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Geographic and Temporal Variation of Carbon Exchange by Ecosystems and Their Sensitivity to Environmental Perturbations

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Through the long-term monitoring of CO₂ concentration at Mauna Loa (Keeling and Whorf 1996) and an expanded network of CO₂ monitoring stations across the globe (Tans et al. 1996), we now possess an ability to observe the “breathing” of the biosphere. In general, the biosphere inhales CO₂ during its hemisphere’s summer and exhales CO₂ during its winter. Superimposed upon this general pattern, however, is much complexity and variability due to temporal and spatial gradients in climate, available resources, plant structure and function, land use, and soil development.

Technically, the biosphere’s breathing can be quantified by assessing net ecosystem productivity, the balance between natural sources and sinks of carbon dioxide. Net ecosystem productivity (NEP; grams of carbon per square meter per year [g C m⁻² y⁻¹]) is defined as the difference between gross primary productivity (GPP) and ecosystem respiration (R_{eco}):

$$NEP = GPP - R_{eco}$$

GPP is defined as the amount carbon dioxide that is assimilated by plants through photosynthesis. Alternatively, we can define GPP as the sum of net primary productivity, NPP , and autotrophic respiration, R_{auto} . As a rule of thumb, autotrophic respiration, or NPP , constitutes about half of GPP (Gifford 1994), and R_{auto} is about two-thirds of ecosystem respiration (Falge et al. 2002).

Ecosystem respiration, R_{eco} , is more complex and consists of autotrophic respiration by the leaves, plant stems, and roots (R_{auto}) and heterotrophic respiration by the microbes and soil fauna (R_{hetero}):

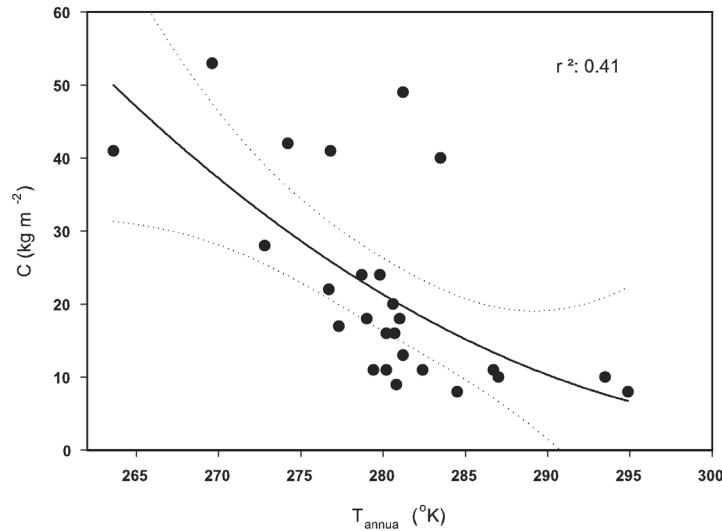


Figure 15.1. Relation between carbon content in the top meter of soil and mean annual temperature. The data are associated with the sites in the FLUXNET network (adapted from Sanderman et al. 2003).

$$R_{eco} = R_{plant} + R_{soil} = R_{auto} + R_{hetero}$$

Over many years, a more relevant measure of carbon balance is net biome productivity (*NBP*), which includes carbon losses due to fire, insect and pathogen damage, and other disturbances (Schulze et al. 2000).

Solar energy, temperature, and soil moisture are the main climate variables that modulate *GPP* on hourly, daily, and seasonal timescales (Leith 1975). Soil respiration is primarily a function of soil temperature, soil moisture, and whether or not the soil is waterlogged. On an annual timescale, soil respiration can be expressed as a function of the ratio between soil carbon content (*C*) and its turnover time (τ). In principle, carbon stores in the soil increase with decreasing temperature (*T*) (Figure 15.1). This occurs, in part, because the soil turnover time decreases with increasing temperature. Whether or not soil respiration increases or decreases with changes in temperature, however, depends upon whether the temperature sensitivity of the numerator (*C*) outpaces that of the denominator (τ) (Sanderman et al. 2003).

Geographic Variability of the Response of *NPP* to Environmental Variables

To assess global carbon exchange of the biosphere, one must assess net carbon exchange for each biome on earth. This task is nontrivial, because each of the world's major bio-

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mes—tropical, temperate, and boreal forests, savannas, shrublands, grasslands, wetlands, tundra, and deserts—contribute differently to the global carbon budget. Factors to consider when constructing carbon budgets include their (1) respective land area; (2) physiological potential to assimilate and respire CO_2 ; (3) the size and perturbation status of carbon pools; and (4) sensitivity of GPP and R_{eco} to environmental drivers (e.g., light, temperature, and soil moisture).

Biogeochemical models provide one tool for assessing the net exchange of carbon between the terrestrial biosphere and atmosphere at continental and global scales (Melillo et al. 1993; Cramer et al. 1999). These models account for the diversity and complexity of the natural world by dividing the terrestrial biosphere into broad vegetation classes that are defined by their function, structure, and climate (Bonan et al. 2002). The type and amount of vegetation at a particular location is evaluated either diagnostically, using remote sensing information derived from satellites (Running et al. 1999), or prognostically, using dynamic vegetation models (Foley et al. 1998). For a given plant class, photosynthesis and respiration are computed using algorithms that are a function of environmental variables, such as light, temperature, and soil moisture (Cramer et al. 1999). The implementation of these algorithms, however, requires weather or climate data for each unit of the model grid. Furthermore, the models require many assumptions about each unit, its representativeness in space, and its uniformity in time.

Nevertheless, with a validated biogeochemical model, one can quantify how spatial gradients in available sunlight, leaf area index, nitrogen content of leaves, and rainfall impose spatial patterns on annual photosynthesis (Churkina and Running 1998; Law et al. 2002) and how respiration scales with temperature, body size, soil moisture, and net primary productivity (Amthor 2000; Enquist 2002; Reichstein et al. 2002a). On a regional basis, NPP is light and temperature limited in northern climates and biomes, has a low degree of light and water limitation in tropical and humid temperate regions, and is limited by water availability in semi-arid climates (Colorplate 10).

Geographic and Temporal Variability of the Response of NEP to Environmental Variables

Although the information in Colorplate 10 is instructive, it leaves many questions unanswered about ecosystem carbon cycling. For instance, how do geographic variations in climate and vegetation affect the responses of NEP to environmental forcings, and how do these forcings cause NEP to vary over the course of a year? Here, we attempt to answer these questions by distilling published data produced by the FLUXNET project (Baldocchi et al. 2001; Falge et al. 2002; Law et al. 2002). Specifically, we examine cases associated with major biomes: (1) temperate broad-leaved forests, (2) boreal and temperate coniferous forests, (3) grasslands, (4) mediterranean-type woodlands, (5) agricultural crops, and (6) northern wetlands. Highlighted in this analysis is the role of environmental switches—leaf on/leaf off; drought, frost (spring/fall), the presence or

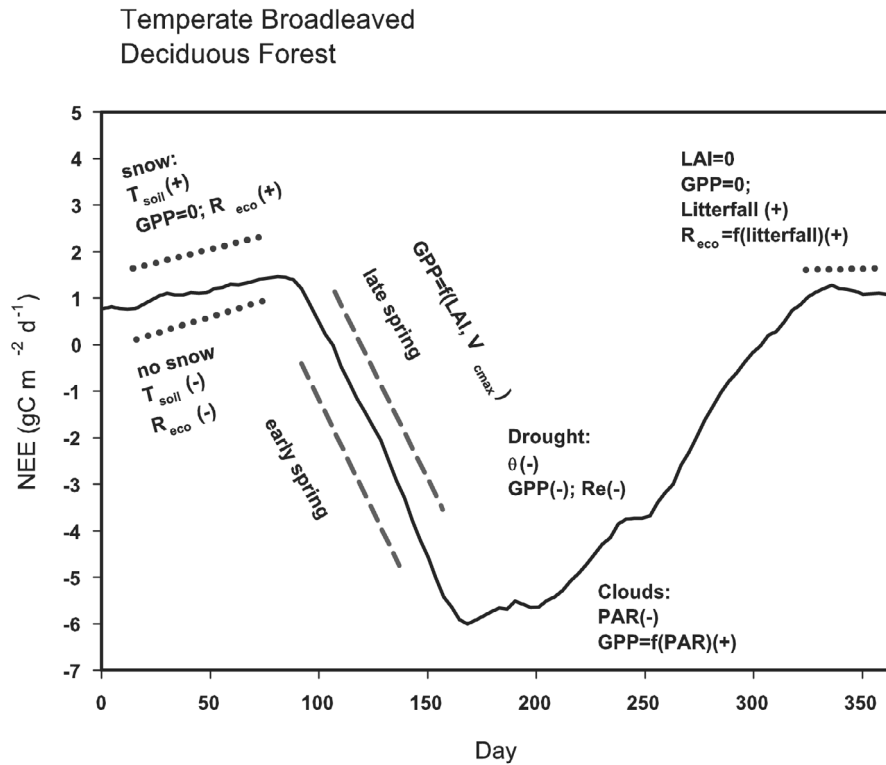


Figure 15.2. Seasonal variation in net CO_2 exchange of a temperate deciduous forest. Also shown are the environmental and biological factors that affect the seasonal dynamics of CO_2 exchange. V_{cmax} represents photosynthetic capacity, LAI is leaf area index, and T is temperature. Data sources: Wofsy et al. (1993); Greco and Baldocchi (1996); Valentini et al. (1996); Goulden et al. (1996); Baldocchi et al. (2000); Granier et al. (2000, 2002); Schmid et al. (2000); Pilegaard et al. (2001); Saigusa et al. (2002). Data are from the Fluxnet database (<http://www-eosdis.ornl.gov/FLUXNET/>) and were gap filled and smoothed.

absence of snow, and, in wetlands, the height of the water table—on ecosystem carbon exchange. Data are presented as net ecosystem carbon exchange (NEE), which is the same quantity as, but opposite in sign from, NEP . NEE is calculated from an atmospheric perspective; it is negative when the atmosphere is losing carbon and the ecosystem is gaining carbon.

Temperate Deciduous Broad-leaved Forests

Temperate deciduous broad-leaved forests exist across large regions of Asia, Europe, and North America, typically north of 30° . Globally, they occupy only 2 percent of the land

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area of the terrestrial biosphere (Melillo et al. 1993), but they contribute significantly to the global carbon budget because they occur in relatively wet and highly productive regions.

During winter, the trees are leafless and dormant, and the ecosystem is respiring (Figure 15.2). The presence or absence of snow has a major impact on soil temperatures and the rates of soil respiration from these forests (Goulden et al. 1996). Snow insulates the soil surface, so soil temperatures are warmer when snow is present. Consequently, greater rates of soil respiration occur from snow-covered ground than from bare soil, which is exposed to the cold winter weather.

During spring, a pronounced peak in ecosystem respiration reflects increased growth respiration as leaves emerge (Greco and Baldocchi 1996; Valentini et al. 1996; Granier et al. 2000, 2002). Daily respiration rates typically range between 5 and 7 g C m⁻² d⁻¹ during this period, which is double to triple respiration rates earlier in the spring. As leaf-out occurs, the ecosystem experiences a pronounced switch from a net source of carbon to a net sink. This switch can represent a net change in the magnitude of carbon exchange that approaches 10 g C m⁻² d⁻¹. Consequently, the date of leaf-out has a major impact on the net annual carbon exchange of this biome.

The date of leaf-out can vary by 30 days at a given site (Goulden et al. 1996; Wilson and Baldocchi 2000) and by more than 100 days across the deciduous forest biome (Figure 15.3). Consequently, differences in length of growing season can alter *NEE* by up to 600 g C m⁻² year⁻¹.

Once a forest has attained full canopy closure, changes in available sunlight explain most of the variability in hourly rates of carbon exchange, with a nonlinear and saturating response (Goulden et al. 1996; Valentini et al. 1996; Baldocchi 1997; Granier et al. 2000; Schmid et al. 2000; Pilegaard et al. 2001). The transparency of the atmosphere, however, complicates the sensitivity of *NEE* to changes in sunlight. At the canopy scale, the initial slope of the light response curve (also known as light use efficiency, *LUE*) increases as the fraction of diffuse radiation increases (Baldocchi 1997; Gu et al. 2002).

The net effect of increasing diffuse radiation, as a consequence of either clouds or atmospheric aerosols, is complex. In general, short-term *NPP* is twice as sensitive to changes in diffuse light as it is to changes in direct light (Gu et al. 2002). On an annual basis, increasing diffuse radiation by 20 percent without affecting total incident radiation (as can occur with aerosol loading in the atmosphere) can theoretically increase annual *NEE* of a temperate deciduous forest by 10–15 percent (Baldocchi et al. 2002), about 70 g C m⁻² year⁻¹. Increasing cloud fraction increases diffuse radiation but lowers total solar radiation. In this situation, an expected reduction in *GPP* (from the decrease in total solar radiation) is minimized at the canopy scale by an increase in light use efficiency (from the increased fraction of diffuse radiation).

Droughts tend to be episodic across the temperate deciduous forest biome. Summer drought and high vapor pressure deficits reduce daytime photosynthesis (Goulden et al. 1996; Greco and Baldocchi 1996; Baldocchi 1997). Drying of the soil also decreases soil

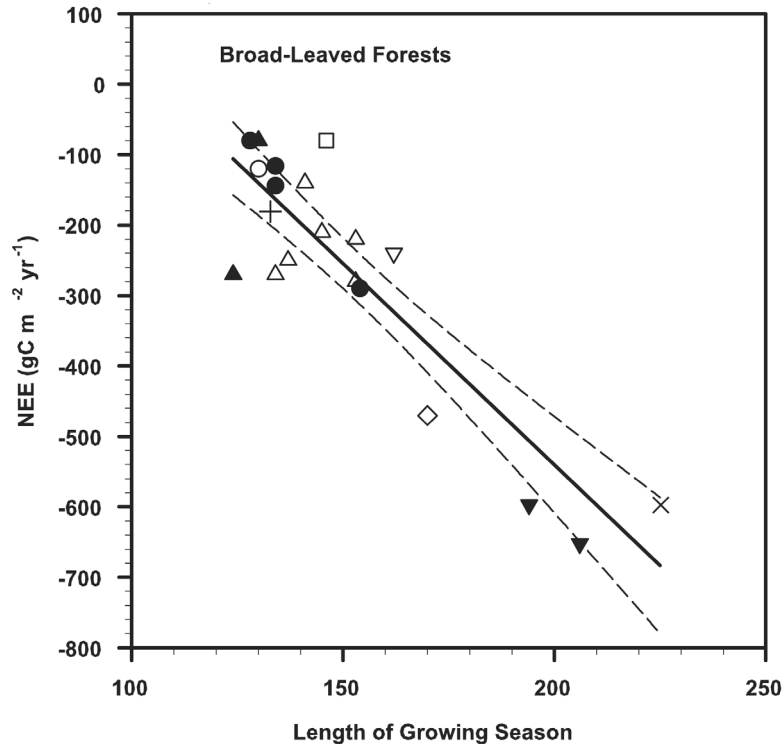


Figure 15.3. Impact of length of growing season on NEE of temperate broad-leaved forests. Length of growing season explains more than 80 percent of the variance of annual NEE across this biome (Baldocchi et al. 2001).

respiration (Hanson et al. 1993). Together, these features reduce *NEE* from values expected during normal, wet summer conditions (Figure 15.2).

In the autumn, photosynthesis ceases, and leaves senesce and drop. Soil respiration, on the other hand, increases because of the input of fresh litter that is readily decomposable, as soils are still warm and autumn rains stimulate litter decomposition (Goulden et al. 1996; Granier et al. 2000, 2002).

On a daily and monthly time scale, ecosystem respiration is mainly a function of soil temperature. The proportionality factor by which ecosystem respiration increases with a 10°C increase in temperature (Q_{10}) ranges between 1.6 and 5.4 (Schmid et al. 2000). Based on such data, one would expect that annual ecosystem respiration would increase as one moves south in the Northern Hemisphere to warmer climates. But across forests in Europe, ecosystem respiration was greater in northern regions (Valentini et al. 2000; Falge et al. 2002). This observation may be an artifact of relatively recent disturbance

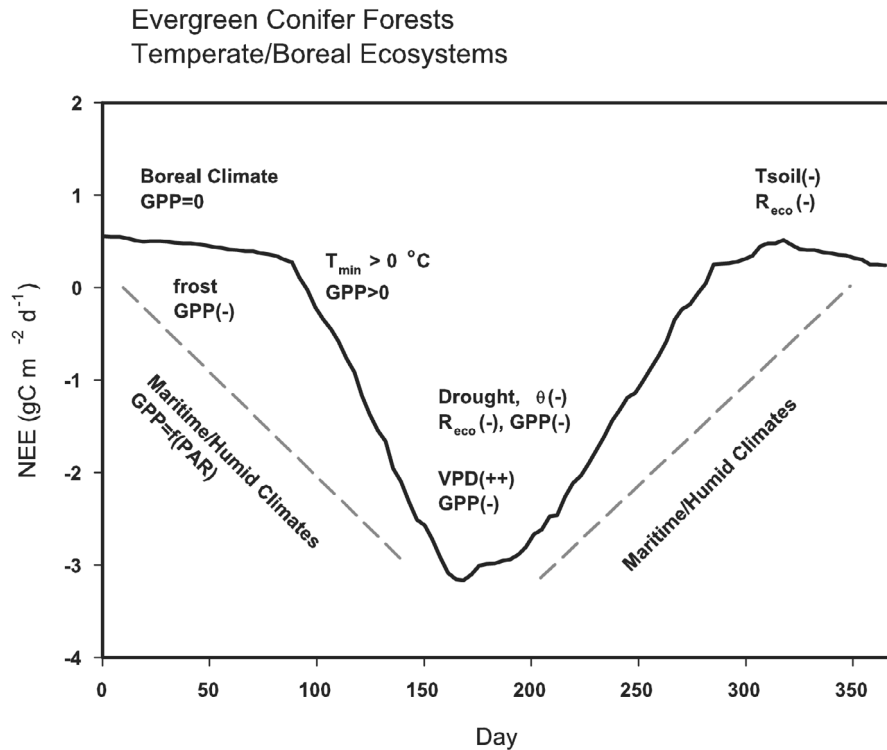


Figure 15.4. Seasonal variation of net CO_2 exchange of temperate, boreal, and alpine conifer forests. Also shown are the environmental and biological factors that affect the seasonal dynamics of CO_2 exchange. VPD is vapor pressure deficit. Data sources: Goulden et al. (1996); Jarvis et al. (1997); Lindroth et al. (1998); Anthoni et al. (2002); Hollinger et al. (1999); Goldstein et al. (2000); Berbigier et al. (2001); Markkanen et al. (2001); Dolman et al. (2002); Monson et al. (2002); Hui et al. (2003).

of carbon pools of northern European forests. Since carbon storage increases with decreasing temperature, any disturbance has the potential to release pools of previously stored carbon and produce relatively low values of NEE (Valentini et al. 2000).

Evergreen Conifer Forests

Evergreen conifer forests occupy a diverse range of climates. They exist at the cold extremes of the boreal zone, in the mild, humid maritime regions, on alpine mountain slopes, and in the semi-arid interior regions of continents. Consequently, the seasonal cycle of carbon exchange of evergreen conifer forests and its sensitivity to environmen-

tal forcings is not universal. Boreal, maritime, and subtropical conifer forests experience different seasonal patterns of CO₂ exchange over a year's time (Figure 15.4).

Forests in maritime climates (Berbigier et al. 2001; Chen et al. 2002) and those growing close to the subtropics (Hui et al. 2003) have the potential to acquire carbon year-round. In contrast, conifer forests in cold boreal or alpine climates experience a restricted period for carbon uptake confined to the summer growing season (Goulden et al. 1996; Jarvis et al. 1997; Lindroth et al. 1998; Hollinger et al. 1999; Markkanen et al. 2001; Monson et al. 2002). During the short summer growing season in the extreme boreal and alpine climate zones, conifer forests frequently lose carbon on individual days. These situations either occur in low-productivity sites on hot, sunny days when high vapor pressure deficits promote stomatal closure (Baldocchi et al. 1997; Hollinger et al. 1999) or on cloudy days when canopy photosynthesis is reduced but the soil is warm and respiration is high (Monson et al. 2002).

Conifer forests in temperate, continental climates experience a longer growing season than forests in boreal and alpine climates. Because temperate conifer forests grow on more productive sites, they maintain higher rates of carbon uptake than do boreal forests (Aubinet et al. 2001; Dolman et al. 2002). Furthermore, they do not experience summer episodes of carbon loss, like boreal forests. Conifers growing in semi-arid regions, such as the western United States, acquire carbon best during the spring and fall and can lose carbon during the prolonged summer drought (Goldstein et al. 2000; Anthoni et al. 2002).

Whether or not conifers gain carbon on fine spring days before the true growing season starts remains an important question. Needles are present and have the potential to assimilate carbon. Physiological studies on *Picea abies* show that uptake rates are low but positive, on fine days with frost events, but that carbon assimilation is suspended when air temperature remains below freezing (Larcher 1975). At the canopy scale, CO₂ uptake for a boreal Scots pine forest is close to zero when the mean air temperature is above, but near, zero Celsius (Markkanen et al. 2001).

Evergreen Broad-leaved Forests

Evergreen broad-leaved forests form dense, closed canopies in humid tropical regions of the Amazon, central Africa, and southeast Asia, as well as the temperate maritime climates of Japan and New Zealand. Evergreen, tropical forests occupy about 15 percent of the global land area. Broad-leaved evergreen trees also exist in a sparser woodlands in seasonally dry climates, such as the Mediterranean-type climates in Australia, California, Chile, Europe, and South Africa. Evergreen woodlands consist of a mix of herbaceous and woody plants, with mixtures ranging from 20/80 to 80/20 (Scholes and Archer 1997). Globally, these woodlands constitute more than 20 percent of the terrestrial biosphere (Melillo et al. 1993).

The aseasonal behavior of the tropical forests contrasts with the strongly seasonal behavior of subtropical and Mediterranean-type forests.

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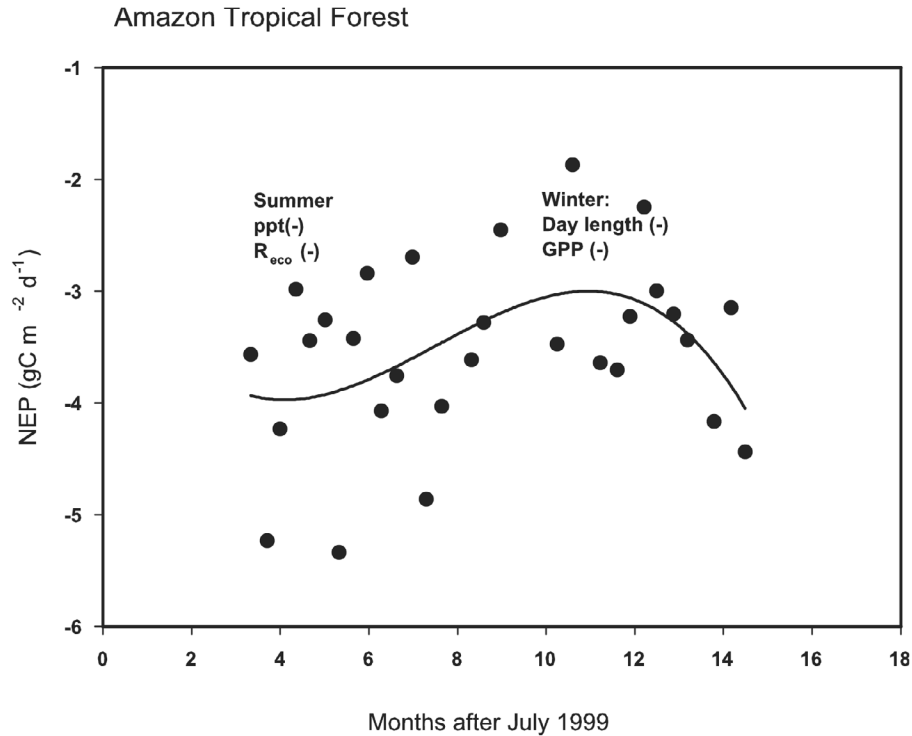


Figure 15.5. Seasonal variation of net ecosystem CO_2 exchange of a tropical forest growing in the Amazon near Manaus, Brazil. Adapted from Araujo et al. (2002).

TROPICAL AND MARITIME CLIMATES

Published data on the seasonal patterns of NEE from evergreen tropical forests are relatively scarce (Grace et al. 1995; Malhi et al. 1998; Araujo et al. 2002). The emerging pattern is that the seasonality of daily-integrated NEE is weak, because of the small range in day length and temperature (Figure 15.5); day length is close to 12 hours long, year-round, and the amplitude of monthly mean air temperatures is less than 4°C . Furthermore, the nearly equal day and night length and warm temperatures experienced by evergreen tropical forests cause them to respire at greater rates and for a longer time than forests, during the growing season, at northern latitudes. As a consequence, daily net rates of carbon exchange are lower in evergreen tropical forests than in temperate broad-leaved forests during the peak of their growing season (Malhi et al. 1998).

Day-to-day variations in GPP are mainly caused by changes in clouds and their modulation of sunlight. Ironically, the seasonal occurrence of drought, which reduces both GPP and R_{eco} , is a major factor modulating NEE of wet tropical forests.

In the temperate maritime climate of New Zealand, broad-leaved, evergreen *Nothofagus* forests experience rates of carbon exchange rates that resemble those of the tropical forests but with lower nocturnal respiration rates (Hollinger et al. 1994). The carbon exchange rates of these forests are also more seasonal than those of tropical forests, operating more like deciduous forests but without the dormant phase. Light-use efficiency of these forests is enhanced by diffuse radiation (Hollinger et al. 1994).

SUBTROPICAL AND MEDITERRANEAN CLIMATES

In the subtropical regions of Africa (tiger bush), Australia (Eucalypt bush), and Brazil (cerrado), the timing of the wet and dry season is the major control on photosynthesis and respiration (Miranda et al. 1997; Eamus et al. 2001; Vourlitis et al. 2001). These woodlands are carbon sinks during the wet season, are carbon neutral during the dry season, and are net sources during the transition period from dry to wet. Changes in vapor pressure deficit and soil moisture are the major modifiers of the maximum value and initial slope of the relationship between sunlight and canopy photosynthesis (Eamus et al. 2001; Vourlitis et al. 2001).

Carbon dioxide exchange of Mediterranean-type ecosystems is out of phase with the seasonal pattern of carbon exchange in temperate forests (Figure 15.6). The prolonged summer drought limits gas exchange (photosynthesis and respiration) (Reichstein et al. 2002a), but rainfall is plentiful during the winter, so the plants are physiologically active when temperatures are cooler, days are shorter, and less sunlight is available than in summer. Consequently, Mediterranean-type ecosystems have less potential to acquire carbon than temperate systems that are active during the warmer and brighter summer.

Another prominent feature, relatively unique to savanna and Mediterranean-type ecosystems, is the effect of episodic rain on soil respiration during the summer (Reichstein et al. 2002b; Rey et al. 2002; Xu and Baldocchi 2003). Two mechanisms may produce enhanced respiration rates after rainfall. One is a physical displacement of soil air and CO₂ by the downward-moving front of water in the soil. But this effect is short-lived, and the volume of air in the soil profile is relatively small. The other mechanism is rapid activation of heterotrophic respiration (Birch 1958).

Grasslands

Grasslands grow in regions with limited annual rainfall (Ehleringer et al. 1997) and possess several modes of function. In the Mediterranean-climate regions of the world, grasslands consist mainly of annual grasses that are functional during the winter and spring growing season and use the C₃ photosynthetic pathway. Grasslands in temperate continental regions are perennial and physiologically active during the summer growing season. Often, C₃ and C₄ grass species coexist, but the proportion of the mixture shifts toward C₄ species as one moves south. In the subtropics, most grasses photosynthesize with the C₄ pathway.

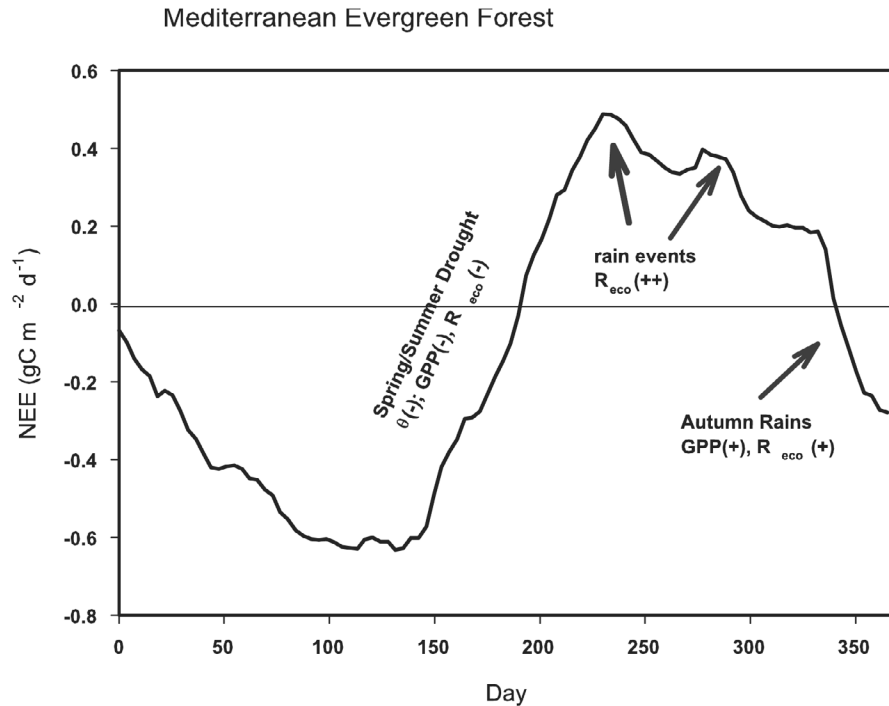


Figure 15.6. Seasonal variation of *NEP* of Mediterranean/subtropical woodland ecosystems and the environmental drivers that perturb the carbon fluxes. Data sources: Leuning and Attiwill (1978); Valentini et al. (1996); Eamus et al. (2001); Reichstein et al. (2002a); unpublished data from Joao Pereira (Fluxnet data archive, <http://www.daac.ornl.gov/FLUXNET/>) and from Baldocchi and Xu (own data and data from AmeriFlux archive).

For Mediterranean-type grasslands, frost limits *GPP* during the winter growing season (Figure 15.7). Rapid growth occurs after the last frosts and ceases when the soil water profile is depleted and the plants die. On a year-to-year basis, timing of cessation of winter rains sets the end of the growing season. Rain pulses during the summer stimulate huge, short-term rates of respiration, as the plants are dead and *GPP* is zero (Xu and Baldocchi 2003). Seed germination and a new growing season commence with the arrival of the autumnal rains. In ecosystems with low *NEE*, such as Mediterranean grasslands, a few large pulses of soil respiration have the potential to change the ecosystem from being a sink of carbon to a source (Xu and Baldocchi 2003).

Perennial temperate grasslands are dormant during the winter, when they are often snow covered. During this period, material in the grass canopy is dead and the system

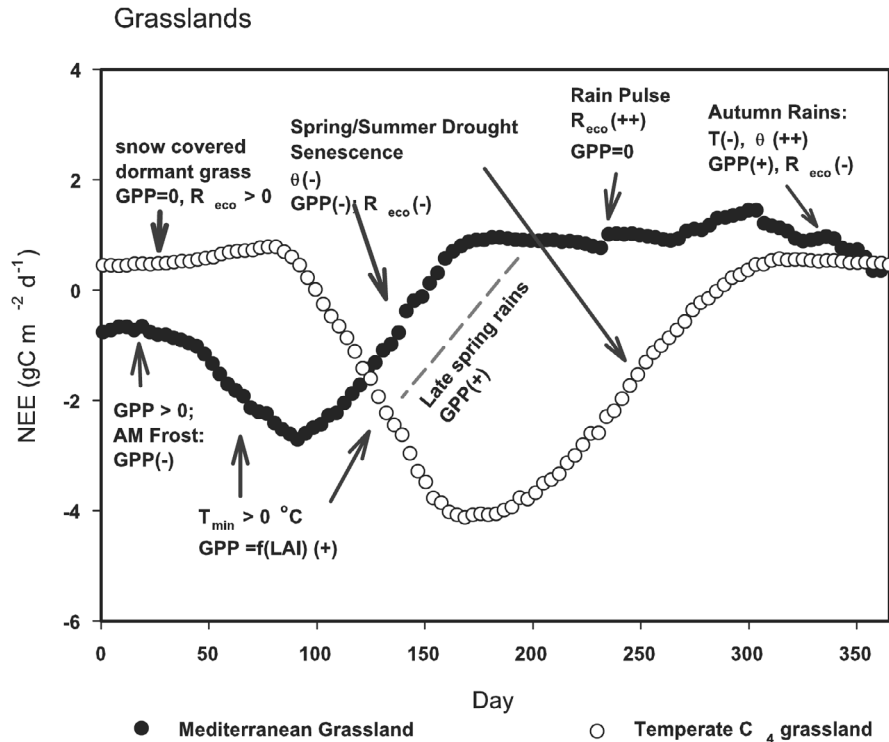


Figure 15.7. Seasonal variation in net CO₂ exchange of a Mediterranean annual grassland and a temperate continental C₄ grassland. Also shown are the environmental and biological factors that affect the seasonal dynamics of CO₂ exchange. Data sources: Valentini et al. (1996); Kim et al. (1992); Saigusa et al. (1998); Meyers (2001); Sukyer and Verma (2001); Flanagan et al. (2002); Xu and Baldocchi (2003).

is respiring. During spring, the grass begins to grow again. Initially, rates of photosynthesis are low, because photons are intercepted by living and dead material. Consequently, the slope of the light response curve changes markedly with leaf area index (Suyker and Verma 2001; Flanagan et al. 2002; Xu and Baldocchi 2003). *NEE* saturates with high sunlight when LAI is low and becomes a quasi-linear function of sunlight as LAI increases and the canopy closes. Summer drought also has a marked effect on *NEE*, limiting photosynthesis and respiration (Kim et al. 1992).

In general, peak rates of CO₂ assimilation are greater for C₄ grasslands than for C₃ grasslands, and they are higher for grasslands with a summer growing season than those with a winter/spring growing season (Figure 15.7).

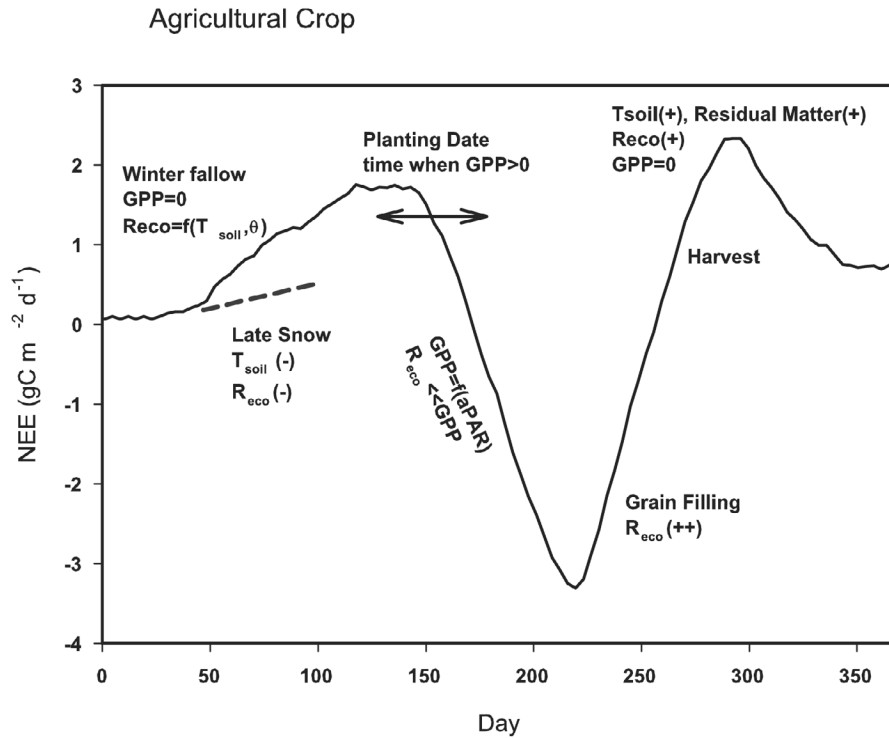


Figure 15.8. Seasonal variation of net CO_2 exchange of an agricultural crop. Also shown are the environmental and biological factors that affect the seasonal dynamics of CO_2 exchange. Data sources: Desjardins (1985); Baldocchi (1994); Rochette et al. (1995); Hanan et al. (2002); Gilmanov et al. (2003); Verma and Sukyer, AmeriFlux (AmeriFlux data archive <http://public.ornl.gov/ameriflux/Participants/Sites/Map/index.cfm>).

Agricultural Crops

The seasonal course of NEE over agricultural regions is much different than that of the native ecosystems we have examined (Figure 15.8). During a long portion of the year, the surface is respiring because it is bare or covered with detritus. At the start of the growing season, the landscape experiences a long period when the canopy is sparse because crops must grow from seed. During this growth period, rates of net CO_2 uptake by crops are relatively low, compared with those of temperate and conifer forests. Maximum rates of carbon uptake occur after the crop achieves closure and are among the highest of all vegetation types, since crops are selected for high productivity, they grow on very fertile soils, they are fertilized, and they tend to have abundant

soil moisture due to rainfall or irrigation (Ruimy et al. 1995). The period during which a crop canopy is closed is rather short, limiting the duration of maximum uptake rates. The occurrence of anthesis is another factor limiting carbon uptake rates of crops during the peak growing period. Respiration in wheat jumps distinctly after anthesis, as a substantial amount of assimilated energy is used to produce reproductive organs, which have high respiration costs (Baldocchi 1994; Rochette et al. 1995). During autumn and after harvest, ecosystem respiration peaks again, owing to the new input of fresh decomposable material and the warmth of the soils. Soil respiration during the fallow period is much lower than in native ecosystems, which have more decaying detritus on the ground or are maintaining the catabolism of a substantial overstory of trees and shrubs.

Because crops are fertilized and grow in regions with ample rainfall or are irrigated, sunlight is the main factor limiting *NEE* of crops. Like grasslands, the light response curve saturates when the canopy is sparse and becomes quasi-linear after full closure (Baldocchi 1994; Rochette et al. 1995; Ruimy et al. 1995). Photosynthetic pathway (C_3 or C_4) also affects maximum rates of CO_2 uptake.

Northern Wetlands/Tundra

Northern wetlands and tundra ecosystems exist in the extremely cold desert climate of the Arctic. Yet, they often remain waterlogged during the summer, as the water balance is positive—precipitation exceeds evaporation. This combination of factors affects the seasonality and rates of carbon exchange experienced by northern wetlands and tundra (Figure 15.9). Despite extreme cold temperatures during the winter, these ecosystems continue to respire (Vourlitis et al. 2000). Respiration occurs because microbes can remain active and decompose organic matter deep in the soil in unfrozen zones.

Since the growing season is very short and the amount of vegetation is low, rates of net carbon uptake during the summer are low. Functionally, soil temperature and solar radiation control net CO_2 balance during the period from snow melt to early autumn. On a seasonal and interannual basis, these ecosystems are sensitive and vulnerable to changes in the water table, as large stores of carbon remain. Lowering the water table allows stored carbon pools to oxidize, causing the ecosystem to be a net source of carbon during the growing season (Vourlitis et al. 2000; Lloyd 2001).

Conclusions

For dominant ecosystems of the world, *NEP* and its component fluxes, *GPP* and R_{eco} , exhibit diverse responses to seasonal changes in weather and climate. Ecosystems growing in a single environment and exposed to the same climate can show remarkable differences in the magnitude of carbon and energy fluxes, as well in their seasonal phasing. The implication of these patterns is that the complex mosaic of geographical

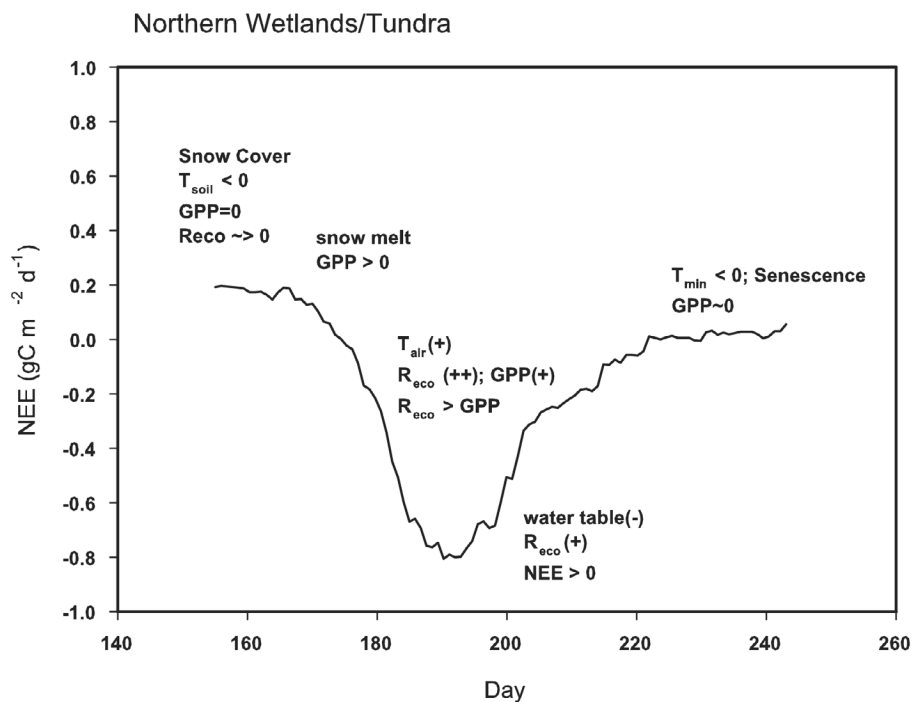


Figure 15.9. Seasonal variation in net CO_2 exchange of a northern wetland and tundra. Also shown are the environmental and biological factors that affect the seasonal dynamics of CO_2 exchange. Data are gap filled and smoothed. Data sources: Shurpali et al. (1995); Griffis et al. (2000); Soegaard et al. (2000); Vourlitis et al. (2000); Lloyd (2001).

variations in a given region cannot be simply represented and modeled as a single “green slab.” A reasonably accurate land use/cover (forests, grasslands, crops, etc.) map is a prerequisite for correctly representing the aggregation of different functional responses and biospheric fluxes.

The examples in this chapter also highlight the vulnerability of the terrestrial carbon sink. Climate changes and disturbance regimes affect the rates and patterns of biospheric carbon exchanges. In boreal regions changes in seasonal dynamics and length of the growing season can have a profound impact on carbon oxidation, even when the annual mean temperature is not perturbed. And if warm and dry spells promote forest fires, the landscape can quickly change from a weak carbon sink to a large source of carbon to the atmosphere. In temperate regions water limitations on soil organic matter decomposition plays a significant role and can limit carbon oxidation, despite changes in temperature. In the tropics light-use efficiency and changes in the ratio of direct versus diffuse radiation can also play an important role in the future carbon exchanges.

These are only few examples of the complexity of the terrestrial ecosystem responses and the parameters that drive their carbon balance. More work is needed to understand these emergent properties, which can have important impacts on the future of the land carbon sink, and to improve our global models. For this reason the concept of “ecosystem physiology,” the integrated response of a vegetation community to environmental factors including carbon, energy, and water, is becoming a useful new tool for understanding the dynamics of the terrestrial biota and its relation with Earth system processes.

Acknowledgments

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