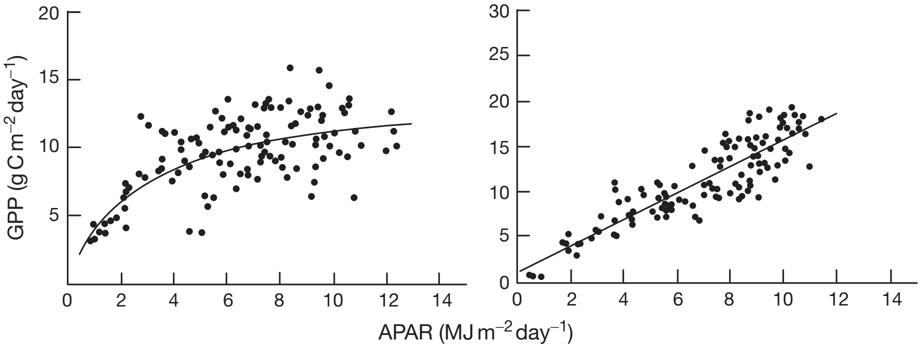

Figure 5 Response of GPP to absorbed photosynthetically active radiation (APAR) in a Massachusetts deciduous forest (left) and a Kansas grassland (right). The forest maintains a relatively constant light-use efficiency (LUE) up to 30–50% of full sun, although there is considerable variability. The grassland maintains a constant LUE over the entire range of naturally occurring irradiance. Redrawn from Turner DP, Urbanski S, Bremer D, et al. (2003) A cross-biome comparison of daily light use efficiency for gross primary production. *Global Change Biology* 9: 383–395. Reproduced with permission from Chapin FS III, Matson PA, and Vitousek PM (2011) *Principles of Terrestrial Ecosystem Ecology*, 2nd edn. New York: Springer.

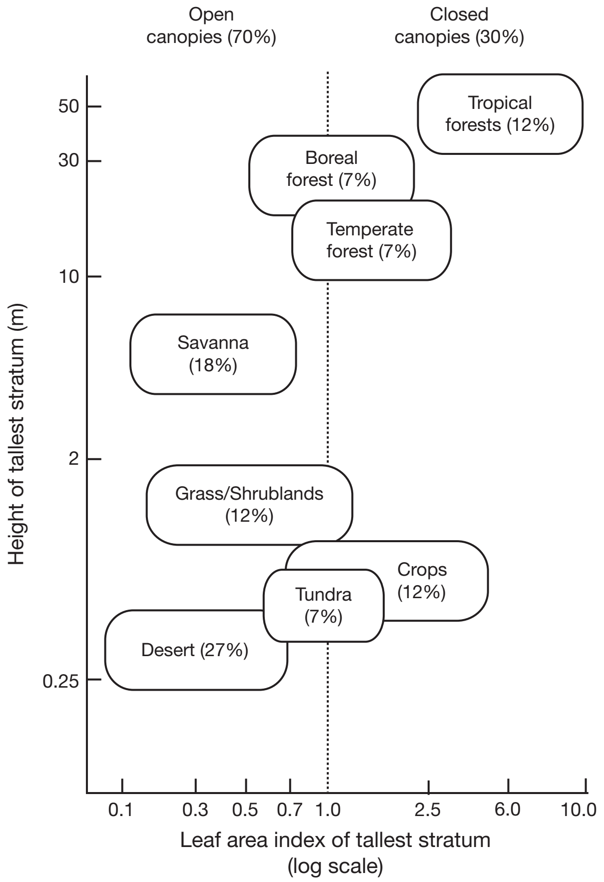

Figure 6 Projected foliage cover and canopy height of the major biomes (Graetz, 1991). Typical values for that biome and the percentage of the terrestrial surface that it occupies are shown. The vertical line shows 100% canopy cover. Reproduced from Graetz RD (1991) The nature and significance of the feedback of change in terrestrial vegetation on global atmospheric and climatic change. *Climatic Change* 18: 147–173, with permission.

constraint on carbon inputs to ecosystems (Körner, 1999). For annuals and deciduous plants, the lack of leaf area is sufficient to explain the absence of photosynthetic carbon gain in the nongrowing season. Lack of water or extremely low temperatures can, however, prevent even evergreen plants from gaining carbon (**Figure 7**; Xiao et al., 2010). In tropical ecosystems where conditions are more continuously favorable for photosynthesis, leaves maintain their photosynthetic machinery from the time they are fully expanded until they are shed. Models that simulate GPP often define the length of the photosynthetic season in terms of thresholds of minimum temperature or moisture below which plants do not produce leaves or do not photosynthesize (Running et al., 2004).

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

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

LUE varies diurnally, being lowest at times of high light. Seasonal patterns of LUE are more complex because they depend not only on light availability but also on seasonal variations in leaf area, canopy nitrogen, and various environmental stresses such as drought and freezing. LUE is highest in high-resource ecosystems such as crops with a high LAI and photosynthetic capacity. It is lowest in low-resource ecosystems such as the boreal forest and arid grasslands (Turner et al., 2003). LUE also declines with increasing temperature (reflecting increases in photorespiration) (Lafont et al., 2002; Turner et al., 2003) and is strongly reduced at extremely low temperatures (Teskey et al., 1995).

10.6.5 Respiration

Respiration provides the energy for a plant to acquire nutrients and to produce and maintain biomass. Total plant respiration can be divided into three functional components: growth respiration, maintenance respiration, and the respiratory cost of ion absorption. Each of these respiratory components involves mitochondrial oxidation of carbohydrates to produce ATP. They differ only in the functions for which ATP is used by the plant.

Growth of new tissue requires biosynthesis of many classes of chemical compounds, including cellulose, proteins, nucleic acids, and lipids. The carbon cost of synthesizing each compound includes the carbon that is incorporated into that compound plus the carbon oxidized to CO_2 to provide the ATP that drives biosynthesis. These carbon costs can be calculated for each class of compound from knowledge of its biosynthetic pathway (Amthor, 2000; Penning de Vries et al., 1974). The cost of producing a gram of tissue can then be calculated from the concentration of each class of chemical compound in a tissue and its carbon cost of synthesis.

There is a threefold range in the carbon cost of synthesis of the major classes of chemical compounds found in plants. The most energetically expensive compounds in plants are proteins, tannins, lignin (vascular land plants only), and lipids. In general, metabolically active tissues, such as leaves, have high concentrations of proteins, tannins, and lipids. The tannins and lipophilic substances such as terpenes serve primarily to defend protein-rich tissues from herbivores and pathogens. Structural tissues have high lignin and low protein, tannin, and lipid concentrations. Leaves of rapidly growing species with high protein concentrations 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

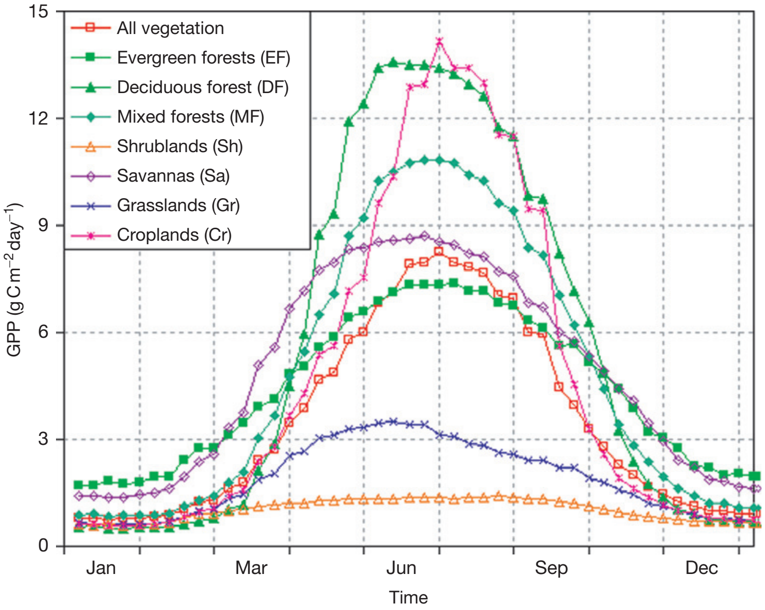

Figure 7 Predicted seasonal pattern of GPP in different biomes of the United States averaged from 2001 to 2006, based on a regression model that uses AmeriFlux GPP measurements and MODIS satellite imagery. Redrawn from Xiao J, Zhuang Q, Law BE, et al. (2010) A continuous measure of gross primary production for the conterminous United States derived from MODIS and Ameriflux data. *Remote Sensing of Environment* 114: 576–591. Reproduced with permission from Chapin FS III, Matson PA, and Vitousek PM (2011) *Principles of Terrestrial Ecosystem Ecology*, 2nd edn. New York: Springer.

differs among plant parts and species. In fact, the carbon cost of producing plant tissue is surprisingly similar across species, tissue types, and ecosystems (Chapin, 1989; Poorter, 1994; Villar et al., 2006). On average, growth respiration accounts for about 20% of the energy expended in growth, and the remaining 80% is incorporated into new biomass. The rates of growth and therefore of growth respiration measured at the ecosystem scale (g C m^{-2} day^{-1}) increase when temperature and moisture favor growth, but growth respiration is a relatively constant fraction of NPP, regardless of environmental conditions.

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

All live cells, even those that are not actively growing, require energy to maintain ion gradients across cell membranes and to replace degraded proteins, membranes, and other constituents. Maintenance respiration provides the ATP for these maintenance and repair functions. About 85% of maintenance respiration is associated with the turnover of proteins (about 2–5% turnover per day), explaining why there is a strong correlation between protein concentration and whole-tissue respiration rate in nongrowing tissues (Penning de Vries, 1975). We therefore expect maintenance respiration to be greatest in ecosystems with high tissue nitrogen concentrations 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 being associated with growth respiration and ion absorption (Lambers et al., 2008).

Maintenance respiration depends on environment as well as tissue chemistry. It increases with temperature because proteins and membrane lipids degrade and must be replaced more rapidly at high temperatures. Drought also imposes short-term metabolic costs associated with the 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 except in strongly fluctuating environments.

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

In summary, studies of the basic components of respiration associated with growth, ion absorption, and maintenance suggest that total plant respiration should be a relatively constant fraction (about half) of GPP (Landsberg and Gower, 1997; Ryan et al., 1994). In other words, plants have a growth efficiency of about 40–50% – the proportion of GPP that is converted to NPP. Variation in maintenance respiration is the most likely cause of variation in this efficiency.

10.6.6 Allocation of NPP

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

Observations in ecosystems are generally consistent with allocation theory. Tundra, grasslands, and shrublands, for example, allocate a larger proportion of NPP below ground than do forests (**Table 2**; Gower et al., 1999; Saugier et al., 2001). Crops, with their relatively favorable water and nutrient supplies, show the least allocation below ground.

Global patterns of leaf area and NPP also suggest that allocation is an important determinant of NPP. Total LAI, when averaged for a biome, varies about sixfold among biomes; the most productive ecosystems generally have the highest LAI (**Table 3**). When growing season NPP is adjusted for differences in leaf area, unproductive ecosystems such as tundra or desert do not differ consistently in NPP from more productive ecosystems (**Table 3**). If anything, the less productive ecosystems may have higher NPP per unit of leaf area and growing season length than do crops and forests. On average, plants in most biomes produce 1–3 g of biomass m^{-2} leaf day^{-1} during the growing season. This is equivalent to a GPP of about 1–3 g C m^{-2} leaf day^{-1}, because NPP is about half of GPP, and biomass is about 50% carbon. Apparent differences among biomes in these values reflect substantial uncertainty in the underlying data. At this point, there is little evidence for strong ecological patterns in NPP per unit leaf area and the length of the growing season.

10.6.7 Tissue Turnover

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

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

10.6.8 Global Patterns of Biomass and NPP

Ecosystems that are close to steady state, that is, not recovering from recent disturbances, show a consistent relationship between climate and plant biomass. Average plant biomass (g m^{-2}) varies 60-fold among the Earth's major terrestrial biomes (**Table 4**). Forests have the most biomass. Among forests, average biomass declines fivefold from the tropics to the low-statured boreal forest, where NPP is low and stand-replacing fires frequently remove biomass. Ecosystems that are dry and cold (deserts and tundra, respectively) have only 1% as much aboveground biomass as do tropical forests.

Tropical forests account for about half of the Earth's total plant biomass and about a third of the Earth's terrestrial NPP, although they occupy only 13% of the ice-free land area; other forests contribute an additional 30% of global biomass and 20% of terrestrial NPP (**Table 4**). Nonforested biomes therefore account for less than 20% of total plant biomass, although they occupy 70% of the ice-free land surface. Crops for example, account for only 1% of terrestrial biomass although they

Table 4 Average biomass, global extent of terrestrial biomes, and their total carbon in plant biomass, and NPP[a]

Biome	*Average biomass (g m^{-2})*	*Area (10^6 km^2)*	*Total plant C pool (Pg C)*	*Total NPP (Pg C $year^{-1}$)*
Tropical forests	38 800	17.5	320	20.6
Temperate forests	26 700	10.4	130	7.6
Boreal forests	8300	13.7	54	2.4
Mediterranean shrublands	12 000	2.8	16	1.3
Tropical savannas/grasslands	5700	27.6	74	14.0
Temperate grasslands	750	15.0	6	5.3
Deserts	700	27.7	9	3.3
Arctic tundra	650	5.6	2	0.5
Crops	610	13.5	4	3.9
Ice		15.5		
Total		149.3	615	58.9

[a] Average biomass per unit area is expressed in units of dry biomass. Total biomass and NPP on the planet are expressed in units of carbon, assuming that plant biomass is 47% carbon (Gower et al., 1999; Sterner and Elser, 2002; Zheng et al., 2003).
Calculated from Saugier et al. (2001).

occupy more than 10% of the ice-free land area and are responsible for 10% of terrestrial production. Grasslands and savannas account for an additional third of terrestrial NPP; these ecosystems are much more important in their contribution to terrestrial production than to biomass. Thus, most of the terrestrial surface has relatively low biomass, which does not necessarily correlate with a system's NPP (**Figure 7**). This observation alone raises concerns about deforestation in the tropics where ecosystem biomass is greatest, independent of the associated species losses.

10.6.9 Nutrient Use

Given the importance of nutrients in controlling NPP, it is important to understand the relationship between nutrient supply and NPP. Plant growth increases linearly with the rate of accumulation of growth-limiting nutrients in laboratory experiments (Ingestad and Ågren, 1988), and NPP increases in response to increased nutrient supply in the field. Tissue nutrient concentrations increase substantially only when other factors begin to limit plant growth.

Nutrient use efficiency (NUE) is the quantity of biomass that an ecosystem produces per unit of nutrient acquired. A useful index of NUE is the ratio of biomass to nutrients lost in litterfall (i.e., the inverse of nutrient concentration in plant litter). This ratio is highest in unproductive sites (Vitousek, 1982), suggesting that plants are more efficient in producing biomass per unit of nutrient acquired and lost if nutrients are in short supply.

There are at least two ways in which a plant might maximize biomass gained per unit of nutrient (Berendse and Aerts, 1987): through (1) a high nutrient productivity, that is, a high instantaneous rate of carbon absorption per unit nutrient or (2) a long residence time, that is, the average time that the nutrient remains in the plant. 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 NUE 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. Similarly, shading reduces tissue loss more strongly than it reduces the capacity to gain carbon (Walters and Reich, 1999).

There is an innate physiological trade-off between nutrient residence time and nutrient productivity (Reich et al., 1997, 1999; Wright et al., 2004). 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 high nutrient productivity grow rapidly and have high photosynthetic rates, which are associated with low tissue density, 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. Shade-tolerant species also produce longer lived leaves than do shade-intolerant species (Reich et al., 1999; Wright et al., 2004). In order for leaves to survive a long time, they must have more structural cells to withstand unfavorable conditions and higher concentrations of lignin and other secondary metabolites to 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 NUE 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 (Craine, 2009; Freschet et al., 2010). A high NUE also reduces rates of decomposition and nutrient mineralization, because well-defended, low-nutrient tissues decompose slowly when they senesce and induce immobilization of nutrients by microorganisms.

Less is known about the trade-offs between root longevity and nutrient absorption rate. Nutrient absorption declines as roots age, lose root hairs, and become suberized, so trade-offs between physiological activity and longevity that have been well documented for leaves probably also exist for roots (Craine, 2009; Freschet et al., 2010). Slow-growing plants often have low nutrient concentrations in their roots as well as low rates of root respiration (Tjoelker et al., 2005), which is consistent with their low capacity for nutrient absorption.

The trade-off between NUE and rate of resource capture explains the diversity of plant types along resource gradients. Low-nutrient environments are dominated by species that conserve nutrients through low rates of tissue turnover, high NUE, 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 infertile environments (Chapin, 1980; Craine, 2009). In high-nutrient environments, species with high rates of resource capture, rapid growth rates, rapid tissue turnover, and consequently, low NUE, outcompete plants with high NUE. In other words, neither a rapid growth rate nor a high NUE is universally advantageous because of inherent physiological trade-offs between these traits. The relative benefit to the plant of efficiency versus rapid growth depends on environment.

10.6.10 Balancing Nutrient Limitation

10.6.10.1 Nutrient Requirements

To this point, we have focused on the mechanisms by which plants minimize 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 adjust their physiology to maximize NPP across a range of limiting factors. Unlike light, CO_2, and water, which are relatively homogeneous in quality, nutrients include many chemical elements, each with different functions and controls.

Because each nutrient performs a different function in plants (**Table 5**), the relative amount of each nutrient required and the plant response to limitation by these nutrients vary. Primary macronutrients are the nutrients needed in the largest amounts. Nitrogen and phosphorus are the macronutrients that most commonly limit plant growth. Plants also require potassium, calcium, magnesium, and sulfur in large quantities, but these nutrients less frequently limit plant growth. Micronutrients are also essential for plants 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 growth and metabolism, and other elements cannot substitute for their function. Beneficial nutrients enhance growth under specific conditions or for specific groups of plants (Marschner, 1995). Ferns, for example, require aluminum, nitrogen-fixing symbionts need cobalt, diatoms need silicon, and Chenopodiaceae need sodium (Larcher, 2003). Other nutrients are not required or are required in such small amounts that even modest levels are harmful (toxic – e.g., selenium). Roots typically exclude these nutrients, although some plants have evolved tolerance and may even accumulate them to high levels as a defense against pathogens and herbivores (Boyd, 2004).

10.6.10.2 Limitation by Different Nutrients

Although all essential nutrients are necessary for plant growth, the particular nutrient that limits plant production varies in time and space. The macronutrients nitrogen and phosphorus most frequently limit NPP. On average, they are about equally limiting to plant growth on land in the short term (**Figure 8**; Elser et al., 2007), although the relative degree of limitation by nitrogen and phosphorus differs within and among ecosystems (Güsewell, 2004). Young- to moderate-aged soils tend to be limited by nitrogen availability, while phosphorus tends to limit plant growth on very old soils (Vitousek and Farrington, 1997), in soils derived from low-P parent material, or at sites where soils form layers that prevent roots from accessing deeper soil layers (Vitousek et al., 2010). Such conditions can be found on some Mediterranean soils (Cowling, 1993; Specht and Rundel, 1990) and on glacial and Aeolian sandy soils in European heathlands (Aerts and Heil, 1993). Thus, lowland tropical forests on ancient weathered soils, for example, tend to respond most strongly to phosphorus addition (Tanner et al., 1998), whereas tundra plants on recently glaciated soils tend to respond more strongly to nitrogen addition (Vitousek and Howarth, 1991). This is consistent with the higher N:P ratios in leaves of tropical than of high-latitude plants (Reich and Oleksyn, 2004; Sterner and Elser, 2002). Sites that would naturally be nitrogen-limited can become phosphorus-limited in areas with high nitrogen deposition (Aerts and Berendse, 1988; Aerts and Bobbink, 1999) and in European fens where

Table 5 Nutrients required by plants and their major functions

Nutrient	*Role in plants*
Macronutrients	Required by all plants in large quantities
Primary	Usually most limiting because used in largest amounts
Nitrogen (N)	Component of proteins, enzymes, phospholipids, and nucleic acids
Phosphorus (P)	Component of proteins, coenzymes, nucleic acids, oils, phospholipids, sugars, and starches Critical in energy transfer (ATP)
Secondary	Major nutrients but less often limiting
Potassium (K)	Component of proteins Role in disease protection, photosynthesis, ion transport, osmotic regulation, and enzyme catalyst
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	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 as a catalyst
Molybdenum (Mo)	Role in N fixation, nitrate-converting enzymes, Fe absorption, and translocation
Zinc (Zn)	Activates enzymes, regulates sugar consumption
Beneficial nutrients	Required by certain plants or by plants under specific environmental conditions
Aluminum (Al)	
Cobalt (Co)	
Iodine (I)	
Nickel (Ni)	
Selenium (Se)	
Silicon (Si)	
Sodium (Na)	
Vanadium (V)	

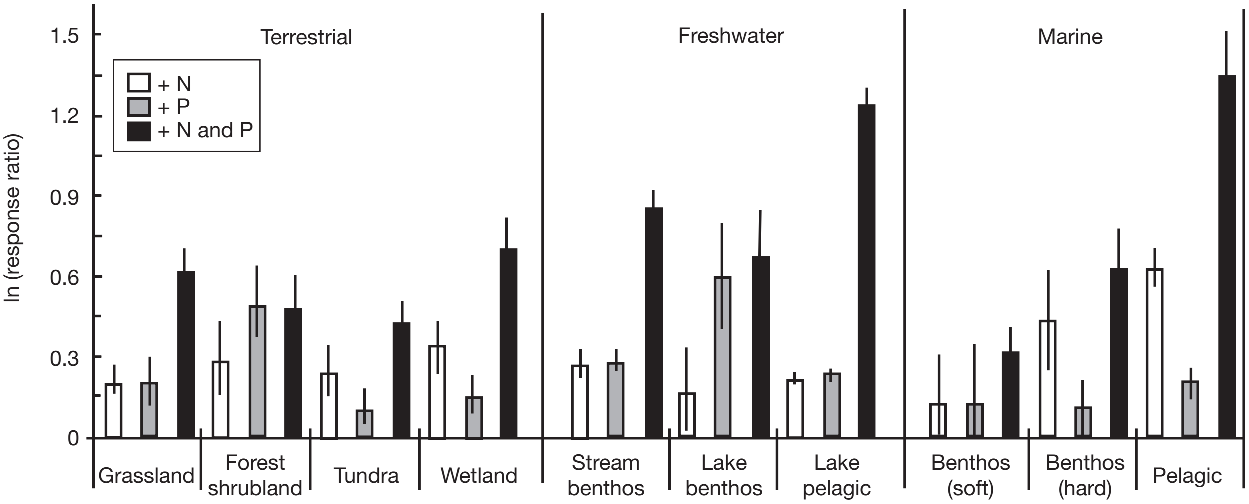

Figure 8 Relative response of plant production to addition of nitrogen or phosphorus or to both nutrients in major habitat types of terrestrial, freshwater, and marine ecosystems. Relative response is calculated as the biomass or production in the enriched treatment divided by its value in the control treatment and then ln-transformed. Redrawn from Elser JJ, Bracken MES, Cleland E, et al. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10: 1135–1142. Reproduced with permission from Chapin FS III, Matson PA, and Vitousek PM (2011) *Principles of Terrestrial Ecosystem Ecology*, 2nd edn. New York: Springer.

long-term mowing treatments have removed substantial phosphorus (Verhoeven and Schmitz, 1991).

On some sites, vegetation composition can influence whether a site is limited by nitrogen or phosphorus. In California grasslands, for example, grass-dominated sites are nitrogen-limited but can be sulfur- and phosphorus-limited if legumes are present (Jones and Martin, 1964; Jones et al., 1970, 1983). Limitation by nitrogen versus phosphorus also changes over the course of soil development, with soils being nitrogen-limited early in primary succession, then becoming phosphorus-limited as P from the parent material is weathered over thousands of years (Vitousek, 2004; Vitousek and Farrington, 1997; Walker and Syers, 1976).

Calcium, magnesium, and potassium virtually disappear due to leaching in old soils, but seldom limit plant growth because of renewal from atmospheric inputs (Chadwick et al., 1999; Vitousek, 2004). There are, however, circumstances when these nutrients do limit NPP. Potassium tends to be limiting in ecosystems with high precipitation 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, 1991). Base cations such as calcium and magnesium can also 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 can occur with manganese (Göransson, 1994), iron (Göransson, 1993), and 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 rainstorms or pulses of litter inputs, can rapidly alter the relative abundance of nutrients, shifting limitation from one nutrient to another at different times. Over an annual cycle, production in most ecosystems responds to both nitrogen and phosphorus and especially to the two nutrients in combination, suggesting colimitation (Craine, 2009; Elser et al., 2007; LeBauer and Treseder, 2008). Whether multiple mineral nutrients are equally important in limiting NPP in the long term depends on species changes and other ecosystem adjustments.

10.6.10.3 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 within the water column and the N:P in the deep sea and upwelling waters, so biotic demand for nitrogen and phosphorus closely matches their availability.

In terrestrial ecosystems, most plants are similar to one another in nutrient ratios, with the general C:N:S:P ratio of land plants being 790:7.6:3.1:1 (Bolin et al., 1983). The widespread use of 'fixed formulas' of nutrients, such as Hoagland's solution, in controlled environments is an indicator of the robustness of this stoichiometric relationship (Ingestad and Ågren, 1988). Departures from such ratios have been used as indicators of nutrient limitation to guide fertilizer application in agricultural systems (Jones and Martin, 1964; Koerselman and Mueleman, 1996; Ulrich and Hills, 1973). However, tissue nutrient ratios 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 are marine phytoplankton (Marschner, 1995).

If the simple stoichiometric control implied by the Redfield ratio were to apply in 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 NUE of plants differs among growing conditions and species. In addition, to be truly comparable to marine systems, the input and recycling of nutrients in dead plant material must 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 the cycling of multiple nutrients and carbon in terrestrial ecosystems.

First, the Redfield ratio is based on an optimal cytoplasmic stoichiometry of single-celled marine organisms. Terrestrial plants are multicellular and have different tissue types and compounds with dramatically different stoichiometries (Bazzaz, 1997; Lambers et al., 2008). As discussed earlier, plants frequently shift their relative allocation among tissues in response to environmental changes. Allocation also differs among species. Thus, even assuming that plants receive an ideal ratio of resources, plant species with inherently different allocation strategies or within-tissue nutrient ratios will differ substantially in the stoichiometry of NPP (Eviner and Chapin, 2003).

The tight coupling of nitrogen and phosphorus cycling hypothesized in marine systems does not occur in terrestrial systems, where nitrogen and phosphorus differ substantially in the controls over mineralization and availability (McGill and Cole, 1981). In addition, litter inputs have a dramatically different stoichiometry from plant demand because nutrients differ in their extent of resorption 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). Hence, unlike marine systems, terrestrial cycling involves significant nutrient storage in plants and soils and slow turnover of nutrients, so the stocks of available nutrients have little relation to fluxes through vegetation.

10.6.10.4 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, 2003; **Figure 9**). In the following sections, we discuss the uncoupling mechanisms that cause NPP in terrestrial ecosystems to depart from a simple stoichiometric model.

10.6.10.4.1 Litterfall and leaching inputs

During the transition from live tissue to litter, the ratios and concentrations of nutrients undergo large changes due to both resorption and leaching (**Figure 9**; Aerts and Chapin, 2000; Marschner, 1995). Plants resorb about half of their leaf nitrogen and phosphorus during senescence, with deciduous plants tending to resorb more nitrogen and evergreens and graminoids resorbing more phosphorus (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 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. The stoichiometry of element returns from plants to soil is

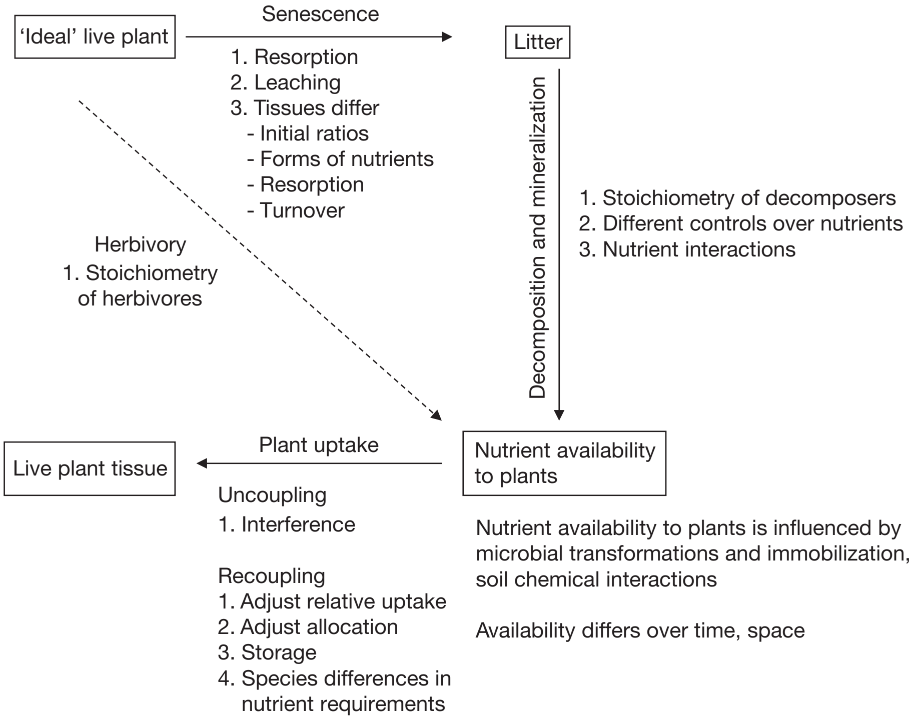

Figure 9 Uncoupling and coupling mechanisms that alter rates of cycling of different plant nutrients relative to the ratios initially present in live plants.

therefore extremely different from the ratios present in plants or those required for plant growth. This contrasts strikingly 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, 2003). Roots, for example, have low nutrient-to-carbon ratios, as does wood, which also has a high calcium concentration. 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), which 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), and there is no evidence of 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 tissues senesce. The stoichiometry of herbivores differs from that of plants (Elser and Urabe, 1999), so herbivores incorporate nutrients and carbon in different ratios than plants supply (e.g., phosphorus sequestration in bone) and therefore excrete excess nutrients (particularly S and N) 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 particulate nutrients sink to the deep ocean and are resupplied in upwelling zones in ratios similar to those in phytoplankton (Mann and Lazier, 2006), the nutrient inputs of terrestrial litter have a stoichiometry decoupled from that of live tissues.

10.6.10.4.2 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. The average plant has a C:N:S:P ratio of 1000:9.6:3.9:1.3 (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 1000:4.8:2.5:0.65. Soil bacterial biomass has a ratio of 1000:100:4.7:23.3, whereas fungi have a ratio of 1000:62:4.3:5.3 (Bolin et al., 1983). Both groups would require ~40% more carbon than the stoichiometric ratios in their biomass would suggest because of the carbon expended in respiration (Paul and Clark, 1996). 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 as much phosphorus per unit of growth than do fungi, that is, bacteria have a higher phosphorus requirement than do fungi.

These stoichiometric differences between bacteria and fungi are consistent with ecosystem-scale patterns of element cycling. Forests, for example, which are dominated by fungi, tend to immobilize nitrogen in microbes and to mineralize phosphorus. In bacterially dominated grasslands and agricultural systems, in contrast, there may be greater tendency to immobilize phosphorus.

The chemical bonds that bind nutrients to dead organic matter also influence patterns of element decoupling during decomposition. Nitrogen is bonded directly to the carbon skeleton of organic matter, so nitrogen can be mineralized to plant-available forms as 'waste products' as microbes oxidize organic compounds for energy (McGill and Cole, 1981; Paul and Clark, 1996). This accounts for the strong relationship between litter C:N ratio 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 immobilize nitrogen. The form of inorganic nitrogen in the soil is governed by a series of redox reactions that are influenced by soil carbon availability, oxygen, pH, and 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 (vs. 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 for microbes and is not involved in soil redox reactions.

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, and, like phosphorus, this ester-bonded sulfur can be mineralized with extracellular enzymes that do not disrupt the carbon skeleton of organic matter. Under sulfur-limiting conditions, plants produce primarily carbon-bonded forms of sulfur, in which case its mineralization depends mainly on microbial carbon demand (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 its supply to plants. The importance of decomposition to magnesium and manganese availability is intermediate between calcium and potassium (Chapin et al., 2011).

Although similar environmental factors can limit both NPP and decomposition, these two processes are differentially affected by these constraints, so the timing and amount of nutrient supply seldom coincide with plant demand. For example, in some ecosystems, a substantial amount of nutrient mineralization occurs beneath the snow pack and is released in spring thaw before plants actively take up nutrients (Bilbrough et al., 2000; Hobbie and Chapin, 1996). Nutrients (particularly nitrogen and phosphorus) 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). These pulses can lead to a temporal decoupling of nutrient availability with plant and microbial uptake, leading to potential loss of nutrients from the ecosystem (Austin et al., 2004; Lodge et al., 1994). 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 depends on microbial demands for energy, and the release of phosphorus depends on microbial phosphorus demands and factors governing microbial turnover.

10.6.10.4.3 Nutrient availability

The ratios at which nutrients are released in their mineral form through decomposition and mineralization do 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 can decrease plant access to these nutrients.

As with mineralization dynamics, nutrients differ in the factors governing their availability after mineralization. Ammonium, for example, diffuses slowly through the soil because its positive charge interacts with negatively charged soil particles, whereas nitrate diffuses rapidly, but is more 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 phosphate from soil solution. Phosphate precipitates with calcium, aluminum, iron, or manganese, forming insoluble compounds. Charged organic compounds, such as the citrate secreted by plant roots in low-phosphorus soils, prevent the formation of these insoluble phosphorus compounds by competing with phosphate for the binding surface of calcium, aluminum, iron, and manganese, thus increasing phosphate 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 for manganese, copper, magnesium, and iron. Waterlogged soils can limit manganese and zinc availability, and iron availability can decrease with enhanced concentrations of phosphorus, manganese, zinc, or copper (Marschner, 1995).

10.6.10.4.4 Element interactions

Elements can also interact to influence one another's dynamics. For example, phosphorus and sulfur can limit nitrogen fixation, and thus nitrogen availability (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 sulfate leaching enhances leaching of cations that precipitate with phosphorus. Nitrogen additions tend to enhance plant phosphatase activity (but not always soil phosphatase activity) (Marklein and Houlton, 2012). Sulfur-releasing enzymes and sulfur mineralization can be inhibited by phosphate and stimulated or inhibited by nitrogen availability (Ghani et al., 1992; McGill and Christie, 1983). 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.

10.6.10.4.5 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 phosphate than plants need and excess calcium and magnesium (Larcher, 2003; 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. In addition, cation uptake decreases at low pH, because hydrogen ion concentrations are high relative to mineral cation concentrations, whereas low pH stimulates or has no effect on anion uptake because of low hydroxyl ion 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 compete for binding sites on the plasma membrane, and the latter have lower transport rates through the plasma membrane. Similarly, ammonium decreases uptake of potassium, calcium, and magnesium; high magnesium can inhibit calcium uptake; potassium and calcium inhibit magnesium uptake; high sulfate decreases molybdenum uptake; and nitrate and chlorine can inhibit one another. There are additional 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, and sodium chloride, and at low pH. Nitrate uptake is also inhibited by the presence of ammonium (Larcher, 2003; Marschner, 1995).

Relatively high concentrations of certain nutrients can also increase the uptake of other elements. For example, ammonium 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, 2003). Calcium has been shown to enhance potassium uptake at low pH but decrease or have no effect on potassium uptake at high pH (Jones and Lunt, 1967). Although many of these examples are situation-specific, it is clear that the stoichiometry of elements available in soil solution can substantially decouple the stoichiometry of plant uptake from supply.

10.6.10.5 Recoupling Mechanisms

In the previous sections, we showed that many processes 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 depended on the relative availability of these nutrients at any one time, NPP would be constrained by a constantly 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, plants respond to nutrient limitation by increasing their root:shoot ratio, increasing their NUE, and by allocating to protective compounds that increase tissue lifespan. Just as water, CO_2, light, and nutrients need to be balanced, plants also adjust their physiology to respond to limitations by specific nutrients. Even those plant adjustments that enhance nutrient acquisition in general, such as increased root length, do not equally relieve limitation by all nutrients. Nitrate diffuses rapidly in the soil, and its uptake increases substantially with a given increase in root length. In contrast, it takes 6–10 times greater root length increase to produce an equivalent increase in phosphate or ammonium uptake because the diffusion zones around 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 its lower mobility in soil (Barber, 1984; Chapin, 1991a; Lambers et al., 2008). For those nutrients that diffuse slowly in soil, plants enhance diffusion by reducing nutrient concentration at the root surface through active uptake of potentially limiting nutrients. Plants substantially enhance absorption of a limiting element (Chapin, 1991a; Lee, 1982; Lee and Rudge, 1986) by increasing the transport proteins specific to that nutrient, while decreasing uptake capacity for nutrients that do not limit growth (Chapin, 1980; Lambers et al., 2008). This is particularly important for the nutrients that most frequently limit plant growth because ammonium, nitrate, potassium, and sulfate 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. Ammonium, nitrate, and amino acids are each 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 different nitrogen forms.

Plants can also balance their uptake of different nutrients through their production of enzymes and other compounds that enhance availability or use of specific nutrients. Nitrate reductase is required to assimilate nitrate into plant biomass, and its production is triggered by the presence of nitrate in the soil solution. Phosphorus limitation induces production of root phosphatase enzymes that cleave organically bound phosphate or siderophores that solubilize iron–phosphorus compounds by chelating iron and perhaps other cations that precipitate phosphorus (Lambers et al., 2008).

Associations with soil microbes such as mycorrhizal fungi also relieve limitations by certain nutrients. Since these fungi greatly increase the effective surface area for nutrient absorption, they particularly enhance uptake of nutrients that diffuse slowly in soil, that is, phosphate and ammonium-nitrogen. Arbuscular mycorrhizae primarily relieve phosphorus limitation, sometimes to an extent that ecosystems become nitrogen-limited (Grogan and Chapin, 2000). In contrast, ectomycorrhizae enhance both phosphorus and nitrogen uptake. Analogously, symbiotic association with nitrogen-fixing bacteria reduces nitrogen limitation for the host plant and indirectly for other plants in the ecosystem. Associations with plant growth-promoting rhizobacteria often stimulate growth under low nutrient conditions (Belimov et al., 2002) through diverse mechanisms including: enhancing nutrient availability (e.g., by releasing exoenzymes or by solubilizing phosphorus), producing compounds that stimulate root growth, or suppressing soil pathogens (Lugtenberg and Kamilova, 2009). However, there are limits to the extent to which plant–microbial interactions can overcome limiting nutrients. Although nitrogen fixation can bring nitrogen from outside ecosystem boundaries, there is no biotic process that can bring new phosphorus into a system. Where rocks are highly weathered in old soils exposed to high rainfall (e.g., tropical soils), phosphorus is likely to represent the ultimate limitation, although both nitrogen and phosphorus may be limiting in the short term (Vitousek et al., 2010).

Although plants have several mechanisms to improve the balance of uptake of multiple nutrients, acquisition of nutrients is rarely in balance at any point in time. Many nutrients are most available in short pulses, or 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, 2003). 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 immobile in the phloem (Nambiar, 1987).

In summary, many mechanisms by which plants adjust to unbalanced supplies of CO_2, water, nutrients, and light enable plants to maximize NPP in situations where the ratio of supply of essential nutrients is far from balanced. One consequence of these adjustments is that plant growth often responds to addition of more than one nutrient (multiple nutrient limitations) over an annual cycle (Elser et al., 2007; Rastetter and Shaver, 1992; Vitousek et al., 2010).

10.6.11 Community-Level Adjustments

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 greatly in the amount of phosphorus they require (Larcher, 2003). Dicots contain twice as much calcium as do monocots, and forbs contain more magnesium than do grasses (Lambers et al., 2008). 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 thereby 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. The 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 tenfold 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 high fine-root biomass in 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). At a more subtle level, species coexistence in arid grasslands depends on species differences in rooting depth and the water sources that they tap (Fargione and Tilman, 2005; Nippert and Knapp, 2007a,b).

Phenological specialization can 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 more active in the warmer, drier part of the growing season than 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 after winter versus summer rains, and in California grasslands, a mixture of early season annuals and late season perennials enhances productivity (Eviner and Chapin, 2001). In all these cases, presence of multiple species differing in phenology probably enhances NPP and nitrogen cycling. In mixed-cropping agricultural systems, 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). The invasion of *Andropogon* in Hawaii has led to boggy conditions because its phenology of maximum evapotranspiration does not coincide with the rainy season (Mueller-Dombois, 1973). 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. Phenology is likely to become increasingly important as multiple global changes impact the seasonality of the multiple resources and environmental conditions that impact NPP (Nord and Lynch, 2009). Plant communities containing mixtures of species that differ in the type, location, and timing of resource uptake often result in higher productivity than could be achieved by any of the component species in monoculture (Hector et al., 2002).

10.6.12 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, that is, those factors that directly regulate ecosystem processes.

10.6.12.1 Species 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 an active nitrogen fixer into a community that lacks such species augments nitrogen availability and cycling. The introduction of the exotic nitrogen-fixing tree, *Morella faya* (formerly *Myrica faya*) in Hawaii, for example, increased nitrogen inputs, litter nitrogen concentration, and nitrogen availability, and the composition of both the plant and soil faunal communities (Vitousek, 2004; Vitousek et al., 1987). A nitrogen-fixing invader is most likely to be successful in ecosystems that are nitrogen-limited, have no symbiotic nitrogen fixers, and have adequate phosphorus, micronutrients, and light (Vitousek and Howarth, 1991).

10.6.12.1.1 Decomposition and nitrogen mineralization

Species differences in tissue quality that govern photosynthesis and nutrient use (see earlier sections) strongly influence litter decomposition rates, primarily as a result of differences in carbon quality, that is, concentrations of lignin, tannins, waxes, and other recalcitrant or toxic compounds. This slow decomposition of litter from species characteristic of nutrient-poor sites (e.g., evergreens) reinforces the low nutrient availability of these sites (Hobbie, 1992; Melillo et al., 1982; Wilson and Agnew, 1992). Species adapted to high-resource sites (e.g., herbs and deciduous species), in contrast, produce rapidly decomposing litter due to its lower concentrations of recalcitrant compounds, enhancing rates of nutrient turnover in nutrient-rich sites (Cornelissen, 1996; De Deyn et al., 2008; Perez-Harguindeguy et al., 2000). In contrast to the strong effects of carbon quality, direct effects of nutrient concentrations in litter or in the soil are seldom seen (Fog, 1988). For example, placing the same litter in soils of different nitrogen availability does not consistently alter decomposition and litters of similar carbon chemistry but different nitrogen concentrations do not differ consistently in decomposition rate (Haynes, 1986; Hobbie and Vitousek, 2000; Knorr et al., 2005; Prescott, 1995; Prescott et al., 1999). To the extent that nutrients influence decomposition, nitrogen is likely to stimulate decomposition of low-lignin litter and inhibit decomposition of high-lignin litter, with no significant overall effect of nitrogen on decomposition (Allison, 2006; Fog, 1988; Janssens et al., 2010).

Litter properties that promote NPP and decomposition also facilitate net nitrogen mineralization, through both carbon quality of substrates and litter nitrogen concentration (Paul and Clark, 1996). There appears to be a universal relationship between litter C:N ratio and nitrogen mineralization or immobilization that depends on substrate quality but is independent of climate (Manzoni et al., 2008; Parton et al., 2007). 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 nitrogen mineralization 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. Experimental planting of species on a common soil shows that species differences in litter quality can alter soil fertility quite quickly. Early-successional prairie grasses, whose litter has a low C:N ratio, for example, enhance net nitrogen mineralization rate of soil within three years, compared to the same soil planted with late-successional species whose litter has a high C:N ratio (Wedin and Tilman, 1990).

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 (Bardgett, 2005; Flanagan and Van Cleve, 1983; Schimel et al., 1992). More than 70% of the soil microbial biomass and grazing fauna occur in the rhizosphere (Ingham et al., 1985). Plant species differ in their effects on the labile carbon pool (Vinton and Burke, 1995) and rhizosphere decomposition (Cheng et al., 2003). 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 tenfold 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; Salih and Bottner, 1988).

10.6.12.1.2 *Water dynamics*

Plant species affect water availability (and therefore NPP) not only through vegetational drawdown of soil moisture to replenish transpirational water losses but also through differential species effects on water availability and distribution (Gordon and Rice, 1993; Gordon et al., 1989; van Vuuren et al., 1992). Some deep-rooted species take up water from deep soil layers and release it passively into surface soils at night, when transpiration ceases. This hydraulic lift occurs in most arid ecosystems and in many moist forests. Sugar maple trees, for example, acquire all their moisture from deep roots during dry periods, but 3–60% of the water used by shallow-rooted herbs in these forests comes from water that has been hydraulically lifted by the maple trees (Dawson, 1993). In the Great Basin deserts of western North America, 20–50% of the water used by shallow-rooted grasses comes from water that is hydraulically lifted by deep-rooted sagebrush shrubs. The water provided by hydraulic lift stimulates decomposition and mineralization in dry shallow soils, augmenting the supplies of both water and nutrients to shallow-rooted species.

Aboveground plant structure may also play a critical role in supplying water to the entire ecosystem in many coastal and montane ecosystems (Weathers, 1999). The coastal redwood trees of California, for example, provide 34% of the annual water input to the ecosystem from fog-derived water during summer, when precipitation is low, but fog occurs frequently (Ewing et al., 2009). This fog water can account for up to 66% of the water use by understory plants and between 13 and 45% of water use by redwood trees, thus dramatically increasing the production of this water-limited system (Dawson, 1998). Similarly, in areas that are climatically marginal for Australian rainforests, the capture of fog and mist by trees can augment rainfall by 40% (Hutley et al., 1997), just as in New Zealand high-elevation tussock grasslands (Mark and Dickinson, 2008).

10.6.12.2 Species Effects on Climate

Species effects on physical microclimate influence ecosystem processes most strongly in extreme environments (Callaway, 1995; Hobbie, 1995; Wilson and Agnew, 1992). Boreal mosses, for example, form thick mats that insulate the soil from warm summer air temperatures (Heijmans et al., 2004). The resulting low soil temperature retards decomposition, contributing to the slow rates of nutrient cycling that characterize these ecosystems (Turetsky et al., 2010; Van Cleve et al., 1991). The sequestration of nitrogen and phosphorus in undecomposed peat reduces growth of vascular plants. In hot environments, the shading of soil by plants is an important factor governing soil microclimate. Establishment of many desert cacti, for example, often occurs in the shade of 'nurse plants' (Nobel, 1984; Turner et al., 1966).

The height, rooting depth, and density of the dominant species in an ecosystem govern surface properties that influence the efficiency of water and energy exchange between ecosystems and the atmosphere and therefore the availability of soil moisture in the transpiring stand and in downwind ecosystems (Chapin et al., 2011). Rough conifer canopies, for example, generate mechanical turbulence, allowing eddies of air from the free atmosphere to penetrate deep within the plant canopy and efficiently carry water vapor from the ecosystem to the atmosphere, whereas the smooth canopies of grasslands or crops transpire less water.

Species differences in water and energy exchange are strong enough to be important to the climate system (Foley et al., 2003). In the Middle East, for example, overgrazing reduced the cover of plant biomass. Model simulations suggest that the resulting increase in albedo (shortwave reflectance) reduced the total energy absorbed, the amount of sensible heat released to the atmosphere, and consequently, the amount of convective uplift of the overlying air. Less moisture was therefore advected (carried inland) from the Mediterranean Sea, resulting in less precipitation and reinforcing the vegetation changes (Charney et al., 1977). These vegetation-induced climate feedbacks could have contributed to the desertification of the Fertile Crescent.

10.6.12.3 Species Effects on Disturbance

Plants also alter the disturbance regime through effects on flammability (D'Antonio and Vitousek, 1992; Grigulis et al., 2005; Johnson, 1992; Mack et al., 2001), wind resistance, soil stability (D'Antonio and Vitousek, 1992), and other properties (Peters et al., 2011). 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. In disturbances that enhance nutrient availability, 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, then disperse to new disturbed sites. As succession proceeds, there is a gradual shift in dominance to species that have lower resource requirements, grow more slowly, and support lower NPP. 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 (Chapin et al., 1994).

10.6.13 Species Interactions and Ecosystem Processes

Most ecosystem processes respond in complex ways to changes in the abundance of species, because *interactions* among species generally govern the extent to which species traits are expressed at the ecosystem level. Species interactions, including mutualism, trophic interactions (predation, parasitism, and herbivory), facilitation, and competition, may affect ecosystem processes directly by modifying pathways of energy and material flow or indirectly by modifying the abundances or traits of species with strong ecosystem effects (Callaway, 1995; Wilson and Agnew, 1992).

Many species effects on ecosystems are indirect and not easily predicted. Species that themselves have small effects on ecosystem processes can have large indirect effects if they influence the abundance of species with large direct ecosystem effects. Thus, a seed disperser or pollinator that has little direct effect on ecosystem processes may be essential for persistence of a canopy species with greater direct ecosystem impact. Mixtures of litter of multiple species decompose and mineralize nitrogen at rates that differ (often more rapid) than would be predicted from each litter type by itself (Gartner and Cardon, 2004). The nature of these litter interactions is sensitive to the environment (Jonsson and Wardle, 2008) and often reflects interactions of nutrients from one litter type and carbon chemistry of other litter types (Dijkstra et al., 2009). Animal–plant–microbe interactions modulate species effects in California grasslands (Eviner and Chapin, 2005). Here experimental plots seeded with goatgrass, which has a low litter quality (high C:N ratio), is associated with a low nitrogen mineralization rate in the absence of disturbance. However, the high root biomass of this species enhances soil cohesion, which reduces the energetic requirement for borrowing by gophers. Gophers are attracted to the goatgrass plots, and the associated disturbance enhances nitrogen mineralization above levels associated with any species in the absence of disturbance. Thus, all types of organism interactions – plants, animal, and microbe – must be considered in understanding the effects of species on NPP. Although each of these examples is unique to a particular ecosystem, the ubiquitous occurrence of species interactions with strong ecosystem effects makes these interactions a general feature of ecosystem functioning (Carpenter and Kitchell, 1993; Chapin et al., 2000). In many cases, changes in these interactions alter the traits that are expressed by species and therefore the effects of species on ecosystem processes. Consequently, simply knowing that a species is present or absent is insufficient to predict its impact on ecosystems. Theoretical frameworks for predicting the types and nature of these interactions are only beginning to emerge (Cardinale et al., 2009; Eviner and Hawkes, 2008; Parker et al., 1999; Polis, 1999).

10.6.14 Summary

NPP is a complex function of resources that are rarely available in the ratios required for plant growth. Vegetation makes many adjustments to improve the balance of resources imposed by state factors through shifts in physiological traits or changes in community composition 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 the C:N ratio. This variation in element stoichiometry enables plants to maximize carbon gain under favorable environmental conditions and to maximize the efficiency of using resources to gain carbon under less favorable conditions. In addition, plants can enhance the availability of limiting resources through their effects on interactive controls, extending 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.

Substantial decreases in NPP are occurring in many ecosystems, contributing to the global decline in ecosystem services (MEA, 2005). Causes of declining NPP vary globally and include forest decline and dieback associated with pollution in many temperate forests (Huettl, 1993; Schulze, 1989); desertification of arid lands, due to changes in climate and land use practices (Reynolds and Stafford Smith, 2002; Schlesinger et al., 1996); erosional loss of topsoil in agricultural lands, managed forests, and natural systems, contributing to a 15–30% decrease in the productivity of rain-fed agricultural land in the last 25 years (Pimentel and Kounang, 1998; Pimentel et al., 1995); widespread cutting of tropical forests; and variable effects of global changes in climate (IPCC, 2007; Knapp and Smith, 2001). Cumulatively, these changes have reduced the capacity of the terrestrial biosphere to capture and sequester carbon (Canadell et al., 2007; Le Quéré et al., 2009). In addition, within a few decades, we will likely be constrained in our ability to manage NPP in phosphorus-limited agricultural systems, as sources of P fertilizer become more scarce (Childers et al., 2011). 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. Only by understanding factors that control NPP can society devise a more sustainable pathway for inhabiting planet Earth.

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