
102: Trophic Dynamics

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The carbon (C) and water cycles are intimately linked in terrestrial ecosystems. Thus, an understanding of the processes regulating transfers of water in terrestrial ecosystems requires an understanding of the carbon cycle, and in particular, the factors constraining carbon movement in the soil-plant-atmosphere continuum and through trophic levels in ecosystems. The linkages between the C and the water cycles are mediated primarily through biological processes, and are bidirectional in nature. For example, precipitation (and hence ecosystem water availability) strongly regulates plant growth and biogeochemical cycling in soils. Subsequently, plant growth and soil biogeochemistry strongly influence evaporation and atmospheric water vapor (and hence precipitation). Plant growth and soil processes are also cyclically linked. Thus, plant and soil interactions can have important implications for water cycling. However, while major climatic variables (including precipitation) may drive biological patterns and processes at large scales, other ecological interactions also regulate both plant and soil processes. An appreciation of these ecological factors is important to understanding the relationship between C and water, and to predicting how global environmental change is likely to affect the interactions between the C and water cycles.

INTRODUCTION

From an ecological perspective, plant photosynthesis regulates the carbon balance and productivity of the biosphere, controls fluxes of C between the biosphere and the atmosphere, and is responsible for virtually all of the biochemical production of organic matter. From an anthropomorphic perspective, biomass produced by autotrophic organisms via photosynthesis is the source of all food, fiber, and fuel in the biosphere, and thus sustains all other life on earth, including humans. Of all the carbon fixed by plants (gross primary production; GPP), some is stored and some is respired. The fraction of C that is fixed but not respired represents net primary production (NPP). Much of the biomass produced by plants is consumed by individuals of higher trophic levels, or moves into soil where it provides substrate for heterotrophic organisms (net ecosystem production; NEP). Inputs of organic matter from plants to soil influence nutrient cycling and soil water retention, and therefore affect further plant production. Understanding the ecological controls on organic matter cycling in terrestrial

ecosystems is fundamental to our understanding of ecosystem water balance, both at present and in the future.

PRIMARY PRODUCTION

Gross Primary Production

In 1942, Lindeman outlined the fundamental ecological concepts of energy flow in ecosystems. At any trophic level, from producer to consumer, energy flow is mediated through the individual organism. Energy is consumed, some is lost as feces, urine, or gas, and part is assimilated and respired or used for the production and growth of new biomass. During each transfer from a lower to a higher trophic level, ~10% of the consumed biomass is directly converted to new biomass; the balance is respired (Smith, 1996). Primary plant production is conceptually similar. Photosynthetically active radiation (PAR; radiation in the 400–700 nm wave band in the visible light spectrum that is utilizable by plants during photosynthesis) may be intercepted by a plant and used to drive photosynthesis. Ultimately, only a tiny fraction of total available light energy is used to convert inorganic carbon to organic molecules

within plants; the majority is lost as long-wave radiation and through sensible and latent heat fluxes. However, this small fraction is sufficient to drive plant production that sustains all organisms occupying higher trophic levels. The total organic carbon produced during plant photosynthesis is known as *gross primary production (GPP)*.

Net Primary Production

The concept of energy flow through ecological trophic levels suggests that not all C fixed by plants during photosynthesis is allocated to growth and biomass production (Figure 1). Plant respiration is also necessary to maintain the energy demands of biomass autotrophic organisms.

Plant respiration, which involves the mitochondrial oxidation of carbohydrates to form ATP, the most important energetic molecule in cells, is the necessary cost of maintaining nonphotosynthetic plant biomass (at all times)

and photosynthetic leaves (at night; Chapin *et al.*, 2002); roughly half of the C fixed by any given individual plant during GPP is respired directly by plants as carbon dioxide (CO_2) back into the atmosphere (Figure 1). The difference between total plant C fixed (GPP) and the C lost through plant respiration represents plant net primary production (NPP). Odum (1971) defined NPP as “the rate of storage of organic matter in plant tissues in excess of the respiratory utilization by plants”. By this definition, NPP includes increases in plant biomass (e.g. growth of roots, shoots, and leaves), incidental losses of fixed C through roots (i.e. root exudation), transfers of fixed C to symbiotic or associated microorganisms (e.g. mycorrhizal fungi and rhizosphere bacteria), and plant production and losses of biogenic hydrocarbons. In Lindeman’s energy transfer model, NPP also represents the amount of photosynthetically fixed C that is available to the first heterotrophic level in an ecosystem (Lindeman, 1942).

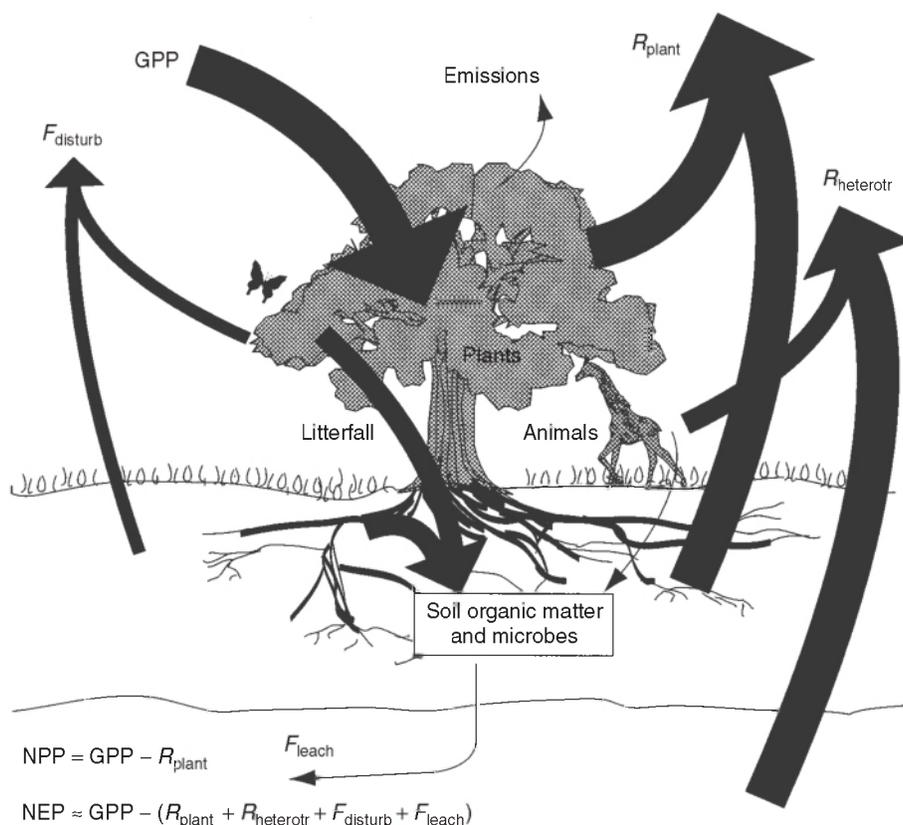


Figure 1 Overview of the major carbon fluxes in an ecosystem. Carbon enters an ecosystem as gross primary production (GPP) through plant photosynthesis. Roots and aboveground plant parts return roughly half of this carbon back to the atmosphere as plant respiration (R_{plant}). Net primary production (NPP) is the difference between GPP and R_{plant} . Most of NPP is transferred to soil organic matter as litterfall, root death, root exudation, and root transfers to symbionts; some NPP is lost to higher trophic levels (e.g. animals). Most carbon entering the soil is lost through microbial respiration, which together with animal respiration, is called *heterotrophic respiration* (R_{hetero}). Additional carbon is lost from soils through leaching and disturbance. Net ecosystem production (NEP) is the net carbon accumulated by an ecosystem; it equals the carbon inputs from GPP minus the various avenues of carbon loss (Reproduced from Chapin *et al.*, 2002 by permission of Springer)

Table 1 Productivity of different ecosystems per day and per unit leaf area

Biome	Season length (d)	Daily NPP per ground area ($\text{g m}^{-2} \text{d}^{-1}$)	Total LAI ($\text{m}^2 \text{m}^{-2}$)	Daily NPP per leaf area
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 and 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

Data from Gower, 2002.

Global Distribution of NPP

NPP is usually measured at the scale of the ecosystem and is expressed in grams of biomass or C per square meter per year (Sala and Austin, 2000). An accurate estimate of NPP represents one of the most fundamentally important characteristics of an ecosystem, and as such, estimates of NPP both within and between ecosystems are plentiful (but see Clark *et al.*, 2001a for discussion of problems in estimating NPP). On the global scale, NPP is spatially heterogeneous, but growing season length is the most important factor explaining differences in biome-specific NPP (Chapin *et al.*, 2002). Like most enzymatic biological processes, photosynthesis is sensitive to extremes in temperature and moisture, and many ecosystems experience times that are too dry, too wet, too cold, or too hot to allow photosynthesis and plant growth to occur. However, when biome-level estimates of NPP are adjusted for growing season length, NPP in different forested ecosystems are nearly identical ($\sim 5 \text{ g m}^{-2} \text{ year}^{-1}$), and NPP in the most productive systems (tropical rain forest ecosystems) is only three times NPP in the least productive systems (desert ecosystems; Table 1). These calculations suggest the importance of growing season length in controlling rates of NPP on a global scale (Chapin *et al.*, 2002).

The Fate of NPP: Plant Allocation

What is the fate of NPP? Plant allocation of the products of NPP varies in both space and time, and from species to species. For example, climatic variability over the range of a single plant species influences the timing of C allocation for leaf bud production and foliar growth, leaf senescence, and flowering and fruiting times, among others. Similarly, allocation patterns in deciduous tree species that annually grow new leaves differ from allocation patterns in evergreen species in an area experiencing identical climatic conditions (e.g. aspens in the spruce-fir ecotone). Thus, while generalizations about plant C allocation are

difficult, in general, plants allocate carbon to minimize limitation by any single resource (Chapin *et al.*, 2002). The relative demand for different resources regulates the direction and flow of carbon through plants (Aber and Melillo, 2001). Plants allocate resources to roots, shoots, or leaves depending on the relative availability of aboveground and belowground resources. When belowground resources (e.g. water or nutrients) are most limiting to plant production, plants may allocate a greater percentage of C to the production and maintenance of belowground biomass. For example, in deserts, water is often the most limiting resource, and light availability is high. Thus, many desert plants produce extensive root systems that include roots at the surface to capture episodic precipitation, and deep roots that effectively capture more consistent water supplies at depth (Chapin *et al.*, 2002). In contrast, plants growing in closed canopy, light limited forests may partition more C to aboveground tissues to maximize their ability to reach the canopy and capture available light (Table 2).

Abiotic Controls on NPP

As discussed, growing season length explains much of the variability in NPP between different ecosystems. What other factors influence rates of NPP? As the driver of the photosynthetic process, light availability strongly regulates ecosystem NPP. Early work by Montieth (1977) demonstrated that the productivity of well-watered and well-fertilized crop plants was linearly related to the amount of light they absorbed. This basic concept has much utility; it combines meteorological constraints of light impinging on a surface with the physiological constraints of light absorption and use by a leaf (Sala and Austin, 2000). Energy absorbed by a leaf (absorbed PAR; APAR) integrates seasonal and diurnal variation in sunlight and climate, and also implicitly includes the quantity of vegetation that is absorbing radiation, or the leaf area index (LAI; Sala and Austin, 2000). A conversion efficiency factor can then be used to convert APAR to growth, or biomass produced.

Table 2 Components of NPP in 12 old-growth tropical rain forest sites

Site	Aboveground biomass (Mg C/ha)	Component of aboveground NPP (Mg C/ha/y)			
		Fine litterfall	Losses to consumers	Volatile organic C	Estimated aboveground NPP
Ivory Coast: L'Anguédédou Forest	151.5	9.3	1.1	0.2	14.3
Thailand: Khaochong	167.0	5.9	0.7	0.2	9.9
USA: Hawaii (Puu Kolekole)	68.5	4.4	0.5	0.2	7.6
Columbia: Magdalena slope	162.9	4.4	0.5	0.3	7.5
Brazil: Egler Reserve	203.0	3.7	0.4	0.2	6.4
Puerto Rico: Colorado Forest	84.8	3.4	0.1	0.2	5.6
Venezuela: San Carlos	118.7	2.8	0.3	0.3	5.2
Jamaica: Blue Mountain Mull Ridge	156.0	2.8	0.3	0.2	5.0
India: Kagneri	230.0	2.0	0.2	0.3	3.9
Mexico: Chamela	40.0	1.7	0.4	0.2	3.2
Puerto Rico: Pico del Este	23.8	1.6	0.1	0.2	2.9
USA: Hawaii (Site 5)	61.5	0.9	0.1	0.2	1.4

Data from Clark *et al.*, 2001b.

Table 3 Primary production and biomass estimates in global terrestrial ecosystems

Ecosystem type	Area (10 ⁶ km ²)	Mean NPP (g C/m ² /year)	Mean biomass (Kg C/m ²)
Tropical rain forest	17.0	900	20
Tropical seasonal forest	7.5	675	16
Temperate evergreen forest	5.0	585	16
Temperate deciduous forest	7.0	540	13.5
Boreal forest	12.0	360	9.0
Woodland, shrubland	8.0	270	2.7
Savanna	15.0	315	1.8
Temperate grassland	9.0	225	0.7
Tundra	8.0	65	0.3
Desert scrub	18.0	32	0.3
Rock, ice, sand	24.0	1.5	0.01
Cultivated land	14.0	290	0.5
Swamp, marsh	2.0	1125	6.8
Lake, stream	2.5	225	0.01

Data from Whittaker and Likens, 1973.

Because APAR can be used to generate estimates of NPP on large scales, combined with the ability to obtain values of APAR using remote sensing, estimates of APAR measured from space are routinely used to generate estimates of plant production.

Large-scale (e.g. biome- to global-scale) patterns in terrestrial primary productivity can also be well explained by climatic variables, most notably average annual temperature and precipitation. In general, primary production is high in ecosystems with warm, moist climates, and low in ecosystems characterized by cold, dry climates (Table 3). Analyses of the empirical relationships between NPP and climate (Schoor, 2003; Lieth, 1975) further validate this observation, and suggest the importance of temperature and precipitation in regulating NPP (Figure 2). Across a

temperature gradient ranging from <10 °C to ~30 °C, NPP increases linearly with increases in temperature (Schoor, 2003). However, precipitation is also highly correlated with ecosystem NPP (Figure 2). This strong positive relationship between ecosystem annual precipitation inputs and NPP represents the first link between C and water cycles depicted in Figure 3.

The relationship between NPP and precipitation has also been verified experimentally. Sala *et al.* (1988) found that mean annual precipitation explained 90% of the variability in mean aboveground NPP in 100 major land resource areas across the central grassland region of North America. These observations illustrate the overwhelming importance of water availability as a control on NPP, at least in some ecosystems. However, while increases in precipitation in

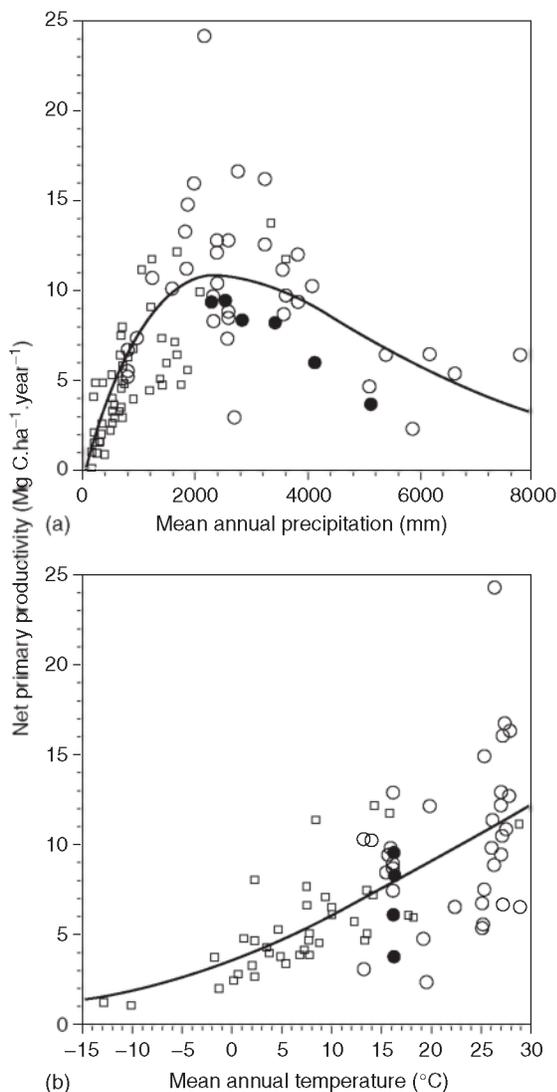


Figure 2 Relationships between net primary production and (a) mean annual precipitation and (b) mean annual temperature in temperate ecosystems (Reproduced from Schuur, 2003 by permission of Ecological Society of America)

many arid and semiarid ecosystems correlate with dramatic increases in NPP, in extremely mesic ecosystems, excessive precipitation inputs may actually correlate with decreases in NPP (Schuur, 2003). Together, these data suggest interesting interactions between precipitation and NPP. Namely, NPP increases with temperature and precipitation, but this effect diminishes in wet, warm ecosystems, where further increases in precipitation or temperature may not be balanced by increases in NPP (Figure 2). The fact that NPP decreases in ecosystems characterized by extremely high precipitation inputs suggests that excessive water availability either directly or indirectly affects plant growth through other feedback mechanisms.

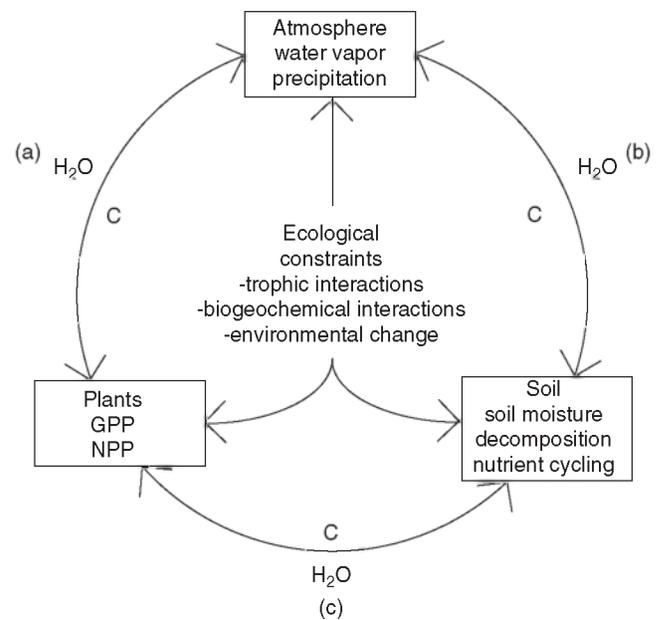


Figure 3 Schematic illustration of the coupling of the carbon and water cycles in terrestrial ecosystems. (a) NPP and evapotranspiration regulate the flow of water and C between plants and the atmosphere; (b) decomposition and evaporation control the flow of water and C between the soil and the atmosphere; and (c) biogeochemistry and soil processes regulate fluxes of C and water in the plant–soil continuum. However, ecological constraints also strongly regulate the fluxes of C and water in terrestrial ecosystems

Evapotranspiration: The Return of Water to the Atmosphere

The emerging linkages between C and water cycling, which include the strong correlation between water availability and NPP, suggest that the relationship may also operate in reverse. In other words, high NPP may also affect atmospheric water content. Empirical evidence suggests a strong relationship between NPP and ecosystem water losses, and these losses, in turn, complete the cycle connecting plant C cycling with atmospheric water content (e.g. Schimel *et al.*, 1997). Respiratory losses of CO₂ are not the only resource costs of maintaining an autotrophic lifestyle; losses of water via evapotranspiration link primary production (C cycle) with the hydrological cycle (*see Chapter 42, Transpiration, Volume 1*). Losses of water from terrestrial ecosystems to the atmosphere occur via two pathways: evaporation, or the direct return of water to the atmosphere from open water bodies and from the land surface (mainly from rock and soil and plant surfaces); and transpiration, the incidental loss of water through plant leaf stomatal openings (*see Chapter 70, Transpiration and Root Water Uptake, Volume 2*). During photosynthesis, plants obtain atmospheric CO₂ for fixation in photosynthesis through their stomata, small pores in the leaf surface.

The size of the stomatal opening regulates stomatal conductance, and high stomatal conductance equates with high fluxes of CO₂ available for photosynthesis. However, as a consequence of high stomatal conductance, a decreasing moisture gradient from the inside of the leaf to the outside creates a flux of water out of the leaf, thus resulting in plant water loss to the atmosphere. Thus, in maximizing CO₂ uptake for photosynthesis, plants necessarily subject themselves to high water losses via transpiration.

Together, transpiration and evaporation are known as *evapotranspiration*, and rates of actual evapotranspiration (AET) are very well correlated with NPP (Figure 4). The high correlation between NPP and AET represents an important feedback loop connecting water and carbon cycling in ecosystems. High rates of precipitation and inputs of solar radiation (energy) stimulate high NPP. Subsequently, high rates of NPP in mesic ecosystems lead to high rates of water loss to the atmosphere via evapotranspiration, which have been shown to complete the feedback system by fueling precipitation into ecosystems. The importance of this feedback between NPP, soils, and precipitation is illustrated by an example from tropical rain forests. In Amazonia, the climate and vegetation are tightly coupled. High rates of evapotranspiration from Amazon forests provide water vapor to the atmosphere. Through convective processes, evaporated and transpired water vapor becomes cumulus clouds and precipitation

(Nobre *et al.*, 1991). Much of the daily rainfall in the Amazon Basin is quickly reevaporated and transpired into the atmosphere, maintaining high atmospheric humidity and generating clouds that provide the following day's rain. Without forest vegetation, most rainfall would enter rivers, resulting in progressive drying of the air, and affecting NPP.

Net Ecosystem Production

With respect to organic C balance, ecosystems can be aggrading (i.e. C accumulating in soils and vegetation), degrading (i.e. net loss of C), or in equilibrium (i.e. carbon inputs matched by carbon losses). The balance between carbon entering and leaving an ecosystem is net ecosystem productivity (NEP; also known as *net ecosystem exchange* [NEE]), and represents the difference between NPP and heterotrophic respiration by animals and microorganisms (Figure 1). Most carbon enters an ecosystem through NPP, and the majority of C that enters an ecosystem is eventually lost through respiration. However, in some ecosystems, leaching of dissolved organic carbon (DOC) or dissolved inorganic carbon (DIC) through soils and into aquatic ecosystems may be important loss vectors for C (Neff and Asner, 2001). This is particularly true in arctic terrestrial ecosystems, where roughly 20% of the CO₂ produced in soils is lost as CO₂ from lakes, streams, or groundwater (Chapin *et al.*, 2002). Losses of fixed C via methane or plant produced hydrocarbon emissions are also significant loss pathways for C in some ecosystems. For example, in wetland systems, or systems where anoxic conditions prevent the aerobic decomposition of organic matter, ecosystem losses of C *via* methanogenesis can be significant. Similarly, many plants have been shown to produce C-rich secondary compounds that are lost as volatile hydrocarbons from ecosystems. Volatile organic carbon (VOC) emissions (e.g. terpenoid and isoprenoid compounds from plants) may account for C losses up to 5% of NPP (Figure 1; Chapin *et al.*, 2002).

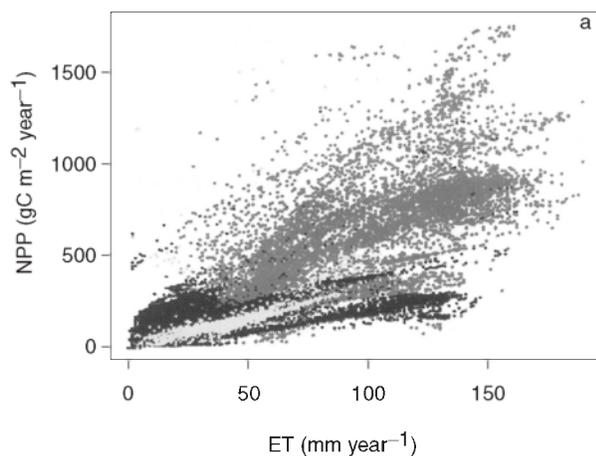


Figure 4 The relationship between NPP and ET ($r^2 = 0.71$) from an integration of the Century ecosystem model for the Northern Hemisphere. Points in dark grey are forest ecosystems, light grey indicates grasslands, and black indicates "mixed" ecosystems that include grasses and trees or shrubs (e.g. savannas) (From Schimel, D.S., Braswell, B.H. and Parton, W.J. (1997). Equilibration of the terrestrial water, nitrogen and carbon cycles. *Proceedings of the National Academy of Sciences*, 94, 8280–8283. ©1997 National Academy of Sciences USA)). A color version of this image is available at <http://www.mrw.interscience.wiley.com/ehs>

DECOMPOSITION

Soil Organic Matter Decomposition

In most ecosystems, the majority of the C fixed during NPP leaves the ecosystem through the activity of heterotrophic microorganisms (Figure 1). The most important conversions of ecosystem organic C to CO₂ (i.e. real losses) occur during heterotrophic respiration; microorganisms utilize dead plant biomass and detritus to respire and build biomass. Decomposition is a fundamental ecological and biogeochemical process; it returns fixed C to the atmosphere, and also returns critical nutrients stored in organic matter back to the soil, thus providing the main source of

annual plant nutrient availability (Paul and Clark, 1996) (see Chapter 96, Nutrient Cycling, Volume 3). Organic matter decomposition is also tightly linked to water inputs, and represents another important link between the C and the water cycles (Figure 3).

Following litterfall and litter accumulation on the soil surface, the first step in organic matter decomposition is leaching of soluble organic material through the litter (and other plant biomass) layer and into the soil. Soluble fluxes of organic C from throughfall (leaching from live plant leaves and other aboveground biomass) and through the fallen litter layer may be 1–19% of the total litterfall C flux, and may represent 1–5% of NPP (References in Neff and Asner, 2001). The rate at which C solubilizes, leaches, and enters the soil is linked to precipitation driving fluxes; the direct movement of water through the vegetation and litter layers drives C fluxes. Experimental evidence suggests that DOC concentrations decrease through the soil horizon, and that the majority of C that enters the soil is biologically available and is utilized and respired by microorganisms (Cleveland *et al.*, 2004).

Abiotic Controls on Decomposition

The decomposition of nonleached plant material accumulated as soil organic matter is strongly linked to climate. For example, temperature affects decomposition directly through its effects on soil microbial activity. Over a broad range, increasing temperature elicits exponential increases in soil respiration (Figure 5). Temperature affects both the physicochemical characteristics of the soil environment as well as the physiological reaction rates of cells. Specifically, in a basic way, microbial decomposition of organic

matter must follow simple reaction kinetics, with reaction rates increasing with temperature to a maximum, and decreasing at excessive temperatures that degrade enzymes. Freeze–thaw cycles can also contribute to decomposition, through the physical effects of freezing on the microorganisms decomposing dead plant material and soil organic matter.

Soil moisture also strongly regulates decomposition. Like plants, decomposer organisms are most productive when water availability is high, provided sufficient oxygen is available in the soil (Paul and Clark, 1996). Microbial decomposition of organic matter is dependent upon diffusion processes in the soil environment. Excessive drying of soil prevents both enzymatic processes and physicochemical processes from allowing decomposition and nutrient mineralization to occur. Evidence suggests that decomposition declines at soil moisture values <30–50%, owing to the reduction in moisture necessary to allow rapid diffusion of necessary resources (Paul and Clark, 1996). Similarly, excess water in soils may also affect soil organic matter decomposition rates, but in the opposite direction. Excessive soil moisture can lead to soil anoxia, and decreased oxygen availability has been linked to decreased rates of decomposition (Schuur, 2003; Schuur *et al.*, 2001). The relationship between water availability and decomposition rate is another important link between the C and water cycles (Figure 3).

The decomposition rate of soil organic material is influenced by many factors. For example, soil temperature, soil moisture, organic matter quality, soil oxygen availability, and the activity of specific microorganisms all influence the rate of conversion of organic C to CO₂. However, as with NPP, an analysis of decomposition at the global scale is useful for determining the role of climate in regulating large-scale variations in decomposition. Meentemeyer (1978) demonstrated that while litter quality strongly correlates with decomposition rates, the slope of the relationship between litter quality and decomposition rate decreases coincidentally with ecosystem actual evapotranspiration (AET; Meentemeyer, 1978). While AET most appropriately represents water losses from a system, it is also a useful proxy for the amount of water (and energy) entering an ecosystem (Schimel *et al.*, 1997). Thus, the observed relationship between AET and decomposition integrates the effect of soil moisture and precipitation inputs on decomposition, and further demonstrates the linkage between precipitation and soil processes, including organic matter decomposition. *In situ* soil respiration, which includes plant root and soil microbial respiration, is also a useful proxy for heterotrophic decomposition. Like with NPP, at large scales, soil respiration is positively related to soil moisture availability (Raich and Schlesinger, 1992; Figure 5).

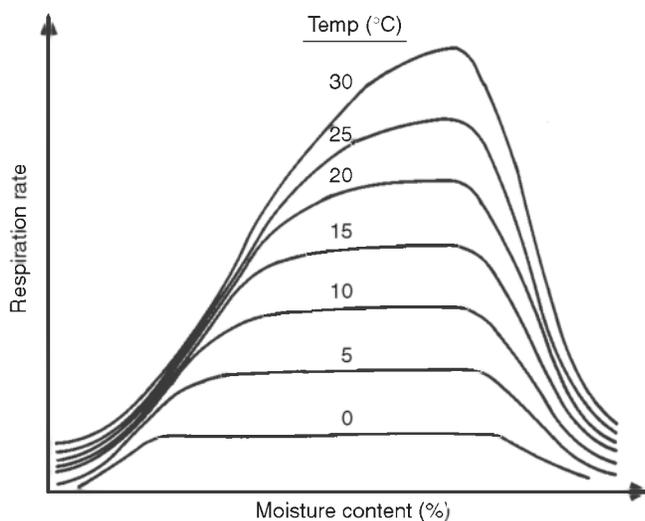


Figure 5 Semiperspective plot of computed soil respiration rate at different soil temperature and soil moisture levels (Reprinted from Paul and Clark, 1996, ©1996 with permission from Elsevier)

Precipitation exerts control on soil processes (including C decomposition) through AET and soil moisture, demonstrating another important linkage between the C cycle and water cycle. However, abundant precipitation not only affects soil processes, but also soil moisture availability, and this constitutes another feedback mechanism linking soil water availability, soil C cycling, and water losses to the atmosphere. Specifically, evaporative losses of water directly from soil are necessarily higher when soil moisture is higher (i.e. the difference between AET and potential evapotranspiration (PET) results from differences in soil moisture) (*see Chapter 42, Transpiration, Volume 1*). High precipitation in mesic ecosystems contributes to high soil moisture, and high soil moisture in ecosystems may perpetuate high precipitation through high rates of AET. Soil is a huge reservoir for water in terrestrial ecosystems, and evaporative processes from soil represent a significant portion of AET. Moreover, variable decomposition rates can affect the amount of organic matter accumulation in ecosystems. Because organic matter in soils often increases water-holding capacity, the linkage between water and C cycles in the atmosphere and soil is completed.

PLANT–SOIL INTERACTIONS

There are important linkages between water availability and both plant and soil processes, and factors affecting these interactions may lead to important feedbacks that further influence the fluxes of water and carbon into and out of ecosystems (Figure 3). However, there are also important interactions that occur between plants and soil, and these interactions affect and are affected by ecosystem C cycling and water status, and hence fluxes of water and C between terrestrial ecosystems and the atmosphere. For example, most inputs of organic matter into ecosystems are the result of primary production. While the fate of soil organic matter is strongly dependent on climatic (e.g. temperature and moisture) and edaphic (e.g. soil texture, soil chemistry) factors, ecosystems with high rates of NPP will have correspondingly high organic matter inputs to soil. Soil organic C decomposition, which is linked to the water cycle through its strong relationship to soil moisture, is also linked to NPP and inputs of organic carbon as the main source of carbon and energy for heterotrophic microorganisms. CO₂ flux from soil is highly correlated with NPP, which supplies organic molecules to decomposers. Across the world's major biomes, Raich and Schlesinger (1992) showed a direct relationship between soil respiration and NPP. Experimental manipulations of C also consistently reveal increases in soil respiration following C inputs (Schlesinger and Andrews, 2000). Thus, precipitation regulates NPP, NPP regulates decomposition

and soil C, soil C regulates soil moisture, which in turn, may regulate precipitation *via* AET (Figure 3).

The interactions between NPP and soil processes also operate in reverse. Precipitation exerts control on soil organic matter decomposition, which in turn represents the major mechanism for nutrient mineralization and nutrient cycling in terrestrial ecosystems. On an annual basis, most of the nutrient demands by plants are met through the activity of soil microorganisms, which liberate important nutrients during soil organic matter (SOM) decomposition. Thus, soil moisture can indirectly affect NPP through decomposition and nutrient mineralization. High levels of NPP also provide increased C substrate and fuel higher levels of soil microbial biomass. In systems where nutrients are extremely rare, high levels of microbial biomass can positively affect nutrient cycling and plant growth (Paul and Clark, 1996).

Some interesting data suggest complexities of the interactions between C and water cycles, and provide evidence for the feedbacks depicted in Figure 3. For example, data from grasslands suggest fascinating interactions between NPP, soil processes, and water availability. First, when grassland sites spanning a precipitation gradient are compared, average NPP increases with precipitation (References in Chapin *et al.*, 2002). Moreover, in a single grassland site, NPP increases during wet years, and responds to experimental water addition, indicating that NPP in grasslands is water limited. However, the apparent water limitation is really nutrient limitation; increased soil moisture increases decomposition rates and nutrient mineralization rates, and hence nutrient supply (Chapin *et al.*, 2002). Arid grasslands are never as productive in wet years as grasslands that regularly receive high moisture inputs, suggesting that arid grasslands lack biomass, species, or soil fertility to exploit high moisture years (Laurenroth and Sala, 1992). Thus water controls NPP, but soil moisture determines NPP in three ways: direct stimulation of NPP, its effect on nutrient supply, and its constraints on species composition and the productive capacity of an ecosystem. This example illustrates the complexity of the interactions between C and water cycles in terrestrial ecosystems.

DEVIATIONS FROM "THE MODEL": BIOTIC REGULATION OF C AND WATER CYCLES

Abiotic factors, including climate and growing season length strongly regulate fluxes of water and carbon into and out of ecosystems. At least on the global scale, there are robust relationships between NPP, soil processes, and precipitation, and these processes link the C and water cycle in ecosystems. Water is a basic requirement for biological organisms. Thus, it is not surprising that water availability regulates biological processes such as NPP and decomposition. These relationships between climatic

variables and ecosystem processes are extremely useful, as they allow estimation of NPP without direct measurement (e.g. Schuur, 2003; Lieth, 1975). However, while climate drives much of the large-scale variability in C cycling, the variability of the data compiled to generate these relationships suggests that other factors influence processes at the plot- to ecosystem-levels (Figure 2). For example, precipitation inputs alone explain 56% of the variability in NPP at the global scale, while temperature alone explains only 47% (Schuur, 2003). Thus, while the relationships are fairly robust, the variability of the data highlights the inability of climate to accurately predict NPP values at small scales. The inability to capture variability at smaller scales suggests that other factors influence plant and soil processes and their effects on C and water cycling.

ECOLOGICAL CONSTRAINTS ON ECOSYSTEM PROCESSES

We refer to the factors other than temperature, moisture, and radiation that may affect plant and soil processes as ecological constraints. An understanding of the effects of ecological constraints on ecosystem processes is critical for predicting interactions between C and water on small scales. The ecological constraints on plant and soil processes can take many forms, and their effects are often complex. Ecological controls on ecosystem processes can vary both spatially and temporally, can have positive or negative consequences, and can have rapid and dramatic effects on ecosystem C cycling. As a result, ecological constraints on plant and soil processes can have profound implications for water cycling at many levels of organization, from the community to the ecosystem scale.

Most ecological constraints on soil and plant processes fall into three general categories: trophic interactions, or the activity of other organisms in an ecosystem that affect plants and soils directly or indirectly (top-down controls); biogeochemical interactions, or the effects of soil nutrient status and soil biogeochemistry on C cycling (and hence water cycling) of an ecosystem (bottom-up controls); and anthropogenic/environmental interactions, or the influence of the many facets of global environmental change (including those driven by human activity) on ecosystem processes. Although many of the consequences of global change on C and water cycling are largely speculative (due to the rate at which the changes are occurring and ecosystems are responding), it is useful to consider some of the major changes and to discuss the state of the science predicting how global change may affect the interactions between C and water cycling.

Trophic Interactions

Herbivory is the consumption of living plant tissue (primary producer) by an organism occupying another trophic

level (consumer), and may influence ecosystem NPP. By the broadest definition, consumers include: parasitic and phytophagous microorganisms (e.g. fungi and algae); phytophagous invertebrates (e.g. stem and foliage feeding insects, root-feeding insects and nematodes and seed predators); and browsing and grazing vertebrates (Barbour *et al.*, 1999). Estimates suggest that on a global scale, ~10–20% of terrestrial NPP is consumed by herbivores, and that the percentage varies by ecosystem. Values of NPP reduction from herbivory in natural ecosystems range from 2–3% in deserts and alpine tundra, 4–7% for forests, 10–15% in lightly grazed grasslands, and 30–60% in heavily grazed grasslands (Barbour *et al.*, 1999). However, periodic outbreaks of herbivore pests such as pathogens or insects may consume up to 100% of NPP.

Grazing

Herbivory in managed ecosystems results in significantly greater reductions in NPP, and thus the associated feedbacks between NPP and the C and water cycles may be impacted to a greater degree than in natural ecosystems (*see Chapter 118, Land Use and Land Cover Effects on Runoff Processes: Agricultural Effects, Volume 3*). In particular, grazing may decrease productivity directly, through a decrease in the potential photosynthetic plant material capable of fixing atmospheric CO₂ into new biomass. An analysis of 276 cases of grazed–ungrazed comparisons over 236 sites, Milchunas and Lauenroth (1993) demonstrated the significance of grazing in heavily managed ecosystems. In general, grazing had predominantly negative impacts on NPP. Grazing decreased above-ground NPP (ANPP) by 44%, 55%, 51%, and 60% in grassland, shrubland, mountain (e.g. alpine), and forest ecosystems, respectively (Milchunas and Lauenroth, 1993).

However, predicting the net effects of decreasing NPP from grazing on C and water cycles are complex. For example, the removal of vegetation by grazing can lead to profound changes in soil properties that can affect water balance. Diminished NPP due to leaf herbivory may contribute to decreased losses of water *via* transpiration. However, leaf herbivory that removes canopy vegetation may alter the balance between light absorbed and reflected (i.e. changes in albedo) and increase the importance of evaporation from soils. Additionally, the effects of grazing and the associated feedbacks on the C and water cycles are not limited to the effects on NPP. Soil trampling and vegetation removal can decrease soil organic matter and soil water-holding capacity. Furthermore, soil compaction can increase soil bulk density and break up soil aggregates, reduce water infiltration, soil stability, soil food-web structure, and nutrient cycling rates (Warren *et al.*, 1986; Ingham *et al.*, 1989). Finally, vegetation removal can increase the amount of bare soil, and leads to soil erosion through both hydrological

and aeolian processes (*see Chapter 118, Land Use and Land Cover Effects on Runoff Processes: Agricultural Effects, Volume 3; Chapter 119, Land Use and Land-cover Effects on Runoff Processes: Forest Harvesting and Road Construction, Volume 3*). All of these potential interactions highlight the complexity of the relationship underpinning the linkage between C and water cycling, and the potential importance of trophic interactions in regulating the relationship.

Insect Herbivory

There are multiple lines of evidence suggesting that grazing of arid lands can have profound effects on ecosystem C cycling which, in turn, could dramatically affect water cycle in terrestrial ecosystems. However, grazing is not the only top-down regulator of ecosystem C cycling. Herbivorous insects and pathogens also play a key role in regulating vegetation growth and dynamics, and represent one of the most important and pervasive agents of disturbance in ecosystems worldwide (Logan *et al.*, 2003). Insects are important components of most ecosystems, and can have both positive and negative effects on ecosystem processes. However, insects have the capacity for extremely high population growth. Thus, when outbreaks of herbivorous insects occur, the effects can be profound. In North American forests, insects affect an area more than 50 times larger than fire on an annual basis, and with substantially greater economic repercussions (Dale *et al.*, 2001).

Insect outbreaks can alter the interactions between C and water cycling in several important ways. First, significant foliage removal or tree mortality resulting from insect herbivory may lead to declines in NPP. In extreme cases, insect defoliation can remove 100% of NPP. At the scale of the individual, decreases in leaf area may lead to declines in plant water uptake and transpiration. At larger scales, this effect can lead to changes in the ways water cycles through the affected ecosystem. For example, landscape-level insect denudation of plant biomass may favor increased water losses as runoff and, thus, lead to decreases in soil moisture across the landscape. Such declines in soil moisture may, in turn, lead to declines in evaporation, plant stand relative humidity and nutrient cycling. Insect outbreaks resulting in large-scale stand mortality may further influence C and water cycling *via* negative effects on nesting birds, mycorrhizal fungi (References in Dale *et al.*, 2001), and on climate (which may affect competitors and natural enemies regulating the abundance of pests and pathogens), creating another potential feedback on insect distribution and abundance (*see Chapter 103, Terrestrial Ecosystems, Volume 3; Chapter 120, Land Use and Land Cover Effects on Runoff Processes: Fire, Volume 3*). Large-scale stand mortality may also accelerate stand fire regimes, further affecting short-term C and water cycling processes.

Interactions between insect outbreaks and water availability are also complex, and are not unidirectional. Specifically, evidence suggests that the potential ecological effects of insect herbivory not only influence ecosystem water balance, but there is also mounting evidence that insect outbreaks in terrestrial ecosystems are related to climate fluctuations, and in particular, water availability (Speer *et al.*, 2001). For example, reductions in soil water potential from low precipitation and soil moisture (drought) have been linked to declines in tree production and health, and such environmental stresses often predispose plant species to attack by insects and other parasites (Hanks *et al.*, 1999). Decreases in tree health resulting from drought often reduce tree resistance to colonization by insects. Thus, in many cases, drought weakens trees, making them more vulnerable to insect infestations. In contrast, using a tree-ring reconstruction, Ryerson *et al.* found evidence that outbreaks of spruce budworm, an insect affecting mixed conifer forests, correspond to increases in moisture. Grassland ecosystem insect susceptibility has also been demonstrated to correlate with changes in precipitation inputs.

A growing body of evidence also suggests that insect herbivory can directly alter nutrient cycling in terrestrial ecosystems, with profound consequences for NPP. Tree damage caused by insect herbivory leads to obvious C losses from trees. These C debits can, in turn, have negative effects on mycorrhizal fungi (Chapin *et al.*, 2002). Mycorrhizal fungi form symbioses with nearly all plants, and their function in the symbiosis is to absorb and translocate important nutrients to their plant host. Mycorrhizal fungi are capable of absorbing mineral nutrients, like phosphorus (P) at much lower concentrations than nonmycorrhizal plant roots. However, the advantages of mycorrhizal infection are reciprocated through a flow of photosynthetically produced C from the host plant to the fungus, providing the C substrates necessary for the fungus to meet much of its energy requirement to grow and sustain biomass. Declines in C available to sustain such symbioses as a result of insect defoliation have clear implications for nutrient acquisition, and thus may also affect ecosystem water fluxes.

Plant Pathogens

Insect infestations also can affect the interactions between C and water cycling *via* interactions with other organisms. For example, plant disease can have a major impact on terrestrial ecosystem dynamics. Chestnut blight in North America and jarrah dieback in Western Australia have severely impacted plant species populations, leading to a cascade of changes to many affected forest ecosystems (References in Rizzo and Garbelotto, 2003). *Phytophthora cinnamomi*, a plant pathogen affecting jarrah, has eliminated most tree species over hundreds and thousands of hectares of the eucalyptus forests of Western Australia, converting them to grassland or shrubland (Rizzo and Garbelotto, 2003).

The severity of such diseases is often related to insect outbreaks. Dutch elm disease, which decimated the population in North America, was spread through the population by elm beetles that carried fungal spores from individual to individual. The wholesale conversion of forest to grassland has profound implications for the water cycle in these affected ecosystems (*see Chapter 103, Terrestrial Ecosystems, Volume 3*). The effects of such feedbacks are likely to increase as introduced exotic diseases spread and impact native plant populations (Rizzo and Garbelotto, 2003).

Biogeochemical Constraints on Ecosystem Processes: NPP

The observed decreases in NPP in ecosystems with high precipitation (Figure 2) suggest that in mesic systems, either excess water inhibits NPP, or that in these ecosystems, other biotic or abiotic processes limit NPP. In many terrestrial ecosystems, nutrient availability strongly regulates NPP and decomposition, and thus the nutrient status of an ecosystem is necessary to understand ecosystem C and water balance. However, nutrient limitation to ecosystem processes is often complex and thus generalizations about nature of nutrient limitation in ecosystems are difficult to make. A substantial amount of data from temperate and high latitude ecosystems suggests that nitrogen (N) commonly limits plant growth (Aber *et al.*, 1991; Vitousek and Howarth, 1991). While nitrogen gas (N₂) comprises ~80% of the atmosphere, N₂ gas must be fixed into reactive forms to be utilized by plants. In the absence of human influence, two major processes convert N₂ into biologically available forms: lightning and biological nitrogen fixation (BNF) by microorganisms (both free-living and in symbiotic associations with plants). However, N₂ fixation by terrestrial BNF is roughly an order of magnitude greater

than that by lightning (Galloway *et al.*, 1995) and is therefore the dominant source of newly fixed N to the landscape.

The N status of ecosystems is largely dependent on the presence and activity of the organisms that can convert N₂ into usable forms. In temperate ecosystems, relatively frequent glaciations effectively remove accumulated N by removing soils and vegetation. The succession of plant and microbial species (and hence soil N accumulation) following deglaciation is relatively slow (10³–10⁴ years), and this phenomenon results in relatively N-poor ecosystems where NPP is N limited. Evidence for N limitation of NPP comes from a wide variety of data, including manipulations of nutrient availability (Figure 6). The pervasiveness of N limitation, and the positive effect of N fertilization on primary production are also clearly illustrated by the magnitude of N applied as fertilizer to the world's agricultural systems. Thus, in temperate ecosystems, an understanding of the factors regulating NPP and the associated feedbacks on water cycling in terrestrial ecosystems requires an understanding of the effects of nutrient status, particularly N status, on primary productivity.

In contrast to temperate and high latitude ecosystems, many tropical forests lie on extremely weathered soils (Vitousek and Sanford, 1986). Many tropical ecosystems have not been influenced by large-scale natural phenomena (e.g. glaciations), and as a result, many tropical ecosystems are rich with free-living N fixers and symbiotic N-fixing species. In these ecosystems, NPP is commonly limited by rock-derived elements (Vitousek and Sanford, 1986). Over millions of years, high rates of precipitation result in rapid chemical and physical weathering of soil, and lead to losses of important, relatively "non-renewable" elements like calcium (Ca), phosphorus (P), magnesium (Mg), or potassium (K). Low levels of these

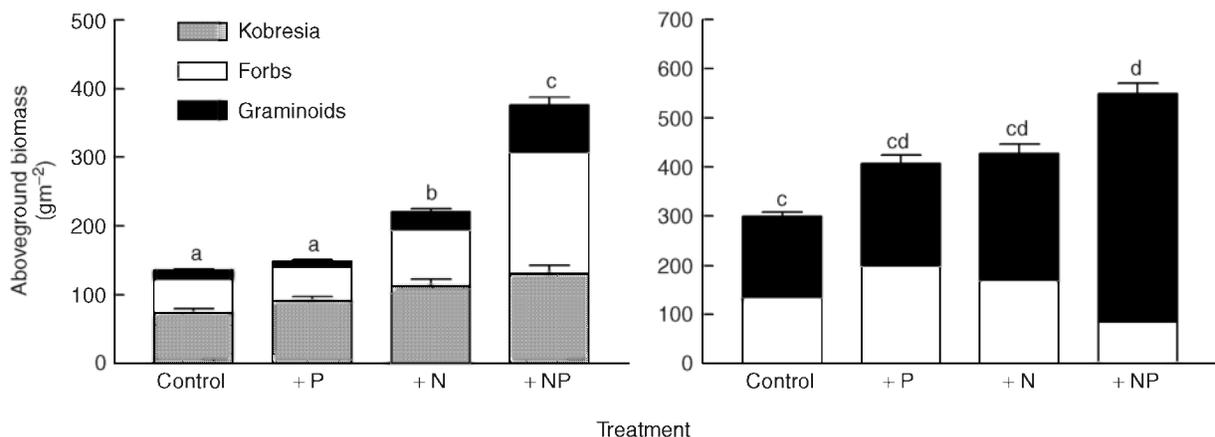


Figure 6 Aboveground biomass production for two alpine tundra communities, dry and wet meadows, under four treatments: control (C), phosphorus (P), nitrogen (N), and N + P treatments. Letters above bars indicate homogeneous means as determined by a Tukey's multiple range test (Reproduced from Bowman *et al.* (1993), by permission of Ecological Society of America)

nutrients may contribute to declines in NPP in tropical ecosystems with high precipitation. Phosphorus is generally believed to be the most limiting element in the majority of tropical forests on older soils (Vitousek, 1984). Indirect attempts to assess nutrient limitation, such as foliar element ratios, strongly suggest P constraints on NPP in many tropical forests on such soils (*see Chapter 96, Nutrient Cycling, Volume 3*). Long-term fertilizations in Hawaiian rainforests have also shown that NPP on older soils is clearly limited by phosphorus (Vitousek and Farrington, 1997), and root in-growth studies under different fertilizer applications suggested phosphorus (and possibly calcium) limitation on one oxisol in the Venezuelan portion of Amazonia (Cuevas and Medina, 1988). In contrast, fertilizer additions to a younger soil in the mountains of western Venezuela showed N to be the primary limiting nutrient (Tanner *et al.*, 1998). Similar results were found on younger soils in Hawaii (Vitousek and Farrington, 1997). The latter data suggest the complexity of nutrient controls on NPP, but clearly illustrate the potential for nutrient constraints of NPP.

Biogeochemical Constraints on Ecosystem Processes: Decomposition

The strong relationship between organic matter decomposition and AET (Meentemeyer, 1978) suggests the importance of ecosystem water availability on nutrient cycling and hence NPP. However, in some cases, microbial decomposition of plant material may also be strongly nutrient limited, and in such cases, may exacerbate plant nutrient limitation. For example, in many nutrient poor ecosystems, the pool of actively cycling nutrients is insufficient to allow rapid microbial decomposition. Hobbie and Vitousek (2000) showed that in a phosphorus limited tropical forest in Hawaii, decomposition was also limited by phosphorus (*see Chapter 96, Nutrient Cycling, Volume 3*). While microbial nutrient immobilization may prevent important nutrient losses in the long-term, in the short-term, the superior ability of soil microorganisms to compete for available soil nutrients may exacerbate plant nutrient limitation, thus impacting NPP.

C AND WATER CYCLES: THE ROLE OF ENVIRONMENTAL CHANGE

The carbon budget of terrestrial ecosystems is tightly coupled to the water cycle, and changes in C cycling in ecosystems can have potentially profound impacts on the water cycle. Moreover, while climate exerts strong control on C cycling at coarse scales, finer scale variations in C cycling (and hence water cycling) are greatly influenced by

ecological processes and interactions. Thus, an understanding of these interactions is critical in assessing the future water balance of terrestrial ecosystems.

Water is a fundamentally important natural resource vital for ecosystem functioning and human well-being. Human use of fresh water, which is expected to triple in the next two decades, and contamination are stressing this important resource, and perturbations to the hydrologic cycle may have profound consequences for people and the environment (Graedel *et al.*, 2001). Consequently, the Natural Research Council of the National Academies of the United States recently suggested that accurate prediction of “changes in fresh water resources and the environment caused by floods, droughts, sedimentation, and contamination in a context of growing demand on water resources” was one of the “Grand Challenges in Environmental Science” (Graedel *et al.*, 2001). Success in this endeavor depends on an appreciation for the tight coupling of the C and water cycles, and an understanding of the complexity of these interactions in a world that is experiencing unprecedented, rapid environmental change.

The global environment is undergoing rapid modification. As the human population and the magnitude of global change continue to grow, an understanding of the structure and functioning of ecosystems will not be possible without an understanding of the strong influence of human activity (Vitousek, 1994). Human activities, including agriculture, industry, fishing, and international commerce have changed the land surface, perturbed global biogeochemical cycles, and altered species dynamics in most of earth's ecosystems. While some of the direct effects are well documented, many of the indirect effects of global change on ecosystem structure and functioning are much more tenuous. However, some of these interactions will undoubtedly result in alterations to global C and water cycles. Specifically, three major categories of global change will play important roles regulating C and water cycling in ecosystems: land transformations, alterations of global biogeochemical cycles, and biotic changes (Vitousek, 1994).

Land Transformations

Humans have caused dramatic changes to the earth's land surface, and this trend is likely to increase well into the future. At present, it is estimated that ~35% of the earth's continental surface (55 million km²) has been cleared and converted to cropland, pasture, and urban settlements (Figure 7; Foley *et al.*, 2003). To date, the majority of human-induced land conversion has occurred in temperate terrestrial ecosystems; the only three significant remaining areas to be exploited are tropical rain forests (in South America, Asia, and Africa), boreal forests (in Canada and Russia), and deserts (Foley *et al.*, 2003). These ecosystems face increasing development pressure as the rising human population demands more forest and agricultural

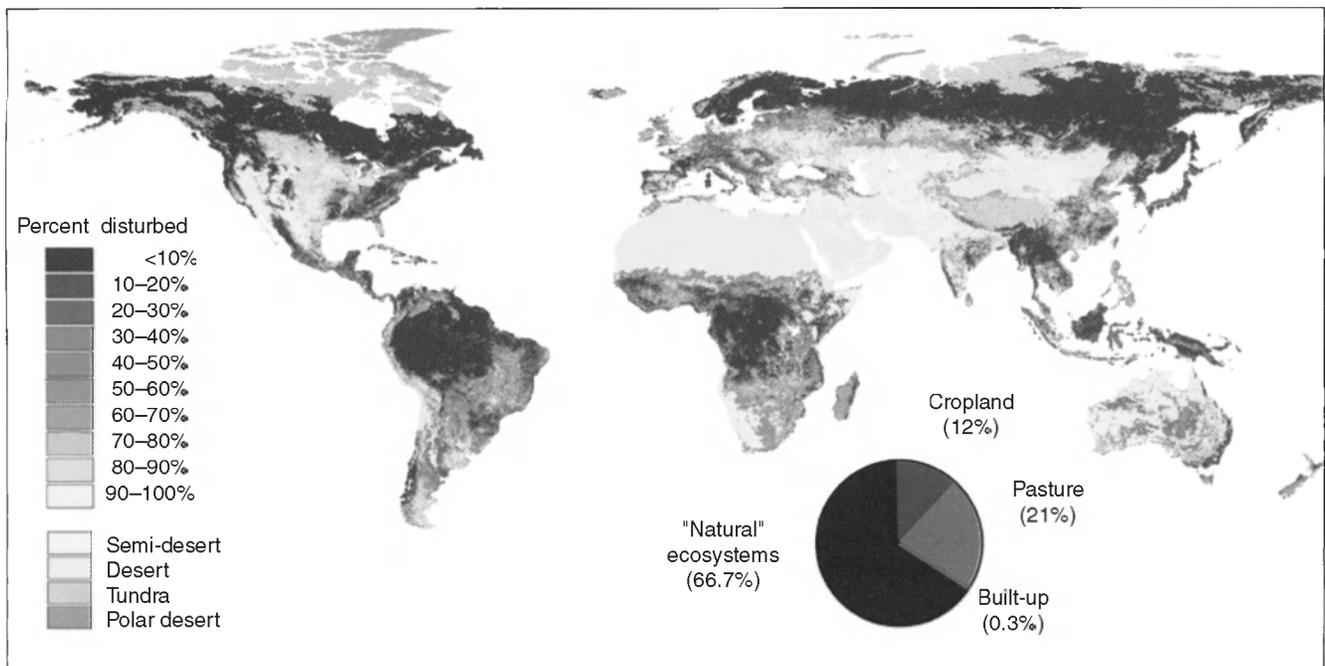


Figure 7 The global extent of human land use, including croplands, pastures, and urban areas across the world (Reproduced from Foley *et al.*, 2003 by permission of Ecological Society of America). A color version of this image is available at <http://www.mrw.interscience.wiley.com/ehs>

products. Activities such as wood extraction, forest conversion to pasture, burning, irrigation, and livestock and poultry management will all affect the biogeochemical cycling of elements, including C and water (*see Chapter 103, Terrestrial Ecosystems, Volume 3*).

Rates of human-induced land conversion are reaching rates unprecedented in history, and the ecological consequences of land conversion and land use change are numerous (*see Chapter 57, Land-cover Classification and Change Detection, Volume 2*). Land conversion leads to losses of indigenous species, introductions of exotic species, rerouting of hydrological flows, and industrial contamination of water, air, and land (Graedel *et al.*, 2001). In addition, land conversion often leads to wholesale changes in the biogeochemical cycling of important elements, including C and water (Vitousek, 1994). However, the specific effects of land use change on C and water cycling are often ecosystem-dependent. For example, in North America, changes in C fluxes following land conversion are related to the fate of converted lands, or the proportion of irrigated to nonirrigated croplands (*see Chapter 118, Land Use and Land Cover Effects on Runoff Processes: Agricultural Effects, Volume 3*) or grazed lands (Ojima *et al.*, 1994). These differences, in turn, affect regional climatic patterns, including precipitation inputs to the landscape (Pielke *et al.*, 1997).

Recent evidence suggests that land conversion and the accompanying ecological changes in tropical rain forests

may lead to profound feedback that alter water cycling in these ecosystems (*see Chapter 103, Terrestrial Ecosystems, Volume 3*). Moist tropical forests comprise one of the world's largest and most diverse biomes, and exchange more carbon, water, and energy with the atmosphere than any other ecosystem. In recent decades, tropical forests have also become one of the world's most threatened biomes, subjected to exceptionally high rates of deforestation and land degradation (e.g. Nepstad, 1999). The effects of land conversion and land use change in tropical rain forests have been thoroughly investigated in recent years (References in Foley *et al.*, 2003). The climatic impacts of such changes are typically evaluated using linked general circulation and biophysical land surface models (Shukla *et al.*, 1990). Most of these analyses suggest that large-scale deforestation and conversion of tropical rain forest will result in a significant temperature increase and decreases in annual evapotranspiration and rainfall (Shukla *et al.*, 1990). Climatic changes are driven largely by shifts in surface energy, water, and momentum balance that accompany deforestation (Figure 8). Lower surface roughness, leaf area, and root depth in pastures relative to forests reduce evapotranspiration, resulting in a decrease in evaporative cooling and surface temperature increases (*see Chapter 45, Actual Evaporation, Volume 1*).

Modeled reductions in precipitation following large-scale tropical deforestation also result from changes in ecosystem water and energy balance. For example, reduced APAR

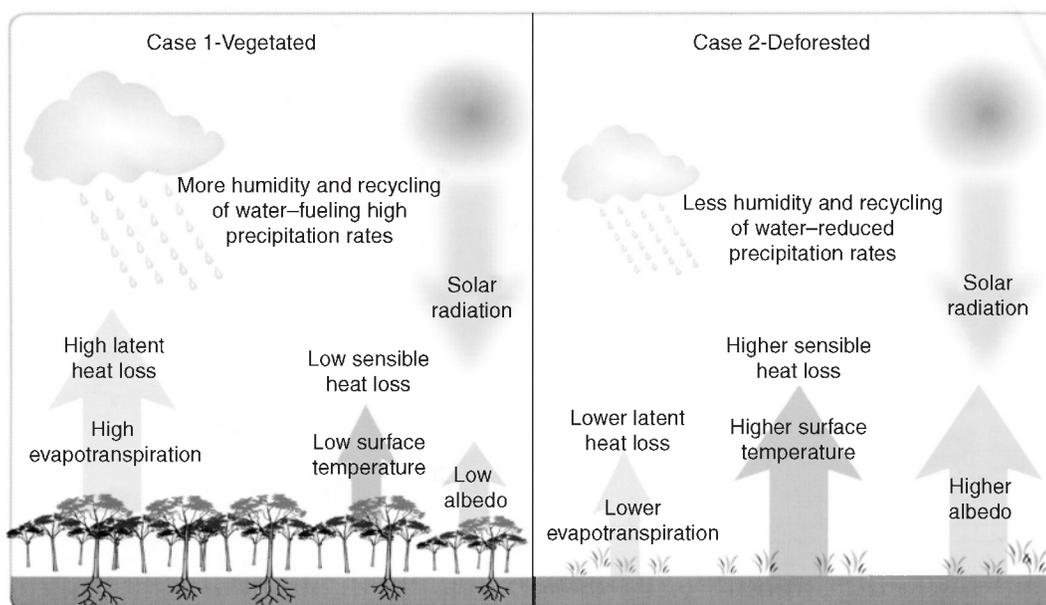


Figure 8 Climatic effects of tropical deforestation on water balance, boundary-layer fluxes, and climate. In vegetation-covered areas (a), the low albedo of the forest canopy provides ample energy for the plants to photosynthesize and transpire, leading to a high latent heat loss that cools the surface. In deforested areas (b), bare soil's higher albedo reduces the amount of energy absorbed at the surface. Latent heat loss is severely reduced and the surface warms, as it has no means of removing the excess energy through transpiration (Reproduced from Foley *et al.*, 2003 by permission of Ecological Society of America). A color version of this image is available at <http://www.mrw.interscience.wiley.com/ehs>

and elevated surface temperatures contribute to a decrease in the net radiative heating of the land, or a decrease in the energy available to fuel atmospheric circulation and convective precipitation (e.g. Wang and Eltahir, 2000a). By reducing AET, land conversion of forests to pastures results in lower atmospheric water availability, contributing to a decrease in rainfall, and may set into motion the feedbacks (Figure 8). For example, water deficits in the Brazilian Amazon are also linked to increased fire susceptibility, another disturbance mechanism that can affect C and water cycling in these areas (Figure 8).

The potentially profound effects of land conversion and land use change on C and water cycling are also observed in analyses of desert ecosystems. For example, the pronounced and persistent drought conditions present in the Sahel region of West Africa for the past three decades have drawn considerable attention. While there are two theories on the physical mechanism behind this drought, the most widely accepted is that intense human activity in the region have significantly altered land cover at the regional scale and caused the prolonged drought conditions (Wang and Eltahir, 2000b). In particular, it is suggested that ecosystem dynamics play an important role in regulating the climate of the region.

Using a coupled biosphere-atmosphere model that incorporated ecosystem dynamics and feedback between the biosphere and atmosphere, Wang and Eltahir (2000b) explored

the relationship between land use change and drought in the Sahel. As discussed previously, vegetation plays a prominent role in the exchange of carbon, water, and energy between the land surface and the atmosphere. Vegetation removal can modify the local carbon, water, and energy balance. Specifically, in the Sahel region, overgrazing, overcultivation of marginal land, slash-and-burn agricultural practices, logging, and poor irrigation techniques have led to widespread land degradation and desertification. Following desertification, ET (and hence surface latent heat flux) significantly decreases, as does precipitation. In simulations, drought conditions are the result of feedbacks involving the response of the natural ecosystem to imposed changes in land cover (Wang and Eltahir, 2000b). Further, when damage to an ecosystem reaches a threshold, climate changes significantly and leads to deterioration of other "healthy" natural ecosystems (Wang and Eltahir, 2000b; Figure 9). Research also suggests that sea surface temperature (SST) is also critical in regulating Sahel climate, but that ecosystem dynamics may dampen the response of the climate system to recover following changes in SST that would promote a return to wetter conditions (Wang and Eltahir, 2000b). Thus, similar to tropical rain forests, land conversion in arid and semiarid ecosystems may lead to changes in regional climate that continue to have feedbacks on C and water cycling.

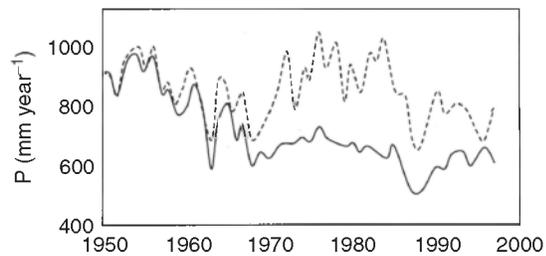


Figure 9 Drought initiation by desertification. Rainfall average over the Sahel region, in the control (dashed line) and desertification (solid line) experiments (Reproduced from Wang and Eltahir, 2000b, by permission of American Geophysical Union)

Alterations to Global Biogeochemical Cycles

Human activities are leading to profound alterations to the earth's major biogeochemical cycles. For example, fertilizer use, legume crop production and fossil fuel combustion have doubled the amount of N entering ecosystems *via* all natural pathways combined (Galloway *et al.*, 1995). Next, it is estimated that humans use 10 to 55% of annual terrestrial NPP for food and fiber or to support grazing animals (Rojs-taczer *et al.*, 2001). Perhaps, the most well-documented aspect of global environmental change is the recent increase in atmospheric CO₂ (Schlesinger, 1997), and rising CO₂ could have profound implications for ecosystem water balance. Rising CO₂ has been postulated to affect plant growth, ecosystem structure, and ecosystem function in many ways. In both laboratory and field experiments, plant photosynthesis often increases under elevated CO₂, and this can lead to changes in C cycling at the ecosystem scale (References in Hungate *et al.*, 1997). Increased CO₂ can lead to decreases in plant stomatal conductance, and corresponding decreases in plant transpiration and evapotranspiration. Changes in stomatal conductance can, in turn, have profound consequences for ecosystem water cycling. Studies conducted in both herbaceous and woody ecosystems have demonstrated reductions in evapotranspiration leading to increases

in soil water content and increased plant water-use efficiency (Figure 10). Increased CO₂ effects on plant water use and transpiration could have feedbacks ranging from changes in soil processes, increased water yield in watersheds, or to altered precipitation regimes. In systems like the Amazon Basin where evapotranspiration provides moisture for convective storms, increased water use efficiency with increased CO₂ may feed back to lower regional precipitation (Shukla *et al.*, 1990; Nobre *et al.*, 1991).

Increasing CO₂ concentrations in the atmosphere has two potential effects on climate. First, the radiative effect of increased CO₂ leads to tropospheric warming (the greenhouse effect). Next, the radiative effect of increased CO₂ warming the troposphere may also increase atmospheric water content (*see Chapter 195, Acceleration of the Global Hydrologic Cycle, Volume 5*) (through more evaporation) and intensify the global water cycle. Such changes would be beneficial to vegetation in regions where water availability or low temperatures limit plant NPP. However, there is also direct impact of changes in atmospheric CO₂ concentration on vegetation through the physiological effects, or through decreases in evapotranspiration. In arid regions, where climate is often driven by vegetation dynamics, relatively small changes in plant physiology resulting from increased atmospheric CO₂ could have profound implications on climate and particularly on precipitation regime in these systems. Thus, changes to the overall water balance of an ecosystem represent the net effects of the biotic and abiotic responses to elevated CO₂ concentrations. Using a coupled biosphere-atmosphere model to simulate the effects of increased atmospheric CO₂ on climate in the Sahel region of Africa, Wang and Eltahir (2002) found that elevated CO₂ did result in significant declines in plant transpiration due to increased plant water-use efficiency. However, the radiative effects of CO₂, which enhance precipitation, overshadowed the physiological effects, and led to more rainfall to the Sahel (Wang and Eltahir, 2002). Under this simulation, precipitation increased and led to increased NPP. In this specific ecosystem, increased water

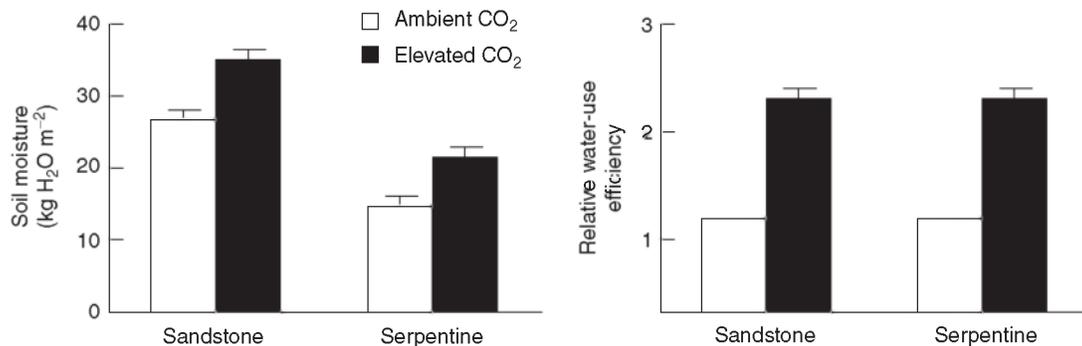


Figure 10 Soil moisture (a) and relative water-use efficiency (b) in untreated and elevated CO₂-treated plots. Values are means \pm S.E. (Reproduced from Hungate *et al.*, 1997 by permission of Springer)

availability led to denser vegetation growth at higher CO₂ concentrations, causing subsequent increases in evapotranspiration (i.e. as a result of an increase in transpiring leaf surface area) and reinforced higher levels of precipitation. This simulated feedback again illustrates the close interaction between C and water cycles, and provides clear evidence of the potential effects of a biogeochemical perturbation (increased CO₂) on regional hydrologic cycles.

Biotic Changes

Human activity has greatly modified the earth's biological resources, and changes to its species and genetically distinct populations are on the rise (Vitousek, 1994). While extinction is a natural phenomenon, current rates of species loss are much higher than "background" levels, and this accelerated extinction rate results in part from the activity of humans. However, human enterprise is not only affecting species loss rates, but causing substantial species redistribution by transporting "exotic" species into areas where they do not occur naturally. In some terrestrial ecosystems, plant invasions have led to complete shifts in species composition, and caused dramatic changes in the structure and functioning of ecosystems. In freshwater ecosystems, accidental species introductions have led to widespread invasions, and often lead to wholesale changes in the hydrologic cycle. In many arid regions in North America and Africa, exotic species have established extensively along watercourses. While harsh growing conditions in arid lands generally limit the extent of exotic plant invasions, riparian areas provide suitable habitat for some exotic species, and their establishment can have profound ecological and hydrological consequences.

For example, saltcedar (*Tamarix*) was first introduced into the western United States, and now dominates many waterways throughout the southwest (Sala *et al.*, 1996). Saltcedar invasion has profound consequences for water cycling in arid ecosystems. Saltcedar traps and stabilizes alluvial sediments, and can greatly decrease river channel width (Graf, 1978). An increase in stabilized deposits along stream channels can decrease the ability of the channel to adjust during high flow events, leading to increased flooding. Saltcedar invasion can also directly affect water cycling in invaded areas. Recent research suggests that saltcedar uses water much more inefficiently than native vegetation, and the increased water losses as a result of saltcedar invasion are profound. In riparian areas where water availability is high, dense saltcedar stands are characterized by extremely high rates of evapotranspiration, and AET in these areas can exceed potential evapotranspiration by a factor of 2 in nonriparian sites within the ecosystem (Sala *et al.*, 1996). Increased riverine water losses due to saltcedar invasion could be extremely important in arid regions that depend on annual reservoir replenishment *via*

riverine inputs to meet the water demand of their growing populations. In this case, saltcedar invasion decreases water that would otherwise be available to meet the growing agricultural and urban water demands in arid regions.

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FURTHER READING

- Aber J. and Melillo J. (2001) *Terrestrial Ecosystems, First Edition*, Harcourt/Academic Press: Burlington.
- Cuevas E. and Medina E. (1985) Nutrient dynamics with Amazonian forest ecosystems I: Nutrient flux in fine litter fall and efficiency of nutrient utilization. *Oecologia*, **76**, 222–235.
- Hungate B.A., Chapin F.S. III, Zhong H., Holland E.A. and Field C.B. (1996) Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. *Oecologia*, **109**, 149–153.
- Lieth H. and Whittaker R.H. (1975) *Primary Productivity of the Biosphere*, Springer-Verlag: New York.
- Sala O.E., Jackson R.B., Mooney H.A. and Howarth R.W. (2000) *Methods in Ecosystem Science*, Springer: New York.

REFERENCES

- Aber J.D., Melillo J.M., Nadelhoffer K.J., Pastor J. and Boone R.D. (1991) Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. *Ecological Applications*, **1**, 303–315.
- Aber J.D. and Melillo J.M. (2001) *Terrestrial Ecosystems, Second Edition*, Harcourt/Academic Press: Burlington.
- Barbour M.G., Burk J.H., Pitts W.D., Gilliam F.S. and Schwartz M.W. (1999) *Terrestrial Plant Ecology, Third Edition*, Benjamin/Cummings: Menlo Park.
- Bowman W.D., Theodose T.A., Schardt J.C. and Conant R.T. (1993) Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology*, **74**, 2085–2097.
- Chapin F.S. III, Matson P.A. and Mooney H.A. (2002) *Principles of Terrestrial Ecosystem Ecology*, Springer: New York.
- Clark D.A., Brown S., Kicklighter D.W., Chambers J.Q., Thomlinson J.R. and Ni J. (2001a) Measuring net primary production in forests: Concepts and field methods. *Ecological Applications*, **11**, 356–370.
- Clark D.A., Brown S., Kicklighter D.W., Chamber J.Q., Thomlinson J.R., Ni J. and Holland E.A. (2001b) Net primary production in tropical forests: An evaluation and synthesis of existing field data. *Ecological Applications*, **11**, 371–384.
- Cleveland C.C., Neff J.C., Townsend A.R. and Hood E. (2004) Composition, dynamics and fate of leached dissolved organic

- matter in terrestrial ecosystems: results from a decomposition experiment. *Ecosystems*, **7**, 275–285.
- Cuevas E. and Medina E. (1988) Nutrient dynamics with amazonian forests II. Fine root growth, nutrient availability, and leaf litter decomposition. *Oecologia* **76**, 222–235.
- Dale V.H., Joyce L.A., McNulty S., Neilson R.P., Ayres M.P., Flannigan M.D., Hanson P.J., Irland L.C., Lugo A.E., Peterson C.J., *et al.* (2001) Climate change and forest disturbances. *Bioscience*, **51**, 723–734.
- Foley J.A., Costa M.H., Delire C., Ramankutty N. and Snyder P. (2003) Green surprise: How terrestrial ecosystems could affect earth's climate. *Frontiers in Ecology and the Environment*, **1**, 38–44.
- Galloway J.N., Schlesinger W.H., Levy H., Michaels A. and Schnoor J.L. (1995) Nitrogen fixation: Anthropogenic enhancement-environmental response. *Global Biogeochemical Cycles*, **9**, 235–252.
- Gower S.T. (2002) Productivity of terrestrial ecosystems. In *Encyclopedia of Global Change*, Mooney H.A. and Canadell J. (Eds.), Blackwell Scientific: Oxford.
- Graedel T.E., Alldredge A., Barron E., Davis M., Field C., Fischhoff B., Frosch R., Gorelick S., Holland E.A., Krewski D., *et al.* (2001) *Grand Challenges in Environmental Sciences*. National Academy of Sciences: Washington, DC, p. 96.
- Graf W.L. (1978) Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. *Geological Society of America Bulletin*, **89**, 1491–1501.
- Hanks L.M., Paine T.D., Millar J.G., Campbell C.D. and Schuch U.K. (1999) Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). *Oecologia*, **119**, 400–407.
- Hobbie S.E. and Vitousek P.M. (2000) Nutrient limitation of decomposition in Hawaiian forests. *Ecology*, **81**, 1867–1877.
- Hungate B.A., Holland E.A., Jackson R.B., Chapin F.S., Mooney H.A. and Field C.B. (1997) The fate of carbon in grasslands under carbon dioxide enrichment. *Nature*, **388**, 576–579.
- Ingham E.R., Coleman D.C. and Moore J.C. (1989) An analysis of food-web structure and function in a shortgrass prairie, a mountain meadow, and a lodgepole pine forest. *Biology and Fertility of Soils*, **8**, 29–37.
- Laurenroth W.K. and Sala O.E. (1992) Long-term forage production on North American shortgrass steppe. *Ecological Applications*, **2**, 397–403.
- Lieth H. (1975) Modeling the primary productivity of the world. In *Primary Productivity of the Biosphere*, Lieth H. and Whittaker R.H. (Eds.), Springer-Verlag: New York, pp. 237–265.
- Lindeman R.L. (1942) The trophic-dynamic aspects of ecology. *Ecology*, **23**, 399–418.
- Logan J., Regniere A.J. and Powell J.A. (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and Evolution*, **1**, 130–137.
- Meentemeyer V. (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**, 465–472.
- Milchunas D.G. and Lauenroth W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327–366.
- Montieth J.L. (1977) Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London*, **281**, 277–294.
- Neff J.C. and Asner G.P. (2001) Dissolved organic carbon in terrestrial ecosystems: Synthesis and a model. *Ecosystems*, **4**, 29–48.
- Nepstad D.C. (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.
- Nobre C.A., Sellers P.J. and Shukla J. (1991) Amazonian deforestation and regional climate change. *Journal of Climate*, **4**, 957–988.
- Odum E. (1971) *Fundamentals of Ecology*, Saunders: Philadelphia.
- Ojima D.S., Galvin K.A. and Turner B.L. (1994) The global impact of land use change. *Bioscience*, **44**, 300–304.
- Paul E.A. and Clark F.E. (1996) *Soil Microbiology and Biochemistry, Second Edition*, Academic Press: San Diego.
- Pielke R.A., Lee T.J., Copeland J.H., Eastman J.L., Ziegler C.L. and Finley C.A. (1997) Use of USGS-provided data to improve weather and climate simulations. *Ecological Applications*, **7**, 3–21.
- Raich J.W. and Schlesinger W.H. (1992) The global carbon dioxide flux in soil respiration and its relationships to vegetation and climate. *Tellus*, **44B**, 81–99.
- Rizzo D.M. and Garbelotto M. (2003) Sudden oak death: Endangering California and Oregon forest ecosystems. *Frontiers in Ecology and the Environment*, **1**, 197–204.
- Rojstaczer S., Sterling S. and Moore N.J. (2001) Human appropriation of photosynthesis products. *Science*, **294**, 2549–2552.
- Sala A., Smith S.D. and Devitt D.A. (1996) Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave Desert floodplain. *Ecological Applications*, **6**, 888–898.
- Sala O.E. and Austin A.T. (2000) Methods of estimating aboveground net primary productivity. In *Methods in Ecosystem Science*, Sala O.E., Jackson R.E., Mooney H.A. and Howarth R.W. (Eds.), Springer: New York, pp. 31–43.
- Sala O.E., Parton W.J., Joyce L.A. and Lauenroth W.K. (1988) Primary production of the central grassland region of the United States. *Ecology*, **69**, 40–45.
- Schimel D.S., Braswell B.H. and Parton W.J. (1997) Equilibration of the terrestrial water, nitrogen, and carbon cycles. *Proceedings of the National Academy of Science*, **94**, 8280–8283.
- Schlesinger W.H. (1997) *Biogeochemistry: An Analysis of Global Change, Second Edition*, Academic Press: San Diego.
- Schlesinger W.H. and Andrews J.A. (2000) Soil respiration and the global carbon cycle. *Biogeochemistry*, **48**, 7–20.
- Schuur E.A. (2003) Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. *Ecology*, **84**, 1165–1170.
- Schuur E.A., Chadwick O.E. and Matson P.A. (2001) Carbon cycling and soil carbon storage in mesic to wet Hawaiian montane forests. *Ecology*, **82**, 3182–3196.
- Shukla J., Nobre C. and Sellers P. (1990) Amazon deforestation and climate change. *Science*, **247**, 1322–1325.
- Smith R.L. (1996) *Ecology and Field Biology, Fifth Edition*, HarperCollins Publishers: New York.

- Speer J.H., Swetnam T.W., Wickman B.E. and Youngblood A. (2001) Changes in pandora moth outbreak dynamics during the past 622 years. *Ecology*, **82**, 697–697.
- Tanner E.V.J., Vitousek P.M. and Cuevas E. (1998) Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology*, **79**, 10–22.
- Vitousek P.M. (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, **65**, 285–298.
- Vitousek P.M. (1994) Beyond global warming: Ecology and global change. *Ecology*, **75**, 1861–1876.
- Vitousek P.M. and Farrington H. (1997) Nutrient limitation and soil development: Experimental test of a biogeochemical theory. *Biogeochemistry*, **37**, 63–75.
- Vitousek P.M. and Howarth R.W. (1991) Nitrogen limitation on land and sea: How can it occur. *Biogeochemistry*, **13**, 87–115.
- Vitousek P.M. and Sanford R.L. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, **17**, 137–167.
- Wang G. and Eltahir E.A.B. (2000a) Biosphere-atmosphere interactions over West Africa. I: Development and validation of a coupled dynamic model. *Quarterly Journal of the Royal Meteorological Society*, **126**, 1239–1260.
- Wang G. and Eltahir E.A.B. (2000b) Ecosystem dynamics and the Sahel drought. *Geophysical Research Letters*, **27**, 795–798.
- Wang G. and Eltahir E.A.B. (2002) Impact of CO₂ concentration changes on the biosphere-atmosphere system of West Africa. *Global Change Biology*, **8**, 1169–1182.
- Warren S.D., Thurow T.L., Blackburn W.H. and Garza N.E. (1986) The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. *Journal of Range Management*, **39**, 491–495.
- Whittaker R.H. and Likens G.E. (1973) Carbon in the biota. In *Carbon and the Biosphere*, CONF 720510, Woodwell G.M. and Pecan E.V. (Eds.), National Technical Information Service: Washington, DC, pp. 281–302.