

10B. Ecosystem and Global Processes: Ecophysiological Controls

1. Introduction

In previous chapters, we emphasized the integration among processes from molecular to whole-plant levels and considered the physiological consequences of interactions between plants and other organisms. In this chapter, we move up in scale to consider relationships between **plant ecophysiological processes** and those occurring at **ecosystem to global scales**. Plant species differ substantially in their responses to environment and to other organisms. It is not surprising that these physiological differences among plants contribute strongly to functional differences among ecosystems.

2. Ecosystem Biomass and Production

2.1 Scaling from Plants to Ecosystems

The supply rates of light, water, and nutrients that govern ecosystem processes are functions of ground area and soil volume. Therefore, a critical initial step in relating the processes in individual plants to those in ecosystems is to determine how **plant size and density** relate to **stand biomass**. In sparse stands of plants, there is no necessary relationship between size and density, so plants increase in mass without changes in density (Fig. 1). As plants begin to compete, however,

mortality reduces plant density in a predictable fashion. Mid- and late-successional communities in approximate equilibrium with their environment, where plant density is determined more by mortality than recruitment, show an inverse relationship between $\ln(\text{biomass})$ and $\ln(\text{density})$, with a slope of about $-3/2$. This **self-thinning line** was initially derived empirically for pure stands under cultivated and natural conditions (Yoda et al. 1963). It has subsequently been observed in a wide array of studies, including mixed communities, both experimental and in the field, in ecosystems ranging from meadows to forests (Weller 1987). The slope and intercept of the self-thinning line vary among species and experimental conditions (Weller 1987, Vandermeer and Goldberg 2003), but the relationship provides an empirical basis to extrapolate from individuals to stands of vegetation. Given that

$$\ln(b) = -3/2 \ln(d) \quad (1)$$

it follows that

$$b = (d)^{-3/2} \text{ or } d = (b)^{-2/3} \quad (2)$$

$$B = b \cdot d = d^{-1/2} = b^{1/3} \quad (3)$$

where b is individual biomass (g plant^{-1}), d is density (plants m^{-2}), and B is stand biomass (g m^{-2}) for a single species growing in competition under specific conditions. These relationships indicate that for a given plant species and environment, increases in stand biomass are typically associated with increased plant size and reduced density. Biomass

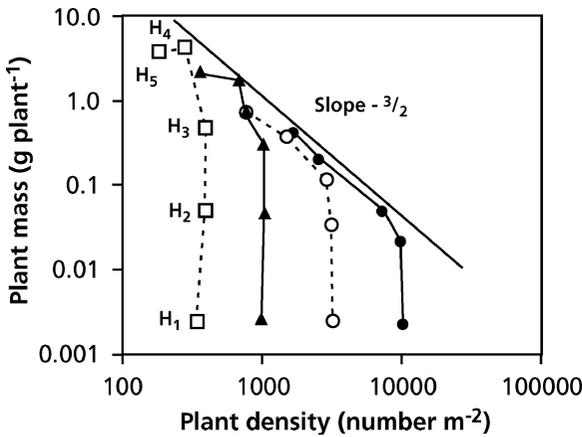


FIGURE 1. Self-thinning in four populations of *Lolium perenne* (perennial ryegrass) planted in glasshouse beds at four densities. H₁–H₅ are replicates harvested at five successive intervals. Following germination, plant biomass increases without change in density due to increased size of individual plants. As plants begin to compete, smaller individuals die, causing a decrease in density and a slower rate of increase in average plant biomass. From this point onward, the biomass–density relationship follows a self-thinning line in which $\ln(\text{biomass})$ and $\ln(\text{density})$ have a slope of $-3/2$ (modified after Kays & Harper 1974). Copyright Blackwell Science Ltd.

per individual can, in turn, be used as a basis for scaling metabolism to the ecosystem scale (Niklas & Enquist 2001).

2.2 Physiological Basis of Productivity

Net primary production (NPP) is the net biomass gain by vegetation per unit time. The main plant traits that govern NPP ($\text{g m}^{-2} \text{ yr}^{-1}$) are **biomass** (g m^{-2}) and **RGR** ($\text{g g}^{-1} \text{ yr}^{-1}$):

$$\text{NPP} = \text{Biomass} \cdot \text{RGR} \quad (4)$$

Most of the woody biomass of trees and shrubs consists of dead cells, so scaling from individuals to stands in woody vegetation (or in vegetation comparisons that include woody species) generally uses leaf biomass rather than total biomass (Niklas & Enquist 2001). Woody biomass is important

primarily as a way for plants to raise their leaves above those of neighbors.

At the **global scale**, **climate** and associated patterns of disturbance (e.g., fire) are the major determinant of NPP (Fig. 2; Schimper 1898) because of constraints on both the growth of individual plants and the types of species that can compete effectively. Highest productivity occurs in rainforests, where warm moist conditions favor plant growth and development of a large plant size; lowest values are in desert and tundra, where low precipitation or temperature, respectively, constrains growth (Table 1). In the tropics, where temperature is not a constraint, rainforests have greater productivity than dry deciduous forests, which are more productive than savannas, i.e., productivity declines with reduced water availability and/or increases in disturbance by fire. Similarly, where moisture is less limiting to growth, productivity is governed by

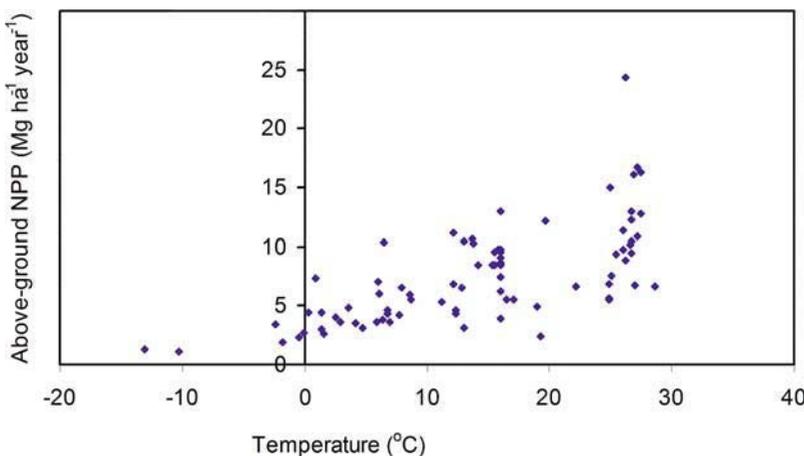


FIGURE 2. The relationships between net primary production and mean annual precipitation (Schoor 2003). Copyright Ecological Society of America.

TABLE 1. Primary production and biomass estimates for the world.

Ecosystem type	Area (10 ⁶ km ²)	Mean biomass (kg C m ⁻²)	Total biomass (10 ⁹ ton C)	Mean NPP (g C m ⁻² yr ⁻¹)	Total NPP (Gt C yr ⁻¹) ^a	RGR (yr ⁻¹)
Tropical rainforest	17.0	20	340	900	15.3	0.045
Tropical seasonal forest	7.5	16	120	675	5.1	0.042
Temperate evergreen forest	5.0	16	80	585	2.9	0.037
Temperate deciduous forest	7.0	13.5	95	540	3.8	0.040
Boreal forest	12.0	9.0	108	360	4.3	0.040
Woodland and shrubland	8.0	2.7	22	270	2.2	0.100
Savanna	15.0	1.8	27	315	4.7	0.175
Temperate grassland	9.0	0.7	6.3	225	2.0	0.321
Tundra and alpine meadow	8.0	0.3	2.4	65	0.5	0.217
Desert scrub	18.0	0.3	5.4	32	0.6	0.107
Rock, ice, and sand	24.0	0.01	0.2	1.5	0.04	–
Cultivated land	14.0	0.5	7.0	290	4.1	0.580
Swamp and marsh	2.0	6.8	13.6	1125	2.2	0.165
Lake and stream	2.5	0.01	0.02	225	0.6	22.5
Total continental	149	5.5	827	324	48.3	0.058
Total marine	361	0.005	1.8	69	24.9	14.1
Total global	510	1.63	829	144	73.2	0.088

Source: Schlesinger (1991).

Note: ^aGigatons (Gt) are 10¹⁵ g.

temperature, decreasing from tropical to temperate to boreal forests and finally to tundra.

At local to regional scales, climate continues to be important, with strong differences in productivity associated with altitudinal gradients in temperature and precipitation and with temperature differences between north- and south-facing slopes. At regional scales, however, differences in soil moisture and nutrients due to topographic variation in drainage and erosional transport of soils and due to differences in parent material (the rocks that give rise to soils) exert increasingly strong controls over productivity. For example, marshes are among the most productive habitats in most climate zones, due to high moisture and nutrient availability. Low-moisture and low-nutrient environments are typically dominated by slowly growing species with low specific leaf area, high leaf mass density, low rates of photosynthesis per unit leaf mass, and low leaf area ratios (Sect. 3 of Chapter 7 on growth and allocation). These plant traits, sometimes combined with low plant density, result in low biomass and productivity.

At the local scale, there can still be important differences in biomass and productivity, due to differences in species traits, even with the same climate

and parent material. Species introductions can result in strikingly different species dominating adjacent sites. For example, in California, *Eucalyptus globulus* (Tasmanian bluegum) forests have been planted on sites that would otherwise be grasslands. The *Eucalyptus globulus* forest has a biomass and productivity much greater than that of the grassland, despite the same climate and parent material. *Eucalyptus globulus* has deeper roots that tap water unavailable to the grasses, thus supporting the larger biomass and productivity (Robles & Chapin 1995). Once the grassland or forest is established, it is difficult for species of contrasting life forms to colonize. Consequently, there can be **alternative stable community types** with strikingly different biomass and productivity in the same environment. Greater water use by the trees compared with grasslands may have significant consequences for the availability of water elsewhere in the landscape. In deserts, deep-rooted **phreatophytes** can tap the water table and support a larger biomass and productivity than do shallow-rooted species. Thus, although climate and resource supply govern large-scale patterns of productivity (Schimper 1898), the actual productivity on a site depends strongly on historical factors that govern the

disturbance regime and species present at a site (Sect. 3 of Chapter 1 on assumptions and approaches).

2.3 Disturbance and Succession

Stand age modifies environmental controls over biomass and productivity. After **disturbance**, the most common initial colonizers are herbaceous weedy species that have high reproductive allocation, effective dispersal and are commonly well represented in the buried seed pool (Sect. 3.1 of Chapter 8 on life cycles). There is initially an exponential increase in plant biomass, due to the exponential nature of plant growth (Sect. 2.1 of Chapter 7 on growth and allocation). Relative growth rate (RGR) declines as plants get larger and begin to compete with one another. In addition, as succession proceeds, there is often a replacement of rapidly growing herbaceous species by woody species that grow more slowly, which are taller and shade out the initial colonizers. This causes a further decline in RGR (Table 2), despite the increase in biomass and productivity through time. In some ecosystems, productivity declines in late succession due to declines in soil nutrient availability and, in some forests, to declines in leaf area and photosynthetic capacity associated with reduced hydraulic conductance of old trees (Sect. 5.2.2 of Chapter 2B on plant respiration, Sect. 5.1 of Chapter 3 on plant water relations). Thus, changes in productivity through succession are governed initially by rates of colonization and RGR, followed by a gradual transition to a woody community that has lower RGR, but whose larger plant size results in further increases in productivity. Finally, over centuries to millennia, soils decline in P availability, causing further decline in the

productivity that can be supported (Sect. 2.1.1 of Chapter 6 on mineral nutrition; Wardle et al. 2004).

Disturbance regime determines the relative proportion of early and late successional stands in a region. For example, **fire** is a natural agent of disturbance that is particularly common at intermediate moisture regimes. In deserts, there is often insufficient fuel to carry a fire, although grass invasions in moist deserts can increase fire probability. By contrast, in temperate and tropical ecosystems with high precipitation or in arctic ecosystems with low evapotranspiration, naturally occurring vegetation is too wet to carry a fire in most years. In grasslands, fire occurs so frequently that woody plants rarely establish, so the region is dominated by herbaceous vegetation with high RGR and modest productivity. These vegetation characteristics are favorable to mammalian grazers, which act as an additional disturbance to prevent colonization by woody plants. Most grasslands have sufficient water and nutrients to support growth of woody plants. It is primarily the disturbance regime that maintains the high-RGR, non-woody nature of grasslands.

Plant traits strongly influence the disturbance regime of ecosystems. In grasslands, grasses produce an abundant fine-structured fuel that burns readily when dry because of the high specific leaf area (SLA), high leaf production rate, and low leaf longevity. Abundant below-ground reserve storage and meristem pools allow grasses to recover after grazing or fire. Thus, there is a common suite of **adaptations** that enable plants to tolerate fire and/or grazing in grasslands. Introduction of grasses into forests, shrublands, or deserts can increase fire frequency and cause a replacement of forest by savanna (D'Antonio & Vitousek 1992). Once the grasses create this disturbance regime with high

TABLE 2. Above-ground biomass, production, and nitrogen flux in major temperate ecosystem types, maximum height, and relative growth rate of species typical of these ecosystem types^a.

Parameter	Grassland	Shrubland	Deciduous forest	Evergreen forest
Above-ground biomass ^a (kg m ⁻²)	0.3 ± 0.02	3.7 ± 0.05	15 ± 2	31 ± 8
Above-ground NPP ^a (kg m ⁻² yr ⁻¹)	0.3 ± 0.02	0.4 ± 0.07	1.0 ± 0.08	0.8 ± 0.08
N flux ^a (g m ⁻² yr ⁻¹)	2.6 ± 0.2	3.9 ± 1.6	7.5 ± 0.5	4.7 ± 0.5
Canopy height ^b (m)	1	4	22	22
Field RGR (yr ⁻¹) ^c	1.0	0.1	0.07	0.03
Laboratory RGR ^b (wk ⁻¹)	1.3	0.8	0.7	0.4

Source: Chapin (1993).

^aNote: Data are means ± SE.

^aBokhari & Singh (1975), Cole & Rapp (1981), Gray & Schlesinger (1981), and Sala et al. (1988).

^bGrime & Hunt (1975), Tilman (1988).

^cAbove-ground production/above-ground biomass.

fire frequency, tree and shrub seedlings can no longer establish. Boreal conifers also create a fire regime that favors their own persistence. They are more flammable than deciduous trees because of their large leaf and twig surface area, low moisture content, and high resin content, an anti-herbivore/pathogen defense (Sect. 3.2 of Chapter 9B on ecological biochemistry; Van Cleve et al. 1991). Thus, there is an increase in fire probability when succession is accompanied by changes in plant functional types. When species shifts do not occur, there is little or no change in flammability with increasing stand age (Schoennagel et al. 2004). The invasion of the North American boreal forest by black spruce (*Picea mariana*) in the mid-Holocene caused an increase in fire frequency (Lynch et al. 2002), clearly showing the role of plant traits in determining community composition through their effects on fire regime.

2.4 Photosynthesis and Absorbed Radiation

One scaling approach is to extrapolate directly from leaf carbon exchange to the ecosystem level based on the relationship between photosynthesis and absorbed radiation. This approach was pioneered in agriculture (Monteith 1977) and has been extended to estimate patterns of carbon exchange in natural ecosystems (Field 1991). The fraction of incident photosynthetically active radiation that is absorbed by plants (**APAR**) is either converted to new biomass (NPP) or is respired. APAR depends on total leaf area, its vertical distribution and its photosynthetic capacity. Both light and leaf N decline in a predictable fashion through the canopy, with N preferentially allocated to the tops of canopies to maximize light utilization (Sect. 3.1 of Chapter 2A on photosynthesis, Box 5.1). Thus, as an initial simplification, the plant canopy can be treated as a **big leaf**, whose photosynthetic capacity depends on total canopy N (Sect. 2 of Chapter 5 on scaling-up; Farquhar 1989, Field 1991). In unstressed crops, dry matter accumulation is roughly proportional to integrated radiation interception over the growing season with a conversion efficiency of about 1.4 g MJ⁻¹ (Monteith 1977). Natural ecosystems vary 10–100-fold in NPP (Table 1). Most of this variation is due to variation in APAR rather than in conversion efficiency, which varies about two-fold among studies. There are no striking ecological patterns in reported values of conversion efficiency, with much of the variation among studies likely due to differences in methodology, rather than inherent differences among ecosystems (Field

1991). Most of the variation in APAR is due to variation in **leaf area index** (LAI) (>50-fold variation among ecosystems), although leaf N concentration can vary nine-fold among ecosystems (Sect. 6.3 of Chapter 2A on photosynthesis; Reich & Oleksyn 2004). Thus, carbon gain and NPP are reduced in unfavorable environments due to the small amount of leaf biomass that can be supported and leaf N concentration that can be attained (Sect. 5 of Chapter 7 on growth and allocation).

The relatively consistent conversion of APAR into plant production among ecosystems provides a tool for estimating global patterns of NPP. APAR can be estimated from satellite-borne sensors, using the **normalized difference vegetation index** (NDVI):

$$\text{NDVI} = (\text{NIR} - \text{VIS}) / (\text{NIR} + \text{VIS}) \quad (5)$$

where NIR (W m⁻²) is reflectance in the near infrared, and VIS (W m⁻²) is reflectance in the visible. NDVI uses the unique absorption spectrum of **chlorophyll** which differs from that of clouds, water, and bare soil to estimate absorbed radiation. Stands with high rates of photosynthesis have a high NDVI because they have low values of reflected VIS and high values of reflected NIR. NDVI is an excellent predictor of APAR and daily net photosynthesis in short-term plot-level studies (Fig. 3). It also provides good estimates of NPP using satellites (Fig. 4). The consistency of this relationship supports the argument that there may be a relatively constant efficiency of converting absorbed radiation into plant biomass. One reason for the modest variation in conversion efficiency between APAR and NPP may be the similarity of growth respiration across plant tissues and species (Sect. 5.2 of Chapter 2B on plant respiration). From a pragmatic perspective, the strong relationship between NDVI and NPP is important because it allows us to estimate NPP directly from satellite images (Fig. 4). In this way, we can estimate **regional and global patterns of NPP** in ways that avoid the errors and biases that are associated with the extrapolation of harvest data to the global scale.

Any factor that alters the leaf area of an ecosystem or the availability of water or N changes the capacity of that ecosystem for carbon gain by moving vegetation along the generalized APAR–NPP relationship. **Climate** has obvious effects on LAI and leaf N (Reich & Oleksyn 2004). The physiological differences among plant species that we have discussed throughout the book also have pronounced effects on the leaf area and leaf N that can be supported in any environment, as mediated by

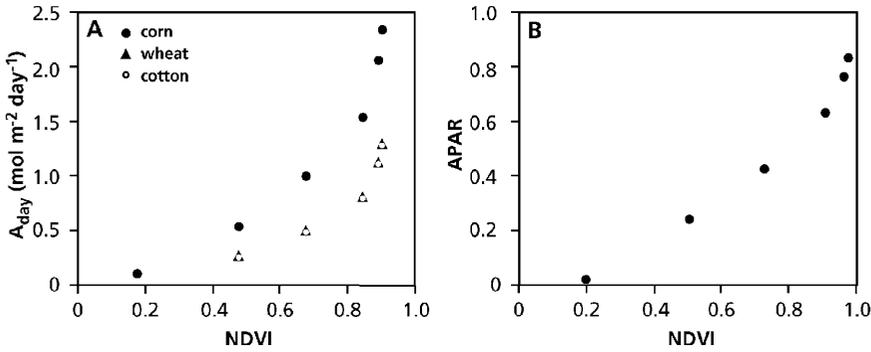


FIGURE 3. Relationship of normalized difference vegetation index (NDVI) to daily net rate of CO₂ assimilation (A_{day}) and to the fraction of absorbed photosynthetically active radiation (APAR). These

relationships were simulated based on data collected from wheat (*Triticum aestivum*), corn (*Zea mays*), and cotton (*Gossypium*) (After Field 1991, as redrawn from Choudhury 1987).

competitive interactions, herbivores, and pathogens. In general, the sorting of species among habitats by competition over the long term probably maximizes APAR and NPP, whereas pathogens and herbivores tend to reduce APAR and NPP. Disturbance regime also influences regional APAR and NPP, as does human land conversion of natural ecosystems to pastures and agriculture.

Satellite-based measurements of NDVI provide evidence for several large-scale changes in NPP. In the tropics and in the southern margin of the boreal forest, there have been decreases in NDVI associated with forest clearing and conversion to agriculture. The West African Sahel and Northern Mexico also show reductions in NDVI associated with land degradation due to overgrazing (Milich & Weiss 2000, Archer et al. 2001). At high latitudes, however, NDVI increased until about 1990, after which it continued increasing in tundra but

declined in boreal forest (Goetz et al. 2005). These high-latitude changes in NDVI are particularly intriguing because they are remote from areas of large-scale anthropogenic land-use change and could reflect broad biospheric responses to changes in climate. High-latitude warming may have increased NPP through increased length of growing season or direct temperature effects on growth (Callaghan et al. 2005). The declining NDVI in boreal forest may reflect warming-induced drought stress or reductions in biomass by insect outbreaks and wild-fire (Goetz et al. 2005), which are increasing in areal extent (Kurz & Apps 1995, Kasischke & Turetsky 2006). There are also potential artifacts associated with lack of calibration of satellite sensors among years that complicate the interpretation. The striking trends in changes in NDVI nevertheless strongly suggest that global NPP can be substantially altered over broad regions of the globe.

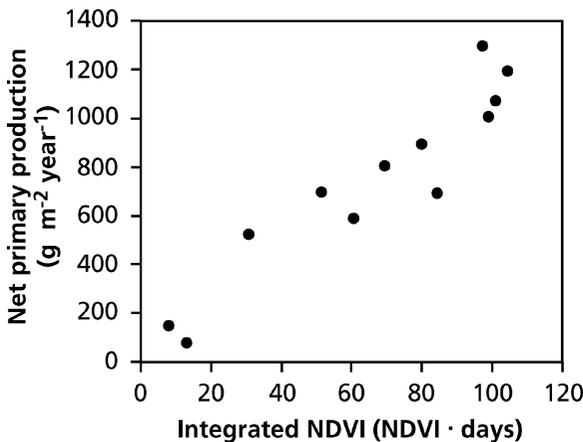


FIGURE 4. Relationship between mean net primary production (NPP) for several biomes and the seasonally integrated normalized difference vegetation index (NDVI) measured from satellites. Each point represents a different biome (after Field 1991, as redrawn from Goward et al. 1985).

2.5 Net Carbon Balance of Ecosystems

Net ecosystem production (NEP, $\text{g C m}^{-2} \text{yr}^{-1}$) of carbon by an ecosystem depends on the balance between **net primary production** (NPP, $\text{g C m}^{-2} \text{yr}^{-1}$) and **heterotrophic respiration** (R_h , $\text{g C m}^{-2} \text{yr}^{-1}$) or between **gross photosynthesis** (P_g , $\text{g C m}^{-2} \text{yr}^{-1}$) and **total ecosystem respiration** (R_e , $\text{g C m}^{-2} \text{yr}^{-1}$), which is the sum of R_h and plant respiration (R_p , $\text{g C m}^{-2} \text{yr}^{-1}$).

$$\text{NEP} = \text{NPP} = R_h = P_g - R_e \quad (6)$$

NEP is important because it is usually the major determinant of **Net Ecosystem Carbon Balance (NECB)**, the increment in carbon stored by an ecosystem. Under some circumstances, however, additional carbon fluxes (e.g., fire, harvest, leaching, lateral transfers of organic or inorganic C, and volatile emission of carbon in forms other than CO_2) are large enough to influence NECB, especially over long time periods (Chapin et al. 2006). We have discussed the plant physiological and environmental constraints on NPP (Sects. 2.2 and 2.4). **Decomposers** account for most of the heterotrophic respiration. Their respiration depends on by moisture and temperature and on the quantity, quality, and location (above or below ground) of organic matter produced by plants (Sect. 3 of Chapter 10A on decomposition). In general, conditions that favor high NPP also favor high R_h . For example, both NPP and decomposition are higher in the tropics than in the arctic and higher in rainforests than in deserts, due to similar environmental sensitivities of NPP and R_h . Similarly, species that are highly productive produce more litter or higher quality litter than do species of low potential productivity. Thus, habitats dominated by productive species are characterized by high decomposition rates (Sect. 3.2 of Chapter 10A on decomposition). There is also a necessary functional linkage between NPP and R_h . NPP provides the organic material that fuels R_h , and R_h releases the minerals that support NPP (Harte & Kinzig 1993). For all these reasons, NPP and R_h tend to be closely matched in ecosystems at steady state (Odum 1969, Wofsy et al. 1993). Therefore, at steady state, by definition, NEP and changes in carbon storage are small and show no correlation with NPP or R_h . In fact **peat bogs**, which are among the least productive ecosystems, are ecosystems with the greatest long-term carbon storage.

NEP is a small difference between two very large fluxes, **gross photosynthesis** (P_g) and **ecosystem respiration** (R_e) (Fig. 5). Although NEP, on average, is close to zero in ecosystems at steady state, it

shows large-enough seasonal variation to cause seasonal fluctuations in atmospheric CO_2 at the global scale (Fig. 2A.55 in Chapter 2A on photosynthesis) with decreases in atmospheric CO_2 concentrations in the northern hemisphere during the summer, when terrestrial photosynthesis is greatest, and increases in winter, when terrestrial photosynthesis declines below the rate of ecosystem respiration. Over long timescale, factors other than NEP also influence NECB. The most clear-cut causes of ecosystem variation in NECB are successional cycles of disturbance and recovery. Most disturbances initially cause a negative NECB. Fire releases carbon directly by combustion (not part of NEP) and indirectly by producing conditions that are favorable for R_h (part of NEP) (Kasischke et al. 1995). For example, removal of vegetation typically reduces transpiration, causing an increase in soil moisture, and increases soil temperature due to greater radiation absorption (lower albedo and greater penetration of solar radiation to the soil surface) (Table 3). The warmer, moister soils enhance R_h , and the reduction in plant biomass reduces NPP, resulting in negative NEP for years after a forest wildfire (Kasischke et al. 1995). Eventually, however, photosynthesis exceeds R_h , leading to carbon accumulation in the ecosystem (a positive NECB). Agricultural tillage breaks up soil aggregates and increases access of soil microbes to soil organic matter, resulting in a similar increase in R_h and negative NEP following conversion of natural ecosystems to agriculture. Prairie soils often lose half their soil carbon within a few decades after conversion to agriculture (Davidson & Ackerman 1993).

NEP can also vary substantially among years, due to different environmental responses of photosynthesis and respiration. For example, northern ecosystems are a net carbon source in warm years and a carbon sink in cool years (Oechel et al. 1993, Zimov et al. 1996) because heterotrophic respiration responds to temperature more strongly than does photosynthesis in cold climates.

2.6 The Global Carbon Cycle

Recent large-scale changes in the global environment (e.g., regional warming, N deposition, and elevated atmospheric CO_2 concentrations) can alter NEP, if they have differential effects on photosynthesis and respiration. For example, photosynthesis responds more strongly to atmospheric CO_2 concentration than does heterotrophic respiration, so the terrestrial biosphere might increase net CO_2 uptake in response to the increases in atmospheric $[\text{CO}_2]$

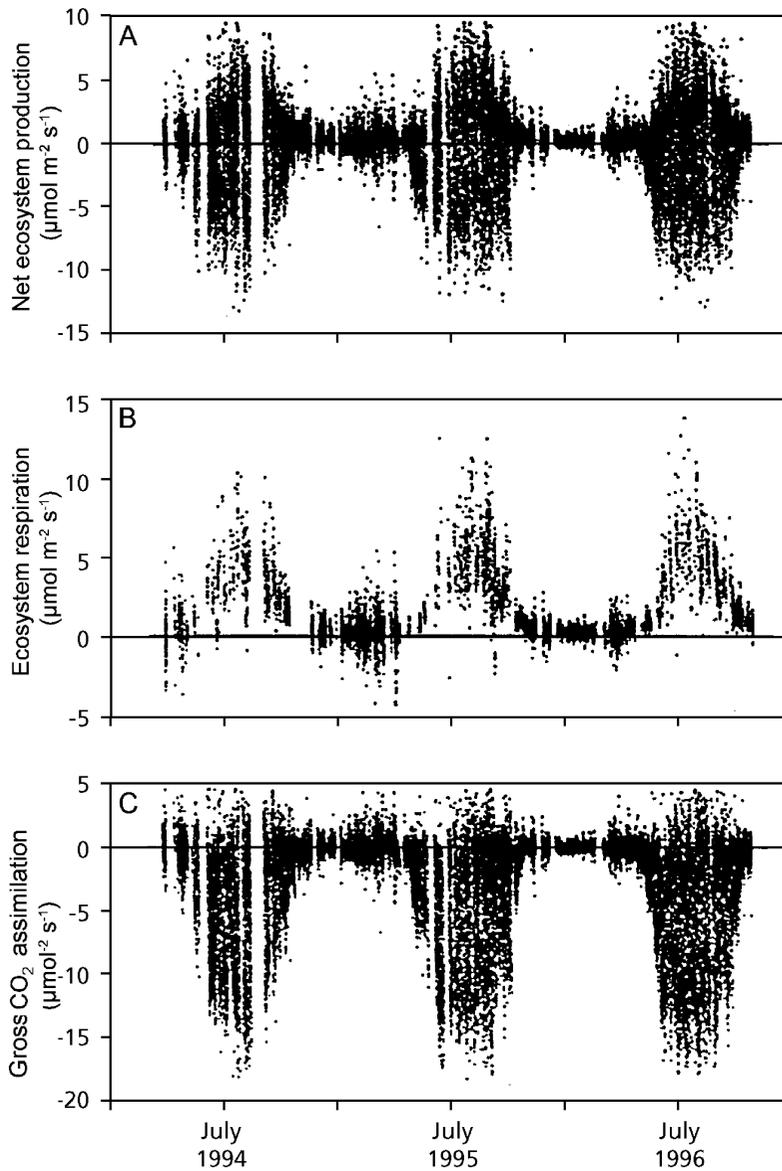


FIGURE 5. Annual course of (A) net ecosystem production (NEP), (B) ecosystem respiration (Resp), and (C) gross CO₂ assimilation (P_g) in an old-growth black spruce (*Picea marina*) forest in northern Canada. Positive values are fluxes from the ecosystem to the atmosphere. Note that fluxes vary considerably from day to day, with largest fluxes of both photosynthesis and respiration in summer (after Goulden et al. 1997).

TABLE 3. Short-wave (150–4000 nm) albedos for various surface types.

Surface type	Measured albedo
Clouds: cumulus	0.85
Clouds: cirrus	0.35
Snow: ice	0.7–0.90
Sands: dry	0.40–0.50
Sands: wet	0.20–0.25
Grasslands	0.15–0.35
Forests	0.10–0.20
Ocean	0.02–0.07

Source: Graetz (1991).

caused by fossil fuel combustion and land-use change. NPP in most terrestrial ecosystems is nutrient-limited, however, strongly constraining the capacity of vegetation to respond to elevated [CO₂]. In relatively young landscapes, N is the key limiting nutrient (Sect. 2.1.1 of Chapter 6 on mineral nutrition). Therefore, the clearest evidence for increases in NPP in response to elevated [CO₂] is in these landscapes with N deposition, where there are widespread increases in tree growth (Kauppi et al. 1992). NPP is only half the story, however: NPP must change more strongly than R_n and disturbance rate, if there is to be an increase in NECB.

Only 45% of the annual anthropogenic input of CO₂ remains in the atmosphere, with the rest being removed by the oceans or the terrestrial biosphere (Sect. 12 of Chapter 2A on photosynthesis). The location of this **missing sink** of atmospheric CO₂ is difficult to identify by direct measurement because its global magnitude (5.0 Gt C yr⁻¹) (Canadell et al. 2007) is only about 5% of global NPP, much smaller than measurement errors and typical interannual variability. Isotopic fractionation in photosynthesis (Box 2A.2) has provided an important key to identifying the magnitude and location of the missing sink. Atmospheric transport models can be run in “inverse mode” (i.e., opposite to the direction of cause to effect) to estimate the global distribution of CO₂ sources and sinks that are required to match the observed geographic and seasonal patterns of concentrations of CO₂ and ¹³CO₂ in the atmosphere (Fig. 2A.55 in Chapter 2A on photosynthesis; Tans et al. 1990, Ciais et al. 1995, Denning et al. 1995). CO₂ uptake by the terrestrial biosphere can be distinguished from the CO₂ that dissolves in the ocean because of the strong **isotopic fractionation** during photosynthesis. Similarly, atmospheric stoichiometry between CO₂ and O₂ separate biological from physical causes of changing atmospheric [CO₂]. Although there are still many uncertainties, these models suggest that terrestrial ecosystems account for about 56% (2.8 Gt C yr⁻¹) of the missing sink, and that these terrestrial sinks are concentrated at mid to high northern latitudes (Canadell et al. 2007). Tropical forests also respond strongly to increased atmospheric [CO₂], but this is offset by high rates of deforestation, which release CO₂ to the atmosphere (Bala et al. 2007, Field et al. 2007).

Human activities have caused the CO₂ concentration to increase 35% since 1750 (half of this increase since 1970), after about 10000 years of relatively stable concentration. Atmospheric [CO₂] is now higher than any time in at least 650000 years (IPCC 2007). The capacity of ecosystems to sequester this anthropogenic CO₂ appears to be saturating for several reasons (Canadell et al. 2007). In part, this is a logical consequence of the A–C_c curve (Fig. 2A.6 in Chapter 2A on photosynthesis), which begins to saturate in most C₃ plants at the current CO₂ concentration (380 mol mol⁻¹) of the atmosphere. This effect is amplified by declines in the photosynthetic capacity of ecosystems due to complex interactions among changes in nutrient and water availability, land-cover change, and pollution; the oceans exhibit an even greater decline in the capacity to sequester CO₂ (Canadell et al. 2007). This sobering observation suggests that we cannot depend on the terrestrial ecosystems to “solve” the problem of rising

concentrations of atmospheric CO₂ and that society must take serious measures to reduce CO₂ emissions, to prevent dangerous rates of climate warming (Stern 2006).

3. Nutrient Cycling

3.1 Vegetation Controls over Nutrient Uptake and Loss

The controls over nutrient uptake and loss by stands of vegetation are basically the same as those described for individual plants (Sect. 2.2 of Chapter 6 on mineral nutrition) (Chapin 2003). Nutrient supply ultimately determines nutrient uptake at the stand level. However, individual plants influence their **acquisition of nutrients** directly by root biomass and the kinetics of ion uptake and indirectly by influencing nutrient supply rate. **Root biomass**, including **mycorrhizas** is the major plant parameter governing stand-level nutrient uptake because a large root biomass is the major mechanism by which plants minimize diffusional limitations of nutrient delivery to the root surface (Sect. 2.2.1 of Chapter 6 on mineral nutrition). The absolute magnitude of root biomass is probably greatest in high-resource environments, where there is a large total plant biomass (e.g., forests; Table 2). Root biomass varies less across ecosystems (Table 5 in Chapter 3), however, than does total biomass because proportional allocation to roots increases in low-resource environments (Sect. 5.4.4 of Chapter 7 on growth and allocation). I_{\max} of ion uptake is generally greatest in plants that grow rapidly (a high plant demand for nutrients) and would therefore contribute to the high nutrient uptake in high-resource environments. In low-nutrient environments, vegetation maximizes nutrient acquisition through high root biomass (an acclimation response rather than adaptation), symbiotic associations (with mycorrhizal fungi and N₂-fixing microorganisms), and by solubilizing scarcely available P or organic N (Sect. 2.2 of Chapter 6 on mineral nutrition and Sects. 2.3, 2.4, 2.5, and 3.7 of Chapter 9A on symbiotic associations). Despite adaptations and acclimations of plants to maximize nutrient acquisition on infertile soils, there is a strong correlation between NPP and nutrient uptake by vegetation, because of the widespread occurrence of nutrient limitation in most ecosystems (Chapin 2003).

Annual **nutrient return** from vegetation to soils is greatest in high-nutrient environments. Where NPP and biomass are high, there is a low mean

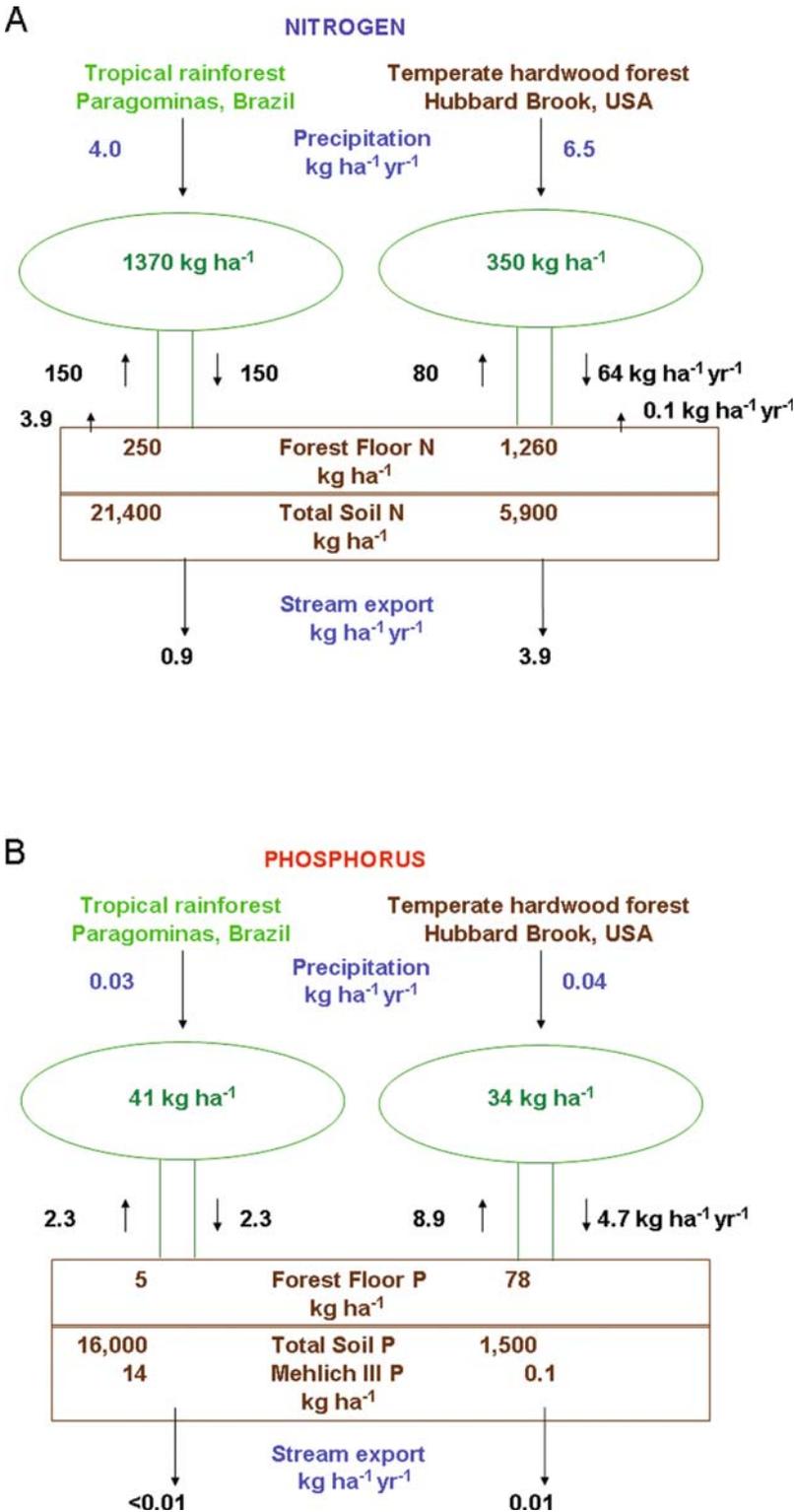


FIGURE 6. Comparison of nutrient cycles at a mature moist tropical evergreen forest at Fazenda Vitória, Paragominas, Pará, Brazil and at a 55-year-old temperate mixed deciduous forest at Hubbard Brook, New Hampshire, United States. (A) N cycle. (B) P cycles. Arrows indicate bulk precipitation inputs, plant uptake, litter and throughfall return to the soil, soil surface emissions of NO+N₂O, and stream export of total dissolved N. Soil stocks are to 8 m depth at Paragominas, whereas the soil depth averages about 0.5 m to the underlying glacial till at Hubbard Brook (after Davidson et al. 2004).

residence time of nutrients in plants (rapid leaf and perhaps root turnover) and high nutrient concentrations in litter (Sect. 4.3.2 of Chapter 6 on mineral nutrition). P is very conservatively cycled, relative to N, in systems where P is a major limiting nutrient, e.g., in Amazon rainforests and Western Australian sandplains, and N is more conservatively cycled where N is limiting, e.g., in a temperate deciduous forest in New Hampshire (Fig. 6; Davidson et al. 2004). Thus, for both plant nutrient uptake and loss, the differences observed among ecosystems are the same as would be predicted by the patterns of acclimation and adaptation of individual plants, but are more pronounced because of the larger size of plants in favorable environments.

3.2 Vegetation Controls over Mineralization

The effects of climate and resource availability on nutrient supply are similar to those described for decomposition (Sect. 2.5, Sect. 2.1.1 of Chapter 6 on mineral nutrition), with high rates of nutrient supply under favorable environmental conditions. Within these environmental constraints, however, **plant traits** strongly influence nutrient supply through their effects on root exudation, microenvironment, and litter quality. Litter quality differs among ecosystems and strongly influences mineralization rates (Sect. 3.1 of Chapter 10A on decomposition). **Root exudates** provide a labile carbon source of sugars, organic acids, and amino acids that can either enhance or reduce mineralization, depending on soil fertility (Sect. 3.3 of Chapter 10A on decomposition). Root exudates may also inhibit **nitrification** (Sect. 2 of Chapter 9B on ecological biochemistry; Lata et al. 2004). Over longer timescales, successional development of vegetation modifies soil temperature (shading), soil moisture (transpiration), and the quantity and quality of organic matter inputs (litter and root exudates) (Sect. 2.2 of Chapter 10A on decomposition).

Over long timescales (decades to centuries), patterns of **nutrient input and loss** exert additional influences over nutrient supply. There is only fragmentary understanding of these long-term controls, although we know that abundance of N₂-fixing plants strongly influences N inputs (Vitousek & Howarth 1991). For example, introduction of the N₂-fixing tree *Myrica faya* (candleberry myrtle) into the Hawaiian Islands greatly increased N inputs, N supply, and annual rates of N cycling (Vitousek 2004). Replacement of perennial grasses by annual grasses, with their shorter period of physiological

activity, may account for autumn N losses from California grasslands. Anthropogenic inputs of N from industrial fixation and planting of legume crops now exceed inputs by natural fixation at the global scale (Vitousek et al. 1997), suggesting that there may be substantial changes in the regulation of inputs and outputs of N in natural ecosystems.

4. Ecosystem Energy Exchange and the Hydrologic Cycle

4.1 Vegetation Effects on Energy Exchange

4.1.1 Albedo

Energy exchange at the ecosystem scale is influenced by the properties of individual leaves and stems (e.g., albedo and the partitioning of dissipated energy between sensible and latent heat) (Sect. 2.1 of Chapter 4A on the plant's energy balance) as well as by any contrasts between plant properties and those of the underlying surface. In addition, canopy complexity reduces albedo because any incoming radiation that is initially reflected by a leaf or stem is more likely to encounter another surface before being reflected back to space. This contributes to the lower albedo of conifers than of trees with round flat canopies. The atmosphere is nearly transparent to the short-wave radiation emitted by the sun, so **air temperature** at local to global scales is primarily determined by the amount of energy absorbed and dissipated by the Earth's surface. Therefore, the influence of vegetation on surface reflectance (**albedo**) can have substantial effects on climate. For example, snow and sand have higher albedos than vegetation, and therefore reduce absorption of radiation at the surface (Table 3). In tundra, any increase in plant height relative to snow depth or increased density of tall shrubs or trees will mask the snow and reduce the albedo (i.e., increase absorbed energy and the energy dissipated to the atmosphere), thus raising the temperature of the overlying air (McGuire et al. 2006). Model simulations suggest that when temperature warmed at the last thermal maximum, 6000 yr ago, the **treeline** moved northward, reducing the regional albedo and increasing energy absorption (Foley et al. 2003b). Approximately half of the **climatic warming** that occurred at that time is estimated to be due to the northward movement of treeline, with the remaining climate warming due to increased solar input (Fig. 7). The warmer regional climate, in turn, favors tree reproduction and establishment at

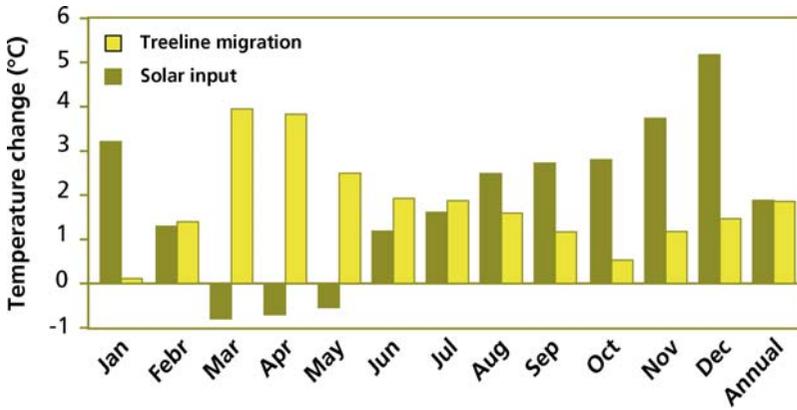


FIGURE 7. The change in arctic air temperature at the last thermal maximum caused directly by changes in solar inputs and caused by the change in albedo associated with northward movement of treeline, as simulated by a general circulation model (redrawn from Foley et al. 1994).

treeline (Payette & Filion 1985, Lloyd et al. 2003), providing a positive feedback to regional warming. Thus, changes in vegetation height, relative to snow depth, could exert a large effect on regional climate. The warming-induced advance in date of snowmelt is already contributing substantially to high-latitude warming (Chapin et al. 2005, Euskirchen et al. 2007).

Vegetation effects on albedo also influence regional climate in arid areas. For example, a 30-year drought in the Sahel at the end of the 20th century reduced plant density, exposed more light-colored soil, and thus reduced absorbed radiation. This reduced heating and convective uplift of the overlying air, resulting in less advection of moisture from the Atlantic and reduced precipitation (Foley et al. 2003a). The resulting increase in drought, compounded by degradation of the land by **overgrazing**, acts as a positive feedback to further reduce plant production and biomass, stabilizing this pattern of regional drought.

Differences in albedo among vegetated surfaces are more subtle than those between vegetation and snow or soil. Vegetation albedo depends primarily on **phenology**. Leaf appearance in deciduous ecosystems increases albedo if the soil surface is dark and reduces albedo over light-colored surfaces. Evergreen communities show minimal seasonal change in albedo. Even the small differences in albedo among plant species could be climatically important. For example, grasslands typically have higher albedo than forests because of their more rapid leaf turnover and retention of dead reflective leaves in the canopy. Similarly, the higher albedo of deciduous than of conifer forests results in less energy absorption and transfer to the atmosphere (Liu et al. 2005). For this reason, forest fires that cause a replacement of late-successional conifers by early successional herbs, shrubs, and deciduous trees act as a negative feedback to climate warming

(Randerson et al. 2006). Policies that seek to promote ecosystem feedbacks to mitigate climate change have focused almost entirely on carbon sequestration associated with expanded forest extent and have ignored the large (and often contrasting) climate feedbacks caused by changes in **energy budget** (Betts 2000, Field et al. 2007). A valuable contribution of climate-change science to the policy arena would be a more comprehensive assessment of **ecosystem feedbacks** to the climate system. For example, the carbon sequestration effect (climate cooling) might prove to be strongest in the tropics, where warm moist conditions speed the carbon cycle, and changing cloudiness ameliorate the albedo effect. In contrast, the albedo effect (climate warming) of increased forest cover is most likely strongest at high latitudes, where there is a large albedo contrast between forests and snow-covered treeless lands. These observations suggest that efforts to reduce deforestation might have most favorable climate consequences in the tropics, where they provide a simultaneous benefit of reducing biodiversity loss.

4.1.2 Surface Roughness and Energy Partitioning

The **roughness of the canopy** surface determines the degree of **coupling** between plants and the atmosphere and the extent to which stomatal conductance influences the partitioning between latent and sensible heat (Sect. 2 of Chapter 5 on scaling-up). Roughness is determined primarily by topography and vegetation structure. Tall uneven canopies have a high surface roughness that creates mechanical turbulence. The resulting eddies of air transport bulk air into the canopy and canopy air back to the free atmosphere. This increases the efficiency of

water, gas, and energy exchange, relative to short-statured canopies such as those of most grasses or annual crops. The lower roughness of short-statured vegetation creates a thicker boundary layer and reduces the influence of stomatal regulation by individual leaves on overall conductance of the canopy to water loss, especially under moist conditions.

On average, the energy absorbed by an ecosystem must be balanced by energy returned to the atmosphere as sensible or latent heat flux. The ratio of sensible to latent heat flux (**Bowen ratio**) varies 100-fold among ecosystems, from less than 0.1 in tropical oceans to 10 in deserts, and depends primarily on climate and soil moisture. Ecosystems with abundant moisture have high rates of evapotranspiration (latent heat flux) and therefore a low Bowen ratio. Strong winds and rough canopies reduce temperature build-up at the surface which drives sensible heat flux, also leading to low Bowen ratios and high evapotranspiration. The Bowen ratio is important because it determines the strength of the linkage between energy exchange and the hydrologic cycle. This linkage is strongest in moist ecosystems with low Bowen ratio, where most of the energy absorbed by the ecosystem is dissipated by water transfer to the atmosphere.

4.2 Vegetation Effects on the Hydrologic Cycle

4.2.1 Evapotranspiration and Runoff

Climate clearly has a critical direct effect on the supply of water to ecosystems as a result of precipitation inputs. In addition, climate determines the rate at which water returns to the atmosphere due to climatic effects on soil moisture availability and the vapor pressure gradient that drives evapotranspiration. However, plant size and leaf area index (LAI) also exert strong controls over **evapotranspiration**. In wet canopies, LAI determines the amount of water that can be intercepted and stored by the canopy, and plant size and canopy roughness determine the rate at which this water evaporates. Similarly, during winter, plant size and canopy roughness determine the amount of snow intercepted by the canopy and returned to the atmosphere by sublimation.

When canopies are dry, soil moisture, climate, and LAI interact in complex ways to control evapotranspiration. Under moist-soil conditions, climate determines the driving forces for evapotranspiration (the net radiation that must be dissipated and the vapor pressure deficit of the bulk air), and plant

size and canopy roughness determine the surface turbulence and boundary layer conductance that control how efficiently this water is transferred to the atmosphere. In general, the moisture content of the air (and the corresponding effect on stomatal conductance) is the most important climatic control over evapotranspiration in well-coupled rough canopies, but net radiation (and the amount of energy to be dissipated) is the most important control in smooth canopies where atmosphere–canopy exchange is less tightly coupled to atmospheric conditions. LAI has surprisingly little influence on evapotranspiration under these moist-soil conditions; it simply determines the extent to which water evaporates from leaves vs. the moist soil surface (Kelliher et al. 1995). As soil moisture and soil surface evaporation decline, however, LAI and stomatal conductance exert increasing importance over evapotranspiration.

Plant biomass indirectly influences evapotranspiration because of its correlation with the quantity of litter on the soil surface which influences the partitioning of water between surface **runoff** and **infiltration** into the soil. Surface **runoff** is negligible in forests and other communities with a well-developed litter layer but can be substantial in dry ecosystems with minimal litter accumulation (Running & Coughlan 1988).

In dry environments, stomatal conductance and rooting depth exert additional influence over evapotranspiration. Desiccation-tolerant species keep their stomata open at times of lower water availability and thus support greater evapotranspiration during dry periods than do species typical of more mesic environments (Schulze & Hall 1982). Tall plants such as trees generally transpire more water than herbs because of their more extensive root systems and greater leaf area and canopy roughness. Consequently, forest harvest reduces evapotranspiration and increases runoff (Bormann & Likens 1979), especially during seasons of rapid plant growth. In summary, plant size, which is a function of resource availability in the environment, is the major determinant of canopy water loss, although the response of stomatal conductance to plant water status becomes important under dry conditions. At the global scale, river runoff has increased during the 20th century, primarily as a result of CO₂-induced reductions in stomatal conductance (Gedney et al. 2006).

The same plant traits that influence evapotranspiration (Sect. 4.1.3) influence **soil moisture**. In northern regions, species characteristic of steppe vegetation have higher rates of evapotranspiration than do mosses and other vegetation characteristic

TABLE 4. Average evapotranspiration rate of tundra and steppe plants from weighing lysimeters under field conditions in northeast Siberia during July.

Surface type	Evapotranspiration rate (mm day ⁻¹)	
	Field capacity	Natural precipitation
Tundra plants		
Lichen	1.6	0.9
Moss	2.8	1.0
Steppe plants		
<i>Agropyron</i>	6.7	2.5
<i>Eriophorum</i>	5.3	3.0
<i>Equisetum</i>	4.0	1.6
<i>Artemisia</i>	6.1	2.3
Probability of tundra-steppe difference	0.03	0.02

Source: Zimov et al. (1995).

Note: Lysimeters were either maintained at field capacity by twice-daily watering or given access only to natural precipitation.

of tundra (Table 4). Either of these vegetation types can persist under the climate typical of tundra, with the higher transpiration rate of steppe plants maintaining the low soil moisture that favors these species and the lower transpiration rate of tundra species causing higher soil moisture that favors tundra species. Zimov et al. (1995) hypothesized that extirpation of mega-herbivores by humans at the end of the Pleistocene shifted the competitive balance from steppe species that tolerate grazing to tundra species. The resulting reduction in evapotranspiration would have increased soil moisture, contributing to the shift from dry steppe to mossy tundra that occurred at the end of the Pleistocene.

4.2.2 Feedbacks to Climate

Species differences in evapotranspiration can have climatic consequences. Simulations suggest that conversion of the Amazon basin from forest to pasture would cause a permanent warming and drying of South America because the shallower roots of grasses would reduce evapotranspiration and cause greater energy dissipation as sensible heat (Foley et al. 2003a). These drier conditions would favor persistence of grasses. In Mexico, the reduction in transpiration that resulted from overgrazing increased sensible heat flux, causing regional warming (Balling 1988). Summer air masses that move from the Arctic Ocean into arctic Canada carry only enough moisture to account for 25% of the

precipitation that occurs on land (Walsh et al. 1994). Thus, the remaining 75% of precipitation must originate from evapotranspiration over land. In other words, recycling of moisture between the land surface and the atmosphere accounts for most of the precipitation in this part of the Arctic (Chapin et al. 1997).

Environmental conditions could influence **vegetation feedbacks** to precipitation. For example, global warming caused by a doubling of atmospheric [CO₂] is predicted to increase precipitation by 8%. The reduction in stomatal conductance caused by this rise in CO₂ concentration (Sect. 10.1 of Chapter 2A on photosynthesis), however, should reduce the magnitude of the expected precipitation increase to only 5% (Henderson-Sellers et al. 1995). On the other hand, increased plant growth and stomatal conductance caused by N deposition might increase evapotranspiration and therefore precipitation. Thus, the interaction among environmental factors that influence plant growth and physiology modulate many of the terrestrial feedbacks to climate (Gedney et al. 2006).

In most ecosystems, there is a close correlation of evapotranspiration with gross photosynthesis because a high leaf area and high stomatal conductance promote both processes. In low-resource communities, however, canopies are sparse, and the soil or surface mosses contribute substantially to evapotranspiration (Chapin et al. 1997). Below an LAI of 4, evapotranspiration becomes increasingly uncoupled from photosynthesis, due to proportional increase in surface evaporation (Schulze et al. 1994).

5. Moving to a Higher Level: Scaling from Physiology to the Globe

Physiological differences among species have important predictable consequences for ecosystem and global processes. Environments with favorable climate and high resource availability support growth forms that are highly productive due to either large size or high RGR, depending on time since disturbance. By contrast, unfavorable environments support slow-growing plants, whose well-developed chemical defenses minimize rates of herbivory and decomposition. Fast-growing plants have high rates of photosynthesis and transpiration (on a mass basis), rapid tissue turnover, herbivory, and decomposition. Plant size is one of the major determinants of exchanges of carbon, nutrients, energy, and water. Vegetation differences in size

and growth rate feed back to reinforce natural environmental differences, largely because large plants reduce soil moisture, and rapidly growing plants produce litter that enhances nutrient availability.

At regional scales, large size and high stomatal conductance promote evapotranspiration and therefore precipitation, whereas small size or sparse vegetative cover dissipates more energy as sensible heat, leading to higher air temperatures. At high latitudes, large size reduces albedo by covering the snow with a dark surface, thereby promoting regional warming during winter and spring. The increasing recognition of the importance of plant traits in influencing ecosystem processes and climate provide a central role for physiological ecology in studies of ecosystem and global processes. These physiological processes are now being incorporated into **Dynamic Global Vegetation Models (DGVMs)** to simulate the changes in competitive balance and species shifts expected to occur in response to climatic change (Cramer et al. 2001, Woodward & Lomas 2004).

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