7 Decomposition and Ecosystem Carbon Budgets

Decomposition breaks down dead organic matter, ultimately releasing carbon to the atmosphere and nutrients in forms that can be used for plant and microbial production. This chapter describes the key controls over decomposition and the carbon balance of ecosystems.

Introduction

Decomposition is the physical and chemical breakdown of detritus (i.e., dead plant, animal, and microbial material). Decomposition causes a decrease in detrital mass, as materials are fragmented, converted to other organic compounds, and ultimately to inorganic nutrients and CO_2. If there were no decomposition, ecosystems would quickly accumulate large quantities of detritus, leading to a sequestration of nutrients in forms that are unavailable to plants and a depletion of atmospheric CO_2. Eventually, many biological processes would grind to a halt. Although this has never happened, there have been times such as the Carboniferous period (see Fig. 2.15) when decomposition did not keep pace with primary production, leading to vast accumulations of carbon- and nitrogen-containing coal and oil. The *balance* between primary production and decomposition therefore strongly influences carbon and nutrient cycling at ecosystem and global scales.

If the climate warming associated with anthropogenic CO_2 emissions were to cause even small changes in the balance between NPP and decomposition, this could greatly alter the CO_2 concentration of the atmosphere and therefore the rate of climate warming. Because of the many critical roles of carbon balance in the biosphere and the Earth System, substantive changes in carbon cycling of plants and ecosystems are an issue of fundamental societal importance.

A Focal Issue

Mismanagement of carbon sequestration of the biosphere amplifies human impacts on climate change. The capacity of natural ecosystems to sequester carbon is generally degraded when lands are cleared for agriculture. Clearing tropical rainforests for oil palm plantations (Fig. 7.1) or plowing prairies to plant corn reduces the capacity of these systems to sequester carbon, and the energy-intensive management of these crops often consumes as much fossil fuels as are offset by the biofuels produced. What happens to soil carbon, when lands are cleared? Is the activity of decomposer organisms determined primarily by environment, by vegetation, or by their own community composition? If the activity of both plants and decomposer microbes is favored by warm, moist conditions, how does climatic change influence the net carbon balance of ecosystems? Given that ecosystems differ in their capacity to store and release carbon, in what locations are human-induced changes in land use and climate likely to have greatest impact on the carbon balance of the biosphere? A clear

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Fig. 7.1 Land-use change greatly alters ecosystem carbon balance. Tropical rainforests, which sequester substantial carbon, have been cleared to grow oil palm, which is used extensively as a food product and increasingly as a source of bioethanol (a substitute for fossil fuels). The loss of potential to sequester carbon due to clearing of rain forest is greater than the climatic benefits due to the substitution of bioethanol for fossil fuels. Extensive development of oil palm plantations is driven more strongly by policy-driven economics than by the logical management of ecosystems for climate regulation. Photograph courtesy of World Land Trust

understanding of the role of the biosphere in the carbon cycle of ecosystems and the planet is essential to any strategy that effectively addresses the accelerating rates of climate change.

Overview of Decomposition and Ecosystem Carbon Balance

The leaching, fragmentation, and chemical alteration of dead organic matter by decomposition ultimately convert detritus to CO_2 and mineral nutrients and a remnant pool of complex organic compounds that resist further microbial breakdown. Most decomposition occurs in the litter layer and in the organic and mineral horizons of the soil (see Chap. 3). Decomposition is a consequence of interacting physical and chemical processes occurring inside and outside of living soil microbes and animals. Decomposition results from three types of processes, each with unique controls and consequences. (1) **Leaching** by water transfers soluble materials away from decomposing organic matter into the environment. These soluble materials are either absorbed by organisms, react with the mineral phase of soil or sediments, or are lost from the system in solution. (2) **Fragmentation** by soil animals breaks large pieces of organic matter into smaller ones, which they eat, and, in the process, create fresh surfaces for microbial colonization. Soil animals also mix the decomposing organic matter into the soil and return organic matter to the soil or sediments as fecal pellets, which have a higher surface-to-volume ratio and provide a more favorable environment for soil microbes (i.e., bacteria and fungi) than does the original material consumed. (3) **Chemical alteration** of dead organic matter results primarily from the activity of soil microbes, although some chemical reactions also occur spontaneously in the soil without microbial mediation.

Dead plant material (leaf, stem, and root **litter**) and animal residues are gradually decomposed until their original identity is no longer recognizable, at which point they are considered **soil organic matter** (SOM). Most compounds in litter are too large and insoluble to pass through microbial membranes. Microbes therefore secrete **exoenzymes** (extracellular enzymes) into their environment to initiate breakdown of litter. These exoenzymes convert macromolecules into soluble products that can be absorbed and metabolized by microbes. Microbes also secrete waste products of metabolism, such as CO_2 and inorganic nitrogen, and produce polysaccharides that enable them to attach to soil particles. When microbes die, their bodies become part of the organic substrate available for decomposition.

Decomposition is largely a consequence of the feeding activity of soil animals (fragmentation) and heterotrophic microbes (chemical alteration). The evolutionary forces that shape decomposition are those that maximize the growth, survival, and reproduction of soil organisms. In other words, decomposition occurs to meet the energetic and nutritional demands of decomposer organisms, not as a community service for the carbon cycle. The ecosystem consequences of decomposition are the **mineralization** of organic matter to inorganic components (CO_2, mineral nutrients, and water) and the **transformation** of some organic matter into complex organic compounds that are often **recalcitrant**, that is, resistant to further microbial breakdown.

The controls over organic matter breakdown change radically once SOM becomes incorporated into mineral soil. The soil moisture, oxygen, and thermal regimes of mineral soil are quite different than in the litter layer. In the mineral soil, SOM can complex with clay minerals or undergo nonenzymatic chemical reactions to form more complex compounds. **Humus**, for example, is a complex mixture of soil organic compounds with highly irregular structure. The long-term persistence of organic matter in soils depends upon chemical recalcitrance, sorption of organic compounds to clay surfaces, and other controls over microbial activity, although the relative importance of these processes is uncertain (Schmidt et al. in press).

Microbes and animals feed on live and dead organic matter to support their energetic and nutritional demands. The associated **heterotrophic respiration** accounts for about half of the CO_2 released from ecosystems to the atmosphere. Carbon is also transferred to the atmosphere through the production of carbon-containing trace gases such as methane and by combustion in wildfires. Finally, carbon leaches from ecosystems in dissolved and particulate forms and moves laterally through erosion and deposition of soil, movement of animals, etc. These lateral fluxes of carbon from terrestrial ecosystems are critical energy subsidies to aquatic ecosystems and constitute a significant component of the carbon budgets of many ecosystems.

In this chapter, we first describe decomposition in terrestrial ecosystems. We then describe important differences in decomposition between terrestrial and aquatic systems and finally integrate carbon loss pathways with carbon inputs to ecosystems (see Chaps. 5 and 6) to assess **net ecosystem carbon balance**.

Leaching of Litter

Leaching is the rate-determining step for mass loss of plant litter when it first senesces. **Leaching** is the physical process by which mineral ions and small water-soluble organic compounds dissolve in water and flow out of the detritus. Leaching begins when tissues are still alive and is most important during and shortly after tissue senescence (see Chap. 8). Soluble compounds are a larger proportion of the mass (and therefore account for more leaching loss) in leaf and fine root litter than in woody stems and roots. Leaching losses from litter are proportionally more important for nutrients than for carbon. Leaching loss from fresh litter occurs most rapidly (minutes to hours) in environments with high rainfall and is negligible under dry conditions. Compounds leached from litter include sugars, amino acids, and other organic compounds that are **labile** (easily broken down) or are absorbed intact by soil microbes.

Litter Fragmentation

Fragmentation creates fresh surfaces for microbial colonization and increases the proportion of the litter mass that is accessible to microbial attack. Fresh detritus is initially covered by a protective layer of cuticle or bark on plants or of skin or exoskeleton on animals. These outer coatings are designed, in part, to protect tissues from microbial attack. Within plant tissues, the labile cell contents are further protected from microbial attack by lignin-impregnated cell walls. Fragmentation of litter greatly enhances microbial decomposition by piercing these protective barriers, by increasing the ratio of litter surface area to mass, and by inoculating the residual mass with soil microbes.

Animals are the main agents of litter fragmentation, although freeze–thaw and wetting–drying cycles can also disrupt the cellular structure of litter. Animals fragment litter as a by-product of their feeding activities. Bears, voles, and other mammals tear apart wood or mix the soil as they search for insects, plant roots, and other food. Soil invertebrates fragment the litter to produce particles that are small enough to ingest. Enzymes in animal guts digest the microbial "jam" that coats the surface of litter particles, providing energy and nutrients to support animal growth and reproduction. The presence of soil invertebrates has a major effect on decomposition rate in moist temperate and tropical ecosystems, but is less important where temperature or moisture strongly constrains decomposition (Wall et al. 2008). The species composition of the invertebrate community, however, causes only a modest (7%) variation in decomposition rate (Wall et al. 2008). Apparently, different soil animals have roughly equivalent effects on fragmentation rates.

Chemical Alteration

Fungi

Fungi and bacteria are the main initial decomposers of terrestrial dead plant material, accounting for about 95% of the total decomposer biomass and respiration. Fungi consist of networks of **hyphae** (i.e., filaments that enable them to grow into new substrates and transport materials through the soil over distances of centimeters to meters). These hyphal networks enable fungi to acquire their carbon in one place and their nitrogen in another, much as plants gain CO_2 from the air but water and nutrients from the soil. Fungi that decompose fresh leaf or woody litter, for example, may acquire carbon from the surface litter and nitrogen from deeper, more decomposed soil horizons. Fungi secrete enzymes that enable them to penetrate the cuticle of dead leaves or the suberized exterior of roots to gain access to the interior of a dead plant organ. Here they proliferate within and between dead plant cells. At a smaller scale, some fungi gain access to the nitrogen, lignin-encrusted cellulose, and other labile constituents of dead cells by breaking down the lignin in cell walls. The large energy investment in lignin-degrading enzymes serves primarily to gain access to these relatively labile compounds.

Fungi produce dense networks of hyphae when resources are plentiful, allowing efficient access to these resources, but sparse hyphal networks when resources are scarce, reallocating resources from one part of the network to exploration of new litter and soil. This flexible growth strategy enables fungi to grow into new areas to explore for substrate, even when current substrates are exhausted. A substantial proportion (perhaps 25%) of the carbon and nitrogen used to support fungal growth are transported from elsewhere in the hyphal network, rather than being absorbed from the immediate environment where the fungal growth occurs (Mary et al. 1996).

Fungi have enzyme systems capable of breaking down all classes of plant compounds. They have a competitive advantage over many bacteria in decomposing tissues with low nutrient concentrations because of their ability to import nitrogen and phosphorus. In addition, fungi typically require less nitrogen per unit biomass than bacteria (i.e., the C:N ratio of fungi is often higher than the C:N ratio of bacteria). This may explain why fungal:bacterial ratios are typically higher in soils with high C:N ratios (Fierer et al. 2009a). White-rot fungi specialize on lignin degradation in wood, whereas brown-rot fungi cleave some of the side chains of lignin but leave the phenol units behind (giving the wood a brown color). White-rot fungi are generally outcompeted by more rapidly growing microbes when nitrogen is abundant, so nitrogen additions have little effect (or sometimes a negative effect) on white-rot fungal decomposition of wood (Waldrop and Zak 2006; Janssens et al. 2010). Most fungi lack a capacity for anaerobic metabolism and are therefore absent from or dormant in anaerobic soils and aquatic sediments.

Mycorrhizae are a symbiotic association between plant roots and fungi in which the plant gains nutrients from the fungus in return for carbohydrates (see Chap. 8). Although mycorrhizal fungi get most of their carbon from plant roots, they also play a role in decomposition by breaking down proteins into amino acids. These amino acids support fungal growth but are also transferred to their host plants (Read 1991; Finlay 2008). Mycorrhizal fungi also produce cellulases to gain entry into plant roots and participate in the breakdown of SOM, but the extent to which mycorrhizal cellulases participate in decomposition of dead organic matter is uncertain.

In the few ecosystems where fungal diversity has been examined using modern molecular techniques, there are 10- to 100-fold more fungal than plant taxa (Fierer et al. 2007; Taylor et al. 2010). Fungal taxa differ in trophic role (mycorrhizal or **saprotrophic** – eating dead organic matter), soil horizon, season of activity, and many other, as yet unknown, dimensions of their ecological niches, with these local sources of diversity often greater than variation among ecosystems (Fierer et al. 2007).

Bacteria and Archaea

The small size and large surface:volume ratio of bacteria and archaea enable them to rapidly absorb soluble substrates and to grow and divide quickly in substrate-rich zones. Archaea are structurally similar but evolutionarily distinct from bacteria. Like bacteria, they are metabolically diverse. The opportunist strategy of bacterial and archaea (which, for convenience, we will label as "bacteria") explain their dominance in the **rhizosphere** (the zone of soil directly influenced by plant roots) and in dead animal carcasses, where labile substrates are abundant. Bacteria are also important in breaking down live and dead bacterial and fungal cells. The major functional limitation resulting from their small size is that each bacterium depends mostly on the substrates that move toward it. Some of these substrates are products of bacterial exoenzymes. These products diffuse to the bacterium along a concentration gradient created by (1) the activity of the exoenzymes, which produce soluble substrates, and (2) the absorption of substrates by the bacterium, which reduces substrate concentrations at the bacterial surface. Other soluble substrates flow past the bacterium in water moving through the soil. This water movement is driven by gradients in water potential associated with plant transpiration, evaporation at the soil surface, and gravitational water movement (see Chap. 4). Water movement (and therefore substrate supply) is most rapid in **macropores** (relatively large air or water spaces between soil aggregates). Bacteria therefore often line macropore surfaces and absorb substrates from the flowing water, just as fishermen net salmon migrating up a stream. Macropores are also preferentially exploited by roots because of the reduced physical resistance to root elongation, providing an additional source of labile substrates to bacteria. Bacteria attached to the exposed surfaces of macropores are vulnerable to predation by protozoa and nematodes, which use the water films in macropores as highways to move through the soil. This leads to rapid bacterial turnover on exposed particle surfaces.

A wide range of bacterial types is present in soils; indeed, we are just beginning to characterize their abundance and diversity through molecular methods, and we can expect much more information to become available as these techniques are refined and applied more widely. Rapidly growing gram-negative bacteria specialize on labile substrates secreted by roots. Actinobacteria are slow-growing, gram-positive bacteria that have a filamentous structure similar to that of fungal hyphae. Like fungi, actinobacteria produce lignin-degrading enzymes and can break down relatively recalcitrant substrates. They often produce antibiotics to reduce competition from other microbes. The best predictor of bacterial community composition and exoenzyme activities appears to be soil pH (Sinsabaugh et al. 2008; Fierer et al. 2009a).

The bacterial communities that coat soil aggregates have a surprisingly complex structure. They often occur as **biofilms**, microbial communities embedded in a matrix of polysaccharides secreted by bacteria. This microbial "slime" protects bacteria from grazing by protozoa and reduces bacterial water stress by holding water like a sponge. The matrix also increases the efficiency of bacterial exoenzymes by preventing them from being swept away by moving water. The bacteria in biofilms often act as a **consortium**, that is, a group of genetically unrelated bacteria, each of which produces only some of the enzymes required to break down complex macromolecules. The breakdown of these molecules to soluble products requires the coordinated production of exoenzymes by several types of bacteria. This is analogous to an assembly line, in which the final product depends on the coordinated action of several consecutive steps, and no bacterium benefits unless all the steps are in place to produce the final product. The evolutionary forces and population interactions that shape the composition and functioning of microbial consortia are poorly understood. Consortia are particularly important in the breakdown of pesticides and other organic residues that people have added to the environment.

Because most bacteria are immobile, a bacterial colony eventually exhausts the substrates in its immediate environment, especially within soil aggregates that have restricted water movement. When this occurs, they become inactive and reduce their respiration to negligible rates. Bacteria may remain inactive for years. Live bacteria have been recovered from permafrost that is three million years old (Gilichinsky et al. 2008). About 50–80% of the bacteria in soils are metabolically inactive (Norton and Firestone 1991). Inactive bacteria reactivate in the presence of labile substrates, for example, when a root grows through the soil and exudes carbohydrates. The inactive bacteria in soils represent a reservoir of decomposition *potential,* analogous to the buried seed pool that provides a source of plant colonizers after a disturbance. Like the buried seed pool, the enzymatic potential of these inactive bacteria may differ from the enzymes produced by the active bacterial community. Consequently, DNA probes or microbiological culturing techniques are better indices of what the soil *could* do (its metabolic diversity and enzymatic potential) than of its current metabolic activity.

Bacterial, archaeal, viral, and fungal communities living in soil are highly diverse (Fierer et al. 2007). However, bacteria and archaea can thrive in a broader range of microenvironments than fungi, including habitats that are anaerobic, have little available carbon or nitrogen, are contaminated with toxic heavy metals, or experience extremes in temperature or UV radiation.

Soil Animals

Soil animals influence decomposition by fragmenting, transforming, and transporting litter, grazing populations of bacteria and fungi, and altering soil structure. **Microfauna** are the smallest animals (<0.1 mm diameter). They include nematodes, protozoans, such as ciliates and amoebae, and rotifers (Fig. 7.2; Wallwork 1976; Lousier and Bamforth 1990). Protozoans are single-celled animals that ingest their prey primarily by **phagocytosis**, that is, by enclosing them in a membrane-bound structure within the cell. Protozoans are usually mobile and are voracious predators of bacteria and other microfauna (Lavelle et al. 1997). Protozoans are particularly important predators in the rhizosphere and other soil microsites with rapid bacterial growth rates (Coleman 1994). The preferential grazing by protozoa on bacteria (even on particular species of bacteria) tends to reduce bacterial:fungal ratios compared to soils from which protozoa are excluded. Nematodes are an abundant and trophically diverse group in which each species specializes on bacteria, fungi, roots, or other soil animals. Bacterial-feeding nematodes in forest litter, for example, can consume about 80 $g\,m^{-2}\,year^{-1}$ of

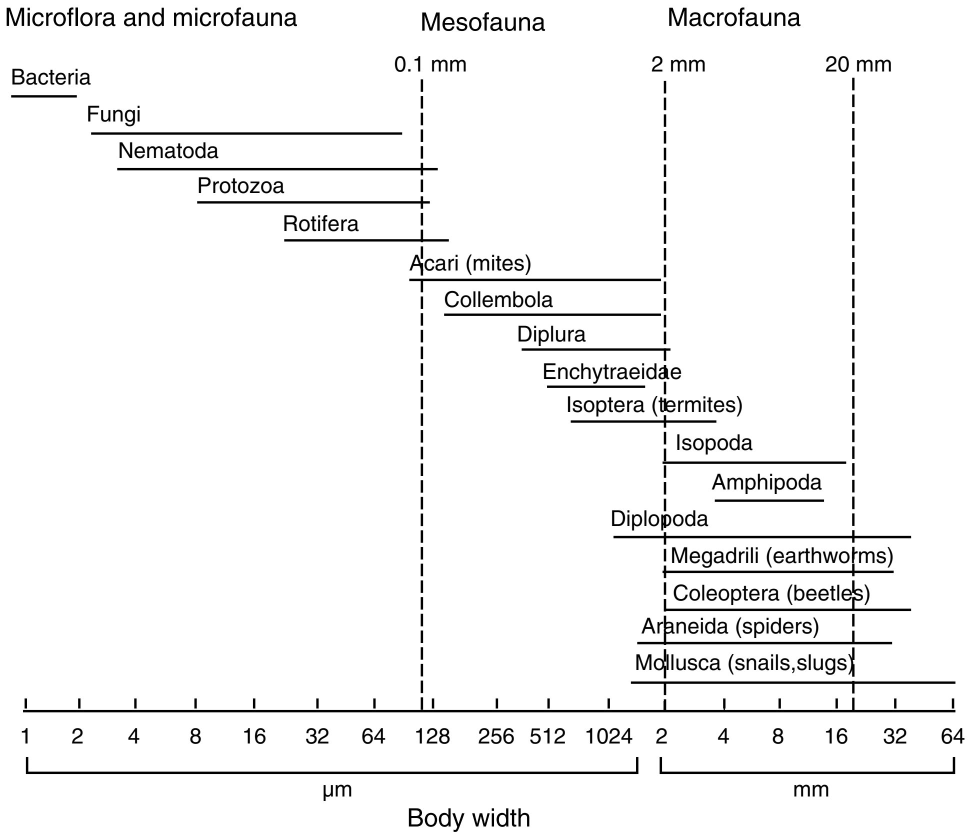

Fig. 7.2 Representative types and sizes (log scale) of soil fauna. Microfauna are most important as predators; mesofauna as organisms that fragment litter; and macrofauna as ecosystem engineers. Redrawn from Swift et al. (1979)

bacteria, resulting in the mineralization of 2–13 $g\,m^{-2}$ $year^{-1}$ of nitrogen, a substantial proportion of the nitrogen that annually cycles through the soil (Anderson et al. 1981). Protozoans and nematodes are aquatic animals that move through water-filled pores between soil particles and are therefore more sensitive to water stress than are fungi and the meso- and macrofauna that fragment soil particles. Their populations fluctuate dramatically, both spatially and temporally, due to drying–wetting events and predation (Beare et al. 1992). When protozoans die, their bodies are rapidly broken down by soil microbes, especially by bacteria.

The **mesofauna** are a numerically abundant and taxonomically diverse group of soil animals 0.1–2 mm in diameter (Fig. 7.2). These are the animals with the greatest effect on decomposition. They fragment and ingest litter coated with microbial biomass, producing large amounts of fecal material with a greater surface area and moisture-holding capacity than the original litter (Lavelle et al. 1997). This altered litter environment is more favorable for decomposition. Mesofauna selectively feed on litter that has been conditioned by microbial activity and also selectively feed on soil fungi, causing changes in fungal community structure. Collembola are small insects that feed primarily on fungi, whereas mites (Acari) are a more trophically diverse group of spider-like animals that consume decomposing litter or feed on bacteria, fungi, or soil animals. Feeding by micro- and mesofauna can significantly alter the biomass and activity of microbial communities and therefore rates of decomposition and nutrient turnover (Bardgett 2005).

Large soil animals (**macrofauna**), such as earthworms and termites, are **ecosystem engineers** that alter resource availability by modifying the physical properties of soils and litter (Jones et al. 1994). Some of them, like the mesofauna, fragment litter (Lavelle et al. 1997). Others burrow or ingest soil, reducing soil bulk density, breaking up soil aggregates, and increasing soil aeration and water infiltration (Beare et al. 1992). The passages created by earthworms create channels in the soil that water and roots easily penetrate. They create patterns of soil structure that promote or constrain the activities of soil microbes and other soil animals. In temperate pastures, earthworms may process 4 kg m^{-2} $year^{-1}$ of soil, moving 3–4 mm of new soil to the ground surface each year (Paul and Clark 1996). This is a geomorphic force that, integrated over time, is orders of magnitude larger than landslides or surface soil erosion (see Table 3.1). In temperate forests, exotic earthworms have substantially reduced soil carbon storage (Bohlen et al. 2004). Soil mixing by earthworms tends to disrupt the formation of distinct soil horizons. Once the soil enters the digestive tract of an earthworm, mixing and secretions by the earthworms stimulate microbial activity, so soil microbes act as gut mutualists. Many of the soil organisms are digested during passage through the gut, which absorbs the resulting products. Earthworms are most abundant in the temperate zone, whereas termites and ants are the dominant ecosystem engineers in tropical soils. Termites eat plant litter directly, digest the cellulose with the aid of mutualistic protozoans and bacteria in their guts, and mix the organic matter into the soil. Dung beetles in tropical grasslands perform a similar function with mammalian dung. This burial of surface organic matter places it in a humid environment where decomposition occurs more rapidly.

The soil fauna is critical to the carbon and nutrient dynamics of soils. Microbes constitute 70–80% of the labile carbon and nitrogen in soils, so exclusion of soil animals from soils or natural variation in their predation on microbes significantly alters carbon and nitrogen turnover in soils, although their net effect is relatively modest (up to 30%; Swift et al. 1979; Verhoef and Brussaard 1990). Sometimes, soil animals *inhibit* decomposition through their direct consumption of microbial biomass, and sometimes they *stimulate* decomposition by reducing the density of microbial predators (Bardgett et al. 2005b).

Because of their high respiration rate, soil animals metabolize much of the microbial carbon they consume to CO_2 and excrete the microbial nitrogen and phosphorus that exceeds their requirements for growth and reproduction. These nutrients become available for absorption by plants or microbes (see Chap. 8). Soil animals account for only about 5% of soil respiration, so their major effect on decomposition is the enhancement of microbial activity through fragmentation (Wall et al. 2001), rather than their own processing of energy derived from detritus.

Temporal and Spatial Heterogeneity of Decomposition

Temporal Pattern

The predominant controls over decomposition change with time. Decomposition is the consequence of the interactions of leaching, fragmentation, and chemical alteration. As soon as a leaf unfolds, it is colonized by aerially borne bacteria and fungal spores that begin breaking down the cuticle and leaf surfaces that have been exposed by herbivores, pathogens, or physical breakage (Haynes 1986). This **phyllosphere decomposition** of live leaves is generally ignored because it is not easily separated from plant-controlled changes in leaf mass and chemistry. Other bacteria and fungi live inside live leaves, producing toxins that reduce herbivory, thereby altering the properties and functioning of leaves (Clay 1990). Both groups provide a microbial inoculum that rapidly initiates decomposition of labile substrates when the leaf falls to the ground. Similarly, the root cortex begins to break down while the conducting tissues of roots still function in water and nutrient transport, blurring the distinction between live and dead roots.

Litter mass initially decreases rapidly as it decomposes, and decomposition rate declines

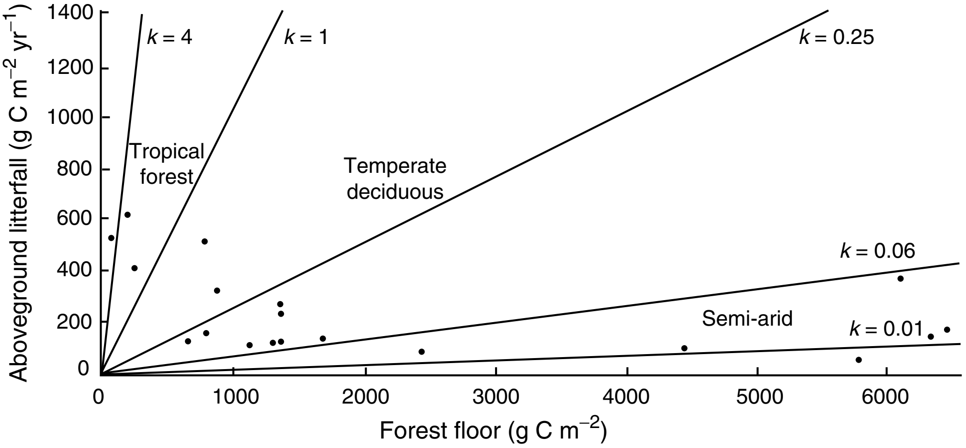

Fig. 7.3 Forest-floor biomass and aboveground litter inputs for selected evergreen forests. Lines show the relationship between forest floor mass and aboveground litterfall for selected decomposition constants (*k*). Redrawn from Olsen (1963)

as litter ages (Haynes 1986; Harmon et al. 2009). This is often described as an exponential relationship, implying that a constant *proportion* of the litter is decomposed each year.

$$L_t = L_0 e^{-kt} \tag{7.1}$$

$$\text{In}\frac{L_t}{L_0} = -kt \tag{7.2}$$

where L_0 is the litter mass at time zero and L_t is the mass at time *t*. The **decomposition rate constant**, *k*, is an exponent that characterizes the decomposition rate of a particular material. The mean **residence time**, that is, the time required for the litter to decompose under steady-state conditions, equals 1/*k*. The residence time of litter can also be estimated as the average pool size of litter divided by the average annual input. Residence time differs substantially among biomes (Fig. 7.3).

$$\frac{l}{k} = \frac{\text{litter pool}}{\text{litterfall}} \quad \text{or} \quad k = \frac{\text{litterfall}}{\text{litter pool}} \tag{7.3}$$

The calculation of residence time from pools and fluxes assumes that the measurements made at a particular time are representative of the steady state, which is seldom the case (see Chap. 12). Year-to-year variation in weather or directional changes in climate cause more rapid changes in litterfall than in the litter pool, creating challenges in estimating residence time. The decomposition constant varies widely with substrate composition. Sugars, for example, have a residence time of hours to days, whereas lignin has a residence time of months to decades, depending on the ecosystem. Plant and animal tissues differ substantially in their chemical composition and therefore in their decay constants. Taken as a whole, leaf and fine-root litter generally has a residence time of months to years, logs a residence time of years to centuries, and organic material mixed with mineral soil a residence time of years to millennia.

The exponential model of decomposition (7.1), which implies a constant proportion of litter decomposed each year, is therefore only a rough approximation of the actual pattern of decline in litter mass with time. The process is more accurately described by multiple curves that describe at least four phases (Fig. 7.4; Adair et al. 2008; Harmon et al. 2009). Leaching of cell solubles dominates the first phase. Fresh leaf or fine-root litter, for example, can lose 5% of its mass in 24 h due to leaching alone. The second phase of decomposition occurs more slowly and involves a combination of fragmentation by soil animals, chemical alteration by soil microbes, and leaching of decay products from the litter. During the

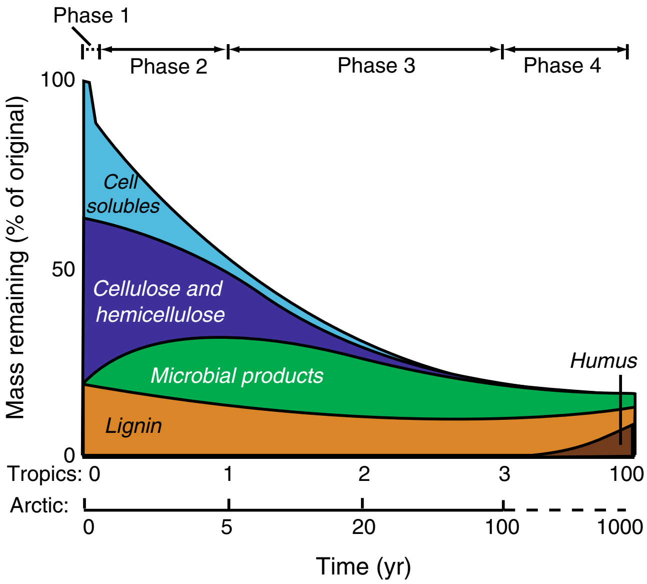

Fig. 7.4 Representative time course of leaf-litter decomposition, showing the major chemical constituents (cell solubles, cellulose and hemicellulose, lignin, microbial products, and humus), the four major phases of litter decomposition, and the timescales commonly found in warm (tropical) and cold (arctic) environments. Leaching dominates the first phase of decomposition. Substrate composition of litter changes during litter decomposition of phases 2 and 3 because labile substrates, such as cell solubles, are broken down more rapidly than recalcitrant compounds such as lignin and microbial cell walls. In phase 4, litter particles contact mineral surfaces, forming soil organic matter

second phase of decomposition, relatively labile substrates are decomposed, leaving behind more recalcitrant ones. The third phase of decomposition involves the same *processes* as the second phase but occurs more slowly because the remaining compounds are recalcitrant and decompose slowly. Decomposition during the second and third phases is often measured as mass loss from dead leaves (Aerts 1997), roots (Berg et al. 1998), or twigs that are tethered on threads or placed in mesh **litterbags** and weighed periodically (Vogt et al. 1986; Robertson and Paul 2000). Logs can be placed on the ground surface. Exponential models of decomposition have been applied primarily to the second and third phases (Harmon et al. 2009). The fourth and final phase of decomposition occurs quite slowly and involves the chemical alteration of organic matter that is mixed with mineral soil and the leaching of breakdown products to other soil layers. Decomposition during this final phase is often estimated from measurements of soil respiration or isotopic tracers, given that mass loss is very slow (Box 7.1; Schlesinger 1977; Trumbore and Harden 1997). The decomposition rate and decomposition rate constant (*k* in 7.1) gradually decline through these four phases of decomposition.

In seasonal environments, microbial respiration often occurs over a longer time period and peaks later in the season than does plant growth. Like plant growth, microbial respiration is favored by warm, moist conditions and is therefore greatest during the season of maximum plant growth. Heterotrophic respiration, however, typically begins earlier in the season and ends later than does plant growth for at least three reasons: (1) Microbial respiration typically occurs over a broader range of temperatures (e.g., −10–40°C) and soil moistures than does plant growth. (2) The soil is buffered from temperature extremes that aboveground parts of plants must cope with. (3) Soil temperature lags behind air temperature, so microbial respiration remains high in late summer and autumn at times when plant activity has begun to decline (Davidson and Janssens 2006). Microbial activity is also influenced by the seasonality of plant activity. Root turnover and exudation are often greatest in mid-season when

Box 7.1 Isotopes and Soil Carbon Turnover

The quantity of soil carbon differs dramatically among ecosystems (Post et al. 1982). The total quantity of carbon in an ecosystem, however, gives relatively little insight into its dynamics. Tropical forests and tundra, for example, have similar quantities of soil carbon, despite their radically different climates and productivities. The simplest measure of soil carbon turnover is its residence time estimated from the pool size and carbon inputs (7.3). These measurements show that, even though tropical forests and arctic tundra have similar-sized soil carbon pools, the turnover may be 500 times more rapid in the tropical forest. More sophisticated approaches to estimating soil carbon turnover using carbon isotopes (Ehleringer et al. 2000) lead to a similar conclusion. In the tropics, 85% of the ^{14}C that entered ecosystems during the era of nuclear testing in the 1960s has been converted to humus, whereas this proportion is only 50% in temperate soils and close to zero in boreal soils (Trumbore 1993; Trumbore and Harden 1997). This comparison clearly indicates more rapid turnover of SOM in the tropics than at high latitudes.

Carbon isotopes can also be used to estimate the impacts of land-use change on carbon turnover in situations where the vegetation change is associated with a change in carbon isotopes. In Hawai'i, for example, replacement of C_3 forests by pastures dominated by C_4 grasses causes a gradual change in the carbon isotope ratio of SOM from values similar to C_3 plants toward values similar to C_4 plants (Townsand et al. 1995). This information can be used to estimate the quantity of the original forest carbon that remains in the ecosystem:

$$\%C_{S1} = \frac{C_{S2} - C_{V2}}{C_{V1} - C_{V2}} \cdot 100 \qquad \text{(B7.1)}$$

where $\%C_{S1}$ is the percentage of soil derived from the initial ecosystem type, C_{S2} is the ^{13}C content of soil from the second soil type, C_{V2} is the ^{13}C content of soil from the second vegetation type, and C_{V1} is the ^{13}C content of vegetation from the initial ecosystem type.

photosynthesis is high, contributing to the mid-season peak in soil respiration. Autumn or dry-season senescence provides an additional input of substrates that supports late-season soil respiration.

Vertical Distribution

Most decomposition occurs near the soil surface, where litter inputs are concentrated. Most aboveground litter (leaves and wood) decomposes and releases nutrients on or near the soil surface. Roots therefore tend to grow in surface soils in order to access these nutrients. Thus most root litter is also produced in surface soils, reinforcing the surface localization of decomposition. There are some deep roots, however, and soil mixing by animals, especially termites and earthworms, as well as leaching of dissolved organic matter to depth. About half of the soil organic carbon therefore is typically below 20 cm depth, even though only a third of the roots are below that depth (Fig. 7.5; Jobbágy and Jackson 2000). On average, the deep-soil carbon is older, more recalcitrant, and more tightly bound to soil minerals than is surface carbon (Trumbore and Harden 1997), but a small fraction of the deep soil C is modern, coming mostly from turnover of deep roots.

Decomposition rates are spatially heterogeneous at several scales. The surface litter layer exhibits large daily changes in temperature and moisture. Decomposition in this layer is dominated by fungi that import nitrogen from below. This is a radically different environment than the mineral soil, where temperature and moisture are more stable, some of the organic matter is humified and recalcitrant, and mineral soil surfaces

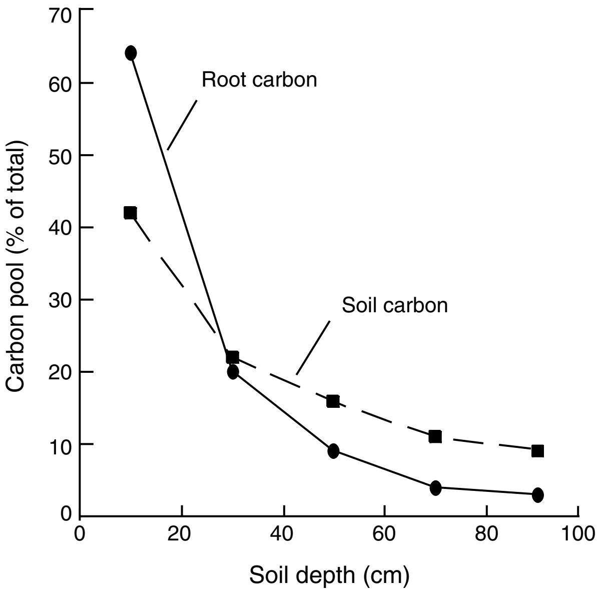

Fig. 7.5 Globally averaged depth profiles of soil organic matter and roots in the top meter of soil. Redrawn from Jobbágy and Jackson (2000)

bind dead organic matter and microbial enzymes. At a finer scale, the rhizosphere around roots is a carbon-rich microenvironment that supports much higher microbial activity than the bulk soil. Finally, the interior of soil aggregates is more likely to be anaerobic than are the surfaces of soil pores. Movement within the soil by roots, water, and soil animals is constantly changing the spatial configuration of these different decomposition environments.

In some ecosystems, such as tropical wet forests, significant quantities of aboveground litter are caught on epiphytes and branches of the canopy. In these wet ecosystems, substantial decomposition, nutrient release, and nutrient absorption by rooted epiphytes occur in the canopy, thereby short-circuiting the soil phase (Nadkarni 1981). Some terrestrial litter and dissolved organic carbon (DOC) also enters streams and lakes, where they become important energy sources for aquatic food webs, as described later. In low-nutrient ecosystems, much of the DOC that enters streams is so recalcitrant that it remains largely unprocessed, leading to the "black-water" rivers that characterize many tropical and boreal forests and temperate swamps.

Factors Controlling Decomposition

Decomposition in ecosystems is controlled by three major factors: substrate quality, characteristics of the microbial community, and physical environment (Swift et al. 1979; Allison 2006). About 75% of terrestrial organic carbon is dead organic matter in soils (see Chap. 14) and represents potential food for decomposer organisms. Given the potent capacity of soil microbes to grow and to break down SOM, why don't they consume it all? In other words, why is the world brown (Allison 2006)? There are multiple contributing factors, but the most important of these appear to be substrate quality, physical environment, and microbial community composition (Allison 2006).

Litter Quality

The availability of belowground resources is the factor governing ecological patterns in litter quality. Plants that grow rapidly, both because of the environment in which they grow and their species properties, typically produce litter that

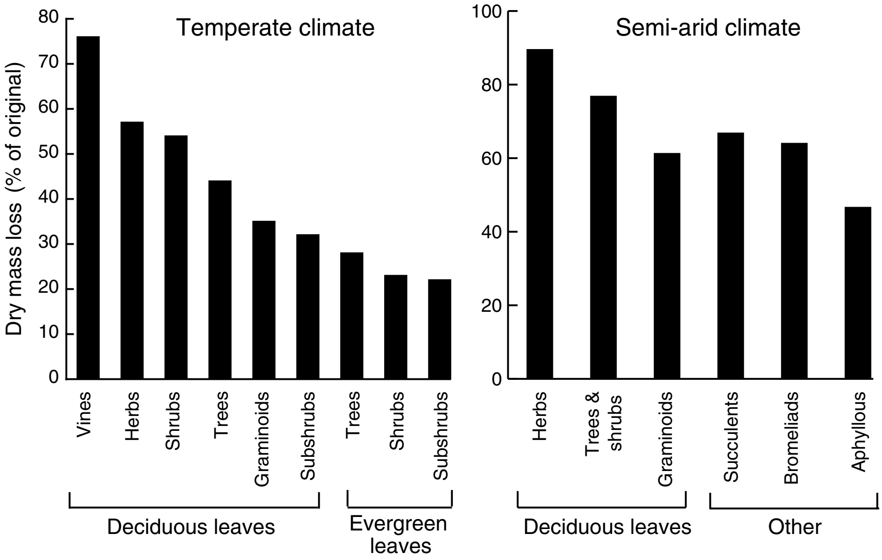

Fig. 7.6 Decomposition rate of leaves of British deciduous and evergreen plant species (*left*) and of deciduous plants and arid-zone plants in Argentina (*right*). Data from Cornelissen (1996) and Perez-Harguindeguy et al. (2000)

decomposes quickly because the same morphological and chemical traits that promote NPP also regulate decomposition (Hobbie 1992; De Deyn et al. 2008). Both NPP and decomposition are enhanced by a high allocation to leaves and by the production of nutrient-rich leaves with a short life span. These tissues decompose rapidly because they have high concentrations of labile compounds such as proteins and low concentrations of recalcitrant cell-wall components such as lignin (Reich et al. 1997). Consequently, species from productive sites produce fine litter that decomposes rapidly (Fig. 7.6; Cornelissen 1996; De Deyn et al. 2008). Species differences in litter quality are an important mechanism by which plant species affect ecosystem processes (see Chap. 11; Hobbie 1992) and are excellent predictors of landscape patterns of initial litter decomposition (Flanagan and Van Cleve 1983). Ecosystems such as forests that produce large quantities of woody stems and roots produce distinct litter types with quite different litter qualities and decomposition rates, with wood decomposing much more slowly than fine litter.

Carbon quality of substrates is the primary chemical determinant of the decomposition of fresh litter. In controlled experiments, differences in substrate **quality**, that is, susceptibility of a substrate to decomposition, give rise to a five- to tenfold range in litter decomposition rate. Animal carcasses decompose more rapidly than plants; leaves decompose more rapidly than wood; deciduous leaves decompose more rapidly than evergreen leaves; and leaves from high-nutrient environments decompose more rapidly than leaves from infertile sites (Figs. 7.6 and 7.7). These differences in decomposition rate are a logical consequence of litter chemistry. Litter compounds can be categorized roughly as: (1) labile metabolic compounds, such as sugars and amino acids, (2) moderately labile structural compounds, such as cellulose and hemicellulose, and (3) recalcitrant structural material, such as lignin, suberin, and cutin. Rapidly decomposing litter generally has higher concentrations of labile substrates and lower concentrations of recalcitrant compounds than does slowly decomposing litter.

Five interrelated chemical properties of organic matter determine substrate quality (J. Schimel, personal communication): size of molecules, types of chemical bonds, regularity of

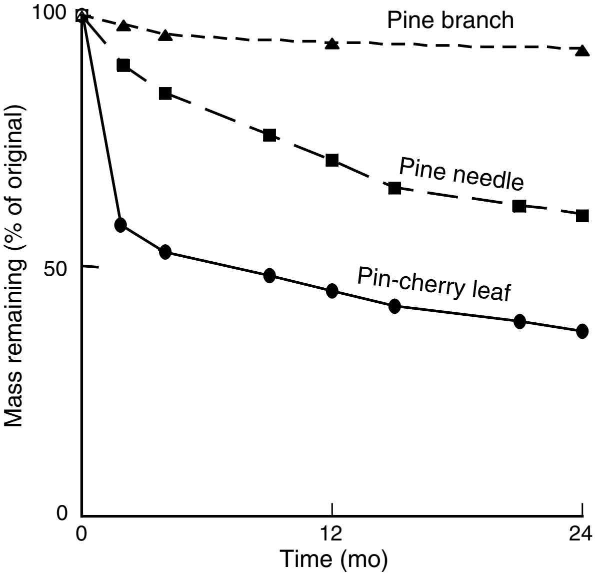

Fig. 7.7 Time course of decomposition of a deciduous leaf, a conifer needle, and wood in a Canadian temperate forest. Data from MacLean and Wein (1978)

structures, toxicity, and nutrient concentrations. (1) Large molecules cannot pass through microbial membranes so they must be processed outside microbial cells by exoenzymes. This limits the degree of control that a given microbe can exert over the detection of substrate availability, delivery of enzymes in response to substrate supply and efficient utilization of breakdown products. Due to differences in molecular size, sugars and amino acids are metabolized more easily than cellulose and proteins, respectively. (2) Some chemical bonds are easier to break than others. Ester linkages that bind phosphate to organic skeletons or peptide bonds that link amino acids to form proteins, for example, are easier to break than the double bonds of aromatic rings. For these reasons, the nitrogen in proteins is much more available to microbes than nitrogen contained in aromatic rings. (3) Compounds like lignin that have a highly irregular structure do not fit the active sites of most enzymes, so they are broken down slowly by nonspecific enzymes (e.g., peroxidases) compared to compounds like cellulose that consist of chains of regularly repeating glucose units. (4) Some soluble compounds such as phenolics and alkaloids are toxic and kill or reduce the activity of microbes that absorb them. (5) Organic compounds containing nitrogen and phosphorus are the major nutrient source supporting microbial growth, so organic matter such as straw that contains low concentrations of these elements may not provide enough nutrients to allow microbes to use fully the carbon present in the litter.

The effects of nutrients on decomposition are largely indirect, mediated by carbon quality of substrates. Although decomposition rates are slow in low-nutrient environments, direct effects of nutrient concentrations in litter or in the soil are seldom seen (Fog 1988; Hobbie 2008). For example, placing the same litter in soils of different nitrogen availability does not consistently alter decomposition, and litters of similar carbon chemistry but different nitrogen concentrations do not differ consistently in decomposition rate (Haynes 1986; Prescott 1995; Prescott et al. 1999; Hobbie and Vitousek 2000; Knorr et al. 2005; Hobbie 2008). Nonetheless, litter with a low ratio of carbon concentration to nitrogen concentration (low **C:N ratio**; high nitrogen concentration) generally decomposes quickly, especially in the early stages of decomposition (Enríquez et al. 1993; Gholz et al. 2000), indicating that C:N ratio is a good *predictor* of initial rates of decomposition. Initial **lignin:nitrogen ratio** of litter is also a good *predictor* of initial

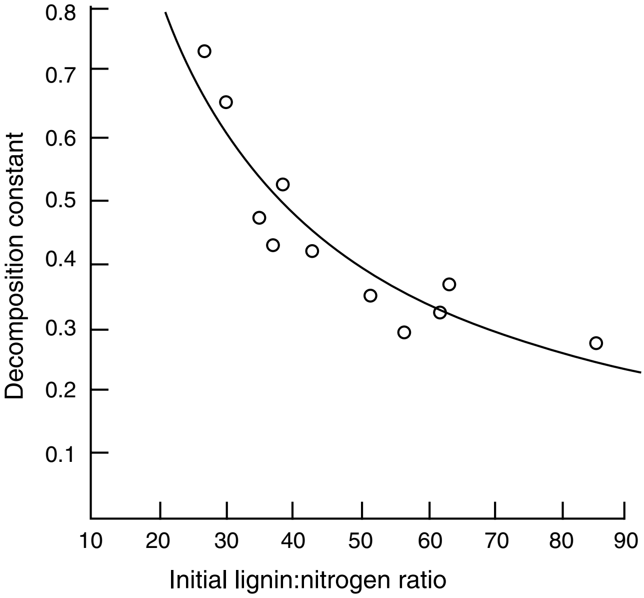

Fig. 7.8 Relationship between the lignin:nitrogen ratio of litter and its decomposition constant. Redrawn from Melillo et al. (1982)

rates of decomposition rate (Fig. 7.8; Berg and Staaf 1980; Melillo et al. 1982; Taylor et al. 1989). To the extent that nutrients influence decomposition, nitrogen is likely to stimulate decomposition of low-lignin litter and inhibit decomposition of high-lignin litter, with no significant overall effect of nitrogen on decomposition (Fog 1988; Allison 2006; Janssens et al. 2010).

Litter nutrient concentrations may influence the fate of carbon metabolized by microbes. Microbes that decompose nitrogen-rich litter, for example, release a larger proportion of the carbon in respiration rather than retaining it in microbial biomass (Manzoni et al. 2008). This may cause high-nitrogen litter to lose its labile carbon so quickly that the remaining litter decomposes quite slowly in the later stages of decomposition (Berg and Meentemeyer 2002).

Both the age and the initial quality of SOM influence its decomposition rate. As litter decomposes, its decomposition rate declines because microbes first consume the more labile substrates, leaving behind more recalcitrant compounds (Fig. 7.4). As microbes die, chitin and other recalcitrant components in their cell walls comprise an increasing proportion of the litter mass. Species effects on litter decomposition rate gradually decline through time as labile substrates are depleted. In addition, older litter fragments that mix downward into mineral soil undergo abiotic chemical reactions and interactions with mineral surfaces that further reduce decomposition rate (Allison 2006). Rates of these later phases of decomposition are difficult to predict (Currie et al. 2010).

The SOM in mineral soils is a mixture of organic compounds of different ages and chemical compositions. It includes fragments of recently shed root, stem, and leaf litter, together with SOM that is thousands of years old (Oades 1989). These different aged components of SOM can be partially separated by density centrifugation because recently produced particles are less dense than older ones and are less likely to be bound to mineral particles. Soils in which a large proportion of the SOM is in the light fraction generally have higher decomposition rates (Robertson and Paul 2000). Alternatively, soil can be chemically separated into distinct fractions, such as water-soluble compounds, **humic acids**, and **fulvic acids** that differ in average age and ease of breakdown. SOM as a whole typically has a mean residence time of 20–50 years, although this can range from 1 to 2 years in cultivated fields to thousands of years in environments where decomposition occurs slowly.

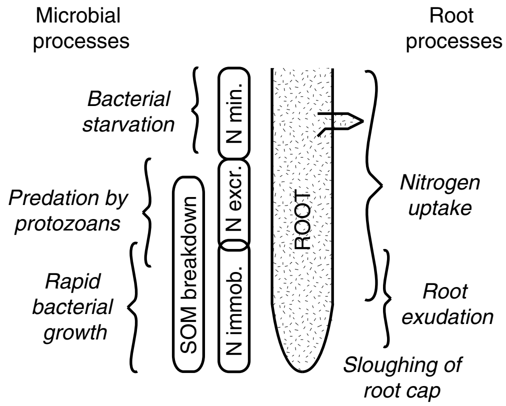

Fig. 7.9 Root and microbial processes in the rhizosphere and the resulting impacts on soil organic matter breakdown and nitrogen dynamics in the rhizosphere

Rhizosphere Stimulation of Decomposition

Plants stimulate decomposition near their roots. The **rhizosphere** is the soil within a few millimeters of plant roots. The rhizosphere comprises virtually all the soil in fine-rooted grasslands, where the average distance between roots is about 1 mm, whereas forests are less densely rooted (often 10 mm between roots; Newman 1985). Roots alter the chemistry of the rhizosphere by secreting carbohydrates and absorbing nutrients. These processes are most active in the zone behind the tips of actively growing roots (Fig. 7.9; Jaeger et al. 1999). The growth of bacteria in the zone of exudation (Norton and Firestone 1991) is supported by high carbon availability (20–40% of NPP; see Table 6.2) and is therefore limited most strongly by nutrients (Cheng et al. 1996). Bacteria use the labile carbon to produce enzymes that "mine" SOM for nutrients.

Microbial immobilization of nutrients in the rhizosphere benefits the plant only if these nutrients are subsequently released and become available to the root. Two processes contribute to the release of nutrients from rhizosphere microbes. First, protozoa and nematodes may graze rhizosphere bacteria, using bacterial carbon to support their high energetic demands and excreting the excess nutrients (Clarholm 1985). Second, as the root matures and exudation rate declines, those bacteria that survive predation may become energy-limited and break down nitrogen-containing compounds in the soil to meet their energy demands, excreting the nitrogen into the rhizosphere as ammonium (Kuzyakov et al. 2000). Food-web interactions among multiple trophic levels complicate these rhizosphere dynamics (Moore et al. 2003).

The relative contribution of grazing and starvation in rhizosphere nutrient release is unknown, but net nitrogen mineralization in the rhizosphere has been estimated to be 30% higher than in bulk soil. In general, the presence of plant roots can stimulate the decomposition of SOM up to threefold, depending on the type of plant species and soil conditions (Cheng et al. 2003). Rhizosphere decomposition may be more sensitive to factors influencing plant carbohydrate status (e.g., light and grazing) than to soil physical environment (Craine et al. 1999; Bardgett et al. 2005a), so the nature of controls over decomposition (soil environment vs. plant carbohydrate status) could differ substantially among ecosystems, depending on the extent of rhizosphere decomposition and the nature of its ecological controls.

Mycorrhizal fungi are functionally an extension of the root system, allowing the root-fungal symbiosis to absorb nutrients at a distance from the root. The **mycorrhizosphere** around mycorrhizal fungal hyphae rapidly moves plant carbon into the bulk soil through a combination of hyphal turnover and exudation (Norton et al. 1990; Finlay 2008). This might also stimulate decomposition, just as in the rhizosphere of roots.

Microbial Community Composition and Enzymatic Capacity

The activity **of soil microbes is more important than their** biomass **in determining decomposition rate**. Microbial biomass is a relatively constant proportion (about 2%) of total soil carbon and therefore has the largest pool size (g m^{-2}) in those stands with the largest quantities of soil carbon (Fierer et al. 2009a); these tend to be the stands with lowest productivity and slowest decomposition (Vance and Chapin 2001). In agricultural soils, microbial biomass also tends to be higher in extremely wet or dry soils, where decomposition is slow, than in moderately moist soils with higher decomposition rate (Insam 1990). Since most microbial biomass is inactive, it is probably more important as a reservoir of nutrients (see Chap. 9) than as a predictor of decomposition rate. This differs from the controls over carbon inputs to ecosystems, where the quantities of plant biomass and leaf area are extremely important determinants of GPP. Those microbial processes like nitrification that are conducted by a restricted number of microbial groups, on the other hand, appear to be sensitive to the population sizes of these groups.

Soil enzyme activity sometimes depends on microbial community composition. The composition of the microbial community is potentially important for decomposition because it influences the types and rates of enzyme production and therefore the rates at which substrates are broken down. Enzymes that break down common substrates like proteins and cellulose are universally present in soils because of their production by most types of microbes (Schimel 2001). Microbial communities that are quite different in composition therefore often have relatively similar decomposition rate and exoenzyme composition (Kemmitt et al. 2008; Fierer et al. 2009b). On the other hand, enzymes involved in processes that occur only in specific environments, such as the anaerobic process of methane production, appear more sensitive to microbial community composition (Gulledge et al. 1997; Schimel 2001). Litter that is decomposed in soils associated with the plant that produces the litter decomposes about 10% faster than in soils from other places (Ayres et al. 2009). This “home field advantage” of decomposition results from the development of distinct microbial communities that are adapted to the litter that they most frequently encounter. These effects of microbial community composition on decomposition are small, however, compared to environmental and substrate-quality effects (Parton et al. 2007; Fierer et al. 2009a).

Soil enzyme activity is also influenced by the binding of enzymes to surfaces or their breakdown by soil proteases. Binding of an enzyme to the external surface of roots or microbes often prolongs its activity in soil, whereas binding to mineral particles can alter the enzyme configuration or block its active site, thereby reducing activity. A brief description of a few soil enzyme systems illustrates some of the microbial and soil controls over exoenzyme activity.

Most soil microbes, including ericoid and ectomycorrhizal fungi, produce enzymes (proteases and peptidases) that break down proteins to amino acids, which are easily absorbed by microbes and used either to produce microbial protein or to provide respiratory energy. Because proteases are subject to attack by other proteases, their lifetime in the soil is short, and soil protease activity tends to mirror microbial activity. Phosphatases, which cleave phosphate from organic phosphate compounds, are, however, more long lived, so their activity in soil is correlated more strongly with the availability of organic phosphate in soil than with microbial activity (Kroehler and Linkins 1991).

Cellulose is the most abundant chemical constituent of plant litter. It consists of chains of glucose units, often thousands of units in length, but none of this glucose is available to support microbial metabolism until acted upon by exoenzymes. Cellulose breakdown requires three separate enzyme systems (Paul and Clark 1996): **Endocellulases** break down the internal bonds to disrupt the crystalline structure of cellulose. **Exocellulases** then cleave off disaccharide units from the ends of chains, forming cellobiose, which is absorbed by microbes and broken down intracellularly to glucose by **cellobiase**. Some soil microbes, including most fungi, produce the entire suite of cellulase enzymes. Other organisms, such as some bacteria, produce only some cellulase enzymes and must function as part of microbial consortia to gain energy from cellulose breakdown.

Lignin is degraded slowly because only some organisms (primarily fungi) produce the necessary enzymes, and these microbes produce enzymes only when nitrogen is unavailable.

Sometimes this is mediated by competition between rapidly growing bacteria that break down labile organic matter and release nitrogen that inhibits more slow-growing lignolytic fungi. Lignin forms non-enzymatically by condensation reactions with phenols and free radicals, creating an irregular structure that does not fit the specificity required by the active site of most enzymes. For this reason, lignin-degrading enzymes use hydrogen peroxide to generate free radicals, which have a low specificity for substrates but are very powerful oxidizers. Oxygen is required to generate the hydrogen peroxide and the subsequent free radicals, so lignin breakdown does not occur in anaerobic soils. Decomposers generally invest more energy in producing lignin-degrading enzymes than they gain by metabolizing its breakdown products (Coûteaux et al. 1995). Lignin appears to be degraded to gain access to the nitrogen in the interior of lignified dead cells or to provide access to lignin-encrusted cellulose (Coûteaux et al. 1995; Adair et al. 2008). Because of the generation of free radicals, some of the enzymes involved in lignin breakdown also modify existing organic matter and generate more complex soil humus.

As discussed earlier, predation by soil animals generally has only a modest effect on decomposition. In the ocean, viruses and other diseases exert an important control over decomposition, but little is known about the role of disease as a "top-down" control over terrestrial decomposition (Allison 2006).

The Environment

Moisture

Decomposition increases with increasing moisture, until soils become so waterlogged that anaerobic conditions inhibit decomposition. Decomposers, like plants, are most productive under warm, moist conditions, if enough oxygen is available. This accounts for the high decomposition rates in tropical forests (Gholz et al. 2000). Decomposition rate of mineral soil generally declines at soil moistures less than 30–50% of dry mass (Haynes 1986), due to the reduced thickness of moisture films on soil surfaces and therefore the rate of diffusion of substrates to microbes (Stark and Firestone 1995). Osmotic effects further restrict the activity of soil microbes in extremely dry or **saline** (salty) soils. Bacteria function at lower water availability than do plant roots, so decomposition continues even in soils that are too dry to support plant activity, perhaps contributing to the low soil organic content of arid ecosystems. Rewetting of very dry soils by dew or rain can influence decomposition by creating an osmotic shock that stresses microbial cells, causing a flush of available carbon. The net effect of drying–wetting cycles is a stimulation of decomposition, if the cycles are infrequent (as generally occurs in soils), but frequent cycles, as in the litter layer, can reduce microbial populations enough to reduce decomposition rates (Clein and Schimel 1994). Drying–wetting cycles tend to stimulate the decomposition of labile substrates (e.g., hemicellulose), which are broken down largely by rapidly growing bacteria, and to retard the decomposition of recalcitrant ones (e.g., lignin; Haynes 1986), which are broken down by slow-growing fungi.

Decomposition is also reduced at high soil moisture (e.g., >100–150% of soil dry mass in mineral soils; Haynes 1986). Oxygen diffuses 10,000 times more slowly through water than through air, so water acts as a barrier to oxygen supply in wet soils or logs, or in wet microsites within aggregates of well-drained soils. Oxygen limitation to decomposition can occur under many circumstances, including topographic controls over drainage, presence of hardpans or permafrost, high clay content, or compaction by animals and agricultural equipment. Irrigation or rain events can lead to short-term oxygen depletion. In warm environments, the solubility of oxygen in water is low, and oxygen is rapidly depleted by root and microbial respiration, making decomposition particularly sensitive to high soil moisture. NPP is generally less limited by high soil moisture than is decomposition because many plants that are adapted to these conditions transport oxygen from leaves to roots. The large accumulations of SOM in histosol soils of swamps and bogs at all latitudes (see Chap. 3)

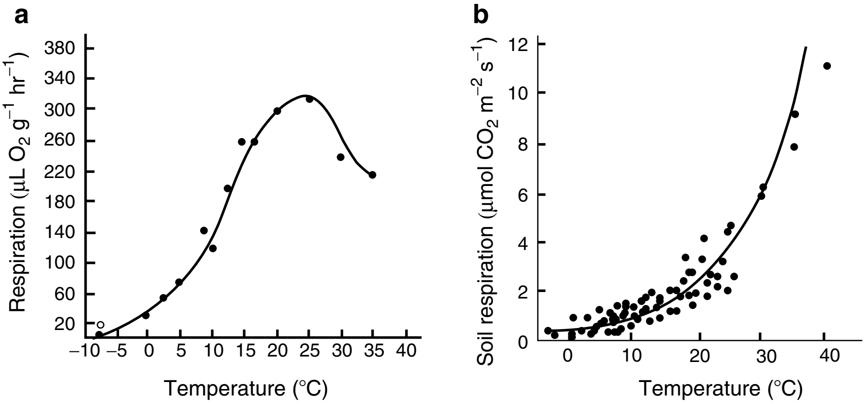

Fig. 7.10 Relationship between temperature and soil respiration in (*left*) laboratory incubations of tundra soils and (*right*) field measurements of soil respiration in 15 globally distributed studies, where data have been fitted to have the same respiration rate at 10°C. Redrawn from Flanagan and Veum (1974) and Lloyd and Taylor (1994)

clearly indicate the importance of oxygen limitation to decomposition.

Decaying logs create their own unique microenvironment and generally have a higher moisture content than adjacent surface litter. In moist environments, log decomposition rate may therefore be limited by oxygen supply at times when microbes in neighboring surface litter are moisture-limited. Oxygen often diffuses along cracks and insect galleries and therefore penetrates to the interior of logs more rapidly than might be predicted from log moisture content (Hicks and Harmon 2002).

Temperature

Although microbial respiration and decomposition increase with temperature in the short term, indirect effects constrain their temperature sensitivity over annual to decadal timescales. Microbial enzyme activity and respiration increase exponentially with short-term increases in temperature over a broad temperature range (Fig. 7.10), speeding up the mineralization of organic carbon to CO_2. The decomposition of recalcitrant substrates is particularly temperature sensitive. A temperature increase from 10 to 20°C, for example, increases the decomposition of the biochemically labile citric acid twofold, the more biochemically recalcitrant tannic acid threefold, and recalcitrant SOM fivefold (Fierer et al. 2005).

Several processes, operating at different timescales, constrain this apparently high temperature sensitivity (Davidson and Janssens 2006). Over days to weeks, microbes may acclimate to higher temperatures by down-regulating respiration (Bradford et al. 2008). Substrate pools decline faster at warmer temperatures, reducing carbon availability and limiting available energy to microbes. Seasonal shifts in microbial community composition to guilds that remain active in each season further reduce the seasonal variation in decomposition rate.

Temperature has many indirect effects on decomposition that act through its effects on other environmental variables (Fig. 7.11). In wet soils or microsites (e.g., aggregates), temperature stimulation of respiration consumes enough oxygen to reduce its availability and therefore microbial respiration. Over longer timescales, however, high temperature reduces soil moisture by augmenting evapotranspiration, which enhances oxygen diffusion. Similarly, at high latitudes, warming thaws the permafrost, improving drainage and the environment for decomposition. Over still longer timescales, vegetation changes alter the quantity and quality of organic matter inputs to soils (see Chap. 12). In summary, the temperature response of decomposition is far from simple. The stimulation of decomposition by warming that is consistently observed on

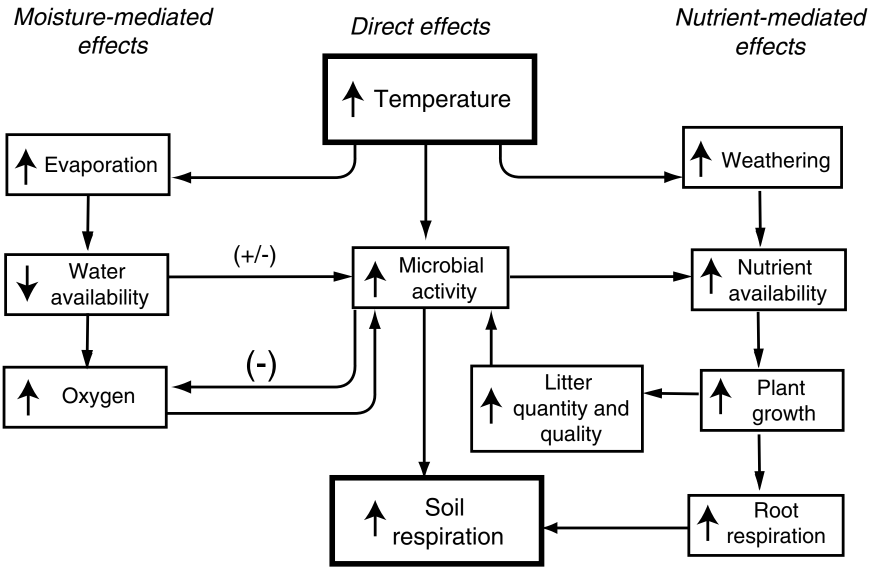

Fig. 7.11 Major direct and indirect effects of temperature on soil respiration

hourly to weekly timescales is increasingly modified by indirect effects over longer timescales, suggesting that the long-term effects of climate warming on decomposition is a fertile topic for future research (Davidson and Janssens 2006; Currie et al. 2010).

Soil Organic Matter

Decomposition of soil organic matter (SOM) is strongly influenced by its reactions with soil minerals. Up to this point, we have focused primarily on the factors controlling the breakdown and loss of litter. Equally important are the processes that reduce rates of decomposition and foster organic accumulation in mineral soils.

Soil Properties

Clay minerals reduce the decomposition rate of soil organic matter, thereby increasing soil organic content. Clays alter the physical environment of soils by increasing water-holding capacity (see Chap. 3). The resulting restriction in oxygen supply can reduce decomposition in wet clay soils. Even at moderate soil moisture, clays enhance organic accumulation by binding SOM (making it less accessible to microbial enzymes), binding microbial enzymes (reducing their capacity to attach to substrates), and binding the soluble products of exoenzyme activity (making these products less available for absorption by soil microbes). This binding of organic matter to clays occurs because the high density of negatively charged sites on clay minerals attract the positive charges on the organic matter (amine groups) or form bridges with polyvalent cations (Ca^{2+}, Fe^{2+}, Al^{3+}, Mn^{4+}) that bind to negative groups (e.g., carboxyl groups) on organic matter (Fig. 7.12). The net effect of this binding by clay minerals is to “protect” SOM and reduce its decomposition rate. SOM protection by clay minerals is most important in ecosystems such as grasslands or tropical forests, where decomposition is relatively rapid and where soil animals rapidly mix fresh litter with mineral soil. Mineral protection of SOM is less important in conifer forests or tundra where much of the decomposition occurs above the mineral soil in a well-developed organic soil horizon (O horizon).

Both the type and quantity of clay influence decomposition. Many tropical clay minerals have a high aluminum concentration that binds tightly

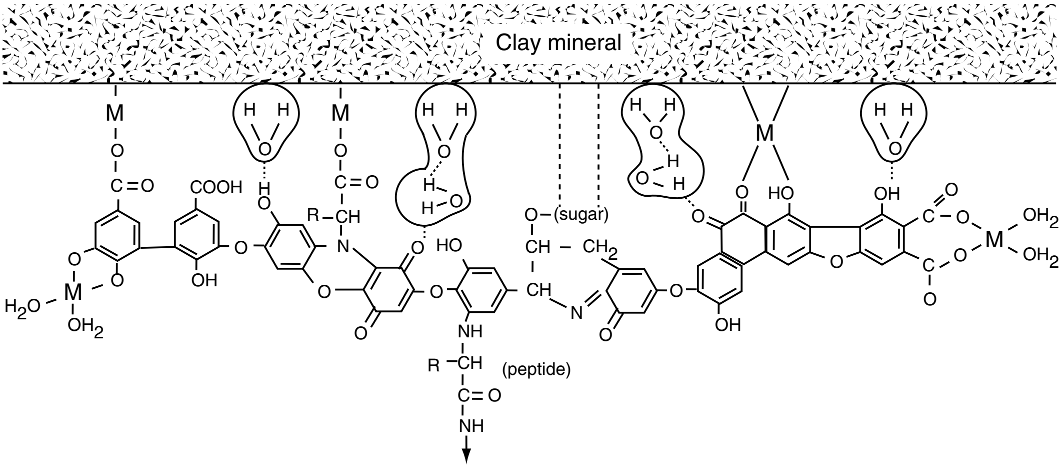

Fig. 7.12 Schematic diagram of the interactions between soil organic matter and clay particles, as mediated by water (H–O–H) and metal ions (M). Redrawn from Stevenson (1994)

to organic matter through covalent bonds. Clays with a multi-layered lattice structure bind organic compounds between the silicate layers, making them particularly effective in SOM protection (see Chap. 3).

All else being equal, soil organic matter decomposes more slowly in acidic than in neutral soils, largely due to indirect effects. Many processes can acidify soils, including cation leaching, acid deposition, and the accumulation of organic acids in highly organic soils. These conditions tend to be associated with low nutrient availability (and therefore low litter quality) and with levels of aluminum that may be toxic to many microbes, especially bacteria.

Soil Disturbance

Soil disturbance increases decomposition by promoting aeration and exposing new surfaces to microbial attack. The mechanism by which disturbance stimulates decomposition is basically the same at all scales, ranging from the movement of earthworms through soils to tillage of agricultural fields. Disturbance disrupts soil aggregates so the organic matter contained within them becomes more exposed to oxygen and microbial colonization. This disturbance effect is most pronounced in warm, wet soils, where the increased aeration has greatest effect on decomposition. In a soil converted to irrigated cotton, for example, tillage caused loss in 3–5 years of half its organic content that had required centuries to millennia to accumulate (Haynes 1986). Similarly, carbon sequestered in soils of restored prairies over 10–20 years (West and Post 2002) can be lost rapidly if these soils are returned to agricultural tillage. The loss of organic matter and disruption of aggregates by plowing eventually impedes the drainage of water, the growth of roots, and the mineralization of soil nutrients.

Humus Formation

In climates that are favorable for decomposition, substantial quantities of carbon persist in mineral soils for thousands of years. It has long been thought that this is primarily soil humus that accumulates due to its recalcitrance (Oades 1989). Recent research suggests, however, that sorption to soil minerals may be a more important protective mechanism and that simple compounds may be just as persistent in soils as the complex ones (Schmidt et al. in press). To the extent that humus formation occurs, the following steps (Fig. 7.13) have been implicated (Zech and Kogel-Knabner 1994):

1. **Selective preservation**. Decomposition selectively degrades labile compounds in detritus, leaving behind recalcitrant materials like

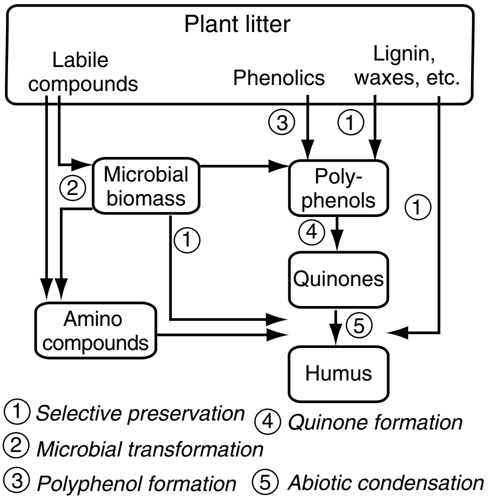

Fig. 7.13 Principle pathways of humus formation. The major steps in humus formation are described in the text

waxes, cutins, suberin, lignin, chitin, and microbial cell walls. Partial microbial breakdown of these recalcitrant “leftovers” may produce compounds with reactive groups and side chains that are reactants in nonspecific soil reactions. There is, however, little direct evidence that lignin is any more persistent than more simple compounds in mineral soils (Schmidt et al. in press).

2. **Microbial transformation**. Enzymatic breakdown of SOM produces low-molecular-weight water-soluble products, some of which may react in humus formation. Amino compounds such as amino acids from protein breakdown and sugar amines from degradation of microbial cell walls may be particularly important (see step 5; Fig. 7.13).
3. **Polyphenol formation**. Soluble phenolic compounds may also be important reactants in humus formation. They come from at least three sources (Haynes 1986): (1) microbial degradation of plant lignin, (2) the synthesis of phenolic polymers by soil microbes from simple non-lignin plant precursors, and (3) polyphenols produced by plants as defenses against herbivores and pathogens.
4. **Quinone formation**. The polyphenol oxidase and peroxidase enzymes produced by fungi to break down lignin and other phenolic compounds also convert polyphenols into highly reactive compounds called quinones.
5. **Abiotic condensation**. Quinones undergo spontaneous condensation reactions with many soil compounds, especially compounds with which they react readily (e.g., compounds with amino groups) or that are abundant (e.g., recalcitrant compounds that accumulate in soils).

The chemical nature of persistent SOM differs among ecosystems (Haynes 1986; Paul and Clark 1996). Forest organic matter includes insoluble compounds with extensive networks of aromatic rings and few side chains. This reflects an abundance of phenolic compounds in leaves and wood that defend plants against herbivores and pathogens. In grasslands, a larger proportion of SOM is water soluble due to extensive side chains and many charged groups.

Peat Accumulation and Trace Gas Emissions

Wet soils contain about a third of Earth’s store of soil organic matter (Schlesinger 1997). In environments where low oxygen availability inhibits decomposition, organic matter accumulates in a relatively undecomposed state. This organic matter accumulates, not because it is chemically recalcitrant, but because environmental conditions constrain the activity of decomposers more strongly than they constrain carbon inputs by plants. In these wet ecosystems, SOM is often quite labile and decomposes quickly whenever soils dry enough for oxygen diffusion to overcome the “environmental protection” of this organic matter (Neff and Hooper 2002). It is important to understand the controls over decomposition in wetland soils because of the large soil carbon reservoir they contain and the sensitivity of this reservoir to environmental change. In addition, anaerobic decomposition in wetlands often releases trace gases (methane and nitrous oxide) that have about 23- and 300-fold, respectively, greater warming effect on the atmosphere per molecule than does CO_2 (see Chap. 2; IPCC 2007).

Within a poorly aerated soil, there is a gradient in decomposition rate from well-oxygenated to oxygen-depleted zones that occur at depth or within the interior of soil aggregates. This gradient in redox potential (see Chap. 3) determines the availability of electron acceptors that organisms can use to support their growth and respiration. Those microbes that transfer electrons from their food (soluble organic compounds they have absorbed) to oxygen, for example, capture the most energy to support their metabolism and growth. As oxygen is depleted, however, only those microbes that are able to transfer electrons from their food (organic substrates) to *other* electron acceptors can metabolize (decompose) organic matter and grow. The amount of energy released to support microbial growth declines progressively with transfer from organic matter to each of the following electron acceptors:

$$O_2 > NO_3^- > Mn^{4+} > Fe^{3+} > SO_4^{2-} > CO_2 > H^+ \tag{7.4}$$

Many soil organisms carry out only one or a few redox reactions. Temporal and spatial variations in the availability of these electron acceptors therefore determine the competitive balance among these organisms and their contribution to decomposition. Organisms that derive more energy from their redox reactions (e.g., aerobic decomposers relative to denitrifiers) have a competitive advantage, when there is an adequate supply of their preferred electron acceptor because they are able to support more growth per unit of organic substrate consumed.

In flooded soils and sediments, there is a dynamic equilibrium determined by the supply of oxygen as an oxidant at the surface and buried organic carbon, which serves as a source of reducing power. As this organic matter is decomposed, microbes consume oxygen and other electron acceptors to support their metabolism and growth. Therefore, aerobic decomposition predominates at the surface and near oxygen-transporting roots, whereas other energy-producing processes become important only when oxygen has been depleted. This results in a vertical zonation of decomposition processes, with aerobic decomposition at the surface, then a zone of denitrification, then zones of manganese and iron reduction, then sulfate reduction, then methane production. Depending on the availability of each of these electron acceptors, the zone can occupy either a significant portion of the vertical profile (and therefore account for substantial decomposition) or can be of negligible importance. Denitrification, for example, is the second most energetically favorable redox reaction, after oxygen has been depleted (7.4). During denitrification, denitrifiers transfer electrons from organic matter to nitrate, producing the gases nitric oxide, nitrous oxide, and di-nitrogen, as waste products. Nitrate availability is often low in anaerobic environments, however, because nitrification, which produces nitrate, is an *aerobic* process (see Chap. 9). Denitrification is therefore relatively unimportant in most wetlands but is important where soil aeration is patchy, for example in anaerobic interiors of soil aggregates of an otherwise aerobic soil, or where water table fluctuates, as in irrigated fields or rice paddies.

As nitrate is depleted, other bacteria, using other electron acceptors, ferment labile organic compounds to produce acetate, other simple organic compounds, and hydrogen. If sulfate is available, as in estuaries, salt marshes, and ocean sediments, sulfate reducers transfer electrons from simple organic compounds to sulfate (7.4), producing hydrogen sulfide and decomposing the organic matter to support their metabolism and growth.

The concentrations of both nitrate and sulfate are low in most non-coastal wetlands and lake sediments (Schlesinger 1997), so methane production is often the predominant mode of anaerobic decomposition in these ecosystems. Conversely, in marine sediments, where sulfate is abundant, methane production is less important. **Methanogens** produce methane (CH_4) when other electron acceptors have been depleted (7.4). Methane production can occur through several pathways. Some methanogens split acetate into CO_2 and CH_4 (7.5). Others use hydrogen (H_2), which is a by-product of fermentation, as an energy source and bicarbonate (derived from CO_2) as an electron acceptor (7.6), much the way NO_3^- or SO_4^{2-} serve as electron acceptors in denitrification and sulfate reduction, respectively.

$$CH_3COOH \rightarrow CO_2 + CH_4 \quad (7.5)$$

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O \quad (7.6)$$

Methane is even more highly reduced than are carbohydrates, so it is a good energy source for organisms that have access to oxygen. Another group of bacteria (**methanotrophs**) that occur in the surface soils of wetlands use methane as an energy source and consume much of the methane as it diffuses from depth toward the atmosphere. Therefore, not all methane produced within an ecosystem actually leaves the system. Methane flux *from the ecosystem* is usually highest when methane escapes through plant gas transport tissues or as bubbles that bypass the zone of methane consumption by methanotrophs (Walter et al. 2006).

Enzymes that convert ammonium to nitrate as part of the nitrogen cycle (see Chap. 9) also react with methane, causing well-aerated soils to be a net sink for methane. Even in wetlands that produce substantial methane, more carbon is generally released as CO_2 by decomposers near the soil surface than as methane by methanogens at depth, so aerobic respiration is still the dominant pathway of carbon return to the atmosphere. Methane is quantitatively more important in its role as a greenhouse gas (see Chap. 2) rather than as a component of the carbon cycle (see Chap. 14).

In summary, conditions that reduce the rate of decomposition (either humification of organic matter under environmental conditions that are favorable for decomposition or peat accumulation in waterlogged soils) contribute to long-term carbon storage in ecosystems. In the next sections, we put these controls over decomposition into the context of whole-ecosystem carbon budgets.

Heterotrophic Respiration

Heterotrophic respiration by soil microbes and animals is one of the largest avenues of carbon loss from ecosystems. Decomposer microbes and their predators account for most of this respiration. Annual heterotrophic respiration correlates closely with NPP across carbon cycling rates that vary at least tenfold globally, suggesting that, on average, respiration by decomposers and other heterotrophs breaks down about the same amount of organic matter that enters the ecosystem each year (Fig. 7.14). This relationship occurs by definition in ecosystems close to steady state (i.e., where there are no large gains or losses of SOM). Both concurrent carbon inputs (e.g., daily GPP) and long-term site productivity (as reflected in LAI) are important predictors of heterotrophic respiration (Migliavacca et al. 2010). Measurements of soil respiration, which includes both heterotrophic and root respiration, are consistent with this generalization. Both soil respiration and heterotrophic respiration (Figs. 7.14 and 7.15) correlate closely with NPP (Raich and Schlesinger 1992; Janssens et al. 2010). About half (25–65%) of soil respiration derives from roots, and the rest comes from decomposition (Raich and Schlesinger 1992; Högberg et al. 2001; Bhupinderpal-Singh et al. 2003).

Heterotrophic respiration shows little relationship with the total quantity of organic matter in soils because most soil carbon is sorbed to mineral surfaces, chemically recalcitrant or in an unfavorable soil environment (e.g., low temperature or low oxygen availability). This means that total soil organic content is not a good predictor

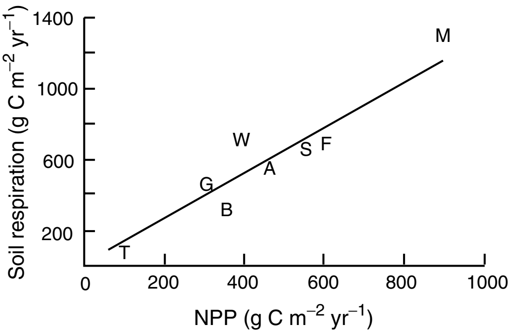

Fig. 7.14 Relationship between average annual NPP and average annual soil respiration rate for Earth's major biomes. Ecosystem types are agricultural lands (A), boreal forest and woodland (B), desert scrub (D), temperate forest (F), temperate grassland (G), tropical wet forest (M), tropical savanna and dry forest (S), tundra (T), and Mediterranean woodland and heath (W). Root respiration probably accounts for the 25% greater soil respiration than NPP at any point along this regression line. Redrawn from Raich and Schlesinger (1992)

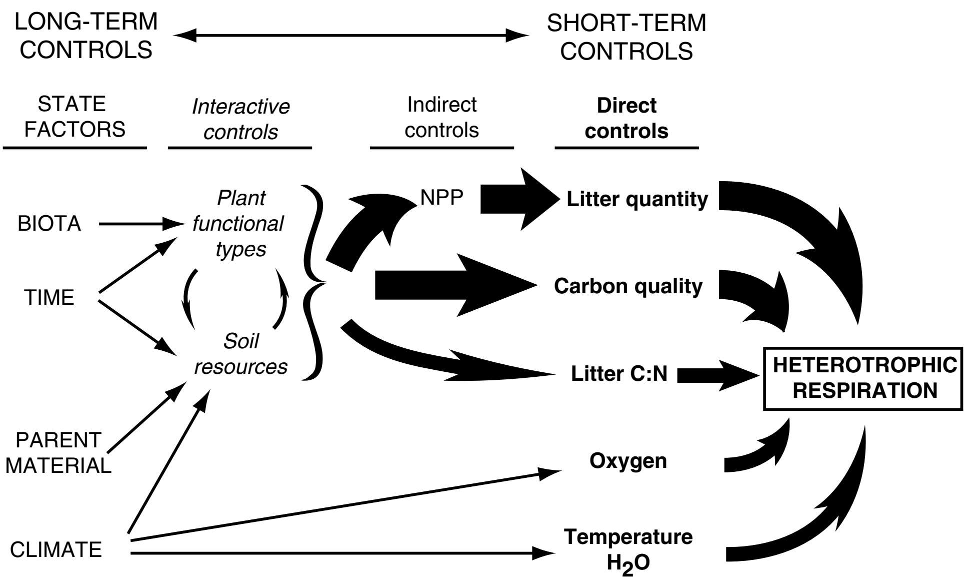

Fig. 7.15 The major factors governing temporal and spatial variation in heterotrophic respiration in ecosystems. These controls range from proximate controls over seasonal variation in heterotrophic respiration to the state factors and interactive controls that are the ultimate causes of ecosystem differences in heterotrophic respiration. Thickness of the *arrows* indicates the strength of the direct and indirect effects. The factors that account for most of the variation in heterotrophic respiration among ecosystems are the quantity and carbon quality of litter inputs, which are ultimately determined by the interacting effects of soil resources, climate, vegetation, and disturbance regime

of stand-level carbon loss (Clein et al. 2000). In fact, the largest soil carbon accumulations often occur in ecosystems such as peat bogs with low NPP but even slower decomposition.

Although nitrogen concentration of litter has a small and inconsistent influence on decomposition, addition of nitrogen to temperate forest soils reduces heterotrophic respiration at the ecosystem scale (Janssens et al. 2010). This is most pronounced in productive sites, where nitrogen limitation of plant production is least likely to occur (Fig. 7.16) and explains why organic matter tends to accumulate in response to nitrogen deposition (Magnani et al. 2007; Sutton et al. 2008; Liu and Greaver 2009). Nitrogen inhibition of heterotrophic respiration is probably the result of multiple effects, including a decline in microbial biomass, particularly of decomposer and mycorrhizal fungi, a reduction in exudation by roots and mycorrhizae, and a decline in the production of lignin-degrading enzymes (Fog 1988; Treseder 2008; Janssens et al. 2010).

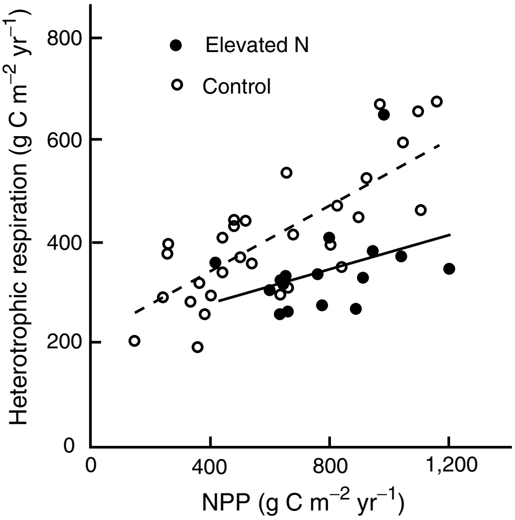

Fig. 7.16 Relationship of heterotrophic respiration to NPP in forests exposed to background or elevated (>0.55 gN m^{-2} year^{-1}) nitrogen deposition. The strong dependence of heterotrophic respiration on NPP is reduced by nitrogen deposition, particularly in productive forests. Redrawn from Janssens et al. (2010)

The linkage of carbon and nutrient cycles constrains potential imbalances between NPP and decomposition. Both plants and microbes require carbon (energy) and nutrients for growth. For example, microbes decomposing fresh litter acquire nitrogen from the substrate or the soil to meet their nitrogen needs for growth (nitrogen **immobilization**). This nitrogen is subsequently released (**mineralized**) when the microbes break down nitrogen-containing compounds to meet their energy needs (see Chap. 9). The magnitude and timing of nitrogen immobilization and release depend on substrate chemistry. Litter produced by nitrogen-limited plants, for example, has a relatively low nitrogen concentration and high concentrations of recalcitrant compounds. Microbes that decompose this litter mineralize nitrogen slowly, constraining the nitrogen supply to plants and therefore NPP. A second important linkage between carbon and nitrogen cycles is mediated by mycorrhizae, whose growth is supported directly by GPP and which mineralize nutrients to support their growth and that of their host plants (Högberg et al. 2001; Finlay 2008). This physiological requirement for both carbon and nutrients for life's processes imposes an inevitable linkage between carbon and nutrient cycles and therefore a rough long-term balance between NPP and decomposition in ecosystems. In Chap. 9, we discuss the processes that modify the balance between carbon and nutrient cycles and therefore the strength of this linkage.

Net Ecosystem Production (NEP)

On short timescales, GPP and respiration typically dominate the carbon balance of terrestrial ecosystems. Their balance is termed **net ecosystem production** (NEP).

$$NEP = GPP - R_{ecosyst} = NPP - R_{het} \qquad (7.7)$$

where

$$R_{ecosyst} = R_{plant} + R_{het} \qquad (7.8)$$

Ecosystem respiration ($R_{ecosyst}$) is the sum of the respiration from plants (R_{plant}) and heterotrophs (R_{het}) – that is, microbes and animals. NEP is a valuable concept because it addresses the major processes by which organisms gain carbon and energy (GPP) and use this energy through respiration to support their growth and maintenance ($R_{ecosyst}$). NEP thus explicitly links the physiology of organisms to the carbon balance of ecosystems (Woodwell and Whittaker 1968; Chapin et al. 2006a; Luyssaert et al. 2007). It is analogous to NPP (GPP − R_{plant}) of plants and can be readily incorporated into process-based models that address the physiology of all organisms in ecosystems.

As discussed later, it is virtually impossible to measure NEP directly. However, in terrestrial ecosystems, gaseous exchange with the bulk atmosphere supplies most of the CO_2 that supports GPP and removes most of the respiratory CO_2. This net CO_2 exchange of the entire ecosystem, termed **net ecosystem exchange**, NEE, is therefore usually a reasonable approximation of NEP, when measured over short time periods. NEE is now being measured in a wide range of ecosystems (Box 7.2). NEE may systematically overestimate NEP in terrestrial ecosystems and underestimate it in freshwater ecosystems, as discussed later, but it probably provides a reasonable proxy for *geographic patterns* of NEP and their environmental controls in those ecosystems that are close to steady state (Baldocchi et al. 2001; Luyssaert et al. 2007; Xiao et al. 2008).

NEE is defined, by convention, as CO_2 flux *from the ecosystem to the atmosphere*. It corresponds to a *negative* carbon input to ecosystems. NEE is defined in this way because atmospheric scientists, who originated the term, seek to document net sources of CO_2 to the atmosphere (i.e., NEE) that account for rising atmospheric CO_2 concentration. Therefore, CO_2 input to the ecosystem is a *negative* NEE.

NEP is determined by factors that cause an imbalance **between GPP and** $R_{ecosyst}$. In ecosystems that have not been recently disturbed, NEP is a small difference between two very large fluxes (Fig. 7.17): (1) photosynthetic carbon gain and (2) carbon loss through respiration (primarily

Box 7.2 Measuring Carbon Fluxes of Ecosystems and Regions

Photosynthesis (GPP) and respiration are usually the largest carbon fluxes between terrestrial ecosystems and the atmosphere. As turbulent eddies of air move across the surface of an ecosystem, like balls rolling across a lawn, the downward-moving limb of the eddy carries atmospheric air into the ecosystem, and the upward-moving limb transports ecosystem air to the free atmosphere. The **eddy covariance technique** takes rapid measurements (about ten times per second) of vertical wind speed and the CO_2 content of upward and downward moving parcels of air. The CO_2 flux can be calculated directly from these measurements (the minute, instantaneous changes in CO_2 concentration times the instantaneous changes in vertical wind velocity that occur as turbulent eddies pass the sensors). When these fluxes are summed over an hour, a day, or a year, they represent the net CO_2 flux between the ecosystem and the atmosphere (i.e., NEE) over that time period (see Fig. 7.22). The technology for measuring these fluxes and correcting for potential artifacts is rapidly improving (Baldocchi 2003). Comparisons of long-term NEE measurements across networks of sites provide a basis for understanding and generalizing about the controls over temporal and spatial variations in NEE among terrestrial ecosystems. This understanding has been incorporated into models that estimate various carbon fluxes (e.g., GPP, ecosystem respiration, and NEP) based on ecosystem properties (e.g., ecosystem type and leaf area) and environmental conditions (e.g., temperature) that can be remotely sensed from space (Running et al. 2004), leading to estimates of carbon fluxes across broad regions (see Fig. 7.19).

NEE measurements can be complemented by measurement of other fluxes, such as CO_2 from wildfire or carbon transfers to groundwater and aquatic ecosystems (Cole et al. 2007). The integration of all these fluxes provides an estimate of net ecosystem carbon balance (NECB) – the rate of carbon accumulation or loss by an ecosystem (Randerson et al. 2002; Chapin et al. 2006a).

An independent check of these flux estimates comes from large-scale atmospheric measurements (see Fig. 7.27). Atmospheric circulation models can calculate, based on measurements, the change in quantity of CO_2 contained in an air mass, as it moves across a continent or ocean. From this information, the net regional flux (regional NEE) between the surface and the atmosphere can be calculated and compared with estimates made from surface measurements and models (Fan et al. 1998; Gurney et al. 2002; Schuh et al. 2010).

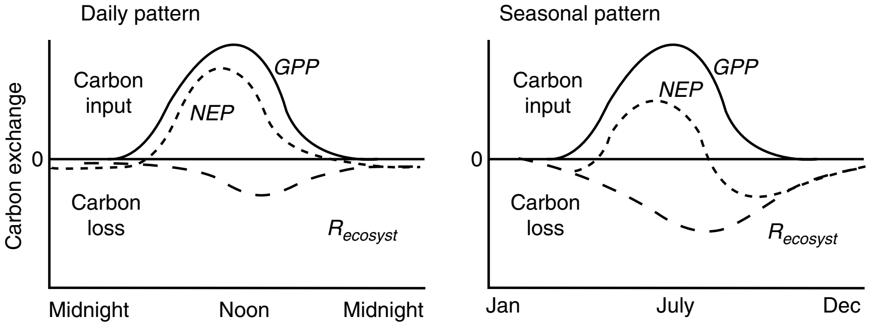

Fig. 7.17 Idealized daily (season of active plant growth) and seasonal pattern of gross primary production (*GPP*), ecosystem respiration ($R_{ecosyst}$), and net ecosystem production (*NEP*) of an ecosystem. *NEP* is the difference between two large fluxes (carbon input as GPP and carbon loss through respiration). In these diagrams, *NEP* is shown as positive over the diurnal cycle (*GPP* > ecosystem respiration during the season of active plant growth) and close to zero over the annual cycles, assuming that the ecosystem is at steady state. The actual pattern of these fluxes varies with environmental conditions, successional status, and other factors (see text). Carbon losses due to leaching and disturbance are assumed to be zero in these diagrams

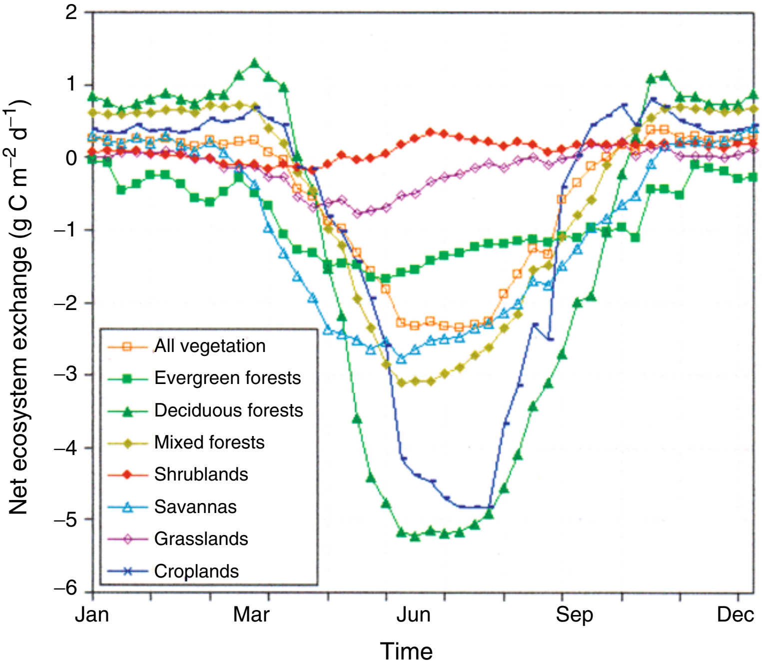

Fig. 7.18 Predicted seasonal pattern of net ecosystem exchange (NEE) of major U.S. vegetation types in 2005, based on a regression model that uses AmeriFlux (a network of ecosystem flux studies) NEE measurements and MODIS satellite imagery. Redrawn from Xiao et al. (2008)

by plants and microbes). In general, GPP is closely correlated with ecosystem respiration on timescales of days to weeks (Migliavacca et al. 2010) because both plant respiration and heterotrophic respiration are strongly affected by the quantity of carbon that enters ecosystems through GPP, as discussed earlier. When GPP exactly equals ecosystem respiration, NEP is, by definition, zero. There is therefore no reason to expect NEP to correlate in any simple way with GPP, NPP, or ecosystem respiration. However, GPP and respiration are seldom perfectly balanced. During the day, photosynthesis exceeds respiration, with the reverse occurring at night. Similarly, during the growing season, NEP is positive because photosynthesis exceeds respiration as plants accumulate biomass. In nongrowing seasons, when photosynthesis is low, heterotrophic respiration dominates, and NEP is negative. This gives rise to very simple and predictable daily and seasonal patterns of NEP (Fig. 7.17).

Consistent with this expected seasonal pattern (Fig. 7.17), NEP is generally positive (or NEE negative) during seasons favorable for plant growth (GPP > ecosystem respiration) and negative (NEE positive) during seasons unfavorable for plant growth (GPP < ecosystem respiration; Fig. 7.18). The magnitude of the seasonal changes in NEP differs among ecosystems. Within the U.S., deciduous forests have the largest positive growing-season NEP and most negative nongrowing-season NEP, and shrublands show least seasonal variation in NEP (Xiao et al. 2008). Coastal evergreen forests show a modest positive NEP throughout the year. Not surprisingly, positive NEP (negative NEE) is most pronounced during summer in the eastern U.S., where deciduous forests dominate, is more evenly distributed throughout the year in coastal evergreen forests of the Pacific Northwest, and is negative (NEE positive) during summer in arid regions of the southwestern U.S. (Fig. 7.19). Midwestern croplands also have a strong positive NEP (negative NEE) during summer. In general, these seasonal variations in NEP are driven more strongly by GPP than by ecosystem respiration because both

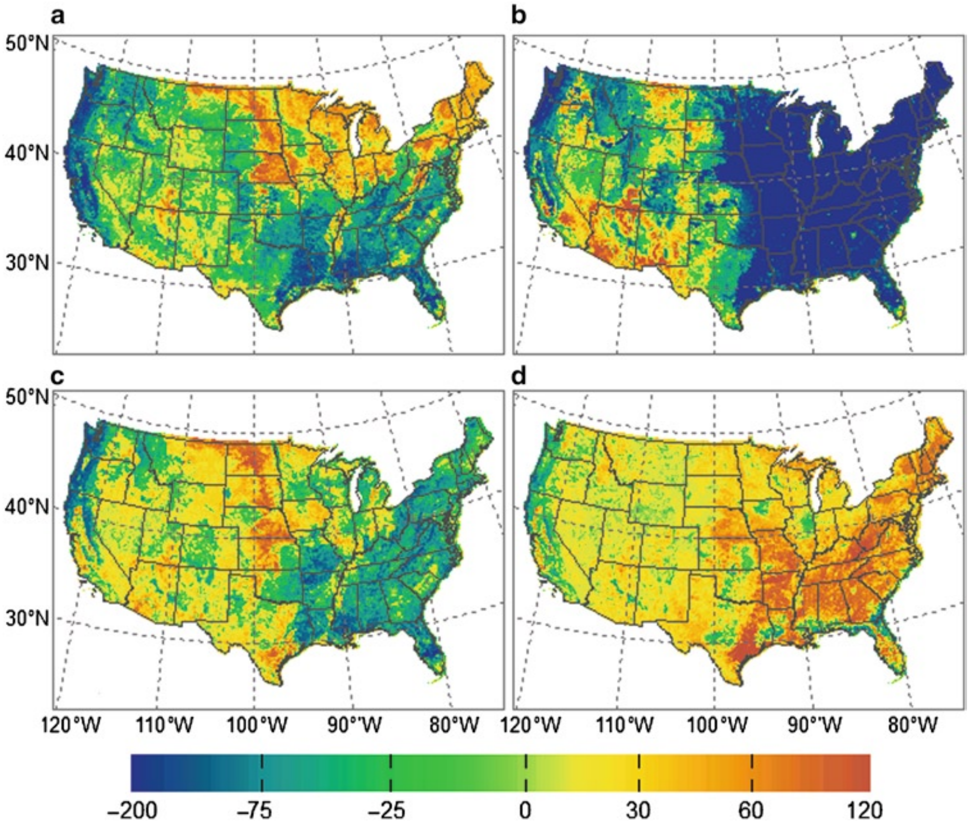

Fig. 7.19 Maps of predicted net ecosystem exchange (NEE) based on a regression model that uses AmeriFlux NEE measurements and MODIS satellite imagery during (**a**) spring (March-May), (**b**) summer (June-August), (**c**) autumn (September-November), and (**d**) winter (December-February). Redrawn from Xiao et al. (2008)

GPP and ecosystem respiration are generally highest during the growing season and GPP declines more strongly than respiration during the nongrowing season.

NEP also varies with time since disturbance. NEP is expected to decline with disturbances such as logging, hurricanes, or wildfire that reduce plant biomass and GPP (see Chap. 12). In addition, heterotrophic respiration often increases after disturbance because of transfer of aboveground biomass to the ground surface (e.g., hurricanes) or environmental changes that favor decomposition. NEP should recover as biomass and GPP increase, then approach zero as GPP comes into equilibrium with ecosystem respiration. What is surprising, however, is that NEP often remains positive, even in forests more than a century old (Fig. 7.20; Luyssaert et al. 2007). Across the U.S., all ecosystem types except

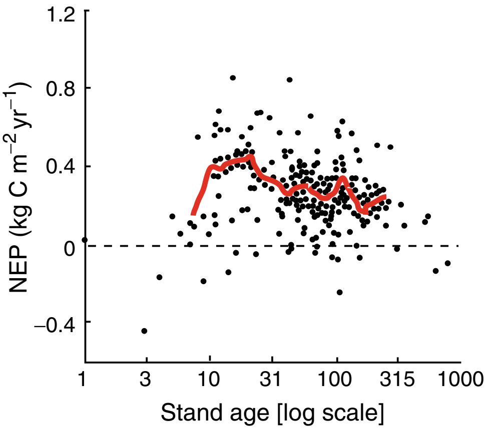

Fig. 7.20 Observed relationship of forest net ecosystem production (NEP) to stand age. Positive values indicate that the forest is a sink for carbon and negative values that it is a source. The line shows the average value of NEP ($n = 500$ forest plots). Maximum NEP occurs at about 20–30 years but usually remains positive for hundreds of years. Redrawn from Luyssaert et al. (2007)

shrublands show, on average, a positive NEP in the absence of recent disturbance (Fig. 7.19; Xiao et al. 2008), as does the terrestrial biosphere as a whole (Le Quéré et al. 2009).

There are at least four potential explanations for the generally positive NEP documented in a wide range of terrestrial ecosystems: (1) This may reflect the expected successional pattern of NEP, with ecosystems being carbon sinks for a very long time after disturbance. In other words, ecosystems may seldom reach steady state before a new disturbance occurs (Luyssaert et al. 2007; Xiao et al. 2008). (2) Recent environmental changes, such as increased atmospheric CO_2 and nitrogen deposition, may have stimulated photosynthesis and reduced respiration, leading to greater carbon sequestration (Magnani et al. 2007; de Vries et al. 2009; Liu and Greaver 2009; Janssens et al. 2010). (3) Carbon loss through leaching and other transfers may be important (but unmeasured) components of the net carbon balance from terrestrial ecosystems; these nongaseous carbon losses would not be detected in measurements of NEE, leading to potential overestimates of NEP (Kling et al. 1991; Randerson et al. 2002; Cole et al. 2007). (4) There may be unintended biases in site selection, measurements, or models (Baldocchi 2003; Sutton et al. 2008). Ecologists are vigorously debating the magnitude and relative importance of these potential explanations for a generally positive NEP measured in terrestrial ecosystems. We now explore these issues in more detail.

NEP generally follows the expected successional pattern. It declines with disturbance. Insect outbreaks, for example, reduce NEP as a result of declines in leaf area (and therefore GPP) and increases in heterotrophic respiration (Kurz et al. 2008). As vegetation recovers, GPP increases more strongly than respiration, leading to increased NEP (Fig. 7.20; see Fig. 12.13). After about 80 years, however, NEP begins to decline as the forest ages (Magnani et al. 2007). As pointed out earlier, NEP seldom declines to zero, even in old forests (Luyssaert et al. 2007; Xiao et al. 2008). About half of the carbon accumulation in forests occurs belowground in roots and soils, and, of the aboveground portion, about two-thirds accumulates in coarse woody debris and the rest in live stems (see Chap. 6). However, even ecosystems such as arctic tundra that seldom experience large-scale disturbances and post-disturbance succession appear to have a positive NEP (McGuire et al. 2009), suggesting that successional dynamics are not the only explanation for the generally positive NEP observed on land.

Global increases in atmospheric CO_2 and nitrogen inputs to ecosystems augment NEP because they stimulate GPP more strongly than ecosystem respiration. Nitrogen deposition associated with acid rain, for example, stimulates carbon storage by about 6% in forests and 2% in agricultural fields, with no detectable change in other natural ecosystems (Sutton et al. 2008; Liu and Greaver 2009). It is more difficult to assess the effects of rising CO_2 on NEP because the CO_2 increase has been relatively uniform across the planet. Experimental studies, however, show that elevated CO_2 concentrations often stimulate NEP, especially in more fertile ecosystems or ecosystems to which nutrients have been added to simulate the effects of nitrogen deposition (McGuire et al. 1995a; Ciais et al. 2005a). Anthropogenic changes in the environment have therefore often enhanced NEP in undisturbed terrestrial ecosystems.

The effects of temporal and spatial variation in climate on NEP are not easy to predict because warm temperatures, improved soil aeration, and improved moisture availability stimulate all components of NEP: GPP, plant respiration, and microbial respiration. In southern Europe, for example, GPP and ecosystem respiration are both strongly moisture-limited. Both of these fluxes increase to a similar extent in moist years or sites, so there is no significant relationship between moisture supply and NEP (Fig. 7.21; Reichstein et al. 2007). Similarly, in northern sites, where GPP and ecosystem respiration are primarily temperature-limited, both of these fluxes increase to a similar extent in warm years and sites, so there is no significant relationship between temperature and NEP (Fig. 7.21; Luyssaert et al. 2007; Magnani et al. 2007; Reichstein et al. 2007; Piao et al. 2009). When considered together, moisture has a stronger effect on NEP than does temperature, primarily because of the strong

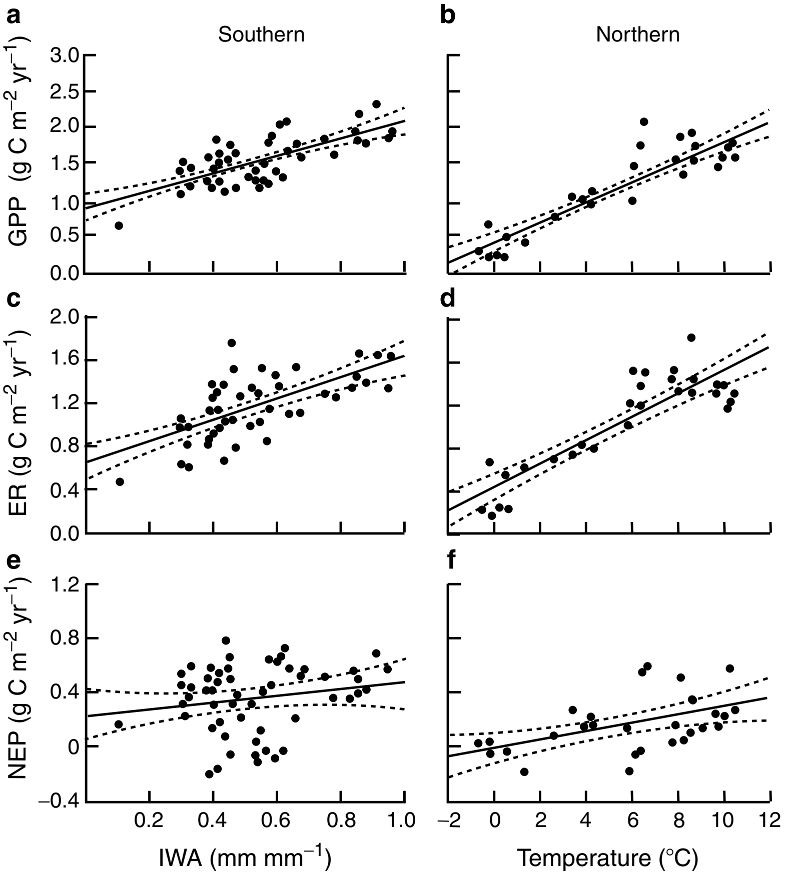

Fig. 7.21 Correlation of carbon fluxes with an index of water availability (IWA; ratio of actual to potential evapotranspiration) in southern European forests and average annual temperature in northern European forests. Fluxes shown are gross primary production (GPP; plots **a** and **b**); ecosystem respiration (ER; plots **c** and **d**); and net ecosystem production (NEP; plots **e** and **f**). The solid and dashed lines are the average and 95% confidence intervals, respectively. GPP and ER are much more strongly correlated with environmental controls than is NEP. Redrawn from Reichstein et al. (2007)

effects of drought in reducing GPP (Reichstein et al. 2007). Thus, interannual variations in climate affect NEP primarily through their effects on GPP rather than ecosystem respiration (Ciais et al. 2005a; Groendahl et al. 2007; Luyssaert et al. 2007; Reichstein et al. 2007), just as observed among seasons within a year.

Despite the modest sensitivity of NEP to variations in temperature and moisture, *changes* in climate drivers may alter NEP over the long term. The magnitude of warming over the last two decades of the twentieth century, for example, explains much of the current variation in NEP among forested sites, even though these sites show little sensitivity of NEP to current year's temperature (Piao et al. 2009). Short-term climate shocks can also have a long-term impact. A severe drought in Europe in July 2003, for example, reduced NEP enough to offset the previous 4 years of carbon sequestration (Ciais et al. 2005b). The seasonality of warming is also important. Spring warming, for example, increases GPP and NEP by advancing the date of snowmelt and the onset of plant growth and photosynthesis (Euskirchen et al. 2006; Lafleur and Humphreys 2007; Piao et al. 2008). In the autumn, however, when sun angle is lower and soils are warmer, warming increases ecosystem respiration more strongly than GPP and therefore reduces autumn NEP. For these reasons, pronounced spring warming in Eurasia leads to increased annual NEP, whereas pronounced autumn warming in North America has reduced annual NEP (Piao et al. 2008).

Changes in water table and soil aeration also cause complex changes in NEP. Drainage of waterlogged peatlands initially reduces NEP because GPP declines (Chivers et al. 2009) and in some cases, heterotrophic respiration increases (Silvola et al. 1996). Over the longer term, invasion of more productive non-peatland species enhance leaf area and GPP, often leading to positive NEP (carbon sequestration; Minkkinen et al. 2002; Laiho et al. 2003). Thawing of permafrost in response to recent climate warming causes ecosystem respiration to increase more strongly than GPP, causing a loss of carbon that accumulated thousands of years ago (Schuur et al. 2009). This negative NEP could become a strong amplifying (positive) feedback to climate warming, given that there is twice as much carbon in the permafrost as in the atmosphere (Zimov et al. 2006; Schuur et al. 2008).

In summary, natural post-disturbance successional processes, climate variations, and human impacts on the atmosphere all influence NEP, primarily through their effects on GPP. Current evidence suggests that human activities substantially influence these controls over the NEP of the biosphere. These effects are exerted through disturbance and land cover change, which can either increase or reduce NEP; nitrogen deposition and increased atmospheric CO_2, which generally increase NEP; and anthropogenic climate warming, which has variable effects on NEP. The net effect of changes in NEP on the climate system and the biosphere depends on the overall changes in ecosystem carbon stocks, as explained in the next section.

Net Ecosystem Carbon Balance

Net ecosystem carbon balance (NECB) is the net rate of carbon accumulation by an ecosystem. It is the balance between carbon entering and leaving the ecosystem, that is, the change in ecosystem carbon stock through time:

$$NECB = \frac{dC}{dt} \tag{7.9}$$

To understand NECB, it is useful to visualize the ecosystem as a defined volume with explicit top, bottom, and sides (Fig. 7.22; Chapin et al. 2006a). The top of this ecosystem "box" in terrestrial ecosystems is above the canopy, the bottom is below the rooting zone, and the sides define the area to be analyzed. Most carbon enters the ecosystem as gross primary production (GPP) and leaves through several processes, including plant and heterotrophic respiration, leaching of DOC and DIC, emissions of volatile organic compounds, methane flux, and disturbance. Lateral transfers such as erosion/deposition, animal movements, or harvest can bring additional carbon into or out of the ecosystem (Fig. 7.22). NECB is the increase (positive value) or loss (negative value) in the quantity of carbon in this ecosystem box.

$$NECB = (gaseous\ inputs - losses) + (dissolved\ inputs - losses) + (particulate\ inputs - losses) \tag{7.10}$$

$$NECB = (-NEE + F_{CO} + F_{CH4} + F_{VOC}) + (F_{DIC} + F_{DOC}) + F_{POC} \tag{7.11}$$

Gaseous Carbon Fluxes

GPP and ecosystem respiration are the dominant gaseous carbon fluxes most of the time. However, wildfire is an additional large episodic cause of CO_2 loss from some ecosystems, and CH_4 and CO fluxes are additional climatically important gaseous emissions. Combustion of organic matter by wildfire is a non-respiratory loss of CO_2 from ecosystems to

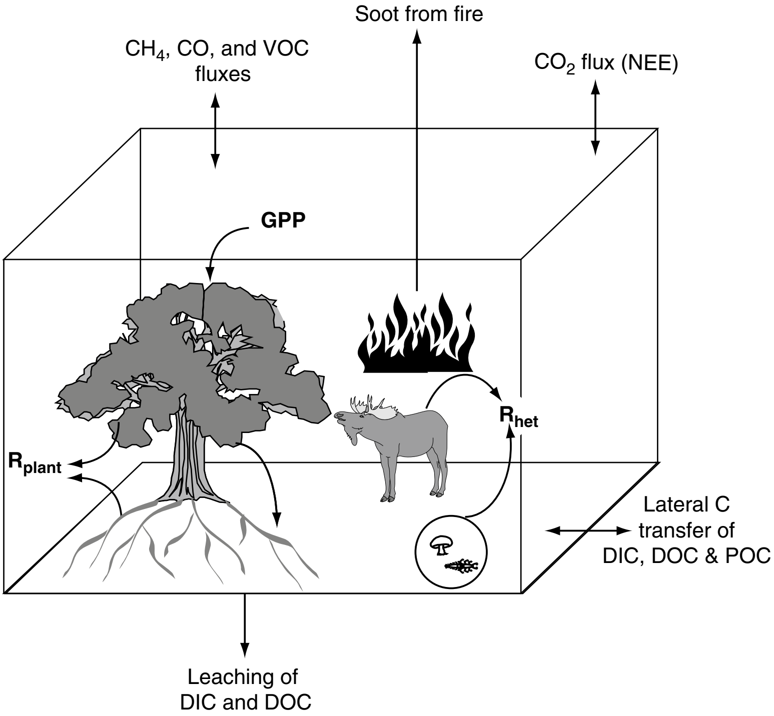

Fig. 7.22 Major components of net ecosystem carbon balance (NECB). The fluxes that determine net ecosystem production (NEP) are shown in bold. The box represents the ecosystem. Fluxes contributing to NECB and NEP are defined in the text. Redrawn from Chapin et al. (2006a)

the atmosphere. Wildfire is therefore an important component of NEE and NECB whenever it occurs, particularly when NEE and NECB are integrated over timescales long enough to incorporate disturbance. Wildfire is *not* a component of NEP (i.e., the balance of GPP and respiration). In many cases, the carbon losses with wildfire are significant components of long-term carbon budgets (Figs. 7.22 and 7.23). Carbon losses during fires in the Canadian boreal forest, for example, are equivalent to about 6–30% of average NPP (Harden et al. 2000; McGuire et al. 2010). Because of their sensitivity to successional status, NECB and NEE estimated at the regional scale depend on the relative abundance of stands of different ages. At times of increasing disturbance frequency, NECB is likely to be negative, as with recent increases in wildfire in western North America. Conversely, areas that have experienced widespread abandonment of agricultural lands in the last century, as in Europe or the northeastern U.S., may experience a positive NECB. Inadequate information on the regional variation in disturbance frequency and NECB is one of the greatest sources of uncertainty in explaining recent changes in the global carbon cycle (see Chap. 14).

Non-CO$_2$ gaseous fluxes can be large components of NECB in ecosystems where net CO$_2$ flux is small. In permafrost- and ice-dominated portions of the northern hemisphere (arctic and boreal lands and the Arctic Ocean), for example, the land and ocean are modest carbon sinks. Large methane emissions from wetlands cause the region to exert a positive greenhouse-gas warming effect on climate (McGuire et al. 2009; McGuire et al. 2010). In addition, the emissions of carbon monoxide from wildfires (47 Tg C year^{-1}) and methane from wetlands and wildfires (31 Tg C year^{-1}) are similar in magnitude to the net sequestration of CO$_2$ (51 Tg C year^{-1}), indicating the importance of multiple gases in regional carbon balance (McGuire et al. 2010).

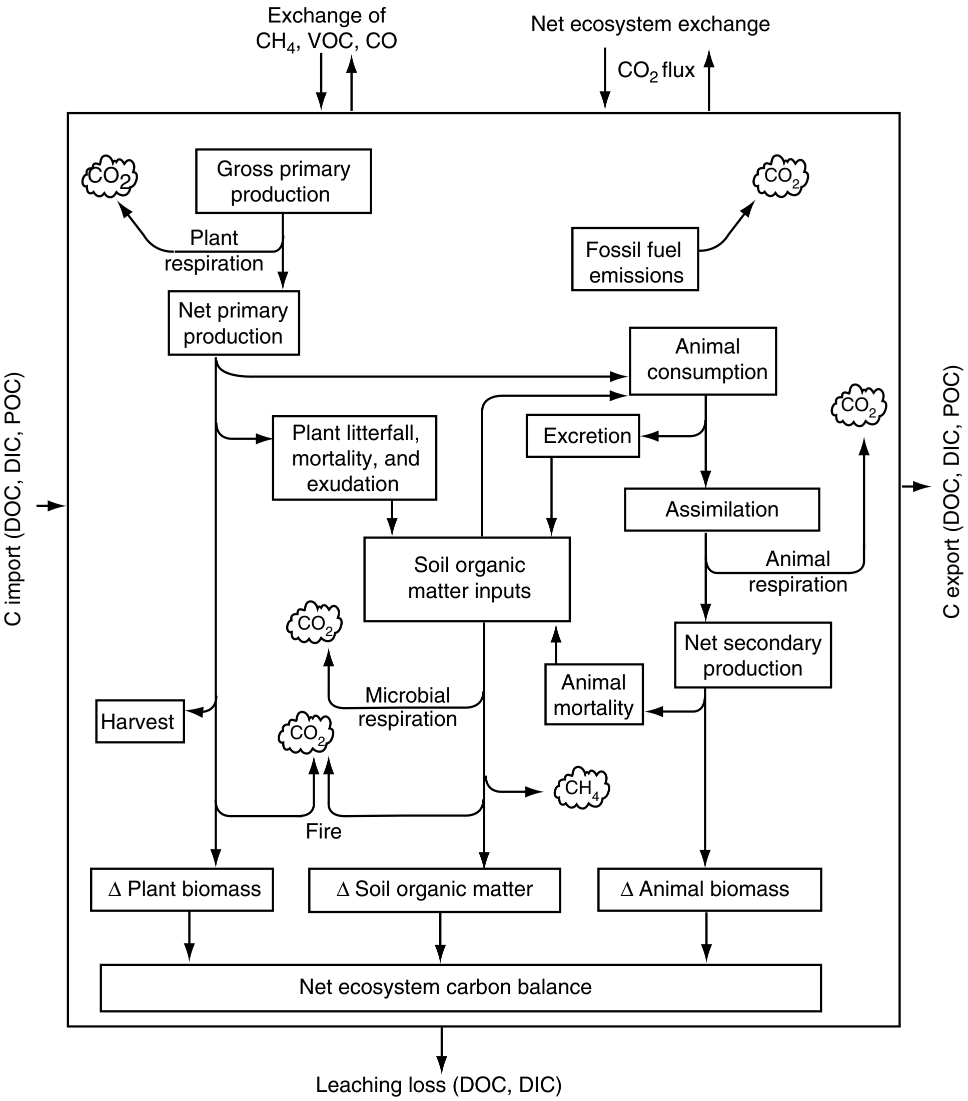

Fig. 7.23 Overview of the carbon fluxes of an ecosystem. The large box represents the ecosystem, which exchanges carbon with the atmosphere, other ecosystems, and groundwater

Disturbances that redistribute carbon within the ecosystem affect NECB only indirectly **because the carbon remains within the ecosystem**. Hurricanes or insect outbreaks, for example, transfer carbon from live plants to soil or to standing dead plants without the carbon being lost from the ecosystem. These disturbances can *indirectly* affect NECB, however, by reducing photosynthetic capacity and increasing the food available to decomposers. In other words, these changes in carbon balance affect NECB through their effects on NEP (= GPP – ecosystem respiration).

Fossil fuel combustion by people is an increasing source of CO_2 to the atmosphere. It is a large carbon flux in industrial agriculture and in many ecosystems such as towns and cities that are occupied by people (see Chap. 14). Fossil-fuel combustion represents a transfer from previously inert geological pools of organic carbon (coal, oil, and natural gas) to the atmosphere.

Particulate Carbon Fluxes

Lateral transfer of particulate carbon into or out of ecosystems can be important to the long-term carbon budgets of ecosystems. Carbon can move laterally into or out of ecosystems through erosion and deposition by wind or water or by movement of animals, including people (Figs. 7.22 and 7.23). In many ecosystems, these lateral transfers are so small that they are undetectable in most years. Over long time periods or during extreme events, such as floods, landslides, or forest harvest, lateral transfers can, however, be quantitatively important. Observations of NEE of Europe, for example, could not be explained based on measured ecosystem fluxes without accounting for food imports from other countries (Ciais et al. 2008). Similarly, within the crop-producing states of the Midwestern U.S., the eastern-most states export most of their crops and are a net CO_2 sink, whereas the western-most states feed these crops to animals, which respire the carbon to the atmosphere, causing little net carbon sequestration (Schuh et al. 2010). Lateral transfers of carbon-containing biomass are significant components of NECB in managed forests, agricultural and grazing ecosystems, and other human-modified ecosystems, which now occupy much of the terrestrial surface (Ellis and Ramankutty 2008).

Dissolved Carbon Fluxes

Leaching of dissolved organic and inorganic carbon (DOC and DIC, respectively) to groundwater and streams is a quantitatively important avenue of carbon loss from some ecosystems (Figs. 7.22 and 7.23). We discuss these in the next section in the context of the carbon balance of streams and rivers.

In summary, fluxes in addition to GPP and ecosystem respiration are important fluxes in most ecosystems, especially over long time periods. Therefore, changes in NEP and NEE tell only part of the story about changes in the carbon balance of terrestrial ecosystems.

Stream Carbon Fluxes

Stream Decomposition

The horizontal flow of carbon in streams is similar to its vertical movement through the soil on land but occurs over much larger distances. The basic steps in decomposition are identical on land and in aquatic ecosystems (Valiela 1995; Wagener et al. 1998; Gessner et al. 2010). These steps include leaching of soluble materials from detritus (up to 25% of initial dry mass in 24 h), fragmentation of litter into small particles by invertebrates and physical processes, and microbial decomposition of labile and recalcitrant substrates (Allan and Castillo 2007). On land, these processes begin at the soil surface, and organic matter moves downward in the soil profile due to mixing by soil invertebrates, burial by new litter, downward leaching, and other processes (Wagener et al. 1998). In stream ecosystems, the same processes occur, but cycling materials are also carried downstream tens of kilometers in the process. Energy and nutrients therefore **spiral** down streams, rather than cycling vertically as they tend to do in most terrestrial ecosystems (Fisher et al. 1998).

In forest headwater streams, the dominant energy input is terrestrial detritus that enters as **coarse particulate organic matter** (CPOM; particles >1 mm) such as leaves and wood (Fig. 7.24). Low light availability limits algal production in these streams (see Chap. 6). The controls over the processing of CPOM are remarkably similar to those that occur on land. Fine litter that enters the stream becomes lodged behind rocks or coarse woody debris, is leached by flowing water and colonized by invertebrates that fragment and ingest small particles, increasing the surface area for microbial colonization (Fig. 7.25). The leaching of **dissolved organic carbon** (DOC; particles <0.5 μm) and export of **fine particulate organic matter** (FPOM; particles >0.5 μm and <1 mm) from leaf packs in the stream leads to an exponential pattern of mass loss with time (Eq. 7.1), just as on land (Allan and Castillo 2007). Decomposition in

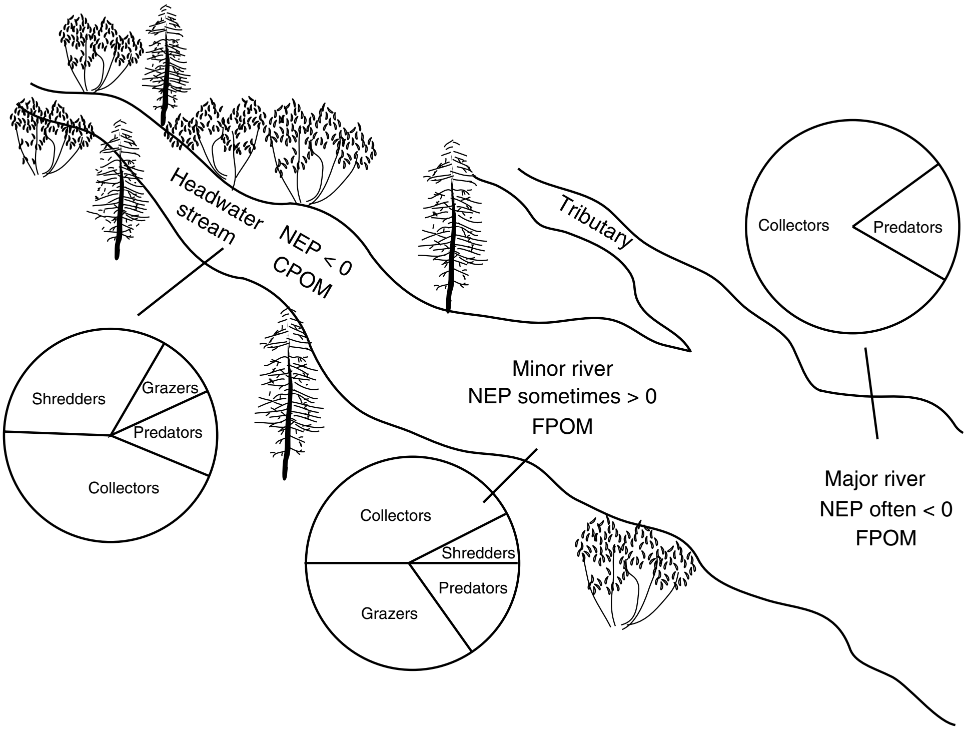

Fig. 7.24 The river continuum concept of a representative river system. Headwater streams have little instream GPP and high heterotrophic respiration, so NEP is negative. Coarse particulate organic matter (CPOM) dominates the detrital pool. Shredders and filter feeders (collectors) are the dominant invertebrates. In middle sections of rivers, more light is available, and GPP sometimes exceeds ecosystem respiration (NEP sometimes positive). Fine particulate organic matter (FPOM) is the dominant form of organic matter, and filter feeders and grazers are the dominant organisms. Large rivers accumulate considerable organic-rich sediments dominated by filter feeders feeding on FPOM from upstream. Ecosystem respiration often exceeds GPP (NEP often negative). Ecosystem respiration generally exceeds GPP (NEP negative) for entire river systems. Based on Vannote et al. (1980)

streams is more rapid than on land because water never limits microbial activity, and fine particles are swept downstream. Most fine (nonwoody) litter in temperate streams loses half its mass in less than a year (Webster and Benfield 1986), whereas it takes more than a year in corresponding terrestrial environments (Fig. 7.6). Stream decomposers are aquatic specialists rather than organisms that enter the streams on the leaves.

Fungi are the dominant decomposers in flowing water, and bacteria dominate in poorly aerated stream sediments (Allan and Castillo 2007). Fungi can either enhance bacterial activity (Gulis and Suberkropp 2003) or compete with bacteria (Wright and Covich 2005; Allan and Castillo 2007). The stimulatory effects of invertebrates on microbial decomposition of litter and the chemical effects of litter quality on decomposition in streams (Allan and Castillo 2007) are virtually identical to the patterns described earlier for terrestrial ecosystems (Gessner et al. 2010).

FPOM comes primarily from within the stream through the processing of CPOM into small particles and feces by invertebrates, release of asexual spores by aquatic fungi, the abrasion of periphyton from rocks, the absorption of DOC by microbes, and other processes. About a third of the leaf material consumed by shredders, for example, is released into the stream as FPOM (Giller and Malmqvist 1998). Stream invertebrates assimilate a relatively small proportion (10–20%) of the organic matter that they ingest (see Chap. 10), resulting in a substantial production of feces. FPOM is generally more recalcitrant than CPOM

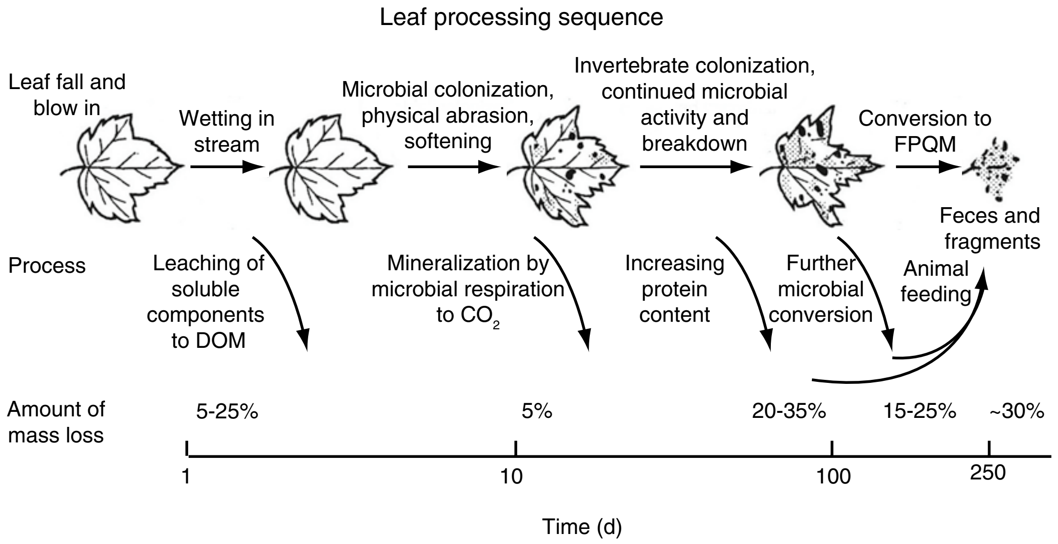

Fig. 7.25 Processes that "condition" a leaf of moderate litter quality in a temperate stream. Redrawn from Allan and Castillo (2007)

because organisms have already removed the labile substrates (Allan and Castillo 2007). In fact, most FPOM appears to be produced by stream organisms rather than being fine particles of terrestrial origin (e.g., leaf fragments). Bacteria are the dominant decomposers of FPOM (Findlay et al. 2002; Allan and Castillo 2007).

DOC is the largest pool of organic carbon in most streams (Karlsson et al. 2005; Allan and Castillo 2007). It derives from both instream processes, such as leaching of fresh litter and excretion by algae, higher plants, and microbes, and as inputs from terrestrial wetlands and riparian areas. Stream DOC contains a diversity of compounds that vary widely in decomposability. Labile DOC is an important energy source for decomposers and higher trophic levels (Allan and Castillo 2007). During spring algal blooms, for example, stream DOC increases by as much as 37% during the day as a result of algal exudation (Kaplan and Bott 1989; Allan and Castillo 2007). Annual pulses of DOC often come from leaching of fish carcasses and autumn leaves. DOC is removed from the stream primarily by microbial absorption but also by abiotic processes such as photo-oxidation and binding to clay particles (Allan and Castillo 2007). Periphyton, the biofilm mixtures of algae and bacteria that create the slimy films on rocks, wood, and macrophytes, appear particularly important in the efficient transfer of algal DOC to bacterial decomposers. In tropical blackwater rivers and boreal peatlands, much of the DOC is tannins and recalcitrant humic and fulvic acids leached from soils. These compounds are processed slowly in streams.

Rivers and streams have a belowground component analogous to terrestrial soils. In the **hyporheic zone**, groundwater moves downstream within the streambed. Substantial decomposition occurs in the hyporheic zone, releasing nutrients that support instream algal production. In intermittent streams, the hyporheic zone is all that remains of the stream during dry periods. Water moves more slowly and therefore has a shorter processing length in the hyporheic zone than in the stream channel, so the spiraling length is much shorter (Fisher et al. 1998).

Stream Carbon Budgets

There is a continuum in stream metabolism from headwaters to the ocean. Stream ecosystems differ dramatically from their terrestrial counterparts in the importance of *lateral linkages* of biogeochemical processes as materials spiral downstream. The **river continuum concept** integrates stream size, energy sources, food webs, and nutrient processing into a longitudinal model of river metabolism from headwaters to the ocean (Fig. 7.24; Vannote et al. 1980). Detrital food webs and heterotrophic processing of energy dominate many headwater streams, particularly in forests, because large terrestrial inputs of litter provide lots of food for microbes, and low light availability limits algal production. These headwater streams therefore have a negative NEP (GPP < ecosystem respiration) and export considerable organic material downstream (Webster and Meyer 1997; Mulholland et al. 2001; Allan and Castillo 2007). Even unshaded headwater streams of tundra, boreal forest, and wetlands are generally heterotrophic because of large inputs of terrestrial organic matter and nutrient limitation of algal production (Peterson et al. 1986). Most headwater streams are dominated by invertebrate **shredders** that break leaves and other detritus into pieces and digest the microbial jam on the surface of these particles, just as occurs in the soil (Wagener et al. 1998). This creates fresh surfaces for microbial attack and produces feces and other fine material that are carried downstream. Desert streams are a major exception to the heterotrophic dominance of headwater streams. Streams in arid environments receive very little litter input or shade and are therefore dominated by algal production and have a positive NEP (GPP > ecosystem respiration; Fisher et al. 1982; Jones et al. 1997).

Downstream, where rivers are wide enough to receive substantial light input, GPP is greater than in headwaters (see Chap. 6), but heterotrophic respiration still generally dominates (negative NEP; Webster and Meyer 1997), depending on light availability, water clarity, and water depth, which influence GPP, and on detrital inputs from upstream (FPOM) or adjacent riverbanks, which influence ecosystem respiration (Howarth et al. 1996b). Some of the fine particles are consumed in suspension by filter feeders like black fly larvae or from benthic sediments by **collectors** like oligochaete worms. The abundance of algae and their **grazers** depends on light availability. Finally, large rivers in their deposition zone have sediments that support substantial hyporheic decomposition. These rivers also support both algal production and bacterial decomposition in the water column if these organisms can reproduce fast enough to offset their downstream export. The shallow gradient and low current velocity in some channels in the deposition zone often allow this to occur (Allan and Castillo 2007). In those rivers where suspended sediments and low water clarity limit algal production, detrital processing tends to dominate (negative NEP; GPP < ecosystem respiration).

Rivers and streams are highly pulsed systems, leading to large temporal fluctuations in carbon metabolism. Seasonal pulses of litterfall cause large seasonal variation in organic matter inputs to streams, just as on land. Snowmelt or heavy rains increase runoff through surface litter and increase the suspension and transport of terrestrial organic and mineral particles, substantially increasing the transfer of organic matter and sediments to streams. In many headwater streams, storm events that account for 1% of the annual discharge transport 70–80% of the annual FPOM throughput of streams (Bilby and Likens 1980; Webster et al. 1990; Allan and Castillo 2007). Finally, flood events dislodge primary producers and transport sediments, woody debris, and other organic matter downstream. Since algal biomass is a strong determinant of GPP and NPP (see Chap. 6), floods constrain the potential of streams to support GPP and a positive NEP. In large unregulated rivers such as the Amazon, flooding converts much of the floodplain from a terrestrial to an aquatic habitat, and 70–90% of the annual carbon inputs to the system come from floodplain inputs during flooding (Bayley 1989; Meyer and Edwards 1990; Lewis et al. 2001; Allan and Castillo 2007). Within a given climatic regime, disturbances that radically reduce primary producer biomass tend to occur much more often in streams than on land. This contributes to the dominance of heterotrophic processes in stream and river ecosystems.

The carbon metabolism of a stream segment (**reach**) is strongly influenced by the site itself (e.g., shade, temperature, and inputs of terrestrial litter) and by upstream processes. Organic matter in rivers typically travels 10–100 km (its **turnover length**) before it is broken down and lost by respiration (Allan and Castillo 2007; Webster 2007). Because heterotrophic headwater streams account for about 85% of the total length of most river systems (Peterson et al. 2001), export of dissolved and particulate carbon from headwater streams has a huge effect on the metabolism of the entire river system.

Taken as a whole, river systems are generally heterotrophic, that is, have a negative NEP (GPP < ecosystem respiration; Cole et al. 2007). This differs strikingly from the generally positive NEP (GPP > ecosystem respiration) of most terrestrial ecosystems. This fundamental difference in carbon metabolism reflects the important role in landscape metabolism of carbon transfer from terrestrial to aquatic systems (see Chap. 13). Clearly, some of terrestrial NEP does not represent carbon sequestered on land but is transferred to aquatic systems where it returns to the atmosphere as CO_2, is stored in sediments of lakes and reservoirs, or is transported to the ocean (Cole et al. 2007).

The terrestrial-to-aquatic carbon transfer has two important components. The first is the transfer of particulate and DOC that supports aquatic heterotrophic respiration, as described earlier. In addition, groundwater that enters streams has extremely high CO_2 concentrations, about 75% of which comes from root and microbial respiration in soils, and 25% from weathering of rocks (Schlesinger 1997; Cole et al. 2007). About 20% of the carbon that appears to be sequestered on land (i.e., positive NEP) moves as DIC (dissolved inorganic carbon [DIC]) to aquatic systems, where it is degassed and returns to the atmosphere (Kling et al. 1991; Algesten et al. 2003; Kortelainen et al. 2006; Cole et al. 2007). In other words, much of the CO_2 release from aquatic ecosystems actually derives from terrestrial respiration, and much of the positive NEP (negative NEE) on land does *not* contribute to terrestrial carbon accumulation (positive NECB).

Of the carbon that enters aquatic systems from the land (as dissolved CO_2 and dead organic matter), about 40% returns to the atmosphere as CO_2, 12% is stored in sediments of lakes and reservoirs, and the remainder (about half) is transported to the ocean, roughly equally as organic and inorganic carbon (Cole et al. 2007).

Lake Carbon Fluxes

Decomposition in lakes is faster than in streams or on land because of the high litter quality of algae. Lignin, which is important for structural support of land plants and which contributes to slow decomposition of terrestrial litter, is not needed in lakes, where primary producers (algae) float in the water or are attached to the bottom. In addition, as in streams, moisture never limits decomposition in lakes. Decomposition in lakes is therefore more rapid than on land, and 70–85% of the decomposition in lakes occurs in the water column before dead organic matter sinks to the sediments (Kalff 2002). An intermediate-sized dead algal cell (nanoplankton of 10 μm diameter) would sink at a rate of about 0.25 $m\,day^{-1}$ and would require 40 days to sink 10 m (Baines and Pace 1994; Kalff 2002). Since the mixing time of water is on the order of half an hour in the mixed layer, a year in bottom waters, and 3 months in the intermediate **metalimnion** (see Fig. 2.21), most detrital particles are repeatedly mixed back into the water column where decomposition continues before they can sink to depth. The only reason that particles can sink in such a turbulent environment is that there is a gradual transition from turbulent flow in the mixed layer to laminar flow at the base of the mixed layer to very little flow at depth. The loss rate of particles from the mixed layer to the metalimnion depends on particle abundance (a function of productivity) and sinking rate of particles just above this boundary layer (Kalff 2002). In lakes with a thin mixed layer (i.e., lakes that are small, protected from wind, or highly stratified), a larger proportion of detrital particles enter the boundary between mixed layer and the nonturbulent waters below and are therefore likely to sink to the bottom. Decomposition continues as particles sink through deeper waters, so the quantity of "lake snow" that reaches the sediments and sediment organic content are lower in deep than in shallow lakes. In summary, lake decomposition is strongly influenced by lake physical properties such as turbulence, stratification, and lake depth. Dead organic matter flux to lake sediments is greatest in lakes that are eutrophic, small, shallow, and protected from winds.

Large particles that are likely to sink out of the mixed layer of lakes derive from large algae, fecal pellets of zooplankton, and the aggregation and flocculation of detrital materials. Large algae dominate in eutrophic lakes and in lakes with abundant zooplankton that consume small algal cells. Large algae tend to be less edible than small algae and are therefore more likely to die before being eaten. Fecal pellets of zooplankton are relatively dense and can sink >100 $m\,day^{-1}$, 400 times faster than an intermediate-sized dead algal cell. Aggregation of dissolved organic matter to particles also influences both its decomposition rate and its probability of sinking out of the mixed layer. Aggregation occurs because organic compounds with their charged groups (e.g., carboxyl and amine groups) interact directly or through cation bridges and are often stabilized by bacterial secretions, just as in soils (see Chap. 3). Aggregation speeds decomposition because it increases the encounter rate between bacteria and their substrate. In small lakes, as much as half the organic matter that enters sediments comes from terrestrial inputs from streams or from the littoral zone rather than from algal production (Kalff 2002).

Grazing influences lake decomposition in complex ways. First grazing "competes" with decomposition by consuming algal cells before they die. Lakes differ dramatically from terrestrial ecosystems in that more energy goes through grazing than through detrital pathways (see Chap. 10). Second, by producing dense fecal pellets and by eating small edible algae, grazers increase the size and sinking rate of dead organic matter and therefore the probability of dead organic matter reaching the sediments. Finally, detrital and plant-based trophic systems are tightly intertwined in pelagic food webs because most grazers select food based more strongly on size than on quality and therefore do not strongly differentiate among live algal cells, dead algal cells, and organic aggregates of appropriate size (see Chap. 10). Grazers therefore contribute directly to the decomposition of dead organic matter in lakes.

About 15–30% of lake decomposition occurs in the sediments. Sediment decomposition is particularly important in lakes that are eutrophic, shallow, or small. Here the controls over decomposition are similar to those in wetland soils and are strongly influenced by oxygen availability. In poorly oxygenated sediments, redox reactions determine the pathway of energy release and whether the product of decomposition is CO_2 or CH_4. In oxygenated sediments, most decomposition occurs aerobically, and mollusks and worms exert important controls over sediment aeration and therefore decomposition, as in coastal ocean sediments.

Transfer of organic matter from the water column to sediments is not a one-way path. Sediment resuspension can return a substantial proportion of surface sediments, particularly recently deposited, loosely consolidated organic matter, to the water column. Turbulence usually drives sediment resuspension and is greatest in shallow waters (e.g., <15 m depth; Kalff 2002). Resuspension is greatest during storms, when water turbulence is high, and during periods of weak stratification, when the mixing depth is greatest. Thus many temperate lakes often experience spring and autumn peaks in resuspension. Development of algal mats and littoral macrophyte beds reduce the magnitude of resuspension.

Sediment resuspension influences not only the interaction between the water column and sediments but also the lateral movement of sediments within the lake basin. Shallow sediments are often resuspended, removing fine particles and leaving behind coarse sediments that facilitate oxygen diffusion. Over the long term, sediments move from shallow depths either to deeper portions of the lake or to littoral macrophyte beds where vascular plants and algal mats stabilize the sediments. The boundary between zones of net resuspension of sediments and net accumulation depends on the turbulence dynamics of the lake (and therefore on size, depth, stratification, and protection from wind). This transition can occur at <3 m in shallow wind-protected lakes with a gradual underwater slope to >40 m in large deep lakes with steep slopes. Sediment accumulation zones are the major locations of carbon storage in lakes.

Lakes are the main sites of carbon sequestration in freshwater ecosystems. On average, about 12% of the terrestrial carbon that enters freshwater systems is deposited in lake sediments (Cole et al. 2007). Reservoirs are particularly important sites of carbon sequestration because former terrestrial soils are suddenly placed in a low-oxygen environment that reduces decomposition rate and favors carbon release as CH_4, a powerful greenhouse gas, rather than as CO_2. In addition, reservoirs are more effective than natural lakes in trapping organic particles that enter from rivers, due to low resuspension rates and long water residence times. Consequently, reservoirs currently bury more carbon than all natural lakes combined and 1.5-fold more carbon than is exported to ocean sediments (Dean and Gorham 1998, Cole et al. 2007). Similarly, sediment delivery from land to the ocean has declined, despite increased sediment delivery to rivers because of sediment capture by reservoirs (see Chap. 3; Syvitski et al. 2005). This illustrates ways in which human activities can inadvertently alter the carbon dynamics and geomorphic processes of landscapes to a degree that, in their aggregate, are important at global scales.

Ocean Carbon Fluxes

Patterns of ocean decomposition are qualitatively similar to those in lakes. This decomposition occurs relatively quickly because the carbon substrates are mostly labile organic compounds of low molecular weight (Fenchel 1994) in contrast to the structurally complex, carbon-rich compounds (cellulose, lignin, phenols, tannins) that dominate terrestrial detritus. Marine decomposition is characterized by rapid leaching of dead cells followed by chemical transformation. This is identical to the decomposition of terrestrial litter, except that the initial "litter" (dead cells) is so small that no invertebrate fragmentation occurs. The chemical controls over decomposition are also very similar to those observed on land (Valiela 1995). Viruses play an important role in planktonic food webs, lysing both phytoplankton and bacteria. Viral lysis may account for 5–25% of bacterial mortality in pelagic ecosystems (Valiela 1995). Dissolved organic matter that is excreted by phytoplankton (about 10% of NPP) or released by lysis of phytoplankton and bacteria or during grazing tends to aggregate into particles that are colonized by bacteria (Valiela 1995), just as in lakes. Pelagic phytoplankton, bacteria, viruses, and particulate dead organic matter are grazed by small (nanoplankton) flagellate protozoans, which in turn are fed upon by larger zooplankton. The detritus-based food web (see Chap. 10) is therefore tightly interwoven with the phytoplankton-based trophic system in pelagic food webs and contributes substantially to the energy and nutrients that support marine fisheries. This **microbial loop** in pelagic ecosystems recycles most of the carbon (80–95%) and nutrients within the euphotic zone before being lost to depth (Fig. 7.26).

Pelagic carbon cycling pumps carbon and nutrients from the ocean surface to depth (Fig. 7.26). Although most of the planktonic carbon acquired through photosynthesis returns to the environment in respiration, just as in terrestrial and freshwater ecosystems, marine pelagic ecosystems also transport 5–20% of the carbon fixed in the euphotic zone into the deeper ocean (Valiela 1995), a somewhat smaller proportion than occurs in most lakes. This process is called the **biological pump**. The carbon flux to depth correlates closely with primary production, so the environmental controls over NPP largely determine the rate of carbon export to the deep ocean. This carbon export consists of particulate dead organic matter (feces and dead cells) and the carbonate exoskeletons that provide structural rigidity to many marine organisms. Carbonate accounts for about 25% of the biotically fixed carbon that rains out of the euphotic zone (Howarth et al. 1996b). The carbonates redissolve under pressure as they sink to depth. Only relatively large particles sink fast enough to reach the sediments before being mostly decomposed.

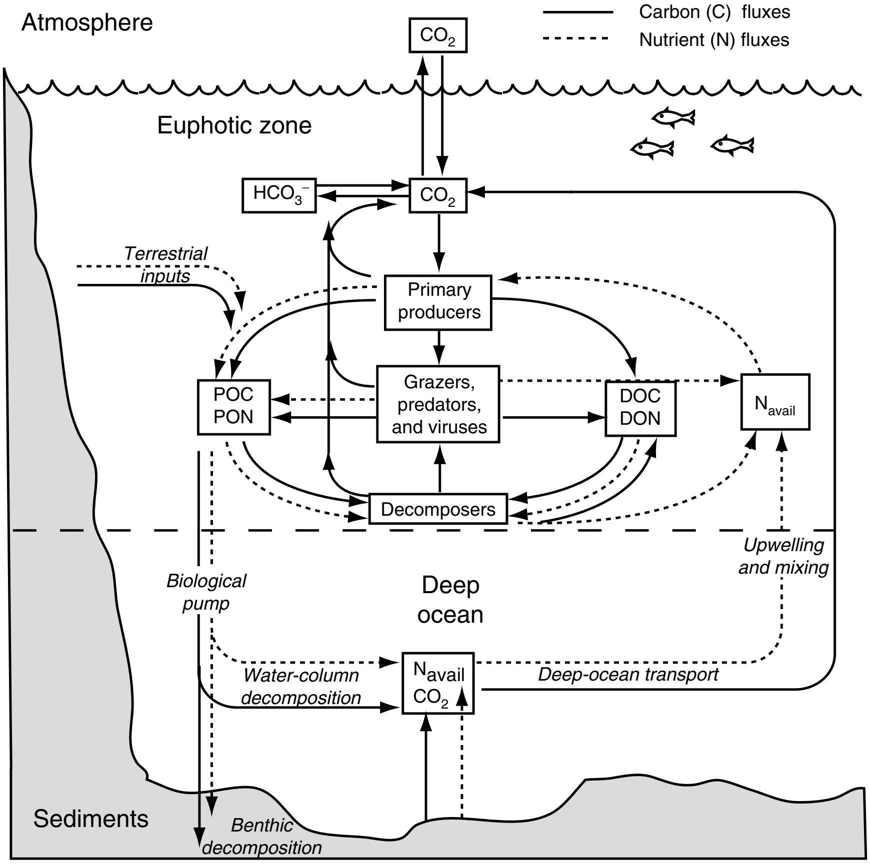

Fig. 7.26 Major pools and net fluxes of carbon (C) and nutrients (N) in the ocean. CO_2 in the euphotic zone equilibrates with bicarbonate (HCO_3^-) in ocean water and with CO_2 in the atmosphere. CO_2 is depleted by photosynthesis by primary producers and is replenished by respiration of organisms and by upwelling and mixing from depth. Grazers consume primary producers and bacteria and are eaten by other animals and lysed by viruses. Each of these organisms releases dissolved and particulate forms of carbon and nutrients (DOC, DON; POC, PON). Animals and decomposers also release available nutrients (N_{avail}). DOC is consumed by bacteria, and available nutrients are absorbed by primary producers. Particulate carbon and nutrients produced by feces and dead organisms sink from the euphotic zone toward the sediments; as they sink, they decompose, releasing CO_2 and available nutrients. Benthic decomposition also releases CO_2 and available nutrients. Bottom waters, which are relatively rich in CO_2 and available nutrients, eventually return to the surface through mixing and upwelling; this augments the supply of available nutrients in the euphotic zone

Over decades to centuries, some of this carbon in deep waters recirculates to the surface through upwelling and mixing. This long-term circulation pattern will cause the impacts of the current increase in atmospheric CO_2 to affect marine biogeochemistry for centuries after its impacts are felt in terrestrial ecosystems. The net effect of the biological pump is to move carbon from the atmosphere to the deep waters and to ocean sediments. Carbon accumulation in mid-ocean sediments is slow (about 0.01% of NPP) because most decomposition occurs in the water column before organic matter reaches the sediments and because these well-oxygenated sediments support decomposition of much of the remaining carbon (Valiela 1995).

The biological pump that transports carbon to depth carries with it the nutrients contained in dead organic matter. The rapid (about weekly) turnover of carbon and nutrients in phytoplankton in the euphotic zone (Falkowski et al. 1998) makes these nutrients vulnerable to loss from the ecosystem and contributes to the relatively open nutrient cycles of pelagic ecosystems. The longer-lived and larger primary producers on land can store and internally recycle nutrients for years. This reduces the proportion of nutrients that are annually cycled and contributes to the tightness of terrestrial nutrient cycles.

Benthic decomposition is more important in estuaries and continental shelves than in the deep ocean because the coastal pelagic system is more productive, generating more detritus, and receives terrestrial organic matter inputs from rivers. In addition, the dead organic matter has less time to decompose before it reaches the sediments. Here oxygen consumption by decomposers depletes the oxygen enough that decomposition becomes oxygen-limited, and organic matter accumulates or becomes a carbon source for anaerobic decomposers such as sulfate reducers, methanogens, and denitrifiers, just as described for terrestrial wetlands. Filter-feeding benthic invertebrates that feed by irrigating their burrows facilitate aerobic decomposition by creating a large surface area for oxygen exchange between the water and the anaerobic sediments. Eutrophication of rivers greatly stimulates the productivity of many estuaries and increases the rain of dead organic matter to the sediments. This augments the oxygen depletion by benthic decomposers, creating dead zones that no longer support fish and macroinvertebrates (see Chap. 9; Howarth et al. 2011). Two-thirds of the estuaries in the U.S. have been degraded in this fashion, and dead zones are becoming more common in estuaries and coastal zones throughout the world (Howarth et al. 2011).

Carbon Exchange at the Global Scale

Seasonal and latitudinal variations in the CO_2 concentration of the atmosphere provide a clear indication of global-scale variation of NEE (Fung et al. 1987; Keeling et al. 1996a; Piao et al. 2008). At high northern latitudes, conditions are warm during summer, and photosynthesis exceeds total respiration (positive NEP, negative NEE), causing a decline in the concentration of atmospheric CO_2 (Fig. 7.27). Conversely, in winter, when photosynthesis is reduced by low

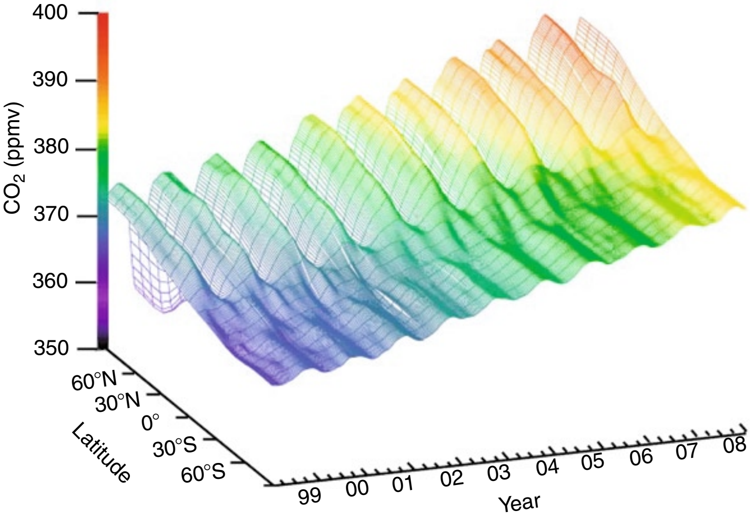

Fig. 7.27 Seasonal and latitudinal variations in the concentration of atmospheric CO_2. Seasonal and latitudinal variations in CO_2 concentration reflect primarily the balance of terrestrial photosynthesis and respiration. The upward trend in concentration across years results from anthropogenic CO_2 inputs to the atmosphere. Figure courtesy of Pieter Tans, http://www.esrl.noaa.gov/gmd/ccgg/

temperature and shedding of leaves, respiration becomes the dominant carbon exchange (positive NEE), causing an increase in atmospheric CO_2. These seasonal changes in the balance between photosynthesis and respiration occur synchronously over broad latitudinal bands, giving rise to regular annual fluctuations in atmospheric CO_2, literally the breathing of the **biosphere** (i.e., all live organisms on Earth; Fung et al. 1987).

Latitudinal variations in climate modify these patterns of annual carbon exchange. In contrast to the striking seasonality of NEE at north temperate and high latitudes, the concentration of atmospheric CO_2 remains nearly constant in the tropics because carbon gain by photosynthesis is balanced by approximately equal carbon loss by respiration throughout the year. In other words, NEP and NEE are close to zero in all seasons. Seasonal changes in atmospheric CO_2 concentration are also relatively small at high southern latitudes where the ocean occupies most of Earth's surface. Carbon exchange with the ocean is largely determined by physical factors, such as wind, temperature, and CO_2 concentration in the surface waters (see Chap. 14), which show less seasonal variation. In summary, the global patterns of variation in atmospheric CO_2 concentration provide convincing evidence that carbon exchange by terrestrial ecosystems is large in scale and sensitive to climate.

The final general pattern evident in the atmospheric CO_2 record is a gradual increase in CO_2 concentration from one year to the next (Fig. 7.27), primarily a result of fossil fuel inputs to the atmosphere that began with the industrial revolution in the nineteenth century (see Chap. 14). The rising concentration of atmospheric CO_2 is an issue of international concern because CO_2 is a greenhouse gas that contributes to climate warming (see Chap. 2). Note that the within-year variation in CO_2 concentration caused by biospheric exchange is about ten times larger than the annual CO_2 increase. If the net carbon gain by ecosystems could be increased over the long term, this might reduce the rate of climate warming. Unfortunately, the capacity of terrestrial and marine ecosystems to remove CO_2 from the atmosphere appears to be declining (Fig. 7.28), as terrestrial vegetation becomes less carbon-limited (see Chap. 5) and as CO_2 saturates the capacity of

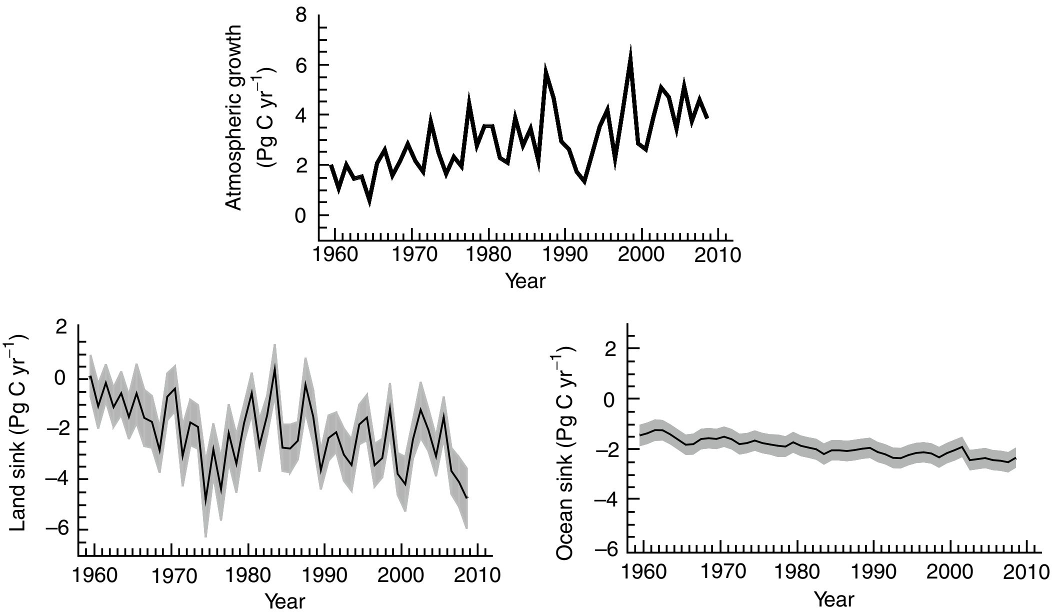

Fig. 7.28 Fraction of fossil fuel CO_2 emissions that remains in the atmosphere, terrestrial ecosystems, and the ocean. Data from Canadell et al. (2007)

the ocean to dissolve more CO_2 (see Chap. 14; Canadell et al. 2007). Ecosystem ecologists are playing a key role in global policy as they seek to link changes in the climate system to carbon fluxes from ecosystems (Fig. 7.22). These advances come through the integration, using computer simulations, of measurements made at leaf-to-global scales.

Summary

Decomposition ultimately converts dead organic matter into CO_2 and inorganic nutrients through leaching, fragmentation, and chemical alteration. Leaching removes soluble materials from decomposing organic matter. Fragmentation by animals breaks large pieces of organic matter into smaller ones that they eat, creating fresh surfaces for microbial colonization. Fragmentation in terrestrial systems also mixes the decomposing organic matter into the soil. Bacteria and fungi carry out most of the chemical alteration of dead organic matter, although some chemical reactions occur spontaneously without microbial mediation.

Decomposition rate is controlled by substrate quality, the physical environment, and composition of the microbial community. Carbon chemistry is a strong determinant of litter quality. Labile substrates, such as sugars and proteins, decompose more rapidly than recalcitrant ones, such as lignin and microbial cell walls. Plants in high-resource environments produce high-quality litter and therefore support rapid decomposition rates. Decomposition rate declines with time, as labile substrates are depleted. Soil animals influence decomposition by fragmenting litter, consuming soil microbes, and mixing the litter into mineral soil. The environmental factors that favor NPP (warm, moist, fertile soils) also promote decomposition, so there is no clear relationship between the amount of carbon that accumulates in soils with either NPP or decomposition rate.

NECB is the rate at which carbon accumulates in ecosystems. This accumulation occurs through gaseous, dissolved, and particulate exchanges with the atmosphere and with other ecosystems. In the absence of large disturbances, net ecosystem production (NEP) – the balance between GPP and ecosystem respiration – is the largest determinant of NECB. This is closely approximated in terrestrial ecosystems by measurement of net ecosystem exchange (NEE) and in aquatic ecosystems by fluxes of DIC. NEP is influenced more strongly by time since disturbance than by the environment. Surprisingly, most terrestrial ecosystems appear to be active sinks for carbon for reasons that are vigorously debated. Some disturbances such as wildfire cause large non-respiratory carbon losses that are not a component of NEP. Inclusion of these disturbances in estimates of NECB provides a more complete accounting of the interactions of ecosystems with the atmosphere. Human activities are altering most of the major controls over NECB at a global scale in ways that are altering global climate.

In contrast to terrestrial ecosystems, most streams and rivers have a negative NEP because of large terrestrial-to-aquatic transfers of organic matter and dissolved CO_2. Decomposition in streams is similar to that on land, except that the products spiral downriver linking stream metabolism horizontally throughout entire river systems. Of the carbon that enters streams from the land (as dissolved CO_2 and dead organic matter), about 40% returns to the atmosphere as CO_2, 12% is stored in sediments of lakes and reservoirs, and the remainder (about half) is transported to the ocean. In lakes and the ocean, most decomposition occurs in the water column, leading to rapid recycling of the nutrients from dead organic matter. About 25% of the carbon sinks to depth (the biological pump).

Review Questions

1. What is decomposition, and why is it important to the functioning of ecosystems?
2. What are the three major processes that contribute to decomposition? What are the major controls over each of these processes? Which of these processes is directly responsible for most of the mass loss from decomposing litter?

3. How do bacteria and fungi differ in their environmental responses and their roles in decomposition?
4. What roles do soil animals play in decomposition? How does this role differ between protozoans and earthworms?
5. Why do decomposer microbes secrete enzymes into the soil rather than breaking down dead organic matter inside their bodies?
6. What chemical traits determine the quality of soil organic matter? How do carbon quality and C:N ratio differ between litter of plants growing on fertile vs. infertile soils?
7. Describe the mechanisms by which temperature and moisture affect decomposition rate.
8. How do roots influence decomposition rate? How does decomposition in the rhizosphere differ from that in the bulk soil? Why?
9. What controls the carbon input to headwater streams? Why is this important to the carbon balance of linked terrestrial–aquatic landscapes?
10. How do the controls over NEP and NECB differ from the controls over GPP and decomposition. Why are these controls different?

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