

# *Biogeochemistry*

**AN ANALYSIS OF**

**GLOBAL CHANGE**

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Third Edition

# 5

**Table 4.9** Estimates of Some Elemental Fluxes to the Ocean in Rivers ( $10^{12}$  g yr $^{-1}$ )<sup>a</sup>

	Ca	Na	Mg	Si	Fe	Cu	Pb	Zn
River particulate load	345	110	209	4430	733	1.55	2.3	5.4
River dissolved load	495	131	129	203	1.5	0.37	0.04	1.1
Total river load	840	241	338	4630	734	1.9	2.3	6.5
Theoretical load <sup>b</sup>	946	298	345	5780	754	0.67	0.33	2.6
Discrepancy	N.S.	N.S.	N.S.	N.S.	N.S.	+1.2	+2.0	+3.9
World mining production	—	—	—	—	—	4.4	3.0	3.9

<sup>a</sup> From Marin and Meybeck (1979). N.S., not significant.

<sup>b</sup> Based on weathering of average rock.

but the inevitable removal of cations results in lower soil pH and base saturation through time (Bockheim 1980). Phosphorus is particularly critical as a soil nutrient, because it is not abundant in crustal rocks and is easily precipitated in unavailable forms in the soil. Old soils in highly weathered landscapes are composed of resistant, residual Fe and Al oxide minerals. In these soils, P is often deficient for plant growth.

### Recommended Readings

- Birkeland, P.W. 1984. *Soils and Geomorphology*. Oxford University Press, Oxford.
- Garrels, R.M. and F.T. MacKenzie. 1971. *Evolution of Sedimentary Rocks*. W.W. Norton, New York.
- Jenny, H. 1980. *The Soil Resource*. Springer-Verlag, New York.
- Likens, G.E. and F.H. Bormann. 1995. *Biogeochemistry of a Forested Ecosystem*, 2nd ed. Springer-Verlag, New York.
- Lindsay, W.L. 1979. *Chemical Equilibria in Soils*. Wiley, New York.
- Reuss, J.O. and D.W. Johnson. 1986. *Acid Deposition and the Acidification of Soils and Waters*. Springer-Verlag, New York.
- Sposito, G. 1989. *The Chemistry of Soils*. Oxford University Press, Oxford.
- Sverdrup, H.U. 1990. *The Kinetics of Base Cation Release Due to Chemical Weathering*. Lund University Press, Lund, Sweden.

## The Biosphere: The Carbon Cycle of Terrestrial Ecosystems

### Introduction

- Photosynthesis
- Water-Use Efficiency in Photosynthesis
- Nutrient-Use Efficiency
- Respiration
- Net Primary Production
- Remote Sensing of Primary Production and Biomass
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### Introduction

Photosynthesis is the biogeochemical process that acts to transfer carbon from its oxidized form, CO<sub>2</sub>, in the atmosphere 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 growth of plants 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 O<sub>2</sub> in our atmosphere provides the striking contrast between the *biogeochemistry* on Earth and the simple geochemistry that characterizes our neighboring planets.

In this chapter we will consider the measurement of net primary production—the rate of accumulation of organic carbon in the tissues of 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, while tropical rainforests can show annual production of >1000 g C/m<sup>2</sup>.

Various environmental factors affect the global 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> (Schlesinger 1977).

## 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 biochemistry. When photosynthetic pigments absorb sunlight, a few of the chlorophyll molecules are oxidized—passing an electron to a sequence of electron transfer proteins that ultimately lead to the reduction of a high-energy molecule, known as nicotinamide adenine dinucleotide phosphate (NADP), to NADPH. These chlorophyll molecules regain an electron from a water molecule, which is split by an enzyme containing manganese, calcium, and chlorine in a recently postulated asymmetrical three-dimensional structure (Pecoraro 1988, Yachandra et al. 1993). This reaction is the origin of O<sub>2</sub> in the Earth's atmosphere:



In all cases, the photosynthetic pigments and proteins are embedded in a cell membrane, which allows protons (e.g., H<sup>+</sup> of Eq. 5.1) to build up to high concentrations on one side of the membrane and for this potential energy to be used to synthesize another 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 CO<sub>2</sub> and build carbohydrate molecules. The reaction begins with the enzyme ribulose bisphosphate carboxylase, also known as *Rubisco*, which adds CO<sub>2</sub> to the basic carbohydrate unit.<sup>1</sup> The overall reaction for photosynthesis is



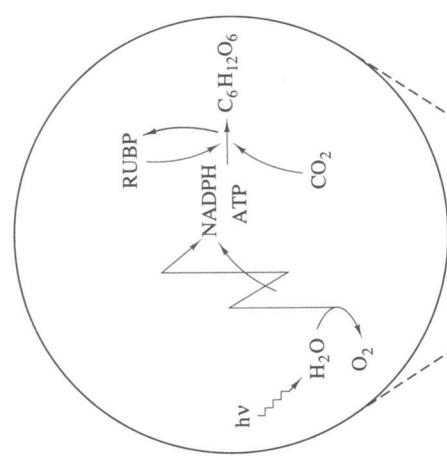
but we should remember that the process occurs in two stages. First, the capture of light energy allows water molecules to be split and high-energy molecules to form. This reaction is followed by carbon reduction, in which CO<sub>2</sub> is converted to carbohydrate.

The carbon dioxide used in photosynthesis diffuses into plant leaves through pores, stomates, that are generally found on the lower surface of broad-leaf plants (Fig. 5.1). One factor that determines the rate of photosynthesis is the stomatal aperture, which plant physiologists express as *stomatal conductance* in units of cm/sec. Stomatal conductance is controlled primarily by the availability of 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 ribulose bisphosphate carboxylase may determine the rate of photosynthesis (Sharkey 1985).

## Water-Use Efficiency in Photosynthesis

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 a major mechanism by which soil moisture is returned to the atmosphere (Table 8.1). 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; streamflow increased by 26–40% when the forest was cut (Pierce et al. 1970). Because water is often in short supply for plant growth (Kramer

<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 21% of global net primary production (Lloyd and Farquhar 1994), 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 isotopic fractionation in their tissues (average –12‰). In fact, various workers have shown that the isotopic ratio of plant debris preserved in soils can be used to trace changes in the distribution of C3 and C4 plants due to past shifts in climate (e.g., Quade et al. 1989, Ambrose and Sikes 1991).



**Figure 5.1** Cross-sectional view of a typical plant leaf, showing the upper (palisade) layer of cells, in which photosynthesis occurs, and the guard cells, which control the diffusion of  $\text{CO}_2$  (in) and  $\text{H}_2\text{O}$  (out) through stomates on the lower surface. A summary of the photosynthetic reaction occurring in the chloroplasts of the palisade cells is shown in the insert.

1982), these large losses of water by plants are somewhat surprising. One might expect natural selection for more efficient use of water by plants, especially in dry environments.

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

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

For most plants, water-use efficiency typically ranges from 0.86 to 1.50 mmol/mol, depending upon environmental conditions (Osmond et al. 1982). Water-use efficiency is higher at lower stomatal conductance. Rising concentrations of  $\text{CO}_2$  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  $\text{CO}_2$  has risen 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 growing in Egypt today (Beerling and Chaloner 1993).

Equation 5.3 largely applies to short-term experiments in the laboratory. For the biogeochemist, long-term average water-use efficiency may be estimated from the carbon isotope composition of plant tissues. This method is based on the observation that the diffusion of  $^{12}\text{CO}_2$ , a lighter molecule, is more rapid than that of  $^{13}\text{CO}_2$ , which composes about 1.1% of atmospheric  $\text{CO}_2$ . Thus, in a given period of time more  $^{12}\text{CO}_2$  enters the leaf than  $^{13}\text{CO}_2$ . Inside the leaf, ribulose bisphosphate carboxylase also has a higher affinity for  $^{12}\text{CO}_2$ . As a result of these factors, plant tissue contains a lower proportion of  $^{13}\text{CO}_2$  than the atmosphere by about 2% (= 20‰) (O'Leary 1988). The discrimination (fractionation) between carbon isotopes is expressed relative to an accepted standard as

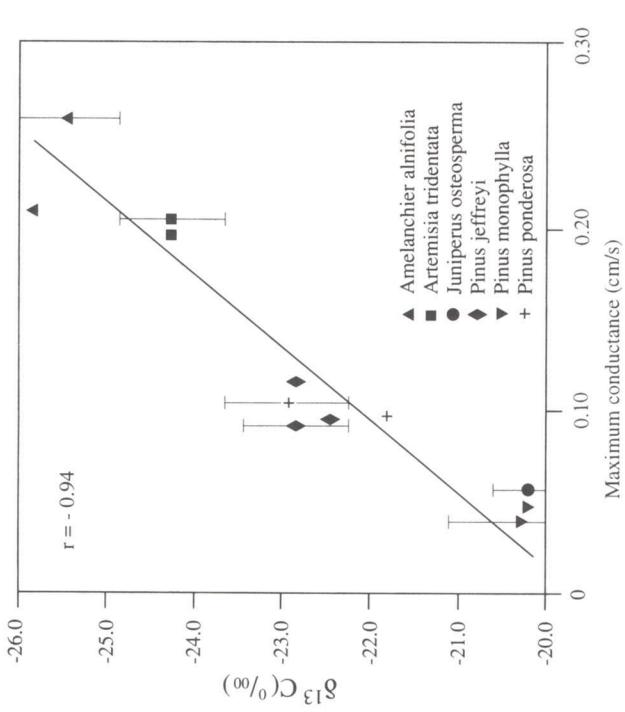
$$\delta^{13}\text{C} = \left[ \frac{\text{^{13}C}/\text{^{12}C}_{\text{sample}} - \text{^{13}C}/\text{^{12}C}_{\text{standard}}}{\text{^{13}C}/\text{^{12}C}_{\text{standard}}} \right] \times 1000 \quad (5.4)$$

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 a  $\delta^{13}\text{C}$  of ca.  $-28\text{\textperthousand}$  [i.e.,  $(-8\text{\textperthousand}) + (-20\text{\textperthousand})$ ]. Sedimentary organic carbon with this isotopic signature is useful in determining the antiquity of photosynthesis as a biochemical process (Fig. 2.6).

The discrimination between  $^{12}\text{CO}_2$  and  $^{13}\text{CO}_2$  during photosynthesis is greatest when stomatal conductance is high (Fig. 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. Thus, 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 indicate that the water-use efficiency of plants has 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).

#### Nutrient-Use Efficiency

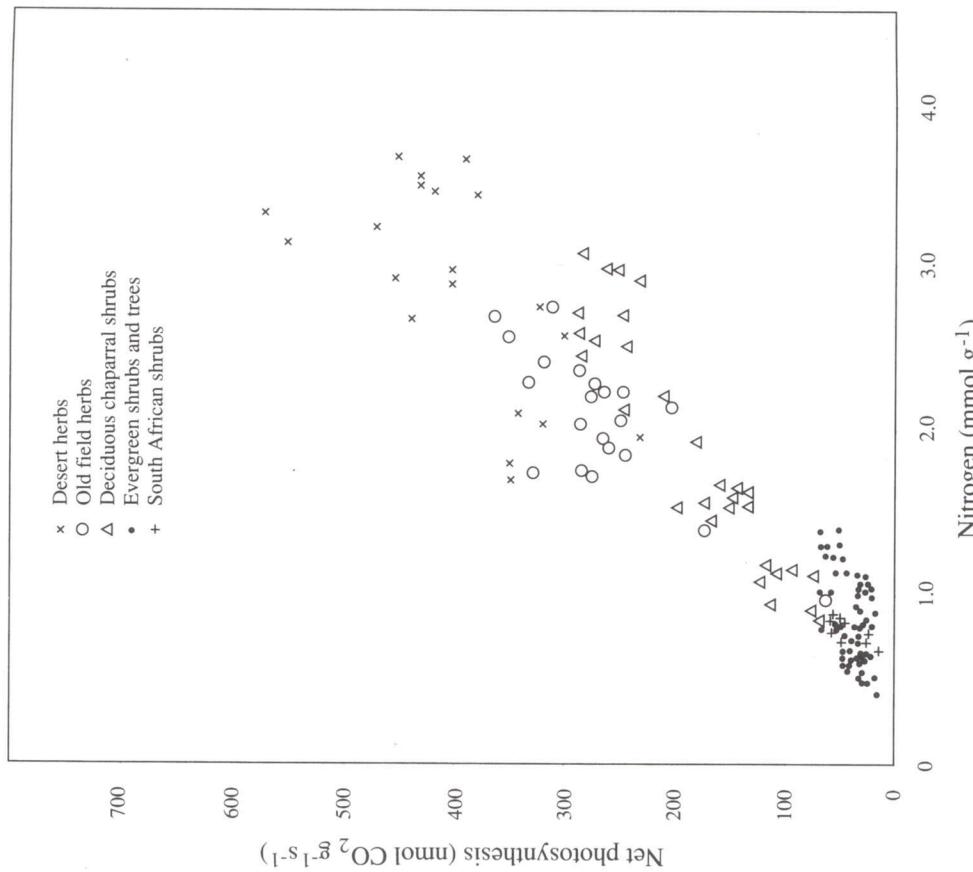
Over a broad range of plant species, the rate of photosynthesis is directly correlated to leaf nitrogen content when both are expressed on a mass basis (Reich et al. 1992, 1995; Fig. 5.3). Most leaf nitrogen is contained in enzymes; by itself, ribulose bisphosphate carboxylase usually accounts for 20 to 30% of leaf nitrogen (Evans 1989). Seemann et al. (1987) found that photosynthetic potential is directly related to the content of ribulose bisphosphate carboxylase and leaf nitrogen in several species, suggesting



**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. Modified from DeLucia et al. (1988).

that the availability of nitrogen determines leaf enzyme contents 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). Despite their central role in the molecules 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. The rate of photosynthesis per unit of leaf nitrogen—the slope of the line in Fig. 5.3—is one measure of nutrient-use efficiency (NUE) (Evans 1989). Overall, the data of Figure 5.3 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).



**Figure 5.3** Relationship between net photosynthesis and leaf nitrogen content among 21 species from different environments. From Field and Mooney (1986).

### Respiration

Photosynthesis is usually measured by placing leaves or whole plants in closed chambers and measuring the uptake of  $\text{CO}_2$  or release of  $\text{O}_2$ . The rates are a measure of *net* photosynthesis by the plant, i.e., the fixation of carbon in excess of the simultaneous release of  $\text{CO}_2$  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 (Fig. 5.4; see also Ryan 1995). In woody plants, a large fraction of the respiration is contributed by stems and roots owing to their large contribution to total

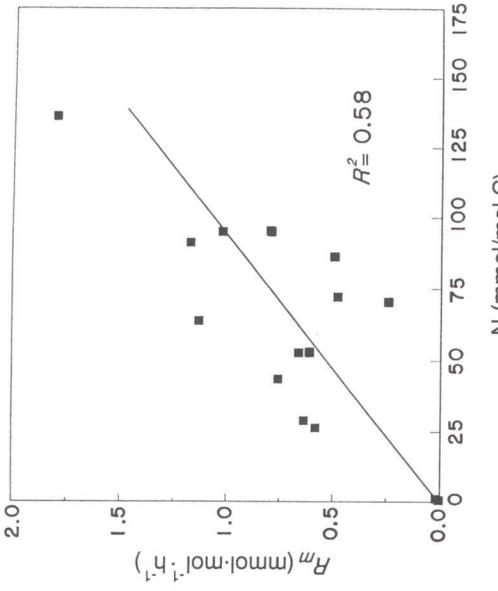


Figure 5.4 Respiration of plant tissues as a function of their nitrogen content. Modified from Ryan (1991).

plant biomass (Amthor 1984, Waring and Schlesinger 1985). For leaf tissues, rates of respiration are higher in the daytime than during the night as a result of the additional process of photorespiration (Sharkey 1988).

Independent measures of respiration suggest that about one-half of the gross carbon fixation by photosynthesis is used by plants, so the actual rate of photosynthesis is often twice that which is measured as plant growth (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, Waring and Schlesinger 1985). 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). Respiration may also increase as plants allocate more tissue to sapwood in hotter, drier environments (Callaway et al. 1994).

### Net Primary Production

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

$$\text{Gross primary production} - \text{plant respiration} = \text{net primary production.}$$

$$(R_p) \quad (NPP) \quad (5.5)$$

Net primary production is, however, not directly equivalent to plant growth as measured by foresters, ranchers, and farmers. Some fraction of NPP is lost to herbivores 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.

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 units 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 in sunlight (Botkin and Malone 1968, Reiners 1972).

The measurement of NPP in the field is not easy, but the methods for estimating aboveground NPP are well developed and reviewed extensively elsewhere for forests (Whittaker and Marks 1975) and grasslands (Singh et al. 1975). Traditional methods for 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. Independent estimates of the seasonal loss of plant parts can be obtained from collections of plant litterfall through the year. In grasslands, there is little or no true increment, and estimates of net primary production 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). These estimates must be corrected for the consumption and loss of tissues during the same period.

Allocation of net primary production varies with vegetation type and age. In forests, 25 to 35% of aboveground production is found in leaves (Whittaker et al. 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 tissue.

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 the tropics—i.e., there is greater wood production per unit of foliage in boreal forests. As a result of their massive structure and

high environmental temperatures, tropical forests may expend a greater percentage of their gross primary production in respiration (Whittaker and Marks 1975, Ryan et al. 1994), leaving less for wood growth. 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 (Fig. 5.5). 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, Caldwell and Camp 1974, Runyon et al. 1994).

Root growth is especially difficult to study, and many estimates of NPP include data only for the aboveground tissues. Nevertheless, when roots have been examined carefully, the annual growth and turnover of root tissues account for a significant fraction of the NPP in most communities. In forests the proportional allocation of photosynthate to root growth varies as an inverse function of site fertility (Axelson 1981, Gower et al. 1992), although the absolute amount of root growth is greatest on sites with

high NPP (Raich and Nadelhoffer 1989). Edwards and Harris (1977) reported that the growth and death of roots delivered 733 g C m<sup>-2</sup> yr<sup>-1</sup> to the soil in a forest in Tennessee, where the aboveground production was 685 g C m<sup>-2</sup> yr<sup>-1</sup> (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 NPP is allocated to root growth in many grassland ecosystems (Lauenroth and Whitman 1977, Warenbourg and Paul 1977). Unfortunately, for the purpose of global estimates, there are no obvious general correlations that allow us to predict the allocation of NPP to aboveground and belowground tissues worldwide (Nadelhoffer and Raich 1992, Gower et al. 1996).

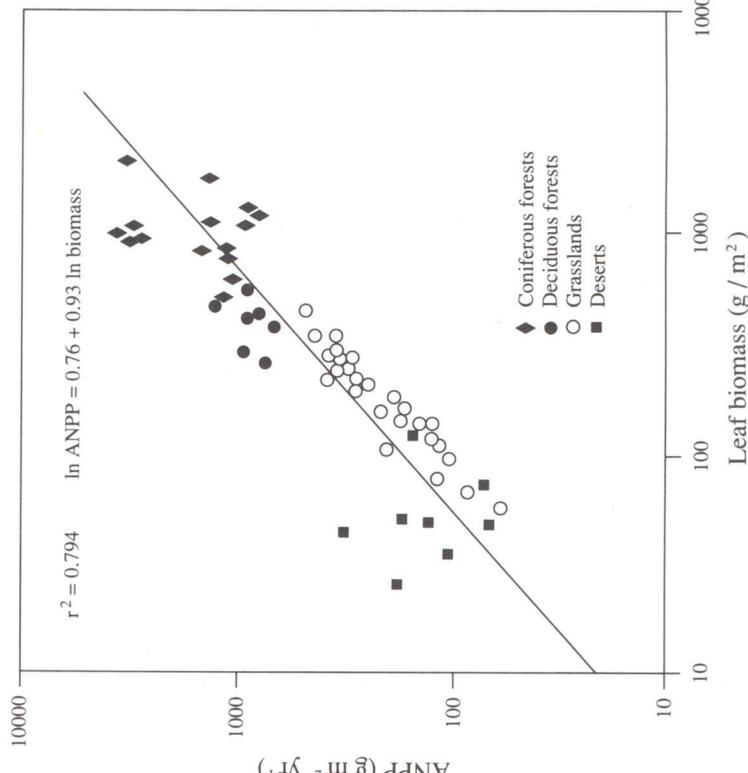
In recent years, ecologists have developed a new approach to estimating the net carbon balance of whole ecosystems—plants as well as soil. The approach is based on the observation that during the day, atmospheric

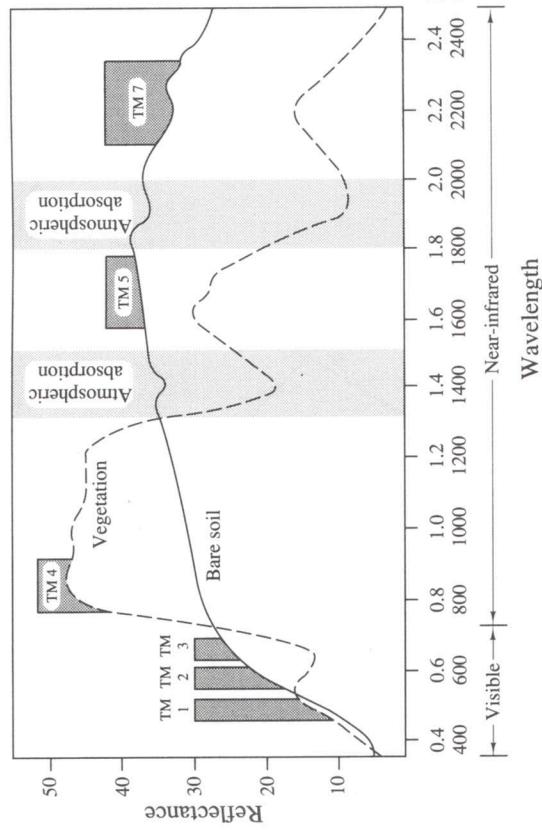
**Table 5.1** Net Primary Production in 23- and 180-yr-old *Abies amabilis* forests in the Cascade Mountains, Washington<sup>a</sup>

	23-yr-old		180-yr-old	
	g m <sup>-2</sup> yr <sup>-1</sup>	% of total	g m <sup>-2</sup> yr <sup>-1</sup>	% of total
<b>Aboveground</b>				
Biomass increment	426		232	
Tree total	6	<1		
Shrub stems			232	9.33
Total	432	18.37		
<b>Detritus production</b>				
Litterfall	151		218	
Mortality	30			
Herb layer turnover	32			
Total	213	9.06	223	5
Total aboveground	645	27.42	455	8.97
				18.30
<b>Belowground</b>				
Roots				
Fine ( $\leq 2$ mm)	650	27.64	1290	51.87
Fibrous-textured	571		1196	
Mycorrhizal (host tissue)	79		94	
Coarse ( $> 2$ 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 belowground	1707	72.58	2032	81.70
Ecosystem total				
			2352	2487

**Figure 5.5** Using data from a variety of ecosystems in North America, Webb et al. (1983) found a strong relation between the annual aboveground net primary production and the biomass of foliage.

<sup>a</sup> From Vogt et al. (1982).





**Figure 5.6** 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.

$\text{CO}_2$  typically shows a concentration gradient from approximately 360 ppm, the tropospheric background (Table 3.1), to lower values in the plant canopy as a result of  $\text{CO}_2$  uptake by vegetation. This gradient develops despite atmospheric mixing that should otherwise cause the concentrations of  $\text{CO}_2$  to be uniform with height. At any rate of mixing, the strength of the gradient is related to the net carbon uptake by vegetation, allowing an estimate of NPP. During the night, the gradient is often reversed, as plant and soil respiration continue in the absence of vegetation uptake (Woodwell and Dykeman 1966, Reiners and Anderson 1968). Known as the eddy-correlation technique, this approach has been applied to a variety of forest and grassland ecosystems (Baldocchi et al. 1987, Wofsy et al. 1988, Kim et al. 1992, Hollinger et al. 1994, Grace et al. 1995).

Using the eddy-correlation approach, Goulden et al. (1996) summed hourly and daily carbon exchange to provide annual estimates of net carbon accumulation in a deciduous forest in Massachusetts. Over five years the forest took up between 1070 and 1210  $\text{g C m}^{-2} \text{ yr}^{-1}$  (GPP), but plant and soil respiration returned 810 to 1140  $\text{g C m}^{-2} \text{ yr}^{-1}$  to the atmosphere, so the net accumulation of carbon in the ecosystem—the true increment—was only 140 to 280  $\text{g C m}^{-2} \text{ yr}^{-1}$ . This value is similar to independent estimates of wood growth in the forest; but, remember that this is less than total NPP, which also includes the production of leaves and other short-lived tissues (Valentini et al. 1996).

#### Remote Sensing of Primary Production and Biomass

Harvest measurements of NPP are labor intensive and necessarily applied only to small areas. Productivity of vegetation may vary greatly over the landscape, so regional estimates of productivity by harvest become prohibitively expensive. Nevertheless, for understanding global change, regional and global estimates of NPP are essential, and various methods using remote sensing to provide integrated estimates of NPP over large areas are currently under development.

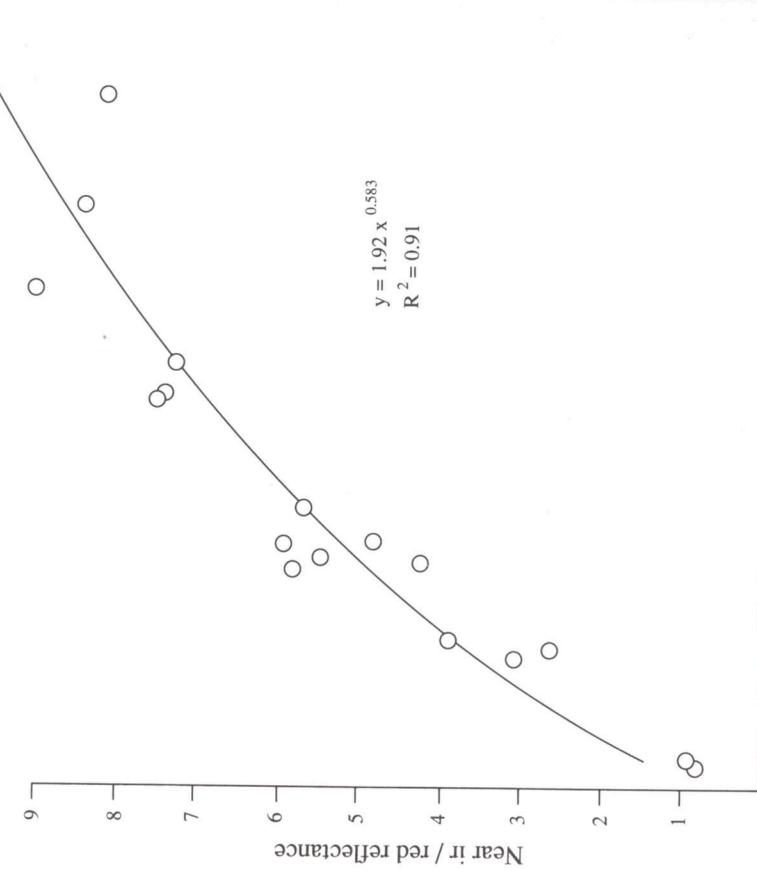
The basis of satellite measurements of NPP is the differential absorption of light by chlorophyll and other leaf pigments. Green plants look green because chlorophyll preferentially absorbs light in the blue and red portions of the solar spectrum, reflecting a large portion of the green light to our eyes. Despite its strong absorption of red light (760 nm), chlorophyll shows little absorption of infrared light with wavelengths of 800 to 1200 nm. Thus, to provide an index of the underlying greenness of the Earth's surface, the LANDSAT (Thematic Mapper) satellites have measured surface reflectance in discrete portions of the visible and infrared spectrum, labeled TM1-7 in Fig. 5.6. Bare soil should show similar reflectance in the TM4 and TM3 wavebands, whereas vegetation shows a TM4/TM3 ratio  $\gg 1.0$  as a result of the absorption of red light by chlorophyll.

The LANDSAT instrument measures the reflectance in each waveband for a 30  $\times$  30-m plot or pixel of land. In the northwestern United States, the TM4/TM3 ratio was directly correlated to leaf area in 17 coniferous forests studied by harvest measurements (Fig. 5.7). In each forest, leaf area was expressed as the leaf-area index (LAI) in units of  $\text{m}^2/\text{m}^2$ —the area of leaves above a square meter of ground surface. Previous studies had shown a direct relation between LAI and NPP in these forests (Fig. 5.8), so the potential extrapolation from satellite measurements of LAI to regional estimates of NPP is obvious. Indeed, Cook et al. (1989) found a good relationship between thematic mapper data and regional estimates of NPP across a range of ecosystem types in North America.

Goward et al. (1985) followed a similar approach using data from an advanced very-high-resolution radiometer (AVHRR) carried on the NOAA-7 satellite. They calculate a normalized difference vegetation index (NDVI),

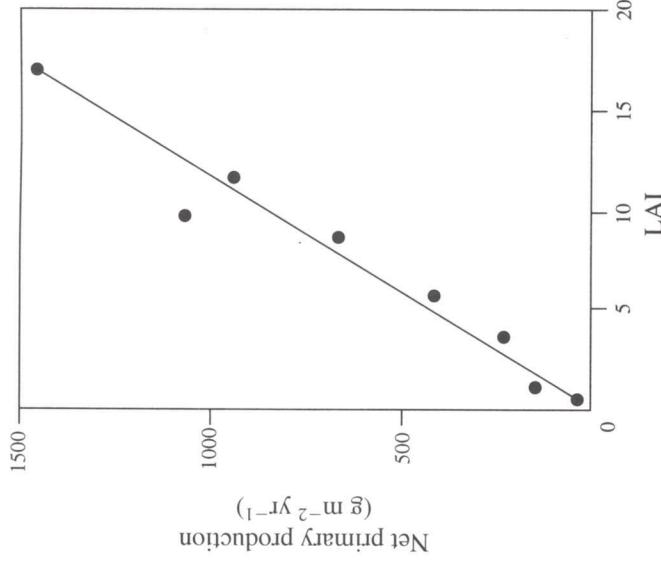
$$\text{NDVI} = (\text{NIR} - \text{VIS}) / (\text{NIR} + \text{VIS}), \quad (5.6)$$

where NIR is reflectance in the near-infrared and VIS is reflectance in the visible 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. Their data allow global mapping of a "greenness" index for the Earth's land surface (Plate 1).



**Figure 5.7** The ratio of light reflected in the near infrared and red spectral bands (wavebands TM4 and TM3 of the LANDSAT satellite; see Fig. 5.6) is related to LAI for forest stands in the northwestern United States. From Peterson et al. (1987).

Satellite measurements of "greenness" may lead to global estimates of NPP, assuming that "greenness" is directly related to leaf area and that LAI is good predictor of NPP (Figs. 5.5 and 5.8). Integrations of NDVI measured at frequent intervals over the growing season show a direct correlation to regional average values of NPP measured by harvest methods (Goward et al. 1985, Box et al. 1989). Recently, Fung et al. (1987) have shown that the seasonal patterns of NDVI for the latitudinal bands of the globe are consistent with the magnitude of the seasonal oscillation of atmospheric CO<sub>2</sub> measured at various latitudinal stations (Fig. 3.6). Although the LANDSAT data have finer resolution than those gathered by AVHRR (1.1 km<sup>2</sup>), the AVHRR data are often more useful in regional and global estimates because the number of pixels covering the land surface remains manageable during data processing. Running et al. (1989) used



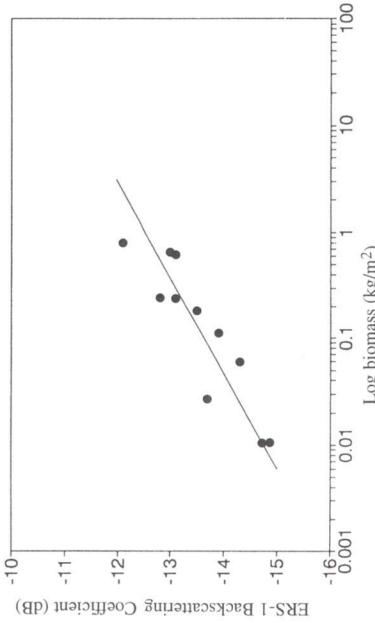
**Figure 5.8** Net primary production is directly related to leaf-area index for forests in the northwestern United States. Modified from Gholz (1982).

AVHRR data to estimate the leaf-area index of forests in western Montana and used the LAI data in a model for forest growth to calculate regional evapotranspiration, NPP, and water-use efficiency.

Remote sensing of leaf area and NPP has proven easier than similar measurements of biomass. However, live woody vegetation absorbs and reflects microwave energy as a function of its height and the volume of water-filled tissue, and this observation has been used as the basis for remote sensing of forest biomass. In most cases a microwave emitter is mounted on an aircraft, which also carries a sensor to measure the proportion of the emitted radiation that is reflected back to the source. Known as synthetic aperture radar (SAR), this technique has been used successfully to measure vegetation biomass, especially the regrowth of forests after clearing (Fig. 5.9).

#### Global Estimates of Net Primary Production and Biomass

Although remote sensing techniques will undoubtedly offer future refinements, most current estimates of global net primary production and biomass are based on compilations of data from harvest measurements. One of the first compilations, that by Whittaker and Likens (1973), is widely cited, but it has been modified repeatedly to incorporate new data from around the



**Figure 5.9** The reflected microwave radiation (backscattering coefficient) measured by an airborne synthetic aperture radar (SAR) for stands of young loblolly pine (*Pinus taeda*) in central North Carolina. Modified from Kasischke et al. (1994).

world (Table 5.2). Most of the estimates of global NPP are in a range of  $45 \times 10^{15}$  g C/yr. Olson et al. (1983) offer the most comprehensive estimate of the total biomass of plants on land; their value is  $560 \times 10^{15}$  g C. The ratio of biomass/NPP is an estimate of the mean residence time for an atom of carbon in plant tissues (cf. Eq. 3.3). The global values yield an overall mean residence time of about 9 years, but this value varies from about 4 in deserts to  $>20$  in some forests (Table 5.2). 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 5.2 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 the full range of variation in the field, because ecologists tend to select mature, well-developed stands for study.

Brown and Lugo (1984) have considered the effect of differences in classification and stand selection on estimates of the biomass of tropical forests. Their data are considerably lower than those reported in Table 5.2. Revised, lower estimates of the biomass in boreal forests (Botkin and Simpson 1990) and deciduous forests (Botkin et al. 1993) of North America are also available. We can expect that global estimates of NPP and biomass by remote sensing will help resolve some of these differences. Similarly, improved classifications of the Earth's vegetation, based on its physiological response to climate, will allow for more consistent compilation of global values for net primary production and biomass (Prentice 1990, Prentice et al. 1992, Neilson 1995, DeFries et al. 1995).

The data in Table 5.2 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. Along a gradient of decreasing precipitation, NPP declines from forests to grasslands, showing very low values in most deserts. Wetland vegetation has high NPP; we will examine wetlands in more detail in Chapter 7.

Evidence for the importance of temperature and moisture is seen in regional comparisons of productivity, especially patterns along gradients of elevation. Whittaker (1975) found that NPP declined with increasing elevation in the forested 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 relation between net primary production and precipitation within the grasslands of the central United States. 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 during the growing season (Grier and Running 1977, Gholtz 1982).

Rosenzweig (1968) combined temperature and precipitation to calculate actual evapotranspiration, which shows a positive correlation to NPP in temperate zone ecosystems (Webb et al. 1978). The overall strength of

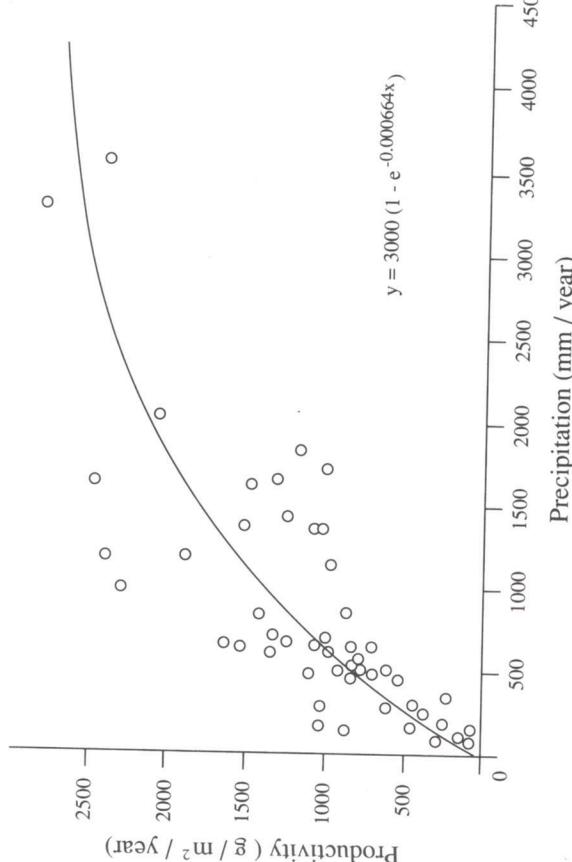
**Table 5.2** Primary Production and Biomass Estimates for the World<sup>a</sup>

Ecosystem	Area ( $10^{12}$ m $^2$ )	Mean plant biomass (kg C/m $^2$ )	Carbon in vegetation ( $10^{15}$ g)	Mean		
				net primary production (g C/m $^2$ /yr)	Net primary productivity ( $10^{15}$ g C/yr)	
Tropical wet and moist forest	10.4	15	156.0	800	8.3	
Tropical dry forest	7.7	6.5	49.7	620	4.8	
Temperate forest	9.2	8	73.3	650	6.0	
Boreal forest	15.0	9.5	143.0	430	6.4	
Tropical woodland and savanna	24.6	2	48.8	450	11.1	
Temperate steppe	15.1	3	43.8	320	4.9	
Desert	18.2	0.3	5.9	80	1.4	
Tundra	11.0	0.8	9.0	130	1.4	
Wetland	2.9	2.7	7.8	1300	3.8	
Cultivated land	15.9	1.4	21.5	760	12.1	
Rock and ice	15.2	0	0.0	0	0.0	
Global total	145.2		558.8		60.2	

<sup>a</sup>From Houghton and Skole (1990).

the relation 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 most important (Brown and Lugo 1982).

One of the earliest systematic attempts to estimate global NPP and biomass focused on climatic variables. Lieth (1975) related NPP at 52 field sites to the mean annual temperature and precipitation recorded in nearby weather stations (Figs. 5.10 and 5.11). He considered temperature to be an index of solar irradiance and to determine the length of the growing season (cf. Bonan 1993). These data provided Lieth with equations that he could use with local weather data to predict productivity in other areas of the world. A map of global productivity was developed using the lower of the two predictions of NPP at each site, to reflect a temperature or moisture limitation on NPP. The global map of NPP (Fig. 5.12) is surprisingly similar to the satellite picture of "greenness" (Plate 1). Lieth's (1975) approach suggests that light and moisture are the main factors determining NPP, with soil nutrients playing a lesser role. His global map suggests a total terrestrial NPP of about  $63 \times 10^{15} \text{ g C yr}^{-1}$ , assuming that the world's land vegetation is undisturbed by humans (Esser et al. 1982).

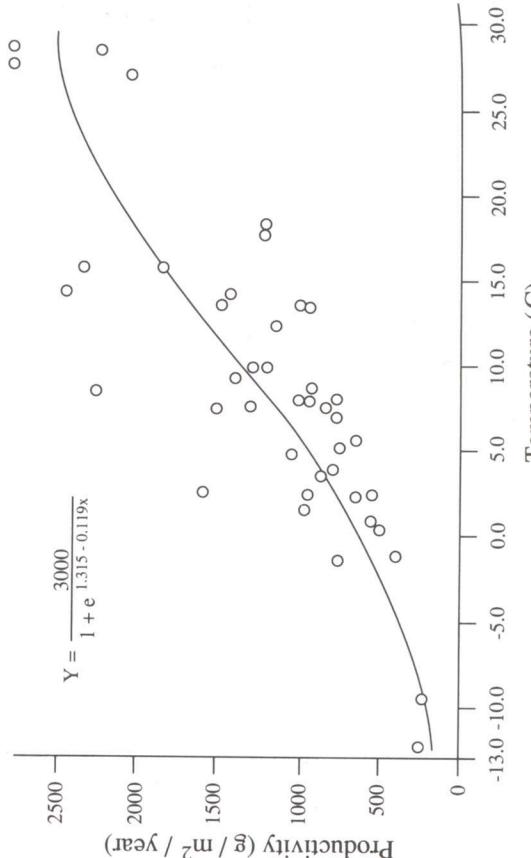


**Figure 5.11** Relationship between NPP and mean annual precipitation for 52 locations around the world. From Lieth (1975).

Recently, several attempts have been made to estimate global NPP by incorporating a large number of factors in global simulation models. Melillo et al. (1993) suggest that for any site,

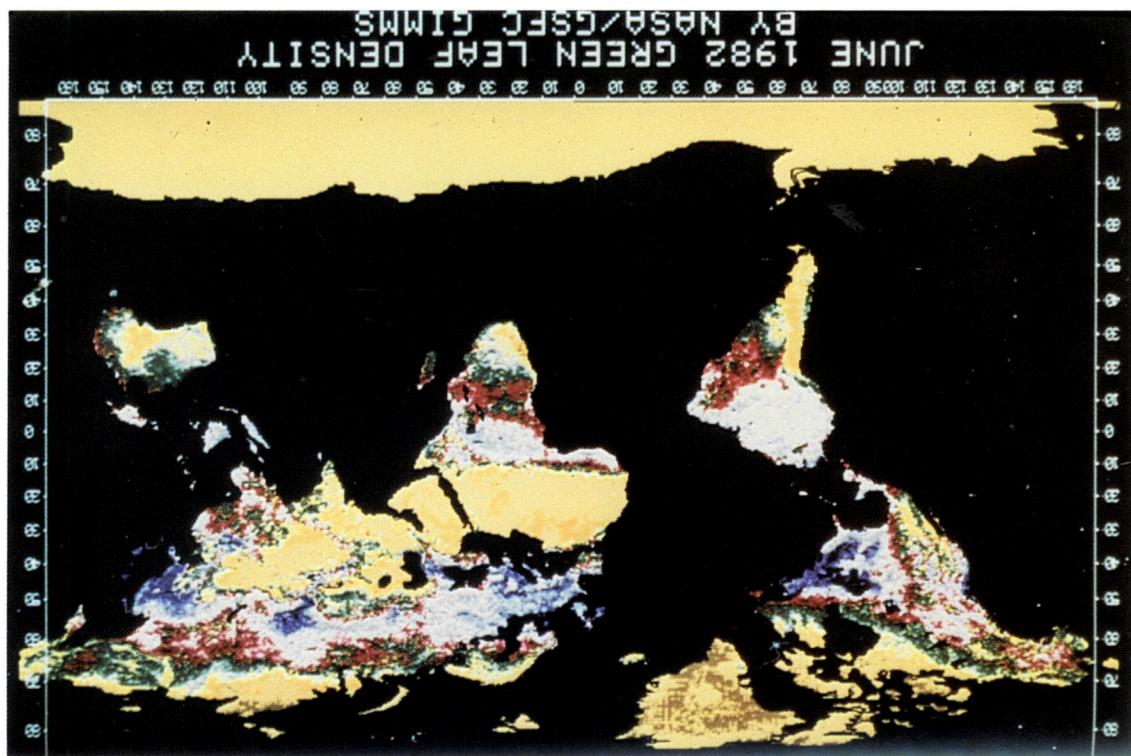
$$\text{NPP} = \text{NPP}_{(\text{max})} \times \text{PAR} \times \text{LAI} \times T \times \text{CO}_2 \times \text{H}_2\text{O} \times \text{NA}, \quad (5.7)$$

where PAR is photosynthetically active radiation,  $T$  is temperature,  $\text{CO}_2$  is the atmospheric concentration of  $\text{CO}_2$ ,  $\text{H}_2\text{O}$  is soil moisture, and NA is an index of nutrient availability. Assuming that the Earth's vegetation is undisturbed by humans, they compiled or estimated these data for >56,000 pixels of the Earth's land surface to calculate a total productivity of  $53.2 \times 10^{15} \text{ g C/yr}$ . A similar approach, using AVHRR to estimate LAI globally, arrives at  $48 \times 10^{15} \text{ g C}$  as a global estimate of NPP—with 70% between  $30^\circ \text{N}$  and  $30^\circ \text{S}$  latitude (Potter et al. 1993, Field et al. 1995). The difference between these values may well represent the effect of human disturbance of the land. These models can be modified to incorporate future changes in the Earth's condition, such as the increase in atmospheric  $\text{CO}_2$  and potential changes in the Earth's temperature and precipitation. For instance, with changes in climate and rising  $\text{CO}_2$ , Melillo et al. (1993) predict an increase in global NPP to more than  $60 \times 10^{15} \text{ g C/yr}$ , assuming no shifts in the distribution of vegetation and no disturbance of the land by humans.

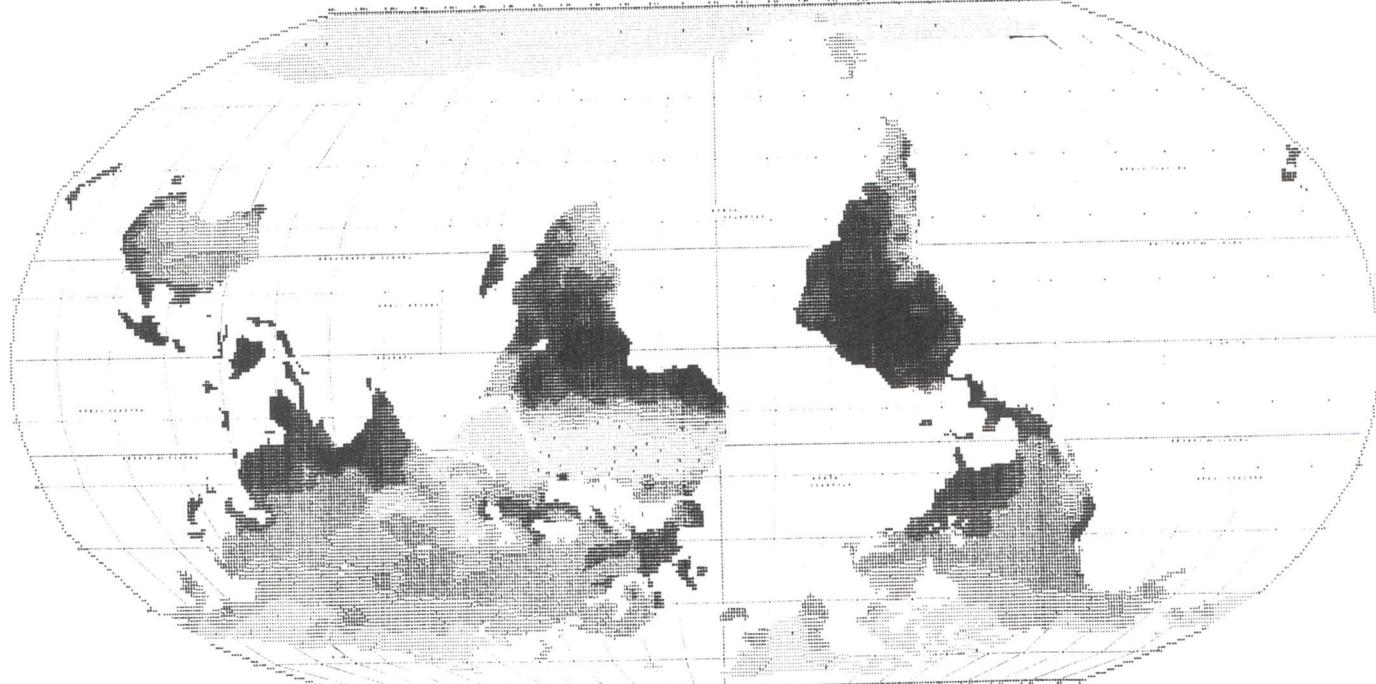


**Figure 5.10** Relationship between NPP determined by harvest and mean annual temperature for 52 studies on various continents. From Lieth (1975).

**Plate 1** Normalized Difference Vegetation Index (NDVI) for June 1982 as obtained from the Advanced Very High Resolution Radiometer on the NOAA satellite. Note that the greatest vegetation density is colored white and blue, whereas green and yellow indicate lower leaf area. The Northern Hemisphere is in mid-summer. From NASA, 1987.



**Figure 5.12** A map of terrestrial net primary production, predicted using the relationships in Figs. 5.10 and 5.11 and local weather data. From Leem (1975).



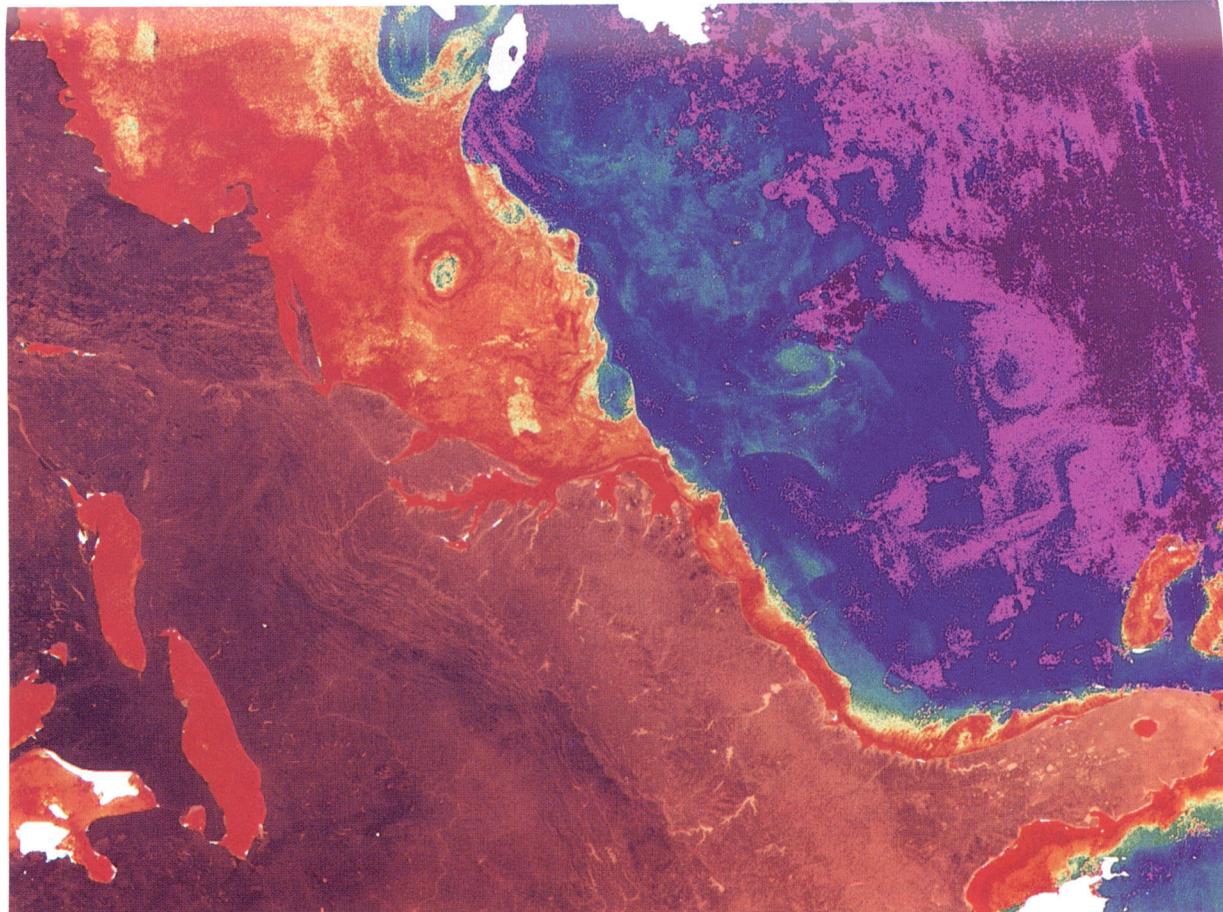
## Net Primary Production and Global Change

The direct harvest of plants for food, fuel, and shelter accounts for about  $3.3 \times 10^{15}$  g C/yr or about 6% of the terrestrial productivity worldwide (Vitousek et al. 1986). As a result of inadvertent activities, such as wildfires and pollution, humans may have reduced total net primary production by up to 25 to 40% (Vitousek et al. 1986; Dobrovolsky 1994, p. 67). Vitousek et al. (1986) suggest that this is probably the largest diversion of primary production to support a single species in the history of life on Earth, certainly a thought-provoking percentage given the current continuing rate of human population growth.

The effect of humans on biomass and net primary productivity is reflected by changes in the global carbon cycle and in the composition of the atmosphere (Chapters 3 and 11). Most of the increase in atmospheric carbon dioxide is due to the burning of fossil fuels, but a significant portion is also due to the destruction of plant biomass, especially in tropical forests. Although fast-growing successional vegetation is found on most areas that are harvested, the rate of carbon accumulation in these areas does not equal the rate of carbon loss during harvest, so there is a net transfer of carbon from biomass to atmospheric CO<sub>2</sub> (Houghton et al. 1983; Harmon et al. 1990). Simply put, the carbon storage in agricultural crops or forest regrowth is less than the carbon contained in the original forest biomass (Table 5.2).

Houghton et al. (1983) attempt to account for the effect of humans on changes in world biomass between 1860 and 1980, compiling land-use statistics to calculate the rate of agricultural expansion and forest harvest. They suggest that world biomass has been reduced by about  $110 \times 10^{15}$  g C since 1860, equivalent to 13% of their estimate of preindustrial biomass ( $827 \times 10^{15}$  g C). The release of carbon from land, including the release from soils, was estimated to be in the range of  $1.8$  to  $4.7 \times 10^{15}$  g C/yr, compared to a release from fossil fuels of  $5 \times 10^{15}$  g C/yr in 1980 (Rotty and Masters 1985). More recent estimates of the net release of carbon from vegetation and soils are somewhat lower, reflecting better estimates of deforestation (Houghton et al. 1987; Houghton 1993). For the decade of the 1980s, the net release was about  $1.6 \times 10^{15}$  g C/yr, reflecting a 3% imbalance between NPP and decomposition on the Earth's land surface (Houghton 1995). Much of the current destruction occurs in tropical forests, which is why an accurate estimate of tropical forest biomass and its rate of deforestation is critical to our understanding of changes in the global carbon cycle (Houghton 1993; Skole and Tucker 1993).

The net destruction of terrestrial vegetation over the last century is reflected in changes in the isotopic composition of atmospheric CO<sub>2</sub>. Remembering that photosynthesis discriminates against <sup>13</sup>CO<sub>2</sub> in favor of <sup>12</sup>CO<sub>2</sub>, we can expect that plant tissues and fossil fuels are depleted in <sup>13</sup>C



**Plate 2** Distribution of chlorophyll in the western North Atlantic Ocean during May 1981, as recorded by the Coastal Zone Color Scanner (CZCS) on the Nimbus-7 satellite. Areas rich in phytoplankton are shown as red ( $> 1$  mg chlorophyll/m<sup>3</sup>); blue and purple areas have lower phytoplankton concentrations ( $< 0.01$  mg/m<sup>3</sup>). Note the high productivity of coastal areas especially

and dilute the atmospheric content of  $^{13}\text{CO}_2$  when they are burned. In addition, fossil fuels contain no  $^{14}\text{C}$ ; that radioactive isotope decays away with a half-life of 5700 years. Thus, the burning of fossil fuels also dilutes the atmospheric content of  $^{14}\text{CO}_2$ . Conveniently, tree rings, gas bubbles trapped in polar ice cores, and direct measurements of atmospheric  $\text{CO}_2$  since the mid-1950s provide a record of the atmospheric content of  $^{13}\text{CO}_2$  and  $^{14}\text{CO}_2$  during the recent past (Leavitt and Long 1988, Siegenthaler and Oeschger 1987). The  $^{13}\text{C}$  content of the atmosphere (i.e.,  $\delta^{13}\text{C}$ , Eq. 5.4) has declined about  $-0.034\text{ \textperthousand}/\text{yr}$  during the last several decades (Keeling et al. 1989). This dilution is greater than what is expected from fossil fuels alone, suggesting a net release from terrestrial vegetation.

Release of carbon from forest destruction in the tropics could, of course, be balanced by the abandonment of farmland and the permanent regrowth of vegetation elsewhere. Forest regrowth in the southeastern United States has apparently been a sink for atmospheric carbon of about  $0.07 \times 10^{15} \text{ g/yr}$  during this century (Delcourt and Harris 1980). Globally, afforestation may sequester about  $0.7 \times 10^{15} \text{ g C/yr}$  (Dixon et al. 1994; see also Chapter 11). We can expect the strength of this regional carbon sink to diminish as reforestation is complete and most forests become mature (Schiffman and Johnson 1989). Of course, the effect of the net sink is lost if these forests are harvested and the wood is converted to short-lived products, such as paper, that are burned.

Some workers have suggested that the primary production of land vegetation will increase as the concentration of atmospheric  $\text{CO}_2$  rises, stimulating photosynthesis by a greater delivery of  $\text{CO}_2$  to the enzyme ribulose bisphosphate carboxylase (Amthor 1995). When plants are maintained at optimal atmospheric  $\text{CO}_2$ , is double the ambient value (Woodward et al. 1991). With irrigation and fertilization, many crop plants show a response of this magnitude in the field (Strain and Cure 1985, Idso and Idso 1994, Wullschleger et al. 1995). There are few long-term experiments with trees, but several indicate a similar response (Curtis 1996, Norby 1996). If this effect is significant globally, then increased productivity by undisturbed vegetation could sequester  $\text{CO}_2$  released by fossil fuels and forest destruction (Idso and Kimball 1993). Evidence for a  $\text{CO}_2$  stimulation of forest growth, as recorded by tree-ring width, is mixed, with some studies showing increases (Graybill and Idso 1993), while others show little or no change over the last 100 years (Graumlich 1991, Jacoby and D'Arrigo 1995). In many areas, the growth of vegetation is limited by other factors, and  $\text{CO}_2$  may have little long-term direct effect (Kramer 1981, Körner 1993, Thomas et al. 1994, Brown 1991). Experimental studies of plant growth at high  $\text{CO}_2$ , often find an increased allocation of NPP to root tissues (Norby et al. 1992, Rogers et al. 1994). These roots may elevate the concentrations of  $\text{CO}_2$  in

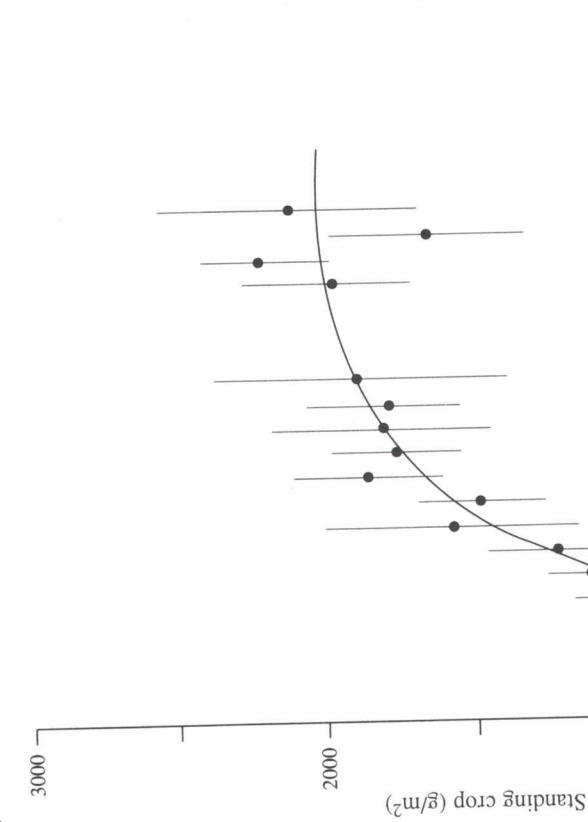
the soil pore space and add to the organic matter stored in soil (D.W. Johnson et al. 1994, Wood et al. 1994).

Elevated  $\text{CO}_2$  concentrations should increase water-use efficiency of vegetation, since stomata show partial closure at high  $\text{CO}_2$  concentrations. Higher water-use efficiency by terrestrial vegetation could leave greater amounts of moisture in the soil, contributing to an increase in the volume of runoff and global riverflow (Idso and Brazel 1984, Probst and Tardy 1987; Chapter 10). Unfortunately, as for the  $\text{CO}_2$  response, most of our work has focused on agricultural plants grown under laboratory conditions. There are few studies that document the response of whole ecosystems to increasing  $\text{CO}_2$ . Soil moisture and streamflow may not increase if plants maintain more leaves at high  $\text{CO}_2$ , compensating for lower transpiration losses per unit of leaf area (Allen 1990, Ellsworth et al. 1995).

Potentially more significant are changes in the distribution of terrestrial vegetation that may occur as a result of a  $\text{CO}_2$ -induced global warming (Overpeck et al. 1991, VEMAP 1995). T.M. Smith et al. (1992) examined the current distribution of world vegetation types and the expected changes in their distribution with changes in global precipitation and temperature. In the northern hemisphere, a northward shift in the distribution of productive forests may increase the rate of carbon storage in some areas, potentially sequestering  $180 \times 10^{15} \text{ g C}$  when the vegetation has fully adjusted to the global warming expected with a doubling of atmospheric  $\text{CO}_2$ . Significantly, however, land vegetation may be an important source of  $\text{CO}_2$  during the adjustment period (Smith and Shugart 1993, Pastor and Post 1993), as warming of the land surface proceeds warming of the oceans and drought becomes widespread (Rind et al. 1990; see Chapter 10). This scenario has dramatic implications for the distribution and productivity of agricultural lands worldwide (R.M. Adams et al. 1990, Rosenzweig and Parry 1994). Changes in the position of well-defined vegetation boundaries, such as continental treeline and the borders of deserts, may be our first indications of global climate change (Tucker et al. 1991, MacDonald et al. 1993, Lescop-Sinclair and Payette 1995, Schlesinger and Gramenopoulos 1996).

### The Fate of Net Primary Production

As communities of long-lived plants develop on land, a certain fraction of net primary production is allocated to perennial, woody tissues that accumulate as biomass through time. Plant communities achieve a steady state in living biomass when the allocation to woody tissue is balanced by the death and loss of older parts (Fig. 5.13). At that point, there is no true increment in biomass, although dead organic matter may still be accumulating in the soil. Odum (1969) summarized these trends in community development, suggesting that increasing fractions of gross primary



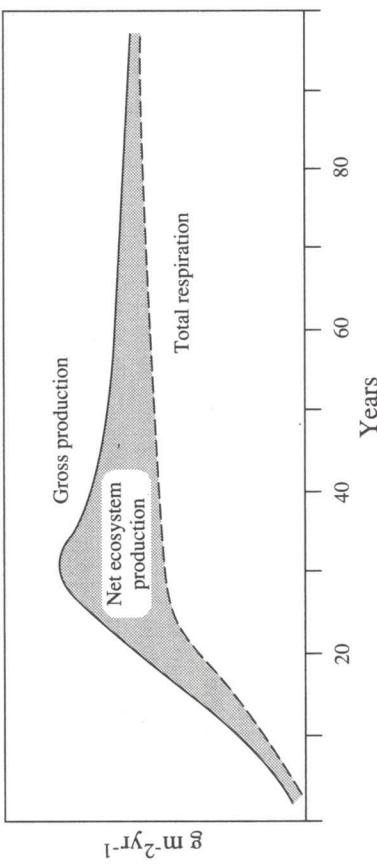
**Figure 5.13** Biomass (solid line) and decomposition through time components of a *Calluna* shrubland during 50 years of recovery after fire. From Chapman et al. (1975).

production are lost to plant respiration and decomposition through time (Fig. 5.14). His work defines *net ecosystem production* (NEP) as

$$\text{NEP} = \text{NPP} - (R_h + R_d), \quad (5.8)$$

where  $R_h$  is respiration of herbivores and  $R_d$  is respiration of decomposers. Remembering that

$$\text{NPP} = \text{GPP} - R_p, \quad (5.9)$$



**Figure 5.14** Generalized trends in primary production and respiration during ecosystem development. Modified from Odum (1969).

we can say that

$$\text{NEP} = \text{GPP} - R_t, \quad (5.10)$$

where  $R_t$  is the total respiratory loss of  $\text{CO}_2$  from the ecosystem.

These relationships suggest that increments in organic matter are possible only during the early stages of plant community development. In older communities, there is no true increment to live biomass, and nearly all the NPP is delivered to the soil, where it is decomposed. The role of animals is relatively minor. 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 NPP (e.g., Mispagel 1978, McNaughton et al. 1989, Cyr and Pace 1993). By consuming leaf area and root tissues, however, herbivores may have an indirect effect on NPP that is larger than estimates of their direct consumption (Reichle et al. 1973b, Llewellyn 1975, Ingham and Detling 1990). Globally, herbivores consume about  $3 \times 10^{15} \text{ g C/yr}$  (Whittaker and Likens 1973).

Fires are analogous to respiration by herbivores and decomposers, rapidly converting long-term accumulations of NEP to  $\text{CO}_2$  and restarting the process of ecosystem development. Globally, the consumption of NPP by fire is estimated to lie between 2 and  $5 \times 10^{15} \text{ g C/yr}$  (Crutzen and Andreae 1990, Hao and Liu 1994), and in recent years humans appear to have increased the frequency and area of land that is subjected to fire, especially in the tropics (Andreae 1991, Prins and Menzel 1994). Whereas boreal forests may have once acted to store atmospheric  $\text{CO}_2$  in biomass, a recent increase in the rate of burning at northern latitudes now makes these ecosystems a potential net source of  $\text{CO}_2$  to the atmosphere (Kasischke et al. 1995).

It is also worth noting, briefly, that vegetation is a source of a wide variety of volatile organic compounds in the atmosphere, including nonmethane hydrocarbons (Greenberg and Zimmerman 1984, Guenther et al. 1994) and carbon monoxide (Jacob and Wofsy 1990). Isoprene is especially abundant in the southeastern United States, where pine forests are widespread (Lamb et al. 1987a, Guenther et al. 1994). Emissions of isoprene, which seem associated with plant response to high temperatures (Sharkey and Singsaas 1995), probably account for about half of the total emission of volatile organic compounds from live vegetation worldwide (Miyoshi et al. 1994, Guenther et al. 1995). Emissions of reduced carbon gases represent NPP that escapes from the terrestrial biosphere to be oxidized in the atmosphere by hydroxyl radicals (Chapter 3). Globally, the emission of reduced carbon compounds from natural vegetation may be as large as  $1.15 \times 10^{15}$  g C/yr, or about 2% of NPP (Cruizen et al. 1985, Guenther et al. 1995).

### *Production of 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 net primary production (Eser et al. 1982). The deposition of litterfall declines with increasing latitude from tropical to boreal forests (Bray and Gorham 1964, Van Cleve et al. 1983, Lonsdale 1988). Leaf tissues account for about 70% of aboveground 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). Following the approach of models for net primary production, Meentemeyer et al. (1982) used actual evapotranspiration to predict global patterns of plant litterfall and to estimate  $54.8 \times 10^{15}$  g for the annual production of aboveground litterfall worldwide.

### *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  $\text{CO}_2$ ,  $\text{H}_2\text{O}$ , 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). 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

$$X/X_0 = e^{-kt}. \quad (5.11)$$

An alternative, the mass-balance approach, suggests that the annual decomposition position 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

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

or

$$\frac{\text{litterfall}}{\text{detrital mass}} = k. \quad (5.13)$$

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, p. 51). 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 estimated in a montane fir forest, 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, there is little surface accumulation and values for  $k$  are greater than 1.0 (e.g., in tropical rain forests; Cuevas and Medina 1988). In such systems, decomposition has the potential to respire more than the annual input of 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 and photooxidation of litter by ultraviolet light (Schaefer et al. 1985). Esser et al. (1982) suggest a global

mean residence time of 3 years (i.e.,  $k = 0.33$ ) for carbon on the surface of the soil.

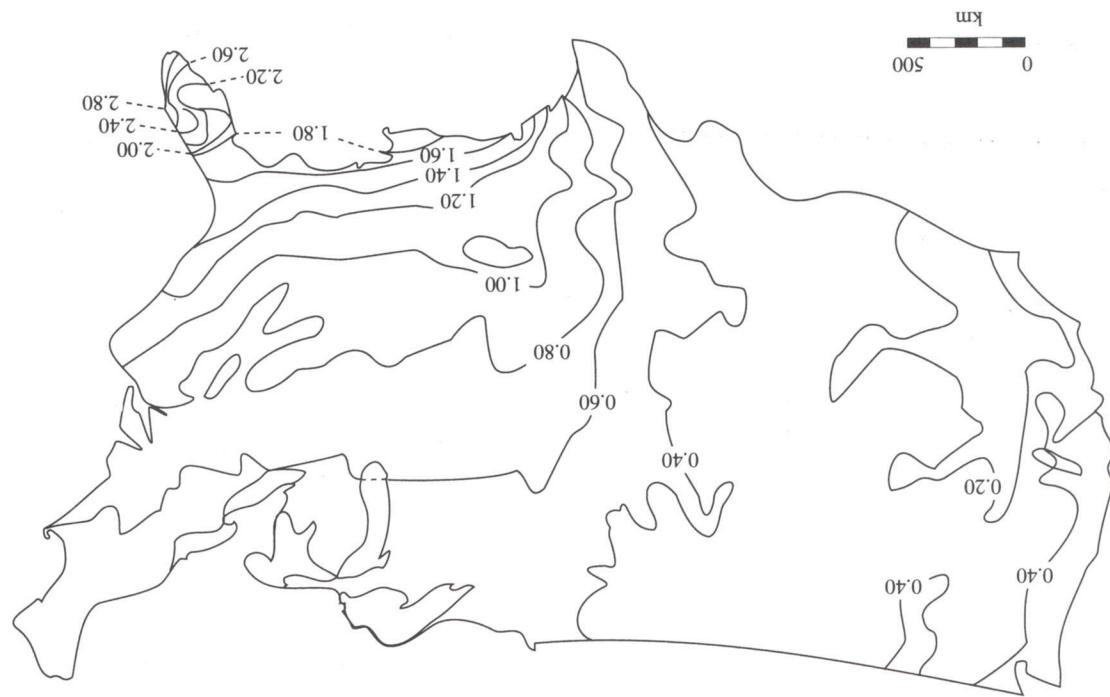
Decomposition rates vary as a function of temperature, moisture, and the chemical composition of the litter material. Microbial activity increases exponentially with increasing temperature (e.g., Edwards 1975). This relation often shows a  $Q_{10}$  of 2.0, i.e., a doubling in activity per  $10^{\circ}\text{C}$  increase in temperature (Singh and Gupta 1977, Raich and Schlesinger 1992, Kirschbaum 1995). 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 (Wielandt et al. 1975, Santos et al. 1984, Amundson et al. 1989). Field experiments suggest that moisture assumes increasing importance when temperate forest soils are warmed (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 (Fig. 5.15). 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). 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 will 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 non-cellular organic matter—humus—that 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 radicals 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), but many scientists believe that a large portion of soil humus is amorphous, with no consistent molecular weight or repeating units of structure. Recent progress in elucidating the chemical structure of humus has been made using  $^{13}\text{C}$  nuclear magnetic resonance (NMR) spectroscopy 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).

**Figure 5.15** Rates of decomposition of fresh litter in the United States predicted by a simulation model using actual evapotranspiration as a predictive variable. Slopelet values are the fractional loss rate ( $k$ ) of mass from fresh litter during the first year of decay. From Meentemeyer (1978a).



Traditional chemical characterizations of humus have been based on the solubility of humic and fulvic acid components in alkaline and acid solutions, respectively (Fig. 5.16). The acid-soluble component of humus, primarily fulvic acid, controls the downward movement of Fe and Al in soils (Chapter 4). Fulvic acids often account for a large fraction of the soil organic matter in the lower soil profile (Beyer et al. 1993), where they are complexed with clay minerals and calcium (Oades 1988). This humus is very resistant to microbial attack. Campbell et al. (1967) extracted humic materials from a forest soil in Saskatchewan and measured a mean  $^{14}\text{C}$  age of 250 to 940 years.

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 (Schlesinger 1977). Table 5.3 provides a global inventory of plant detritus and soil organic matter, totaling  $1456 \times 10^{15} \text{ g C}$ . Alternative estimates based on soil groups or climatic regions are similar (Post et al. 1982, Eswaran et al. 1993, Baatjes 1996). The global estimate of soil organic matter, divided by the estimate of global litterfall, suggests a mean residence time of about 30 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 (Fig. 5.17).

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, Harrison et al. 1993). O'Brien and Stout (1978) used radiocarbon dating to find that 16% of the organic matter in a pasture soil had a minimum age of 5700 years, while the rest was of recent

Table 5.3 Distribution of Soil Organic Matter by Ecosystem Types<sup>a</sup>

Ecosystem type	Mean soil organic matter ( $\text{kg C m}^{-2}$ )	World area ( $\text{ha} \times 10^8$ )	Total world soil organic carbon ( $\text{mt C} \times 10^9$ )	Amount in surface litter ( $\text{mt C} \times 10^9$ )
Tropical forest	10.4	24.5	255	3.6
Temperate forest	11.8	12	142	14.5
Boreal forest	14.9	12	179	24.0
Woodland and shrubland	6.9	8.5	59	2.4
Tropical savanna	3.7	15	56	1.5
Temperate grassland	19.2	9	173	1.8
Tundra and alpine	21.6	8	173	4.0
Desert scrub	5.6	18	101	0.2
Extreme desert, rock, and ice	0.1	24	3	0.02
Cultivated	12.7	14	178	0.7
Swamp and marsh	68.6	2	137	2.5
Totals	147	1456	55.2	

<sup>a</sup> From Schlesinger (1977).

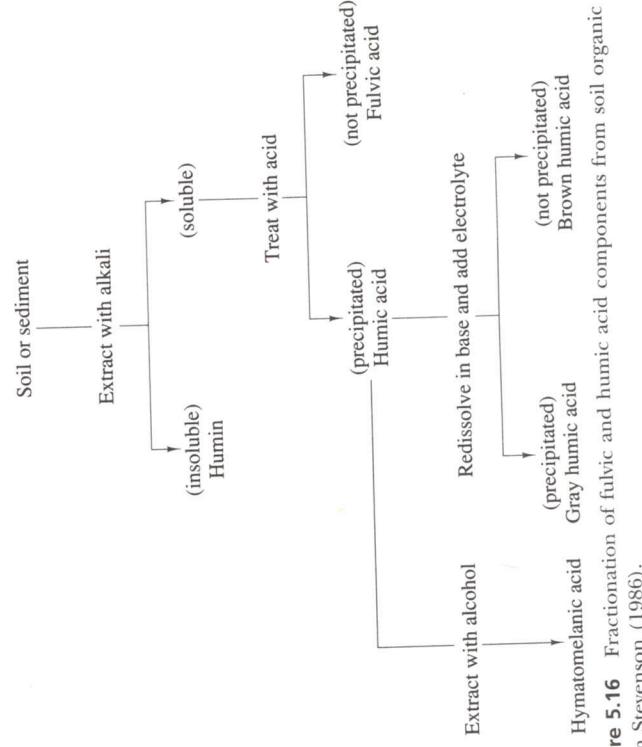


Figure 5.16 Fractionation of fulvic and humic acid components from soil organic matter. From Stevenson (1986).

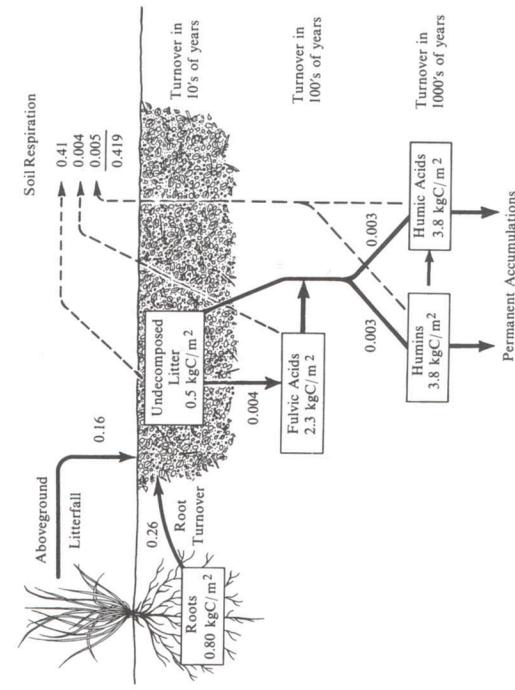


Figure 5.17 Turnover of litter and soil organic fractions in a grassland soil. Note that mean residence time can be calculated for each fraction from measurements of the quantity in the soil and the annual production or loss (respiration) from that fraction. Flux estimates are in  $\text{kg C m}^{-2} \text{ yr}^{-1}$ . From Schlesinger (1977).

origin and concentrated near the surface. Because of different turnover times, decomposition constants,  $k$ , for surface litter cannot be applied to the entire mass of organic matter in the soil profile.

Field measurements of the flux of  $\text{CO}_2$  from the soil surface provide an estimate of the total respiration in the soil, and a potential alternative approach to estimating the turnover of the humus pool (Raich and Schlesinger 1992). 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).

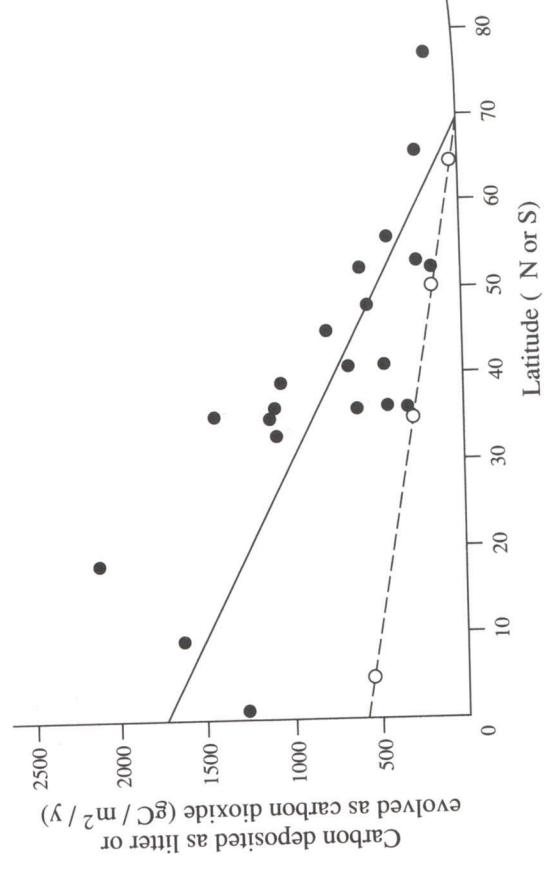
Unfortunately, the respiration of living roots makes it difficult to use estimates of  $\text{CO}_2$  flux in calculations of turnover of the soil organic pool. In a compilation of values, Schlesinger (1977) found that  $\text{CO}_2$  evolution exceeded the deposition of aboveground litter by a factor of about 2.5 (Fig. 5.18). The additional  $\text{CO}_2$  is presumably derived from root metabolism

and the decomposition of root detritus (Raich and Nadelhoffer 1989). Global soil respiration is  $68 \times 10^{15} \text{ g C/yr}$  (Raich and Schlesinger 1992, Raich and Potter 1995), with about  $\frac{1}{3}$  derived from the respiration of live roots and the remainder from decomposition. Soil respiration shows a strong correlation with temperature and NPP in world ecosystems (cf. Fig. 4.3).

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. Accumulations of soil organic matter are greatest in wetland ecosystems and least in deserts (Table 5.3). Among forests, accumulations increase from tropical to 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 (Fig. 5.18). Worldwide, the accumulation of soil organic matter seems more related to factors controlling decomposition than to the NPP of terrestrial ecosystems (Cebrián and Duarte 1995).

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 low soil organic content, perhaps due to frequent fire (Kadaba 1978, Jones 1973).

Storage of soil organic matter represents the net ecosystem production (NEP) in terrestrial ecosystems. Although many wetland ecosystems may show long-term net accumulations (Chapter 7), the mass of soil organic matter in most upland ecosystems is likely to have been fairly constant before widespread human disturbance of soils. Studies of soil chronosequences suggest that humus accumulates at a rates of about  $1\text{--}12 \text{ g C m}^{-2} \text{ yr}^{-1}$  during soil development (Table 5.4; Chadwick et al. 1994), with the highest rates under cool, wet conditions. Globally, the annual net production of humus substances is  $<0.4 \times 10^{15} \text{ g C/yr}$  (Schlesinger 1990). When soils show a steady state in soil organic content, the production of humic compounds must be equal to their removal from soils by erosion. Thus, an estimate of the transport of organic carbon in rivers is an alternative upper limit for terrestrial NEP (Lugo and Brown 1986). Recent estimates of the global transport of organic carbon in rivers are also about  $0.4 \times 10^{15} \text{ g C/yr}$  (Schlesinger and Melack 1981, Meybeck 1982), so either approach suggests that terrestrial NEP for the globe is not likely to be more



**Figure 5.18** 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 of  $\text{CO}_2$  from the surface. The difference between these lines represents the loss of  $\text{CO}_2$  from root respiration and from the respiration of root detritus and mycorrhizae. From Schlesinger (1977).

**Table 5.4** Long-Term Rates of Accumulation of Organic Carbon in Holocene-Age Soils

Ecosystem type	Vegetation in terminal state	Soil origin	Accumulation interval (yr)	Long-term rate of accumulation ( $\text{g C m}^{-2} \text{ yr}^{-1}$ )	
				Glacial retreat	Glacial retreat
Tundra	Polar desert	Glacial retreat	8,000	0.2	
	Polar desert	Glacial retreat	9,000	0.2	
	Polar desert	Glacial retreat	2,600	2.4	
	Sedge moss	Glacial retreat	1,000	2.4	
	Sedge moss	Glacial retreat	9,000	1.1	
	Sedge moss	Glacial retreat	8,700	0.7*	
Boreal forest	Spruce	Glacial retreat	3,500	11.7	
	Spruce-fir	Glacial retreat	5,435	0.8	
	Spruce-fir	Glacial retreat	2,740	2.2	
Temperate forest	Broadleaf evergreen	Volcanic ash	1,277	12.0	
	Coniferous	Volcanic mudflow	1,200	10.0	
	Deciduous	Alluvium	1,955	5.1	
	Deciduous	Dunes	10,000	0.7	
	Podocarpus	Dunes	10,000	2.1	
	<i>Angophora</i>	Dunes	4,200	1.7	
	<i>Eucalyptus</i>	Dunes	6,500	1.4	
	<i>Eucalyptus</i>	Dunes	5,500	2.1	
	Low forest	Glacial deposits	9,000	2.5	
Tropical forest	<i>Metrosideros</i>	Volcanic ash	3,500	2.5	
	Rain forest	Volcanic ash	8,620	2.3	
Temperate grassland	<i>Chionochloa</i>	Glacial deposits	9,000	2.2	
Temperate desert	Grassland	Alluvium	3,040	0.8	

From Schlesinger (1990); citations to original literature are given therein.

\* Corrected from value given in original publication.

soil organic matter has accumulated at rates of about  $1.35 \text{ g C m}^{-2} \text{ yr}^{-1}$  during the Holocene period. The current rate of storage in northern ecosystems ( $0.04 \times 10^{15} \text{ g C/yr}$ ) is too small to be a significant sink for human releases of  $\text{CO}_2$  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,  $1456 \times 10^{15} \text{ g}$  or  $121 \times 10^{15}$  moles, can account for only 0.3% of the  $\text{O}_2$  content of the atmosphere, given that the storage of organic carbon and the release of  $\text{O}_2$  occur on a mole-for-mole basis during photosynthesis (Eq. 5.2). Thus, accumulations of atmospheric  $\text{O}_2$  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).

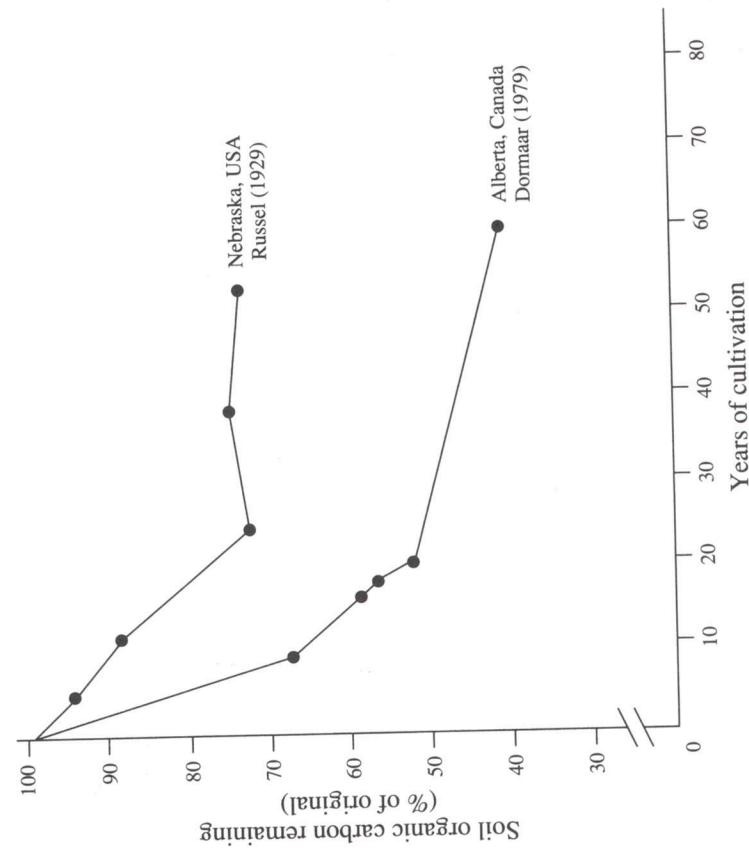
### Soil Organic Matter and Global Change

When soils are brought under cultivation, their content of soil organic matter declines (Fig. 5.19). Losses from many soils are typically 20 to 30% within the first few decades of cultivation (Schlesinger 1986, Mann 1986, Detwiler 1986, Davidson and Ackerman 1993, Scholes and Schlesinger 1995). The loss is greatest during the first few years of cultivation. Eventually a new, lower level of soil organic matter is achieved that is in equilibrium with the lower production of plant detritus and the greater rates of decomposition under cropland (Jenkinson and Rayner 1977). Some of the soil organic matter is lost in erosion, but most is probably oxidized to  $\text{CO}_2$  and released to the atmosphere. With about 10% of the world's soils under cultivation (Table 5.3), losses of organic matter from agricultural soils have been a major component of the past increase in atmospheric  $\text{CO}_2$  (Schlesinger 1984). The current rate of release from soils, as much as  $0.8 \times 10^{15} \text{ g C/yr}$ , is largely dependent upon the current rate at which natural ecosystems, especially in the tropics, are being converted to agriculture. Especially large losses of soil carbon are seen when organic soils in wetlands and peatlands are drained (Armentano and Menges 1986, Hutchinson 1980).

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 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 (Fig. 5.16), 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 fraction-

than 0.7% of NPP (Schlesinger 1990, Dobrovolsky 1994, p. 114). Despite the stability of humus substances in the soil profile, 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).

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 glacial, covering  $29.5 \times 10^6 \text{ km}^2$  of the present land area (Flint 1971), now contains roughly  $400 \times 10^{15} \text{ g C}$ , or about 25% of the carbon contained in all soils of the world (Table 5.3). In these areas,



**Figure 5.19** Decline in soil organic matter following conversion of native soil to agriculture in two grassland soils. From Schlesinger (1986).

ation, 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 (Foster 1981, Tiessen and Stewart 1983, Dalal and Mayer 1986a, 1986b). 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 due to losses from the light fraction (Buyanovsky et al. 1994, Cambardella and Elliott 1994). Significantly, soil organic matter can accumulate fairly rapidly when agricultural soils are abandoned (Table 5.5). The formation of charcoal during forest fires is a source of recalcitrant organic matter which accumulates in soils. Fearnside et al. (1993) calculate

**Table 5.5** Accumulation of Soil Organic Matter in Abandoned Agricultural Soils and in Other Disturbed Sites, Which are Allowed to Return to Native Vegetation

Ecosystem type	Previous land use	Period of abandonment (yr)	Rate of accumulation ( $\text{g C m}^{-2} \text{yr}^{-1}$ )	Reference
Subtropical forest	Cultivation	40	30–50	Lugo et al. (1986)
Temperate deciduous forest	Cultivation	100	45	Jenkinson (1990)
Temperate coniferous forest	Cultivation	50	21–26	Schiffman and Johnson (1989)
Temperate coniferous forest	Diked soils	100	26	Bekke (1990)
Temperate deciduous forest	Mine spoils	50	55	Leisman (1957)
Temperate grassland	Mine spoils	28–40	28*	Anderson (1977)
Temperate grassland	Cultivation	53	1.55	Burke et al. (1995)
Temperate grassland	Cultivation	5	110.0	Gebhart et al. (1994)

that about 2.7% of the aboveground biomass in tropical rainforests is converted to charcoal when they burn. Pine forests on the Virginia Piedmont contain  $0.46 \text{ kg C/m}^2$  as charcoal in the forest floor (Schiffman and Johnson 1989), and Sanford et al. (1985) found 0.23 to  $0.70 \text{ kg C/m}^2$  of charcoal in three soils of Brazilian rainforest. Unfortunately, we know relatively little about the long-term dynamics of charcoal in soils (Shneour 1966). Although the charcoal content of soils is typically only a small portion of the total pool of organic matter (Table 5.3), the apparent rate of accumulation of charcoal (0.4 to  $2.8 \text{ g C m}^{-1} \text{ yr}^{-1}$ ) in the Brazilian rainforest soils is similar to the overall rate of humus formation in many ecosystems (Table 5.4). However, despite increasing rates of biomass burning by humans, it is not likely that an additional storage of carbon in charcoal is a significant flux in models of the global carbon cycle (Suman et al. 1997; Chapter 11).

In addition to changes in the pool of organic carbon as a result of cultivation and fire, soil carbon will change with climatic warming, which should stimulate rates of decomposition and the loss of soil organic matter in many ecosystems (Schleser 1982, Jenkinson et al. 1991, Peterjohn et al. 1994, Kirschbaum 1995, Trumbore et al. 1996). The effect of temperature will interact with other factors. For example, several experiments show that warming of organic soils in the tundra will increase the flux of  $\text{CO}_2$  from the soil, but the loss is especially large if the water table is also lowered due to melting of permafrost (Billings et al. 1982, Moore and Dalva 1993, Funk et al. 1994). Oechel et al. (1993, 1995) suggest that a loss of carbon from some tundra soils is associated with unusually warm conditions over the last few decades. However, when tundra ecosystems are exposed to both high temperature and elevated  $\text{CO}_2$ , at levels chosen to resemble

presumed atmospheric conditions of the next century, they show a net storage of carbon (Oechel et al. 1994). Inasmuch as many tundra ecosystems are nutrient limited (Billings et al. 1984), an increased storage of carbon in vegetation may be allowed by a greater rate of decomposition and nutrient release in warmer soils. The most accurate predictions of future changes in net ecosystem production may be derived from simulation models that include these interactive factors (e.g., Pastor and Post 1986; Seastedt et al. 1994; Schimel et al. 1994). Changes in soil carbon storage will be closely associated with changes in the distribution and productivity of vegetation discussed earlier.

### Summary

Photosynthesis provides the energy that powers the biochemical reactions of life. That energy is captured from sunlight. Globally, net primary production of about  $60 \times 10^{15} \text{ g C yr}^{-1}$  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 the display of leaf area and NPP (Figs. 5.5 and 5.8). 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. 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.

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  $\text{O}_2$ .

### Recommended Readings

- Reichle, D.E. (ed.). 1981. *Dynamic Properties of Forest Ecosystems*. Cambridge University Press, Cambridge.

- Solomon, A.H. and H. Shugart (eds.). 1993. *Vegetation Dynamics and Global Change*. Chapman and Hall, New York.
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