

# The Biosphere

## The Carbon Cycle of Terrestrial Ecosystems

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### INTRODUCTION

Photosynthesis is the biogeochemical process that transfers carbon from its oxidized form, CO<sub>2</sub>, to the reduced (organic) forms that result in plant growth. Directly or indirectly, photosynthesis provides the energy for all other forms of life in the biosphere, and the use of plant products for food, fuel, and shelter brings photosynthesis into our daily lives. The fossil fuels that power modern society are derived from plant photosynthesis in the geologic past (Dukes 2003). Plant growth affects the composition of the atmosphere (Chapter 3) and the development

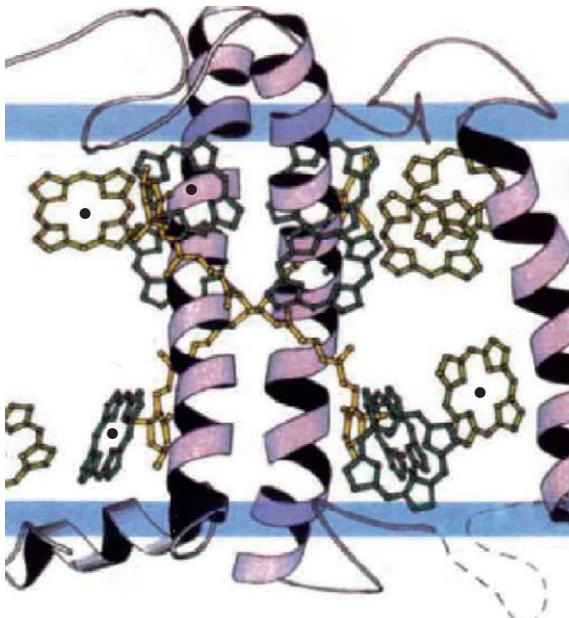
of soils (Chapter 4), linking photosynthesis to other aspects of global biogeochemistry. Indeed, the presence of organic carbon in soils and sediments and O<sub>2</sub> in our atmosphere provides a striking contrast between the *biogeochemistry* on Earth and the simple geochemistry that characterizes our neighboring planets.

In this chapter we consider the measurement of net primary production—the rate of accumulation of organic carbon in land plants. A similar treatment of photosynthesis in the world's oceans is given in Chapter 9. The rate of plant growth varies widely over the land surface. Deserts and continental ice masses may have little or no net primary production (NPP), while tropical rainforests can show annual production of >1000 g C/m<sup>2</sup>.

Various environmental factors affect the rate of net primary productivity on land and the total storage of organic carbon in plant tissues (biomass), dead plant parts (detritus), and soil organic matter. As any home gardener knows, light and water are important, but plant growth is also determined by the stock of available nutrients in the soil. These nutrients are ultimately derived from the atmosphere or from the underlying bedrock (Table 4.5). The overall storage of carbon on land is determined by the balance between primary production and decomposition, which returns carbon to the atmosphere as CO<sub>2</sub>.

## PHOTOSYNTHESIS

Containing a central atom of magnesium, the chlorophyll molecule is a prime example of how plants have incorporated an abundant product of rock weathering as an essential element in their biochemistry (Figure 5.1). When photosynthetic pigments absorb sunlight, a few of the chlorophyll molecules are oxidized—passing an electron to a sequence of proteins



**FIGURE 5.1** Molecular structure of the light-harvesting complex of photosystem II, showing the position of the Mg-porphyrin groups, shown with black dots. Source: From Kuhlbrandt et al. (1994).

that ultimately add the electron to a high-energy molecule, known as nicotinamide adenine dinucleotide phosphate ( $\text{NADP}^+$ ), which is thus reduced to form NADPH. The chlorophyll molecule regains an electron from a water molecule, which is split by an enzyme containing manganese, calcium, and chlorine, in a complex three-dimensional structure (Yano et al. 2006, Guskov et al. 2009, Umena et al. 2011). This reaction is the origin of  $\text{O}_2$  in the Earth's atmosphere:



In all cases, the photosynthetic pigments and proteins are embedded in a cell membrane, which allows protons (e.g.,  $\text{H}^+$  of Eq. 5.1) to build up to high concentrations on one side of the membrane and for this potential energy to be captured in a high-energy compound, adenosine triphosphate or ATP. In higher plants, the accumulation of protons occurs within the chloroplasts of leaf cells, whereas in photosynthetic bacteria, the reaction is conducted across the external cell membrane.

The high-energy compounds NADPH and ATP are then used by a suite of enzymes to reduce  $\text{CO}_2$  and build carbohydrate molecules. The reaction begins with the enzyme ribulose bisphosphate carboxylase, also known as *Rubisco*, which adds  $\text{CO}_2$  to the basic carbohydrate unit.<sup>1</sup> The overall reaction for photosynthesis is shown in the following equation,



but we should remember that the process occurs in two stages.

First, the capture of light energy allows water molecules to be split and high-energy molecules to form. This drives a second reaction in which  $\text{CO}_2$  is converted to carbohydrate. The efficiency of photosynthesis relative to the sunlight absorbed by chlorophyll is known as the *quantum yield efficiency*, which is normally close to 0.081 moles of  $\text{CO}_2$  captured in carbohydrate per mole of photons absorbed, when soil water and other environmental factors are optimal (Singsaas et al. 2001). Photosynthesis can occur in markedly low-light environments, such as beneath snow and ice and under translucent rocks (Starr and Oberbauer 2003, Gradinger 1995, Schlesinger et al. 2003); moonlight, however, is not enough (Raven and Cockell 2006).

The carbon dioxide used in photosynthesis diffuses into plant leaves through pores, known as *stomates*, which are generally found on the lower surface of broad-leaf plants. One factor that determines the rate of photosynthesis is the stomatal aperture, which plant

<sup>1</sup> For understanding global biogeochemistry, we focus on the photosynthesis of C3 plants, which account for the overwhelming proportion of plant biomass and net primary productivity on Earth. C3 plants are so named because the first product of the photosynthetic reaction is a carbohydrate containing three carbon atoms. However, some plant species, largely warm-climate grasses, conduct photosynthesis by another biochemical pathway, known as C4 photosynthesis (Ehleringer and Monson 1993). C4 plants may account for up to 23% of global net primary production (Lloyd and Farquhar 1994, Still et al. 2003), but their contribution to global biomass is small because most species are not woody. The overall photosynthetic reaction is identical to Eq. 5.2, but C4 plants have different water-use efficiency and a different C-isotopic fractionation in their tissues (average  $-12\text{\textperthousand}$ ). The isotopic ratio of plant debris preserved in soils can be used to trace changes in the past distribution of C3 and C4 plants (e.g., Quade et al. 1989a, Ambrose and Sikes 1991).

physiologists express as stomatal *conductance* in units of cm/sec. Stomatal conductance is controlled primarily by the availability of light and water to the plant and the concentration of CO<sub>2</sub> inside the leaf, where it is consumed by photosynthesis. When well-watered plants are actively photosynthesizing, internal CO<sub>2</sub> is relatively low and stomates show maximum conductance. Under such conditions, the amount and activity of Rubisco may determine the rate of photosynthesis (Sharkey 1985).

## Water-Use Efficiency

There is a trade-off in photosynthesis; when plant stomates are open, allowing CO<sub>2</sub> to diffuse inward, O<sub>2</sub> and H<sub>2</sub>O diffuse outward to the atmosphere. The loss of water through stomates, *transpiration*, is the major mechanism by which soil moisture is returned to the atmosphere (Chapter 10). In the Hubbard Brook Experimental Forest in New Hampshire (see Chapter 4), about 25% of the annual precipitation is lost by plant uptake and transpiration; stream flow increased by 26 to 40% when the forest was cut (Pierce et al. 1970). Because water for plant growth is often in short supply (Kramer 1982), these large losses of water by plants are somewhat surprising. One might expect natural selection for more efficient use of water by plants.

Plant physiologists express the loss of water relative to photosynthesis as water-use efficiency (WUE), namely,

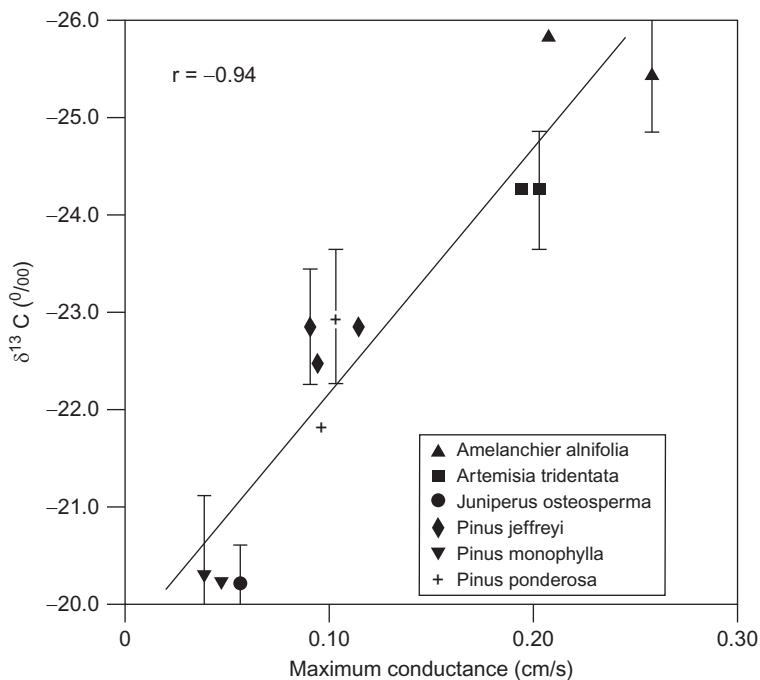
$$\text{WUE} = \text{mmoles of CO}_2 \text{ fixed}/\text{moles of H}_2\text{O lost}. \quad (5.3)$$

For most plants, water-use efficiency typically ranges from 0.86 to 1.50 mmol/mol, depending on environmental conditions (Osmond et al. 1982). Water-use efficiency is higher at lower stomatal conductance.

Rising concentrations of CO<sub>2</sub> in the atmosphere allow the same rate of photosynthesis to occur at lower stomatal conductance, thus increasing WUE (Bazzaz 1990, Ceulemans and Mousseau 1994). There is also some evidence that the number of stomates per unit of leaf surface has declined as atmospheric CO<sub>2</sub> rose during the Industrial Revolution (Woodward 1987, 1993; Peñuelas and Matamala 1990). The olive leaves preserved in King Tut's tomb (1327 B.C.) have a higher density of stomates than the leaves of the same species now growing in Egypt (Beerling and Chaloner 1993a).

Equation 5.3 largely applies to short-term experiments in the laboratory. For the biogeochemist, long-term average WUE can be estimated from the carbon isotope composition of plant tissues, especially tree rings. This method is based on the observation that the diffusion of <sup>12</sup>CO<sub>2</sub> is more rapid than that of <sup>13</sup>CO<sub>2</sub>, which has a slightly higher molecular weight. Thus, over any time period, a greater proportion of <sup>12</sup>CO<sub>2</sub> enters the leaf than <sup>13</sup>CO<sub>2</sub>. Inside the leaf, ribulose bisphosphate carboxylase also has a higher affinity for <sup>12</sup>CO<sub>2</sub>. As a result of these factors, plant tissue contains a lower proportion of <sup>13</sup>CO<sub>2</sub> than the atmosphere by about 2% (= 20‰) (O'Leary 1988). The discrimination (*fractionation*) between carbon isotopes is expressed relative to an accepted standard as

$$\delta^{13}\text{C} = \left[ \frac{{}^{13}\text{C}/{}^{12}\text{C}_{\text{sample}} - {}^{13}\text{C}/{}^{12}\text{C}_{\text{standard}}}{{}^{13}\text{C}/{}^{12}\text{C}_{\text{standard}}} \right] \times 1000 \quad (5.4)$$



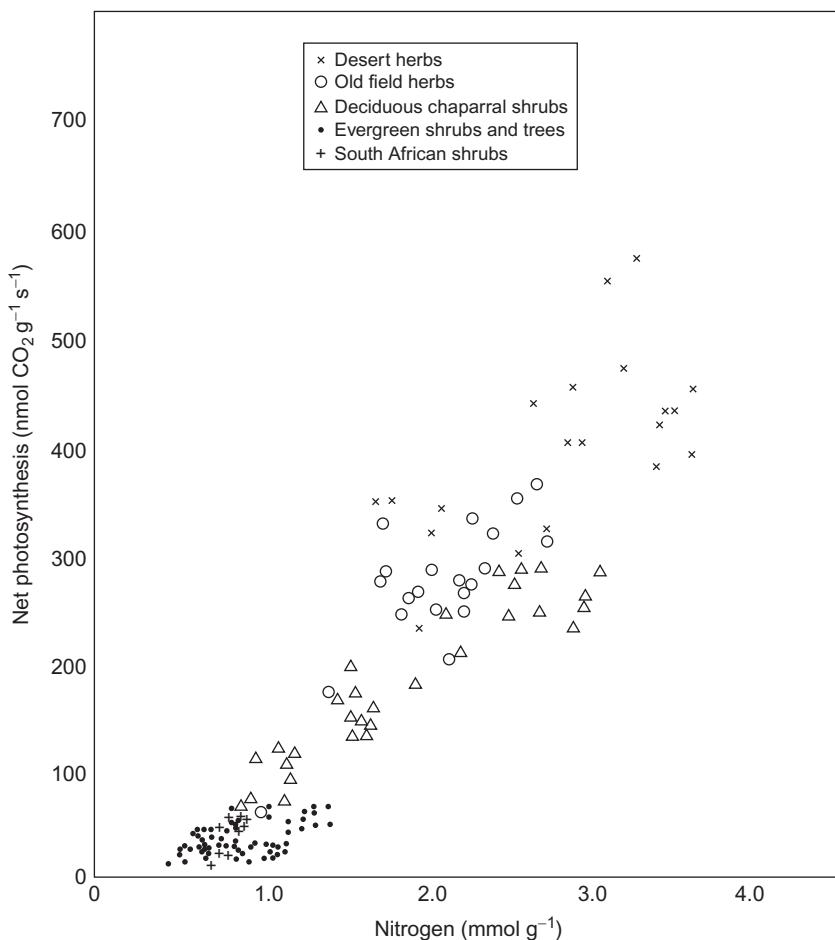
**FIGURE 5.2** Relationship between the content of  $^{13}\text{C}$  in plant tissues (expressed as  $\delta^{13}\text{C}$ ) and stomatal conductance for a variety of plant species in western Nevada. Source: Modified from DeLucia et al. (1988).

using the units of parts per thousand parts (‰). Because atmospheric  $\text{CO}_2$  shows an isotopic ratio of  $-8.0\text{\textperthousand}$  versus the standard, most plant tissues show  $\delta^{13}\text{C}$  of about  $-28\text{\textperthousand}$ —that is,  $(-8\text{\textperthousand}) + (-20\text{\textperthousand})$ . Sedimentary organic carbon with this isotopic signature is useful in determining the antiquity of photosynthesis as a biochemical process (Figure 2.6).

The discrimination between  $^{12}\text{CO}_2$  and  $^{13}\text{CO}_2$  during photosynthesis is greatest (most negative  $\delta^{13}\text{C}$ ) when stomatal conductance is high (Figure 5.2). When stomates are partially or completely closed, nearly all of the  $\text{CO}_2$  inside the leaf reacts with ribulose bisphosphate carboxylase and there is less fractionation of the isotopes. Therefore, the isotopic ratio of plant tissue is directly related to the average stomatal conductance during its growth, providing a long-term index of water-use efficiency (Farquhar et al. 1989). Significantly,  $\delta^{13}\text{C}$  values of preserved plant materials and tree rings indicate that WUE of plants increased as the concentration of atmospheric  $\text{CO}_2$  rose at the end of the last glacial period (Van de Water et al. 1994) and during the last several hundred years (Peñuelas and Azcón-Bieto 1992, Feng 1999, Sauer et al. 2004, Watmough et al. 2001, Kohler et al. 2010).

## Nutrient-Use Efficiency

Over a broad range of plant species, the rate of photosynthesis is directly correlated to leaf nitrogen content when both are expressed on a mass basis (Reich et al. 1992, 1999, Atkinson et al. 2010; Figure 5.3). Most leaf nitrogen is contained in enzymes; by itself, ribulose bisphosphate carboxylase usually accounts for 20 to 30% of leaf nitrogen (Evans 1989). Seemann et al.



**FIGURE 5.3** Relationship between net photosynthesis and leaf nitrogen content among 21 species from different environments. Source: From Field and Mooney (1986). Used with permission of Cambridge University Press.

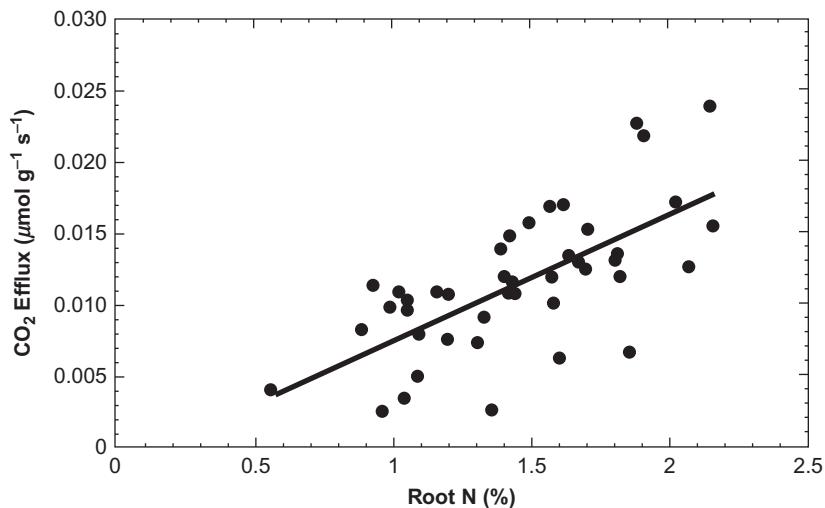
(1987) found that photosynthetic potential is directly related to the content of ribulose bisphosphate carboxylase and leaf nitrogen in several species, suggesting that the availability of nitrogen determines leaf enzyme content and, thus, the rate of photosynthesis in land plants. In addition to nitrogen, leaf phosphorus content may be an important determinant of photosynthetic capacity in some species (Reich and Schoettle 1988, DeLucia and Schlesinger 1995, Raaijmakers et al. 1995), and adequate P often determines the relationship of photosynthesis to N (Reich et al. 2009). Despite their central role in the biochemistry of photosynthesis, magnesium and manganese are seldom in short supply for plant growth.

Because most land plants grow under conditions of nitrogen deficiency, we might expect adjustments in nutrient use to maximize photosynthesis under varying conditions of soil fertility. The rate of photosynthesis per unit of leaf nitrogen—the slope of the line in Figure 5.3—would be one measure of nutrient-use efficiency (NUE) (Evans 1989). Overall, the data of this figure would seem to indicate that most species have similar photosynthetic

NUE, but subtle variations in NUE are seen among different types of plants (Reich et al. 1995) and among plants grown at different levels of fertility (Reich et al. 1994). For many plant species, when leaf nutrient content increases (by fertilization), NUE declines (Ingestad 1979a, Lajtha and Whitford 1989). Nutrient-use efficiency also appears inversely correlated to WUE across many species (Field et al. 1983, DeLucia and Schlesinger 1991).

## RESPIRATION

Photosynthesis is usually measured by placing leaves or whole plants in closed chambers and measuring the uptake of CO<sub>2</sub> or release of O<sub>2</sub>. The rates are a measure of *net* photosynthesis by the plant—that is, the fixation of carbon in excess of the simultaneous release of CO<sub>2</sub> by plant metabolism. Plant metabolism, known as respiration, is largely the result of mitochondrial activity in plant cells, and it is correlated to the nitrogen content, which is a good index of metabolic activity in most plant tissues (Figure 5.4; see also Ryan 1995, Vose and Ryan 2002, Reich et al. 2006). In woody plants, a large fraction of the respiration is contributed by stems and roots owing to their large contribution to total plant biomass (Amthor 1984, Ryan et al. 1994). For leaf tissues, rates of respiration are higher in the daytime than during the night as a result of the additional process of photorespiration.<sup>2</sup>



**FIGURE 5.4** Root respiration as a function of nitrogen content (%) in roots of loblolly and ponderosa pine. Source: From Griffin et al. (1997). Used with permission of Springer.

<sup>2</sup> Photorespiration is not simply respiration during the day, but a higher level of plant respiration that is observed in sunlight as a result of a competitive reaction of Rubisco with O<sub>2</sub>, which the plant must expend energy to reverse (Sharkey 1988). The reaction with O<sub>2</sub> is a function of the O<sub>2</sub>/CO<sub>2</sub> ratio in the chloroplast, which is greater at high temperatures and during drought. Although photorespiration has generally been regarded as detrimental to plant growth, there is some evidence that the process is important to nitrate assimilation in land plants (Rachmilevitch et al. 2004) and to the protection of the photosynthetic mechanism at high light during periods of drought (Mahall and Schlesinger 1982).

About one-half of the carbon fixation by photosynthesis is resired by plants, so the gross rate of photosynthesis is often twice the measured rate of carbon uptake (Farrar 1985, Amthor 1989). For long-lived woody plants, maintenance respiration increases with stand age, consuming an increasing fraction of the gross photosynthesis and contributing to the reduction in the rate of plant growth with age (Kira and Shidei 1967, DeLucia et al. 2007, Piao et al. 2010). Plant respiration generally increases with increasing temperature, accounting for high rates of respiration in tropical forests and potentially higher rates of plant respiration with global warming (Ryan 1991; Ryan et al. 1994, 1995). In desert environments, total respiration in trees may increase as plants allocate more tissue to sapwood (Callaway et al. 1994). The increase in plant respiration in warmer conditions, versus the relatively insensitive response of photosynthesis to temperature, has important implications for global net primary production in the face of ongoing global climate change (Dillaway and Kruger 2010, Cai et al. 2009, Piao et al. 2010).

## NET PRIMARY PRODUCTION

The rate of plant growth, *net primary production* (NPP), measured by ecologists in the field is analogous to the rate of net photosynthesis measured by plant physiologists in the laboratory. For plants in nature, we say that

$$\text{Gross primary production} - \text{plant respiration} = \text{net primary production} \quad (5.5)$$

NPP is, however, not directly equivalent to plant growth as measured by foresters, ranchers, and farmers. Some fraction of NPP is lost to herbivores, fires, and in the death and loss of tissues, known collectively as *litterfall*. Foresters frequently call the NPP that remains the *true increment*, which may add to the accumulation of biomass over many years. When mortality occurs during forest development, the true increment is the net increase in the mass of woody tissue in living plants, after subtracting the mass of individuals that die over the same interval (Clark et al. 2001).

The annual accumulation of organic matter per unit of land is a measure of NPP, often expressed in units of  $\text{g m}^{-2} \text{ yr}^{-1}$ . Plant tissue typically contains about 45 to 50% carbon, so division by two is a convenient way to convert the accumulation of organic matter to carbon fixation (Reichle et al. 1973a). Net primary production can also be expressed in units of energy, by measurements of the caloric content of various plant tissues (Paine 1971, Darling 1976). Calories are particularly useful for expressing the efficiency of photosynthesis relative to the receipt of sunlight energy. Net primary production typically increases as a function of intercepted radiation (e.g., Runyon et al. 1994), but even in forests, photosynthesis usually captures only about 1% of the total energy received from sunlight (Botkin and Malone 1968, Reiners 1972, Schulze et al. 2010). Even crop plants show maximum efficiencies of <5% of incident sunlight (Amthor 2010).

### Measurement and Allocation of NPP

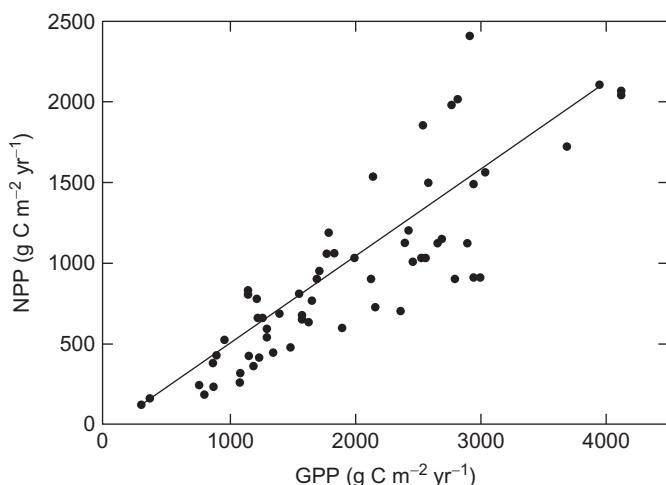
Traditional methods for measuring NPP in forests and shrublands involve the harvest of vegetation and calculation of the annual growth of wood and the mass of foliage at the peak of annual leaf display (Clark et al. 2001). The harvest data of a few individuals are used to

calculate the mass and increment in plants of varying size by virtue of tightly constrained relationships between diameter, height, mass, and growth of individual plants—known as *plant allometry* (Whittaker and Marks 1975, Enquist et al. 2007, Niklas and Enquist 2002).

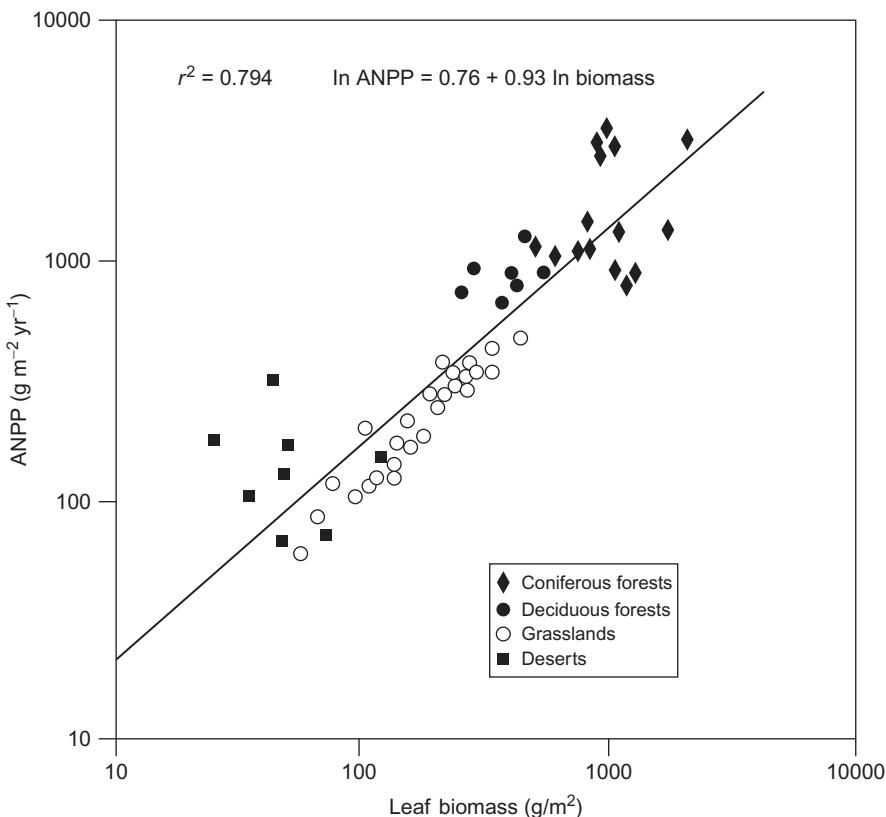
Independent estimates of the seasonal loss of plant parts can be obtained from collections of plant litterfall throughout the year. In grasslands, where there is little or no true increment, estimates of NPP generally involve the difference between the mass of tissue harvested from small plots at the beginning and the end of the growing season (e.g., Wiegert and Evans 1964, Lauenroth and Whitman 1977, Singh et al. 1975). These estimates must be corrected for the consumption and loss of tissues during the same period. Similar approaches are used to measure the growth of roots by sequential coring throughout the growing season (Neill 1992, Vogt et al. 1998, Makkonen and Helmisaari 1999).

Allocation of net primary production varies with vegetation type and age. In forests, 25 to 35% of aboveground production is found in leaves (Whittaker 1974), with this percentage tending to decrease with stand age. Allocation to foliage in shrublands is generally greater, ranging from 35 to 60% in desert and chaparral shrubs (Whittaker and Niering 1975, Gray 1982). In grassland communities, essentially all aboveground net primary production is found in photosynthetic tissues. Across a broad range of species, allocation of photosynthate to leaf growth relative to stem growth is 0.53 (Niklas and Enquist 2002).

As seen in laboratory studies of photosynthesis, plant respiration accounts for about half of GPP in ecosystem studies (Waring et al. 1998, Litton et al. 2007; [Figure 5.5](#)). As a result of their massive structure and high environmental temperatures, tropical forests may expend a greater percentage of their GPP in respiration (Whittaker and Marks 1975, Ryan et al. 1994, Luyssaert et al. 2007, Piao et al. 2010), leaving less for wood growth. Comparing plant communities in different regions, Jordan (1971) found that the proportional allocation of NPP to wood growth was greater in boreal forests than in tropical forests—that is, there is greater wood production per unit of foliage in boreal forests. Webb et al. (1983) found a logarithmic relationship between total aboveground NPP and foliage biomass for a variety of plant communities in North America, with some deserts showing exceptionally high values of this ratio



**FIGURE 5.5** Relationship between net primary production (NPP) and gross primary production (GPP) in different forest types. Source: From DeLucia et al. (2007).



**FIGURE 5.6** Using data from a variety of ecosystems in North America, Webb et al. (1983) found a strong relation between the annual aboveground NPP and leaf biomass.

(Figure 5.6). Compared to communities with abundant precipitation, however, desert shrublands show relatively low allocation of NPP to wood production (Jordan 1971), perhaps as a result of a large allocation to roots (Wallace et al. 1974, Mokany et al. 2006).

Because measurements of roots are difficult, many studies of NPP include data only for the aboveground tissues. Root biomass ranges between 20 and 40% of total biomass in forest ecosystems (Vogt et al. 1996, Poorter et al. 2012), and the annual growth of root tissues accounts for a significant fraction of the total NPP in most communities—averaging about 15 to 25% across a broad range of plant size (Pan et al. 2006; Niklas and Enquist 2002; K. Niklas, personal communication, 2010). Some NPP is lost in soluble organic compounds released from roots, perhaps as much as 20% in some circumstances (van Hees et al. 2005, Fahey et al. 2005).<sup>3</sup> Trees allocate proportionally more photosynthate to root growth in low-fertility soils (Axelsson

<sup>3</sup> Various workers use “total belowground allocation” to describe the total allocation of GPP to root and mycorrhizal respiration, to leakage of root exudates, and to root production—only the latter has traditionally been considered a component of NPP (Raich and Nadelhoffer 1989).

1981, Gower et al. 1992, Powers et al. 2005), although the absolute amount of root growth is greatest on sites with high NPP (Raich and Nadelhoffer 1989, Aerts and Chapin 2000).

Edwards and Harris (1977) reported that the growth and death of roots in a forest in Tennessee delivered  $733 \text{ g C m}^{-2} \text{ yr}^{-1}$  to the soil, whereas the aboveground production was  $685 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Reichle et al. 1973a). Similarly, roots composed more than half of the NPP in coniferous forests in Washington (Table 5.1) and in the deciduous forest at Hubbard Brook (Fahey and Hughes 1994). An even larger proportion of total NPP is allocated to root growth in many grassland ecosystems (Lauenroth and Whitman 1977, Warembourg and Paul 1977).

Although there are strong relations between above- and belowground biomass (Cairns et al. 1997, Enquist and Niklas 2002, Mokany et al. 2006, Cheng and Niklas 2007), there are no obvious generalizations that allow us to predict the allocation of NPP to the growth of shoots and roots worldwide (Nadelhoffer and Raich 1992, Gower et al. 1996, Litton et al. 2007).

Much of the plant photosynthate that is allocated belowground supports the growth of roots  $< 2 \text{ mm}$  diameter, known as fine roots. In grasslands, the total length of fine roots may exceed 100 km beneath each square meter of the soil (Jackson et al. 1997). In most ecosystems,

**TABLE 5.1** Net Primary Production in 23- and 180-yr-old *Abies amabilis* Forests in the Cascade Mountains in Washington

Aboveground	23-yr-old		180-yr-old	
	$\text{g m}^{-2} \text{ yr}^{-1}$	% of total	$\text{g m}^{-2} \text{ yr}^{-1}$	% of total
Biomass increment				
Tree total	426		232	
Shrub stems	6		<1	
Total	432	18.37	232	9.33
Detritus production				
Litterfall	151		218	
Mortality	30			
Herb layer turnover	32		5	
Total	213	9.06	223	8.97
<b>Total aboveground</b>	<b>645</b>	<b>27.42</b>	<b>455</b>	<b>18.30</b>
Belowground				
Roots				
Fine ( $\leq 2 \text{ mm}$ )	650	27.64	1290	51.87
Fibrous-textured	571		1196	
Mycorrhizal	79		94	
Coarse ( $> 2 \text{ mm}$ )	358		324	
Angiosperm fine root turnover	373		44	
Total root turnover	1381	58.72	1658	66.67
Mycorrhizal fungal component	326	13.86	374	15.04
Total below ground	1707	72.58	2032	81.70
<b>Ecosystem total</b>	<b>2352</b>	<b>2352</b>	<b>2487</b>	

Source: Form Vogt et al. (1982). Used with permission of Ecological Society of America.

about half of these roots die each year (Gill and Jackson 2000), consistent with observations of roots using transparent soil tubes, known as *minirhizotrons* (Strand et al. 2008, Eissenstat and Yanai 1997). However, studies following the disappearance of carbon from isotopic-labeled root systems indicate considerable longevity of some fine roots—sometimes exceeding 5 years (Matamala et al. 2003, Gaudinski et al. 2001, Riley et al. 2009). It is likely that many root systems consist of a large fraction of roots with relatively short longevity and a smaller population that lasts several years (Joslin et al. 2006, Gaudinski et al. 2010).

## NET ECOSYSTEM PRODUCTION AND EDDY-COVARIANCE STUDIES

As long as they are growing, plants allocate some NPP to the accumulation of biomass, with the remaining NPP passing to herbivores or decomposers, which convert organic carbon to CO<sub>2</sub> and return it to the atmosphere. We define *net ecosystem production* (NEP) as

$$\text{NEP} = \text{NPP} - (\text{R}_h + \text{R}_d); \quad (5.6)$$

thus,

$$\text{NEP} = \text{GPP} - (\text{R}_p + \text{R}_h + \text{R}_d), \quad (5.7)$$

where R<sub>p</sub>, R<sub>h</sub>, and R<sub>d</sub> represent the respiration of plants, herbivores, and decomposers, respectively.<sup>4</sup> Except in unusual circumstances, NEP will be a partial fraction of NPP. In young forests, NEP may be 50% of NPP, but in older stands, when vegetation is not accumulating biomass, nearly all the NEP will be found in small increments to soil organic matter (Schlesinger 1990, Law et al. 2003, Pregitzer and Euskirchen 2004).

In recent years, atmospheric scientists have made indirect measurement of net ecosystem production of whole ecosystems by calculating the net uptake of CO<sub>2</sub> within a hypothetical column of the atmosphere with a small ground “footprint,” typically 1 m<sup>2</sup>. Substantial theory underlies this approach. Namely, if there is no carbon exchange between the atmosphere and the biosphere, such as over the surface of a parking lot, we would expect the atmosphere to show a uniform concentration of CO<sub>2</sub> at all heights above the surface—with values close to the global average in the troposphere (~400 ppm; Table 3.1). In contrast, inside the canopy of a forest, photosynthesis will deplete CO<sub>2</sub> during the day, while CO<sub>2</sub> will be enriched in samples taken near the soil surface, where it is emitted by the activity of decomposers. These differences in CO<sub>2</sub> concentration with height persist in the face of winds that might transport fresh air from outside the ecosystem or mix air within the forest, resulting in a uniform concentration of CO<sub>2</sub>. Thus, if we measure the concentration of CO<sub>2</sub> at various heights within the forest and the delivery of fresh air at each height, then we can estimate the carbon uptake, or CO<sub>2</sub> release, necessary to maintain the differences in CO<sub>2</sub> at different heights. Integrating over height and time, these measurements would indicate the net exchange of CO<sub>2</sub>—net ecosystem production—in a forest or other types of vegetation.

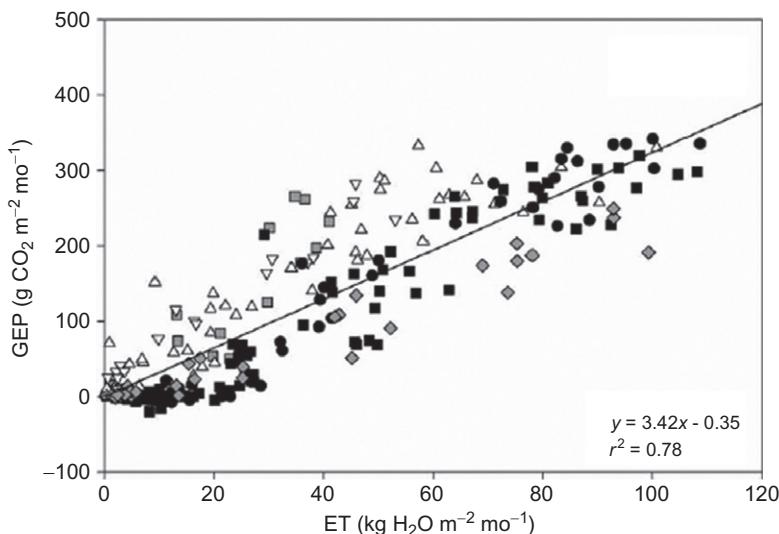
<sup>4</sup> When calculated for large areas, NEP is sometimes called net biome production (NBP) (Randerson et al. 2002).



**FIGURE 5.7** An eddy-covariance (flux) tower in a deciduous forest in North Carolina. *Photo courtesy of G. Katul, Duke University.*

Now consider the height-profile of carbon dioxide in the middle of a uniform expanse of vegetation. The air moving through the column above a hypothetical 1-m<sup>2</sup> ground footprint will arrive and leave with the same distribution of CO<sub>2</sub> with height. The only net exchange with the atmosphere will occur from above the canopy as a result of wind- and eddy-driven transport into or out of the vegetation. *Eddy-covariance measurements* of net carbon exchange, so named because they trace the simultaneous variation in CO<sub>2</sub> concentrations and vertical wind velocity, have been made in a large number of sites worldwide. The method requires a tower with wind speed and CO<sub>2</sub> analyzers at varying heights (Figure 5.7), and works best in large areas of relatively uniform vegetation and flat topography, where the effects of turbulence are minimized (Baldocchi 2003). Eddy-covariance studies can provide simultaneous measurements of the net flux of several gases, such as CO<sub>2</sub> and H<sub>2</sub>O, providing an estimate of the WUE of photosynthesis at the ecosystem level (Figure 5.8)<sup>5</sup>. At night, the outward flux of CO<sub>2</sub> would represent the total respiration

<sup>5</sup> Developed by atmospheric scientists who were interested in the disappearance of CO<sub>2</sub> from the atmosphere, eddy-covariance studies assign plant uptake of CO<sub>2</sub> a negative value. Ecologists, using harvests to estimate increases in carbon storage in an ecosystem, express NEP as a positive value. Thus, NEP of -100 g C m<sup>-2</sup> yr<sup>-1</sup> reported by an eddy-covariance study is equivalent to +100 g C m<sup>-2</sup> yr<sup>-1</sup> reported by foresters, and both indicate net carbon storage in the ecosystem. In this book, we follow the latter convention and assign a positive value to all NPP and NEP estimates that indicate net carbon uptake by vegetation.



**FIGURE 5.8** Monthly gross primary production and evaporation in various temperate deciduous forests, measured by eddy-covariance techniques. The slope of the line is an estimate of water-use efficiency, here equivalent to 1.4 mmol/mol (see Eq. 5.3). Source: From Law *et al.* (2002).

in the ecosystem. GPP can be calculated from NEP using Eq. 5.7, with the assumption that the respiration flux measured during the night applies during the 24-hour period.<sup>6</sup>

It is interesting to compare traditional harvest estimates to NEP obtained from eddy-covariance studies (Table 5.2). Barford *et al.* (2001) used eddy-covariance to estimate GPP of 1300 g C m<sup>-2</sup> yr<sup>-1</sup> during an 8-year study in a deciduous woodland at Harvard Forest in Massachusetts. Total respiration was 1100 g C m<sup>-2</sup> yr<sup>-1</sup>, resulting in NEP of 200 g C m<sup>-2</sup> yr<sup>-1</sup>—a preliminary estimate of net carbon sequestration in wood and soil organic matter. Independent measurements of NEP from traditional harvests indicate net carbon storage of 160 g C m<sup>-2</sup> yr<sup>-1</sup> showing agreement within 20 to 25%.

In an experimental forest in Michigan, Gough *et al.* (2008) concluded that the differences between biometric (harvest) and meteorological (eddy-covariance) estimates of NPP were related to late-season photosynthesis which was allocated to storage rather than growth. NPP measured by these techniques agreed within 1% when data were averaged over 5 years. Unfortunately, many investigators using eddy-covariance techniques have not simultaneously used traditional methods to validate the carbon accumulation at their field sites (Luyssaert *et al.* 2009).

Eddy-covariance studies of carbon uptake can be applied in a wide variety of situations, including ecosystem-level studies of the net carbon balance of cities. Despite harboring

<sup>6</sup> Net carbon uptake in eddy-covariance studies is sometimes known as net ecosystem exchange (NEE).

**TABLE 5.2** GPP, NPP, and NEP for Some Young Temperate and Boreal Forest Ecosystems  
Measured by Harvest (H) and Eddy Covariance (CV) Methods

Ecosystem type	Age	Method	GPP	NPP	NEP	References
<i>Pinus sylvestris</i> (Finland)	40	CV	1005	185	228	Kolari et al. 2004
		H				
<i>Picea rubens</i> (Maine)	90	CV	1339		174	Hollinger et al. 2004
<i>Pinus taeda</i> (North Carolina)	16	CV	2238	986	433	Juang et al. 2006
		H			428	Hamilton et al. 2002
						McCarthy et al. 2010
<i>Pinus elliottii</i> (Florida)	24	CV	2606	675	745	Clark et al. 2004
		H				
<i>Pinus ponderosa</i> (Oregon)	56–89	CV	1208	400	324	Law et al. 2000
		H			118	Law et al. 2003
Mixed deciduous (Massachusetts)	60	CV	1300	200	160	Barford et al. 2001
		H				
Mixed deciduous (Michigan)	85	CV	654	151	153	Gough et al. 2008
		H				

Note: All data in  $\text{g C m}^{-2} \text{ yr}^{-1}$

considerable forest cover, suburban areas in Baltimore show a net release of  $361 \text{ g C m}^{-2} \text{ yr}^{-1}$  or  $241 \text{ kg C yr}^{-1}$  for each inhabitant (Crawford et al. 2011). Other world cities have even higher rates of net efflux, reflecting the balance between  $\text{CO}_2$  uptake by vegetation vs.  $\text{CO}_2$  release by fossil fuel combustion for heating and transport (Crawford et al. 2011, Bergeron and Strachan 2011).

## THE FATE OF NET PRIMARY PRODUCTION

As defined in Eq. 5.6, NEP would seem equivalent to the incremental accumulation of organic matter in an ecosystem—largely in wood growth and increments of soil organic matter. Even old forests that have stopped growing continue to store some organic matter in soils (Luyssaert et al. 2008, Law et al. 2003, Schlesinger 1990, Zhou et al. 2006). Only a small amount of carbon from photosynthesis accumulates in ecosystems in other forms, including calcium oxalate and calcium carbonate in plant tissues (Stone and Boonkirk 1963, Braissant et al. 2004, Cailleau et al. 2004) and calcium carbonate in soils (Chapter 4). If it survives the appetite of herbivores, most of the remaining NPP passes to the decomposers, where it is respired to  $\text{CO}_2$ . Terrestrial vegetation is also subject to fire, with a yearly frequency in some

grasslands and century-long return intervals for fire in some forests. Fires return carbon to the atmosphere, largely as CO<sub>2</sub>, analogous to a large, generalist herbivore.

Although herbivory may play a role in controlling forest productivity and nutrient cycling ([Chapter 6](#)), the consumption of plant tissues by herbivores is nearly always <20% of terrestrial NPP (e.g., Mispagel 1978, McNaughton et al. 1989, Cyr and Pace 1993, Cebrian and Lartigue 2004). Higher values are nearly always associated with insect outbreaks (e.g., Kurz et al. 2008). By consuming leaf area and root biomass, herbivores may have an indirect effect on NPP that is larger than their direct consumption (Reichle et al. 1973b, Llewellyn 1975, Ingham and Detling 1990). Globally, herbivores consume about 5% of terrestrial NPP (Whittaker and Likens 1973). Respiration by decomposers consumes most of the rest ([Chapter 11](#)).

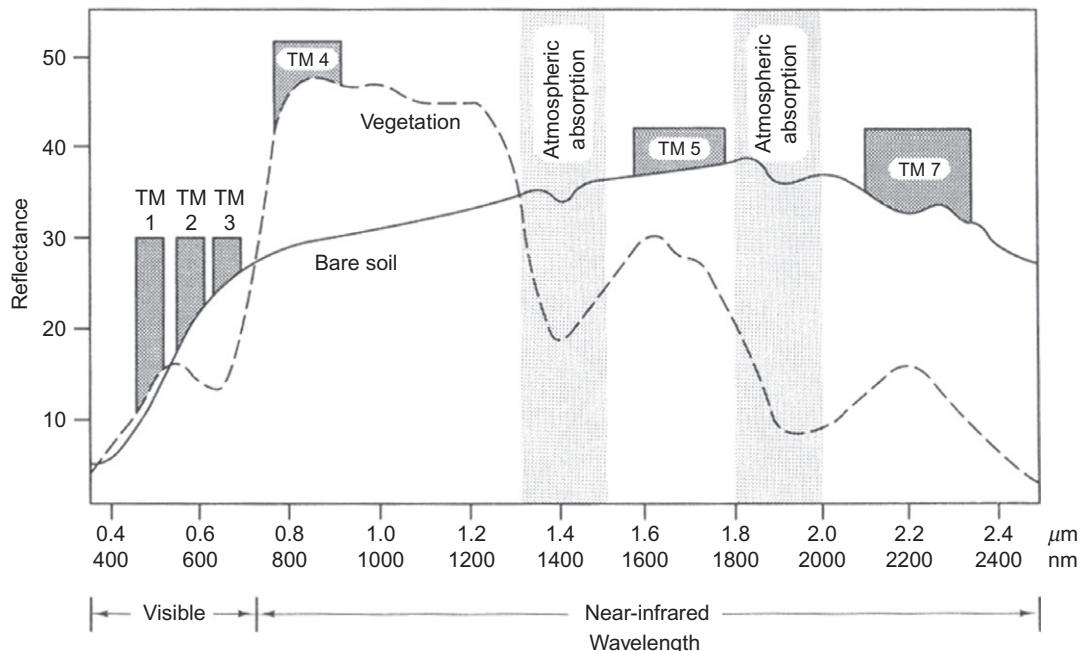
A small amount of carbon is lost from ecosystems in organic materials that are carried by streamwaters and groundwaters ([Chapter 8](#)) and respired to CO<sub>2</sub> outside the boundaries of the ecosystem, typically amounting to 1 to 10 g C m<sup>-2</sup> yr<sup>-1</sup>, or less than 1% of global terrestrial NPP (Schlesinger and Melack 1981). Similarly, when volatile organic compounds (VOCs) are produced by plants and lost to the atmosphere, they represent a small portion of NPP that is oxidized by hydroxyl radicals outside of the ecosystem ([Chapter 3](#); Kesselmeier et al. 2002). Emissions of isoprene have been measured using eddy-covariance methods (Rinne et al. 2000).

Globally, the emission of reduced carbon compounds from natural vegetation may exceed  $1 \times 10^{15}$  g C/yr, or about 2% of NPP (Guenther 2002, Laothawornkitkul et al. 2009). This small fraction accounts for much of the CO and CH<sub>4</sub> in the atmosphere ([Chapter 11](#)). Losses of organic carbon compounds in streamwaters and as volatile organics explain why NEP is not always directly equivalent to new incremental storage of organic matter in the ecosystem (Lovett et al. 2006, Chapin et al. 2006, Kindler et al. 2011).

## REMOTE SENSING OF PRIMARY PRODUCTION AND BIOMASS

Harvest measurements and eddy-covariance studies of NPP are labor intensive and necessarily applied only to small areas. Since the productivity of vegetation may vary greatly over the landscape, regional estimates of productivity by harvest are often prohibitively expensive. For the past decade, a NASA satellite, known as Moderate Resolution Imaging Spectroradiometer (MODIS), has provided integrated estimates of GPP over large areas for studies of global change (Running et al. 2004). MODIS replaces a number of older satellites, including LANDSAT and NOAA-AVHRR, which provided early estimates of global NPP using similar approaches (Box et al. 1989, Field et al. 1998).

The basis of satellite measurements of GPP is the differential absorption of light by chlorophyll and other leaf pigments. Green plants look green because chlorophyll preferentially absorbs light in the blue and red portions of the solar spectrum, reflecting a large portion of the green light to our eyes. Despite its strong absorption of red light (760 nm), chlorophyll shows little absorption of infrared light at wavelengths of 800 to 1200 nm. Thus, to provide an index of the underlying “greenness” of the Earth’s surface, satellites measure the surface reflectance in discrete portions of the visible and infrared spectrum ([Figure 5.9](#)). Bare soil



**FIGURE 5.9** A portion of the solar spectrum showing the typical reflectance from soil (—) and leaf (---) surfaces and the portions of the spectrum that are measured by the LANDSAT satellite.

shows similar reflectance in the infrared and red wavebands, whereas vegetation shows an infrared/red ratio  $\gg 1.0$  as a result of the absorption of red light by chlorophyll.

The normalized difference vegetation index (NDVI) is calculated as:

$$\text{NDVI} = (\text{NIR} - \text{VIS}) / (\text{NIR} + \text{VIS}), \quad (5.8)$$

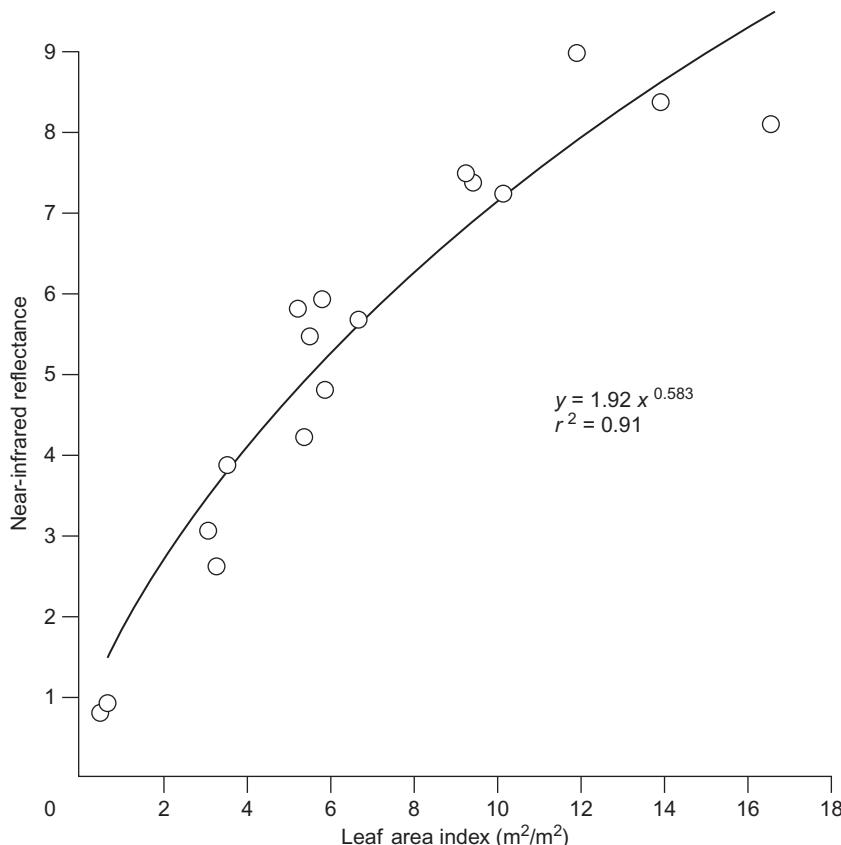
where NIR is reflectance in the near-infrared and VIS is reflectance in the visible red wavebands, respectively. This index minimizes the effects of variations in background reflectance and emphasizes variations in the data that occur because of the density of green vegetation. NDVI allows global mapping of a greenness index for the Earth's land surface, and satellite measurements of greenness can provide estimates of NPP, assuming that greenness is directly related to leaf area<sup>7</sup> and that LAI is a good predictor of NPP (Gholz 1982; Figures 5.6 and 5.10).

For the past decade, the MODIS satellite has provided an estimate of GPP by assuming that

$$\text{GPP} = \varepsilon \times \text{NDVI} \times \text{PAR}, \quad (5.9)$$

where  $\varepsilon$  is a measured coefficient expressing the efficiency of conversion of sunlight energy into plant growth in various ecosystems (Field et al. 1995), and PAR is a measure of

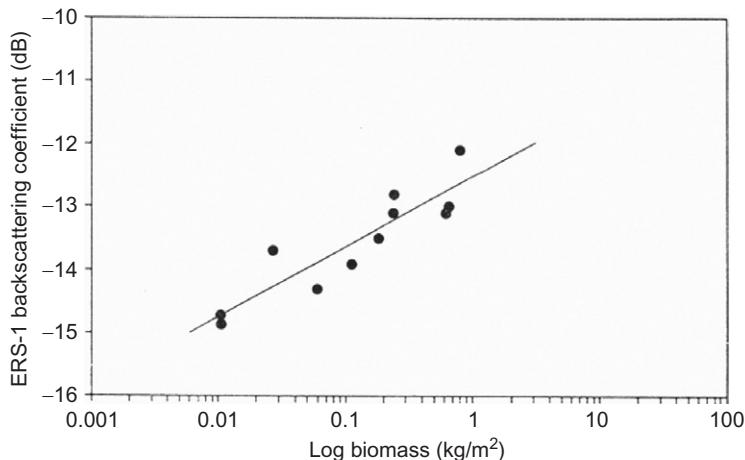
<sup>7</sup> Ecosystem ecologists often express leaf area as the area of leaves exposed above 1 m<sup>2</sup> of ground surface. The term, *leaf area index* or LAI, has the units of m<sup>2</sup>/m<sup>2</sup>.



**FIGURE 5.10** The ratio of light reflected in the near-infrared and red spectral bands (wavebands TM4 and TM3 of the LANDSAT satellite; see Figure 5.9) is related to LAI for forest stands in the northwestern United States. *Source:* From Peterson *et al.* (1987).

photosynthetically active radiation. The estimate is computed every 8 days for the Earth's land surface at 1-km spatial resolution (Running *et al.* 2004). Currently, the satellite measurements of NDVI are coupled to independent measurements of surface climate conditions that affect  $\epsilon$ . It is possible that direct satellite estimates of  $\epsilon$  may be possible in the near future (Grace *et al.* 2007, Hilker *et al.* 2011, Frankenberg *et al.* 2011).

Remote sensing of biomass is more difficult than for LAI and NPP. Synthetic aperture radar (SAR) is used to measure vegetation biomass based on the absorption of microwave radiation by the water held in woody biomass (Le Toan *et al.* 2011; Figure 5.11). Biomass estimates have used radar or LiDAR to estimate forest height, which is often directly related to biomass (Treuhhaft *et al.* 2004, 2010; Shugart *et al.* 2010). Boudreau *et al.* (2008) used a combination of field measurements and aircraft and satellite LiDAR systems to estimate forest biomass from measurements of its height in Quebec. Similar techniques have been applied to tropical rainforests in Costa Rica and Brazil (Dubayah *et al.* 2010, Drake *et al.* 2003, Asner *et al.* 2010, Clark *et al.* 2011).



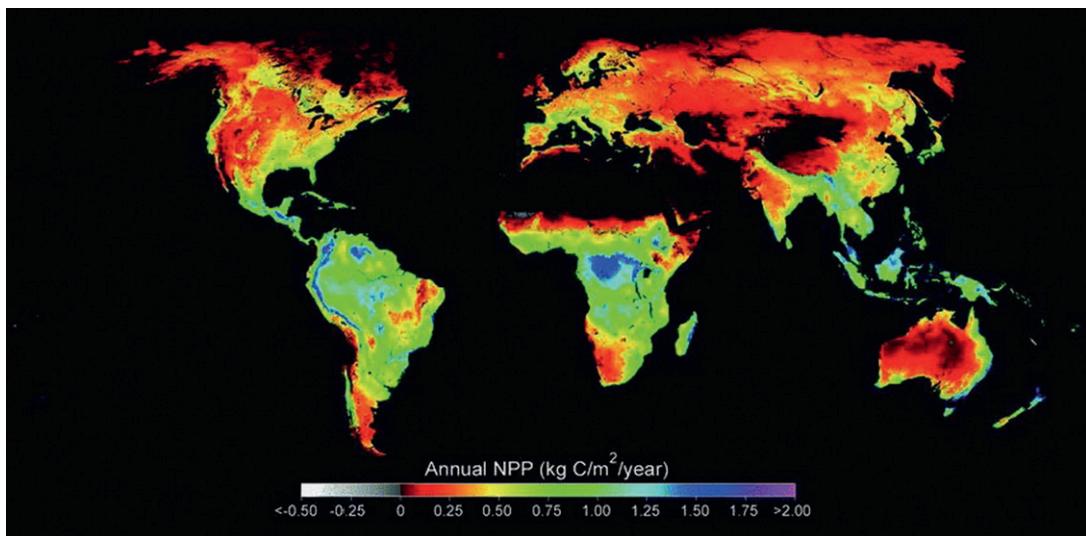
**FIGURE 5.11** The reflected microwave radiation (backscattering coefficient) measured by an airborne SAR for stands of young loblolly pine (*Pinus taeda*) in central North Carolina. Source: Modified from Kasischke *et al.* (1994).

## GLOBAL ESTIMATES OF NET PRIMARY PRODUCTION AND BIOMASS

Beer et al. (2010) estimate  $123 \times 10^{15}$  g C/yr of global GPP based on 8 years of observations of the land surface by the MODIS satellite (compare Jung et al. 2011). Since one-half of the GPP is normally consumed by respiration, the indicated global terrestrial net primary production is about  $60 \times 10^{15}$  g C/yr—near the high end of the range of earlier estimates based on the modeling and aggregation of harvest data ( $45 - 65 \times 10^{15}$  g C/yr) of the following authors in order: Whittaker and Likens (1973), Lieth (1975), Melillo *et al.* (1993), Field *et al.* (1998), Saugier *et al.* (2001), Del Grosso *et al.* (2008), and Ito (2011). As expected, a global map of terrestrial NPP shows the highest values in tropical rainforests and the lowest values in areas of extreme desert and ice (Figure 5.12).

Aggregations of data from harvest and eddy-covariance studies also suggest that the primary productivity of forests is greatest in the tropics and declines with increasing latitude to low values in boreal forests and shrub tundra (Table 5.3). In seasonal environments, photosynthetic rates often acclimate to changes in temperature (Lange *et al.* 1974, Gunderson *et al.* 2010). Thus, daily values for NPP are relatively similar in many ecosystems; it is the length of the growing season, as determined by temperature and moisture, that determines annual NPP (Kerkhoff *et al.* 2005). Among European forests, net ecosystem production is lower in northern forests as a result of a greater effect of low temperatures on the length of the growing season, reducing GPP relative to ecosystem respiration (Valentini *et al.* 2000, Janssens *et al.* 2001, Van Dijk and Dolman 2004). Along a gradient of decreasing precipitation, NPP declines from forests to grasslands, showing very low values in most deserts (Knapp and Smith 2001). In all biomes, rain-use efficiency by vegetation is greatest during dry years, when it approaches a value of 0.21 g C in aboveground NPP per mm of precipitation (WUE = 0.315 mmol/mol) across a broad range of ecosystems (see Eq. 5.3; Huxman *et al.* 2004).

Evidence for the importance of temperature and moisture as controls of NPP is seen in regional comparisons of productivity, especially patterns along gradients of elevation. Whittaker (1975) found that net primary production declined with increasing elevation in the forested



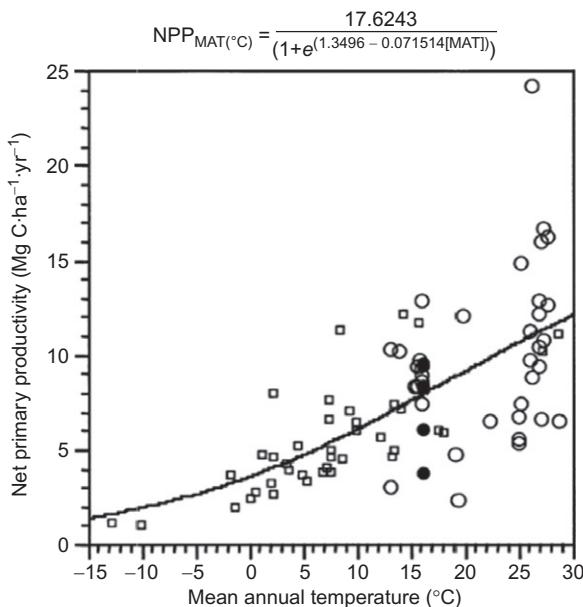
**FIGURE 5.12** Distribution of global NPP on land for 2002, computed from MODIS data. Source: From Running et al. 2004, Figure 5 in BioScience, June 2004; used with permission.

**TABLE 5.3** Biomass and Net Primary Production in Terrestrial Ecosystems

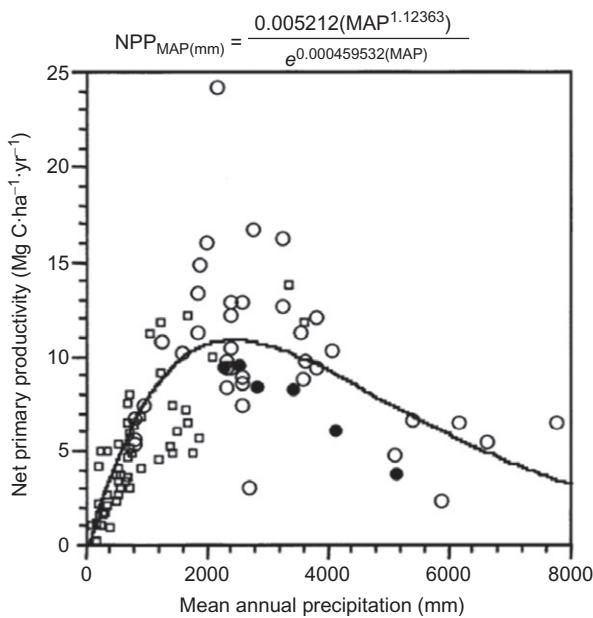
Biome	Area ( $10^6 \text{ km}^2$ )	NPP ( $\text{g C m}^{-2} \text{ yr}^{-1}$ )	Total NPP ( $10^{15} \text{ g C yr}^{-1}$ )	Biomass ( $\text{g C m}^{-2}$ )	Total plant C pool ( $10^{15} \text{ g C}$ )
Tropical forests	17.5	1250	20.6	19,400	320
Temperate forests	10.4	775	7.6	13,350	130
Boreal forests	13.7	190	2.4	4150	54
Mediterranean shrublands	2.8	500	1.3	6000	16
Tropical savannas/grasslands	27.6	540	14.0	2850	74
Temperate grasslands	15.0	375	5.3	375	6
Deserts	27.7	125	3.3	350	9
Arctic tundra	5.6	90	0.5	325	2
Crops	13.5	305	3.9	305	4
Ice	15.5				
<b>Total</b>	<b>149.3</b>		<b>58.9</b>		<b>615</b>

From data compiled by Saugier et al. 2001, assuming a 50% carbon content in plant tissues.

mountains of the eastern United States, presumably reflecting the influence of declining temperatures (i.e., a shorter growing season). In the southwestern United States, where precipitation is more limited, NPP tends to increase with elevation in communities ranging from desert shrublands to montane forests (Whittaker and Niering 1975). Sala et al. (1988) show a direct relationship between NPP and precipitation within the grasslands of the central United



**FIGURE 5.13** NPP in world forests versus mean annual temperature. *Source:* From Schuur (2003). Used with permission of the Ecological Society of America.



**FIGURE 5.14** NPP in world forests versus mean annual precipitation. *Source:* From Schuur (2003). Used with the permission of the Ecological Society of America.

States. Compilations of data from various world biomes show strong relations of NPP to temperature and mean annual precipitation (Scurlock and Olson 2002; Figures 5.13 and 5.14).

In forests of the northwestern United States, NPP and LAI are directly related to site water balance, which is the difference between precipitation inputs and losses of soil moisture by

runoff and evapotranspiration during the growing season (Grier and Running 1977, Gholz 1982). Rosenzweig (1968) combined temperature and precipitation to calculate actual evapotranspiration, which shows a positive correlation to NPP in temperate zone ecosystems (compare Webb et al. 1978). The overall strength of the relationship may partially derive from the influence of these variables on microbial processes that speed nutrient turnover in the soil (Chapter 6). Nutrient availability often determines local differences in net primary productivity among sites within the temperate zone (e.g., Pastor et al. 1984). In tropical rainforests, where both light and moisture are abundant, the relationship of NPP to these variables is weak, and local soil conditions determining fertility are potentially more important (Brown and Lugo 1982, Cleveland et al. 2011).

Estimates of the total biomass of land plants range from  $560$  to  $615 \times 10^{15}$  g C, derived from the aggregation of harvest data worldwide (Olson et al. 1983, Saugier et al. 2001). Based on a random sampling of land areas, total biomass in U.S. forests is about  $18 \times 10^{15}$  g C (Blackard et al. 2008), whereas forests in China and India contain about  $4.75 \times 10^{15}$  g C and  $2.9 \times 10^{15}$  g C, respectively (Fang et al. 2011, Kaul et al. 2011). By comparison, total biomass in the tropical forests of Brazil may be as large as  $50 \times 10^{15}$  g C (Nogueira et al. 2008). The ratio of biomass/NPP is an estimate of the mean residence time for an atom of carbon in plant tissues (compare to Eq. 3.3). The global values yield an overall mean residence time of about 10 years, but this value varies from about 4 in deserts to >20 in some forests (see Table 5.3; compare to Fahey et al. 2005). For the United States, the mean residence time of C in vegetation is about 5 years—that is, forest biomass of  $18 \times 10^{15}$  g C divided by NPP of  $3.5 \times 10^{15}$  g C/yr, which is calculated from Xiao et al. (2010). Of course, we must remember that these are weighted averages. In forests some tissues, such as leaves, may last only a few months, while wood may last for centuries.

Estimates, such as those in Table 5.3, are calculated by classifying the land vegetation into a small number of categories and by assigning a mean value to the NPP and biomass of each category based on data from the widest possible number of field studies. The classification of vegetation is arbitrary, and estimates of the land area in each category often vary considerably (Golley 1972). Moreover, the NPP data often do not reflect average values because ecologists tend to select mature, well-developed stands for study. Random site selection often produces lower regional values (Botkin and Simpson 1990, Botkin et al. 1993, Jenkins et al. 2001). Remote sensing estimates of NPP and biomass have the advantage of including the full range of variation seen in the field (Zhang and Kondragunta 2006). MODIS offers continuous, realistic estimates of NPP over large scales, with some loss of accuracy at local sites (Pan et al. 2006).

## NET PRIMARY PRODUCTION AND GLOBAL CHANGE

Since the beginning of civilization, humans have harvested the Earth's net primary production for food, fuel, and fiber. Indeed, the pages of this book were once part of a living tree. Cultivated lands and pasture now occupy about 40% of the world's land surface (Ellis et al. 2010, Goldewijk et al. 2010, Ramankutty and Foley 1998, Sterling and Ducharme

2008), and rates of tropical deforestation, largely for new cultivation, are estimated at 5.6 to  $5.8 \times 10^6$  ha/yr (Archard et al. 2002, DeFries et al. 2002).<sup>8</sup> Directly and indirectly humans now use 11 to 24% of potential NPP on the land surface (Haberl et al. 2007, Imhoff et al. 2004b), with most of the carbon released to the atmosphere as CO<sub>2</sub>. Ancillary human impacts on the land surface may raise our total appropriation of photosynthesis to 40% annually (Vitousek et al. 1986). These high values for the consumption of NPP by a single species do not bode well for the future of other species on the planet.

The human harvest of natural vegetation is not uniform across the planet. High rates of harvest in the tropics are balanced by the abandonment and regrowth of cultivated land elsewhere (Imhoff et al. 2004b). In the southeastern U.S. coastal plain, young forests are storing 90,000 tC/yr, which is equivalent to NEP of 100 g C/m<sup>2</sup>/yr ( $90 \times 10^9$  g/yr) (Binford et al. 2006, Delcourt and Harris 1980). Similarly, in Europe regrowing forests provide a net storage of carbon (Peters et al. 2010, Luyssaert et al. 2010). Nevertheless, as a result of expanding urban areas, overall NPP has declined by 0.4% in the Southeast (Milesi et al. 2003). Imhoff et al. (2004a) estimate a 1.6% loss of NPP due to urbanization across the entire United States.

In the Great Plains of the United States, irrigated and fertilized lands have potentially increased NPP by 10% above the level of native ecosystems in that region (Bradford et al. 2005); however, in most areas, agricultural lands are a net source of CO<sub>2</sub> to the atmosphere (i.e., negative NEP), especially when ancillary CO<sub>2</sub> emissions, such as those from diesel fuel, are included (West et al. 2010).

Fires are a normal part of the Earth's terrestrial ecosystems, especially in areas of tropical savanna (Cahoon et al. 1992). However, much of the land-clearing by humans has increased the global extent of fire (Bowman et al. 2009, Mouillet and Field 2005). Global estimates of CO<sub>2</sub> emissions from fires range from 1.4 to  $3.6 \times 10^{15}$  g C/yr (van der Werf et al. 2003, Mouillet et al. 2006, Schultz et al. 2008, Mieville et al. 2010); fires also contribute to global sources of a variety of trace gases (Andreae and Merlet 2001, Jain et al. 2006; Chapter 3 and 6). Large fires in Kalimantan, Indonesia, in 1997 are estimated to have released between 0.81 and  $2.57 \times 10^{15}$  g C into the atmosphere in a single year (Page et al. 2002). Large fires have also resulted in major losses of carbon from boreal forests in recent years (Kasischke et al. 1995, Bond-Lamberty et al. 2007). Many ecologists anticipate a greater frequency of fires as a result of global climate change.

The rising concentration of carbon dioxide in the atmosphere from fossil fuel combustion and biomass burning increases the availability of a basic reactant for photosynthesis (Eq. 5.2). Early studies of plant response to high CO<sub>2</sub> showed an average 31% increase in growth with a doubling of CO<sub>2</sub> concentrations for woody plants in controlled experiments (Curtis and Wang 1998, Wang et al. 2012). When it was noted that the growth responses were much lower in the absence of fertilization (Thomas et al. 1994, Hattenschwiler et al. 1997, Poorter and Perez-Soba 2001),

<sup>8</sup>Country-specific statistics for the extent of forests are given in The Global Forest Resources Assessment of the Food and Agriculture Organization. [www.fao.org/forestry/fra/fra2010/en/](http://www.fao.org/forestry/fra/fra2010/en/). The gross rate of forest cover loss is approximately 4 times larger than the net rate as a result of the regrowth of forests on some disturbed lands (Hansen et al. 2010). In the Amazon basin, the rate of deforestation declined significantly between 2004 and 2011 (Davidson et al. 2012). For the United States, the gross rate of deforestation is about  $1 \times 10^6$  ha/yr (Masek et al. 2011), but as a result of reforestation and afforestation, there has been a net increase in forest area during the last decade.



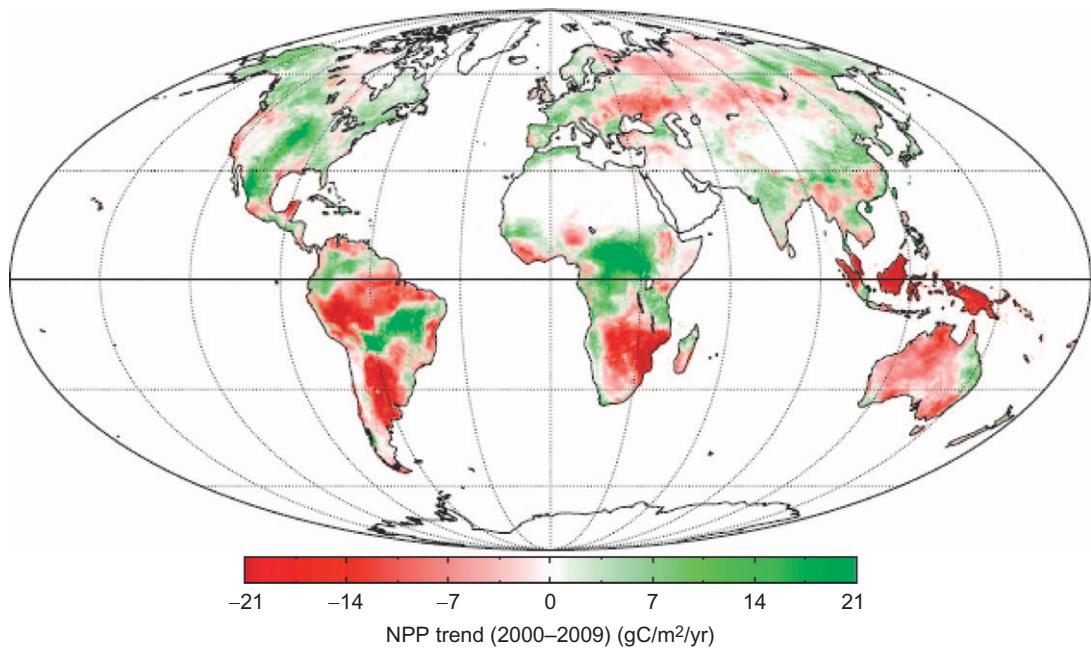
**FIGURE 5.15** The Free-Air CO<sub>2</sub> Enrichment experiment in Duke Forest in central North Carolina. Each plot is 30 m in diameter and surrounded by 16 towers, which emit CO<sub>2</sub> so as to maintain a specified concentration in the cylindrical volume of the plot to the height of the forest canopy. All other factors, including soil fertility, are allowed to vary naturally in the control and experimental plots.

investigators established large-scale, long-term experiments in a variety of ecosystems using Free-Air CO<sub>2</sub> Enrichment (FACE) technology (see [Figure 5.15](#) and Hendrey et al. 1999).

The results from various forest FACE experiments show an 18% increase in NPP with growth at +200 ppm CO<sub>2</sub>—the atmospheric levels expected globally in 2050 (Norby et al. 2005). Crop plants show growth stimulations ranging from 12 to 14% in rice, wheat, and soybeans (Long et al. 2006). In all species, growth at high CO<sub>2</sub> stimulates the proportional allocation of NPP to roots, which may increase the delivery of carbon to soils (Rogers et al. 1994, Jackson et al. 2009). There seems little doubt that the rise of CO<sub>2</sub> in Earth's atmosphere and thus the rate of anticipated climate change would be greater if it were not for CO<sub>2</sub> uptake in areas of undisturbed vegetation and the regrowth of vegetation on previously cleared lands.

Along with exposure to high CO<sub>2</sub>, humans have increased the exposure of forests to ozone, acid rain, and various forms of reactive nitrogen, with variable effects on growth. Nitrogen deposition from the atmosphere, producing a number of changes in soil biogeochemistry ([Chapter 6](#)), is likely to increase carbon uptake and storage in forests through its effect as a plant fertilizer (Magnani et al. 2007, Thomas et al. 2010). On the other hand, ozone reduces the growth of most plants when concentrations exceed 100 ppb (Richardson et al. 1992, Gregg et al. 2003), although growth at high CO<sub>2</sub> partially compensates for the ozone effect (Reid and Fiscus 1998, King et al. 2005, Poorter and Perez-Soba 2001, Penuelas et al. 2011). Losses of photosynthetic efficiency from air pollutants are noted even among plants in high northern latitudes, where one might expect relatively low pollution loads (Odasz-Albrigtsen et al. 2000, Savva and Berninger 2010).

With the onslaught of human effects on terrestrial NPP, it is worth asking whether we have produced measurable changes in global NPP in recent years. Tree-ring records are equivocal—some showing recent increases in growth (Soule and Knapp 2006), others showing little or no effect, perhaps due to concurrent drought (Barber et al. 2000, Gedalof and Berg 2010, Andreu-Hayles et al. 2011, Penuelas et al. 2011). Using satellite data to monitor NDVI ([Eq. 5.8](#)), several studies noted increases in global NPP during the 1980s and 1990s, largely through changes in high northern latitudes (Myneni et al. 1997), and perhaps globally (Nemani et al. 2003). Most of the change was attributed to changes in temperature, which determines the



**FIGURE 5.16** Change in terrestrial NPP from 2000 to 2009 from MODIS. Source: From Zhao and Running 2010. Used with permission of the American Association for the Advancement of Science.

length of the growing season. Strangely, this effect seems to be reversed in the MODIS-derived NPP record from 2000 to 2009 which shows a 1% decline in global NPP attributed to increasing drought in the Southern Hemisphere (Figure 5.16; Piao et al. 2011). Eddy-covariance studies in Europe show a severe reduction in NPP during 2003 due to heat and drought, so that the region became a source of CO<sub>2</sub> to the atmosphere (i.e., negative NEP; Ciais et al. 2005).

Certainly, global changes in NPP and biomass accompanied past climate changes associated with glacial intervals. At the last glacial maximum 19,000 years ago, carbon storage in land plants and soils was 30 to 50% lower than today (Bird et al. 1994, Beerling 1999, Kohler and Fischer 2004). NPP on the world's land surface was presumably depressed as well, because of lower plant cover; cold, dry climates; and low atmospheric CO<sub>2</sub> (Gerhart and Ward 2010). At the last glacial maximum, Landais et al. (2007) estimate that terrestrial NPP was only 65 to 70% of today's value. With the future climate changes due to greenhouse warming, plant biomass may increase up to 10% over present-day conditions (Smith et al. 1992c), although a transient period of drought may reduce terrestrial productivity during the next few decades (Rind et al. 1990, Smith and Shugart 1993). Overall, we might expect higher terrestrial NPP on a warmer, wetter world in the future (Wu et al. 2011).

## DETRITUS

The largest fraction of NPP is delivered to the soil as dead organic matter. Global patterns in the deposition of plant litterfall are similar to global patterns in NPP (Matthews 1997). The deposition of litterfall declines with increasing latitude from tropical to boreal forests (Vogt et al.

1986, Lonsdale 1988, Berg et al. 1999). Leaf tissues account for about 70% of litterfall in forests (O'Neill and De Angelis 1981, Meentemeyer et al. 1982), but the deposition of woody litter tends to increase with forest age, and fallen logs may be a conspicuous component of the forest floor in old-growth forests (Lang and Forman 1978, Harmon et al. 1986). In grassland ecosystems, where little of the aboveground production is contained in perennial tissues, the annual litterfall is nearly equal to annual net primary production.

In most areas, the annual growth and death of fine roots contributes a large amount of detritus to the soil, which has been overlooked by studies that only consider aboveground litterfall (Vogt et al. 1986, Nadelhoffer and Raich 1992). Using actual evapotranspiration to predict global patterns of litterfall; Meentemeyer et al. (1982) estimated  $27 \times 10^{15}$  g C for the annual production of aboveground litterfall worldwide. Matthews (1997) indicates total detritus production of  $\sim 50 \times 10^{15}$  g C/yr, suggesting that about half of global NPP occurs belowground. Her value is slightly smaller than current estimates of terrestrial NPP, which allows us to accommodate ancillary losses of organic carbon to the atmosphere and to streams and groundwater.

## The Decomposition Process

Most detritus, whether from litterfall or root turnover, is delivered to the upper layers of the soil where it is subject to the decomposition by microfauna, bacteria, and fungi (Swift et al. 1979, Schaefer 1990). Decomposition leads to the release of CO<sub>2</sub>, H<sub>2</sub>O, and nutrient elements, and to the microbial production of highly resistant organic compounds known as *humus*. Humus compounds accumulate in the lower soil profile (Chapter 4) and compose the bulk of soil organic matter (Schlesinger 1977, Rumpel and Kogel-Knabner 2011). The dynamics of the pool of carbon in soils is best viewed in two stages—processes leading to rapid turnover of the majority of litter at the surface and processes leading to the slower production, accumulation, and turnover of humus at depth.

The litterbag approach is widely used to study decomposition at the surface of the soil. Fresh litter is confined in mesh bags that are placed on the ground and collected for measurements at periodic intervals (Singh and Gupta 1977). Simple models of decay are based on an exponential pattern of loss, where the fraction remaining after 1 year is given by

$$X/X_0 = e^{-k} \quad (5.10)$$

An alternative, the mass-balance approach, suggests that the annual decomposition should equal the annual input of fresh debris so that the mass of detritus stays constant. Under these assumptions, a constant fraction, *k*, of the detrital mass decomposes, so that

$$\text{litterfall} = k(\text{detrital mass}), \quad (5.11)$$

or

$$\text{litterfall/detrital mass} = k. \quad (5.12)$$

When the detritus is in steady state, the values for *k* calculated from the litterbag and mass-balance approaches should be equivalent, and mean residence time for plant debris is  $1/k$  (Olson 1963; see also footnote on p. 55). For a forest in the Pacific Northwest, Vogt et al. (1983) shows the importance of fine roots in the calculation of mean residence times by the mass-balance approach. When root turnover was included, the mean residence time for

organic matter in the forest floor was 8.2 to 15.6 years, compared to 31.7 to 68.6 years calculated from aboveground litter alone.

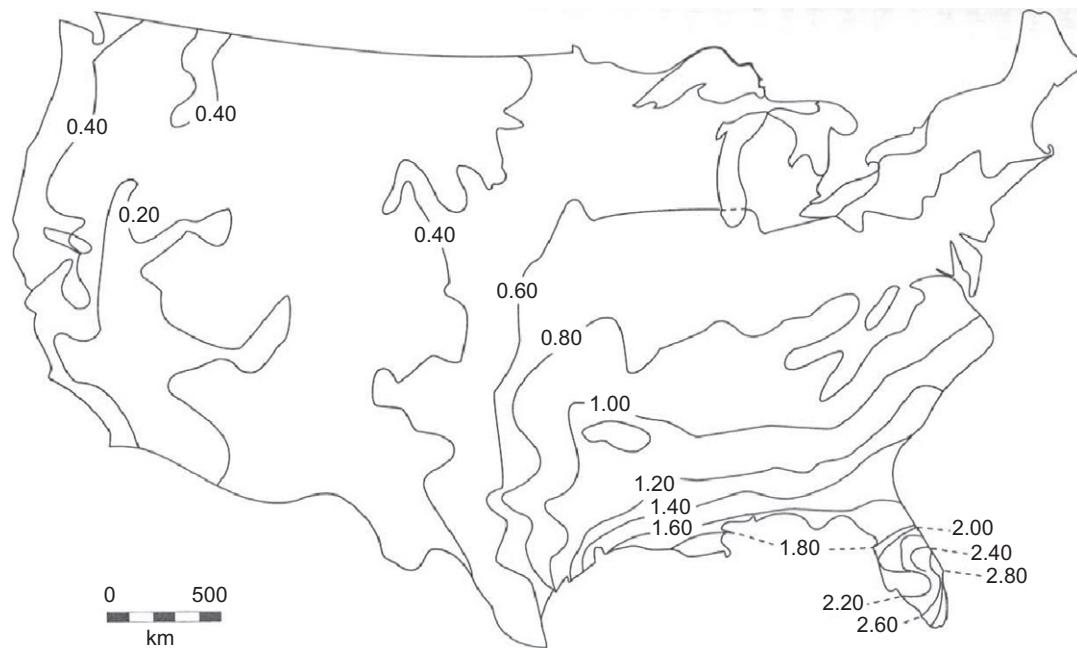
With either approach, when decomposition rates are rapid, values for  $k$  are greater than 1.0, and there is little surface accumulation (e.g., in tropical rainforests; Cuevas and Medina 1988, Gholz et al. 2000, Powers et al. 2009). In such systems, decomposition has the potential to respike more than the annual input of organic carbon in litterfall. In contrast, in some peatlands values for  $k$  are very small (e.g., 0.001; Olson 1963). Decomposition in grasslands shows a range of 0.20 to 0.60 in values for  $k$  (Vossbrinck et al. 1979, Seastedt 1988), but values for deserts may be as high as 1.00 due to the action of termites (Schaefer and Whitford 1981) and photooxidation of litter by ultraviolet light (Austin and Vivanco 2006, Gallo et al. 2009). In many ecosystems, decomposition shows a rapid initial phase of decomposition, followed by a slower phase in which some material may persist for decades (Harmon et al. 2009). Two- or three-phase exponential models are often best to describe this pattern of decomposition and for the most accurate estimates of  $k$  (Minderman 1968, Adair et al. 2008).

Decomposition rates vary as a function of temperature, moisture, and the chemical composition of the litter material. Microbial activity increases exponentially with increasing temperature (e.g., Edwards 1975). For plant litter, this relation often shows a  $Q_{10}$  of  $\geq 2.0$ , that is a doubling in activity per  $10^{\circ}\text{C}$  increase in temperature (Raich and Schlesinger 1992, Kirschbaum 1995, Katterer et al. 1998). Van Cleve et al. (1981) found that the thickness of the forest floor in black spruce forests in Alaska was inversely related to the cumulative degree days favorable to decomposition each year. In contrast, soil moisture often limits the rate of decomposition in arid and semiarid regions (Strojan et al. 1987, Amundson et al. 1989, Epstein et al. 2002), and moisture assumes increasing importance when temperate forest soils are subject to experimental warming, which dries them (Peterjohn et al. 1994).

Meentemeyer (1978a) compiled data from various decomposition studies to relate surface decomposition to actual evapotranspiration, and used the resulting equation to predict regional patterns of decomposition ([Figure 5.17](#)). His predictions are consistent with observations of surface litter in much of the United States (e.g., Lang and Forman 1978). Actual evapotranspiration is also a good predictor of decomposition in Europe (Berg et al. 1993), but less successful in predicting the decomposition of fine roots (Silver and Miya 2001). Improvements in these predictions are found when chemical parameters, such as lignin and nitrogen, are also considered (Meentemeyer 1978b, Melillo et al. 1982), but we defer a discussion of the dynamics of nutrient elements during decomposition until [Chapter 6](#).

## Humus Formation and Soil Organic Matter

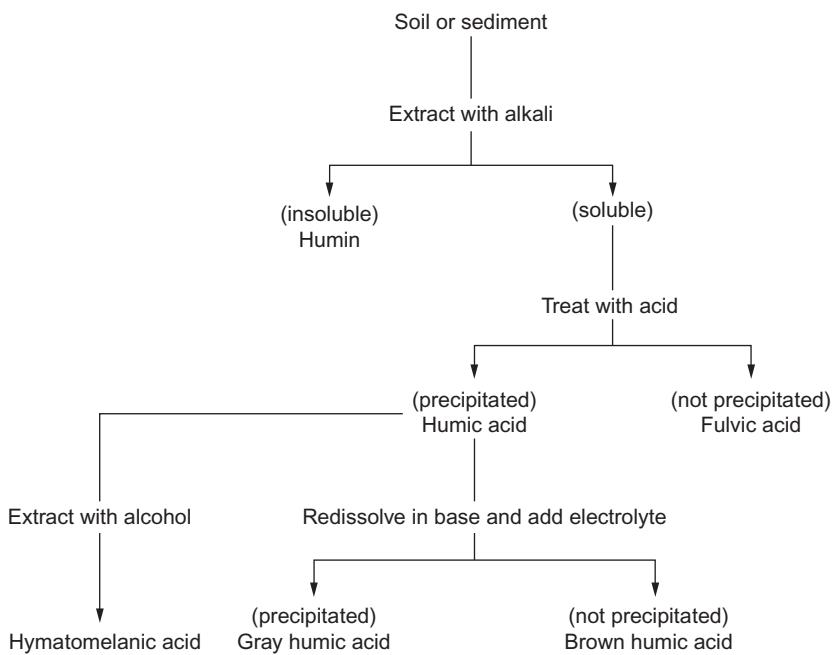
Plant litter and soil microbes constitute the cellular fraction of soil organic matter. As decomposition proceeds, there is an increasing content of noncellular organic matter (i.e., humus) which appears to result from microbial activity. The structure of humus is poorly known, but it contains numerous aromatic rings with phenolic ( $-OH$ ) and organic acid ( $-COOH$ ) groups (Flaig et al. 1975, Stevenson 1986). As we saw in [Chapter 4](#), these groups offer a major source of cation exchange capacity in many soils. Some tentative models have been proposed for the complete molecular structure of humus (Schulten and Schnitzer 1993, 1997), but many scientists believe that a large portion of soil humus is amorphous, with no consistent molecular weight or repeating units.



**FIGURE 5.17** Rates of decomposition of fresh litter in the United States predicted by a stimulation model using actual evapotranspiration as a predictive variable. Isopleth values are the fractional loss rate ( $k$ ) of mass from fresh litter during the first year of decomposition. *Source: From Meentemeyer (1978a.)*

The structure of humic substances also changes dramatically in response to changes in the pH, ion strength and complexing ions in the soil solution (Myneni et al. 1999). Recent progress in elucidating the chemical structure of humus has been made using  $^{13}\text{C}$  nuclear magnetic resonance (NMR) spectroscopy (Mahieu et al. 1999, Baldock et al. 2004) and pyrolysis-field ionization mass spectrometry (Py-FIMS) (Schnitzer and Schulten 1992). The most recalcitrant fractions of soil humus appear to have a large component of polymethylene ( $\text{C}=\text{C}=\text{C}$ ) groups that are synthesized by microorganisms (Baldock et al. 1992).

Traditional chemical characterizations of humus have been based on the solubility of humic and fulvic acid components in alkaline and acid solutions, respectively (Figure 5.18). The acid-soluble component of humus, primarily fulvic acid, controls the downward movement of Fe and Al in soils (Chapter 4). Percolating downward from the forest floor and A-horizon, fulvic acids often account for a large fraction of the soil organic matter in the lower soil profile, where they are complexed with clay minerals and calcium (Beyer et al. 1993, Oades 1988, Kalbitz et al. 2000). Noncrystalline forms of Fe- and Al-oxides are particularly effective in preserving organic matter with surface adsorption (Torn et al. 1997, Mikutta et al. 2006, Powers and Veldkamp 2005). This humus is very resistant to microbial attack; extracted humic materials from forest soil in Saskatchewan had a measured mean  $^{14}\text{C}$  age of 250 to 940 years (Campbell et al. 1967).



**FIGURE 5.18** Fractionation of fulvic and humic acid components from soil organic matter. Source: From Stevenson (1986).

Under most vegetation, the mass of humus in the soil profile exceeds the combined content of organic matter in the forest floor and aboveground biomass. Globally the pool of organic carbon in world soils amounts to about  $1500 \times 10^{15}$  g to 1-m depth (Schlesinger 1977, Batjes 1996, Amundson 2001). Many tropical soils contain small amounts of soil organic matter dispersed in the lower profile. Table 5.4 provides a global inventory of plant detritus and soil organic matter, totaling  $2344 \times 10^{15}$  g C to 3-m depth (Jobbágy and Jackson 2000). Even that value may underestimate the total mass of organic material stored in regions of permafrost (Tarnocai et al. 2009).

The global estimate of soil organic matter, divided by the estimate of global litterfall, suggests a mean residence time of about 50 years for the total pool of organic carbon in soils, but the mean residence time varies over several orders of magnitude between the surface litter and the various humus fractions (Figure 5.19). In the temperate zone, the mass of soil organic matter and its mean residence time increase from warm-temperate to boreal forests (Schlesinger 1977, Garten 2011, Frank et al. 2012). Regional inventories of the distribution and abundance of soil organic carbon (0–100 cm) are available for the United States ( $74 \times 10^{15}$  g C; Guo et al. 2006), China (84 to  $89 \times 10^{15}$  g C; Yu et al. 2007, Li et al. 2007), India ( $63 \times 10^{15}$  g C; Lal 2004), and other nations as part of recent national accounts of carbon storage in vegetation and soils.

## Turnover

The incorporation of nuclear-bomb-derived radiocarbon ( $^{14}\text{C}$ ) into different fractions of soil organic matter shows promise as a means of estimating their turnover (Trumbore 1993). O'Brien and Stout (1978) used radiocarbon dating to find that 16% of the organic matter

**TABLE 5.4** Distribution of Soil Organic Matter by Ecosystem Types

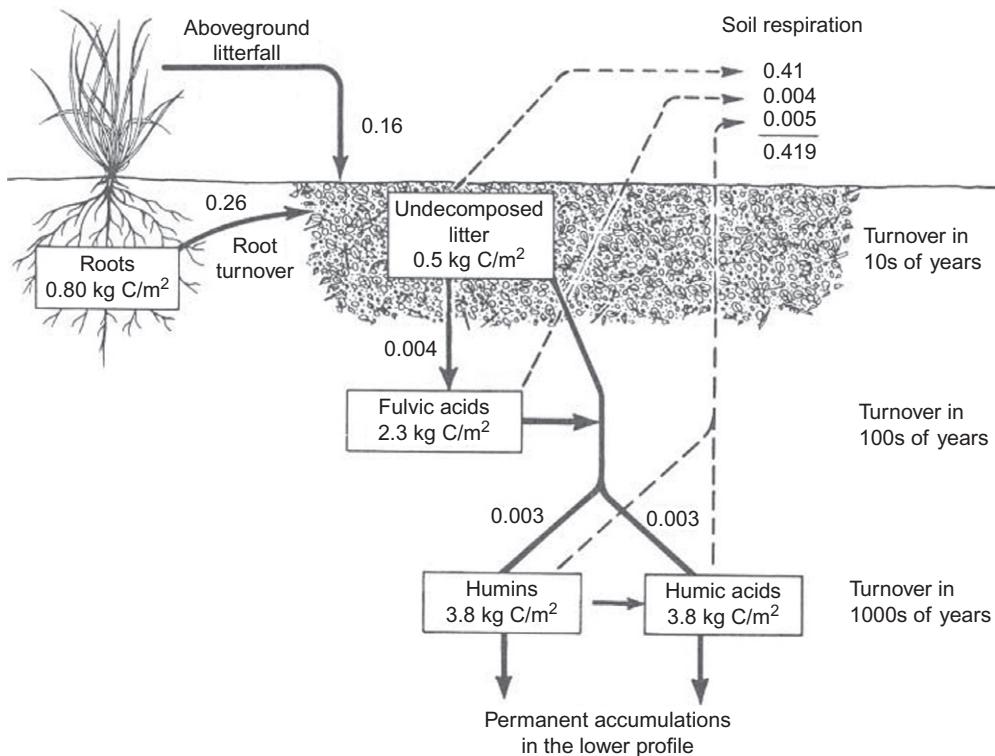
Biome	World area ( $10^6 \text{ km}^2$ )	Mean soil profile carbon ( $\text{kgC/m}^2$ )		Total soil carbon pool ( $10^{15} \text{ gC}$ ) 0–300 cm
		0–100 cm	0–300 cm	
Tropical forests				
Deciduous	7.5	15.8	29.1	218
Evergreen	17.0	18.6	27.9	474
Temperate forests				
Deciduous	7	17.4	22.8	160
Evergreen	5	14.5	20.4	102
Boreal forests	12	9.3	12.5	150
Mediterranean shrublands	8.5	8.9	14.6	124
Tropical savannas/grasslands	15	13.2	23.0	345
Temperate grasslands	9	11.7	19.1	172
Deserts	18	6.2	11.5	208*
Arctic tundra	8	14.2	18.0	144
Crops	14	11.2	17.7	248
Extreme desert, rock and ice	15.5			
<b>Total</b>	<b>136.5</b>			<b>2344</b>

Note: Excludes soil carbonates, which may contain an additional  $930 \times 10^{15} \text{ gC}$  (Schlesinger 1985).

Source: From Jobbágy and Jackson (2000). Used with permission of the Ecological Society of America.

in a pasture soil had a minimum age of 5700 years, while the rest was of recent origin and concentrated near the surface. In British deciduous woodlands, the distribution of radio-carbon is also compatible with two pools of carbon, each with about  $3.5 \text{ kg/m}^2$  to 15-cm depth (Tipping et al. 2009). Because of different turnover times, there is no universal decomposition constant,  $k$ , that can be applied to the entire mass of organic matter in the soil profile (Trumbore 1997, Gaudinski et al. 2000).

Field measurements of the flux of  $\text{CO}_2$  from the soil surface provide an estimate of the total respiration in the soil. Most of the production of  $\text{CO}_2$  occurs in the surface litter where decomposition is rapid and a large proportion of the fine root biomass is found (Bowden et al. 1993). Edwards and Sollins (1973) found that only 17% of the annual production of  $\text{CO}_2$  in a temperate forest soil was contributed by soil layers below 15 cm. Flux of  $\text{CO}_2$  from the deeper soil layers is presumably due to the decomposition of humus substances. Production of  $\text{CO}_2$  in the soil leads to the accumulation of  $\text{CO}_2$  in the soil pore space, which drives carbonation weathering in the lower profile (Chapter 4). Geologic sources of  $\text{CO}_2$  diffusing upward to the soil surface are normally very small (Keller and Bacon 1998).

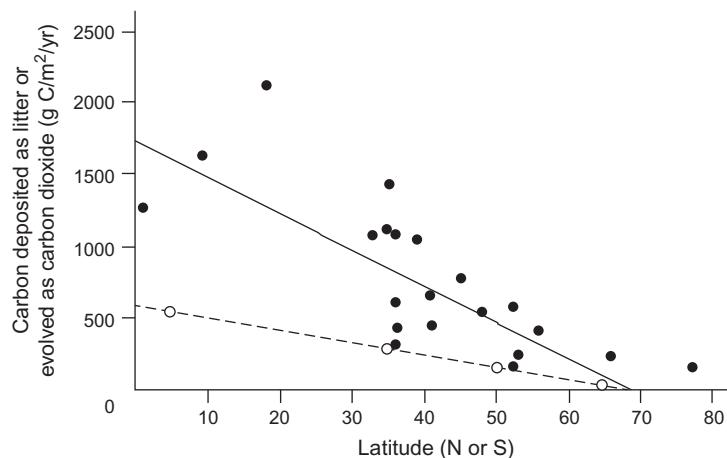


**FIGURE 5.19** Turnover of detritus and soil organic fractions in a grassland soil, in units of  $\text{kgC m}^{-2} \text{ yr}^{-1}$ . Note that mean residence time can be calculated for each fraction from measurements of the quantity in the soil and the annual production or loss (respiration) from that fraction. *Source: From Schlesinger (1977).*

Unfortunately, the respiration of living roots makes it impossible to use estimates of  $\text{CO}_2$  flux from the soil surface to calculate turnover of the soil organic pool (Fahey et al. 2005). In a compilation of values, Schlesinger (1977) found that  $\text{CO}_2$  evolution exceeded the deposition of aboveground litter by a factor of about 2.5 (Figure 5.20). The additional  $\text{CO}_2$  is presumably derived from root and mycorrhizal metabolism and the decomposition of root detritus (Raich and Nadelhoffer 1989, Subke et al. 2011).

In a field experiment using girdling of trees to eliminate the transport of new photosynthate to roots, Hogberg et al. (2001) reported a 54% decline in soil respiration; presumably the remaining respiration was due to decomposers in the soil (compare to Andrews et al. 1999, Hanson et al. 2000). Globally, soil respiration is  $80$  to  $100 \times 10^{15} \text{ g C/yr}$ , with about half derived from the respiration of live roots and the remainder from decomposition (Raich et al. 2002, Subke et al. 2006, Bond-Lamberty and Thomson 2010). Soil respiration shows a strong correlation with NPP and detritus inputs in world ecosystems (Raich and Tufekcioglu 2000, Bond-Lamberty et al. 2004, Hibbard et al. 2005).

The global distribution of soil organic matter shows how moisture and temperature control the balance between primary production and decomposition in surface and lower soil layers (Amundson 2001). Among forests, accumulations in the forest floor increase from tropical to

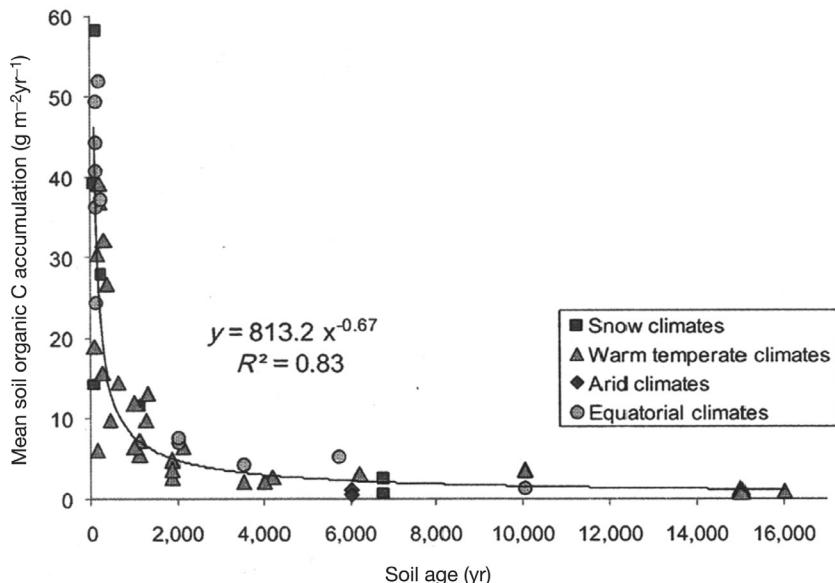


**FIGURE 5.20** Latitudinal trends for carbon dynamics in forest and woodland soils of the world. The *dashed line* shows the mean annual input of organic carbon to the soil by litterfall. The *solid line* shows the loss of carbon, measured as the flux  $\text{CO}_2$  from the surface. The difference between these lines represents the loss of  $\text{CO}_2$  from root and mycorrhizae respiration and from the decomposition of root detritus and exudates. *Source:* From Schlesinger (1977).

boreal climates. Net primary productivity shows the opposite trend, so the accumulation of soil organic matter is largely due to differences in decomposition. Thus, compared to the process of primary production, soil microbes are more sensitive to regional differences in temperature and moisture (Figure 5.20). Worldwide, the accumulation of organic matter in surface litter seems more related to factors controlling decomposition than to the NPP of terrestrial ecosystems (Cebrián and Duarte 1995, Valentini et al. 2000; but see Frank et al. 2012).

Parton et al. (1987) developed a model based on the differential turnover of soil organic fractions to predict the accumulation of soil organic matter in grassland ecosystems. Accurate predictions were achieved when temperature, moisture, soil texture, and plant lignin content were included as variables. Despite relatively low NPP, soils of temperate grasslands contain large amounts of soil organic matter (Sanchez et al. 1982b) due to relatively low rates of decomposition and a larger fraction of plant debris that is derived from root turnover (Oades 1988). In contrast, tropical grasslands and savannas have relatively small accumulations of surface litter, perhaps due to frequent fire (Kadeba 1978, Jones 1973).

Storage of soil organic matter represents a component of net ecosystem production (NEP) in terrestrial ecosystems. Studies of soil chronosequences show that soil organic matter accumulates rapidly on disturbed sites, but rates decline to 1 to  $12 \text{ g C m}^{-2} \text{ yr}^{-1}$  during long-term soil development (Figure 5.21; Schlesinger 1990, Chadwick et al. 1994), with the highest rates under cool, wet conditions. Many wetland soils also show large rates of organic accumulation due to anoxic conditions in their sediments (Chapter 7). The low rate of accumulation of soil organic matter in upland soils speaks strongly for the efficiency of decomposers using aerobic metabolic pathways of degradation (Gale and Gilmour 1988). With relatively high nutrient content, humic substances are not inherently resistant to decomposition, but they are stabilized by interactions with soil minerals (Schmidt et al. 2011, Allison 2006). Globally, the annual



**FIGURE 5.21** The rate of accumulation of organic matter in soil chronosequences of different age and climate zones, all derived from volcanic materials. *Source: From Zehetner (2010).*

net production of humus substances is  $<0.4 \times 10^{15}$  g C/yr or only about 0.7% of NPP (Schlesinger 1990).

The mass of soil organic matter in most upland ecosystems is likely to have been fairly constant before widespread human disturbance of soils. When soils show a steady state in organic content, the production of humic compounds must be equal to their removal from soils by erosion. Coincidentally, estimates of the global transport of organic carbon in rivers are also about  $0.4 \times 10^{15}$  g C/yr (Schlesinger and Melack 1981, Meybeck 1982), suggesting that before human impacts, NEP for the Earth's land surface was essentially zero.

For areas covered by the last continental glaciation, the total accumulation of soil organic matter represents NEP for the last 10,000 years. The maximum extent of the last glaciations, covering  $29.5 \times 10^6$  km<sup>2</sup> of the present land area (Flint 1971), now contains roughly  $300 \times 10^{15}$  g C—that is, more than 10% of the organic carbon contained in all the world's soils (Table 5.4). In these areas, soil organic matter has accumulated at rates of about  $1.35$  g C m<sup>-2</sup> yr<sup>-1</sup> during the Holocene period. The current rate of storage in northern ecosystems ( $0.015$  to  $0.035 \times 10^{15}$  g C/yr) is too small to be a significant sink for human releases of CO<sub>2</sub> to the atmosphere from fossil fuels, nor is it likely to have increased significantly during the last century (Gorham 1991, Harden et al. 1992).

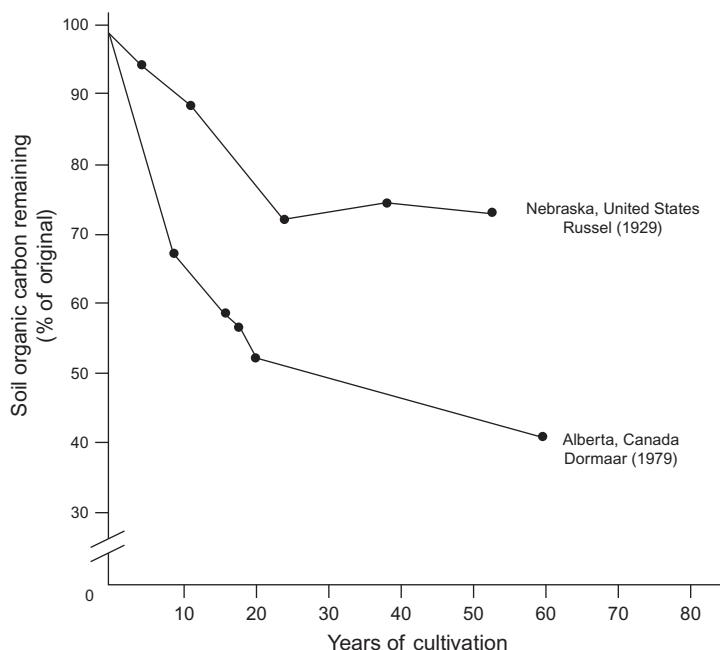
Total storage of carbon in soils,  $1456 \times 10^{15}$  g or  $121 \times 10^{15}$  moles, can account for only 0.3% of the O<sub>2</sub> content of the atmosphere, given that the storage of organic carbon and the release of O<sub>2</sub> occur on a mole-for-mole basis during photosynthesis (Eq. 5.2). Thus, accumulations of atmospheric O<sub>2</sub> cannot be the result of the storage of organic carbon on land. Long-term storage of organic carbon appears to be dominated by accumulations in anoxic marine sediments (Chapter 9).

## SOIL ORGANIC MATTER AND GLOBAL CHANGE

When soils are brought under cultivation, the content of organic matter in soil declines. Most cultivation reduces the inputs of fresh plant debris and increases the rate of decomposition of soil organic matter as a result of better soil moisture and aeration conditions. Losses from many soils are typically 20 to 30% within the first few decades of cultivation (e.g., Figure 5.22, Don et al. 2011). The loss is greatest during the first years of cultivation. Eventually a new, lower level of soil organic matter is achieved that is in equilibrium with the plant production and decomposition in cropland (Jenkinson and Rayner 1977). Some of the soil organic matter is lost as a result of erosion and buried elsewhere, but most is probably oxidized to CO<sub>2</sub> and released to the atmosphere (Van Oost et al. 2007).

With about 10% of the world's soils under cultivation (refer to Table 5.4), losses of organic matter from agricultural soils have been a major component of the increase in atmospheric CO<sub>2</sub> during the past several centuries (Schlesinger 1984). The current rate of release from soils, as much as  $0.8 \times 10^{15}$  g C/yr, is largely dependent on the rate at which natural ecosystems, especially in the tropics, are being converted to agriculture (Maia et al. 2010, Don et al. 2011). Especially large losses of soil carbon are seen when organic soils in wetlands and peatlands are drained (Armentano and Menges 1986, Hutchinson 1980; Chapter 7).

The dynamics of soil organic matter are illustrated by the pattern of loss after land is converted to agriculture. Recall that soil organic matter consists of a labile and a resistant



**FIGURE 5.22** Decline in soil organic matter following conversion of native soil to agriculture in two grassland soils. Source: From Schlesinger (1986).

fraction. The labile fraction is composed of fresh plant materials that are subject to rapid decomposition, whereas the resistant fraction is composed of humic materials that are often complexed with clay minerals. Rather than using biochemical fractionations (refer to Figure 5.18), some workers have used size or density fractionation to quantify the labile and resistant organic matter. Density fractionations are performed by adding soil samples to solutions of increasing specific gravity and collecting the material that floats to the surface (Spycher et al. 1983).

In size fractionation, soils are passed through screens of varying mesh (Tisdall and Oades 1982, Elliott 1986). Most of the turnover of soil organic matter is in the “light” or large fractions that represent fresh plant materials (Tiessen and Stewart 1983). The “heavy” fraction is composed of polysaccharides (sugars) and humic materials that are complexed with clay minerals to form microaggregates of relatively high specific gravity (Tisdall and Oades 1982, Tiessen and Stewart 1988). The radiocarbon age of the different size or weight fractions indicates their rate of turnover. Anderson and Paul (1984) reported a  $^{14}\text{C}$  age of 1255 years for organic matter in the clay fraction of a soil for which the overall age was 795 years. The decline in soil organic matter in agricultural soils is largely the result of losses from the light fraction (Buyanovsky et al. 1994, Cambardella and Elliott 1994).

Losses of soil organic matter with cultivation contribute to the rise of atmospheric  $\text{CO}_2$ , but also to the hope that better management of agricultural soils might restore their native soil carbon and act to store  $\text{CO}_2$  that would otherwise accumulate in the atmosphere. A reduced frequency of tillage results in the accumulation of soil carbon in many circumstances (West and Marland 2002). Successful management of agricultural soils may benefit from the preservation of their organic microaggregate structure by reduced tillage.

Greater returns of crop residues, stimulated by fertilizer and irrigation, can also result in accumulations of soil organic matter, although in most circumstances the enhanced soil carbon storage is less than the  $\text{CO}_2$  emitted during the manufacture or delivery of these amendments (Schlesinger 2000, Russell et al. 2005, Khan et al. 2007, Townsend-Small and Czimczik 2010). Additions of biochar also increase soil organic matter in some circumstances (Woolf et al. 2010). When ancillary and offsite emissions are considered, most agricultural lands in the United States show negative NEP (West et al. 2010). Indeed, allowing vegetation to regrow on abandoned agricultural lands seems the only certain way to increase soil carbon (Vuichard et al. 2008, McLauchlan et al. 2006).

Significantly, soil organic matter can accumulate fairly rapidly when agricultural soils are abandoned, with rates averaging  $33 \text{ g C m}^{-2} \text{ yr}^{-1}$  in a wide review of published values (Post and Kwon 2000, Guo and Gifford 2002, Clark and Johnson 2011)—much higher than the accumulation under undisturbed vegetation (see Figure 5.21). Soils in urban environments—lawns, parks, and golf courses—can also show increases in soil carbon storage with intensive management (Golubiewski 2006, Pouyat et al. 2009, Raciti et al. 2011). In all cases of natural succession, the accumulation of carbon in soil organic matter is dwarfed by the accumulation in regrowing woody vegetation (Richter et al. 1996, Johnson et al. 2003, Hooker and Compton 2003).

Growth at high  $\text{CO}_2$  increases the productivity of vegetation, especially belowground, so it is natural to expect increasing storage of soil carbon as a result. Nevertheless, various high  $\text{CO}_2$  experiments using FACE technology in forests report only small differences in soil carbon storage (Jastrow et al. 2005, Hagedorn et al. 2003, Lichter et al. 2008, Hungate et al. 2009).

Soil carbon shows no significant increase in Russian grassland soils during the last 100 years, while atmospheric CO<sub>2</sub> has increased 30% (Torn et al. 2002). Rates of soil respiration increase in forests exposed to high CO<sub>2</sub>, reflecting greater rates of decomposition (Bernhardt et al. 2006, Dieleman et al. 2010). Greater inputs of plant residues appear to stimulate the decomposition of existing soil organic matter, in what is known as the “priming effect” (Van Kessel et al. 2000, Hoosbeek et al. 2004, Fontaine et al. 2007, Langley et al. 2009a).

Global patterns in the distribution and abundance of soil organic carbon (refer to Table 5.4) show the greatest accumulations in cold, wet conditions. Future, warmer conditions are likely to increase the decomposition of organic matter in boreal and arctic ecosystems, where much organic matter is held in the permafrost (Niklinska et al. 1999, Zimov et al. 2006, Ping et al. 2008, Tarnocai et al. 2009). The increasing flux of CO<sub>2</sub> to the atmosphere from large pools of soil carbon at these latitudes could exacerbate global warming (Trumbore et al. 1996, Oechel et al. 2000, Schuur et al. 2009, Dorrepaal et al. 2009). In the tundra of Alaska, changes in the depth of the water table—as might be expected by melting permafrost—appear to have a greater effect on soil carbon than changes in soil temperature alone (Huemmrich et al. 2010). Throughout the arctic and boreal regions, the organic carbon in deep soil horizons is relatively labile and subject to rapid decomposition in warmer, drier climates (Waldrop et al. 2010, Dorrepaal et al. 2009, Nowinski et al. 2010).

Various soil-warming experiments have resulted in greater plant growth and greater soil respiration, especially in cold regions (Billings et al. 1982, Rustad et al. 2001). Experimental ecosystem warming in the montane region of the Rocky Mountains has shown that the greatest changes in NPP appear to derive from an early start to the spring growing season, which subsequently leads to increasing drought later in the year (Saleska et al. 1999). Nearly all experiments imposing soil warming on intact ecosystems report an increase in the decomposition of soil organic matter and a greater release of nutrients (Van Cleve et al. 1990, Melillo et al. 2002, Conant et al. 2011, Harte et al. 2006). The losses of soil organic matter are greatest in the first years of these experiments, presumably due to depletion of the labile fractions and acclimation of soil microbial populations to the change in temperature (Allison et al. 2010).

Losses of soil organic matter due to climate change may be partially mediated by soil mineralogy, especially in areas where organic compounds are bound to Fe- and Al minerals (Rasmussen et al. 2006, Powers and Veldkamp 2005). With global warming, some of the carbon lost from soils is likely to be captured by enhanced growth of vegetation (Schuur et al. 2009, Melillo et al. 2011). It is important not to forget that large amounts of carbon were stored in vegetation and soils of high northern latitudes during the Holocene, when these areas experienced warmer climates at the end of the last continental glaciation (Harden et al. 1992, compare Chen et al. 2006b).

## SUMMARY

Photosynthesis provides the energy that powers the biochemical reactions of life. That energy is captured from sunlight and stored in carbohydrates (organic matter). Globally, net primary production of about  $60 \times 10^{15}$  g C yr<sup>-1</sup> is available in the terrestrial biosphere. Although that is a large value, NPP typically captures less than 1% of the available sunlight

energy. Most of the remaining energy evaporates water and heats the air, resulting in the global circulation of the atmosphere (Chapters 3 and 10). Thus, the terrestrial biosphere is fueled by a relatively inefficient initial process.

During photosynthesis, plants take up moisture from the soil and lose it to the atmosphere in the process of transpiration. Available moisture appears to be a primary factor determining global variation in leaf area and NPP. Among communities with adequate soil moisture, net primary production is determined by the length of the growing season and mean annual temperature; both are an index of the receipt of solar energy. Soil nutrients appear to be of secondary importance to NPP on land, perhaps because plants have various adaptations for obtaining and recycling nutrients efficiently when they are in short supply (Chapter 6).

Most net primary production is delivered to the soil, where it is decomposed by a variety of organisms. The decomposition process is remarkably efficient, so only small amounts of NPP are added to the long-term storage of soil organic matter or humus each year. Soil organic matter consists of a dynamic pool near the surface in which there is rapid turnover of fresh plant detritus and little long-term accumulation, and a large refractory pool of humic substances that are dispersed throughout the soil profile. Thus, the turnover time of organic carbon in the soil ranges from about 3 years for the litter to thousands of years for humus. For the United States, the mean residence time of carbon in terrestrial ecosystems is about 46 years (Zhou and Luo 2008).

Humans have altered the processes of net primary production and decomposition on land, resulting in the transfer of organic carbon to the atmosphere, and perhaps a permanent reduction in the global rate of NPP. This disruption has produced global changes in the biogeochemical cycle of carbon, but little change in the atmospheric concentration of O<sub>2</sub>.

## Recommended Readings

- Chapin, F.S., P.A. Matson, and P.M. Vitousek. 2012. *Principles of Terrestrial Ecosystem Ecology*. Springer.
- Fahey, T.J., A.K. Knapp. 2007. *Principles and Standards for Measuring Primary Production*. Oxford University Press.
- Reichle, D.E. (ed.). 1981. *Dynamic Properties of Forest Ecosystems*. Cambridge University Press.
- Roy, J., B. Saugier, and H.A. Mooney. 2001. *Terrestrial Global Productivity*. Academic Press.
- Swift, M.J., O.W. Heal, and J.M. Anderson. 1979. *Decomposition in Terrestrial Ecosystems*. University of California Press.
- Waring, R.H., and S.W. Running. 2007. *Forest Ecosystems: Analysis at Multiple Scales* (third ed.). Elsevier.

## PROBLEMS

1. Fick's law of diffusion states that the Flux = Gradient/Resistance. For a plant leaf, the concentration of CO<sub>2</sub> typically ranges from about 100 µl/l inside the leaf to 400 µl/l in the atmosphere. For water vapor, the gradient of concentration ranges from saturation inside the leaf to the vapor pressure of the free atmosphere, as determined by relative humidity and temperature outside the leaf. Assume stomatal resistance is 5 sec/cm. What is the flux of CO<sub>2</sub> into the leaf and water vapor out of the leaf at 25 °C and 30% relative humidity? (Remember to consider the different value of diffusivity for each of these gases in air). If the stomatal aperture decreases, so that the resistance increases to 10 sec/cm, what is the flux of these two gases? What do these calculations suggest as to why the water-use efficiency of vegetation is so low?
  2. Assume that the shape of a tree trunk approximates that of a cone and that only that outermost ring of wood, with 2-mm thickness, is metabolically active (i.e., it respires at a rate of 0.005 µmol CO<sub>2</sub>/cm<sup>3</sup>/sec) and functional in water transport. In a cross-section of the trunk at the base, if each cm<sup>2</sup> of these outer layers of wood support 0.50 m<sup>2</sup> of leaf area, and each unit of leaf area fixes carbon at a rate of 10 µmol CO<sub>2</sub>/m<sup>2</sup>/sec, what fraction of the photosynthate generated by a tree of 50-cm diameter will go to the support of wood tissue when it is 15-m tall? (Assume a 12-hour daylight period, each day for a 365-day growing season.)
  3. Physiologists often use the expression Q<sub>10</sub> to express the change in a metabolic process that occurs with a 10°C rise in temperature. In many areas, the Q<sub>10</sub> for soil respiration is about 2.4. What will be the annual global increase in soil respiration with a 3°C rise in global temperature during the next century? How does this compare to fossil fuel emissions?
  4. There is a total of 10.4 kg C/m<sup>2</sup> in the grassland soil pictured in [Figure 5.19](#). Calculate the turnover of the soil organic carbon with respect to each of the three components of soil respiration and with respect to total soil respiration. Then, calculate the overall turnover time with respect to total inputs to the soil. How do these compare? Is the overall turnover time controlled by the pools with rapid or slow turnover?
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