10.7 Biogeochemistry of Decomposition and Detrital Processing

J Sanderman and R Amundson, University of California, Berkeley, CA, USA

This article is reproduced from the previous edition, volume 8, pp. 249–316, © 2003, Elsevier Ltd.

10.7.1 Introduction

Decomposition is a key ecological process that roughly balances net primary production in terrestrial ecosystems and is an essential process in resupplying nutrients to the plant community. Decomposition consists of three concurrent processes: communition or fragmentation, leaching of water-soluble compounds, and microbial catabolism. Decomposition can also be viewed as a sequential process, what Eijsackers and Zehnder (1990) compare to a Russian matriochka doll. Soil macrofauna fragment and partially solubilize plant residues, facilitating establishment of a community of decomposer microorganisms. This decomposer community will gradually shift as the most easily degraded plant compounds are utilized and the more recalcitrant materials begin to accumulate. Given enough time and the proper environmental conditions, most naturally occurring compounds can completely be mineralized to inorganic forms. Simultaneously with mineralization, the process of humification acts to transform a fraction of the plant residues into stable soil organic matter (SOM) or humus. For reference, Schlesinger (1990) estimated that only ~0.7% of detritus eventually becomes stabilized into humus.

Decomposition plays a key role in the cycling of most plant macro- and micronutrients and in the formation of humus. **Figure 1** places the roles of detrital processing and mineralization within the context of the biogeochemical cycling of essential plant nutrients. Chapin (1991) found that while the atmosphere supplied 4% and mineral weathering supplied no nitrogen and <1% of phosphorus, internal nutrient recycling is the source for >95% of all the nitrogen and

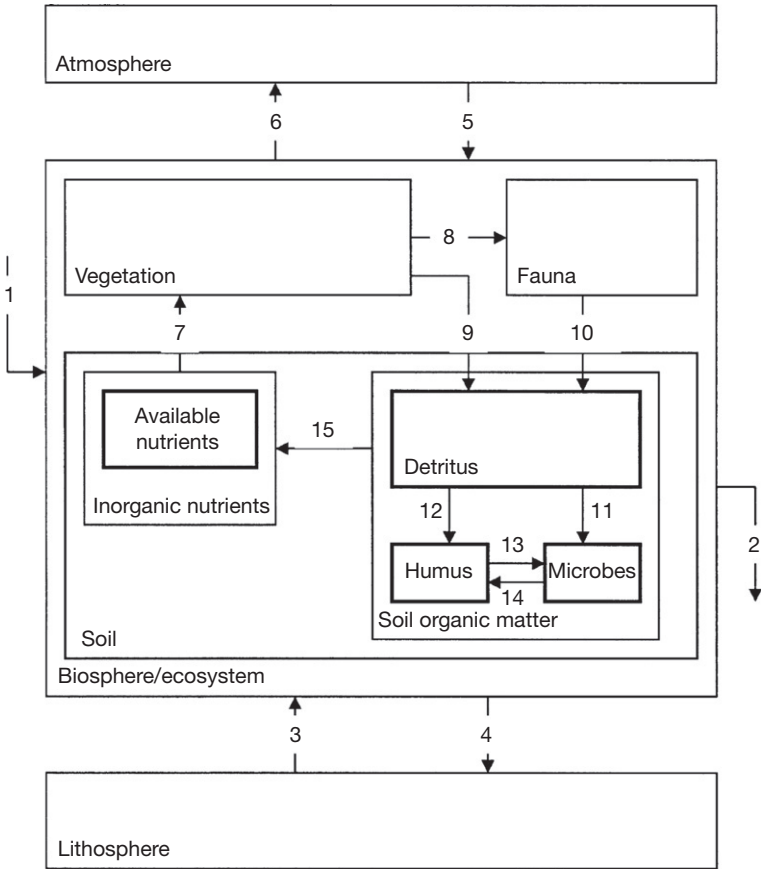

Figure 1 A decomposition-centric biogeochemical model of nutrient cycling. Although there is significant external input (1) and output (2) from neighboring ecosystems (such as erosion), weathering of primary minerals (3), loss of secondary minerals (4), atmospheric deposition and N-fixation (5) and volatilization (6), the majority of plant- available nutrients are supplied by internal recycling through decomposition. Nutrients that are taken up by plants (7) are either consumed by fauna (8) and returned to the soil through defecation and mortality (10) or returned to the soil through litterfall and mortality (9). Detritus and humus can be immobilized into microbial biomass (11 and 13). Humus is formed by the transformation and stabilization of detrital (12) and microbial (14) compounds. During these transformations, SOM is being continually mineralized by the microorganisms (15) replenishing the inorganic nutrient pool (after Swift et al., 1979).

phosphorus uptake by tundra species in Barrow, Alaska. In a cool temperate forest, nutrient recycling accounted for 93%, 89%, 88%, and 65% of total sources for nitrogen, phosphorus, potassium, and calcium, respectively (Chapin, 1991).

The second major ecosystem role of decomposition is in the formation and stabilization of humus. The cycling and stabilization of SOM in the litter–soil system is presented in a conceptual model in Figure 2. Parallel with litterfall and most root turnover, detrital processing is concentrated at or near the soil surface. As labile SOM is preferentially degraded, there is a progressive shift from labile to passive SOM with increasing depth. There are three basic mechanisms for SOM accumulation in the mineral soil: bioturbation or physical mixing of the soil by burrowing animals (e.g., earthworms, gophers, etc.), *in situ* decomposition of roots and root exudates, and the leaching of soluble organic compounds. In the absence of bioturbation, distinct litter layers often accumulate above the mineral soil. In grasslands where the majority of net primary productivity (NPP) is allocated belowground, root inputs will dominate. In sandy soils with ample rainfall, leaching may be the major process incorporating carbon into the soil.

There exists an amazing body of literature on the subject of decomposition that draws from many disciplines—including ecology, soil science, microbiology, plant physiology, biochemistry, and zoology. In this chapter, we have attempted to draw information from all of these fields to present an integrated analysis of decomposition in a biogeochemical context. We begin by reviewing the composition of detrital resources and SOM (Section 10.7.2), the organisms responsible for decomposition (Section 10.7.3), and some methods for quantifying decomposition rates (Section 10.7.4). This is followed by a discussion of the mechanisms behind decomposition (Section 10.7.5), humification (Section 10.7.6), and the controls on these processes (Section 10.7.7). We conclude the chapter with a brief discussion on how current biogeochemical models incorporate this information (Section 10.7.8).

10.7.2 Composition of Decomposer Resources

A wide range of substrates are available to the decomposer organisms. Table 1 highlights the large range in biomass and

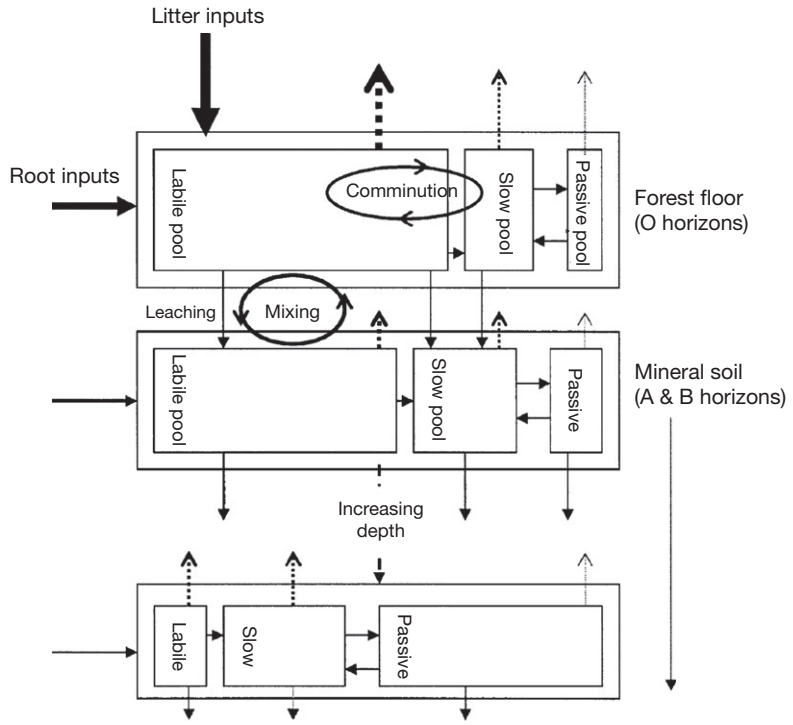

Figure 2 Conceptual model of carbon cycling in the litter-soil system. In each horizon or depth increment, SOM is represented by three pools: labile SOM, slow SOM, and passive SOM. Inputs include aboveground litterfall and belowground root turnover and exudates, which will be distributed among the pools based on the biochemical nature of the material. Outputs from each pool include mineralization to CO_2 (dashed lines), humification (labile→slow→passive), and downward transport due to leaching and physical mixing. Communition by soil fauna will accelerate the decomposition process and reveal previously inaccessible materials. Soil mixing and other disturbances can also make physically protected passive SOM available to microbial attack (passive→slow).

production values within and across three major biomes. Not only are the absolute amounts of litter important in determining decomposition dynamics, but its spatial distribution, molecular composition and physical properties will also have a large controlling effects on both its degradation and stabilization as SOM (see **Section 10.7.7**). The microbial biomass is an important secondary resource and its varied composition and properties are now believed to be a significant starting material for SOM formation (see **Section 10.7.5**). In this section, we will describe the physical and molecular composition of detritus. For additional information on this subject, see reviews by De Leeuw and Largeau (1993) and Kogel-Knabner (2002).

10.7.2.1 Plant Litter

Leaves, whether broadleaf foliage or coniferous needles, are the dominant aboveground inputs to most soils. Other aboveground inputs—such as branches, bark, and fruits—account for only 20% in temperate deciduous forests (Jensen, 1984) and 20–40% in coniferous forests (Millar, 1974) of total litterfall. Herbaceous understory vegetation contributes only a small fraction to the total litterfall in most temperate forests. Whether or not a forest is managed for timber production will have a major impact on the composition of the aboveground litter. In mature natural forests, coarse woody debris may contribute 40–60% or more to the total detrital biomass (Vogt, 1991). Aboveground input in grasslands and other semi- arid ecosystems can be an order of magnitude lower than in forests (**Table 1**). Additionally, grazing will have a significant impact on how much of the aboveground NPP is returned to be decomposed (Sims and Singh, 1978a,b).

The timing of litterfall will also have a big impact on detrital processing and carbon dynamics in terrestrial ecosystems. Deciduous forests have a single annual pulse of fresh inputs in the fall, while evergreen coniferous and tropical forests have a somewhat continuous rate of litterfall which tends to fluctuate with water availability. Plants in grasslands and other semi-arid to arid ecosystems often turn over in response to drought stress.

Plants are predominantly composed of parenchyma and woody tissues. Parenchyma cells dominate the green tissues in leaves and are composed of a protein-rich protoplast surrounded by a cellulose wall. Woody plant cells dominate all support (sclerenchyma) and transport (xylem and phloem) structures in a plant. They are composed of several layers (middle lamella, primary wall, secondary wall, and tertiary wall) with varying proportions of cellulose, hemicellulose, and lignin (Fengel and Wegener, 1984).

In general, intracellular spaces are comprised of easily degraded energy-rich proteins and starches, while plant cell walls contain macro- molecular polysaccharides (cellulose and hemi- cellulose), lignin, lipids, and various polyphenols with varying degrees of decomposability (Kogel-Knabner, 2002). **Table 2** shows the distribution of these major organic components in several primary and secondary resources as

determined by wet chemical techniques. The structure and degradation pathways of each of these compounds are discussed in Section 10.7.5.4.

10.7.2.2 Roots

Plants allocate a significant portion of their C and energy resources to root production. Vogt (1991) estimated that belowground net primary production (BNPP) accounts for 30–50% of total NPP in temperate forests, while temperate grasslands can allocate as much as 86% of NPP to belowground production (Sims and Singh, 1978b). Jackson et al. (1996) found that as a global average, 50% and 75% of total root biomass occurs in the top 20 cm and 40 cm of soil, respectively. Reviewing the root literature, Gill and Jackson (2000) found that annual root turnover or mortality, defined as BNPP/maximum belowground standing crop, was 10% for entire tree root systems, 34% for total shrubland roots, 53% for grassland fine roots (<5 mm diameter), 55% for wetland fine roots (<5 mm), and 56% for forest fine roots (<5 mm). In addition, minirhizotron studies have shown the existence of a highly dynamic pool of roots (generally <1 mm) with a lifespan of days to weeks (Hendrick and Pregitzer, 1997; Tingey et al., 2000). However, Gaudinski et al. (2001) noted the possibility of long-lived fine roots (<2 mm) based on radiocarbon measurements. Reconciling these results is an area of active research with major ramifications on terrestrial carbon cycling dynamics.

Despite its importance in detrital processing and long-term carbon storage, the biochemical composition of belowground carbon inputs has received much less attention. Most current biogeochemical models assume that the chemical composition of roots is similar to that of above ground litter. Root diameter will have a large impact on the ratio of woody to nonwoody tissues, with the proportion of woody tissues increasing with diameter (Gill and Jackson, 2000).

Rhizodeposition represents a small but significant carbon substrate available to the decomposer organisms. Rhizodeposition, a term that describes the loss of carbon from a living root (Whipps and Lynch, 1985), includes: (1) water-soluble exudates such as sugars, amino acids, and organic acids which passively leak from roots; (2) highermolecular-weight secretions such as complex carbohydrates and enzymes which are metabolically moved out of the root; (3) lysates from the autolysis of cells within the root; (4) mucilage coating on roots which is composed of polysaccharides and polygalacturonic acids; and (5) gases such as ethylene and CO_2 (Grayston et al., 1996; Lynch and Whipps, 1990). The amount of net fixed carbon lost as nongaseous rhizodeposition has been estimated to range from 1% to 10% in most perennial plants (Grayston et al., 1996), with annual plants ranging from 6% to 17% (Lynch and Whipps, 1990). The majority of this carbon is readily utilized by the highly active microbial community in the rhizosphere and only a small fraction will end up incorporated into SOM (Cheng et al., 1994; Grayston, 2000).

Readily assimilable root exudates are believed to have a large impact on plant nutrient availability (Uren and Reisenauer, 1988). Exuded organic acids can increase the solubility of inorganic nutrients such as phosphorus and manganese. However, the largest effect rhizode- position has on nutrient availability is indirectly through the stimulation of microorganisms and their subsequent acceleration of the biogeochemical cycling of most essential plant nutrients (Grayston et al., 1996). Additionally, it has been hypothesized that root exudates act as a primer for the decomposition of bulk SOM through the stimulation of microorganisms in the rhizosphere (Bottner et al., 1988; Sallih and Bottner, 1988).

Table 1 Range of biomass and productivity for temperate forests, temperate grasslands, and moist to wet tropical forests

	Temperate forest	*Temperate grassland*	*Temperate forest*
Biomass (tC ha^{-1})			
Total living	1.3–281	22–27	209–473
Aboveground	5.7–220	0.5–1.8	146–431
Below ground	7.0–41	1.7–25	11–120
Litter layer	2.8–75	0.5–4.2	1.8–16.5
Soil organic matter	27–158	17–207[a]	50–599
Production (tC ha $^{-1}$ yr^{-1})			
NPP	4.3–24	2.3–14.3	11.1–20.8
Aboveground NPP	1.6–15	0.5–5.2	9.6–18.2
Litterfall	0.4–2.7	0.3–3.1	6.4–15.3
Belowground NPP	1.9–6.4	1.5–2.2	1.5–5.5
Root turnover	0.6–6.0	0.5–2.2	1.0–3.6[b]

[a]±1 SD of mean listed for cool temperate steppe ecosystems in Post et al. (1982).
[b]Estimated from root turnover rates listed for tropical forests in Gill and Jackson (2000).
Sources: temperate forests—Vogt (1991); temperate grasslands—Sims and Singh (1978a,b); and tropical forests—Brown and Lugo (1982).

Table 2 Major organic components of plant and microbial resources determined by wet chemical methods

	Deciduous leaf *Quercus*	Conifer needle *Pinus*	Grass leaf *D. flexuosa*	Grass root *Loudetia simplex*	Deciduous Wood	Bacteria	Fungi
Lipid (ether soluble)	8	24	2	11	2–6	10–35	1–42
Storage/metabolc carbohydrate (cold and hot water soluble)	22	7	13	35	1–2	5–30	8–60
Cell wall polysaccharide, hemicellulose (alkali soluble)	13	19	24	16	19–24	4–32	2–15
Cellulose (strong acid)	16	16	33	11	45–48	0	0
Lignin (residue)	21	23	14	34	17–26	0	0
Protein($N \times$ 6.25)	9	2	2	2		50–60	14–52
Ash (incineratio)	6	2		5	0.3–1.1	5–15	5–12

Adapted from Swift et al. (1979) and Lavelle and Spain (2001).

10.7.2.3 Secondary Resources

Microbial biomass only contributes 1–5% to the total SOM pool. However, this highly dynamic protein-rich carbon pool represents a major nutrient sink and as such many organisms are capable of degrading most microbially synthesized materials. Microbial biomass is usually measured indirectly by monitoring CO2 production (Anderson and Domsch, 1978; Jenkinson and Powlson, 1986) or levels of specific enzymes and unique biochemical compounds (Tunlid and White, 1992; West et al., 1987). The chloroform ($CHCl_3$) fumigation–incubation technique, developed by Jenkinson and Powlson (1986), measures the extra CO_2 evolved (assumes that dead microorganisms are rapidly decomposed) from a soil following fumigation relative to a control soil. First proposed by Anderson and Domsch (1978), the substrate-induced respiration method measures the initial respiratory response of the microbial population following amendment with an excess carbon and energy source.

Fungal cell walls are composed primarily of the highly crystalline polysaccharides, chitin and β-glucan, and various nonhydrolyzable melanins (Peberdy, 1990). **Section 10.7.5.4** describes the structure and decomposition of chitin. While chitin has been well studied, very little is known about the structure or *in situ* decomposition of melanins (Butler and Day, 1998). However, melanins are thought to be a possible humus precursor because of their similarities with humic acids (Saiz-Jimenez, 1996).

Peptidoglucan, a heteropolymer with carbohydrate and amino acid subunits, is the dominant material in bacterial cell walls (Rogers et al., 1980). Bacteria and a number of algae also contain considerable amounts of insoluble, nonhydrolyzable aliphatic compounds, termed bacteran and algaenan (Kogel-Knabner, 2002). Although more research is needed, these highly recalcitrant macromolecules also have the potential to be humus precursors (Augris et al., 1998).

10.7.2.4 Soil Organic Matter

SOM is composed of a continuum of organic resources from fresh plant residues to stabilized organic matter (OM) or humus (Stevenson, 1994). Although this definition of SOM includes intact plant litter, in this review we will often distinguish between decomposition of litter on the soil surface and decomposition/stabilization of OM within the mineral soil. Within the mineral soil, SOM is often divided into four categories: the "light" fraction, microbial biomass (discussed above), dissolved organic matter (DOM), and stable humic substances.

Maintaining adequate levels of humus in agriculture soils is recognized as one of the key factors in sustaining productivity (Weil, 1992). Humus imparts the typical dark color of many soils; greatly increases water retention; facilitates cementation of clay particles into aggregates; acts as a large pool of nutrients for plant growth; enhances micronutrient availability by forming stable complexes with many polyvalent cations; helps buffer the soil from pH changes; and greatly increases the cation exchange capacity of the soil (Stevenson, 1994).

Light fraction. The light fraction, so termed because it is the material that floats in liquids with densities ranging from 1.6 g cm^{-3} to 2.0 g cm^{-3}, consists of partially decomposed plant residues. In an undisturbed forest and grassland soils, the light fraction can constitute as much as 30% of the total SOM (Stevenson, 1994). However, in agriculture soils, the light fraction will typically contribute only a few percent to total SOM. Under a microscope, the majority of the light fraction can still be recognized as belonging to plant litter. As determined by ^{13}C nuclear magnetic reasonance (NMR) spectroscopy, the gross chemical composition of the light fraction has been found to be comparable to that of plant litter (Skjemstad et al., 1986). The light fraction combined with the microbial biomass is what many researchers have termed the labile or active SOM fraction— the highly dynamic, rapidly cycling component of SOM responsible for supplying most of the nutrients for plant growth (Stevenson, 1994; Townsend et al., 1997).

Dissolved organic matter. The water-soluble matter or DOM is a small but important component of SOM. Typical concentrations of dissolved organic carbon (DOC) in forest soil solutions are 10–50 mg L^{-1} with annual fluxes decreasing from 10–80 g C m^{-2} yr^{-1} in the surface horizons (0–20 cm) to <10 g C m^{-2} yr^{-1} in the subsurface (20–100 cm) (Neff and Asner, 2001; Qualls et al., 1991). The dissolved phase of SOM is a major source of plant-available nutrients (i.e., Qualls and Haines, 1991) and it has been implicated in the alleviation of metal toxicities (i.e., Pohlman and McColl, 1988) and in movement of organic carbon into the mineral soil (i.e., Guggenberger, 1992). DOM fluxes leaving the litter layer consist mostly of simple carbohydrates and amino acids, while fluxes through the mineral horizons often contain complex biopolymers that are thought to be of microbial origin (see **Section 10.7.5.3** for more details).

Humic substances. In most soils, humic substances comprise ~60–80% of SOM. Humic substances are distinguished from nonhumic substances in that they are unique to the soil or sediment environment and are composed of relatively high-molecular-weight compounds that can neither be characterized as biopolymers of microorganisms nor higher plants (Stevenson, 1994).

Researchers have devised numerous extraction and fractionation schemes to deal with the heterogeneous nature of humic substances. Traditionally, the operational definition of humic substances as used by the International Humic Substances Society (Hayes et al., 1989) is based on the solubility in a series of acids and bases. In this scheme, humic substances are classified into three chemical groupings: (1) fulvic acid, soluble in both alkali and acid solutions, has the lowest molecular weight and is generally considered the most susceptible to microbial degradation; (2) humic acid, soluble in alkali but not in acid, is intermediate in molecular weight and decomposability; and (3) humin, insoluble in both alkali and acid solutions, is the most complex and recalcitrant humus fraction in this scheme (Brady and Weil, 2002). Although widely applied, this fractionation scheme has been criticized because the resulting fractions are still heterogeneous mixtures of compounds that will differ between soils and do not necessarily correlate with the biochemical processes of decomposition and humification (Kogel-Knabner, 1993; Oades, 1988).

Methods of characterization. Other physical and chemical fractionation schemes attempt to separate humus in terms of biodegradability or degree of humification. With decreasing particle size or increasing density, the recalcitrance, as defined by numerous

methods, of the associated organic material often increases (Christensen, 1992). Additional chemical treatments can be applied to a sample, such as HCl or H_2SO_4 hydrolysis which removes labile carbohydrates and proteinaceous materials. Trumbore et al. (1996) combined density separation with hydrolysis to separate bulk SOM into three pools with increasing mean residence times based on ^{14}C analysis: a low-density (<2.0 g cm^{-3}) fraction with rapid turnover; a high-density hydrolyzable fraction with intermediate turnover; and a highdensity nonhydrolyzable fraction with very slow turnover times.

Kogel-Knabner (2002) stressed that conventional chemical degradative techniques, such as those used to produce **Table 2**, can only account for 50–60% of the total organic material in plant litter and SOM (Kogel et al., 1988) and that these methods are often not specific for single compound classes (Preston et al., 1998; Ryan et al., 1990). Although these conventional chemical techniques have limitations, the majority of decomposition studies have relied on them. Recently, numerous advances have been made in the study of decomposition and humification utilizing solid-state ^{13}C NMR spectroscopy, pyrolysis in combination with gas chromatography (Py-GC) and mass spectrometry, and other advanced analytical techniques (Baldock et al., 1997; Kogel-Knabner, 1997).

In NMR spectroscopy, certain nuclei (e.g.,^{1}H,^{13}C,^{15}N, and ^{31}P) will precess about their axis parallel with an externally applied magnetic field. When a second magnetic field is applied at a right angle, the nuclei will resonate, thereby inducing a measurable voltage change. Each nucleus is influenced by its neighbors and will only resonate in a specific magnetic field strength, so by varying the strength of the magnetic field a spectrum of electromagnetic radiation is produced. To make quantitative comparisons, results are always expressed as a "chemical shift" (δ) relative to a reference standard, usually tetra- methylsilane (TMS). Solid organic samples often show broad overlapping peaks due to dipolar interactions between ^{13}C and the much more common ^{1}H nuclei and interference due to paramagnetic materials such as iron oxides in the soil. The techniques of cross-polarization and magic-angle spinning (CPMAS) have been developed to greatly reduce line broadening due to ^{1}H (Wilson et al., 1981). Treatment with HF will both concentrate the organic material and remove paramagnetic materials (Schmidt et al., 1997; Skjemstad et al., 1994). For much more detail on theory and application of NMR spectroscopy to OM studies, see Malcolm (1989), Wilson (1989), Kogel-Knabner (1997) and Veeman (1997), and others.

Solid-state CPMAS ^{13}C NMR spectroscopy yields information on the abundance of different functional groups in a sample. In general, the four most commonly used chemical shift regions are: alkyl carbon (0–45 ppm) associated with lipids, cutin, suberin, proteins, aliphatic biopolymers, and several uncharacterized compounds; O-alkyl carbon (45–110 ppm) associated with carbohydrates and methoxyl groups; aromatic carbon (110–160 ppm) associated with lignin and tannins; and carboxyl C (160–210 ppm) associated with numerous compounds (Zech et al., 1992). The ^{13}C NMR spectrum of humic acid extracted from a grassland soil along with the chemical shift regions for selected functional groups is shown in Figure 3. As this example illustrates, humic acid is a heterogeneous mixture of organic materials dominated by aromatic carbon ($\delta = 130$ ppm), followed by near equal contributions of

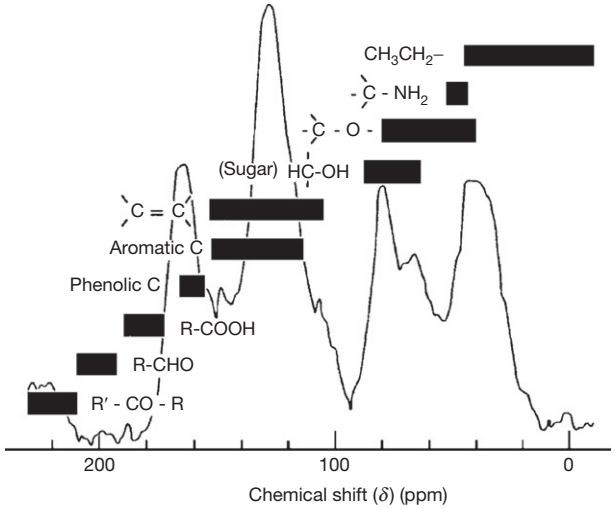

Figure 3 Solid-state CPMAS ^{13}C NMR spectrum of humic acid extracted from a grassland soil with the chemical shift ranges for select functional groups relative to TMS (after Schnitzer, 1990; Wilson, 1990).

carboxyl (178 ppm), aliphatic (25–32 ppm) and carbohydrate (75 ppm) carbon, and slightly smaller quantities of proteinaceous (58 ppm) and phenolic carbon (152 ppm).

While ^{13}C NMR studies reveal the gross chemical composition of OM, this technique cannot identify specific compounds. However, the thermal degradative technique of analytical pyrolysis, especially when coupled with mass spectrometry, can provide information on the specific compounds present in a sample. Bracewell et al. (1989), Saiz-Jimenez (1994), Kogel-Knabner (2000), and others have reviewed the application of pyrolysis techniques to OM studies.

10.7.2.5 Summary

The quantity and biochemical composition of aboveground litter inputs has been well characterized by wet chemical analyses such as the classical Klason lignin or van Soest analysis of proximate fractions. However, there is a dearth of data on belowground carbon inputs (i.e. roots, root exudates, and microbial biomass). Due to its importance in ecosystem functioning and in longterm carbon storage, many aspects of below ground carbon inputs are being actively researched.

Despite the fact that the classical degradative techniques have potentially serious analytical problems (Kogel et al., 1988; Zech et al., 1987), they are still commonly employed in decomposition studies and the majority of biogeochemical models have been parametrized using these data. Significant advances in the understanding of the macromolecular composition of detritus are being made using spectroscopic, thermolytic, and other analytical techniques (Kogel-Knabner, 2002). Where appropriate, we have attempted to integrate some recent ^{13}C NMR spectroscopy data into this review.

10.7.3 The Decomposer Organisms

When examining decomposition at a large scale, we tend to obscure the fact that decomposition and detrital recycling

occurs as a result of the direct and indirect actions of a myriad of soil flora and fauna. A well-developed soil may contain a thousand species of soil animals with a much greater number of microbial taxa. In fact, soil microorganisms may constitute upwards of 98% of all life (Pace, 1996), with only a fraction of a percent having been classified. Even more impressive than the shear diversity of soil dwelling organisms is their abundance. In a single gram of soil, there may be one hundred million bacterial cells supporting a population of one hundred thousand predatory protozoa (**Table 3**).

This taxonomic diversity emphasizes the challenges facing any analysis of the decomposer community and highlights the need to simplify the classification of the roles these organisms play in the process of decomposition (Swift et al., 1979). In this section, we will first outline a functional ecology for decomposer organisms and then highlight some details of several of the major groups of soil organisms. For more detailed information on the biology and ecology of soil organisms, the reader is referred to the texts of Burges and Raw (1967), Dindal (1990), Dix and Webster (1995), and Reddy (1995b).

10.7.3.1 Functional Ecology

Depending on the interests of the particular investigator, soil organisms regardless of taxonomic identity can be classified by body size or by various physiological traits related to trophic function. In studies of decomposition, the functional division of the decomposer community based on body size has become common since Edwards and Heath (1963) introduced the mesh litter bag as a field tool for studying detrital processing (details of the litter bag technique can be found in **Section 10.7.4**). On the basis of what organisms can or cannot enter a specific mesh size, the appropriate dimension to consider would be body width (**Figure 4**) not length as researchers have traditionally done (e.g., Wallwork, 1970). Under this scheme bacteria and fungi are considered *microflora*. The protozoa, nematodes, rotifers, tardigrades, and the smallest mites (Acari), and Collembola are classified as *microfauna*. The major functional role of the microfauna is as bacterial and fungal predators. The organisms generally responsible for communition and redistribution of plant litter most often are categorized as *macrofauna*. The macrofauna include several groups which when present have inordinate impacts on the decomposition subsystem, mainly the earthworms (Oligochaeta) and the termites (Isoptera).

Alternately, the decomposer organisms can be subdivided by their respective trophic positions. The traditionally well-described food chains of herbivore–carnivore systems for higher animals often fail to capture the complexity and diversity of roles in the decomposer community. Swift et al. (1979) describe the food web of the decomposer community as "a more fluid, interactive structure with individual species operating on several levels which might be distinguished as trophically different." The trophic-level classification of fungus and food source devised by Lewis (1973) has been widely adopted to describe the general decomposer community (e.g., Swift et al., 1979). Lewis (1973) defines three main trophic roles: *necrotrophs*, *biotrophs*, and *saprotrophs*.

The *necrotrophs* exploit other living organisms resulting in the rapid death of the food resource. They include parasitic microorganisms (individuals of which can feed on and kill both plant tissue and higher soil fauna) and the major microflora predators (i.e., the protozoa and nematodes). The *biotrophs* form a more mutualistic relationship whereby their continued existence depends on the health of the host (many root-feeders and the mycorrhizal fungi fall into this category). The majority of the decomposer organisms are classified as *saprotrophs*, organisms that utilize dead OM as their main food source. The saprotrophs can further be divided into the type of OM they consume, i.e., *primary* or *secondary* (Swift et al., 1979). In terms of ecological strategies (Macarthur and Wilson, 1967), the necrotrophs are primarily opportunistic *r*-selected species (short lifespan, early reproduction, low biomass, and the potential to produce large numbers of offspring in a short period of time), the biotrophs are dominated by long-lived *K*-strategists (in fact, the largest and oldest known organism may be mycelial fungi), and the saprotrophs are represented by the full spectrum of ecological strategies.

Table 3 Relative abundance and biomass of soil fauna and flora commonly found in the surface 15 cm of soil

Organisms	Number		Biomass[b]	
	m^{-2}	g^{-1}	$kg\ ha^{-1}$	$g\ m^{-2}$
Microflora				
Bacteria	10^{13}–10^{14}	10^{8}–10^{9}	400–5000	40–500
Actinomycetes	10^{12}–10^{13}	10^{7}–10^{8}	400–5000	40–500
Fungi	10^{10}–10^{11}	10^{5}–10^{6}	1000–15 000	100–1500
Algae	10^{9}–10^{10}	10^{4}–10^{5}	10–500	1–50
Soil fauna				
Protozoa	10^{9}–10^{10}	10^{4}–10^{5}	20–200	2–20
Nematodes	10^{6}–10^{7}	10–10^{2}	10–150	1–15
Mites	10^{3}–10^{6}	1–10	5–150	0.5–1.5
Collembola	10^{3}–10^{6}	1–10	5–150	0.5–1.5
Earthworms[a]	10–10^{3}		100–1500	10–150
Other fauna	10^{2}–10^{4}		10–100	1–10

[a]A greater depth was used for earthworms. [b] Biomass values are on a liveweight basis. Dry weights are ~20–25% of these values.
Source: Brady and Weil (2002).

10.7.3.2 Soil Microorganisms

The diversity of microbial life is, in part, a result of the interactions between an extremely heterogeneous and complex habitat (the soil), variable nutrition sources (both in structure and availability), numerous trophic interactions (including competition and predation), and multiple methods of gene flow. For additional information on soil microorganisms the reader is referred to the texts of Paul and Clark (1996) and Sylvia et al. (1999).

The soil habitat. Soil is a dynamic and diverse medium—the result of a complex interplay between the local climate (especially temperature and precipitation), parent material (bedrock, alluvium, aeolian sands, etc.), living biota (especially the native vegetation), topography (slope and relief), and time (Jenny, 1941). Soils vary horizontally and continually across the landscape as a result of variations in these soilforming factors. Vertical heterogeneity in a soil profile results from

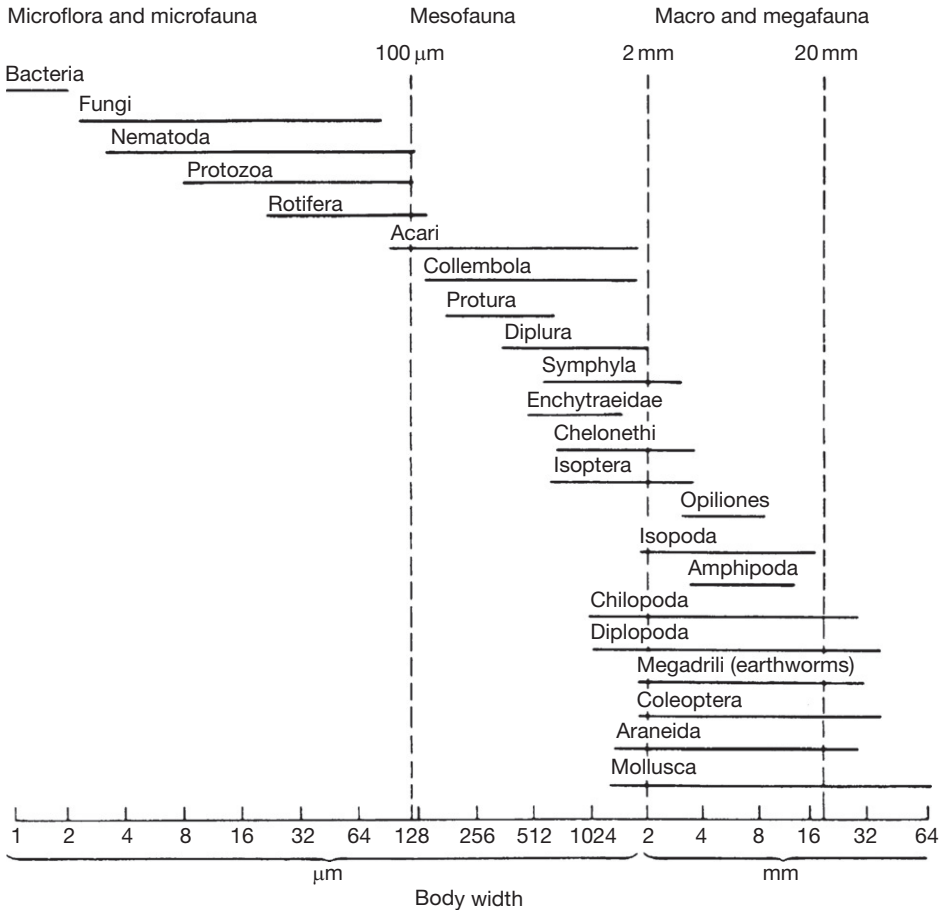

Figure 4 Size classification of organisms in decomposer food webs by body width (Swift et al., 1979) (reproduced by permission of University of California Press from *Decomposition in Terrestrial Ecosystems*, 1979).

variations in chemical weathering and leaching of weathering products down a profile, asymmetric inputs of OM as litter at the surface or as root exudates at localized positions within the soil, and turbation by both biotic and abiotic factors.

A given volume of soil will contain ~50% solid particles of which less than 5% is typically defined as OM and 50% as pore space which can then be further divided into water- and air-filled pores. The ratio of water/air will depend on the water content of the soil. The mineral fraction can be defined by texture—the mixture of sand (diameters from 0.05 mm to 2.0 mm), silt (0.002 mm to 0.5 mm), and clay size (less than 0.002 mm) particles. The soil texture, especially the clay percentage due to its very high surface area, is critical in determining many properties relevant to soil microorganisms and detrital processing: (1) soil structure and the distribution of pore sizes; (2) water-holding capacity of the soil; (3) soil aeration; and (4) the ability to retain nutrient elements (cation exchange capacity).

Perhaps the single most important factor determining the distribution of microorganisms in a soil is the water potential. Nearly all microorganisms and many of the smallest soil animals rely on the thin film of water surrounding soil aggregates and in soil pores for the basic necessities of life. The soil water potential (Ψ) is a measure of the potential energy of water in the soil relative to the potential energy of pure, free water. Ψ is always negative in a soil due primarily to attractive forces of soil particles (matric potential, Ψ_m) and solute ions (osmotic potential, Ψ_π). Table 4 shows the relationship between matric potential, water film thickness, and the limitations on microbial activity. If Ψ falls too low, microorganisms must either enter a quiescent resting phase or perish from desiccation. Just as drying has dramatic effects on microbial populations, rapid rewetting can cause massive mortality and turnover (discussed in detail in Section 10.7.7).

Table 4 Microbial tolerance to matric-controlled (Ψ_m) water stress

Waterpotential *(MPa)*	Water film thickness	Microbial activity limited (example of genus)
−0.03	4.0 μm	movement of protozoa,
−0.1	1.5 μm	zoospores, and bacteria
−0.5	0.5 μm	
−1.5	<3.0 μm	nitrification; sulfur oxidation
−4.0	<1.5 μm	bacterial growth *(Bacillus)*
−10.0	<1.5 nm	fungal growth *(Fusarium)*
−40.0	<0.9 nm	fungal growth (Penicillium)

Although representing less than 5% and often less than 1% of the soil, OM plays several critical roles in the soil system. It is the substrate for all heterotrophic microbial life. The high

cation exchange capacity of OM acts as a store of plant and microbe available nutrients. OM, especially fungal muscigels and root exudates, in combination with mycelial microorganisms act to bind mineral particles into soil aggregates. The microhabitat within soil aggregates can be extremely different than that of the aggregate surface. Diffusion is limited by the increased bulk density and anaerobic interiors to aggregates are found often only a few millimeters from the aggregate surface (Tokunaga et al., 2001). Anaerobic interiors offer a refuge for strict anaerobic bacteria and also play a major role in protecting and preserving OM in soils. The diversity of microhabitats created by soil aggregates is highlighted in **Figure 5**.

Methods of quantification. A major hindrance to the study of soil microorganisms and particularly to bacteria is the lack of appropriate methods for characterizing the community structure (Hill et al., 2000). Torsvik et al. (1996) estimate that less than 0.1% of the microbes found in a typical agricultural soil can be cultured using current culturing techniques. A quote from Zak et al. (1994) expresses the difficulties inherent in studying microbial biodiversity: "we understand little about the degree to which genetic diversity is translated into taxonomic diversity, and even less about the manner in which genetic and taxonomic diversity affects functional diversity or ecosystem properties."

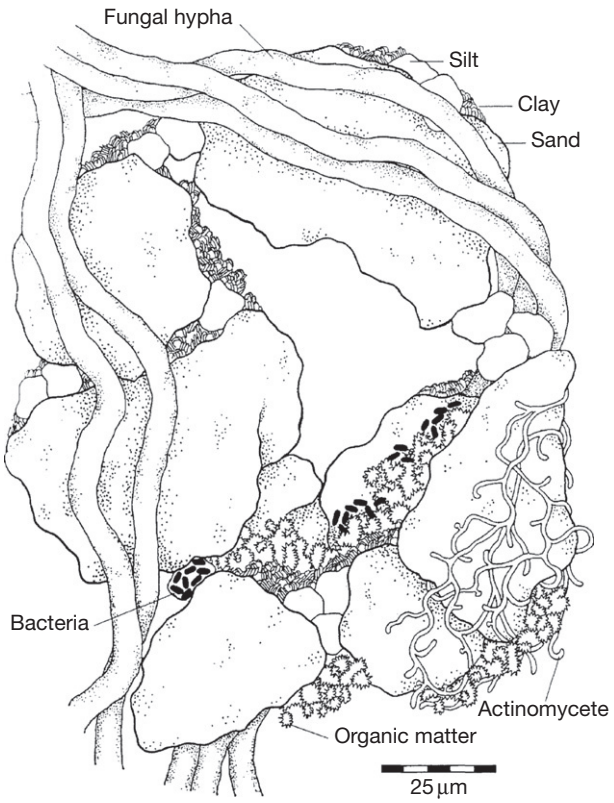

Figure 5 A typical soil aggregate. Sand, silt, and clay particles, cemented by organic matter, precipitated inorganic materials, and microorganisms, bind the soil particles together to form an aggregate. Original drawing by Kim Luoma (Fuhrmann, 1999) (reproduced by permission of Prentice Hall from *Principles and Applications of Soil* Microbiology, **1999**).

One culture-dependent method that is now being widely utilized in analysis of community-level physiological profiles (Garland and Mills, 1991; Zak et al., 1994) is available commercially as the BIOLOG® system. This system is based on the microbial utilization (detected by the reduction of a tetrazolium dye) of a suite of 95 different carbon sources that can be categorized into several substrate guilds: carbohydrates, carboxylic acids, polymers, amines/amides, amino acids, and miscellaneous (Zak et al., 1994). A major drawback of the commercially available substrates on the BIOLOG® plates is that the substrates are often not ecologically relevant and likely do not reflect the diversity of substrates found in the natural environment (Insam, 1997; Konopka et al., 1998). With this and several other methodological considerations (Hill et al., 2000) in mind, the BIOLOG® system has been extensively and successfully employed to characterize the functional diversity between both microbial communities and individual isolates (Garland, 1996; Lehman et al., 1995; Zak et al., 1994).

Culture-independent methods of soil microbial community analysis include methods based on: (1) the extraction, quantification, and identification of molecules (most commonly, phospholipids fatty acids (PLFAs) and nucleic acids) from the soil that are unique to certain microorganisms or microbial groups; or (2) fluorescence microscopic techniques where DNA segments are hybridized with labeled taxon-specific oligonucleotide probes and then scanned for cells that have incorporated the probe (Hill et al., 2000). Fluorescent *in situ* hybridization (FISH) has proven to be a useful technique for direct identification and quantification of prokaryotic communities within their natural habitat (Amann et al., 1995; Macnaughton et al., 1996). A particularly powerful technique for assessing the decomposer community in terms of what organisms are using which substrate is to combine ^{13}C isotopic analysis with the PLFA analysis (Petersen et al., 1997). These methods and applications are reviewed by Zarda et al. (1997), Atlas and Bartha (1998), Hill et al. (2000), and Ward et al. (1992).

Bacteria. The bacteria are single-celled prokaryotic organisms representing two of the three phylogenetic domains of life: the Bacteria and the Archea (Woese, 1987). Bacteria are a ubiquitous feature of terrestrial ecosystems—from the dry deserts of the Antarctic to the tropical rainforest soils of the Amazon. For a perspective on the diversity and abundance of prokaryotic life, see Whitman et al. (1998). Perhaps, most importantly, it is the variety of metabolic capabilities and the ability to rapidly reproduce and exploit a food source which make bacteria so crucial in the processes of OM decomposition, nutrient cycling, and soil formation (Sylvia et al., 1999). In general, the Bacteria are mesophiles while the Archea are tolerant of harsh environments, with both utilizing an array of nutrient and energy sources (Paul and Clark, 1996). Several of the more important soil dwelling members of the Bacteria domain are the subgroups (Paul and Clark, 1996): purple bacteria (diverse group of gram negative bacteria), green sulfur bacteria (obligate anaerobic photolithotrophs), actinomycetes (slender, filamentous growth form), sporogenic bacilli (capable of forming an endospore), and the cyanobacteria (obligate phototrophs). Within the Archea, we find the extreme halophiles, methanogens, extreme thermophiles, and the thermoacidophiles (Noll, 1992).

Bacteria, as well as fungi, can only transport simple monomers and some dimers across their cell walls and as such must

excrete a suite of extracellular enzymes to break down large and complex organic molecules (discussed in detail in **Section 10.7.5**). The production of extracellular enzymes by an individual microbe can be seen as a metabolically costly and potentially wasteful process. However, many bacteria have developed mechanisms for intercellular communication that allow homogenous populations to coordinate enzyme production and in a sense behave as a multicellular organism (Dworkin, 1998). Bacteria constantly excrete diffusible signals or "pheromones" into the environment which when at a critical concentration can induce or repress gene expression for a number of important traits (Gray, 1997; Kaiser and Losick, 1993). This density-dependent or "quorum" sensing mechanism allows for more efficient exploitation of heterogeneous carbon sources by timing the production of exoenzymes to times of high bacterial population density and substrate availability (Benedik and Strych, 1998; Chernin et al., 1998). New research in the field of quorum sensing shows that plants can even excrete substances that mimic the bacterial signals (Teplitski et al., 2000) which can have profound impacts on how we picture nutrient cycling.

Fungi. The fungi comprise a diverse group of multicellular eukaryotic organisms that exhibit an amazing array of morphologies, both vegetative and reproductive, and of life cycles (Carlile and Watkinson, 1994; Cooke and Rayner, 1984; Dix and Webster, 1995). On a wet biomass basis, fungi are the most abundant soil organism with biomasses ranging from 1000 kg wet biomass ha^{-1} to 15 000 kg wet biomass ha^{-1} (see **Table 3**). Additionally, fungi are the dominant agents of OM decomposition in most soils (Paul and Clark, 1996). As with the bacteria, the diversity and ubiquity of fungi cannot be overemphasized. Cornejo et al. (1994) found over 500 morphospecies from litter of only five different tropical tree species using a single culture medium. Perhaps the most striking contrast to the bacteria is the mycelial growth form that allows a fungus to grow indefinitely towards nutrient sources and provide some protection from adverse environmental conditions (Sylvia et al., 1999). Additionally, the presence of unique reproductive structures in many taxa of fungi has allowed for simple isolation and determination of basic ecological characteristics. In fact, many of these general trends in fungal decomposer community dynamics first outlined in an excellent review by Hudson (1968), still hold today.

The decomposer fungi can be classified functionally by substrate-utilization/enzyme-production and by position, both spatially and temporally, along the SOM continuum. There exists an active biotrophic community of fungi on photosynthesizing leafs, such as the common leafsurface fungus, *Aureobasidium pullulans*, which often become the first wave of primary saprotrophs as a leaf senesces (Swift et al., 1979). After contact with the soil surface, the litter-dwelling primary saprophytic fungi, which can rapidly utilize simple and readily available carbohydrates, begin to colonize the leaf. These fungi are often referred to as the "sugar fungi" and are commonly members of the class Zygomycetes. After assimilation of these readily available energy sources, the cellulose decomposers (numerous genera of the ascomycetes) and associated secondary, often soil-borne, saprophytic sugar fungi that are dependent upon the hydrolytic products of the cellulose decomposers for nutrition become dominant (Garrett, 1981). Researchers often further distinguish the primary and secondary colonizers as surface or interior colonizers. Osono and Takeda (1999) summarize the differences between these groups: "The interior colonizers grow over the mesophyll and utilize such substrates as lignocellulose or readily available hexoses and pentoses. However, surface colonizers utilize two kinds of nutrients: endogenous substrates originating from relatively recalcitrant cuticular components above the epidermal cell walls, and exogenous substrates that deposit on the surface." The final stage in this generalized succession on leaf litter is the establishment of the lignin degrading and associated fungal communities (Garrett, 1981). This generalized succession has been demonstrated on many litter types including grain sorghum litter (Beare et al., 1993), black alder litter (Rosenbrock et al., 1995), and pine litter (Tokumasu, 1998).

Another important class of fungi are the Basidiomycetes which contain the dominant wood-rot species responsible for the decay of coarse woody debris (Paul and Clark, 1996). The wood-rot fungi are commonly divided into the white-rot and brown-rot fungi. The brown-rot fungi lack the ability to degrade lignin thus leaving behind a brown residue, while the white rots can simultaneously degrade lignin and complex carbohydrates (cellulose and hemicellulose) (Griffin, 1994). Paul and Clark (1996) also note that many of the basidiomycetes are facultatively parasitic—attacking and killing living trees and then growing as a saprotroph on the dead wood.

10.7.3.3 Soil Fauna

> Soil animals exist.I like soil animals.They respire too little.Ergo, they must CONTROL something!
>
> Faunophilic logic by O. Andrén

The term soil fauna encompasses a broad range of organisms from single-celled protozoa to burrowing earthworms to highly social insects such as the termites to mammals, e.g., pocket gophers and ground squirrels. In this review, we will limit the discussion to select groups of soil invertebrates. Although playing a small role in the direct mineralization of OM to CO_2, soil fauna greatly affect the functioning of the decomposer microorganisms both directly and indirectly as a result of their feeding habits (Seastedt, 1984). There are four basic roles that individual soil fauna play in detrital processing: (1) increasing microbial access to litter through communition and fragmentation; (2) ameliorating harsh environmental conditions that would hinder microbial processing; (3) mineralizing immobilized nutrients by grazing on microflora and fauna; and (4) stimulation and dispersal of microorganisms.

Protozoa. These single-celled eukaryotic organisms, lacking adaptations for a truly terrestrial existence, are restricted in habitat to the thin films of water in the soil matrix. Their distribution in soil is largely influenced by pore space size with flagellates and small amoebae occupying the smallest and most abundant pores. Small pores often are inaccessable to predators and stay moist due to presence of capillary water, protecting these smallest protozoa from desiccation. Larger pores, home to most amoebae, ciliates, and testecea, are subject to increased moisture variations leading to periods of low activity and encystment (Bamforth and Lousier, 1995). Typical population densities

range from 10^2 g^{-1} soil for desert sites to $>10^6$ g^{-1} soil in humid forest soils (Lousier and Bamforth, 1990).

Soil-dwelling protozoa obtain most of their nutrition through predation on bacteria. As a result of this feeding habit, protozoa play two important roles in detrital processing: (1) increased mineralization of nutrients through bacterial predation and (2) transformation of bacterial biomass into higher trophic levels (Bamforth and Lousier, 1995). As an example, Lousier and Parkinson (1984) found that the mean biomass of testacea in an aspen woodland was 72 g m^{-2}, with an annual production of 206 g m^{-2} resulting from the consumption of 1377 gm^{-2} of bacteria per year. These protozoa consumed 60 times the annual standing crop of bacteria in this system.

Nematodes. The importance of nematodes in decomposition and detrital processing is exemplified by the quote from B. G. Chitwood and M. B. H. Chitwood (1974): "Soil nematodes are of chief importance in the destruction of dead plant material, but they also take part in the decomposition of animal matter. Their inter-relationships with other organisms, both dead and alive, might easily be so great that if tomorrow they all disappear, a few weeks hence the foul odour of death might pervade the whole earth as the balance of life was destroyed." Nematodes occur in nearly all soils and feed on an incredibly diverse range of food. Sharma and Sharma (1995) identify three roles in decomposition: (1) the dispersal of microorganisms by carrying them on their body surface, by ingestion and subsequent defecation of bacteria and fungal spores, and by development of microflora in their faeces; (2) mineralization of nutrients by predation on microbes; and (3) their bodies act as stores of energy and nutrients for consumption by higher trophic levels.

The nematodes can be divided into groups based on general feeding habits. **Figure 6** highlights the diversity in mouth parts and digestive systems found in the soil nematodes. R. Sharma and S. B. Sharma (1995) recognized five functional groups of soil nematodes: (1) Plant feeders (order Tylenchida) are obligate parasites that feed using a stylet to pierce plant cell walls, predominately root tissue, and to suck sap. Wasilewska (1991) found that phytophagous nematodes can consume 3–20% of net root production in a drained peat soil. (2) Fungal feeders also use a stylet to pierce and withdraw hyphae contents. Many fungal feeders can also parasitize roots. (3) Bacterial feeders, such as Rhabditida, ingest material of suitable size and shape, but will only digest bacteria and some decaying OM. (4) Omnifeeders consume whole diatoms, blue-green algae, bacteria, and protozoa by sucking food particles into their oesophagus. (5) Predatory nematodes (e.g., order Mononchida) possess powerful teeth, jaws, or denticles with which they puncture, shred, or bite prey. Prey include protozoa, other nematodes, rotifers, tradigrads, and even small oligochaetes.

Nematode distribution follows the distribution of organic carbon sources in the soil. In an evergreen oak forest, fungal and bacterial feeders dominate in the rapidly decomposing surface litter with populations decreasing with increasing depth in the soil (Tanaka et al., 1978). In this study, Tanaka et al. (1978) also found that densities of nematodes in the surface litter varied by an order of magnitude between the wet and dry seasons. Actively feeding nematodes cannot tolerate desiccation and as such will be forced to either move away from dry regions or shift into a quiescent resting state. Starvation can also induce this anhydrobiotic state (Anderson et al., 1981).

Oligochaeta. This class includes the Enchytraeidae (the white worms) and the diverse group commonly referred to as the earthworms. The main differences between these two groups can be considered in terms of ecological strategies. The enchytraeids are largely *r*-selected species with a small body size, rapid development, a short life span, and high reproductive output (Dash, 1995). Alternatively, the earthworms can be generalized as *K*-selected species with a relatively large body size and long life span.

The enchytraeids through their grazing on litter and fungal populations play an important role in decomposition. Besides the indirect effects of microbial grazing listed above, the enchytraeids possess gut enzymes, including cellulase, indicating that they also play a direct role in the decomposition of plant litter (Dash et al., 1981). Populations reach maximums of 2×10^4 individuals m^{-2} in tropics and 10 times that number in many temperate regions (Dash, 1995). In a typical soil, an

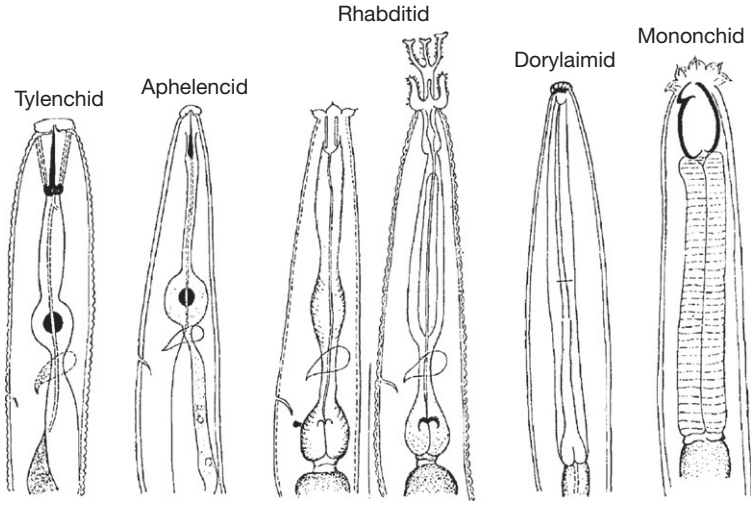

Figure 6 Diagram of mouth parts and oesophageal regions of selected soil nematodes (Sharma and Sharma, 1995) (reproduced by permission of Westview Press from *Soil Organisms and Litter Decomposition in the Tropics*, **1995**, pp. 75–88).

enchytraeid biomass of ~6 g m^{-2} can consume 3–20% of the annual energy input to the forest floor based on oxygen consumption data reviewed by Dash (1990).

Charles Darwin (1881) wrote: "It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures." The importance of earthworms in ecosystem functioning has indeed been recognized for centuries. Gilbert White (1789) wrote: "worms seem to eat earth, or perhaps rotten vegetables turning to earth... they perforate, loosen, and meliorate the soil, rendering it pervious to rains, the fibres of plants, and... without worms, perhaps vegetation would go on but lamely."

Edwards and Bohlen (1996) identified five major terrestrial earthworm families, with the Megoscolides (important in subtropical and tropical environments) and the Lumbricidae (temperate systems) being the most common. Earthworms occur across the globe, but rarely in extreme environments—deserts, permafrost, high mountains, and other regions lacking a well-developed soil. Most terrestrial earthworms are intolerant of salts, sensitive to very low or high pH, high temperatures, low soil moisture, and very clayey soil textures (Lee, 1985)—thus creating limits on their range. In many temperate regions earthworms dominate the soil faunal biomass (see **Table 3**). Fragoso and Lavelle (1992) compared soil faunal communities across a range of tropical forests and found that earthworms account for 51% of total biomass, followed by termites at 13%. A comprehensive review of earthworm biology and ecology is beyond the scope of this chapter. The interested reader is referred to the texts of Lee (1985) and Edwards and Bohlen (1996). Here we focus our review on the importance of earthworms in detrital processing.

Bouché (1977) identified three dominant ecological groups for the European lumbricid (**Table 5**), which have since been widely adopted to describe earthworms in all regions of the world. The epigenic worms live in the litter or upper organic horizons and feed almost exclusively on plant litter. These litter feeders are primarily agents of communition and fragmentation. The endogenic worms live in the mineral soil and feed by indiscriminately ingesting mineral soil. The anecic earthworms live in the mineral soil in permanent vertical burrows and consume partially decomposed litter after pulling the litter into their burrows. Anecic earthworms can comprise 50–75% of worm biomass in temperate zone, while often less than 10% in dry tropics (Edwards and Bohlen, 1996). Anderson and Swift (1983) state that no tropical earthworms are known to draw leaves down into the soil, but Fragoso and Lavelle (1992) showed that some earthworm communities are dominated by epigenic and anecic worms in tropical rainforests. Lavelle (1988) further divided the endogenic category into polyhumic (ingest soil with high OM content), mesohumic (feed indiscriminately on both mineral and organic particles), and oligohumic (feed on deep soil poor in OM) feeders.

During a normal wet year (1250 mm rainfall) at Lamto on the Ivory Coast of Africa, earthworm communities in this savannah contain 2000–4100 individuals ha^{-1}, weighing 350–550 kg fresh weight, which ingest 800–1250 Mg dry soil ha^{-1} containing 14–15 Mg OM ha^{-1} (Lavelle and Martin, 1992). At this site, Lavelle (1978) estimated that upwards of 60% of the humic pool in the upper 10 cm of the soil passes through the gut of earthworms annually (Martin, 1991). However, these high activity levels only result in 5–6% of the total soil heterotrophic respiration due to low assimilation of the worms (2–18%) (Edwards and Bohlen, 1996). Scheu (1991) found that 37% of the total carbon loss from a geophagous earthworm, *Octolasion lacteum*, was respired and 63% was excreted as high-energy, water-soluble mucous compounds. Most of the ingested soil material is excreted in discrete casts enriched in OM relative to the bulk soil. The sizes of the casts range from a few millimeters to several centimeters in length (Lee, 1985). The implications of these castings on detrital processing are discussed in detail in **Section 10.7.7**.

Most endogenic species form mutualistic relationships with microflora enabling digestion of low-quality substrates (Barois

Table 5 General diagnostic features of the major ecological groups of European lumbricid earthworms as described by Bouché (1977)

Diagnostic feature	*Epigeic species*	*Anecic species*	*Endogeic species*
Food	Decomposing litter on the soil surface; little or no soil ingested	Decomposing litter on soil surface, some of which is pulled into burrows; some soil ingested	Mineral soil with preference for material rich in organic matter
Pigmentation	Heavy, usually both ventrally and dorsally	Medium–heavy, usually only dorsally	Unpigmented or lightly pigmented
Size of adults	Small–medium	Large	Medium
Burrows	None; some burrowing in upper few cm of soil by intermediate species	Large, permanent, vertical burrows extending into mineral soil horizon	Continuous, extensive, subhorizontal burrows, usually in the upper 10–15 cm of soil
Mobility	Rapid movement in response to disturbance	Rapid withdrawal into burrow but more sluggish than epigeics	Generally sluggish
Longevity	Relatively short lived	Relatively long lived	Intermediate
Generation time	Shorter	Longer	Shorter
Drought survival	Survives drought in the cocoon stage	Becomes quiescent during drought	Enters diapause in response to drought
Predation	Very high, particularly from birds, mammals, and predatory arthropods	High, especially when they are at the surface; somewhat protected in their burrows	Low; some predation by ground-dwelling mammals and predatory arthropods

Source: Edwards and Bohlen (1996).

and Lavelle, 1986; Martin et al., 1992). Gut microorganisms are generally the same species found in soils; however, many earthworms also produce cellulose and chitin degrading enzymes (Edwards and Bohlen, 1996). Kristufek et al. (1992) examined the bacterial counts in the fore-, mid-, and hindguts of a detritivore *Lumbricus rubellus* and a geophagous earthworm *Aporrectodea caliginosa* and found that bacterial counts increased down the digestive pathway in the detritivore while they decreased in the geophage. Kristufek et al. (1992) concluded that the digestive canal could be considered as a fermentor of fresh plant residues for *L. rubellus*, while *A. caliginosa* cannot support a gut community due to the low quality of SOM and that this earthworm may, in fact, utilize the microbes as nutrient sources. Casts generally have higher fungi, actinomycetes, bacteria populations, and enzyme activity than surrounding soil (Dkhas and Mishra, 1986; Tiwari and Mishra, 1993). Microbial populations show a similar trend in burrows. Bhatnagar (1975) in a French grassland found 42% of soil aerobic nitrogen fixers, 13% of anaerobic nitrogen fixers, and 16% of denitrifiers associated with burrows.

Earthworm activity can influence microbial decomposition for a number of reasons (Lavelle and Martin, 1992): (i) there is a greater nitrogen concentration in casts; (ii) gut passage can stimulate dormant microbes; and (iii) increased bacteria/fungal ratio due to increase in soluble OM from mucus secretions. Trigo and Lavelle (1993) describe this relationship between earthworms and microflora as a mutualistic digestive system—the earthworms secrete mucus for the microorganisms in return for increased decomposition and nutrient release within the gut. A similar mutualistic relationship is believed to exist between plants and rhizosphere bacteria whereby the plants supply high-energy root exudates that the bacteria can rapidly mineralize, thus resupplying nutrients to the plant (Anderson et al., 1981).

Litter arthropods. In general, the dominant groups of litter arthropods are the mites (order Acari) and Collembola, with the Acarina dominating in monocotyledonous and deciduous leaf litter and the Collembola dominating in coniferous litters (Reddy, 1995a). The dominance of these two groups of mesofauna is diminished in the tropics, where the influence of several groups of macroarthropods, notably the termites, are greater (Swift et al., 1979). We will discuss the termites (order Isoptera) separately due to their disproportionate impact on decomposition processes in ecosystems where they are abundant.

Population densities of most litter arthropods are often correlated with substrate availability and microclimate. Many arthropods cannot tolerate dry conditions. Reddy and Venkataiah (1989) found that Collembola and Acarina were almost completely absent from *Eucalyptus* leaf litter during the hot dry summer months in Warrangal, India. Ecologically, the litter arthropods can be divided by food preference: litter or microbial feeders. Rihani et al. (1995a) studied the food preferences of three oribatid mites on a decomposition gradient of beech litter from fresh litter to fungal mycelium. They found that the mite *Damaeus verticillipes* preferred fungal hyphae in the leaves (microphytophage); *Steganacarus magnus* preferred the easily digestible parenchyma tissue in the leaves (macrophytophage); and *Achipteria coleoptrata* was intermediate in food preference (panphytophage). These feeding habits are supported by the gut enzyme activities (see **Section 10.7.5** for details on enzyme activities) of these three species—*S. magnus* showed only cellulase activity, while *D. verticillipes* showed chitinase and trehalase activity (Luxton, 1982).

Termites. The termites (order Isoptera), can be divided into six families (Kambhampati and Eggleton, 2000): Hodotermitidae (harvester termites); Termopsidae (rottenwood termites); Mastotermitidae (primitive Australian termites); Kalotermitidae (dampwood and drywood termites); Rhinotermitidae (subterranean termites); and Termitidae (higher termites). Approximately 85% of all known termites are considered higher termites which are differentiated phylo-genetically because they harbor only bacteria in their gut instead of a mix of protozoa and bacteria (Kambhampati and Eggleton, 2000). **Figure 7** highlights the dominantly tropical and subtropical distribution of termite diversity. The Rhinotermitidae can range 1000 km north of all other genera, because they make shelter tubes that keep them warm and moist (Eggleton, 2000). Termites are important agents in the decomposition of litter, wood, and soil humus.

The primary reason for the importance of termites in detrital processing stems from their symbiotic relationships with bacteria, fungi, and protozoa. Direct microscopic counts reveal densities of 10^9–10^{11} cells ml^{-1} of gut fluid, where often greater than 90% of the gut volume is occupied by protozoa in the lower termites (Breznak, 2000; Krasil'nikov and Satdykov, 1969). A very interesting and poorly understood observation is that these protozoa contain their own bacterial symbionts, often methanogens consuming the CO_2 and H_2 produced by the protozoa (Breznak, 2000; Lee et al., 1987). These gut symbioses are discussed in length in the text of Abe et al. (2000). Globally, the fermenting activity of termite-gut symbionts may add 10–50 Tg CH_4 to the atmosphere annually (Houghton, 1996).

The higher termites, especially the Macrotermitinae, have evolved symbiotic relationships where they cultivate a fungus (*termitomyces* spp.) on elaborate combs within more or less developed mounds or subterranean nests. Jones (1990) described this cultivation of fungus as a "short-circuiting" of the nutrient cycling and soil food web, resulting in greatly enhanced decomposition rates. These termite-fungal systems can process an extraordinary amount of litter. For example, Buxton (1981) observed that Macro-termitinae reprocessed greater than 90% of the dry wood in a semi-arid savanna in Kenya; Collins (1981) reported that 25% of the total litter fall (leaf + wood) was consumed annually by termites in a Nigerian savanna; and Whitford et al. (1982) estimated that termites may be responsible for upwards of 100% of all litter consumption in many dry regions of the world. Collins (1981) concluded that mound structure determines seasonality of feeding habits, with the more complex mounds having the most stable microclimate. *Macrotermes bellicosus* builds the most complex nest in the Nigerian savanna: the individual colonies of *M. bellicosus* can cultivate a fungal comb 3 m in diameter with a mound reaching 6 m in height (Collins, 1979).

10.7.3.4 Interactions

It is often tempting to describe decomposition as a purely biochemical process where enzymes catalyze the chemical breakdown of complex organic molecules. By ignoring the soil organisms, we would not only be missing a beautifully

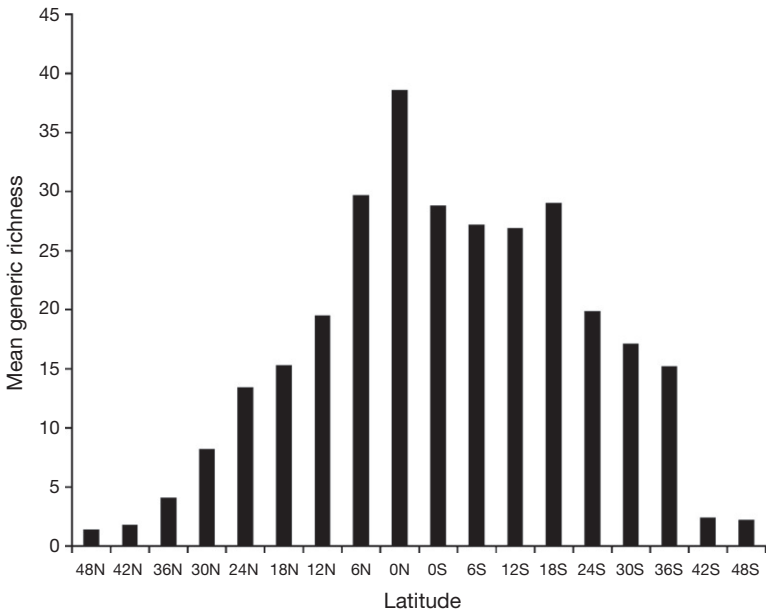

Figure 7 Latitudinal gradients of termite generic richness north and south of the equator (source Eggleton, 2000).

complex ecological system but also be missing important interactions that can have a profound effect on decomposition and nutrient cycling. In terms of carbon mineralization, microorganisms are the primary agents of decomposition and are often responsible for greater than 90% of the total heterotrophic respiration (Foissner, 1987). Soil fauna, alternatively, play a minor direct role in carbon mineralization but can have major indirect impacts on decomposition rates through their actions, including—communition and fragmentation of leaf litter; mixing of litter into the mineral soil; dramatically changing soil physical properties; predation on life plant tissue and on microorganisms; stimulation and dispersal of microbial communities; and mineralization of immobilized nutrients (see references within).

10.7.4 Methods for Studying Decomposition

Researchers have employed numerous techniques for studying OM cycling in the soil. We can broadly divide these methods into: (1) laboratory- or field-based techniques; and (2) litter- (including roots) or SOM-specific techniques. When trying to derive a mechanistic understanding of the controls on decomposition, Kirschbaum (2000) considered laboratory incubations to give a truer indication of the response to a manipulation of a single variable. By working in a highly controlled environment, laboratory studies will minimize the indirect effects of that manipulation which can often swamp the direct response. A simple example of this is that in Mediterranean environments soil moisture levels will often vary inversely with temperature (Xu and Qi, 2001). However, due to the numerous indirect controls on decomposition and SOM stabilization (Lavelle et al., 1993; Sollins et al., 1996), the true microbial response to a single variable measured in the laboratory may never be realized. The choice of field or laboratory methods will thus depend on the scope of the study: for microbial physiological studies, laboratory studies may be more appropriate, while field-based techniques may be more appropriate for deriving empirically based biogeochemical models of detrital processing.

10.7.4.1 Litter Techniques

In regions of the world where litter accumulates on the forest floor, annual decay rates can be estimated simply by measuring the litter fall *(L)* and the standing stock of recognizable litter (Olsen, 1963):

$$k = \frac{L}{X_{ss}} \quad (1)$$

where X_{ss} is the steady-state forest floor mass. More precisely, the mass/nutrient loss of a single cohort of litter can be followed through time and k can be estimated based on the shape of the decay curve. This is the basic premise behind both litterbag and isotopic labeling techniques for studying litter decomposition both in the field and in laboratory microcosms.

Confining a known mass of litter in a mesh bag and periodically measuring the mass loss and nutrient concentrations has proven to be an easy and cost effective method in litter decay studies. In addition, confining litter in bags with varying mesh sizes is an effective method for measuring the impacts of soil fauna on detrital processing (Seastedt, 1984). Seastedt (1984) presents a nice conceptual model of faunal influences on mass loss in a litterbag (**Figure 8**). A drawback of using large mesh sizes is that undigested fragments of litter can be lost from the bag, thus leading to an overestimate of the decomposition rate. Although communition is a critical aspect of decomposition in as far as it exposes more surface area to the microbial community, communition *per se* does not directly affect mass loss or nutrient mineralization (Witkamp and Olson, 1963). Confining litter in a small mesh bag may also affect fungal productivity (St. John, 1980); however, decay

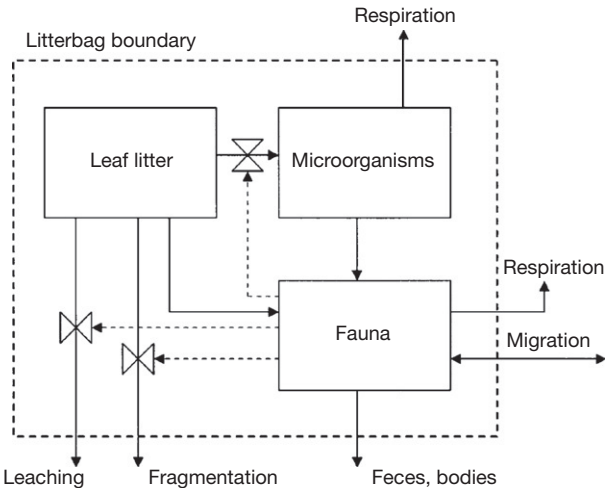

Figure 8 Conceptual model of mass loss of litter contained in litterbags. Solid arrows represent direct flows and indirect regulation by soil fauna is indicated by the dashed arrows (after Seastedt, 1984).

rates obtained from litterbag studies usually agree with results from laboratory microcosms (Seastedt, 1984).

Isotope techniques for studying litter decomposition include both natural ^{13}C abundance experiments (Balesdent et al., 1987) and ^{14}C and ^{15}N labeling experiments (Durall et al., 1994; Harmon et al., 1990b; Scheu, 1992; Van Veen et al., 1985). Natural abundance experiments take advantage of the 12–15‰ difference in the $\delta^{13}C$ value of vegetation from different photosynthetic pathways. $\delta^{13}C$ (‰) is defined as

$$\delta^{13}C = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1,000 \quad (2)$$

where R is the ratio of $^{13}C/^{12}C$ and the standard is Pee Dee Belemnite (PDB). For example, unconfined C4 grass litter ($\delta^{13}C \approx -13‰$) can be incubated with soil derived from a C3 forested site ($\delta^{13}C \approx -26‰$) and the CO_2 evolved can be divided into litter- and native SOM-derived CO_2 using a two-member mixing model:

$$f_{litter} = \frac{\delta_{CO_2} - \delta_{soil}}{\delta_{litter} - \delta_{soil}} \quad (3)$$

where f_{litter} is the fraction of litter-derived CO2 and δ_{CO2}, δ_{soil}, and δ_{litter} are the $\delta^{13}C$ of the evolved CO_2, the soil, and the litter, respectively (Balesdent et al., 1990). ^{14}C-labeling experiments follow the same premise, but the ^{14}C-CO_2 evolved can be measured directly by scintillation counting (Dalias et al., 2001b).

In studies of mass loss through time decomposition rate constants are not measured directly, necessitating the modeling of mass loss versus time to calculate a k value. The simplest model for this relationship is a zero-order decomposition model where mass loss progressively decreases with time. However, this model often does not capture observed trends and will yield unrealistic predictions as time gets large (Andren and Paustian, 1987). Most often, decomposition dynamics are represented as a first-order process—i.e., decomposition is proportional to the amount of material present:

$$M_t = M_0 e^{-kt} \quad (4)$$

Many authors find that a better fit is achieved with a parallel first-order model where the carbon substrate is divided into pools of similar decom posability (Dalias et al., 2001a). For example, a two-pool model with a labile, l, and recalcitrant, r, component:

$$M_t = M_0 \alpha e^{-k_l t} + M_0(1-\alpha)e^{-k_r t} \quad (5)$$

where α is the empirically derived labile carbon fraction of M. It is important to keep in mind that the α values obtained using a model such as Equation (5) to fit mass loss data do not necessarily represent any distinct pool of carbon that can be isolated in the laboratory.

Litterbags have become the primary tool for studying litter decomposition and nutrient dynamics in field studies. Although both litterbags and labeling studies are used in the laboratory, isotope labeling methods offer several advantages over litterbags. The decomposition products can be followed as they are incorporated into the mineral soil as more humified materials (Christensen and Sorenson, 1985). Additionally, researchers have labeled individual plant components, such as lignin (Scheu, 1992) and cellulose (Amato and Ladd, 1980).

10.7.4.2 SOM Techniques

Given that soils only contain a few percent OM by mass, direct measurement of SOM mass loss is much more difficult than for litter studies. The four most common techniques for measuring soil organic carbon (SOC) turnover are: (1) laboratory incubations; (2) *in situ* soil respiration measurements; (3) stable isotope measurements; and (4) radiocarbon methods. We will introduce the basic methodology and highlight some of the strengths and weaknesses of each of these four techniques. For much more detailed discussions of these methods, see the references cited within.

Laboratory incubations. Incubating sieved and homogenized soils in the laboratory under controlled moisture and temperature conditions and measuring the CO_2 evolution over a period of time is a simple and effective means of calculating the decomposition rate of SOM (Townsend et al., 1997). CO_2 evolution can be measured either by trapping the CO_2 released in an airtight chamber using an alkaline absorber such as granular soda lime (Edwards, 1982) or NaOH solution (Leiros et al., 1999), or by periodically measuring the CO_2 efflux rate via an infrared gas analyzer (IRGA) (Fang and Moncrieff, 2001). Decomposition rates (k) can then be calculated either by following the drop in respiration rates with time or by assuming steady-state conditions and dividing the respiration rate by the stock of carbon in the incubation (similar to Equation (1)). Theoretically, most of the initial CO_2 flux in an incubation experiment should be dominated by mineralization of the labile pool of SOM. This pool will be rapidly depleted without continued plant inputs, leaving a background mineralization rate of the much larger stabilized SOM pool (Townsend et al., 1997). This conceptual model is shown in **Figure 9**.

Kirschbaum (2000) believes that laboratory incubations give the truest microbial response to manipulations of temperature and moisture, because by sieving the soil roots have been removed and soil macrostructure, which can limit microbial

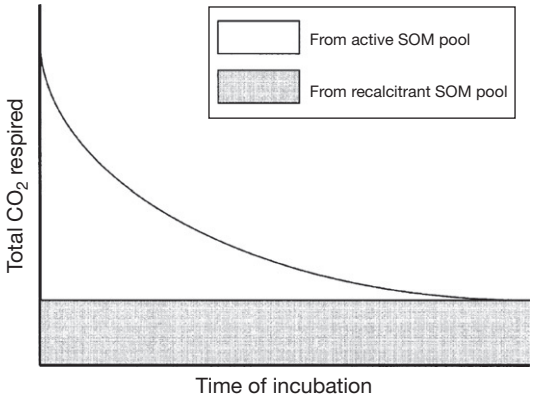

Figure 9 Theoretical contribution of active and recalcitrant SOM pools to total CO_2 respiration during a long-term laboratory incubation (after Townsend et al., 1997).

access to carbon (see **Section 10.7.7**), has been destroyed. In fact, Kirschbaum (2000) found that the temperature dependence of SOM decomposition was much more sensitive for laboratory techniques than for other techniques. However, this high-temperature sensitivity may never be realized *in situ* because of the complex array of direct and indirect controls on decomposition rates.

In situ *soil respiration measurements.* Respiration can be measured directly in the field to avoid the methodological artifacts discussed in the preceding section. A number of techniques have been used to measure the CO_2 efflux rate, including the soda lime and infrared gas analysis techniques mentioned above. Each of these techniques has its own strengths and weaknesses which have been compared and reviewed by several authors (Janssens et al., 2000, 2001; Pongracic et al., 1997). In order to get at the SOM decomposition rate, root respiration must be separated from microbial metabolism (i.e., heterotrophic respiration). This can be done analytically by assuming that roots contribute a fixed percentage to total soil respiration (Raich and Schlesinger, 1992) or experimentally by digging a trench around a plot and removing all aboveground vegetation (Boone et al., 1998; Melillo et al., 1996). Once the influence of roots is removed, decomposition rates can again be calculated using the simple steady-state model (heterotrophic respiration divided by the stock of carbon in the soil).

Stable isotopes studies. Numerous researchers have taken advantage of the difference in carbon isotope fractionation during photosynthesis of plants with C3 and C4 photosynthetic pathways as a natural tracer to study soil carbon dynamics (Balesdent et al., 1987). If a C3 forest is converted to a C4 pasture or C4 agricultural field, the whole soil carbon turnover time (τ) can be calculated as

$$\tau = \frac{-X}{\mathrm{In}\left((\mathrm{C3} - \mathrm{C}_{\mathrm{present}})/(\mathrm{C3} - \mathrm{C}_{\mathrm{initial}})\right)} \qquad (6)$$

where X is the time since conversion, C3-$C_{prefient}$ and C3-$C_{initial}$ are quantities of C3 forested-derived carbon at the present sampling (derived from a simple two-member mixing model similar to Equation (3)) and at time of conversion (usually an adjacent forested stand is used as a surrogate) (Giardina and Ryan, 2000). This technique can be expanded beyond the bulk soil by examining the amount of C4-C that has been incorporated into different size or density separates (Christensen, 1992). This method for calculating turnover time assumes that there is no fractionation as the new carbon is incorporated into the soil and that the soils are at steady state (i.e., the soils have not accumulated or lost any carbon since conversion).

An additional consideration is that if X is large enough (perhaps only 20–50 years depending on the climate), then much, if not all, of the original C3-derived carbon will have been mineralized long before the *present* sampling date (Neill et al., 1996), thus leading to an overestimation of the turnover time.

Radiocarbon approaches. Carbon-14 has proven to be a particularly powerful tool for studying the dynamics of C cycling in soils (Amundson et al., 1998; Trumbore, 1993). In particular, the "bomb-spike" of ^{14}C released to the atmosphere due to nuclear weapons testing has been utilized to study nearly all aspects of the biogeochemical cycling of carbon. In order to model the turnover of SOM using ^{14}C, several assumptions must be met (Gaudinski et al., 2000): (i) each SOM fraction is homogeneous with respect to decomposition; (ii) newly fixed photosynthate reflects the ratio of $^{14}C/^{12}C$ of that year's atmosphere; and (iii) ^{14}C does not fractionate during respiration. Based on these assumptions, the fraction of modern carbon in the soil (post-1950) normalized to a standard, F_s, which would be expected given a specific decay constant, k, in any given year, can be modeled as (Trumbore et al., 1996)

$$F_{s(t)} = \frac{C_{s(t-1)}F_{s(t-1)}(1 - k - \lambda) + (I)F_{\mathrm{atm}(t)}}{C_{s(t-1)}} \qquad (7)$$

where C_s is the carbon stock in a given pool at year t, λ is the radioactive decay of ^{14}C, and I is the annual carbon inputs to the whole soil. **Figure 10** shows the atmospheric record of ^{14}C as well as the expected values for soil carbon pools with turnover times of 5 yr and 50 yr based on Equation (7). To better constrain this model, ^{14}C measurements of archived soils can be compared to modern samples (Trumbore et al., 1996).

10.7.5 Detrital Processing

In this section, we will highlight the major biogeochemical pathways effecting detritus throughout the decomposition process. Swift et al. (1979) identified three distinct processes that combine to result in what is generally termed decomposition: comminution, leaching, and catabolism. The relative importance of these three processes will depend on numerous factors, including the location and type of litter, the soil faunal community, and the climate regime. These controls on detrital processes will be discussed in length in **Section 10.7.7**. Here we will examine the rates of decomposition, the roles of comminution, leaching, and catabolism in detrital processing, and the fate of nutrients during the decay process.

10.7.5.1 Time Course of Litter Decomposition

Long-term studies of litter decomposition have been primarily conducted in temperate forested ecosystems (Aber et al., 1990; Berg, 1984b; Berg and Staaf, 1980; Melillo et al., 1989). In a 77-month litterbag study at the Harvard Forest, MA, Melillo

and co-workers (Aber et al., 1990; Melillo et al., 1989) found that for two litters (red pine needles and paper birch leaves), decomposition can be described by a two-phase system: (i) a relatively constant fractional mass loss until ~20% of the original mass remains and (ii) a second phase of negligible rates of mass loss (**Figure 11**). Decay in phase I was best described by an exponential curve for the more palatable paper birch foliage, while the lignin-rich red pine needle was best fit by a simple linear function (see **Section 10.7.7.2** for the influence of resource quality on decomposition rates). Melillo et al. (1989) developed a simple decomposition model where the initial litter quality (i.e., nutrient concentrations and lignin to nutrient ratios) controls the decay rate until a point where the lignocellulose index (LCI) (ratio of lignin to lignin + cellulose) reaches 0.7–0.8, at which time the factors governing the decay of lignin will control the overall decomposition rate. Berg (1984b) found that decomposition of Scots pine root litter also followed this general two-phase model.

When litter accumulates to form a well-stratified organic layer on the soil surface (morsoils), litter depth can be used as a surrogate for time of decay (Gourbiére, 1982; Scheu and Parkinson, 1995). This allows for practical study of the products of late stages of decay. Gourbiére (1982) was able to identify 10 years worth of decaying Spruce needles in the

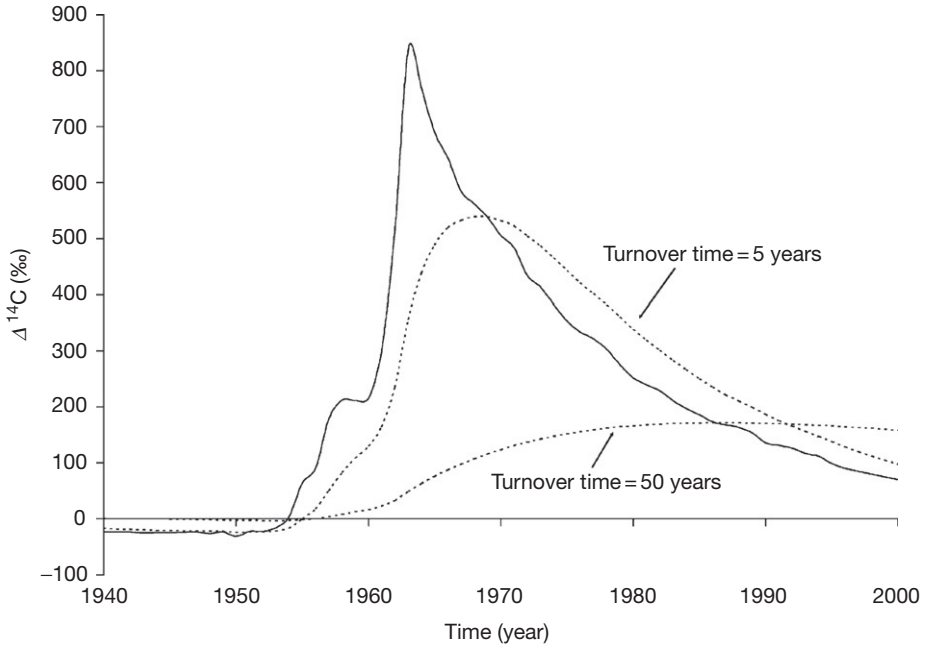

Figure 10 The atmospheric ^{14}C record in the Northern Hemisphere (solid line). Also shown are the modeled $\Delta^{14}C$ content of a homogenous, steady-state carbon pool with turnover times of 5 years and 50 years (Equation (7)) (dashed line).

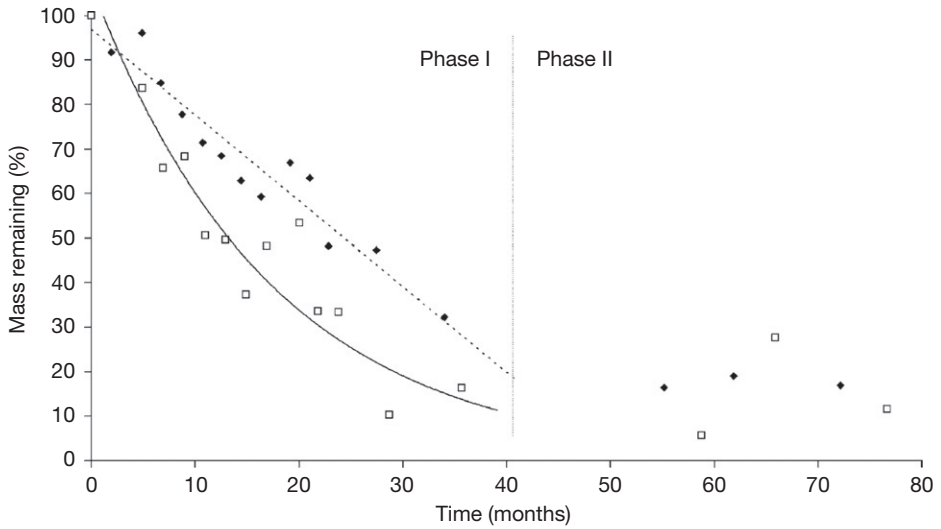

Figure 11 Percent of original mass remaining for red pine needle litter (filled diamonds) and paper birch foliage litter (open squares) versus time in months (sources Melillo et al., 1989; Aber et al., 1990).

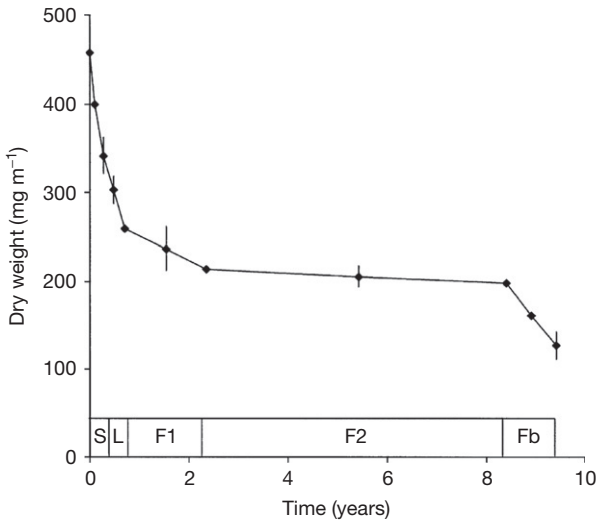

Figure 12 Decomposition dynamics of Spruce needles as indicated by increasing depth in the litter layers (S, L, F1, F2, and Fb). Fb = F layer that has been invaded by white-rot fungi (after Gourbiére, 1982).

organic horizons of a cool temperate forest (Figure 12). An initial phase of rapid decomposition occurred in years 0–2.5. This was followed by a long phase of relative inhibition of decomposition (years 2.5–8.5). Finally, a third stage consisting of rapid mass loss occurred as a result of the establishment of a community of white-rot fungi. If edaphic conditions favor bacteria over fungi, this third phase may not be present in a particular ecosystem.

Baldock et al., (1992) presented a model describing decomposition based on CPMAS ^{13}C NMR spectra obtained for decreasing particle size fractions (Figure 13). Decreasing particle size fractions have commonly been employed as a surrogate for extent of degradation, with fresh plant residues being associated with the largest size fractions (.>20 μm), partially degraded residues in the intermediate fractions (2–20 μm), and the most humified material associated with the finest fractions (<2 μm) (Christensen, 1992). As shown in Figure 13, the O-alkyl carbon peak at 73 ppm (simple carbohydrates, cellulose, and hemicellu lose) dominated the ^{13}C NMR spectra for the largest size fraction. Baldock et al. (1992) proposed that the relative increase in alkyl (32 ppm) and aromatic carbon

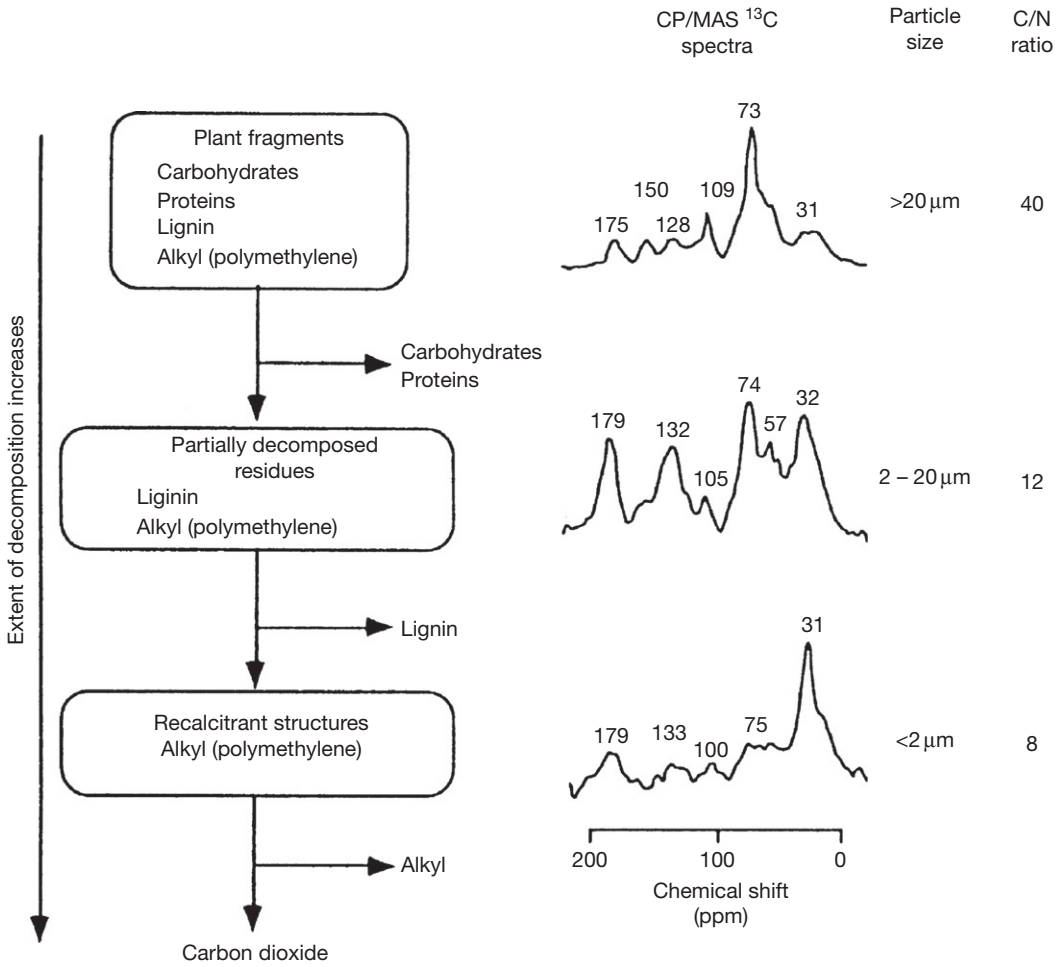

Figure 13 Decomposition model of Baldock et al. (1992) based on CPMAS ^{13}C NMR spectroscopy of a Mollisol (reproduced by permission of Kluwer Academic Publishers from *Biogeochemistry*, **1992**, *16*, 1–42).

(132 ppm) in the intermediate size fraction was due to the preferential degradation of carbohydrates and proteins with the selective preservation of more recalcitrant plant polymers. Microbial biomass was thought to be reason for the continued presence of O-alkyl carbon in this fraction. In the finest size fraction, aromatic carbon was lost indicating substantial lignin degradation. Baldock et al. (1992) proposed that the dominance of alkyl carbon in this fraction was due to the microbial synthesis of highly resistant compounds.

10.7.5.2 Comminution

The physical fragmentation of coarse litter by the feeding habits of soil invertebrates can significantly enhance the accessibility of organic compounds to leaching (Reddy and Venkataiah, 1989) and microbial attack (Wolters, 2000). Comminution also stimulates microbes by increasing the surface area of litter available for colonization (Kheirallah, 1990). Maraun and Scheu (1995) found a large increase in the maximum initial respiratory response of the microbial community when beech litter was fragmented to <25 mm^2. For a wide variety of deciduous litters, Seastedt (1984) found that microarthropods increased the average decay rate by 23% (litterbag exclusion studies lasting from 9 months to 30 months). The grinding of soil aggregates by geophagous fauna can also increase SOM accessibility by disrupting the bonds between soil particles (Lavelle and Martin, 1992; Wolters, 2000). Additional examples of soil faunal controls through comminution on decomposition can be found in **Section 10.7.7.1**.

10.7.5.3 Leaching

The infrequent sampling intervals in long-term litter decomposition experiments shown in **Figure 11** missed a small, but significant, fraction of the mass loss by leaching which occurs in the first few days to weeks of decomposition. Leaching not only contributes to the initial phases of decomposition (Ibrahima et al., 1995; Reddy and Venkataiah, 1989), but also transports organic C to underlying mineral horizons (Guggenberger and Zech, 1994). The degree to which leaching is a significant factor in the decomposition and stabilization processes depends on the local soil moisture regime, hydrologic properties, and the nature of the litter and its reaction products.

Leaching is often implicated as a reason for the faster than predicted loss based on exponential models (MacLean and Wein, 1978; Parsons et al., 1990). These models otherwise yield reasonable fits with most litter decomposition data (Taylor and Parkinson, 1988b). Mass loss attributable to leaching and that due to the microbial metabolism of water-soluble compounds are often hard to separate (Andren and Paustian, 1987). Laboratory studies where fresh litter is submerged in deionized water provide data on leaching losses (Nykvist, 1959, 1961; Taylor and Parkinson, 1988b). Water absorption and leaching loss curves are shown in **Figure 14** for aspen and pine litter. The striking differences in the curves for aspen and pine litter can be best explained in terms of the complexity of leaf architecture. In aspen leaves, water only has to penetrate the cuticle to access hydrophilic compounds, while in pine needles, lignified tissues protect much of the potentially soluble materials (Taylor and Parkinson, 1988b).

Because low-molecular-weight compounds such as sugars, simple carbohydrates, and ionic nutrients are preferentially leached from fresh litter (Berg and Wessen, 1984), the remaining chemical components become more recalcitrant. This will alter the decomposability of the remaining litter (**Figure 15**). Parsons et al. (1990) found that the preleached litter had lost 32% of total mass and nearly 60% of labile materials, and decomposed at a significantly reduced rate relative to the intact litter. Using a single exponential model, the underestimate in the intercept for the unleached aspen litter corresponded closely with the amount of mass loss that Parsons et al. (1990) attributed to leaching.

Physical fragmentation of litter also influences the leaching rates. By comparing mass and nutrient loss rates from litter in fine- and coarse-meshed litterbags that were both suspended and on the ground, Reddy and Venkataiah (1989) found that leaching losses were only significant in litter that was comminuted by soil fauna. Potassium is generally considered to be a highly mobile element that is not required by microorganisms to mineralize OM (Witkamp and Crossley, 1966). Potassium concentrations decreased nearly 50% in the first month for the litter altered by soil fauna, while litter in suspended litterbags only lost ~15% of the initial potassium concentration (Reddy and Venkataiah, 1989).

On longer timescales, leaching of DOM from the organic layer to the underlying mineral soil plays an important role in soil development and long-term carbon storage by transporting carbon deep within a profile. For three forest soils, Guggenberger (1992) estimated that between 66% and 91% of the annual carbon inputs to the mineral soil are due to DOC fluxes from the organic horizons (Guggenberger and Zech, 1994). Neff and Asner (2001) estimated that the annual carbon flux from the organic horizons in a temperate forest was 10–40 g DOC m^{-2}, which contributed 25% of the total soil profile carbon. Based on a review of DOC chemical characterization literature, Currie and Aber (1997) found that the majority of the forest floor leachate is comprised of fairly recalcitrant lignocellulose-associated materials and that only 15% could be considered labile materials. This DOC leaving the organic horizons is comprised mainly of partially degraded plant compounds and microbial biooxidation products, and can be considered important humus precursors (Guggenberger and Zech, 1994).

DOC transport through the soil and its concentration leaving a soil profile depends on abiotic sorption and desorption reactions with mineral surfaces. The tendency for organics to be strongly sorbed to soil particles through a variety of bonds can explain the order of magnitude drop in DOC fluxes in subsurface horizons (Neff and Asner, 2001; Ugolini et al., 1977). For example, at the Harvard Forest, Massachusetts, Currie et al., (1996) found that greater than 50% of the total dissolved nitrogen (TDN) and DOC leached from the organic horizons are retained in the underlying mineral soil (**Table 6**). **Table 6** also highlights the fact that DON is the dominant form of nitrogen leached from this system. In a mixed hardwood forest in North Carolina, Qualls et al., (1991) found that although throughfall consisted of 50% inorganic nitrogen, leachate from the base of the Oa horizon consisted of >90% DON. Additionally, across a range of unpolluted South American forests, Perakis and Hedin (2002) showed that nitrogen losses were dominated by DON.

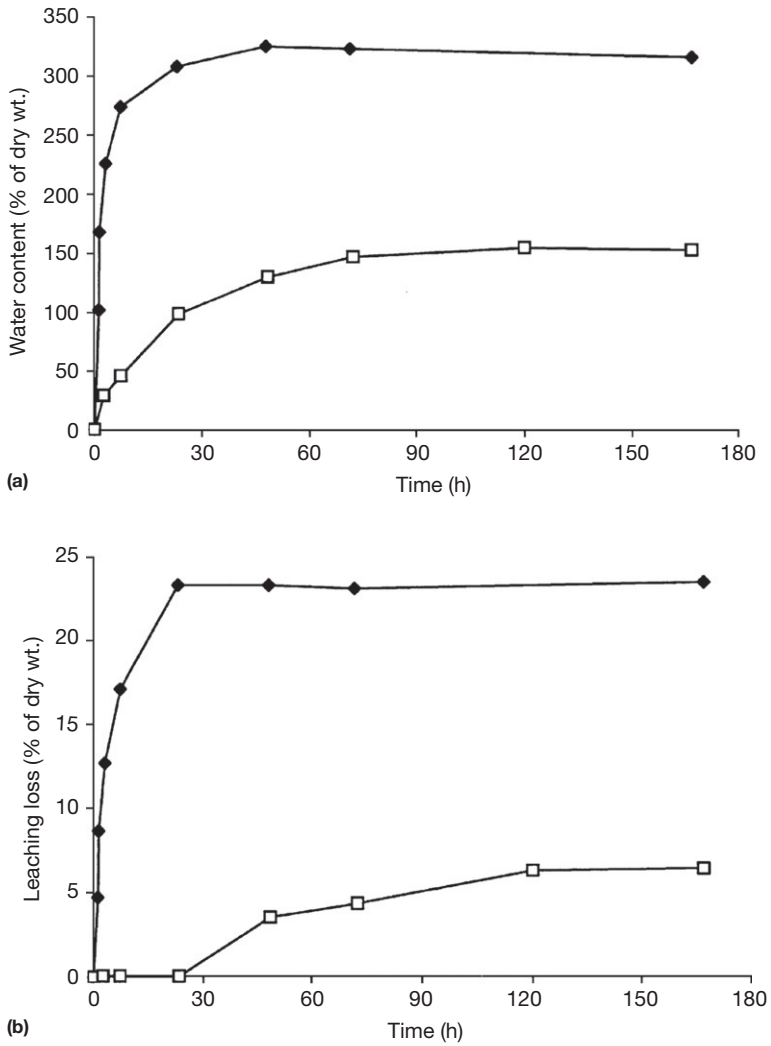

Figure 14 Rates of: (a) water absorption and (b) leaching loss from 5 g of pine needles (open squares) and aspen leaves (filled diamonds) immersed in 1.5 L of deionized water (after Taylor and Parkinson, 1988b).

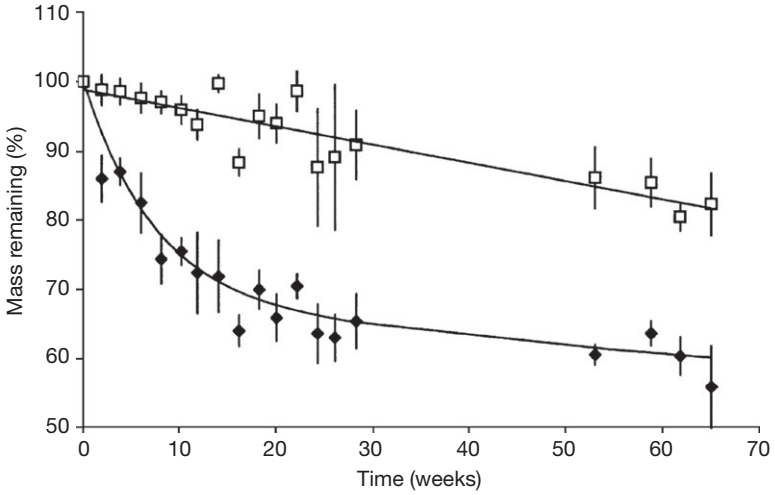

Figure 15 Mass loss (% original mass remaining) from intact (filled diamonds) and preleached (open squares) aspen leaf litter. Preleached litter had lost 31.7% of original mass before onset of incubation. A linear regression best described the mass loss of the preleached litter ($r^2 = 0.57$ $P < 0.05$), while a double exponential model (i.e., Equation (5)) best described the mass loss of the intact litter ($r^2 = 0.79$ $P < 0.01$) (after Parsons et al., 1990).

10.7.5.4 Catabolism

There are very few materials, natural or man made, that microorganisms cannot degrade (Ratledge, 1994). Upwards of 95% of total heterotrophic respiration is derived from microbial mineralization of OM (Lavelle and Spain, 2001). However, fungi and bacteria are only capable of ingesting monomeric and some dimeric compounds. These organisms digest macromolecular complexes *in situ* by secreting numerous extracellular enzymes (Griffin, 1994). Extracellular enzymes catalyze the cleavage of large molecules into monomeric subunits which can then be transported into the cell where intracellular enzymes will help complete the metabolic process. **Table 7** lists the major classes of enzymes and the reactions that each catalyze. Of these enzyme classes, the hydrolases are especially important because they catalyze many of the reactions involved in the biogeochemical transformations of C, N, P, and S, and are an integral component of detrital processing (Taylor et al., 2002).

The major biochemical constituents of detritus (i.e., water-soluble carbohydrates, cellulose, hemicellulose, lignin, proteins, phenols, lipids, waxes, and other secondary plant compounds) differ in their ease of microbial degradation (Minderman, 1968). Microorganisms degrading fresh litter will preferentially metabolize the easily accessible, high energy-yielding compounds first. Numerous field studies have found that lignin degradation is often delayed by several years (Berg et al., 1982; Gourbiere, 1982;

Table 6 Annual solute fluxes for a red pine and mixed hardwood stand in the Harvard Forest, MA

Flux or flux difference	NO_3^-N *($g m^{-2} yr^{-1}$)*	NH_4^-N *($g m^{-2} yr^{-1}$)*	DON *($g m^{-2} yr^{-1}$)*	TDN[a] *($g m^{-2} yr^{-1}$)*	DOC *($g m^{-2} yr^{-1}$)*
Red pine stand					
Throughfall	0.696	0.223	0.348	1.27	13.9
From Oa	0.604	0.138	0.953	1.70	39.8
From subsurface	<0.001	0.010	0.536	0.549	16.7
Illuviated and retained[b]	0.604	0.128	0.417	1.15	23.1
Hardwood stand					
Throughfall	0.488	0.181	0.268	0.938	11.7
From Oa	0.199	0.104	0.611	0.915	22.5
From subsurface	0.002	0.003	0.319	0.324	12.3
Illuviated and retained[b]	0.197	0.101	0.292	0.591	10.2

[a]TDN = total dissolved nitrogen

[b]Material illuviated into mineral soil and retained there, calculated as flux from Oa minus flux from subsurface.

Source: Currie et al. (1996).

Table 7 Major classes and subclasses of enzymes and the corresponding types of reactions catalyzed

Class	*Representative subclasses*	*Types of reactions catalyzed by enzyme class*
Oxireductases	Dehydrogenases Oxidases Reductases Oxygenases Peroxidases Catalases	Catalyze oxidation–reduction reactions. Important in fermentation and respiration pathways.
Transferases	Aminotransferases Kinases	Catalyze the transfer of molecular constituents among molecules.
Hydrolases	Glycosidases Peptidases Phosphatases Ribonucleases	Catalyze the hydrolytic cleavage of chemical bonds.
Lyases	Decarboxylases Synthases Lyases	Catalyze the addition or removal of chemical groups such as carbon dioxide, ammonia, and water.
Isomerases	Racemases Isomerases	Catalyze inversions at asymmetric carbon atoms and the intramolecular transfer of molecular constituents.
Ligases	Synthetases Carboxylases	Catalyze the binding of two molecules with the expenditure of ATP. Important in anabolic pathways.

Source: Fuhrmann (1999).

Scheu and Parkinson, 1995) until the appropriate fungal communities become established in the litter and begin producing the enzymes required to degrade these complex substrates. **Figure 16** illustrates this fact: crude proteins and soluble components are the first materials to be degraded and their relative proportions decrease rapidly; polysaccharides that comprise the semicrystalline cellulose (glucans) and hemicellulose (most of the nonglucan poly saccarides) remain in their initial abundances for over one year; and the absolute amount of lignin did not change for over two years (Berg et al., 1982).

Microbial metabolism can be divided into two general functions, the anabolic building of structural and functional components of the organism and the catabolic extraction of energy through the breaking of chemical bonds. Swift et al. (1979) defined catabolism as "the biochemical term which describes an energy-yielding enzymatic reaction, or chain of reactions, usually involving the transformation of complex organic compounds to smaller and simpler molecules." Anabolism, the synthesis of cellular materials from simpler metabolic and nutritive sources, is dependent upon catabolism for both energy in the form of ATP, NAPH, and NADPH, and the production of critical reaction intermediates (Griffin, 1994). More information on microbial metabolism and the biochemistry of microbial catabolism is available in the texts of Griffin (1994) and Ratledge (1994). In this section, we highlight some important molecular aspects of the biochemical degradation of the major plant and microbial materials.

Water-soluble organic compounds such as simple sugars, free amino acids, and organic acids are readily available for utilization by the vast majority of microorganisms. Root exudates also contribute significantly to the water-soluble pool of rapidly metabolized organic materials. Simple sugars and free amino acids can directly be transported into the cell and undergo glycolysis and then enter the appropriate metabolic pathway (Ramsh et al., 1994; Wagner and Wolf, 1999). Depending on microbial species, disaccharides can be transported directly into the cell to undergo hydrolysis or the molecule can be hydrolyzed outside the cell and then transported (Griffin, 1994). For example, Sutton and Lampen (1962) found that the yeast *Saccharomyces cerevisae* converted sucrose to glucose and fructose at the cell surface then transported the monomeric compounds into the cell. In a similar manner, peptidase will catalyze the cleavage of the peptide bonds of polymeric proteins and then the individual amino acids can be transported into the cell.

The structural components of most plant cells contain most of their carbon in the form of complex carbohydrates, the most common being cellulose (**Figure 17**). Cellulose consists of a pseudocrystalline array of linear β-1, 4-glucan molecules, interspersed with amorphously linked regions, with hydrogen bond cross-links between chains (Paul and Clark, 1996). Individual cellulose molecules may contain upwards of 10^4 glucose units (Wagner and Wolf, 1999). Microbial cellulolysis is a complex process involving a number of extracellular enzymes that will vary with species (Wood and Garcia-Campayo, 1994). The aerobic soft-rot and white-rot fungi, and some aerobic bacteria, use a three-enzyme system consisting of an exoglucanase (normally cellobio-hydrolase), endoglucanase, and β-glucosidase (Eriksson and Wood, 1985). Exoglucanase cleaves disaccharide cellobiose units from the nonreducing ends of cellulose chains and is mainly responsible for breaking interchain hydrogen bonds. Endoglucanase hydrolyzes the internal bonds of cellulose chains, while β-glucosidase hydrolyzes cellobiose to glucose (Griffin, 1994). Brown-rot fungi do not produce exoglucanases and likely use a decomposition mechanism involving H_2O_2 (Wood and Garcia-Campayo, 1994). The anaerobic bacteria use

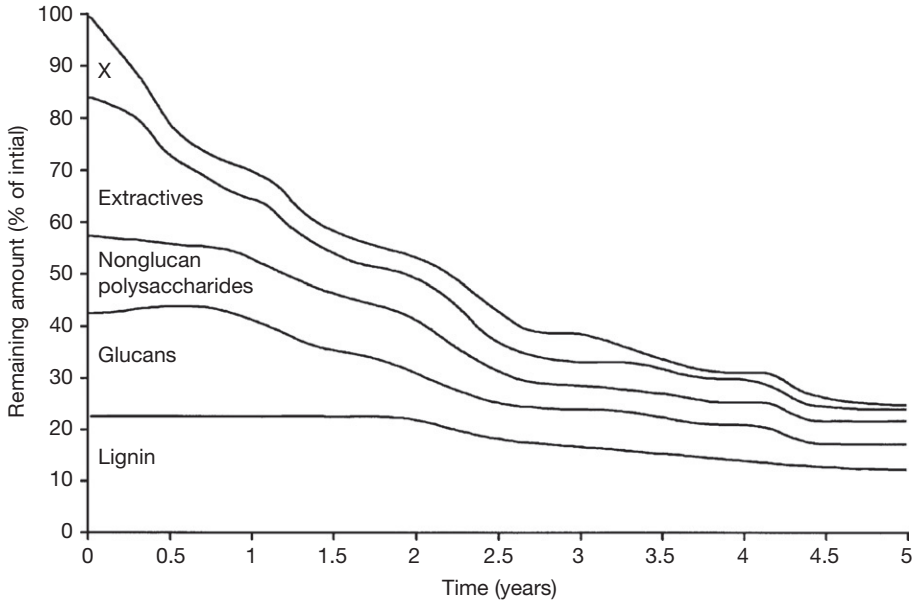

Figure 16 Changes in the composition of Scots pine needle litter during five years of decomposition. X corresponds to crude proteins, polyurinodes, ash, and unspecified products (after Berg et al., 1982).

a membrane-bound multi- component protein-enzyme complex called a cellulosome, of which the detailed biochemistry is just beginning to be worked out (Schwarz, 2001).

While the composition of cellulose is consistent between groups of plants, the composition of hemicellulose and lignin can vary dramatically. Generally found in association with cellulose in the secondary walls of plants, hemicelluloses are branched heteropolymers containing several simple sugars, including xylose, mannose, glucose, galacatose, arabanose, and glucuronic acid (Griffin, 1994; Wagner and Wolf, 1999). Hardwood hemicellulose is often comprised of a glucoxylan backbone with uronic acid branches (**Figure 18**), softwood hemicellulose is comprised of glucomannan backbone with uronic acid branches, and grasses (graminaceous plants) can have either of these general configurations (Dekker, 1985; Jeffries, 1994). Numerous endo and exo-xylanases and mannanases acting on specific cross-linkages have been characterized (Jeffries, 1994). Several accessory enzymes including esterases, arabinofuranosidases, and glucuranosidases are also required for hemicellulose biodegradation (Jeffries, 1994). Despite the complex array of enzymes required to degrade hemicellulose, hemicellulose is often observed to decay at a rapid rate (e.g., **Figure 16**).

Lignin is synthesized by a polycondensation process involving free radicals in plant cells from three phenol propane building blocks: coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol (Jeffries, 1994). Due to the random nature of its synthesis, lignin does not show a specific structure (Paul and Clark, 1996) and the relative proportions of the phenol propanoid units will vary according to plant source (Griffin, 1994). However, a generalized structure highlighting the propanoid units and the various linkages and side chains can be drawn (**Figure 19**). In plant cells, lignin is the impregnating material that protects the cellulose and hemicellulose matrix from enzymatic attack (Griffin, 1994). Lignin decomposition differs greatly from the biodegradation of all other plant materials for several reasons. First, only a particular group of basidiomycete fungi called the white-rot fungi have been shown to completely mineralize lignin to CO_2. Second, lignin is degraded by oxidative rather than hydrolytic attack. Third, lignin degradation requires an accompanying cometabolizable substrate to provide the carbon and energy for fungal growth (Buswell, 1991). Additionally, strict aerobic conditions and nitrogen limitations have been shown to be required for active lignin degradation (Buswell, 1991; Fog, 1988). Because of the energy costs involved in its decomposition, lignin decomposition probably only occurs because it is protecting a substantial amount of simpler carbon- and nitrogen-containing materials. Before lignin degradation can begin, the cellulose-rich secondary wall must be at least partially degraded in order for the fungi to attack the lignin. Rihani et al. (1995b) found that lignin loss rates in beech litter increased significantly after two weeks of incubation when ~20% of the cellulose content had disappeared.

Three families of extracellular enzymes have been implicated in lignin degradation: lignin peroxidases (ligninases),

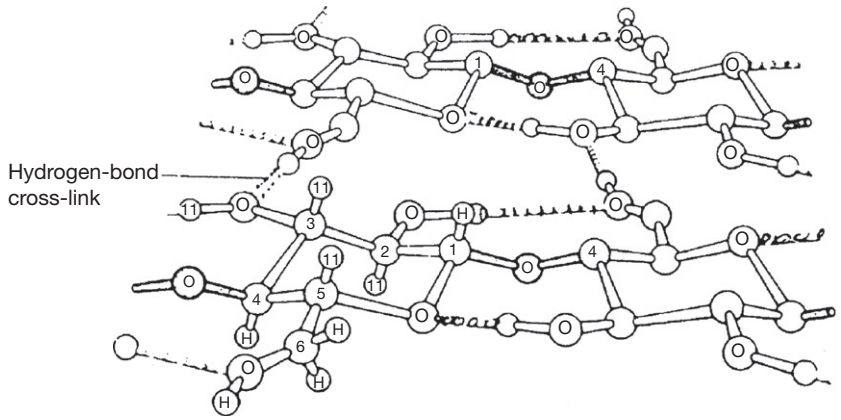

Figure 17 The structure of cellulose (Paul and Clark, 1996) (reproduced by permission of Elsevier from *Soil Microbiology and Biochemistry*, **1996**).

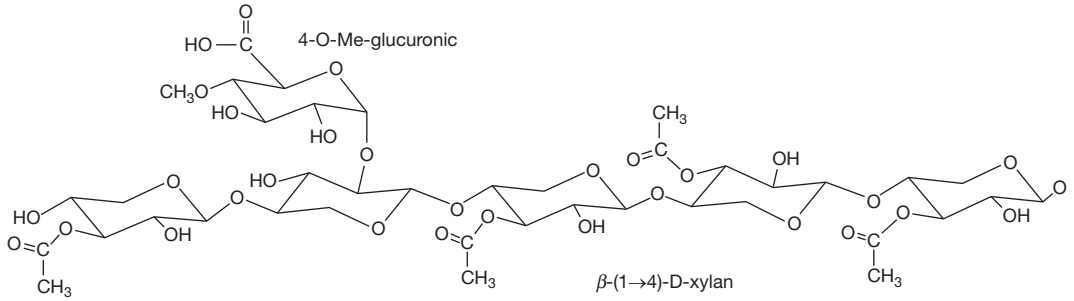

Figure 18 *O*-Acetyl-4-*O*-methyl-D-glucuronoxylan, a type of hemicellulose, structure from angiosperms (Dekker, 1985) (reproduced by permission of Academic Press from *Biosynthesis and Biodegradation of Wood Components*, **1985**).

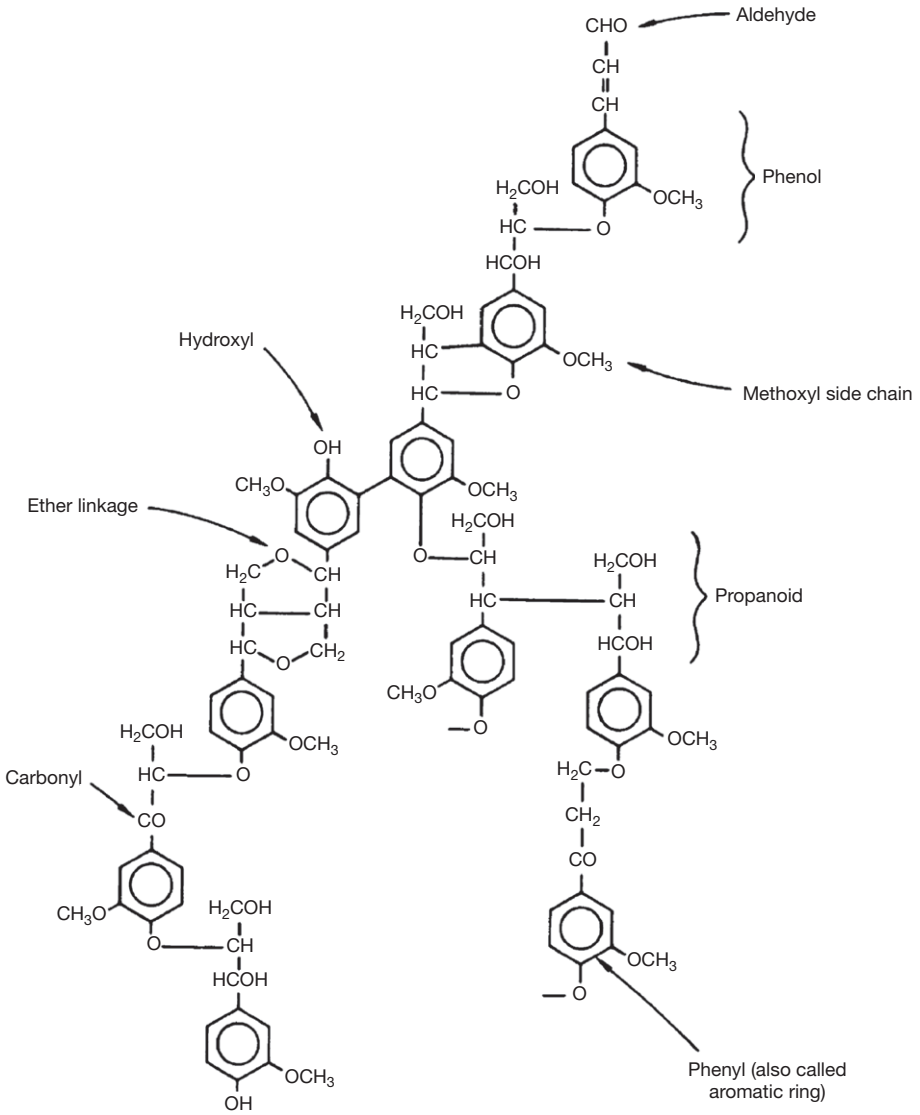

Figure 19 Generalized lignin structure, showing the common functional groups (Paul and Clark, 1996) (reproduced by permission of Elsevier from *Soil Microbiology and Biochemistry*, **1996**).

manganese-dependent peroxidases, and phenol oxidases (Griffin, 1994). The ligninase enzyme system consists of a heme-protein (iron containing) that interacts with H_2O_2 in cyclic oxidation–reduction reactions that results in the oxidative cleavage and removal of a variety of functional groups (Buswell, 1991; Kirk and Farrell, 1987). The manganese peroxidases are distinguished from lignin peroxidases by their requirement of Mn^{2+} and by their ability to catalyze the demethoxylation of aromatic methyl esters, to act as a methyl esterase, and to oxidize several phenols (Buswell, 1991). Lignin peroxidase uses the iron in the heme-protein as an electron donor, while manganese peroxidase, which also contains the heme-protein, uses manganese as the electron donor. White-rot fungi also produce several phenol oxidases, including the copper-containing laccase (Griffin, 1994). The exact biodegradative role of laccase and other phenol oxidases has been difficult to ascertain, because polymerization reactions dominate *in vitro* experiments (Buswell, 1991). *In vivo*, quinine-oxidoreductases are thought to limit phenol polymerization reactions (Buswell, 1991; Chung et al.,2000).

In soils, microbial cell walls make up a significant portion of the organic nutrient reserves. Bacteria have a peptidogylcan cell wall composed of repeating units of *N*-acetylglucosamine and *N*-acetylmuramic acid joined by amino acids through peptide linkages (Paul and Clark, 1996). Fungal cell walls also contain significant amounts of chitin, a crystalline chain of *N*-acetylglucosa-mine with $\beta(1\rightarrow4)$ linkages (**Figure 20**). Many bacteria and fungi are capable of degrading microbial cell walls producing both glucanase and chitinase degrading enzyme systems. Most commonly, chitin is degraded by the hydrolysis of glycosidic bonds (Gooday, 1994): exochitinase cleaves diacetylchitobiose from the ends of chitin chains; endochitinase cleaves glycosidic linkages randomly along chitin chains; and the diacetylchitobiose will be hydrolyzed to *N*-acetyl-glucosimane by *β*-*N*-acetylglucosaminidase. An

alternative pathway utilized by some microorganisms is via deacetylation of chitin to chitosan which is then hydrolyzed by chitosanase to chitobiose, which, in turn, is cleaved by glucosaminidase to yield individual glucosamine units (Gooday, 1994).

10.7.5.5 Change in Nutrient Status

The combined action of comminution, leaching, and catabolism results in patterns of mass loss such as shown in Figures 11 and 12. As the dominant element in plant tissues, carbon loss will mirror the mass loss. However, the rates at which other important nutrient elements are lost may vary significantly. Changes in nutrient status during decomposition can be generalized into three phases: initial leaching, bioaccumulation/ immobilization, and final mineralization (Berg and Staaf, 1981; Cornejo et al., 1994; Gosz et al., 1973). Nutrients that are nonlimiting to microbial growth such as potassium, magnesium, and sodium will rapidly be leached and mineralized (Bubb et al., 1998), while limiting nutrients such as nitrogen and phosphorus will follow this three-phase model (Staaf and Berg, 1982). **Figure 21** highlights the differential behavior of nutrient loss for Scots pine litter decomposition in central Sweden. Gosz et al. (1973) hypothesized that when nutrient loss is greater than mass loss leaching must be the dominant removal pathway, and when nutrient loss is less than or equal to mass loss mineralization will dominate the eventual release of the nutrient.

Numerous researchers have reported a mobility series for major nutrients released during the decomposition of different litters (**Table 8**). In the chaparral of southern California, Schlesinger and Hasey (1981) found that after one year, potassium was almost completely lost from both *Salvia* and

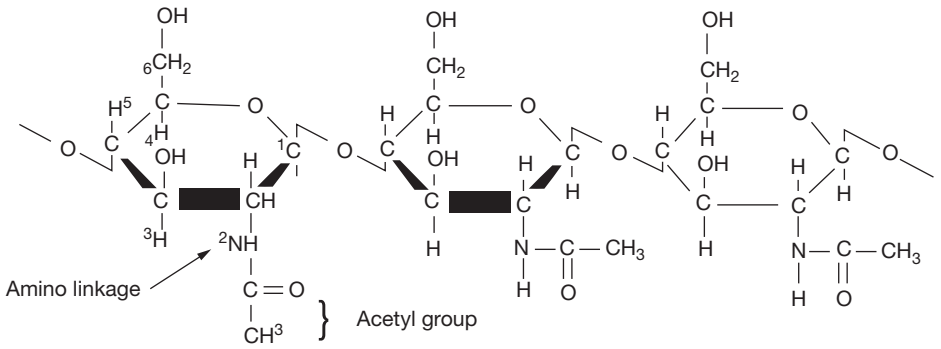

Figure 20 The structure of chitin (Paul and Clark, 1996) (reproduced by permission of Elsevier from *Soil Microbiology and Biochemistry*, **1996**).

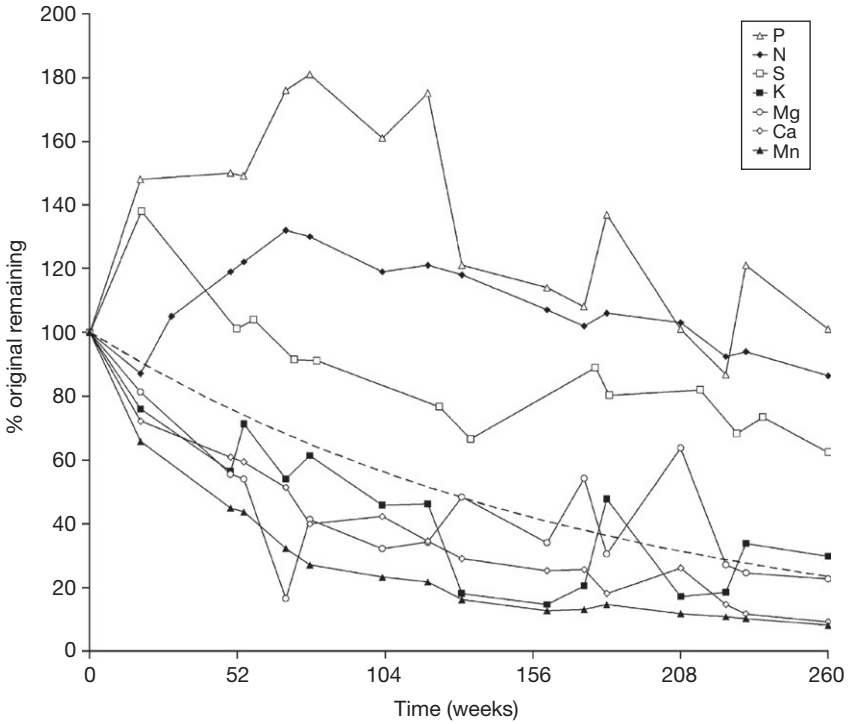

Figure 21 Changes in absolute amounts of plant nutrients for Scots pine needle litter during five years of decomposition. The dashed line shows the fitted exponential decay for mass loss of organic matter (after Staaf and Berg, 1982).

Table 8 Nutrient mobility series for decomposition of various litters

Litter species	*Ecosystem*	*Ref.*[a]	*Mobility series*
Scots pine	Boreal forest	1	Mn > Ca > K > Mg > S > N > P
Mixed hardwood	Temperate forest	2	K > Mg > P > Ca ≈ S > C > N
Beech and fir	Temperate forest	3	K > P > Mg > Ca ≈ N
Ceanothus	Chaparral	4	K > Mg > Ca ≥ N > P
Salvia	Chaparral	4	K > P > Mg > Ca > N
Evergreen oak and stone pine	Mediterranean	5	K > P ≈ Mg ≈ C > Ca > N
Hoop pine	Subtropical forest	6	K > Na > C > Mg > P > N > Ca > Mn
Three legume species	Tropical plantation	7	K > P ≈ N ≈ Mg > C > Ca

[a]References: 1. Staaf and Berg (1982); 2. Gosz et al. (1973); 3. Rutigliano et al. (1998); 4. Schlesinger and Hasey (1981b); 5. Regina (2001); 6. Bubb et al. (1998); and 7. Palm and Sanchez (1990).

Ceanothus litter, phosphorus showed a 50% decline in the phosphorus-rich *Salvia* but actually bioaccumulated in the phosphorus-poor *Ceanothus* litter, magnesium and calcium were lost at a slightly greater rate than overall mass loss for both species, and nitrogen showed a net immobilization over the one-year study period. In a seasonally dry tropical forest, Cornejo et al. (1994) found that for several deciduous litter species potassium and phosphorus were rapidly leached, nitrogen was bioaccumulated, and magnesium and calcium concentrations increased because of abiotic exchange reactions. These authors concluded that the divalent cations, magnesium and calcium, were preferentially absorbed as the more mobile monovalent cations were leached from exchange sites on clays and OM. Calcium is also known to accumulate as calcium oxalate in fungal biomass reducing its relative mobility (Cromack et al., 1975; Palm and Sanchez, 1990).

Gosz et al. (1973) found that carbon-to-nutrient ratios are critical in determining both the percent increase or decrease in a particular nutrient's concentration as well as the initiation of nutrient release. **Figure 22** highlights the importance of the initial carbon-to-nutrient ratios in determining the final nutrient content after two years of decomposition (Rutigliano et al., 1998). Researchers recognize a critical C : N ratio in forest soils between 20 and 30 (Lutz and Chandler, 1946). At higher ratios nitrogen is immobilized, while at lower ratios nitrogen is released or mineralized. In most ecosystems, the preferential degradation of simple carbohydrates in the initial phases of decomposition leads to an increase in the concentration of nitrogen (Berg and Staaf, 1987; Lousier and Parkinson, 1978; Rustad, 1994; Rutigliano et al., 1998). However, researchers have also found that the *absolute* quantity of nitrogen increases (Berg and Staaf, 1980; Gosz et al., 1973; Lousier and Parkinson, 1978; Schlesinger, 1985). This indicates that the litter-degrading microorganisms are accessing and immobilizing an exogenous supply of nitrogen.

As decomposition proceeds, the C:N ratio declines as organic carbon is lost from the system as CO_2 and the C : N ratio of stabilized SOM approaches the C : N ratio of the microbial biomass. In a forest soil, Scheu and Parkinson (1995) found that the C:N ratio dropped from 37.5 in fresh litter to 20.7 in the organic horizons and to 9.3 in the first mineral horizon.

Results from fertilization experiments generally support the contention that nitrogen is often a limiting nutrient to microbial growth during the initial phase of litter decomposition (French, 1988). Additionally, the form of applied nitrogen can exert a strong influence on the microbial response (Rastin et al., 1990; Scheu and Parkinson, 1995). In a temperate forest, Scheu and Parkinson (1995) found that ammonium, not nitrate, stimulated microbial respiration.

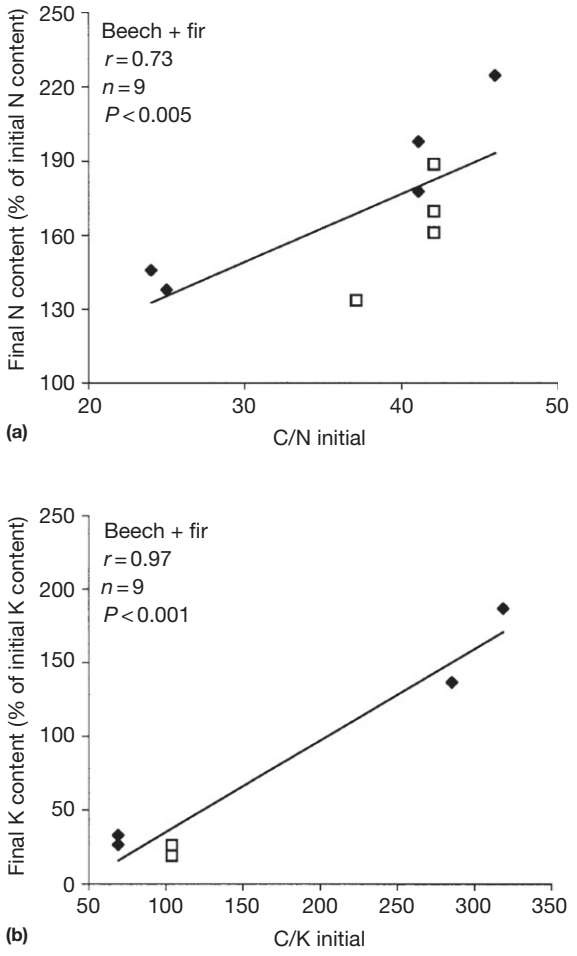

Figure 22 Relationship between: (a) final N and (b) K content (as percent of initial nutrient content) and initial C/nutrient ratio for beech (filled diamonds) and fir (open squares) litters (source Rutigliano et al., 1998).

Phosphorus is often a limiting nutrient for decomposition in old highly weathered soils (Crews et al., 1995; Vitousek and

Sanford, 1986). In contrast to nitrogen, the dominant source of phosphorus is from the chemical weathering of parent material (Schlesinger, 1991) or from atmospheric deposition (Chadwick et al., 1999). Phosphate, PO_4^-, the biologically available anionic form, will be tightly bound to sesquioxide clays in well-developed soils and allophane in young volcanic soils that have a high affinity for anionic compounds (Vitousek and Sanford, 1986). Along the Hawaiian archipelago chronosequence, Crews et al. (1995) found that during a 1.5-year *Metrosideros polymorpha* litter decomposition study, phosphorus was immobilized at the youngest (an Andisol) and oldest landforms (an Oxisol), but was lost at a similar rate to the overall mass loss at the nutrient-rich intermediate-aged sites (**Table 9**). The rapid mass and nutrient loss observed at the intermediate-aged sites was likely the combined result of the soils having more available nutrients and the leaf litter having higher nutrient contents (Crews et al., 1995).

Several researchers have also found that root and leaf litter decomposition often have contrasting patterns of immobilization and release of limiting nutrients (Moretto et al., 2001; Ostertag and Hobbie, 1999; Prescott et al., 1993; Seastedt et al., 1992). For M. *polymorpha* along the Hawaiian chronosequence, Ostertag and Hobbie (1999) found that although fine roots (<2 mm) decomposed faster than leaves possibly due to lower lignin : N and lignin : P ratios in the roots, root decomposition immobilized nitrogen regardless of site fertility, while nitrogen was released from leaf litter. For phosphorus, these authors found that only the roots at the old phosphorus-limited site showed significant phosphorus immobilization. In a semi-arid grassland in Argentina, Moretto et al. (2001) found that roots released nitrogen and phosphorus regardless of initial nutrient content; while leaf litter of the unpalatable grass (low nitrogen and phosphorus and high lignin content) immobilized phosphorus and the more palatable grasses released both nitrogen and phosphorus. Summarizing these studies, it would seem that differences in nutrient release patterns between leaf and root litter are primarily driven by those in initial resource quality and in the decomposition environment.

10.7.5.6 Priming Effect on Native SOM

Experimental additions of carbon- and nitrogen-labeled plant residues often show an increase in the mineralization rates of nonlabeled or native carbon and nitrogen relative to a control treatment (Bottner et al., 1988; Cheng and Johnson, 1998; Fu and Cheng, 2002; Sallih and Bottner, 1988). Kuzyakov et al. (2000) define priming effects as "strong short-term changes in the turnover of SOM caused by comparatively moderate treatments of the soil." In considering the biogeochemistry of decomposition, the priming effects that would be of most interest involve additions of easily available organic substances (i.e., fresh litter and rhizodeposition). Positive priming effects following additions of organic material are attributed to an increase in microbial activity and an acceleration of SOM mineralization through co-metabolism (Asmar et al., 1994; Breland and Hansen, 1998). Negative priming effects have also been observed following the addition of organic materials (Cheng, 1996; Sparling et al., 1982). Kuzyakov et al. (2000) largely attribute the negative effects to a switch in microbial metabolism of SOM to the newly added readily available substrates.

The accumulating literature on priming effects (reviewed by Kuzyakov et al., 2000) indicates that both the direction of and the mechanism driving the priming effect may depend on the study system. For example, Fu and Cheng (2002) found that in soybeans potted in soil dominated by C4 OM, native SOM decomposition increased by 70%, but when sorghum was planted in soil with C3 OM, SOM decomposition decreased by 9% relative to control soil. Priming effects can have large quantitative impacts on belowground nutrient cycling which are not included in most existing models of carbon and nitrogen dynamics (Kuzyakov et al., 2000).

10.7.6 Humification

The transformation of plant detritus into stabilized humic substances is one of the most complex and least understood biogeochemical processes in the carbon cycle (Stevenson, 1994). Traditionally, decomposition and humification of plant residues was thought to be dominated by the mineralization of labile materials, while more recalcitrant aromatic compounds accumulate in the soil. The application of modern analytical techniques—including solid-state ^{13}C NMR spectroscopy, pyrolysis gas chromatography, and degradative chemical techniques—to the study of decomposition and humification has significantly altered this simple view of carbon transformation in the soil (Baldock et al., 1997; Kogel-Knabner, 1997).

The formation of humus in most soils is likely the result of a combination of several processes, which Kogel-Knabner (1993) has summarized as *selective preservation* of recalcitrant

Table 9 Percent of initial C, N, and P remaining in *M.* polymorpha leaf litter decomposed *in situ* for 1.5 years along a chronosequence in Hawaii

Elapsed time *(yr)*	Thurston *(300 yr)*			Laupahoehoe *(20 kyr)*			Kohala *(150 kyr)*			Kokee *(4.1 Myr)*		
	C	N	P	C	N	P	C	N	P	C	N	P
0.083	97	75	94	98	90	88	97	100	87	98		
0.25	94	81	91	87	97	87	91	96	82	96	88	78
0.50	88	90	97	62	95	96	74	83	81	92	80	90
1.00	74	89	143	29	43	55	37	64	58	85	119	146
1.50	64	81	146	18	39	36	31	69	66	80	104	194

After Crews et al. (1995).

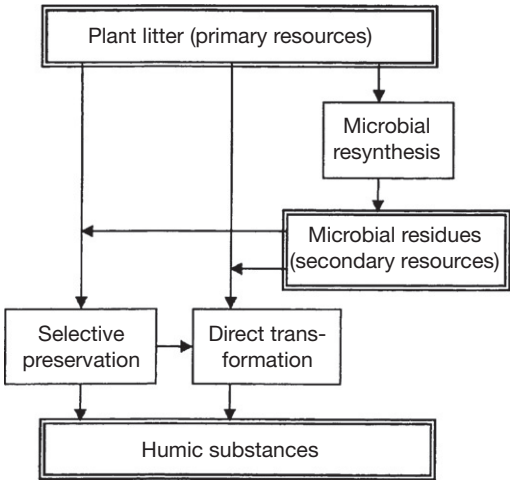

Figure 23 Different humification processes operating in the transformation of litter to humic compounds (after Kogel-Knabner, 1993).

plant and microbial biopolymers, *direct transformation* and *microbial resynthesis* (**Figure 23**). The relative importance of each of these processes will vary with resource type and soil environmental conditions. In this section, we will highlight the leading theories of humus synthesis with emphasis on some recent advances arising from the use of modern chromatographic and spectroscopic techniques. For more detailed information, the reader is referred to several excellent reviews (Baldock et al., 1997; Hatcher and Spiker, 1988; Hedges, 1988; Kogel-Knabner, 1993; Kononova, 1966; Zech et al., 1997).

10.7.6.1 Selective Preservation

Certain recalcitrant plant and microbial biopolymers are thought to be incorporated into stable SOM with only minor modification by microorganisms (Hatcher and Spiker, 1988; Lichtfouse, 1999; Waksman, 1932). Early investigators held the view, popularized by the Waks-man (1932) lignin-protein theory, that humus was derived primarily from the incomplete utilization of lignin by microorganisms. In this theory, lignin is progressively altered by microbial attack on the exposed methyl groups and terminal side chains. Demethylation and oxidation of side chains results in products enriched in acidic functional groups (COOH and phenolic OH) which can then undergo various condensation reactions with nitrogen-containing compounds to form humic acids (Stevenson, 1994). Much of the evidence that Waksman cited in support of this theory stems from the similar biochemistry between lignin and humic acid.

Based on detailed analyses of the chemical nature of SOM, Hatcher and Spiker (1988) have extended this humification model to include other resistant biopolymers, including plant cutin and suberin, and microbial melanins and paraffinic macromolecules. During decomposition, these biopolymers are selectively preserved and modified to become part of what can be operationally defined as humin (acid and alkali insoluble component of humus) (Hatcher and Spiker, 1988; Rice, 2001). The humin becomes progressively enriched in acidic groups leading to the formation of first humic acids and then fulvic acids, which under this "degradative" scheme of SOM formation would be regarded as the most humified of humic substances (Stevenson, 1994).

Under aerobic conditions, the long-term preservation of relatively unaltered lignin seems unlikely. Several groups of fungi have been identified with the ability to completely mineralize lignin to CO_2 (Griffin, 1994). Solid-state ^{13}C NMR studies have found that the aromatic carbon (predominantly, lignin and tannins) content often decreases with depth (Baldock et al., 1997) and with decreasing particle size (Baldock et al., 1992). Additionally, CuO oxidation studies often find an increase in the acid/aldehyde ratio of individual phenylpropane units with depth (Kogel, 1986), indicating increased biodegradation of lignin via ring cleavage and side chain oxidation (Kogel-Knabner, 1993). These studies suggest that the selective preservation of lignin may not be as important as previously thought.

The relatively recent work combining isotopic and structural information (pyrolysis gas chromatography with mass spectrometry) has revealed several biopolymers that appear to be selectively preserved in soils (Kracht and Gleixner, 2000). Working in a *Spagnum* moss bog, Kracht and Gleixner (2000) found that the relative amount of several plant biopolymers increased with increasing depth in the bog, while the $\delta^{13}C$ of the individual components remained constant relative to fresh moss samples. These authors concluded that no change in the isotopic ratio indicated that these biopolymers were being selectively preserved rather than being synthesized by microorganisms. In a maize agricultural soil, Lichtfouse et al. (1998) found evidence for the selective preservation of a highly aliphatic, straight-chain biopolymer which was thought to be of microbial origin. Other researchers have found and ascribed these highly aliphatic polymers to the cutans and suberans of higher plants (Augris et al., 1998; Nierop, 1998). In contrast, Poirier et al. (2000) found that aliphatic entities contributed only a minor amount to the refractory (nonhydrolyzable during drastic chemical treatment) organic fraction.

Charcoal or "black carbon" resulting from the incomplete combustion of plant residues during fires is another potentially important preservation pathway for SOM (Goldberg, 1985). Several researchers have shown that black carbon can account for a significant fraction of the total soil organic carbon, especially in fire-dominated landscapes (Glaser et al., 1998; Golchin et al., 1997; Skjemstad et al., 1996). Applying ^{13}C NMR spectroscopy to UV-photo-oxidized SOM from the $<53\,\mu m$ size fraction of five different Australian soils, Knicker and Skjemstad (2000) found that charred material comprised most of the physically protected "passive" OM. Additionally, Poirier et al. (2000, 2002) found that the refractory organic fraction in both a temperate cultivated soil and a deep tropical savanna soil consisted of substantial amounts of black carbon. The black carbon in the tropical savanna soil was characteristic of forest vegetation which was thought to be replaced by savanna over 3,000 years BP (Poirier et al., 2002).

10.7.6.2 Condensation Models

In contrast to the selective preservation theory, the condensation pathway proposes that humic substances are derived from the polymerization and condensation of low-molecular-weight molecules that are products of the partial microbial degradation of organic residues (Kogel-Knabner, 1993). Under this

scheme of increasing complexation, fulvic acids would be the first humic substances synthesized, followed by humic acids and then humin (Stevenson, 1994). The two commonly accepted condensation models are the polyphenol theory and the sugar-amine or mela-noidin theory.

The polyphenol theory views humus as a result of enzymatic conversion of polyphenols to quinones, which polymerize in the company or absence of amino compounds (Stevenson, 1994). Sources of polyphenol humic-precursors are thought to include the phenylpropane structural units of lignin released as a result of lignin biodegradation (Flaig et al., 1975) and the synthesis products of microorganisms during xylem cellulose degradation (Kononova, 1966). Martin and Haider (1971) found that, when several different *Imperfecti* fungi were grown on cultures of plant residues, significant amounts of humic-acid-like compounds were produced. Upon structural determination, these phenol polymers were found to be composed of both biodegraded lignin subunits (i.e., syringyl and guaiacyl acids and their derivatives) and microbially derived products (i.e., flavinoids). Adding support to observations that peat derived from lignin-free mosses contained substantial amounts of humus, Martin and Haider (1969) and Martin et al. (1972) found that fungi grown on lignin-free cultures synthesized appreciable quantities of humic-acid-like substances.

Polyphenols derived from lignin biodegradation and by microbial synthesis can be viewed as reaction intermediates in the polyphenol theory of humus formation. The oxidation of phenols to quinones is mostly likely catalyzed by the extracellular polyphenoloxidase enzyme produced by numerous decomposer microorganisms (Kononova, 1966). There is also evidence that this reaction can occur spontaneously in an alkaline media (Stevenson, 1994). Quinones, being relatively unstable in soil, will undergo condensation and polymerization reactions with other quinones and amino compounds to form humic substances (Hedges, 1988; Kononova, 1966). In cultures of microorganisms, Flaig et al. (1975) found that the lignin degradation products, vanillin and vanillic acid, in the presence of various amino acids formed brown nitrogenous polymers with properties similar to natural humic acids. Additionally, Bondiett et al. (1972) found that similar humic-acid-like polymers could be produced from the reaction of phenol derivatives with amino sugars.

Formed by the condensation of simple carbohydrates and amino acids, melanoidins are complex brown nitrogenous macromolecules that are insoluble and resistant to chemical degradation. This reaction, commonly observed during food dehydration, was initially proposed by Maillard (1917) to be important during humus formation. The substrates for the melanoidin model, simple sugars and amino acids, are available in large quantities in plant residues; however, they are also readily metabolized by most microorganisms leading to low abundances in the mineral soil where most humus is found (Kogel-Knabner, 1993; Stevenson, 1994). Additionally, synthetically derived melanoidins have different structural characteristics from naturally occurring humic substances, as determined by solid-state ^{13}C NMR spectroscopy (Hedges, 1988; Kogel- Knabner, 1993). Despite these and other criticisms, the melanoidin theory has been supported by several researchers (Ikan et al., 1986; Poirier et al., 2000; Van Bergen et al., 1998). In fact, Poirier et al. (2000) revised earlier results (Augris et al., 1998) that indicated selective preservation of highly aliphatic macromolecules in the refractory humus pool to invoke the participation of melanoidins.

The field of humus research is an exciting and rapidly developing field. Newly developed methods combining structural and isotopic information with compound specific analyses hold the greatest potential in elucidating the various humification pathways. Despite these advances, there has been little conclusive evidence supporting one theory of humification over another. Humification likely involves both selective preservation and condensation reactions. The soil environment (via temperature and moisture regimes and interactions with clay minerals) will have a large impact upon the degree to which either of these processes operates.

10.7.7 Control of Decomposition and Stabilization

Decomposition and stabilization of detritus as SOM are regulated by three general categories of driving variables (Swift et al., 1979): the physicochemical environment, the resource quality, and the decomposer organisms. The physicochemical environment can be further divided into climatic and edaphic components. Communition and catabolism of detritus are influenced by all three variables, while leaching is primarily controlled by the climate and resource quality of the litter. Swift et al. (1979) considered these driving variables as three points on a triangle with each variable interacting and influencing the other.

In experiments designed to test these controls on decomposition, researchers often find that not all of these factors are equally important in all ecosystems. Heneghan et al. (1999) comparing a single substrate between a temperate and two tropical sites found that soil fauna are not important in controlling decomposition in the temperate forest, but soil fauna are important and could explain the differences between the two tropical sites. In a three-factorial experiment (climate, litter quality, and biota), Gonzalez and Seastedt (2001) found that climate and litter quality had dominant effects at a temperate and dry tropical site, while all three factors were important in the wet tropical site.

In a review of the decomposition literature, Lavelle et al. (1993) suggest a general model where decomposition is controlled by a hierarchy of factors which regulate microbial activity at decreasing spatial and temporal timescales (**Figure 24**). This hierarchical model best integrates seemingly disparate results—acutal evapo transpiration (AET) can explain over 90% of the variation in decomposition rates across large geographic regions (Berg et al., 1993a); litter quality, as measured by lignin and nitrogen content, can explain 88% of the variation in decomposition between four Rocky Mountain coniferous forests (Taylor et al., 1991); and at a given site, differences in the abundance and assemblage of soil fauna can lead to threefold increases in decomposition rates (Whitford et al., 1982). A corollary to this model is that when climatic and edaphic factors are ideal or at least not limiting, litter quality and mutualistic relationships between macro- and microorganisms become much more important in governing decomposition rates (Lavelle et al., 1993). In this section, we will use this hierarchical model to describe the controls on decomposition beginning with the proximal controls of the decomposer organisms and ending with the more distal climatic factors.

10.7.7.1 Decomposer Organisms

Section 10.7.3 outlined the basic biology and ecology of the major decomposer organisms and Section 10.7.5 reviewed how these organisms breakdown and metabolize detritus. Here, we will highlight some of the more interesting controls that decomposer organisms have on the decomposition/stabilization process.

Microorganisms. Microorganisms are the primary agent of carbon mineralization in the detritus–soil continuum. Greater than 90% of total heterotrophic respiration is attributable to the metabolic activity of the microflora (Foissner, 1987). While acknowledging that microorganisms play a paramount role in decomposition, most biogeochemical models only implicitly include the microbial ecology (Schimel, 2001). According to Schimel (2001), two key assumptions in most biogeochemical models are: (1) microbial physiologies are global, i.e., they have an equivalent response across a range of environmental conditions and (2) microbial population sizes are never limiting and they rapidly adjust to stresses. These assumptions usually hold for processes that are aggregates of several microbial processes (i.e., soil respiration); however, as processes get more specific (i.e., nitrification or CH_4 production), these assumptions may not hold (Schimel, 2001).

Although microbial degradation is constrained by external factors (i.e., climate, edaphic conditions, etc.), the interactions between various microorganisms can have significant impacts on decomposition rates. Cox et al. (2001) showed the importance of individual species versus functional communities in the decomposition of pine litter; initially, a group of "sugar fungi" soon out-competed *Marasmius androsaceus* (basidiomycetes, lignocellulose degrader), but once the most labile substrates were consumed *M. androsaceus* regained dominance. An antagonistic relationship between microorganisms was also demonstrated by Møller et al. (1999) where mineralization of one-year-old beech leaves was reduced by 50% when bacteria was added to a soil containing a cellulolytic fungi (*Humicola* sp.) due to carbon limitation and competition. Cox et al. (2001) also demonstrated that the celluolytic antagonistic fungi *Trichoderma viride* can prevent any other species from entering a volume of soil for six months.

Microorganisms also affect decomposition indirectly through the adhesive qualities of metabolic products, and the entanglement of soil particles by filamentous fungi can lead to a significant increase in soil aggregation (Caesar-TonThat and Cochran, 2000; Tisdall et al., 1997). In a laboratory study on sterile sandy soil, Caesar-TonThat and Cochran (2000) demonstrated that water-stable aggregates (WSAs) increased when saprolytic fungi were present, and that carbon amendments greatly increased WSA formation because the fungus was carbon limited. Scanning electron microscopy by Caesar-TonThat and Cochran (2000) showed the extensive hyphal binding of soil particles (**Figure 25**). Tisdall et al. (1997), working with both saprophytic and mycorrhizal fungi, provided support for Miller and Jastrow's (1992) hypotheses that vesicular – arbuscular mycorrhizae (VAM) hyphae bring mineral soil and organic material together to from small

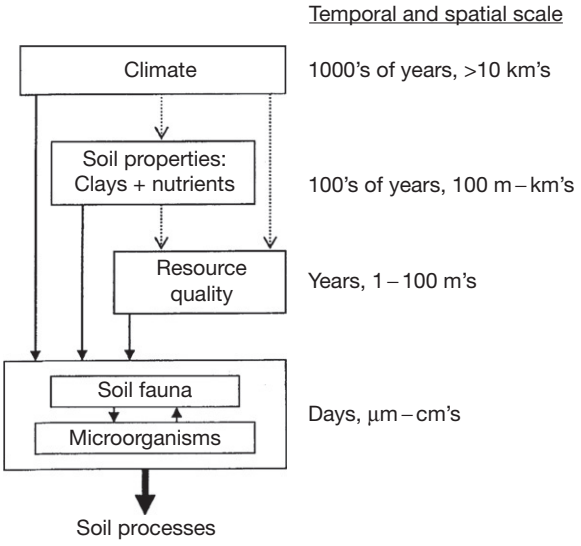

Figure 24 A hierarchical model of the factors controlling many soil processes in terrestrial ecosystems. Solid arrows represent direct regulation of biological processes and dashed arrows represent indirect controls (after Lavelle et al., 1993).

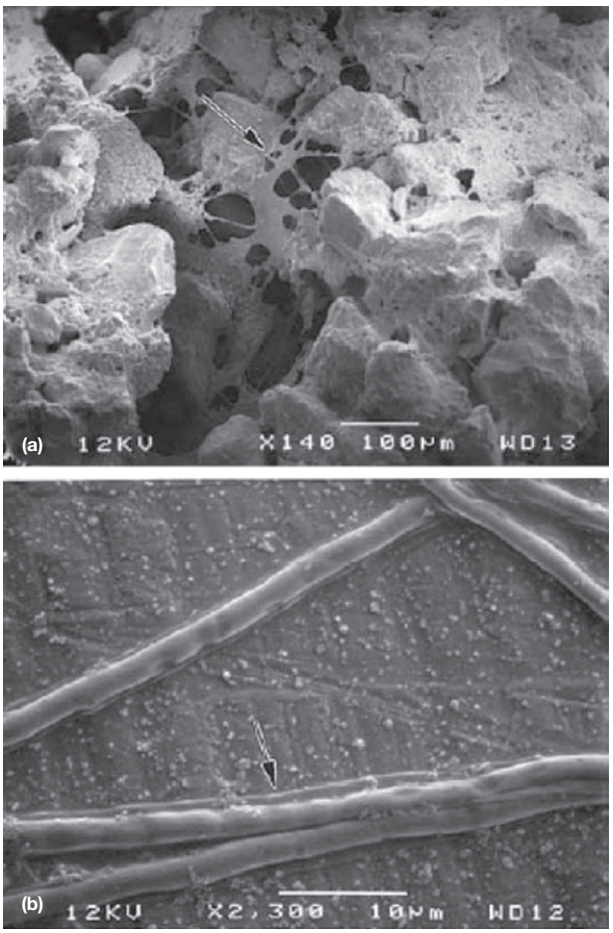

Figure 25 Low-temperature scanning electron microscopy of: (a) a portion of a soil macroaggregate with fungal material bridging soil particles (*arrow*) and (b) mucigel produced along fungal hyphae (*arrow*) (Caesar-TonThat and Cochran, 2000) (reproduced by permission of Springer Verlag from *Biol. Fert Soils*, **2000**, *32*, 374–380).

microaggregates and the hyphae enmesh and bind microaggregates into larger macroaggregates (>50 μm) with the help of root exudates.

Soil fauna. In a review of soil invertebrate control on SOM stability, Wolters (2000) noted that soil fauna affect the recalcitrance of, microbial accessibility to, and interactions with SOM. Direct effects of soil fauna include the communition, incorporation, and redistribution of organic materials (Seastedt, 1984). Soil fauna indirectly effect decomposition through numerous interactions with the microbial community (Shaw, 1992; Wolters, 2000). The mixing, aggregating, and channeling of soil material are another class of important indirect effects that can affect SOM stability and turnover. The summation of these direct and indirect effects of soil fauna can result in substantially increased decomposition rates. For a wide variety of deciduous litters, Seastedt (1984) found that microarthropods, predominately mites and collembolans, increased the average decay rate by 23% (median value of 17%) for litterbag exclusion studies lasting 9–30 months.

Anderson et al. (1981) showed that CO_2 production increased in the presence of nematodes because grazing increased the turnover of the bacterial population (i.e., more rapid growth). Anderson et al. (1981) also found that although decomposition was similar with or without nematodes after 65 days, greater nitrogen and phosphorus mineralization rates were observed with nematodes present because nematodes have low production efficiencies, ranging from 15% to 40% (Sohlenius, 1980). Net mineralization of nitrogen and phosphorus due to bacterial grazing by nematodes can also be argued based on C:N and C:P ratios—nematodes have higher carbon-to-nutrient ratios than bacteria; thus, they cannot assimilate all of the nitrogen and phosphorus in the bacteria food source (Anderson et al., 1981). This observation suggests that secondary sapro-phages (i.e., microbial consumers) facilitate efficient nutrient cycling in soils (Bardgett et al., 1999; Savin et al., 2001).

A study by Rihani et al. (1995a) highlighted the synergistic interaction between the direct decomposition effects of faunal ingestion and the indirect effects it causes by simulating the microbial population. These authors found that the litter feeding mite *Steganacarus magnus* digested 8% of beech leaf litter alone, a white-rot fungus decomposed 24% of litter, while together the two organisms decomposed 37% of the litter. Maraun and Scheu (1996) found that fragmentation of beech leaf litter by the millipede *Glomeris marginata* resulted in initial increases in microbial biomass due to increased access to carbon, but later microbial biomass was depressed, relative to control, due to reduced carbon availabilty. *G. marginata* also significantly altered the microbial community directly through the preferential digestion of fungi, as shown by changes in ergosterol levels in the soil (Maraun and Scheu, 1996). In the same study, Maraun and Scheu (1996) also demonstrated that microbial growth in the faecal pellets of *G. marginata* is carbon limited while microbial growth in the original beech litter is nutrient limited, thereby changing the limiting factor of decomposition.

Perhaps no other soil invertebrate has such well-documented controls on decomposition and stabilization of SOM as the burrowing anecic earthworms, such as *Lumbricus terrestris*. These organisms are capable of directly incorporating surface litter into the soil, and often the absence of a surface organic horizon is due to the presence of these organisms (Edwards and Bohlen, 1996). Langmaid (1964) reported that it took only three to four years after invasion of worms to thoroughly mix a well-developed spodosol in New Brunswick, Canada. Clements et al. (1991) found that after earthworms had been absent from a grassland soil for 20 years, there was a significant increase in the depth of the litter layer and a large reduction in the OM content of the underlying soil. Based on radiocarbon measurements, O'Brian and Stout (1978) estimated that the introduction of earthworms led to an increase in the annual carbon flux from 300 kg ha^{-1} to 1000 kg ha^{-1}, and the residence time of SOM decreased from 180 years to 67 years in a New Zealand pasture.

Earthworms only assimilate a low proportion of ingested OM. Lavelle and Martin (1992) reported that *Millsonia anomala* assimilates only 2–6% of the OM that passes through its gut, although the communition of litter and particulation of soil aggregates can have important secondary effects. Kanyonyo (1984), cited within Lavelle and Martin (1992), found that in the tropical anecic *Millsonia lamtoiana*, communition plus assimilation decreased the recognizable fragments of tree leaves, roots, grasses, and seeds by 83%, 71%, 41%, and 31%, respectively. Free-living microbial populations that have been ingested along with soil and litter are greatly stimulated during gut passage by the addition of water and labile intestinal mucus secretions. In this respect carbon cycling is stimulated in the drilosphere, the region of soil influenced by earthworms (i.e., burrow and casts), much like that is known to occur in the rhizosphere due to the exudation of labile root exudates that stimulate nutrient turnover (Anderson et al., 1981). During gut transport, by the time material reaches the second half of the gut, most of the added mucus has been metabolized and the now active microbial community begins to degrade soil OM into assimilable compounds which are used by both the earthworms and the microorganisms (Barois and Lavelle, 1986; Edwards and Bohlen, 1996).

Microbial metabolism of soil SOM during gut transport and the excretion of urine by earthworms into their guts both result in the release of available nutrients which may be expelled in casts. The volume of casts in earthworm- dominated soils can be enormous. In a tropical savanna at Lamto, Ivory Coast, Blanchart et al. (1993) found that 50% of the soil volume and 65% of the soil weight consisted of high bulk density (1.97 g cm^{-3}) casts, while the remaining soil volume had a bulk density near 1.0 g cm^{-3}. In a temperate cultivated soil, *L. terrestris* casts contained 21.9 μg $N\text{-}NO_3^-$ g^{-1} soil and 150 μg P g^{-1} soil while the surrounding bulk soil contained only 4.7 μg $N\text{-}NO_3^-$ g^{-1} soil and 20.8 μg P g^{-1} soil (Lunt and Jacobson, 1944). In a tropical savanna, Lavelle and Martin (1992) reported that fresh casts of *M. anomala* contained an average of 26.4 μg $N\text{-}NH_4^+$ g^{-1} soil and only traces of NO_3^-, while the control soil contained 1.5–7.5 μg $N\text{-}NH_4^+$ g^{-1} soil and no NO_3^-. Generally, fresh fecal material shows elevated decomposition relative to bulk SOM due to increased accessibility of labile carbon and nutrients, and the stimulation of bacterial populations during gut passage (Wolters, 2000). In a 30-day laboratory incubation, Cortez et al. (1989) found that the presence of the earthworm *Nicodrilus longus* increased CO_2 production threefold over soil without earthworms (**Figure 26**).

As earthworm casts age, mineralization is often reduced relative to uningested soil. Martin (1991) found that carbon

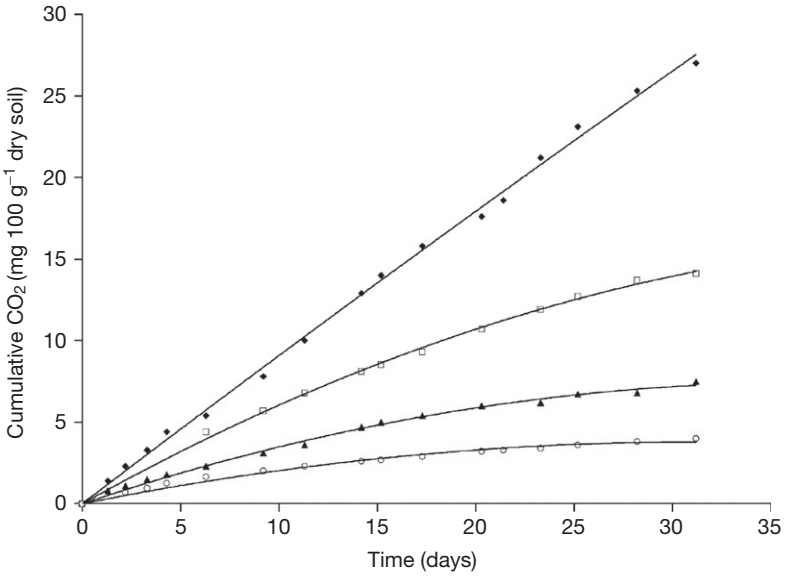

Figure 26 Cumulative CO_2 released from soil alone (open circles), soil + wheat straw litter (filled triangles), soil + earthworms (open squares), and soil + earthworms + litter (filled diamonds) (source Cortez et al., 1989).

in the aged casts of the tropical endogenic *M. anomala* mineralized at a rate of 3% yr^{-1}, while the control soil mineralized at 11% yr^{-1}. McInerney and Bolger (2000a) showed that earthworm-cast microaggregate structure was responsible for the decreased decomposition rates in temperate oak litter casts due to fewer macropores and more micropores, which reduce accessibility by most microorganisms. Blanchart et al. (1993) concluded that water re-adsorption in the hindgut pulls fine particles to the outside of the cast creating a crust (~25 μm thick) that has micropores and which prevents water movement. Shipitalo and Protz (1989) discussed the cast formation process, and suggested that aggregate stability in the casts increases via cation bridges and coordinated complexes between clay minerals and SOM.

Martin et al. (1992) found that the tropical geophage *M. anomala* assimilated both fresh plant material (coarse OM) and fine soil OM (resistant pool) into biomass by measuring changes in $\delta^{13}C$ of the earthworms switched from a C3 forest to a C4 grassland (or vice versa). Studies of earthworm invasions have shown that worms can metabolize recalcitrant SOM (Burtelow et al., 1998; O'Brian and Stout, 1978). These studies raise the question: in earthworm- dominated systems is there really any resistant SOM? The digestion of humified OM during earthworm invasions would result in a significant release of nitrogen due to the low C/N ratios of stable SOM. Martin (1991) estimated that 12–17 kg N ha^{-1} yr^{-1} is incorporated into casts, 60% of which originated from the clay-associated OM. However, increased mineralization of the humic pool during earthworm digestion may be balanced by decreased mineralization of the remaining carbon in the resulting casts. While there is ample evidence to suggest that earthworms dramatically alter the cycling dynamics and structure of OM in soil, these competing factors make it hard to predict whether earthworms act to increase or decrease the overall storage of carbon (Blaire et al., 1994).

Many of the effects on carbon decomposition and stabilization discussed above for earthworms can be generalized to many groups of soil fauna. **Table 10** summarizes the mechanisms by which soil invertebrates control decomposition and stabilization of OM in soils. Wolters (2000) hypothesized that soil invertebrates externally influence SOM destabilization by microorganisms in two ways: (1) directly, by selectively grazing on fast-growing fungi, thereby allowing the slower growing lignolytic fungi to gain a competitive advantage (Doube and Brown, 1998; Moody, 1993) and (2) indirectly, by altering the availability of nutrients in a way which is advantageous to the microorganisms capable of metabolizing recalcitrant compounds (Scheu, 1992). Humus formation is directly promoted through decreased access to carbon in aged casts (Shipitalo and Protz, 1989) and increased soil aggregation via the excretion of polysaccharides (Sollins et al., 1996). Indirect controls on humus formation include a range of processes that favor condensation of humic products and humic precursors (Hartenstein, 1982; Wolters, 2000).

10.7.7.2 Resource Quality

The primary carbon sources, originating from plants, available to the decomposer community comprise a wide variety of tissues that differ in both physical and chemical properties (Swift et al., 1979). The aboveground components (leaves, stems, and reproductive organs) and the below-ground components (roots) will each show characteristic patterns of decomposition that vary between species and possibly within species in differing ecosystems. Swift et al. (1979) showed that decay rates, calculated as litter fall divided by standing crop, from both a temperate and a tropical forest followed the same pattern—fleshy reproductive organs decayed faster than leaves, which decayed much faster than woody parts. Differences in the apparent decay rates of these plant parts are due not only to the palatability to the decomposers, but also to the loss of water-soluble compounds (Ibrahima et al., 1995; Kuiters and Sarink, 1986; Nykvist, 1961; Taylor and Parkinson, 1988b).

One of the first detailed studies to highlight the importance of the chemical nature of detritus upon decomposition was

Table 10 Overview of the mechanisms by which invertebrates control the turnover of humic substances

Process	*Level of control*[a]		*Mechanism*
Humus formation	Internal	Direct	Production of gut enzymes that favor the condensation reactions Biosynthesis of waxes, etc.
		Indirect	Production of enzymes that favor humification by gut symbionts
	External	Indirect	Facilitation of the microbial production of polymers and extracellular enzymes
			Altering distal factors affecting SOM stability by: (i) affecting the condensation of intermediates and (ii) stimulating the formation of stable organometallic complexes
Humus degradation	Internal	Direct	Disturbance of soil structure and associated disaggregation
		Indirect	Degradation of recalcitrant organic compounds aided by obligate or facultative symbionts
	External	Indirect	Increase in the competitive capacity of humus-degrading microorganisms by: (i) alterations in carbon and nutrient availability and (ii) selective grazing of fast-growing fungi and on microorganisms capable of degrading recalcitrant compounds
Other effects	Internal	Direct	Selective ingestion of less recalcitrant compounds leads to the enrichment of recalcitrant SOM
		Direct and indirect	Degradation of more labile compounds in the gut gradually increases the average recalcitrance of nonassimilated carbon
	External	Direct	Selective translocation of SOM leads to enrichment either of less or of more recalcitrant SOM
		Indirect	Rapid depletion of nutrients and labile carbon compounds shortly after defecation leads to an increase in recalcitrant components

After Wolters, (2000).

[a]Internal control refers to effects of ingestion and digestion, while external control refers to any process occurring outside of the invertebrate's body.

reported in a series of papers by Tenney and Waksman (1929) and Waksman and Tenney (1927, 1928). Since then, differences in decay rates between plant species have been shown to be controlled by a wide variety of chemical properties (Aerts, 1997), including the lignin concentration or lignin-to-nutrient ratios (Aerts and De Caluwe, 1997; Berg, 1984a; Meentemyer, 1978; Melillo and Aber, 1982; Tian et al., 1992b; Van Vuuren et al., 1993), the nitrogen concentration or the C/N ratio (Coulson and Butterfield, 1978; Perez-Harguindeguy et al., 2000; Taylor et al., 1989; Tian et al., 1992a), phosphorus concentrations or C/P ratios (Berg et al., 1987; Coulson and Butterfield, 1978; Schlesinger and Hasey, 1981a; Staaf and Berg, 1982; Vitousek et al., 1994), and polyphenol content (Northup et al., 1998; Yu et al., 1999).

Plant physical traits that protect against biotic attack and harsh environmental conditions (Herms and Mattson, 1992) produce tissues with higher lignin, polyphenol, and wax contents and higher lignin/N and C/N ratios that decompose more slowly (Perez-Harguindeguy et al., 2000). Grime et al. (1996) presented evidence that the least palatable litters to two herbivores also decomposed at the slowest rates. Perez-Harguindeguy et al. (2000) showed that litter mass loss is highly correlated ($r = -0.86$, $p = 0.014$, $n = 7$) to leaf tensile strength across a wide range of plant functional types in central Argentina (**Figure 27**). Although not a direct measure of the chemical nature of the litter, tensile strength is a relative measure of leaf toughness (Cornelissen et al., 1999; Cornelissen and Thompson, 1997). When these same litters were moved to the temperate climate of Sheffield, UK (mean temperature of experiment = 7.7 °C versus 20 °C in Argentina), Perez-Harguindeguy et al. (2000) found the same trend of mass loss versus tensile strength, but that there was a 25% reduction in overall mass loss.

Table 11 summarizes the effect of initial litter quality on decay rates, k, for selected studies (Aber et al., 1990; Fioretto et al., 1998; Harmon et al., 1990a; McClaugherty et al., 1985; Melillo and Aber, 1982; Taylor et al., 1989, 1991; White et al., 1988). Included are forested sites that span a range of climates from mediterranean to temperate rainforest and that include a variety of litter sources (leaf, needle, and fine root) with greatly contrasting chemistry. For these sites, neither the nitrogen concentration nor the C/N ratio predicted k. However, a simple exponential model explained most of the variance between k and lignin content across all sites. The addition of nitrogen either in the form of the lignin/N ratio or in a multiple linear regression significantly improved the prediction for the Hubbard Brook, Kananaskis Valley, and Olympic National Park sites (**Table 11**). Aber et al. (1990) suggested that the ratio of lignin to lignin + cellulose (the lignocellulose index (LCI)) is a good predictor of k. For the data in **Table 11**, the LCI significantly increases the coefficient of determination to 0.73 and 0.94 for the Olympic National Park and Blackhawk Island sites, respectively. These results indicate that at a given site, lignin is the primary control on the decomposition rate, and that nutrient content is a secondary influence (Taylor et al., 1991).

For a range of lignin concentrations wider than evaluated in **Table 11**; Taylor et al. (1991) found a rapid decrease in mass loss with increasing lignin up to a critical content of 28% lignin and a lignin-to-nitrogen ratio of 50 : 1, after which constant

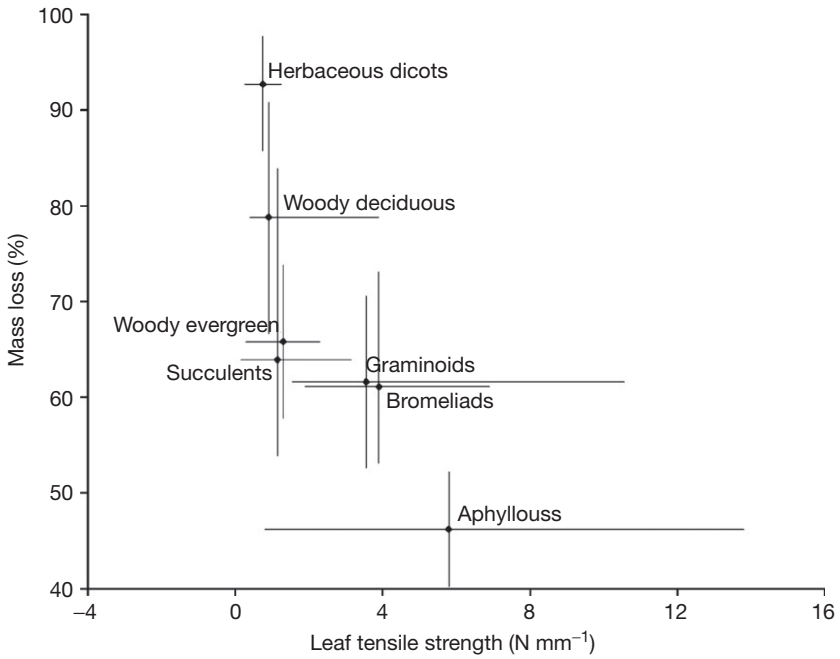

Figure 27 Relationship between leaf tensile strength and mass loss for different functional types of central Argentina. Points represent median values and error bars reprsent the quartiles 25% and 85% (source Perez-Harguindeguy et al., 2000).

Table 11 Regression summary of litter chemistry controls on the decay rates of leaf and fine root (< 1 mm) litter for selected sites spanning a range of climates (as indicated by MAT, MAP, AET, DEFAC, and mean *k* values for each site). Values are the coefficients of determination for a linear regression between the natural log (*k*) and the litter chemistry variable in each column. Also shown is the results of a multiple linear regression between ln (*k*) and %N and %lignin

Site	Ref.[a]	MAT (°C)	MAP (mm)	AET (mm)	DEFAC[b]	n	mean k	Multiple Regression parameters					
								%N	%lignin	C : N	LCI	lignin : N	%N, % liognin
Kananaskis Valley, Alberta	5	2.1	660	385	0.13	10	0.14	0.09	0.81***[c]	0.03	ND[d]	0.87***	0.90*,***
Hubbard Brook, NH	4	5.0	1300	552	0.24	6	0.25	0.00	0.55*	ND	ND	0.99***	0.99**,***
Blackhawk Island, WI	1	7.0	810	605	0.26	8	0.41	0.29	0.90***	ND	0.94***	0.06	0.92⁻,**
Harvard Forest, MA	3	7.0	1120	578	0.26	4	0.55	0.26	0.96*	ND	0.65**	0.69	0.998⁻,*
Olympic National Park, WA	6	8.9	3550	525	0.33	9	0.81	0.33	0.44*	ND	0.73**	0.55*	0.55⁻
Coweeta, NC	2	13.0	1800	702	0.37	6	0.94	0.27	0.96***	0.25	0.85**	0.44	0.98⁻,**

[a]References: (1) McClaugherty et al. (1985), (2) White et al. (1988), (3) Aber et al. (1990), (4) Melillo and Aber (1982) (5) Taylor et al. (1989, 1991), and (6) Harmon et al. (1990a).
[b]DEFAC = synthetic climate variable used in the Century model (see text for explanation).
[c]Significance of each regression is denoted by astericks (for the multiple regression: significance of %N term, %lignin term):
*P < 0:1;
**P < 0:01;
***P < 0:001
[d]ND = not determined.

loss rates occurred. However, this interpretation may be confounded by the fact that all of the high lignin substrates were large woody litters (branches, cones, and roots) which may exhibit more complex decay patterns due to their three-dimensional structure (Edmonds et al., 1986). In the Pacific Northwest, Edmonds (1988) found no correlation between five-year mass loss and lignin content for branch, twig, and cone litter.

In a review of global patterns of root decomposition, Silver and Miya (2001) found that the substrate quality parameters,

root Ca^{++} concentration and C/N ratio, could explain the greatest proportion of the variance in decay rates across a range of sites and species ($r^2 = 0.89$, $n = 17$):

$$\ln(k) = 3.79 + 0.74 \times \ln(\mathrm{Ca}) - 1.22 \times \ln(\mathrm{C:N}) \quad (8)$$

This result is in accord with Lavelle et al.'s (1993) hierarchical model—when climate is ameliorated as a limiting variable, resource quality becomes much more important in determining decomposition dynamics. In the soil, roots and the associated decomposer organisms are sheltered from climatic extremes relative to the surface litter system. Additionally, Silver and Miya (2001) proposed two explanations for the strong role of root calcium in predicting decay rates: (1) high levels of calcium in the root may indicate high levels of mycorrhizal fungal associations which upon root death may act as a readily available carbon substrate for heterotrophic organisms and (2) high root calcium levels may indicate nutrient-rich soil conditions that in turn would promote accelerated decomposition rates.

At the San Dimas Experimental Forest in southern California, a large lysimeter installation established in 1937 is an excellent experiment on the effects of differing monocultures of native vegetation (chamise, ceanothus, scrub oak, and Coulter pine) on soil properties and processes without the confounding influence of other factors (Colman and Hamilton, 1947). The lysimeters are large (5.3 m × 5.3 m horizontally and 2.1 m deep) earthen-walled pits that were filled with a homogenized fine sandy loam (58% sand, 31% silt, 11% clay) with only 0.2% organic carbon at time of filling (Colman and Hamilton, 1947). Previous research has addressed the influence of vegetation on soil morphological development (Graham and Wood, 1991), aggregate stability (Graham et al., 1995), soil nutrient content (Ulery et al., 1995), and mineralogy (Tice et al., 1996). Perhaps the most striking finding is that the soil under oak has developed a dark, 7 cm thick "A" horizon overlain by a thin (6 cm) litter layer while the soil under pine has a thick "O" horizon (10 cm), minimal darkening in the A horizon, and an argillic horizon (a subsurface concentration of clay by elluvial processes) had developed in only four decades (Graham and Wood, 1991). Graham and Wood (1991) report that while worms are completely absent from the pine soil, there is substantial earthworm activity in the oak soil and that the A horizon is comprised of 95% earthworm casts.

Quideau and co-workers have compared the soil carbon cycling dynamics of the oak and pine lysimeters using physical fractionation (Quideau et al., 1998), radiocarbon (Quideau et al., 2001), and ^{13}C NMR techniques (Quideau et al., 2000). Based on radiocarbon measurements, Quideau et al. (2001) found that the decomposition rates were much faster under oak han under pine for both the litter layer and for nearly all SOM fractions in the A horizon (**Table 12**). Not only are the turnover rates faster under oak, but significantly more OM is being incorporated in the mineral soil, mainly a result of bioturbation by earthworms (Graham and Wood, 1991). Results from Quideau et al.'s (2000) NMR analysis suggest two separate patterns of decomposition (**Figure 28**).

Table 12 Carbon storage, radiocarbon content, and the estimated decomposition constant (k) for the O and A horizons under oak and pine vegetation.

Horizon[a]	Depth *(cm)*	*C (g m^{-2})*	□^{14}C *(‰)*	*K (yr^{-1})*
Oak lysimeter				
Oi	6	493	212	0.61
A-WS	7	2,093	259	0.08
FL		963	319	0.07
SA		492	154	0.09
FS		331	274	0.08
CL		308	225	0.13
Pine lysimeter				
Oi1	4	107	216	0.51
Oi2	2	65	238	0.27
Oe	4	347	343	0.03
A-WS	1	172	90	0.04
FL		56	220	0.08
SA		49	–90	0.005
FS		31	108	0.07
CL		37	115	0.02

After Quideau et al. (2001).

[a]WS = whole soil (< 2 mm), FL = floatables (50–2,000 □m), SA = sand + coarse and medium silt (5–2,000 □m), FS = fine silt (2–5 □m), CL = clay (< 2 □m).

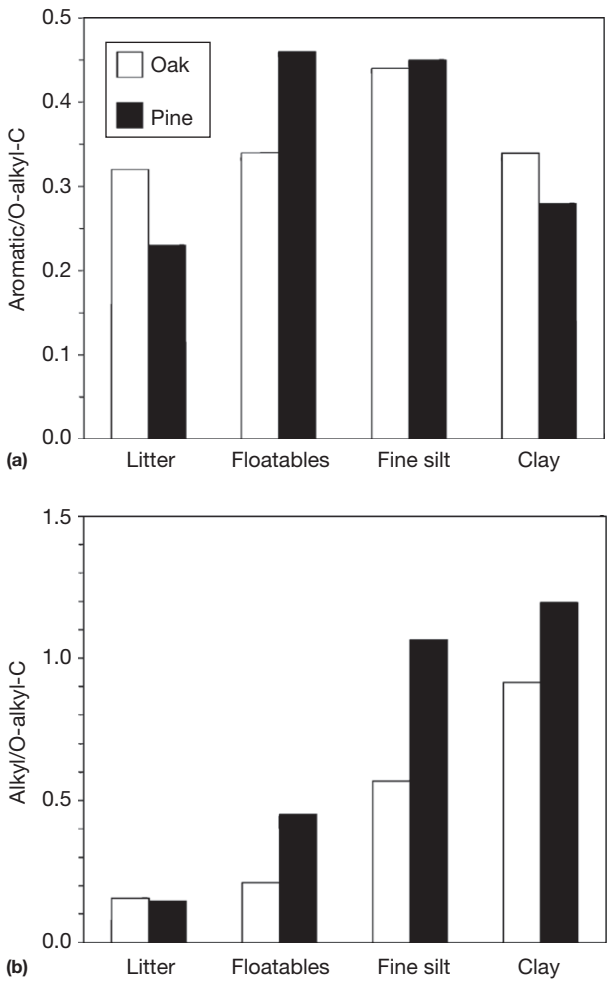

Figure 28 (a) Aromatic/O-alkyl-C and (b) alkyl/O-alkyl-C ratios in litter and particle size fractions from A horizon samples under oak and pine vegetation in the San Dimas lysimeters experiments (source Quideau et al., 2000).

The small increase in the aromatic/O-alkyl-C ratio from the litter to floatable fraction of the A horizon under oak indicates little microbial metabolism of the labile carbon components, while substantial degradation has occurred under pine. Fragmentation and mixing of the litter into the A horizon may dominate the initial stages of decomposition under oak, followed by a more traditional pattern (Baldock et al., 1992) of microbial degradation of labile (O-alkyl carbon rich), and then more recalcitrant (high in aromatic-C and alkyl-C) components. In the pine soil, without the influence of earthworms, much more microbial degradation occurs in the litter layer and transport into the mineral soil is much slower, resulting in more recalcitrant SOM as indicated by the higher alkyl/O-alkyl-C ratios in all size fractions (**Figure 28**). Consistent with this pattern, particle size analysis of the OM in the A horizon showed that most of the carbon was associated with the sand fraction under oak, while most of the carbon was associated with the silt and clay fractions under pine vegetation (Quideau et al., 1998).

10.7.7.3 Soil Characteristics

In this section, we will consider the effects of soil texture and soil nutrient status on decomposition. The initial stages of leaf litter decomposition will be at least partially decoupled from control by edaphic properties of the soil environment. For example, Scott et al. (1996) found that while SOM decomposition varies significantly with soil texture, the CO_2 evolution from surface litter does not. However, as partially decomposed litter is incorporated into the soil both through abiotic and biotic means, the physical characteristics of the soil begin to play an important role in the overall degradation and stabilization of the organic inputs.

Christensen (2001) suggested a conceptual model for SOM dynamics organized around three levels of structural complexity: (1) primary organomineral complexes, (2) soil aggregates, and (3) the whole soil. In terms of SOM, the organo-mineral complexes associated with the sand-, silt- and clay-sized soil fractions represent the basic structural and functional units. At the scale of a soil particle, surface area and charge properties will be the dominant influences stabilizing OM from microbial degradation. Within soil aggregates, water and gas diffusion become important limiting controls on rates of carbon mineralization. At the scale of the whole soil, nutrient availability, macroporosity, the activity of soil fauna and roots, and exogenous disturbance become important influences on decomposition processes (Christensen, 2001).

Soil texture. In many biogeochemical models, soil texture, in the form of the clay + silt fraction, is suspected of being one of the key variables influencing both the decomposition rate of the active SOM pool and the efficiency of stabilizing active SOM into slow SOM (e.g., Parton et al., 1987).

In a laboratory incubation of Danish soils of varying texture, Sørensen (1981) found that the proportion of labeled cellulose that decomposed after 90 days varied inversely with clay content ($r^2 = 0.99$, $P = 0.006$, $n = 4$) and that the amount of labeled carbon remaining in the soil after 1600 days was twice as large in the high clay soil compared to the sandy soil. McInerney and Bolger (2000b) showed that CO_2 produced per gram soil carbon was 15% higher in a loam versus a clayey soil, indicating a reduction in decomposition rates. Schimel et al. (1985), working on a toposequence in southwestern North Dakota, also report that the amount of CO2-C respired, normalized to carbon content, decreases with increasing clay. Giardina et al. (2001) found a strong, but nonsignificant ($r^2 = 0.51$, $P = 0.11$, $n = 6$) trend of decreasing CO_2 efflux with increasing clay content in lodgepole pine forest soils but not for soils under an aspen stand ($r^2 = 0.11$, $P = 0.46$, $n = 6$). When the Scott et al., (1996) data on carbon mineralization rates are normalized by carbon content, we find that the clay-rich soils decompose slower than the sandy soil. However, other studies have found weak (Motavalli et al., 1994) or nonexistent trends (Giardina and Ryan, 2000; Thomsen et al., 1999). It is not surprising that conflicting results are reported since clay content is affected by state factors (i.e., climate and parent material) which in turn influence decay rates and affect a number of soil properties (i.e., porosity, water-holding capacity, and aggregate stability). The latter can also significantly alter decay rates (Sollins et al., 1996).

Analyses of SOM dynamics on particle size and density separates (Christensen, 1992) support the general concept that the clay- and silt-associated OM is a more recalcitrant pool with slower turnover times (Stevenson, 1994). Christensen (1987) found that the sand-associated OM decomposed faster than the clay fraction which, in turn, decomposed faster than the silt fraction. Overall decomposition rates were higher in the finer textured soil, because most of the OM was associated with the clay fraction which decomposed faster than silt-associated OM (Christensen, 1987). Several other particle size fraction studies support the finding that the silt-SOM is the most stable fraction (Amato and Ladd, 1980; Ladd et al., 1977); however, turnover times derived from ^{14}C data usually show that the clay fraction is the most stable pool (Anderson and Paul, 1984; Christensen, 1992). During particle size fractionation, without rigorous pretreatment, silt-sized aggregates of clay particles can settle out with the silt- sized fraction, possibly reconciling these two disparate results.

Geologists are also beginning to recognize the importance of the role of clay minerals in the long-term burial and preservation of OC in shale deposits. Kennedy et al. (2002) showed that 85% of the variance in total OC can be explained by mineral surface area in two Cretaceous black shale deposits.

The importance of clays in stabilizing OM comes from results of labeling studies which find that the clay fraction is often most enriched, relative to the whole soil (Chichester, 1970). This enrichment is relatively more important in sandy than in clayey soils (**Figure 29**). However, the turnover of clay-associated SOM in sandy soils is faster (Gregorich et al., 1989), suggesting that these soils are less efficient in stabilizing and storing SOM than clay-rich soils (Christensen, 1992). Cheshire and Mundie (1981) found that plant-derived carbohydrates (glucose, xylose, and arabinose) were dominant in the sand separates (20–2000 μm), while microbial sugars (mannose, rhamnose, and fucose) were found in greatest concentration in the clay fraction. As the OM ages and becomes more humified, structural complexity and size can increase, possibly explaining the relatively greater role silt plays in holding old (native) SOM in long-term labeling studies (Christensen and Sorenson, 1985). Several studies using solid-state ^{13}C NMR spectroscopy on size separates found that the aromaticity of silt-SOM fraction is

higher than the clay fraction (Catroux and Schnitzer, 1987; Oades etal., 1987; Schnitzer and Schuppli, 1989).

The evidence from studies that track the change in $\delta^{13}C$ values following a vegetation shift also indicates that OM associated with the coarse fractions decomposes at the fastest rate. Twenty-three years after the conversion of a pine forest (C3) to maize (C4), Balesdent et al. (1987) found that SOM in silt contained the least maize-derived carbon (12%), and thus the slowest turnover, while the coarse sand had 61% maize-SOM. However, 97 years after a prairie was converted to wheat cultivation, Balesdent et al., (1988) found that the fine clay-SOM (<0.2 μm) fraction had the slowest turnover and that the major losses, occurring during the first 27 years, were from the macro-OM in separates >25 μm and the fine silt-SOM (2–25 μm). For an Oxisol in the humid tropics, whose vegetation had shifted from grass savanna (C4) to dense woodland (C3), Martin et al. (1990) found turnover times increased from clay (70% savanna-derived C) to fine silt (56% savanna-C) to coarse silt (28% savanna-C) to the >50 μm fraction (<15% savanna-C).

Although there is ample observational evidence for soil textural effects on SOM decomposition and stabilization, mechanisms for the observations are difficult to verify. Perhaps the most straightforward hypothesis is that clays have a high surface area and possess the majority of the surface charges of the soil particles, thereby creating more opportunities to hold organic additions to the soil. Oades (1988) has suggested that SOM stabilization to clay is due to adsorption reactions (i.e., electrostatic bonding, hydrogen bonding, van der Waals forces, hydrophobic bonding, coordination, and ligand exchange (Stevenson, 1994)) of organics onto surfaces of clays and other organic complexes. It would, therefore, seem that the type of clay present, due to differences in particle size, surface area, and charge density, will have a large effect on the carbon dynamics (**Table 13**). Nelson et al. (1997) found that the ability to retain OM was less in an illite- and kaolinite-dominated soil than in a smectite-dominated soil, even though no difference in the structural stability of aggregates occurred between the two soils (Barzegar et al., 1997).

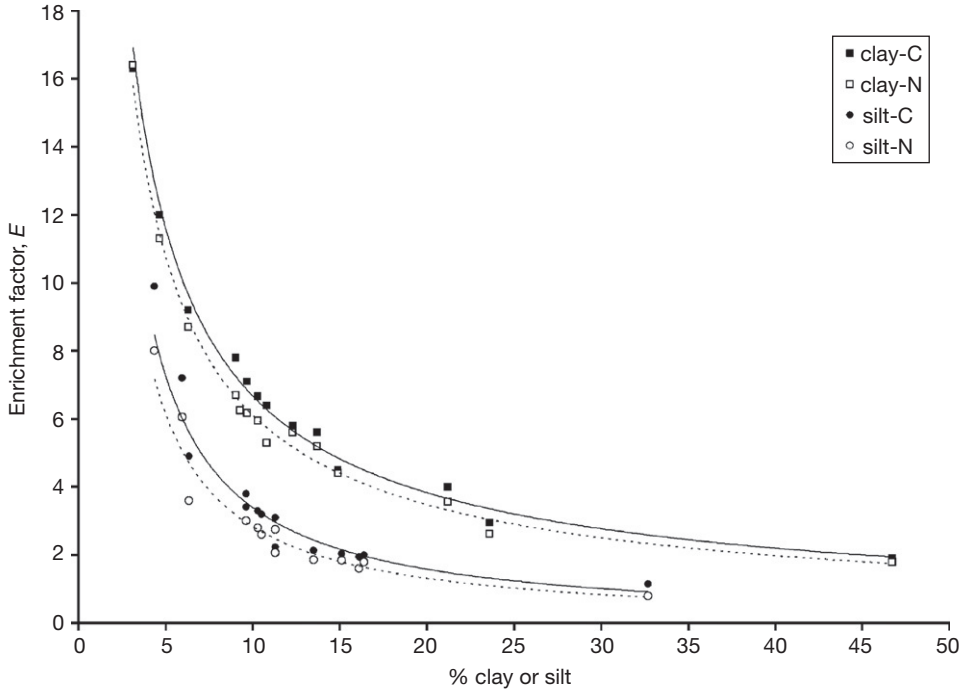

Figure 29 Relationship between fraction size and C and N enrichment factors (*E* = percent of C or N in fraction to percent in whole soil) for clay (<2 μm) and silt (2–20 μm) isolated from a range of Danish agriculture soils (source Christensen, 1992 and references within).

Table 13 Surface characteristics of various clay minerals

Clay mineral	Size (*μm*)	Surface area ($m^2\ g^{-1}$)	Negative charge ($cmol_c\ kg^{-1}$)	Positive charge ($cmol_c\ kg^{-1}$)
Smectite	0.01–1.0	600–800	80–120	0
Vermiculite	0.1–5.0	600–800	100–180	0
Illite	0.2–2.0	70–100	10–40	0
Kaolinite	0.1–5.0	10–30	3–15	2
Gibbsite (Al oxide)	0.1–0.2	5–20	0–4	0–5
Goethite (Fe oxide)	0.01–0.2	25–95	0–4	0–5
Allophane		70–300	0–30	0–15

Sources: Brady and Weil (2002); Stevenson (1994), and others.

Across a chronosequence of soils on the Hawaiian islands (Crews et al., 1995), Torn et al. (1997) found that both the quantity of stored carbon and its turnover time correlated with the noncrystalline (allophane, imogolite, and ferrihydrite) mineral content of the soil (Figure 30). These amorphous minerals possess a unique geometry with a very high surface area (Table 13) which facilitates the formation of highly stable bonds with SOM (Oades, 1988).

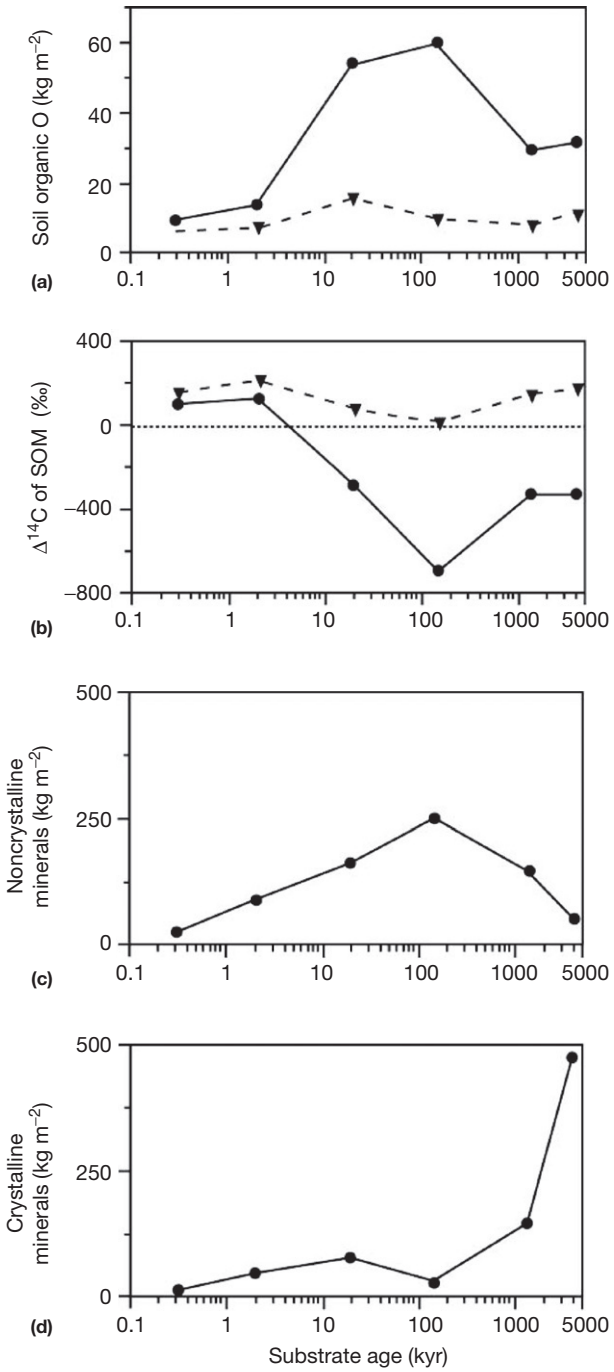

Figure 30 Content of: (a) organic C, (b) Δ^{14}C, (c) noncrystalline minerals, and (d) crystalline minerals versus age along a chronosequence of soils on the Hawaiian Islands. Filled circles represent total soil profile and filled triangles represent surface (O and A) horizons only (Torn et al., 1997) (reproduced by permission of Nature Publishing Group from *Nature*, **1997**, *389*, 170–173).

Textural differences may influence microbial activity and decomposition rates indirectly by modifying the physiochemical environment (Nelson et al., 1997). Indirect mechanisms include entrapment of organic particles in the interiors of aggregates (Van Veen and Kuikman, 1990) and in micropores (Hassink et al., 1993) where microbes are physically excluded. Van Veen et al. (1985) suggest that in fine textured soils, products released from dead bacterial cells are retained in the vicinity of surviving bacteria which minimizes the leaching of labile carbon. A similar mechanism has been proposed for the observed decrease in decomposition in earthworm casts (Martin, 1991) where increased organo-clay bonding (Zhang and Schrader, 1993) can reduce the amount of leachate in casts versus bulk soil (Mclnerney and Bolger, 2000b).

Soil texture is a major control on the distribution of pore sizes in a volume of soil, which, in turn, largely determines both the water holding capacity and the soil water potential (Ψ, MPa) for a given volumetric water content (θ, m^3 water m^{-3} soil). The water potential limits to microbial activity are listed in Table 4. Studying native SOM mineralization rates across a range of soils, Scott et al. (1996) found a significant interaction between soil texture and Ψ (Figure 31), which could best be explained in terms of the percentage water-filled pore space (WFPS). As clay increased from 7% to 20%, SOM mineralized per kg of soil increased linearly with increasing WFPS ($r^2 = 0.71$, $P < 0.01$). However as WFPS increases towards 100%, it might be expected that O_2 limitations would begin to decrease the activity of the microorganisms. Thomsen et al. (1999) incorporated the soil textural interactions with water availability by defining microbially accessible water (MAW) as the difference between volumetric water content (θ) and the volume of inaccessible water (IW). IW was defined as the water content at the permanent wilting point ($\Psi = -1.5$ MPa), which increases with increasing clay and SOM content. In a ^{14}C-labeled residue addition experiment, MAW significantly improved predictions of $^{14}CO_2$ evolution from a series of soils with increasing clay content from $r^2 = 0.55$ for θ to 0.88 for MAW (Thomsen et al., 1999).

Soil structure. Mature soils often exhibit well-developed macrostructure as a result of physical binding between organo-metal–mineral complexes (Tisdall and Oades, 1982) and polysaccharides excreted by roots (Traore et al., 2000) and soil organisms (Tisdall, 1994) and through the enmeshment of soil particles by fine roots and fungal hyphae (Tisdall et al., 1997). Although Tisdall and Oades (1982) propose that clay particle binding to bacterial colonies is a major factor in promoting microaggregate formation, Bossuyt et al. (2001) found that fungi, not bacteria, were the dominant agents in macro-aggregate (>2000 µm) formation. Factors which affect fungal biomass—such as resource quality, predation, and nutrient availability—will impact the formation of macroaggregates in the soil (Bossuyt et al., 2001).

The effect of cultivation on aggregate stability, and carbon cycling, is important for carbon storage, and the disruption of this structure may be the fundamental mechanism behind the rapid and large loss of soil carbon that occurs following the initiation of agriculture (Paul et al., 1997). Beare et al. (1994b)

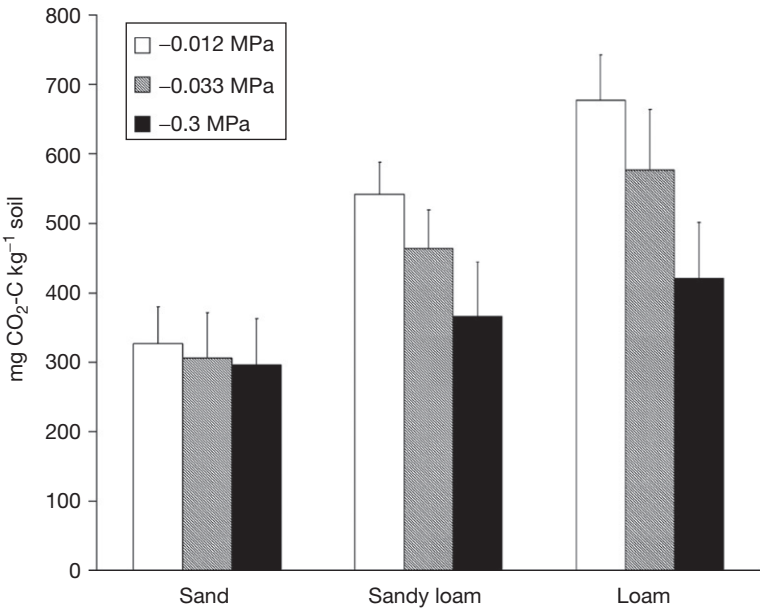

Figure 31 Interaction between soil texture and water pressure on total native soil C mineralization during a 91-day incubation. Error bars represent 1 standard error (source Scott et al., 1996).

found that WSAs were larger, more abundant, and more stable in no-till agriculture versus conventional tillage, resulting in a fourfold increase in the protected nitrogen pool. An important finding of this study was that the macroaggregate-protected OM was more labile than the unprotected inter-aggregate OM (Beare et al., 1994a). These authors suggested that the unprotected inter-aggregate OM has been more processed by microorganisms. Six et al. (2001), using multiple methods of SOM characterization, confirmed that inter-aggregate particulate OM is more decomposed than coarse intra-aggregate particulate OM.

Following the ^{13}C content after six years of continuous maize production, Puget et al. (2000) found that stable macroaggregates (2–3 mm diameter) contained 62% young carbon (maize derived) mostly in the form of particulate OM, whereas aggregates of medium stability contained 38% young carbon, and unstable aggregates contained only 5% young carbon. At a site that had been under maize for 23 years, the differences in maize-derived or young carbon between stability classes were less pronounced, although similar percentages of particulate OM were found relative to the six-year site, indicating that the macroag-gregates are transient in nature (Puget et al., 2000). These differences in aggregate structure and stability across cropping regimes result in substantially increased decomposition rates in fields under conventional tillage. For example, Balesdent et al. (1990) found that ^{13}C-derived turnover times decreased from 127 years for no-tillage to 68 years for superficial-tillage to 56 years for conventional-tillage after only 17 years of maize production.

Nutrient availability. Nutrient-deficient soils can limit decomposition rates directly due to nutrient limitation of the microbial community, and indirectly through the production of lower quality litter by nutrient-stressed plants. Gosz (1981) found that when climate was held constant, plants growing on nitrogen-rich sites produce leaf litter with greater nutrient concentrations that decompose more quickly than litter from nitrogen-poor sites. On a long-term age gradient of soils on the Hawaiian islands, Ostertag and Hobbie (1999) found that one-year mass loss for leaf and fine root litter is least for the old phosphorus-limited site, intermediate for the young nitrogen-limited site, and greatest at the intermediate-aged fertile site (neither nitrogen nor phosphorus limiting). This indirect effect of fertility on resource quality can often explain most of the variation in decay rates between sites of differing fertility (Hobbie, 1992; Ostertag and Hobbie, 1999; Prescott, 1995).

If nutrient availability was limiting decomposition especially of low-quality litters (high C/N and lignin/N ratios), fertilization should relieve this microbial limitation and decomposition rates will increase. Several studies report increases in k following nutrient additions to soil, indicating that decomposer organisms are nutrient limited (Ostertag and Hobbie, 1999; Prescott et al., 1992). However in a review of nitrogen effects on decomposition, Fog (1988) cited more than 60 papers that reported neutral or negative effects on decomposition following nitrogen fertilization. As an explanation for this observation, microbiologists often attribute the lack of a decomposition response after fertilization to the fact that microbes are primarily limited by substrate (carbon) not by nutrient availability (McClaugherty et al., 1985; Ostertag and Hobbie, 1999; Prescott et al., 1992). In line with this, Fog (1988) found that positive effects of fertilization were most commonly reported for easily degrad-able substrates, which in effect were not substrate limited.

Several mechanisms have been proposed to explain the negative effects of nitrogen fertilization on decomposition rates (Fog, 1988): (1) the competitive balance in the microbial community is shifted to bacteria and fungi which rapidly utilize the additional nutrients at the expense of the slower growing lignolytic basidomycetes; (2) the production of ligninase is repressed in the presence of available nitrogen and recalcitrant lignocellulose accumulates preferentially; and (3) polymerization reactions

with polyphenols are enhanced by the presence of amino compounds resulting in the formation of more recalcitrant compounds. These proposed mechanisms leading to decreased decomposition in the presence of nitrogen fertilizers are very similar to several theories on humification (see **Section 10.7.6**).

While the influence of nutrient availability on litter decomposition has been well documented, its influence on SOM turnover has received much less attention. Working along the same age gradient as Ostertag and Hobbie (1999), Torn et al. (in review) found that the slow SOM pool (turnover times of decades) in the O and A horizons turned over two to three slower in the young nitrogen-limited and old phosphorus-limited sites than in the non-nutrient limiting sites of intermediate age. Additionally, experimental fertilization at the young and old sites had only small and inconsistent effects on SOM turnover (Torn et al., in review). These results in combination suggest that nutrient availability does not directly influence microorganisms ability to degrade SOM (consistent with the assumption that microorganisms are primarily carbon-substrate limited, not nutrient limited), but, rather, indirectly through the quality of the litter resource being incorporated into the soil (similar to the conclusions for leaf and root litter from Ostertag and Hobbie, 1999).

Soil texture also plays a major indirect role in regulating decomposition dynamics by effecting nutrient availability. The exchange capacity due to clay mineralogy will have a big impact on the nutrient cycling in a soil. Soils with a high cation exchange capacity will better retain nutrient cations (i.e., K^+, NH_4^+, Ca^{2+}, Mg^{2+}, etc.), whereas soils with appreciable anion exchange capacity will better retain nutrient anions (i.e., NO_3^-, PO_4^-, SO_4^{2-}, etc.) (**Table 13**). Working with akaolonite-, Al- and Fe-oxide dominated textural gradient in Para, Brazil, Silver et al. (2000) found that total phosphorus increased fourfold from a sandy to clayey soil and that extractable (available) phosphorus decreased threefold. A similar pattern of phosphorus availability was observed by Tiessen et al. (1994).

10.7.7.4 Climate

Beginning with the work of Tenny and Waksman (1929), studies of detrital processing have often emphasized the importance of the climate of the decomposition environment. In developing their generalized conceptual decomposition model (**Figure 24**), Lavelle et al. (1993) recognized that the temperature and moisture regimes usually exert the dominant control on decay.

Meentemyer (1995) asked the question: "Is the climate of decay processes measured at weather stations?" The microclimate at the scale of an individual leaf may be nearly fully decoupled from what a nearby weather station measures. For field studies following decomposition processes at short time intervals, this decoupling may have important consequences. However, for studies comparing annual mass losses across large geographic regions, the average climate at the weather station will probably suffice. Additionally, as Lavelle et al. (1993) noted, climate is not an equally important constraint across all ecosystems. Whitford (1989) hypothesized that abiotic controls on decomposer food webs are least important in moist, closed-canopy forests and most important in hot deserts.

Most research has shown that temperature and moisture regimes are the relevant climatic controls on decomposition. How these "regimes" are represented as measurable variables is not universally agreed upon and will often depend on the scale of investigation. Temperature of air or soil can be represented as an average, maximum, or minimum for any given temporal scale. It can also be incorporated into time-dependent models by regressing mass loss against degree-day data (Andren and Paustian, 1987). Moisture can be represented simply by the amount of precipitation or more directly as the volumetric water content (θ) or soil water potential (Ψ). These variables can be combined with knowledge of the water-holding capacity of the soil into the AET, what many researchers (Berg et al., 1993a; Meentemyer, 1978) consider to be a more robust measure of climate. In this section, we will consider how each of these groups of variables controls both litter and SOM processing across a range of scales.

Temperature. In controlled laboratory incubations of single substrates where only temperature varies and moisture is nonlimiting, investigators often find a strong positive correlation between mineralization rate and temperature (Moore, 1986; Nicolardot et al., 1994; Sorensen, 1981). Similar observations have been made for fresh litter and mineral-associated OM (e.g., Kirschbaum, 1995). Swift et al. (1979) proposed that litters of differing quality have consistent differences in decay rates regardless of temperature or moisture regimes. However, Taylor and Parkinson (1988a) observed that pine and aspen litters have different initial (16-week) responses to temperature (**Figure 32**).

This differential response is generally not seen in laboratory studies of SOM mineralization (Fang and Moncrieff, 2001; Katterer et al., 1998; Kirschbaum, 1995) or in an analysis of field studies conducted in nonmoisture limiting systems (Lloyd and Taylor, 1994). For example, Katterer et al. (1998) empirically fit two-component exponential decay models (Equation (5)) to 25 sets of incubation data and found that a single nonlinear model could explain 96% of the variance in the SOM decay rate response (r) factor to temperature (**Figure 33**). The r-factor is simply a scalar that adjusts all k_1 and k_2 values to a common temperature ($r = 1$ at 30 °C), i.e.,

$$k_1 = r k_1^{T=30} \tag{9}$$

In fitting their model, Katterer et al. (1998) assumed that temperature affects the decay constants of the labile and recalcitrant fractions equally. There is evidence from litter decomposition studies that this assumption may not be valid. Studying the decomposition of a ^{14}C-labeled standard plant litter along an altitudinal gradient in Venezuela, Couteaux et al. (2002) found that the labile fraction decayed rapidly regardless of temperature, whereas $k_{\text{recalcitrant}}$ was strongly correlated with temperature. Nicolardot et al. (1994) also found nonproportional responses of glucose and holocellulose carbon and nitrogen mineralization rates to increasing temperature in a laboratory microcosm study.

Researchers have fit a variety of empirical models to describe the temperature dependence of soil respiration and OM decomposition. Lloyd and Taylor (1994) and Fang and Moncrieff (2001) have excellent discussions of many of these models. **Figure 34** illustrates the relationship between the mean residence times of SOM with mean annual temperature (MAT) for a wide range of forested sites (Sanderman et al., 2003). We will use this data set to discuss the fit and appropriateness of several common

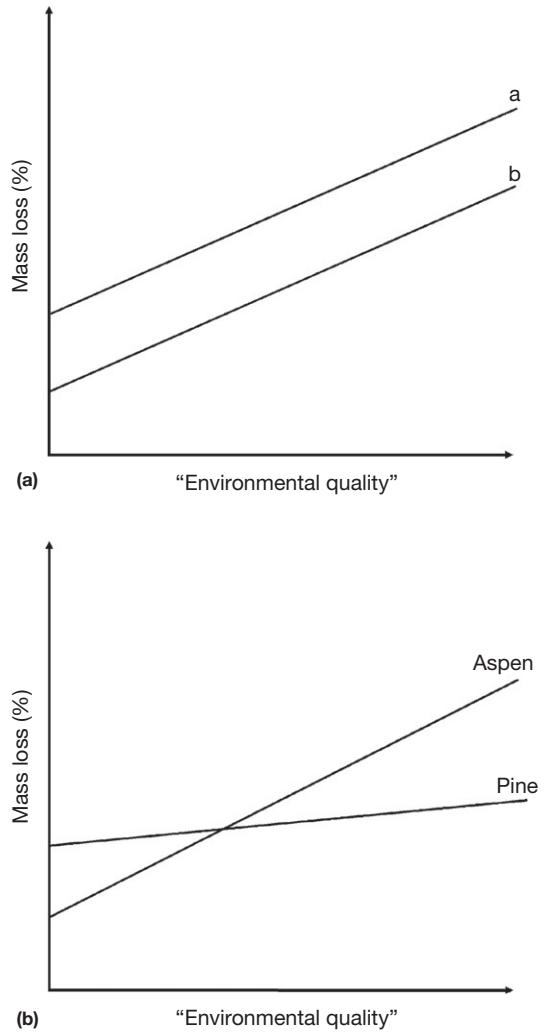

Figure 32 Graphical depiction of the response of litter decomposition rate to changes in climate and edaphic factors that favor decomposition ("environmental quality"). (a) Theoretical response that substrate "a" decomposes faster than substrate "b" under all conditions (b) The observed response of pine needles and aspen leaf litter mass loss to changing conditions. (after Taylor and Parkinson, 1988a).

temperature-dependent decomposition models. Linear and exponential equations are simple empirical expressions relating turnover time with increasing temperature, although they lack any theoretical basis (Fang and Moncrieff, 2001). While some researchers have found a good linear fit for decomposition of specific substrates (Nicolardot et al., 1994), a cursory examination of **Figure 34** reveals its inappropriateness. A common log–transform of the data produces a more reasonable fit ($r^2 = 0.77$, $P < 0.0001$, $n = 21$). However, as Fang and Moncrieff (2001) found, an examination of the distribution of residuals reveals that turnover times are underestimated at low temperatures and overestimated at high temperatures.

The exponential equation is given as

$$\tau = \tau_0 e^{\beta(T-\bar{T})} \tag{10}$$

where β is a fitted parameter and τ_0 is the turnover time at the MAT, yields a very good fit to the data in **Figure 34** ($r^2 = 0.81$, $P < 0.0001$, $n = 21$). The rate increase of any reaction to a 10 °C increase in temperature is termed the Q_{10} value (Kirschbaum, 2000). We calculated Q_{10} for these data (where $Q_{10} = e^{10\beta}$) to be 2.9 for this regression at a MAT of 281 K. Although the model produces an excellent fit with the data, fitting a constant Q_{10} is not biologically realistic (Fang and Moncrieff, 2001; Kirschbaum, 1995). In a review of laboratory incubation data, Kirschbaum (1995) found a greater temperature sensitivity of decomposition at lower temperatures. To accommodate this, the Arrhenius equation can be expressed in terms of turnover time at 10 °C (as illustrated in Lloyd and Taylor, 1994):

$$\tau = \tau_{10} \exp\left[\frac{E^*}{R}\left(\frac{1}{283.15} - \frac{1}{T}\right)\right] \tag{11}$$

where E^* is the activation energy and R is the universal gas constant (8.314 $\mathrm{Jmol^{-1}\,K^{-1}}$). Although the empirical fit of Equation (11) in **Figure 34** is similar to a simple exponential model ($r^2 = 0.81$), this equation is theoretically more justifiable because it is derived from basic biochemical principles (Moore, 1986). A plot of the natural logarithm of decay rates versus the inverse of absolute temperature (the "Arrhenius graph") should reveal a linear range whose slope is the activation energy. Beyond this range, decomposition rates drop sharply due to microbial limitations in extreme cold and hot environments.

Lloyd and Taylor (1994) suggested that the assumption of a constant activation energy across a range of ecosystems, that likely have vastly different microbial communities, may not be valid. Plotting the data of both Lloyd and Taylor (1994) and Sanderman et al. (2003) reveals a nonlinear decrease in the ln *(k)* with decreasing *T*. Based on this observation, Lloyd and Taylor modified Equation (11) to account for the effect of a nonconstant activation energy:

$$\tau = \tau_{10} \exp E_0\left(\frac{1}{283.15 - T_0} - \frac{1}{T - \bar{T}_0}\right) \tag{12}$$

where E_0 and T_0 are fitted parameters and τ_{10} is the turnover time at 10 °C. This equation is no longer directly related to biochemical principles but Lloyd and Taylor (1994) suggested that this "semi-empirical formulation effectively gives a decrease in activation energy with increasing temperature." Equation (12) fit to the data in **Figure 34** produces a similar, albeit more gradual, temperature response than reported by Kirsch–baum (1995) where the calculated Q_{10} decreases from 4 to 2 across a 36 °C temperature range.

Dalias et al. (2001b) incubated soils from different latitudes with a common ^{14}C-labeled substrate and found that the temperature response optima (similar to the *r*-factor of Katterer et al., 1998) varied with latitudinal origin of soil and decreased with time for some soils. This finding is consistent with the notion that the native microbial community is adapted to function optimally within the normal range of temperatures they are acclimated to. Additionally, these researchers found that the proportion of litter acting as labile carbon (α in Equation (8)) decreased with increasing temperature. In a companion study, Dalias et al. (2001a) confirmed this temperature-dependent stabilization by moving soils, initially incubated at different temperatures until a common percent mass loss was achieved, to a common temperature. The litter conditioned at the highest temperature had the slowest mass

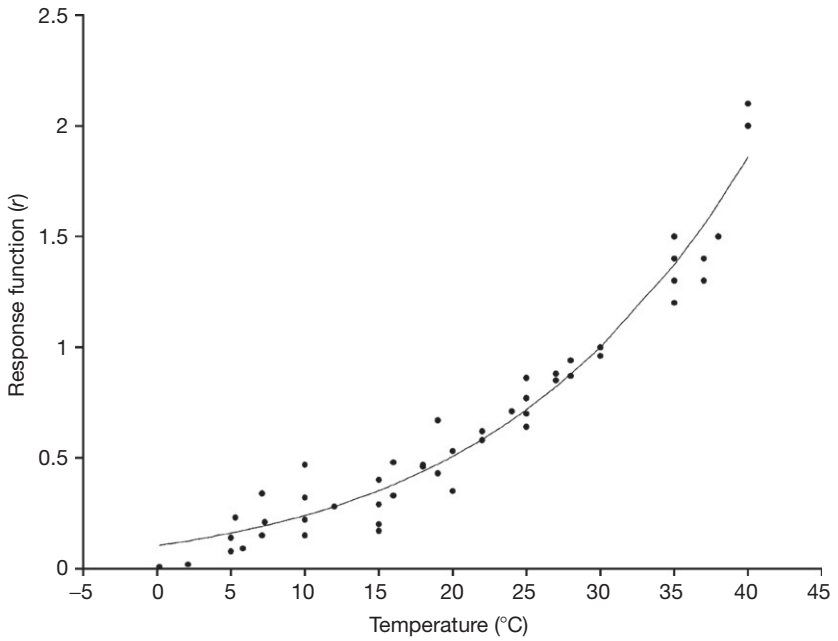

Figure 33 The temperature response function r of the first-order decomposition rate constants k_l and k_r. The r-function is a scalar that relates k at any given temperature to its maximal rate at a reference temperature ($T_{ref} = 30\,^{\circ}C$, see text for details). Also shown is the modeled fit of the Lloyed and Taylor equation (Equation (12), $r^2 = 0.96$). (after Katterer et al., 1998).

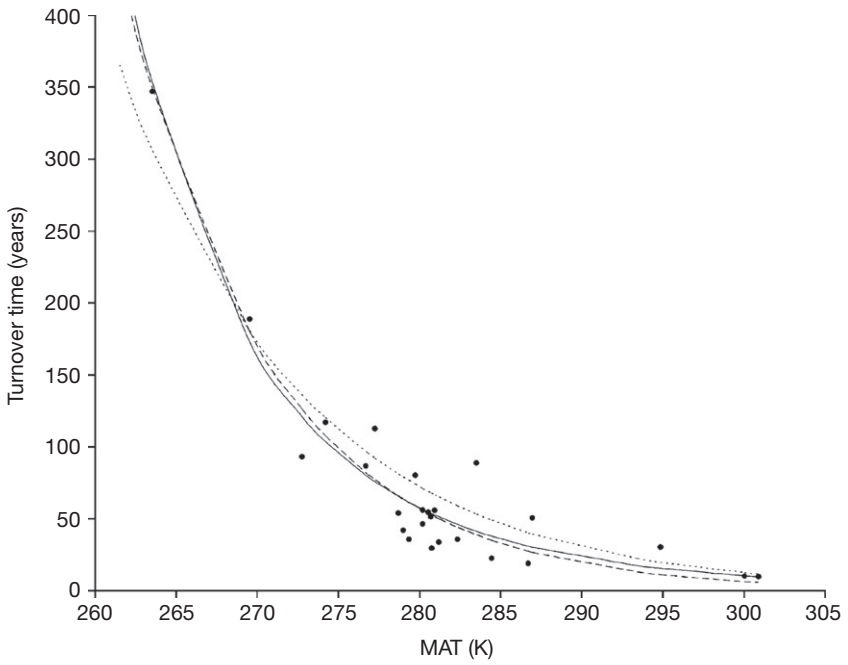

Figure 34 Steady-state SOM mean residence times derived from eddy covariance data plotted against MAT. Bold solid curve is Lloyd and Taylor fit; bold dashed curve is the Q_{10} best fit; and light dashed curve represents a linear regression wit, the common log of turnover time (source Sanderman et al., 2003).

loss rate when incubated at a common temperature, indicating a greater fraction of recalcitrant carbon. Finding similar results, Zogg et al. (1997) concluded that this response to temperature may be due to a shift in the microbial community away from lignin degraders which cannot compete with fast-growing bacteria at the higher temperatures. Berg et al. (1993b) and Johansson et al. (1995) also found that in long-term litter studies, a greater percentage of remaining mass was lignified at the warmer site. Dalias et al. (2001a) cautioned that results such as these may invalidate models that assume constant pool sizes with different temperatures. Additionally, this observed shift in the temperature optima with mass loss of litter has

important implications for decay studies in general: generating thermal response functions from a single cohort or input of litter followed through time may be misleading, because there will be a progressive shift in recalcitrance and hence a non-steady-state response with temperature. In this case, steady-state methods for determining decomposition rates may be of more general use.

Most simply, steady-state annual decomposition rates can be calculated by dividing the standing stock of carbon in the forest floor or mineral soil by the annual flow in (litter production; Olsen, 1963) or out (heterotrophic respiration; Raich and Schlesinger, 1992), respectively. Although single-pool models are gross simplifications of complex systems, they offer the advantage of being inexpensive and easy ways to compare turnover times at large spatial scales. Based on estimates of the steady-state turnover of SOM using the shift in $\delta^{13}C$ following vegetation change across a range of sites, Giardina and Ryan (2000) found no relationship between mean residence time and MAT. This data set contained study sites that were forests converted to pasture, forests converted to various agricultural practices, and pastures that were re-invaded by forests. The varying disturbance histories between these sites may have masked any real trends in climate. By limiting the data set to one land-use type (i.e., forest converted to pasture), Sanderman et al. (2003) found that the $\delta^{13}C$-derived turnover times do indeed decrease exponentially with increasing MAT ($r^2 = 0.59$, $P = 0.001$, $n = 14$). By calculating steady-state turnover times from ^{14}C measurements of density separates of paired pre/post atomic bomb testing soils along an altitudinal transect in the Sierra Nevada, Trumbore et al. (1996) reported a very similar trend to that depicted in **Figure 34** for the mass-weighted mean of the low-density (<2.0 g cm^{-3}) and hydrozylable portion of the dense fraction (>2.0 g cm^{-3}) of the surface horizons.

Moisture. Microorganisms rely on the thin film of water surrounding soil particles and in soil pores for the basic necessities of life. As water potential drops, microorganisms must either enter a quiescent resting phase or perish (**Table 4**). In laboratory incubations at constant temperatures of both litter (Donnelly et al., 1990; Taylor and Parkinson, 1988a) and SOM (Orchard and Cook, 1983; Thomsen et al., 1999), carbon mineralization rates are strongly correlated with soil moisture levels. For example, Donnelly et al. (1990) found that at 12 °C increasing θ from 0.2 m^3 m^{23} to 0.6 m^3 m^{-3} increased microbial biomass fourfold and increased cellulose degradation by over 60-fold and lignin degradation by sixfold. In a 77-day incubation of a silt loam pasture soil at 25 °C, Orchard and Cook (1983) found that microbial activity measured as CO_2 evolution increased linearly with the common logarithm of water potential (**Figure 35**). Unfortunately, many soil moisture experiments only report volumetric water content (θ), which is hard to compare physiologically across different soils (Walse et al., 1998). For any value of θ, the soil water potential (Ψ), which may be of greater physiological significance, will be higher for a fine textured soil than a coarse textured soil.

In field studies, soil moisture can affect decomposition dynamics in a number of ways. In systems where soil moisture is nonlimiting, researchers find little, if any, correlation between soil respiration and soil water potential (Davidson et al., 1998). However in the same study, Davidson et al. (1998) found that including matrix potential with soil temperature could significantly improve soil flux predictions at sites that are affected by seasonally low Ψ (**Figure 36**). Xu and Qi (2001) found a similar seasonal pattern in a ponderosa pine plantation in the Mediterranean climate of northern California—soil CO_2 efflux increases sharply with increasing spring temperatures until the soil dries out a few months later

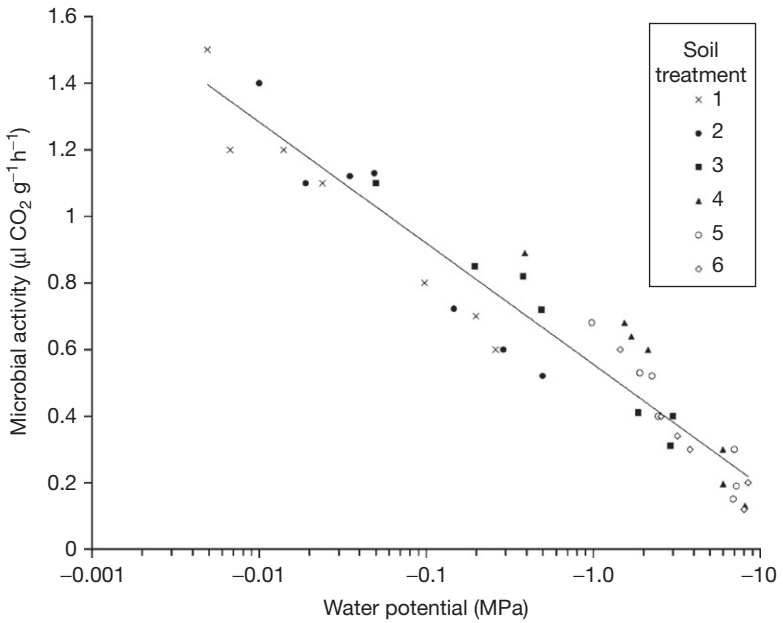

Figure 35 Relationship between water potential (MPa) and microbial respiration during a 77-day incubation of a silt loam with six different initial water potentials: −0.005 MPa, −0.01 MPa, −0.05 MPa, −0.4 MPa, −1.0 MPa, and −1.5 MPa, for treatments 1–6, respectively (source Orchid and Cook, 1983).

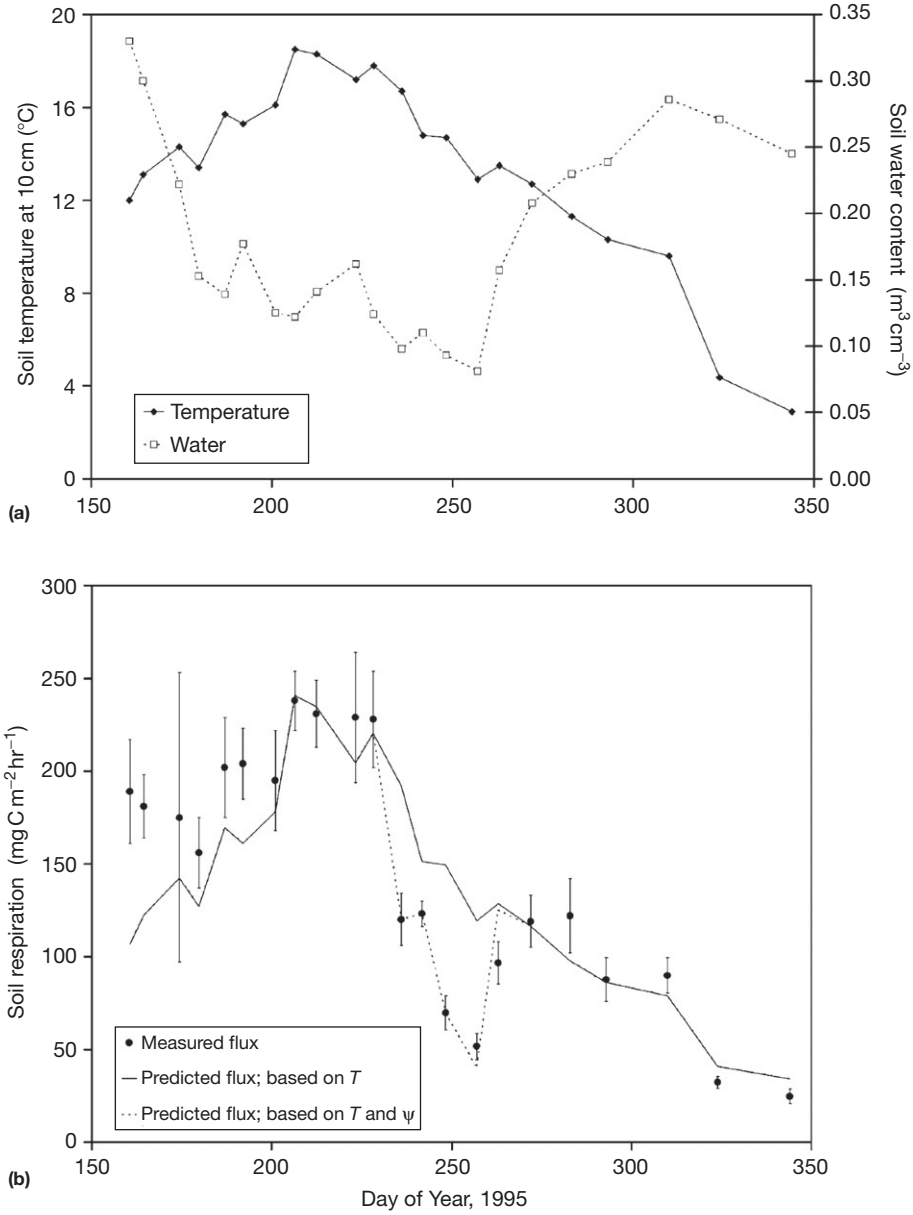

Figure 36 Seasonal variation in mean soil temperature and soil water content for well-drained soils at the Harvard Forest, MA. Also shown is the measured flux (error bars = 1 standard error) and predicted flux based on temperature alone (solid line) and based on temperature and soil water potential (dashed line) (after Davidson et al., 1998).

and flux rates drop sharply. Bryant et al. (1998) concluded that soil moisture was the primary control on surface litter decomposition in an alpine tundra ecosystem.

In the wet tropics, rapid forest floor (O horizon) decomposition begins with leaf fall, and nutrient releases reflect leaf fall seasonality (Anderson and Swift, 1983). In contrast, in dry tropics, the nutrient flush is delayed until the onset of the rainy season resulting in a strong, highly seasonal, pulse of nutrients to the ecosystem (Cornejo et al., 1994). In Cornejo et al.'s study, mass loss was greater under irrigation during the dry season than in the control (no irrigation) due primarily to leaching, and secondarily to microbial enhancement. Similarly, Swift et al. (1981) found that during the dry season, substantial amounts of phosphorus, nitrogen, and other nutrients accumulated on the forest floor in undecomposed leaf litter, and within four weeks of the onset of rains all of the accumulated phosphorus and half of the nitrogen was released through decomposition (reported in Anderson and Swift, 1983). In cool temperate forest soils, West et al. (1992) found that drying produced only a small reduction in microbial biomass, but rewetting caused basal respiration and carbon mineralization to increase strongly. West et al. (1992) attributed this strong increase in mineralization to enhanced microbial turnover and subsequent release of immobilized nutrients. Rapid rewetting imposes osmotic stresses that many microorganisms cannot tolerate resulting in ruptured

of the cell walls, and a large turnover of the microbial biomass (Kieft et al., 1987). Consistent with general microbial ecology, the bacterial populations are often observed to recover faster from drying/rewetting events, than the slower growing fungal communities (Scheu and Parkinson, 1994; Van Gestel et al,. 1993). Studying the effects of wetting/drying cycles on earthworm casts, McInerney and Bolger (2000b) found that supersaturation of casts can swell clays enough to break the organo-clay bonds and reduce the structural stability of the cast, leading to a reduction in the protection of the SOM within.

Working along a well-controlled precipitation gradient on the island of Hawaii, Austin and Vitousek (2000) found a clear increase in *M. polymorpha* litter decomposition rates with mean annual precipitation (MAP) increasing from 500 mm to 5500 mm. To tease apart direct versus indirect effects of increasing MAP, these authors studied the decomposition of *in situ* litter, common substrates across sites, and litter taken from each site and decomposed at the common site. The decay rates for the common substrates of varying quality all increased with MAP; as did the *in situ* litters despite the fact that palatability, as measured by mass loss at the common site, decreased with increasing MAP of the site where the litter was obtained (Austin and Vitousek, 2000). Along this gradient, climate exerts a direct control on microbial metabolism, and indirect effects on nutrient (phosphorus) availability in the soils (Austin and Vitousek, 1998), which are manifest in the decreasing litter quality from the dry to wet sites. A second important indirect effect of soil moisture that several investigators have also observed is that as soil moisture content declines the temperature sensitivity or Q_{10} value decreases in both lab-based litter incubations (Moore, 1986) and field-based soil respiration studies (Xu and Qi, 2001).

AET. Combining temperature and moisture into a multivariate model is often complicated by the fact that these two factors co-vary in many ecosystems. Many researchers believe that AET best combines these interactions between temperature and precipitation along with soil physical parameters in predicting decomposition dynamics (Berg et al., 1993a; Gonzalez and Seastedt, 2001; Meentemyer, 1977). Studying the first-year mass loss of a common pine needle substrate, Meentemyer and Berg (1986) found that 80% ($P<0.0001$, $n=14$) of the variance between pine forests along a latitudinal transect in Sweden could be explained by AET. Berg et al. (1993a) expanded this study to include pine forests in the eastern United States and across Europe and again found a strong linear trend between first–year mass loss and AET (adjusted $R^2=0.5$, $P<0.0001$, $n=39$). However, Whitford et al. (1981) suggested that this simple AET model is not appropriate in very low-AET (i.e., desert) ecosystems and in very disturbed systems (i.e., clear-cut forests) because of biotic adaptations and marked differences in microclimate, respectively.

In cross-site studies designed to examine climatic controls on litter decomposition, a common practice is to use a "standardized litter" from one forest and place it in all of the treatment sites (Berg et al., 1993a; Gholz et al., 2000; Gonzalez and Seastedt, 2001). This experimental design raises the question: Is there a "home field advantage" (Gholz et al., 2000) for native litters? Based on a comparison of a short-grass prairie, a mountain meadow, and a lodgepole pine ecosystem, Hunt et al., (1988) suggested that the decomposer community in a particular ecosystem may be adapted to the native litter of that ecosystem. Berg et al. (1993b) attempted to limit this treatment effect by restricting their study to a variety of coniferous forests. In a comparison of long-term (five-year) litter dynamics across 28 long-term ecological research (LTER) sites, Gholz et al. (2000) found that when k was normalized by AET, leaf litter from the tropical hardwood *Drypetes glauca* decomposed nearly 3 times faster in broadleaf forests than in coniferous forests ($k=1.37$ and 0.43, respectively) and needle litter from *Pinus resinous* decomposed 30% faster in coniferous forests than in the broadleaf forests.

With this qualification in mind, Gholz et al. (2000) reported that the synthetic climate variable DEFAC, a composite of temperature and moisture influences on decay rates (see **Section 10.7.8**), developed for predicting the climate influence on litter, and SOM decomposition in the Century model (Parton et al., 1993) is a better predictor of litter decay rates than AET across the LTER sites (**Figure 37**). Gholz et al. (2000) concluded that DEFAC is applicable over a wider range of ecosystems because it "places a primary emphasis on temperature over a relatively broad range of moisture availability, and still maintains some decomposition at very low precipitation." For the studies listed in **Table 11**, DEFAC (Pearson's $r=0.94$, $P<0.01$, $n=6$) does a better job in predicting the mean k across a range of litter types than AET (Pearson's $r=0.70$, $P>0.2$, $n=6$).

The studies presented in this section indicate that not only does climate play a large direct role in litter decomposition and SOM turnover, but the indirect effects of climate on the structure of the microbial community (Zogg et al., 1997), litter chemistry (Alvarez and Lavado, 1998), soil texture (Alvarez and Lavado, 1998), and nutrient status (Vitousek et al., 1994) combine to make climate the overriding influence on detrital processing when comparing across large spatial and temporal scales. This is especially evident in studies that calculate turnover times from an aggregate of substrates with varying quality (e.g., CO_2 efflux studies and isotopic studies on bulk samples).

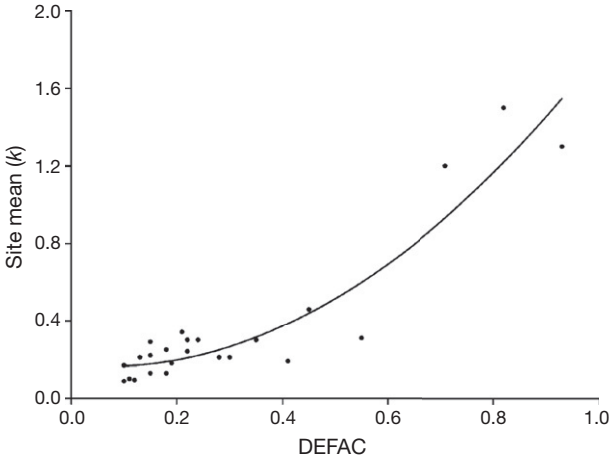

Figure 37 Relationship between the mean decomposition rate constant k for the leaf and root litter of *D. glauca* and *Pinus elliotii*, and DEFAC, a synthetic climate variable (see text for explanation), across a range of N. American sites. Solid line is a quadratic fit with the data ($r^2=0.88$, $n=28$) (source Gholz et al., 2000).

10.7.7.5 Multiple Constraints

In developing a model that incorporates both AET and litter quality (i.e., lignin concentration), Meentemyer (1978) found that mass loss is more sensitive to changes in AET when the litter is of higher quality. However, in nature litter quality will often co-vary with climate, making it harder to tease apart the relative strength of climate versus resource quality controls on decomposition. In a review of 44 litter decomposition data sets, Aerts (1997) was able to separate the relative contributions of direct and indirect controls of climate and litter quality (lignin/N) on decomposition rates using the multiple regression technique of path analysis (**Figure 38**). In this "triangular relationship," AET is significantly correlated with both k and the lignin/N ratio which, in turn, is also significantly correlated with k. More importantly, ~20% of the relationship between k and AET can be explained by the indirect effects of the lignin/N ratio (Aerts, 1997).

The lignin concentration increase rate (LCIR) as defined by Berg et al. (1993b) is the slope of a plot of lignin concentration versus mass loss. The LCIR for Scots pine litter is highest under favorable climate conditions (and/or soil nutrient status) which can actually lead in the long term to the formation of more recalcitrant SOM. In colder/dryer conditions, LCIR is lower because mass loss of labile components is slower leading to an accumulation of easily decomposable SOM. This line of reasoning can help explain why SOM at colder sites is relatively more sensitive to changes in temperature. These results also support the model of Berg and Staaf (1980) that in early stages of litter decay, climate, or nutrient status controls mass loss of labile components; then in later stages, lignin loss rate is rate limiting factor.

The models of Meentemyer (1978), Parton et al. (1987), and Aerts (1997) consider climate and litter quality as the dominant controls on decomposition rates. Of these studies, only Aerts (1997) has included tropical sites in developing his regressions. For the tropical sites only, no significant regressions could be developed with AET and the lignin/N ratio could only explain a little more than 50% of the variance in k. Lavelle et al. (1993) and others have suggested that in the humid tropics where macroinvertebrate populations are large, biological regulation of decomposition becomes much more important. In **Section 10.7.7.1**, we have reviewed numerous studies where soil fauna play an important, if not dominant, role in detrital processing. Gonzalez and Seastedt (2001) designed a three-factorial (climate, litter quality, and macrofauna) experiment to test the hypothesis that the soil biota become significant factors in controlling litter decay rates. These authors found that climate and litter quality were significant at all three sites (temperate, dry tropical, and wet tropical), while the faunal exclusion only produced significant effects in the wet tropical site.

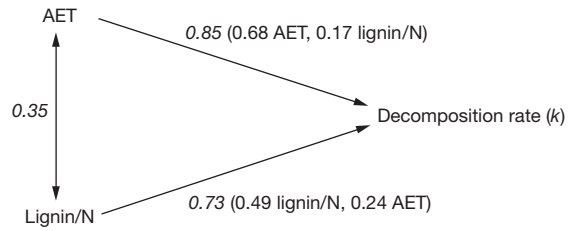

Figure 38 Path diagram describing the structure of the relationship between decomposition rate constants *(k)* and climate (AET) and litter quality (lignin/N ratio) for first-year decomposition from 44 locations. Numbers in bold type are the Pearson correlation coefficients among variables and the numbers in parentheses partition the coefficients into direct and indirect effects of the predictor variables (AET and lignin/N) (source Aerts, 1997).

Detrital processing can be thought of as a continuum from fresh litter to stabilized SOM (Agren and Bosatta, 2002). At different stages in this continuum, the relative importance of each of these environmental and biological factors that have been identified as controlling decomposition dynamics will likely vary. The initial stages of mass loss are characteristically most affected by climate, resource quality, and, when abundant, soil macrofauna. The physical soil environment also needs to be considered as an important control on the turnover of more humified SOM in the mineral horizons. It is also evident from this literature review that observed correlations between decay rates and "decomposition" factors are often attributable to both the direct effects of that factor on microbial metabolism and to the indirect interactions with other factors.

10.7.8 Modeling Approaches

Modeling has been critical to the development and advancement of biogeochemistry. Models are tools for both synthesizing and extrapolating to broader spatial and temporal scales, and for testing and refining hypotheses. Decomposition and detrital processing in terrestrial ecosystems has been represented in a number of biogeochemical-process-based simulation models, including Century (Parton et al., 1987, 1993), Introductory Carbon Balance Model (ICBM) (Katterer and Andren, 2001), G'Day (Comins and McMurtrie, 1993), Linkages (Pastor and Post, 1986), and Terrestrial Ecosystem Model (TEM) (McGuire et al., 1992). The use of first-order kinetics to describe decomposition rates and division of SOM into a number of pools based on decomposability are traits common to all of these models with roots dating back to the original work of Tenney and Waksman (1929). These simulation models differ from the empirical models presented in the previous sections in that they can be potentially parametrized for application across a range of ecosystems.

Complex bottom-up modeling (e.g., food webs) of decomposition and detrital processing is often impossibly difficult at the ecosystem level. To quote Andrén et al. (1999): "How do we construct an ecosystem out of a square meter harboring 50000 microorganism species, 50 mite species, 10 enchytraied species, 1000 insect species, 100 plant species, etc.? And the adjacent square meter, where careful sampling revealed a slightly, but statistically significant, different species composition, is that another ecosystem?" To deal with this amazing genetic diversity, most ecosystem models use top–down or process-based approaches where the organismal physiology and their population size are only implicitly included (see Schimel (2001) for an excellent discussion on this topic). When applying a process-based model to environmental change, Andrén et al. (1999) suggested five crucial questions that should be addressed to determine if implicitly including the biota is sufficient: (1) Are there any keystone species?

(2) Are there species-poor functional groups? (3) Are there functional groups with low dispersal abilities? (4) Are there important "narrow–physiology" microbes? and (5) Are there significant interactions that may vanish or appear?

The underlying assumption in implicitly including decomposer organisms, and microorganisms in particular, is that microbes are primarily carbon limited and the microbial community can rapidly expand and adapt to handle even extreme environmental changes (Finlay et al., 1997; Schimel, 2001). As shown in numerous examples throughout this chapter, these assumptions seem to hold in most situations. However, as Schimel (2001) highlights, there are numerous situations where these assumptions may not hold and an explicit characterization of the microbial biomass and physiology would result in a more accurate model.

The basic representation of decomposition using first-order kinetics has already been discussed. Here we will highlight how the widely used Century model represents decomposition, SOM cycling, and the controls on these processes (Parton et al., 1987, 1993). We choose this model due to its intensive development, and its wide use and availability to the scientific community. For a detailed description, instructions, and to download the version 5 of Century (latest as of early 2003) see www.nrel.colostate.edu/projects/century5/. A box model representation of the SOM dynamics in Century version 5 is shown in Figure 39. Litter, both aboveground and belowground, is divided into structural and metabolic carbon based on its lignin/N ratio. Surface metabolic carbon is incorporated into the microbial carbon pool, whereas the belowground metabolic carbon pool flows into the active carbon (~0.5 yr turnover time). However, as McGill (1996) noted, the microbial carbon pool is essentially indistinguishable from the active carbon pool. Most structural and active carbon is incorporated into the slow carbon pool (turnover of 20–40 yr), which can further be transformed into passive carbon (200–1500 yr). Both slow and passive carbon can be transformed back onto active carbon. During each microbially mediated transformation, a percentage of the carbon is mineralized to CO_2. For each carbon pool, there is an analogous nitrogen, phosphorus, and sulfur pool, which is linked directly to the carbon flows by the carbon-to-nutrient ratios.

Decomposition of each pool is calculated as

$$\frac{dC_i}{dt} = K_i L_C A T_m C_i \tag{13}$$

where C_i = carbon in the ith pool, K_i = maximum decomposition rate for the ith pool, L_C is the impact of lignin on structural decomposition, A is the combined effect of temperature and

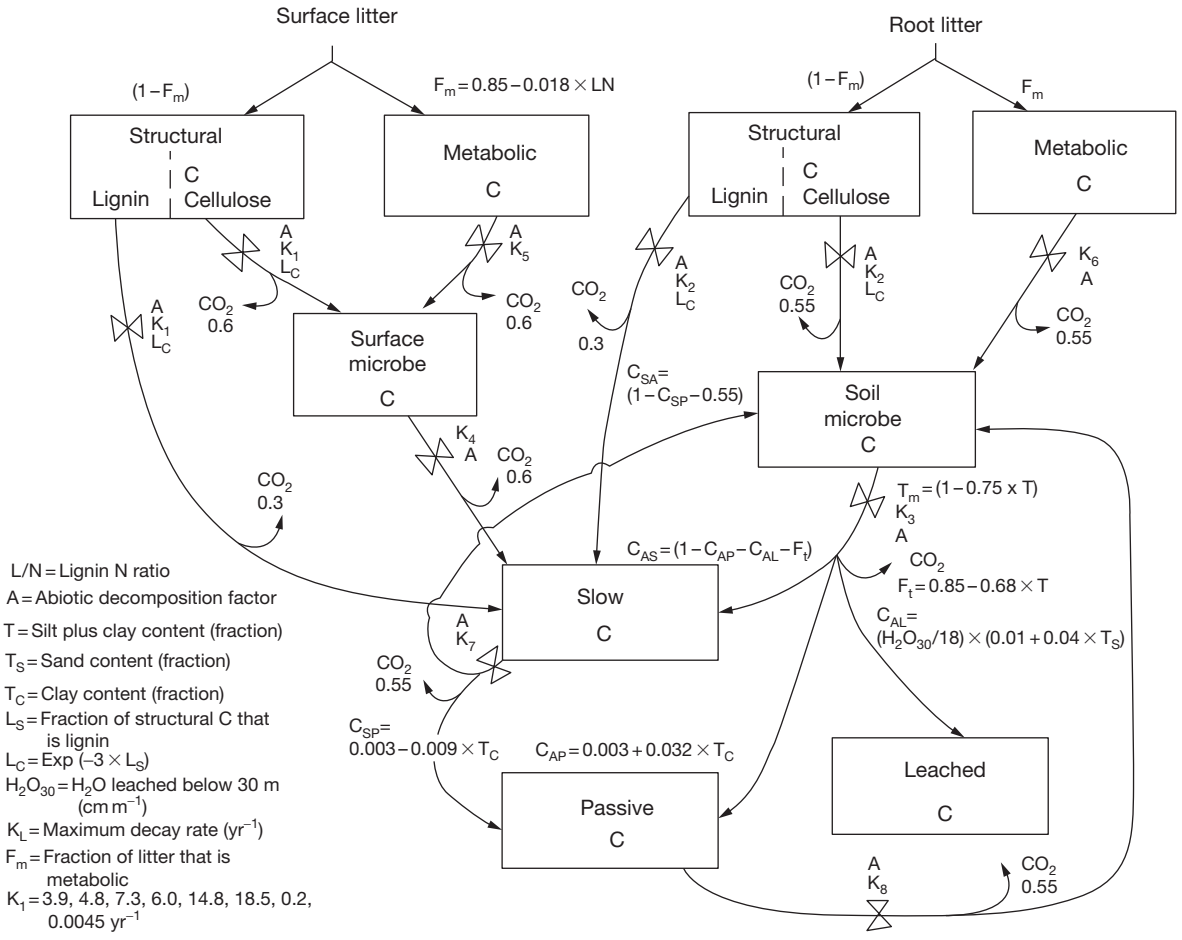

Figure 39 Diagram of carbon pools and flows in the Century version 5 agroecosystem model (Parton et al., 1993) (reproduced by permission of the American Geophysical Union from *Global Biogeochem. Cycles*, **1993**, *7*, 785–809). See text for discussion.

moisture on decomposition, and *Tm* is the effect of soil texture (defined as the silt + clay content of the soil) (Parton et al., 1994). All of the effects on K_i are scaled from 0 to 1, so that if any of the variables are suboptimal, the maximum decomposition rate will not be realized. As shown in **Figure 39**, most transformations are controlled by only a subset of these scalars. The shapes of the soil temperature and moisture effect curves are shown in **Figure 40**.

The general structure of most terrestrial bio–geochemistry models is similar to what we have described for the Century model; however, these models do vary significantly in how they treat the controls on decomposition (Burke et al., 2003). For example, TEM uses an exponentially increasing temperature scalar ($Q_{10} = 2.0$), while Century uses a generalized Poisson function that drops off rapidly above 40 °C (shown in **Figure 40(a)**). Similar differences between models are found when comparing the moisture, textural, and litter quality controls. These differences become strikingly apparent when several models are used to simulate ecosystem dynamics in highly contrasting ecosystems (Moorhead et al., 1999).

Part of these discrepancies can be attributed to the fact that many of these models are based on a limited number of empirical studies. In Century, the temperature response function that is *the same for all pools* of carbon was derived from the Sørensen (1981) 90-day laboratory incubation study on the decomposition of labeled cellulose at three different temperatures (10 °C, 20 °C, and 30 °C) (Parton et al., 1987). It is unlikely that microbial physiology developed to digest cellulose will respond to temperature the same way as physiologies designed to digest lignin and other recalcitrant polymers. In fact, Taylor and Parkinson (1988a) found that pine and aspen litters had different initial responses to changing temperature, with the more palatable aspen leaves being more sensitive to changes in temperature (**Figure 32**).

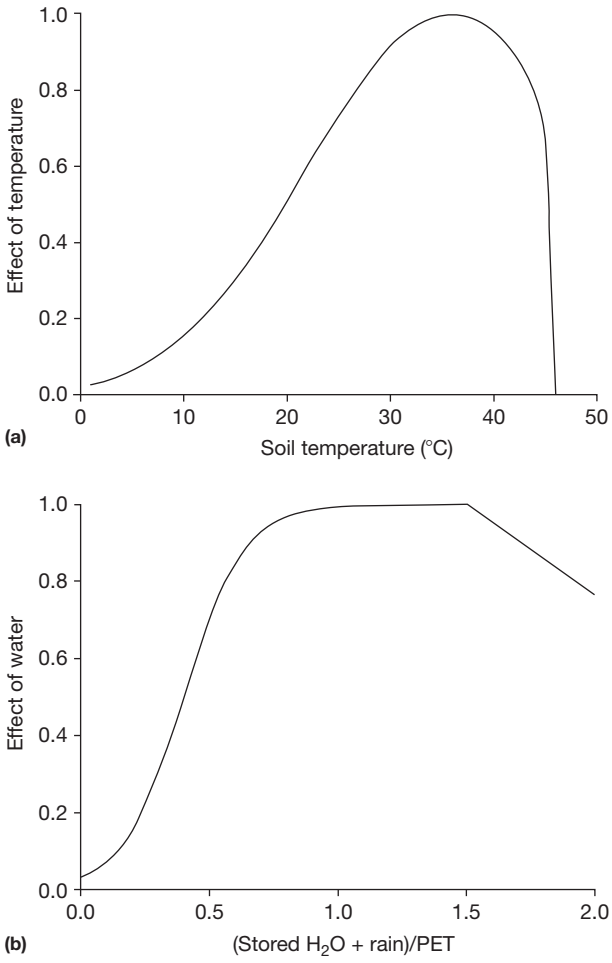

Figure 40 The effect of: (a) soil temperature and (b) soil water on decomposition in the Century model.

In Century, as well as other models, soil texture has a significant influence on the turnover rate of the active carbon pool (i.e., $T_m = 1 - 0.75\,T$ where T is the silt + clay content of the soil) and the rate of stabilization into the slow and passive carbon pools. This formulation of T_m is based on data from the Sørensen (1981) study in Danish agricultural soils and validated with a series of semi-arid grassland soils (Gregorich et al., 1991; Schimel et al., 1985; Van Veen et al., 1985). The applicability of this relationship to soils with a different mineralogy, especially variably charged clays found in many tropical regions, is questionable (e.g., Giardina and Ryan, 2000, 2001). Additionally, the disruption of soil aggregates in the original laboratory experiments (Sørensen, 1981) can result in significantly different carbon dynamics than in an intact soil (see **Section 10.7.7.3**).

Despite these and other potential limitations, Century and other biogeochemistry models are able to reasonably simulate the carbon and nitrogen dynamics in many ecosystems (see Parton et al., 1994 for example). The success of these models in simulating current conditions, given proper parametrization, gives scientists and policy makers greater confidence in believing model predictions under climate change and differing management regimes. However, caution should be used in interpreting these predictions given the uncertainties in the data used for model development, such as those described above. Greater attention should be given to designing experiments that test these models' assumptions regarding the controls on decomposition (Burke et al., 2003) and on the underlying microbiology (Schimel, 2001).

10.7.9 Conclusions

Decomposition is essentially a microbial process whose rate is regulated by a suite of physical and biological controls. At the microscopic level, many of the biochemical details of microbial degradation of specific carbon and nitrogen compounds have been well documented. However, beyond this scale, most of our understanding of decomposition becomes empirical in nature. As we have highlighted in this review, there exists a wealth of data on the decomposition of plant litter while root and soil OM have received significantly less attention. The composition and activity of soil fauna, initial resource quality, soil properties such as texture and nutrient availability, and climatic factors such as temperature and moisture must all be considered. These factors can directly affect a microorganism's ability to degrade a resource or indirectly affect biodegradation by altering one or more of the above factors in a way that affects microbial activity. Most biogeochemical models

incorporate only a subset of these controls and rarely incorporate the numerous indirect effects. As carbon cycling and sequestration becomes more and more of a sociopolitical issue, the demand for more precise biogeochemical models that incorporate all of these direct and indirect effects will likely increase.

References

Abe T, Bignell DE, and Higashi M (2000) *Termites: Evolution, Sociality, Symbioses, Ecology*. Kluwer Academic.

Aber JD, Melillo JM, and McClaugherty CA (1990) Predicting long–term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can. J. Botany* 68(10): 2201–2208.

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79(3): 439–449.

Aerts R and De Caluwe H (1997) Nutritional and plant– mediated controls on leaf litter decomposition of Carex species. *Ecology (Washington, DC)* 78(1): 244–260.

Agren GI and Bosatta E (2002) Reconciling differences in predictions of temperature response of soil organic matter. *Soil Biol. Biochem.* 34(1): 129–132.

Alvarez R and Lavado RS (1998) Climate, organic matter and clay content relationships in the Pampa and Chaco soils, Argentina. *Geoderma* 83(1–2): 127–141.

Amann RI, Ludwig W, and Schleifer K-H (1995) Phylogenetic identification and *in situ* detection of individual microbial cells without cultivation. *Microbiol. Rev.* 59(1): 143–169.

Amato M and Ladd JN (1980) Studies of nitrogen immobilization and mineralization in calcareous soils: V. Formation and distribution of isotope–labelled biomass during decomposition of 14C- and 15 N-labelled plant material. *Soil Biol. Biochem.* 12: 405–411.

Amundson R, Stern L, Baisden T, and Wang Y (1998) The isotopic composition of soil and soil–respired CO_2. *Geoderma* 82(1–3): 83–114.

Anderson DW and Paul EA (1984) Organo–mineral complexes and their study by radiocarbon dating. *Soil Sci. Soc. Am. J.* 48: 298–301.

Anderson JM and Swift MJ (1983) Decomposition in tropical forests. In: Sutton SL, Whitmore TC, and Chadwick AC (eds.) *Tropical Rain Forest: Ecology and Management*, pp. 210–287. Blackwell.

Anderson JPE and Domsch KH (1978) A physiological method for the quantitative measurement of microbial biomass in soils. *Soil Biol. Biochem.* 10: 215–221.

Anderson RV, Coleman DC, Cole CV, and Elliott ET (1981) Effect of nematodes *Acrobeloides* sp. and *Mesodi– plogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization in soil. *Ecology* 62: 549–555.

Andrén O, Brussaard L, and Clarholm M (1999) Soil organism influence on ecosystem–level processes bypassing the ecological hierarchy? *Appl. Soil Ecol.* 11(2–3): 177–188.

Andren O and Paustian K (1987) Barley straw decomposition in the field A comparison of models. *Ecology (Tempe)* 68(5): 1190–1200.

Asmar F, Eiland F, and Nielsen NE (1994) Effect of extracellular-enzyme activities on solubilization rate of soil organic nitrogen. *Biol. Fertility Soils* 17(1): 32–38.

Atlas RM and Bartha R (1998) *Microbial Ecology: Fundamentals and Applications*. Benjamin/Cummings.

Augris N, Balesdent J, Mariotti A, and Derenne S (1998) Structure and origin of insoluble and non–hydrolysable, aliphatic organic matter in a forest soil. *Org. Geochem.* 28: 119–124.

Austin AT and Vitousek PM (1998) Nutrient dynamics on a precipitation gradient in Hawai'i. *Oecologia (Berlin)* 113(4): 519–529.

Austin AT and Vitousek PM (2000) Precipitation, decomposition and litter decomposability of Metrosideros polymorpha in native forests on Hawai'i. *J. Ecol.* 88(1): 129–138.

Baldock JA, Oades JM, Waters AG, Peng X, Vassallo AM, and Wilson MA (1992) Aspects of the chemical structure of soil organic materials as revealed by solid–state carbon-13 NMR spectroscopy. *Biogeochemistry (Dordrecht)* 16(1): 1–42.

Baldock JA, Oades JM, Nelson PN, Skene TM, Golchin A, and Clarke P (1997) Assessing the extent of decomposition of natural organic materials using solid-state 13C NMR spectroscopy. *Austral. J. Soil Res.* 35(5): 1061–1083.

Balesdent J, Mariotti A, and Guillet B (1987) Natural carbon– 13 abundance as a tracer for studies of soil organic matter dynamics. *Soil Biol. Biochem.* 19(1): 25–30.

Balesdent J, Wagner GH, and Mariotti A (1988) Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. *Soil Sci. Soc. Am. J.* 52(1): 118–124.

Balesdent J, Mariotti A, and Boisogntier D (1990) Effect of tillage on soil organic carbon mineralization estimated from carbon-13 abundance in maize fields. *J. Soil Sci.* 41(4): 587–596.

Bamforth SS and Lousier JD (1995) Protozoa in tropical litter decomposition. In: Reddy MV (ed.) *Soil Organisms and Litter Decomposition in the Tropics*, pp. 59–74. Westview Press.

Bardgett RD, Cook R, Yeates GW, and Denton CS (1999) The influence of nematodes on below-ground processes in grassland ecosystems. *Plant Soil* 212(1): 23–33.

Barois I and Lavelle P (1986) Changes in respiration rate and some physicochemical properties of a tropical soil during transit through Pontoscolex corethrurus (Glossoscolecidae, Oligochaeta). *Soil Biol. Biochem.* 18(5): 539–542.

Barzegar AR, Nelson PN, Oades JM, and Rengasamy P (1997) Organic matter, sodicity, and clay type: influence on soil aggregation. *Soil Sci. Soc. Am. J.* 61(4): 1131–1137.

Beare MH, Pohlad BR, Wright DH, and Coleman DC (1993) Residue placement and fungicide effects on fungal communities in conventional and no-tillage soils. *Soil Sci. Soc. Am. J.* 57(2): 392–399.

Beare MH, Cabrera ML, Hendrix PF, and Coleman DC (1994a) Aggregate–protected and unprotected organic matter pools in conventional– and no–tillage soils. *Soil Sci. Soc. Am. J.* 58(3): 787–795.

Beare MH, Hendrix PF, and Coleman DC (1994b) Water– stable aggregates and organic matter fractions in conventional– and no–tillage soils. *Soil Sci. Soc. Am. J.* 58(3): 777–786.

Benedik MJ and Strych U (1998) Serratia marcescens and its extracellular nuclease. *FEMS Microbiol. Lett.* 165(1): 1–13.

Berg B (1984a) Decomposition of moss litter in a mature Scots pine forest. *Pedobiologia* 26(5): 301–308.

Berg B (1984b) Decomposition of root litter and some factors regulating the process—long–term root litter decomposition in a Scots pine forest. *Soil Biol. Biochem.* 16(6): 609–617.

Berg B and Staaf H (1980) Decomposition rate and chemical changes of Scots pine needle litter: II. Influence of chemical composition. *Ecol. Bull. (Stockholm)* 32: 363–372.

Berg B and Staaf H (1981) Leaching, accumulation and release of nitrogen in decomposing litter. In: Clark FE and Rosswall T (eds.) *Terrestrial Nitrogen Cycles*, *Ecological Bulletins*, vol. 33, 163–178.

Berg B and Staaf H (1987) Release of nutrients from decomposing white birch leaves and Scots pine needle litter. *Pedobiologia* 30(1): 55–63.

Berg B and Wessen B (1984) Changes in organic–chemical components and ingrowth of fungal mycelium in decomposing birch leaf litter as compared to pine needles. *Pedobiologia* 26: 285–298.

Berg B, Hannus K, Popoff T, and Theander O (1982) Changes in organic chemical components of needle litter during decomposition: long-term decomposition in a Scots pine forest: I. *Can. J. Botany* 60: 1310–1319.

Berg B, Muller M, and Wessen B (1987) Decomposition of red clover *(Trifolium pratense*) roots. *Soil Biol. Biochem.* 19: 589–594.

Berg B, Berg MP, Bottner P, et al. (1993a) Litter mass loss rates in pine forests of Europe and Eastern United States: some relationship with climate and litter quality. *Biogeochemistry (Dordrecht)* 20(3): 127–159.

Berg B, McClaugherty C, and Johansson M-B (1993b) Litter mass–loss rates in late stages of decomposition at some climatically and nutritionally different pine sites: long-term decomposition in a Scots pine forest: VIII. *Can. J. Botany* 71(5): 680–692.

Bhatnagar T (1975) Lombriciens et humification: un aspect noveau de l'incorporation microbienne d'azote induite par les vers de terre. In: Kilbertus G, Reisinger O, Mourney A, and Cancela Da Fonseca JA (eds.) *Biodegradation et Humification*. pp. 169–182 Pierron.

Blaire JM, Parmelee RW, and Lavelle P (1994) Influences of earthworms on biogeochemistry. In: Hendrix PF (ed.) *Earthworm Ecology and Biogeography in North America*, pp. 127–158. Lewis Publishers.

Blanchart E, Bruand A, and Lavelle P (1993) The physical structure of casts of Millsonia anomala (Oligochaeta: Megascolecidae) in shrub savanna soils (Cote d'Ivoire). *Geoderma* 56(1–4): 119–132.

Bondiett E, Martin JP, and Haider K (1972) Stabilization of amino sugar units in humic–type polymers. *Soil Sci. Soc. Am. Proc.* 36(4): 597–602.

Boone RD, Nadelhoffer KJ, Canary JD, and Kaye JP (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature (London)* 396(6711): 570–572.

Bossuyt H, Denef K, Six J, Frey SD, Merckx R, and Paustian K (2001) Influence of microbial populations and residue quality on aggregate stability. *Appl. Soil Ecol.* 16(3): 195–208.

Bottner P, Sallih Z, and Billes G (1988) Root activity and carbon metabolism in soils. *Biol. Fertility Soils* 7(1): 71–78.

Bouché MB (1977) Strategies lombriciennes. *Ecol. Bull. (Stockholm)* 25: 122–132.

Bracewell JM, Haider K, Larter SR, and Schulten HR (1989) Thermal degradation relevant to structural studies of humic substances. In: Hayes MHB, MacCarthy P,

Malcolm RL, and Swift MJ (eds.) *Humic Substances II: In Search of Structure*, pp. 181–222. Wiley.
Brady NC and Weil RR (2002) *The nature and property of soils*. Prentice Hall.
Breland TA and Hansen S (1998) Comparison of the difference method and 15 N technique for studying the fate of nitrogen from plant residues in soil. *Biol. Fertility Soils* 26(3): 164–168.
Breznak JA (2000) Ecology of prokaryotic microbes in the guts of wood- and litter-feeding termites. In: Abe T, Bignell DE, and Higashi M (eds.) *Termites: Evolution, Sociality, Symbioses, Ecology*, pp. 209–231. Kluwer Academic.
Brown S and Lugo AE (1982) The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14: 161–187.
Bryant DM, Holland EA, Seastedt TR, and Walker MD (1998) Analysis of litter decomposition in an alpine tundra. *Can. J. Botany: Rev. Can. Botanique* 76(7): 1295–1304.
Bubb KA, Xu ZH, Simpson JA, and Saffigna PG (1998) Some nutrient dynamics associated with litterfall and litter decomposition in hoop pine plantations of southeast Queensland. Australia. *Forest Ecol. Manage.* 110(1–3): 343–352.
Burges A and Raw F (1967) *Soil Biology*. Academic Press.
Burke IC, Kaye JP, Bird SP, Hall SA, McCulley RL, and Sommerville GL (2003) Evaluating and testing models of terrestrial biogeochemistry: The role of temperature in controlling decomposition. In: Canham CD, Cole JJ, and Lauenroth WK (eds.) *Models in Ecosystem Science*, pp. 225–253. Princeton: Princeton University Press.
Burtelow AE, Bohlen PJ, and Groffman PM (1998) Influence of exotic earthworm invasion on soil organic matter, microbial biomass and denitrification potential in forest soils of the northeastern United States. *Appl. Soil Ecol.* 9: 197–202.
Buswell JA (1991) Fungal degradation of lignin. In: Arora DK, Rai B, Mukerji KG, and Knudsen GR (eds.) *Handbook of Applied Mycology*, vol. 1, pp. 425–480. Dekker.
Butler MJ and Day AW (1998) Fungal melanins: a review. *Can. J. Microbiol.* 44(12): 1115–1136.
Buxton RD (1981) Termites and turn-over of dead wood in an arid tropical environment. *Oecologia* 51: 379–384.
Caesar–TonThat TC and Cochran VL (2000) Soil aggregate stabilization by a saprophytic lignin-decomposing basidio-mycete fungus: I. Microbiological aspects. *Biol. Fertility Soils* 32(5): 374–380.
Carlile MJ and Watkinson SC (1994) *The Fungi*. Academic Press.
Catroux G and Schnitzer M (1987) Chemical spectroscopic and biological characteristics of the organic matter in particle size fractions separated from an Aquoll. *Soil Sci. Soc. Am. J.* 51(5): 1200–1207.
Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, and Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. *Nature (London)* 397(6719): 491–497.
Chapin FS III (1991) *Effects of Multiple Environmental Stresses on Nutrient Availability and Use*. Academic Press.
Cheng W (1996) Measurement of rhizosphere respiration and organic matter decomposition using natural 13C. *Plant Soil* 183(2): 263–268.
Cheng W and Johnson DW (1998) Elevated CO_2, rhizo-sphere processes, and soil organic matter decomposition. *Plant Soil* 202(2): 167–174.
Cheng WX, Coleman DC, Carroll CR, and Hoffman CA (1994) Investigating short–term carbon flows in the rhizo-spheres of different plant species, using isotopic trapping. *Agron. J.* 86(5): 782–788.
Chernin LS, Winson MK, Thompson JM, et al. (1998) Chitinolytic activity in *Chromobacterium violaceum*: substrate analysis and regulation by quorum sensing. *J. Bacteriol.* 180(17): 4435–4441.
Cheshire MV and Mundie CM (1981) The distribution of labelled sugars in soil particle size fractions as a means of distinguishing plant and microbial carbohydrate residue. *J. Soil Sci.* 32: 605–618.
Chichester FW (1970) Tranformations of fertilizer nitrogen in soil: II. Total and N15-labelled nitrogen of soil organo-mineral sedimentation fractions. *Plant Soil* 33: 437–456.
Chitwood BG and Chitwood MBH (1974) *Introduction to Nematology*. University Park Press.
Christensen BT (1987) Decomposability of organic matter in particle size fractions from field soils with straw incorporation. *Soil Biol. Biochem.* 19(4): 429–436.
Christensen BT (1992) Physical fractionation of soil and organic matter in primary particle size and density separates. *Adv. Soil Sci.* 20: 1–90.
Christensen BT (2001) Physical fractionation of soil and structural and functional complexity in organic matter turnover. *Euro. J. Soil Sci.* 52(3): 345–353.
Christensen BT and Sørensen LH (1985) The distribution of native and labelled carbon between soil particle size fractions isolated from long-term incubation experiments. *J. Soil Sci.* 36: 219–229.
Chung NH, Lee IS, Song HS, and Bang WG (2000) Mechanisms used by white-rot fungus to degrade lignin and toxic chemicals. *J. Microbiol. Biotechnol.* 10(6): 737–752.
Clements RO, Murray PJ, and Sturdy RG (1991) The impact of 20 years' absence of earthworms and three levels of nitrogen fertilizer on a grassland soil environment. *Agri. Ecosys. Environ.* 36: 75–86.
Collins NM (1979) The nests of *Macrotermes bellicosus* (Smeathman) from Mokwa. Nigeria. *Insectes Soc.* 26: 240–246.
Collins NM (1981) The role of termites in the decomposition of wood and leaf litter in the southern guinea savanna of Nigeria. *Oecologia* 51: 389–399.
Colman E. A. and Hamilton E. L. (1947) The San Dimas lysimeters. Research Note 47, US Forest Service, Forest Range Experiment Station.
Comins HN and McMurtrie RE (1993) Long-term response of nutrient-limited forests to CO_2 enrichment—equilibrium behavior of plant-soil models. *Ecol. Appl.* 3(4): 666–681.
Cooke RC and Rayner ADM (1984) *Ecology of Saprotrophic Fungi*. Longman.
Cornejo FH, Varela A, and Wright SJ (1994) Tropical forest litter decomposition under seasonal drought: nutrient release, fungi and bacteria. *Oikos* 70(2): 183–190.
Cornelissen JHC and Thompson K (1997) Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytol.* 135(1): 109–114.
Cornelissen JHC, Perez–Harguindeguy N, Diaz S, et al. (1999) Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytol* 143(1): 191–200.
Cortez J, Hameed R, and Bouche MB (1989) Carbon and nitrogen transfer in soil with or without earthworms fed with carbon-14 and nitrogen-15 labelled wheat straw. *Soil Biol. Biochem.* 21(4): 491–498.
Coulson JC and Butterfield J (1978) Investigation of biotic factors determining rates of plant decomposition on blanket bog. *J. Ecol.* 66(2): 631–650.
Couteaux MM, Sarmiento L, Bottner P, Acevedo D, and Thiery JM (2002) Decomposition of standard plant material along an altitudinal transect (65–3,968 m) in the tropical Andes. *Soil Biol. Biochem.* 34(1): 69–78.
Cox P, Wilkinson SP, and Anderson JM (2001) Effects of fungal inocula on the decomposition of lignin and structural polysaccharides in Pinus sylvestris litter. *Biol. Fertility Soils* 33(3): 246–251.
Crews TE, Kitayama K, Fownes JH, et al. (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology (Washington, DC)* 76(5): 1407–1424.
Cromack K Jr., Todd RL, and Monk CD (1975) Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. *Soil Biol. Biochem.* 7: 265–268.
Currie WS and Aber JD (1997) Modeling leaching as a decomposition process in humid montane forests. *Ecology (Washington, DC)* 78(6): 1844–1860.
Currie WS, Aber JD, McDowell WH, Boone RD, and Magill AH (1996) Vertical transport of dissolved organic C and N under long-term N amendments in pine and hardwood forests. *Biogeochemistry (Dordrecht)* 35(3): 471–505.
Dalias P, Anderson JM, Bottner P, and Couteaux MM (2001a) Long-term effects of temperature on carbon mineralisation processes. *Soil Biol. Biochem.* 33(7–8): 1049–1057.
Dalias P, Anderson JM, Bottner P, and Couteaux MM (2001b) Temperature responses of carbon mineralization in conifer forest soils from different regional climates incubated under standard laboratory conditions. *Global Change Biol.* 7(2): 181–192.
Darwin C (1881) *The Formation of Vegetable Mould, through the Action of Worms: with Observations on their Habits*. J. Murray.
Dash MC (1990) Oligochaeta: Enchytraeidae. In: Dindal DL (ed.) *Soil Biology Guide*, pp. 311–340. Wiley.
Dash MC (1995) The Enchytraeidae. In: Reddy MV (ed.) *Soil Organisms and Litter Decomposition in the Tropics*, pp. 89–102. Westview Press.
Dash MC, Nanda B, and Mishra PC (1981) Digestive enzymes in three species of tropical Enchytraeidae (Oligo-chaeta). *Oikos* 36: 316–318.
Davidson EA, Belk E, and Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4(2): 217–227.
Dekker RFH (1985) Biodegradation of the hemicelluloses. In: Higuchi T (ed.) *Biosynthesis and Biodegradation of Wood Components*. Academic Press.
De Leeuw JW and Largeau C (1993) A review of macromolecular organic compounds that comprise living organisms and their role in kerogen, coal, and petroleum formation. In: Engel MH and Macko SA (eds.) *Organic Geochemistry*, pp. 23–72. Plenum.
Dindal DL (1990) *Soil Biology Guide*. Wiley.
Dix NJ and Webster J (1995) *Fungal Ecology*. Chapman and Hall.
Dkhas MC and Mishra RR (1986) Microflora in earthworm casts. *J. Soil Biol. Ecol.* 6: 24–31.
Donnelly PK, Entry JA, Crawford DL, and Cromack K Jr. (1990) Cellulose and lignin degradation in forest soils: response to moisture, temperature, and acidity. *Microbial Ecol.* 20(3): 289–296.

Doube BM and Brown GG (1998) Life in a complex community: functional interactions between earthworms, organic matter, microorganisms, and plants. In: Edwards CA (ed.) *Earthworm Ecology*, pp. 179–211. Boca Raton, FL: Lucie Press.
Durall DM, Todd AW, and Trappe JM (1994) Decomposition of 14C-labelled substrates by ectomycor-rhizal fungi in association with Douglas fir. *New Phytol*. 127(4): 725–729.
Dworkin M (1998) Multiculturalism versus the single microbe. In: Shapiro JA and Dworkin M (eds.) *Bacteria as Multicellular Organisms*, pp. 3–13. Oxford University Press.
Edmonds RL (1988) Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington. USA. *Can. J. Forest Res*. 17(6): 499–509.
Edmonds RL, Vogt DJ, Sandberg DH, and Driver CH (1986) Decomposition of Douglas–fir [Pseudotsuga menzie-sii] and red alder [Alnus rubra] wood in clear-cuttings. *Can. J. Forest Res*. 16(4): 822–831.
Edwards CA and Bohlen PJ (1996) *Biology and Ecology of Earthworms*. Chapman and Hall.
Edwards CS and Heath G (1963) The role of soil animals in breakdown of leaf material. In: Doeksen J and van der Drift J (eds.) *Soil Organisms*, pp. 76–84. North Holland.
Edwards NT (1982) The use of soda-lime for measuring respiration rates in terrestrial systems. *Pedobiologia* 23: 321–330.
Eggleton P (2000) Global patterns of termite diversity. In: Abe T, Bignell DE, and Higashi M (eds.) *Termites: Evolution, Sociality, Symbioses, Ecology*, pp. 25–51. Kluwer Academic.
Eijsackers H and Zehnder AJB (1990) Litter decomposition—a Russian Matriochka doll. *Biogeochemistry* 11(3): 153–174.
Eriksson KE and Wood TM (1985) Biodegradation of cellulose. In: Higuchi T (ed.) *Biosynthesis and Biodegradation of Wood Components*, pp. 469–504. Academic Press.
Fang C and Moncrieff JB (2001) The dependence of soil CO_2 efflux on temperature. *Soil Biol. Biochem*. 33(2): 155–165.
Fengel D and Wegener G (1984) *Wood: Chemistry, Ultra-structure*. Reactions. de Gruyter.
Finlay BJ, Maberly SC, and Cooper JI (1997) Microbial diversity and ecosystem function. *Oikos* 80(2): 209–213.
Fioretto A, Musacchio A, Andolfi G, and De Santo V (1998) Decomposition dynamics of litters of various pine species in a Corsican pine forest. *Soil Biol. Biochem*. 30(6): 721–727.
Flaig W, Beutelspacher H, and Rietz E (1975) Chemical composition and physical properties of humic substances. In: Gieseking JE (ed.) *Soil Components: Vol. I. Organic Components*, pp. 1–211. Springer.
Fog K (1988) The effect of added nitrogen on the rate of decomposition of organic matter. *Biol. Rev. Cambridge Phil. Soc*. 63(3): 433–462.
Foissner W (1987) Soil protozoa fundamental problems ecological significance adaptations in ciliates and Testaceans Bioindicators and Guide to the Literature. *Prog. Protist*. 2: 69–212.
Fragoso C and Lavelle P (1992) Earthworm communities of tropical rain forests. *Soil. Biol. Biochem*. 24(12): 1397–1408.
French DD (1988) Some effects of changing soil chemistry on decomposition of plant litters and cellulose on a Scottish [UK] moor. *Oecologia (Berlin)* 75(4): 608–618.
Fu S and Cheng W (2002) Rhizosphere priming effects on the decomposition of soil organic matter in C_4 and C_3 grassland soils. *Plant Soil* 238: 289–294.
Fuhrmann JJ (1999) Microbial metabolism. In: Sylvia DM, Fuhrmann JJ, Hartel PG, and Zuberer DA (eds.) *Principles and Applications of Soil Microbiology*, pp. 189–217. Prentice Hall.
Garland JL (1996) Patterns of potential C source utilization by rhizosphere communities. *Soil Biol. Biochem*. 28(2): 223–230.
Garland JL and Mills AL (1991) Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole-carbon-source utilization. *Appl. Environ. Microbiol*. 57(8): 2351–2359.
Garrett SD (1981) *Soil Fungi and Soil Fertility: An Introduction to Soil Mycology*. Pergamon.
Gaudinski JB, Trumbore SE, Davidson EA, and Zheng S (2000) Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. *Biogeochemistry (Dordrecht)* 51(1): 33–69.
Gaudinski JB, Trumbore SE, Davidson EA, Cook AC, Markewitz D, and Richter DD (2001) The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. *Oecologia (Berlin)* 129(3): 420–429.
Gholz HL, Wedin DA, Smitherman SM, Harmon ME, and Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biol*. 6(7): 751–765.
Giardina CP and Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature (London)* 404(6780): 858–861.
Giardina CP, Ryan MG, Hubbard RM, and Binkley D (2001) Tree species and soil textural controls on carbon and nitrogen mineralization rates. *Soil Sci. Soc. Am. J*. 65(4): 1272–1279.
Gill RA and Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytol*. 147(1): 13–31.
Glaser B, Haumaier L, Guggenberger G, and Zech W (1998) Black carbon in soils: the use of benzenecarboxylic acids as specific markers. *Org. Geochem*. 29(4): 811–819.
Golchin A, Clarke P, Baldock JA, Higashi T, Skjemstad JO, and Oades JM (1997) The effects of vegetation and burning on the chemical composition of soil organic matter in a volcanic ash soil as shown by C-13 NMR spectroscopy: 1. Whole soil and humic acid fraction. *Geoderma* 76(3–4): 155–174.
Goldberg ED (1985) *Black Carbon in the Environment*. Wiley.
Gonzalez G and Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82(4): 955–964.
Gooday GW (1994) Physiology of microbial degradation of chitin and chitosan. In: Ratledge C (ed.) *Biochemistry of Microbial Degradation*, pp. 279–312. Kluwer Academic.
Gosz JR (1981) Nitrogen cycling in coniferous ecosystems. In: Clark FE and Rosswall T (eds.) *Terrestrial Nitrogen Cycles*, pp. 405–426. Ecological Bulletin.
Gosz JR, Likens GE, and Bormann FH (1973) Nutrient release from decomposing lead and branch litter in the Hubbard Brook Forest, New Hamsphire. *Ecol. Monogr*. 43: 173–191.
Gourbière F (1982) White rot of Abies-alba mill litter: 1. Modification of litter during the activity of basidiomycetes of the genus collybia. *Revue D Ecologie Et De Biologie Du Sol* 19(2): 163–175.
Graham RC and Wood HB (1991) Morphologic development and clay redistribution in lysimeter soils under chaparral and pine. *Soil Sci. Soc. Am. J*. 55(6): 1638–1646.
Graham RC, Ervin JO, and Wood HB (1995) Aggregate stability under oak and pine after four decades of soil development. *Soil Sci. Soc. Am. J*. 59(6): 1740–1744.
Gray KM (1997) Intercellular communication and group behavior in bacteria. *Trends Microbiol*. 5(5): 184–188.
Grayston SJ (2000) Rhizodeposition and its impact on microbial community structure and function in trees. *Phyton (Horn)* 40(4): 27–36.
Grayston SJ, Vaughan D, and Jones D (1996) Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. *Appl. Soil Ecol*. 5(1): 29–56.
Gregorich EG, Kachanoski RG, and Voroney RP (1989) Carbon mineralization in soil size fractions after various amounts of aggregate disruption. *J. Soil Sci*. 40(3): 649–660.
Gregorich EG, Voroney RP, and Kachanoski RG (1991) Turnover of carbon through the microbial biomass in soils with different textures. *Soil Biol. Biochem*. 23(8): 799–805.
Griffin DH (1994) *Fungal Physiology*. Wiley-Liss.
Grime JP, Cornelissen JHC, Thompson K, and Hodgson JG (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos* 77(3): 489–494.
Guggenberger G (1992) Eigenschaften und Dynamik geloster organischer Substanzen (DOM) auf unterschiedlich immissionsgeschadigten Fictenstandorten. *Bayreauther Boden-kundl. Ber*. 26: 1–164.
Guggenberger G and Zech W (1994) Dissolved organic carbon in forest floor leachates: simple degradation products or humic substances? *Sci Total Environ*. 152(1): 37–47.
Harmon ME, Baker GA, Spycher G, and Greene SE (1990a) Leaf litter decomposition in the Picea, Tsuga forests of Olympic National Park, Washington. USA. *Forest Ecol. Manage*. 31(1–2): 55–66.
Harmon ME, Ferrell WK, and Franklin JF (1990b) Effects on carbon storage of conversion of old-growth forests to young forests. *Science (Washington, DC)* 247(4943): 699–702.
Hartel PG (1999) The soil habitat. In: Sylvia DM, Fuhrmann JJ, Hartel PG, and Zuberer DA (eds.) *Principles and Applications of Soil Microbiology*, pp. 21–43. Prentice Hall.
Hartenstein R (1982) Soil macroinvertebrates, aldehyde oxidase, catalase, cellulase and peroxidase. *Soil Biol. Biochem*. 14: 387–391.
Hassink J, Bouwman LA, Zwart KB, and Brussaard L (1993) Relationships between habitable pore space, soil biota and mineralization rates in grassland soils. *Soil Biol. Biochem*. 25(1): 47–55.
Hatcher PG and Spiker EC (1988) Selective degradation of plant biomolecules. In: Frimmel FH and Christman RF (eds.) *Humic Substances and their Role in the Environment*, pp. 59–74. Wiley.
Hayes MHB, MacCarthy P, Malcolm RL, and Swift RS (1989) The search for structure: setting the scene. In: Hayes MHB, MacCarthy P, Malcolm RL, and Swift RS (eds.) *Humic Substances II: In Search if Structure*, vol. 2, pp. 3–31. Wiley.
Hedges JI (1988) Polymerization of humic substances in natural environments. In: Frimmel FH and Christman RF (eds.) *Humic Substances and their Role in the Environment*, pp. 45–58. Wiley.
Hendrick RL and Pregitzer KS (1997) The relationship between fine root demography and the soil environment in northern hardwood forests. *Ecoscience* 4(1): 99–105.

Heneghan L, Coleman DC, Zou X, Crossley DA, and Haines BL (1999) Soil microarthropod contributions to decomposition dynamics: tropical-temperate comparisons of a single substrate. *Ecology* 80(6): 1873–1882.

Herms DA and Mattson WJ (1992) The dilemma of plants to grow or defend. *Quart. Rev. Biol.* 67(3): 283–335.

Hill GT, Mitkowski NA, Aldrich–Wolfe L, et al. (2000) Methods for assessing the composition and diversity of soil microbial communities. *Appl. Soil Ecol.* 15(1): 25–36.

Hobbie SE (1992) Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* 7(10): 336–339.

Houghton JT (1996) *Climate Change 1995: The Science of Climate Change*. Cambridge University Press.

Hudson HJ (1968) The ecology of fungi on plant remains above the soil. *New Phytol.* 67: 837–874.

Hunt HW, Ingham ER, Coleman DC, Elliott ET, and Reid CPP (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. *Ecology (Tempe)* 69(4): 1009–1016.

Ibrahima A, Joffre R, and Gillon D (1995) Changes in litter during the initial leaching phase—an experiment on the leaf-litter of Mediterranean species. *Soil Biol. Biochem.* 27(7): 931–939.

Ikan P, Rubinsztain Y, Ioselis P, et al. (1986) Carbon–13 cross polarized magic–angle spinning nuclear magnetic resonance of melanoidins. *Org. Geochem.* 9(3): 199–212.

Insam H (1997) A new set of substrates proposed for community characterization in environmental samples. In: Insam H and Rangger A (eds.) *Microbial Communities: Functional versus Structural Approaches*, pp. 259–260. Springer.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, and Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia (Berlin)* 108(3): 389–411.

Janssens IA, Kowalski AS, Longdoz B, and Ceulemans R (2000) Assessing forest soil CO_2 efflux: an *in situ* comparison of four techniques. *Tree Physiol.* 20(1): 23–32.

Janssens IA, Kowalski AS, and Ceulemans R (2001) Forest floor CO_2 fluxes estimated by eddy covariance and chamber-based model. *Agri. Forest Meteorol.* 106(1): 61–69.

Jeffries TW (1994) Biodegradation of lignin and hemi-celluloses. In: Ratledge C (ed.) *Biochemistry of Microbial Degradation*, pp. 233–277. Kluwer Academic.

Jenkinson DS and Powlson DS (1986) The effects of biocidal treatments on metabolism in soil: V. A method for measuring soil biomass. *Soil Biol. Biochem.* 8: 209–213.

Jenny H (1941) *Factors of Soil Formation: A System of Quantitative Pedology*. McGraw–Hill.

Jensen V (1984) Decomposition of angiosperm tree leaf litter. In: Dickinson CH and Pugh GJF (eds.) *Biology of Plant Litter Decomposition*, vol. 1, pp. 69–104. Academic Press.

Johansson M-B, Berg B, and Meentemyer V (1995) Litter mass-loss rates in late stages of decomposition in a climatic transect of pine forests: long-term decomposition in a Scots pine forest: IX. *Can. J. Botany* 73(10): 1509–1521.

Jones JA (1990) Termites, soil fertility and carbon cycling in dry tropical Africa: a hypothesis. *J. Tropical Ecol.* 6(3): 291–305.

Kaiser D and Losick R (1993) How and why bacteria talk to each other. *Cell* 73(5): 873–885.

Kambhampati S and Eggleton P (2000) Taxonomy and phylogeny of termites. In: Abe T, Bignell DE, and Higashi M (eds.) *Termites: Evolution, Sociality, Symbioses, Ecology*, pp. 1–23. Kluwer Academic.

Kanyonyo KK (1984) *Ecologie alimentaire du ver de terre anecique africain* Millisonia lamtoiana *(Acanthodrilidae, Oligochetes) dans la savane de Lamto (Cote d'Ivoire)*. Doctoral: Paris VI University.

Katterer T and Andren O (2001) The ICBM family of analytically solved models of soil carbon, nitrogen, and microbial biomass dynamics: descriptions and application examples. *Ecol. Model.* 136(2–3): 191–207.

Katterer T, Reichstein M, Andren O, and Lomander A (1998) Temperature dependence of organic matter decomposition: a critical review using literature data analyzed with different models. *Biol. Fertility Soils* 27(3): 258–262.

Kennedy MJ, Pevear DR, and Hill RJ (2002) Mineral surface control of organic carbon in black shale. *Science* 295: 657–660.

Kheirallah AM (1990) Fragmentation of leaf litter by a natural population of the millipede Julus scandinavius (Latzel 1884). *Biol. Fertility Soils* 10(3): 202–206.

Kieft TL, Soroker E, and Firestone MK (1987) Microbial biomass response to a rapid increase in water potential when dry soil is wetted. *Soil Biol. Biochem.* 19(2): 119–126.

Kirk TK and Farrell RL (1987) Enzymatic combustion— the microbial-degradation of lignin. *Annu. Rev. Microbiol.* 41: 465–505.

Kirschbaum MUF (1995) The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic–C storage. *Soil Biol. Biochem.* 27(6): 753–760.

Kirschbaum MUF (2000) Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* 48(1): 21–51.

Knicker H and Skjemstad JO (2000) Nature of organic carbon and nitrogen in physically protected organic matter of some Australian soils as revealed by solid-state C–13 and N–15 NMR spectroscopy. *Austral. J. Soil Res.* 38(1): 113–127.

Kogel I (1986) Estimation and decomposition pattern of the lignin component in forest soils. *Soil Biol. Biochem.* 18: 589–594.

Kogel I, Hempfling R, Zech W, Hatcher PG, and Schulten HR (1988) Chemical composition of the organic matter in forest soils: 1. Forest litter. *Soil Sci.* 146(2): 124–136.

Kogel–Knabner I (1993) *Biodegradation and Humification Processes in Forest Soils*. Dekker.

Kogel–Knabner I (1997) 13C and 15 N NMR spectroscopy as a tool in soil organic matter studies. *Geoderma* 80(3–4): 243–270.

Kogel–Knabner I (2000) Analytical approaches for characterizing soil organic matter. *Org. Geochem.* 31(7–8): 609–625.

Kogel–Knabner I (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biol. Biochem.* 34: 139–162.

Kononova MM (1966) *Soil Organic Matter: Its Nature, Its Role in Soil Formation and in Soil*. Fertility: Pergamon.

Konopka A, Oliver L, and Turco RF (1998) The use of carbon substrate utilization patterns in environmental and ecological microbiology. *Microbial Ecol.* 35(2): 103–115.

Kracht O and Gleixner G (2000) Isotope analysis of pyrolysis products from Sphagnum peat and dissolved organic matter from bog water. *Org. Geochem.* 31(7–8): 645–654.

Krasil'nikov NA and Satdykov SI (1969) Estimation of the total bacteria in the intestines of termites. *Mikrobiologiya* 38: 346–350.

Kristufek V, Ravasz K, and Pizl V (1992) Changes in densities of bacteria and microfungi during Gut transit in Lumbricus-Rubellus and Aporrectodea-Caliginosa Oligochaeta Lumbricidae. *Soil Biol. Biochem.* 24(12): 1499–1500.

Kuiters AT and Sarink HM (1986) Leaching of phenolic-compounds from leaf and needle litter of several deciduous and coniferous trees. *Soil Biol. Biochem.* 18(5): 475–480.

Kuzyakov Y, Friedel JK, and Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32(11–12): 1485–1498.

Ladd JN, Parsons JW, and Amato M (1977) Studies of nitrogen immobilization and mineralization in calcareous soils: II. Mineralization of immobilized nitrogen from soil fractions of different particle size and density. *Soil Biol. Biochem.* 9: 319–325.

Langmaid KK (1964) Some effects of earthworm invasion in virgin podsols. *Can. J. Soil Sci.* 44: 34–37.

Lavelle P (1978) *Les vers de terre de la savane de Lamanto (Cote d'Ivoire): peuplements, populations et fonctions dans l'ecosysteme*. University of Paris PhD Dissertation.

Lavelle P (1988) Earthworm activities and the soil system. *Biol. Fertility Soils* 6(3): 237–251.

Lavelle P and Martin A (1992) Small-scale and large-scale effects of endogeic earthworms on soil organic matter dynamics in soils of the humid tropics. *Soil Biol. Biochem.* 24(12): 1491–1498.

Lavelle P and Spain A (2001) *Soil Ecology*. Kluwer Academic.

Lavelle P, Blanchart E, Martin A, et al. (1993) A hierarchical model for decomposition in Terrestrial ecosystems— application to soils of the humid tropics. *Biotropica* 25(2): 130–150.

Lee KE (1985) *Earthworms: Their Ecology and Relationships with Soils and Land Use*. Academic Press.

Lee MJ, Schreurs PJ, Messer AC, and Zinder SH (1987) Associationofmethanogenicbacteriawithflagellatedprotozoa from a termite hindgut. *Current Microbiol.* 15(6): 337–342.

Lehman RM, Colwell FS, Ringelberg DB, and White DC (1995) Combined microbial community-level analyses for quality assurance of terrestrial subsurface cores. *J. Microbiol. Meth.* 22(3): 263–281.

Leiros MC, Trasar-Cepeda C, Seoane S, and Gil-Sotres F (1999) Dependence of mineralization of soil organic matter on temperature and moisture. *Soil Biol. Biochem.* 31(3): 327–335.

Lewis DH (1973) Concepts in fungal nutrition and the origin of biotrophy. *Biol. Rev.* 48: 261–278.

Lichtfouse E (1999) A novel model of humin. *Analusis* 27(5): 385–386.

Lichtfouse E, Chenu C, Baudin F, et al. (1998) A novel pathway of soil organic matter formation by selective preservation of resistant straight-chain biopolymers: chemical and isotope evidence. *Org. Geochem.* 28(6): 411–415.
Lloyd J and Taylor JA (1994) On the temperature dependence of soil respiration. *Funct. Ecol*. 8(3): 315–323.
Lousier JD and Bamforth SS (1990) Soil protozoa. In: Dindal DL (ed.) *Soil Biology Guide*, pp. 97–136. Wiley.
Lousier JD and Parkinson D (1978) Chemical element dynamics in decomposing leaf litter. *Can. J. Botany* 56: 2795–2812.
Lousier JD and Parkinson D (1984) Annual population dynamics and production ecology of testacea (Protozoa, Rhizopoda) in an aspen woodland soil. *Soil Biol. Biochem.* 16: 103–114.
Lunt HA and Jacobson GM (1944) The chemical composition of earthworm casts. *Soil Sci*. 58: 367–374.
Lutz HJ and Chandler RFJ (1946) *Forest Soils*. Wiley.
Luxton M (1982) Studies on the oribatid mites of a Danish beech wood soil. *Pedobiologia* 12: 434–463.
Lynch JM and Whipps JM (1990) Substrate Flow in the Rhizosphere. *Plant Soil* 129(1): 1–10.
Macarthur RH and Wilson ED (1967) *The Theory of Island Biogeography*. Princeton University Press.
MacLean DA and Wein RW (1978) Weight loss and nutrient changes in decomposing litter and forest floor material in New Brunswick forest stands. *Can. J. Botany* 56: 2730–2749.
Macnaughton SJ, Booth T, Embley TM, and O'Donnell AG (1996) Physical stabilization and confocal microscopy of bacteria on roots using 16S rRNA targeted, fluorescent-labeled oligonucleotide probes. *J. Microbiol. Meth*. 26(3): 279–285.
Maillard LC (1917) Identité des matières humiques de synthèse avec les materières humiques naturelles. *Annales de Chimie (Paris)* 7: 113–152.
Malcolm RL (1989) Application of solid-state 13C NMR spectroscopy to geochemical studies of humic substances. In: Hayes MHB, MacCarthy P, Malcolm RL, and Swift MJ (eds.) *Humic Substances II: In Search of Structure*, pp. 339–372. Wiley.
Maraun M and Scheu S (1995) Influence of beech litter fragmentation and glucose concentration on the microbial biomass in three different litter layers of a beechwood. *Biol. Fertility Soils* 19(2–3): 155–158.
Maraun M and Scheu S (1996) Changes in microbial biomass, respiration and nutrient status of beech (Fagus sylvatica) leaf litter processed by millipedes (Glomeris marginata). *Oecologia (Berlin)* 107(1): 131–140.
Martin A (1991) Short-term and long-term effects of the endogenic earthworm Millsonia anomala (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas on soil organic matter. *Biol. Fertility Soils* 11(3): 234–238.
Martin JP and Haider K (1969) Phenolic polymers of Stachybotrys Atra Strachybotrys Chartarum and Epicoccum Nigrum in relation to humic acid formation. *Soil Sci*. 107(4): 260–270.
Martin JP and Haider K (1971) Microbial activity in relation to soil humus formation. *Soil Sci*. 111(1): 54–59.
Martin A, Mariotti A, Balesdent J, Lavelle P, and Vuattoux R (1990) Estimate of organic matter turnover rate in a savanna soil by carbon-13 natural abundance measurements. *Soil Biol. Biochem.* 22(4): 517–524.
Martin A, Mariotti A, Balesdent J, and Lavelle P (1992) Soil organic matter assimilation by a geophagous tropical earthworm based on carbon-13 measurements. *Ecology (Tempe)* 73(1): 118–128.
Martin JP, Wolf D, and Haider K (1972) Synthesis of phenols and phenolic polymers by Hendersonula Toruloidea in relation to humic acid formation. *Soil Sci. Soc. Am. Proc*. 36(2): 311–315.
McClaugherty CA, Pastor J, Aber JD, and Melillo JM (1985) Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology (Tempe)* 66(1): 266–275.
McGill WB (1996) Review and classification of ten soil organic matter (SOM) models. In: Powlson DS, Smith P, and Smith JU (eds.) *Evaluation of Soil Organic Matter Models*, pp. 111–132. Springer.
McGuire AD, Melillo JM, Joyce LA, et al. (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochem. Cycles* 6(2): 101–124.
McInerney M and Bolger T (2000a) Decomposition of Quercus petraea litter: influence of burial, comminution and earthworms. *Soil Biol. Biochem*. 32(14): 1989–2000.
McInerney M and Bolger T (2000b) Temperature, wetting cycles and soil texture effects on carbon and nitrogen dynamics in stabilized earthworm casts. *Soil Biol. Biochem.* 32(3): 335–349.
Meentemyer V (1977) Macroclimate regulation of decomposition rates of organic matter in terrestrial ecosystems. In: Adriano DC and Brisbin IL (eds.) Environmental Chemistry and Cycling Processes, US DOE Symposium Series CONF-760429, pp. 779–789. US DOE.
Meentemyer V (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology* 59(3): 465–472.
Meentemyer V (1995) Meteorologic control of litter decomposition with an emphasis on tropical environments. In: Reddy MV (ed.) *Soil Organisms and Litter Decomposition in the Tropics*, pp. 153–182. Westview Press.
Meentemyer V and Berg B (1986) Regional variation in rate of mass loss of Pinus sylvestris needle litter in Swedish pine forests as influenced by climate and litter quality. *Scand. J. Forest Res*. 1(2): 167–180.
Melillo JM and Aber JD (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63(3): 621–626.
Melillo JM, Aber JD, Linkins AE, Ricca A, Fry B, and Nadelhoffer KJ (1989) Carbon and nitrogen dynamics along the decay continuum plant litter to soil organic matter. *Plant Soil* 115(2): 189–198.
Melillo JM, Newkirk KM, Catricala CE, et al. (1996) The soil warming experiment at Harvard forest 1991–1996. *Bull. Ecol. Soc. Am* 77(3 suppl. Part 2): 300.
Millar CS (1974) Decomposition of coniferous leaf litter. In: Dickinson CH and Pugh GJF (eds.) *Biology of Plant Leaf Litter Decomposition*, vol. 1, pp. 105–128. Academic Press.
Miller RM and Jastrow JD (1992) The role of mycorrhizal fungi in soil conservation. In: Bethlenfalvay CJ and Linderman RG (eds.) *Mycorrhizae in Sustainable Agriculture*, pp. 29–44. Soil Science Society of America.
Minderman G (1968) Addition, decomposition and accumulation of organic matter in forests. *J. Ecol*. 56: 355–362.
Møller J, Miller M, and Kjoller A (1999) Fungal-bacterial interaction on beech leaves: influence on decomposition and dissolved organic carbon quality. *Soil Biol. Biochem.* 31(3): 367–374.
Moody SA (1993) Selective consumption of decomposing wheat straw by earthworms. *Soil Biol. Biochem*. 27: 1209–1213.
Moore AM (1986) Temperature and moisture dependence of decomposition rates of hardwood and coniferous leaf litter. *Soil Biol. Biochem.* 18(4): 427–435.
Moorhead DL, Currie WS, Rastetter EB, Parton WJ, and Harmon ME (1999) Climate and litter quality controls on decomposition: an analysis of modeling approaches. *Global Biogeochem. Cycles* 13(2): 575–589.
Moretto AS, Distel RA, and Didone NG (2001) Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. *Appl. Soil Ecol*. 18(1): 31–37.
Motavalli PP, Palm CA, Parton WJ, Elliott ET, and Frey SD (1994) Comparison of laboratory and modeling simulation methods for estimating soil carbon pools in tropical forest soils. *Soil Biol. Biochem.* 26(8): 934–944.
Neff JC and Asner GP (2001) Dissolved organic carbon in terrestrial ecosystems: synthesis and a model. *Ecosystems* 4(1): 29–48.
Neill C, Fry B, Melillo JM, Steudler PA, Moraes JFL, and Cerri CC (1996) Forest- and pasture-derived carbon contributions to carbon stocks and microbial respiration of tropical pasture soils. *Oecologia (Berlin)* 107(1): 113–119.
Nelson PN, Barzegar AR, and Oades JM (1997) Sodicity and clay type: influence on decomposition of added organic matter. *Soil Sci. Soc. Am. J*. 61(4): 1052–1057.
Nicolardot B, Fauvet G, and Cheneby D (1994) Carbon and nitrogen cycling through soil microbial biomass at various temperatures. *Soil Biol. Biochem.* 26(2): 253–261.
Nierop KGJ (1998) Origin of aliphatic compounds in a forest soil. *Org. Geochem.* 29: 1000–1019.
Noll KM (1992) Archaebacteria Archaea. In: Lederberg J (ed.) *Encyclopedia of Microbiology*, vol. 1, pp. 149–160. Academic Press.
Northup RR, Dahlgren RA, and McColl JG (1998) Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: a positive feedback? *Biogeochemistry* 42(1–2): 189–220.
Nykvist N (1959) Leaching and decomposition of litter: I. Experiments on leaf litter of *Fraxinus Excelsior*. *Oikos* 10: 190–211.
Nykvist N (1961) Leaching and decomposition of litter: III. Experiments on leaf litter of *Betula Verrucosa*. *Oikos* 12(2): 249–263.
Oades JM (1988) The retention of organic matter in soils. *Biogeochemistry (Dordrecht)* 5(1): 35–70.
Oades JM, Vassallo AM, Waters AG, and Wilson MA (1987) Characterization of organic matter in particle size and density fractions from a red-brown earth by solid-state carbon-13 NMR. *Austral. J. Soil Res*. 25(1): 71–82.
O'Brian BJ and Stout JD (1978) Movement and turnover of soil organic matter as indicated by carbon isotope measurements. *Soil Biol. Biochem.* 10: 309–317.
Olsen JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44(2): 322–331.
Orchard VA and Cook F (1983) Relationship between soil respiration and soil moisture. *Soil Biol. Biochem.* 15: 447–453.

Osono T and Takeda H (1999) Decomposing ability of interior and surface fungal colonizers of beech leaves with reference to lignin decomposition. *Euro. J. Soil Biol.* 35(2): 51–56.

Ostertag R and Hobbie SE (1999) Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. *Oecologia (Berlin)* 121(4): 564–573.

Pace NR (1996) New perspective on the natural microbial world: molecular microbial ecology. *Am. Soc. Microbiol. News* 62: 463–470.

Palm CA and Sanchez PA (1990) Decomposition and nutrient release patterns of the leaves of 3 tropical legumes. *Biotropica* 22(4): 330–338.

Parsons WFJ, Taylor BR, and Parkinson D (1990) Decomposition of aspen (Populus tremuloides) leaf litter modified by leaching. *Can. J. Forest Res.* 20(7): 943–951.

Parton WJ, Schimel DS, Cole CV, and Ojima DS (1987) Analysis of factors controlling soil organic matter levels in great plains grasslands USA. *Soil Sci. Soc. Am. J.* 51(5): 1173–1179.

Parton WJ, Scurlock JMO, Ojima DS, et al. (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochem. Cycles* 7(4): 785–809.

Parton WJ, Ojima DS, Cole CV, and Schimel DS (1994) A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: Bryant RB and Arnold RW (eds.) *Quantitative Modeling of Soil Forming Processes*, vol. 39, pp. 147–167. SSSA SSSA Special Publication.

Pastor J and Post WM (1986) Influence of climate, soil moisture, and succession of forest carbon and nitrogen cycles. *Biogeochemistry* 2: 3–27.

Paul EA and Clark FE (1996) *Soil Microbiology and Biochemistry*. Academic Press.

Paul EA, Paustian K, Elliott EA, and Cole CV (1997) *Soil Organic Matter in Temperate Agroecosystems: Long-term Experiments in North America*. CRC Press.

Peberdy JF (1990) Fungal cell walls—a review. In: Kuhn PJ, Trinci APJ, Jung MJ, Goosey MW, and Copping LG (eds.) *Biochemistry of Cell Walls and Membranes in Fungi*, pp. 5–30. Springer.

Perakis SS and Hedin LO (2002) Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature (London)* 415(6870): 416–419.

Perez–Harguindeguy N, Diaz S, Cornelissen JHC, Vendramini F, Cabido M, and Castellanos A (2000) Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant Soil* 218(1–2): 21–30.

Petersen SO, Debosz K, Schjonning P, Christensen BT, and Elmholt S (1997) Phospholipid fatty acid profiles and C availability in wet-stable macro-aggregates from conventionally and organically farmed soils. *Geoderma* 78(3–4): 181–196.

Pohlman AA and McColl JG (1988) Soluble organics from forest litter and their role in metal dissolution. *Soil Sci. Soc. Am. J.* 52(1): 265–271.

Poirier N, Derenne S, Rouzaud JN, et al. (2000) Chemical structure and sources of the macromolecular, resistant, organic fraction isolated from a forest soil (Lacadee, south-west France). *Org. Geochem.* 31(9): 813–827.

Poirier N, Derenne S, Balesdent J, Rouzaud JN, Mariotti A, and Largeau C (2002) Abundance and composition of the refractory organic fraction of an ancient, tropical soil (Pointe Noire, Congo). *Org. Geochem.* 33(3): 383–391.

Pongracic S, Kirschbaum MUF, and Raison RJ (1997) Comparison of soda lime and infrared gas analysis techniques for *in situ* measurement of forest soil respiration. *Can. J. Forest Res.* 27(11): 1890–1895.

Post WM, Emanuel WR, Zinke PJ, and Stangenberger AG (1982) Soil carbon pools and world life zones. *Nature* 298: 156–159.

Prescott CE (1995) Does nitrogen availability control rates of litter decomposition in forests? *Plant Soil* 168–169(0): 83–88.

Prescott CE, Corbin JP, and Parkinson D (1992) Immobilization and availability of nitrogen and phosphorus in the forest floors of fertilized Rocky Mountain coniferous forests. *Plant Soil* 143(1): 1–10.

Prescott CE, Taylor BR, Parsons WFJ, Durall DM, and Parkinson D (1993) Nutrient release from decomposing litter in Rocky-Mountain coniferous forests-influence of nutrient availability. *Can. J. Forest Res. Revue Canadienne De Recherche Forestiere* 23(8): 1576–1586.

Preston CM, Trofymow JA, Sayer BG, and Niu JN (1998) C-13 nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning investigation of the proximate-analysis fractions used to assess litter quality in decomposition studies. *Can. J. Botany: Rev. Can. Botanique* 75(9): 1601–1613.

Puget P, Chenu C, and Balesdent J (2000) Dynamics of soil organic matter associated with particle-size fractions of water-stable aggregates. *Euro. J. Soil Sci.* 51(4): 595–605.

Qualls RG and Haines BL (1991) Geochemistry of dissolved organic nutrients in water percolating through a forest ecosystem. *Soil Sci. Soc. Am. J.* 55(4): 1112–1123.

Qualls RG, Haines BL, and Swank WT (1991) Fluxes of dissolved organic nutrients and humic substances in a deciduous forest. *Ecology (Tempe)* 72(1): 254–266.

Quideau SA, Graham RC, Chadwick OA, and Wood HB (1998) Organic carbon sequestration under chaparral and pine after four decades of soil development. *Geoderma* 83(3–4): 227–242.

Quideau SA, Anderson MA, Graham RC, Chadwick OA, and Trumbore SE (2000) Soil organic matter processes: characterization by C-13 NMR and C-14 measurements. *Forest Ecol. Manage.* 138(1–3): 19–27.

Quideau SA, Chadwick OA, Trumbore SE, Johnson-Maynard JL, Graham RC, and Anderson MA (2001) Vegetation control on soil organic matter dynamics. *Org. Geochem.* 32(2): 247–252.

Raich JW and Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Ser. B: Chem. Phys. Meteorol.* 44(2): 81–99.

Ramsh MV, Saha BC, Mathupala SP, Podkovyrov S, and Zeikus JG (1994) Biodegradation of starch and alpha-glycan polmyers. In: Ratledge C (ed.) *Biochemistry of Microbial Degradation*. Kluwer Academic.

Rastin N, Schlechte G, Huettermann A, and Rosenplaenter K (1990) Seasonal fluctuation of some biological and biochemical soil factors and their dependence on certain soil factors on the upper and lower slope of a spruce forest. *Soil Biol. Biochem.* 22(8): 1049–1062.

Ratledge C (1994) *Biochemistry of Microbial Degradation*. Kluwer Academic.

Reddy MV (1995a) Litter Arthropods. In: Reddy MV (ed.) *Soil Organisms and Litter Decomposition in the Tropics*, pp. 113–140. Westview Press.

Reddy MV (1995b) *Soil Organisms and Litter Decomposition in the Tropics*. Westview Press.

Reddy MV and Venkataiah B (1989) Influence of microarthropod abundance and climatic factors on weight loss and mineral nutrient contents of Eucalyptus leaf litter during decomposition. *Biol. Fertility Soils* 8(4): 319–324.

Regina IS (2001) Litter fall, decomposition and nutrient release in three semi-arid forests of the Duero basin, Spain. *Forestry* 74(4): 347–358.

Rice JA (2001) *Humin. Soil Sci.* 166(11): 848–857.

Rihani M, Cancela Da Fonseca JP, and Kiffer E (1995a) Decomposition of beech leaf litter by microflora and mesofauna: II. *Food preferences and action of oribatid mites on different substrates. Euro. J. Soil Biol.* 31(2): 67–79.

Rihani M, Kiffer E, and Botton B (1995b) Decomposition of beech leaf litter microflora and mesofauna: I. in vitro action of white-rot fungi on beech leaves and foliar components. *Euro. J. Soil Biol* 31(2): 57–66.

Rogers HJ, Perkins HR, and Ward JB (1980) *Microbial Cell Walls and Membranes*. Chapman and Hall.

Rosenbrock P, Buscot F, and Munuch JC (1995) Fungal succession and changes in the fungal degradation potential during the initial stage of litter decomposition in a black alder forest (*Alnus glutinosa* (L.) Gaertn.). *Euro. J. Soil Biol* 31(1): 1–11.

Rustad LE (1994) Element dynamics along a decay continuum in a red spruce ecosystem in Maine, USA. *Ecology (Tempe)* 85(4): 867–879.

Rutigliano FA, Alfani A, Bellini L, and De Santo AV (1998) Nutrient dynamics in decaying leaves of Fagus sylvatica L. and needles of Abies alba Mill. *Biol. Fertility Soils* 27(2): 119–126.

Ryan MG, Melillo JM, and Ricca A (1990) A comparison of methods for determining proximate carbon fractions of forest litter. *Can. J. Forest Res.: J. Canadien De La Recherche Forestiere* 20(2): 166–171.

Saiz–Jimenez C (1994) Analytical pyrolysis of humic substances—pitfalls, limitations, and possible solutions. *Environ. Sci. Technol.* 28(11): 1773–1780.

Saiz–Jimenez C (1996) The chemical structure of humic substances: recent advances. In: Piccolo A (ed.) *Humic Substances in Terrestrial Ecosystems*, pp. 1–44. Elsevier.

Sallih Z and Bottner P (1988) Effect of wheat (Triticum aestivum) roots on mineralization rates of soil organic matter. *Biol. Fertility Soils* 7(1): 67–70.

Sanderman J, Amundson R, and Baldocchi DD (2003) Application of eddy covariance measurements to the temperature dependence of soil organic matter mean residence times. *Global Biogeochem. Cycles* 17(2): 1061.

Savin MC, Gorres JH, Neher DA, and Amador JA (2001) Uncoupling of carbon and nitrogen mineralization: role of microbivorous nematodes. *Soil Biol. Biochem.* 33(11): 1463–1472.

Scheu S (1991) Mucus excretion and carbon turnover of endogeic earthworms. *Biol. Fertility Soils* 12(3): 217–220.

Scheu S (1992) Decomposition of lignin in soil microcompartments: a methodical study with three different carbon-14- labelled lignin substrates. *Biol. Fertility Soils* 13(3): 160–164.

Scheu S and Parkinson D (1994) Changes in bacterial and fungal biomass C, bacterial and fungal biovolume and ergosterol content after drying, remoistening and incubation of different layers of cool temperate forest soils. *Soil Biol. Biochem.* 26(11): 1515–1525.

Scheu S and Parkinson D (1995) Successional changes in microbial biomass, respiration and nutrient status during litter decomposition in an aspen and pine forest. *Biol. Fertility Soils* 19(4): 327–332.

Schimel DS, Coleman DC, and Horton KA (1985) Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. *Geoderma* 36: 201–214.
Schimel J (2001) Biogeochemical models: implicit versus explicit microbiology. In: Schulze ED, Heimann M, Harrison S, Holland EA, Lloyd J, Prentice IC, and Schimel D (eds.) *Global Biogeochemical Cylces in the Climate System*, pp. 177–183. Academic Press.
Schlesinger WH (1985) Decomposition of chaparral shrub foliage. *Ecology (Tempe)* 66(4): 1353–1359.
Schlesinger WH (1990) Evidence from Chronosequence Studies for a low carbon-storage potential of soils. *Nature (London)* 348(6298): 232–234.
Schlesinger WH (1991) *Biogeochemistry: An Analysis of Global Change*. Academic Press.
Schlesinger WH and Hasey MM (1981) Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology* 62(3): 762–774.
Schmidt MWI, Knicker H, Hatcher PG, and Koegel-Knabner I (1997) Improvement of C-13 and N-15 CPMAS NMR spectra of bulk soils, particle size fractions and organic material by treatment with 10% hydrofluoric acid. *Euro. J. Soil Sci*. 48(2): 319–328.
Schnitzer M (1990) Selected methods for the characterization of soil humic substances. In: MacCarthy P, Clapp CE, Malcolm RL, and Bloom PR (eds.) *Humic Substances in Soil and Crop Sciences: Selected Readings*, pp. 65–89. American Society of Agronomy.
Schnitzer M and Schuppli P (1989) The extraction of organic matter from selected soils and particle size fractions with 0.5 M sodium hydroxide and 0.1 M tetrasodium pyrophosphate solutions. *Can. J. Soil Sci* 69(2): 253–262.
Schwarz WH (2001) The cellulosome and cellulose degradation by anaerobic bacteria. *Appl. Microbiol. Bio. technol* 56(5–6): 634–649.
Scott NA, Cole CV, Elliott ET, and Huffman SA (1996) Soil textural control on decomposition and soil organic matter dynamics. *Soil Sci. Soc. Am. J.* 60(4): 1102–1109.
Seastedt TR (1984) The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol*. 29: 25–46.
Seastedt TR, Parton WW, and Ojima DS (1992) Mass loss and nitrogen dynamics of decaying litter of grassland: the apparent low nitrogen immobilization potential of root detritus. *Can. J. Botany* 70(2): 384–391.
Sharma R and Sharma SB (1995) Nematodes and tropical litter decomposition. In: Reddy MV (ed.) *Soil Organisms and Litter Decomposition in the Tropics*, pp. 75–88. Westview Press.
Shaw PJA (1992) Fungi, fungivores and fungal foodwebs. In: Carroll GC and Wicklow DT (eds.) *The Fungal Community—Its Organization and Role in the Ecosystem*, pp. 295–310. Dekker.
Shipitalo MJ and Protz R (1989) Chemistry and micromorphology of aggregation in earthworm casts. *Geoderma* 45(3–4): 357–374.
Silver WL and Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* V129(N3): 407–419.
Silver WL, Neff J, McGroddy M, Veldkamp E, Keller M, and Cosme R (2000) Effects of soil texture on belowground carbon and nutrient storage in a lowland Amazonian forest ecosystem. *Ecosystems* V3(N2): 193–209.
Sims PL and Singh JS (1978a) The structure and function of tem western North American grasslands: I. *Abiotic and vegetational characteristics. J. Ecol*. 66: 251–285.
Sims PL and Singh JS (1978b) The structure and function of ten western North American grasslands: III. Net primary production, turnover and efficiencies of energy capture and water use. *J. Ecol*. 66: 573–597.
Six J, Guggenberger G, Paustian K, Haumaier L, Elliott ET, and Zech W (2001) Sources and composition of soil organic matter fractions between and within soil aggregates. *Euro. J. Soil Sci*. 52(4): 607–618.
Skjemstad JO, Dalal RC, and Barron PF (1986) Spectroscopic investigations of cultivation effects on organic matter of vertisols. *Soil Sci. Soc. Am. J*. 50(2): 354–359.
Skjemstad JO, Clarke P, Taylor JA, Oades JM, and Newman RH (1994) The Removal of magnetic materials from surface soils—a solid state C-13 Cp/Mas Nmr study. *Austral. J. Soil Res*. 32(6): 1215–1229.
Skjemstad JO, Clarke P, Taylor JA, Oades JM, and McClure SG (1996) The chemistry and nature of protected carbon in soil. *Austral. J. Soil Res*. 34(2): 251–271.
Sohlenius B (1980) Abundance, biomass, and contribution to energy flow by soil nematodes in terrestrial ecosystems. *Oikos* 34: 186–194.
Sollins P, Homann P, and Caldwell BA (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma* 74(1–2): 65–105.
Sørensen LH (1981) Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biol. Biochem*. 13: 313–321.
Sparling GS, Cheshire MV, and Mundie CM (1982) Effect of barley plants on the decomposition of 14C-labelled soil organic matter. *J. Soil Sci*. 33: 89–100.
St. John TV (1980) Influences of litterbags on growth of fungal vegetative structures. *Oecologia* 46: 130–132.
Staaf H and Berg B (1982) Accumulation and release of plant nutrients in decomposing Scots pine needle litter— long-term decomposition in a Scots pine forest: 2. *Can. J. Botany: Revue Canadienne De Botanique* 60(8): 1561–1568.
Stevenson FJ (1994) *Humus Chemistry: Genesis, Composition*. Reactions: Wiley.
Sutton DD and Lampen JO (1962) Localization of sucrose and maltose fermenting systems in *Saccharomyces cerevisiae. Biochim. Biophys. Acta* 56: 303–312.
Swift MJ, Heal OW, and Anderson JM (1979) *Decomposition in Terrestrial Ecosystems*. University of California Press.
Swift MJ, Russel–Smith A, and Perfect TJ (1981) Decomposition and mineral nutrient dynamics of plant litter in a regenerating bush-fallow in the sub-humid tropics. *J. Ecol*. 69: 981–995.
Sylvia DM, Fuhrmann JJ, Hartel PG, and Zuberer DA (1999) *Principles and Applications of Soil Microbiology*. Prentice–Hall.
Tanaka M, Sugi Y, Tanaka S, Mishima Y, and Hamada R (1978) Animal population, biomass and production. Soil invertebrates. In: Kira T, Ono Y, and Hosokawa T (eds.) *Biological Production in a Warm Temperate Evergreen Oak Forest of Japan*, pp. 147–163. University of Tokyo Press.
Taylor BR and Parkinson D (1988a) Aspen and pine leaf litter decomposition in laboratory microcosms: 2. Interactions of temperature and moisture level. *Can. J. Botany: Rev. Can. Botanique* 66(10): 1966–1973.
Taylor BR and Parkinson D (1988b) Patterns of water- absorption and leaching in pine and aspen leaf litter. *Soil Biol. Biochem*. 20(2): 257–258.
Taylor BR, Parkinson D, and Parsons WFJ (1989) Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology (Tempe)* 70(1): 97–104.
Taylor BR, Prescott CE, Parsons WJF, and Parkinson D (1991) Substrate control of litter decomposition of four Rocky Mountain coniferous forests. *Can. J. Botany* 69(10): 2242–2250.
Taylor JP, Wilson B, Mills MS, and Burns RG (2002) Comparison of microbial numbers and enzymatic activities in surface soils and subsoils using various techniques. *Soil Biol. Biochem*. 34(3): 387–401.
Tenney FG and Waksman SA (1929) Composition of natural organic materials and their decomposition in the soil: IV. The nature and rapidity of decomposition of the various organic complexes in different plant materials, under aerobic conditions. *Soil Sci* 28: 55–84.
Teplitski M, Robinson JB, and Bauer WD (2000) Plants secrete substances that mimic bacterial *N*–acyl homoserine lactone signal activities and affect population density-dependent behaviors in associated bacteria. *Molecul. Plant-Microbe Interact* 13(6): 637–648.
Thomsen IK, Schjonning P, Jensen B, Kristensen K, and Christensen BT (1999) Turnover of organic matter in differently textured soils: II. *Microbial activity as influenced by soil water regimes. Geoderma* 89(3–4): 199–218.
Tian G, Kang BT, and Brussaard L (1992a) Biological effects of plant residues with contrasting chemical—compositions under humid tropical conditions—decomposition and nutrient release. *Soil Biol. Biochem*. 24(10): 1051–1060.
Tian G, Kang BT, and Brussaard L (1992b) Effects of chemical-composition on N, Ca, and Mg release during incubation of leaves from selected agroforestry and fallow plant-species. *Biogeochemistry* 16(2): 103–119.
Tice KR, Graham RC, and Wood HB (1996) Transformations of 2:1 phyllosilicates in 41-year-old soils under oak and pine. *Geoderma* 70(1): 49–62.
Tiessen H, Chacon P, and Cuevas E (1994) Phosphorus and nitrogen status in soils and vegetation along a toposequences of dystrophic rainforests on the upper Rio Negro. *Oecologia (Berlin)* 99(1–2): 145–150.
Tingey DT, Phillips DL, and Johnson MG (2000) Elevated CO_2 and conifer roots: effects on growth, life span and turnover. *New Phytol*. 147(1): 87–103.
Tisdall JM (1994) Possible role of soil microorganisms in aggregation in soils. *Plant Soil* 159: 115–121.
Tisdall JM and Oades JM (1982) Organic matter and water stable aggregates in soils. *J. Soil Sci*. 33: 141–161.
Tisdall JM, Smith SE, and Rengasamy P (1997) Aggregation of soil by fungal hyphae. *Austral. J. Soil Res*. 35(1): 55–60.
Tiwari SC and Mishra RR (1993) Fungal abundance and diversity in earthworm casts and in uningested soil. *Biol. Fertility Soils* 16(2): 131–134.
Tokumasu S (1998) Fungal successions on pine needles fallen at different seasons: the succession of interior colonizers. *Mycoscience* 39(4): 409–416.
Tokunaga TK, Wan J, Firestone MK, et al. (2001) Chromium diffusion and reduction in soil aggregates. *Environ. Sci. Technol*. 35(15): 3169–3174.
Torn MS, Trumbore SE, Chadwick OA, Vitousek PM, and Hendricks DM (1997) Mineral control of soil organic carbon storage and turnover. *Nature (London)* 389(6647): 170–173.

Torn M. S., Vitousek P. M., and Trumbore S. E. (in review) The influence of nutrient availability on soil organic matter turnover estimated by incubations and radiocarbon modeling. *Ecology*.
Torsvik V, Sorheim R, and Goksoyr J (1996) Total bacterial diversity in soil and sediment communities: a review. *J. Indust. Microbiol.* 17(3–4): 170–178.
Townsend AR, Vitousek PM, Desmarais DJ, and Tharpe A (1997) Soil carbon pool structure and temperature sensitivity inferred using CO-2 and 13CO-2 incubation fluxes from five Hawaiian soils. *Biogeochemistry (Dordrecht)* 38(1): 1–17.
Traore O, Groleau-Renaud V, Plantureux S, Tubeileh A, and Boeuf-Tremblay V (2000) Effect of root mucilage and modelled root exudates on soil structure. *Euro. J. Soil Sci.* 51(4): 575–581.
Trigo D and Lavelle P (1993) Changes in respiration rate and some physicochemical properties of soil during gut transit through Allolobophora molleri (Lumbricidae, Oligochaeta). *Biol. Fertility Soils* 15(3): 185–188.
Trumbore SE (1993) Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. *Global Biogeochem. Cycles* 7(2): 275–290.
Trumbore SE, Chadwick OA, and Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science* 272(5260): 393–396.
Tunlid A and White DC (1992) Biochemical analyses of biomass. *community structure, nutritional status, and metabolic activity of microbial communities in soil. In Soil Biochemistry (ed. G. Stotzky). Dekker* 7: 229–262.
Ugolini FC, Dawson H, and Zachara J (1977) Direct evidence of particle migration in soil solution of a podzol. *Science* 198(4317): 603–605.
Ulery AL, Graham RC, Chadwick OA, and Wood HB (1995) Decade-scale changes of soil carbon, nitrogen and exchangeable cations under chaparral and pine. *Geoderma* 65(1–2): 121–134.
Uren NC and Reisenauer HM (1988) The role of root exudates in nutrient acquisition. In: Tinker PB and Lauchli A (eds.) *Advances in Plant Nutrition*, pp. 79–114. Praeger.
Van Bergen PF, Nott CJ, Bull ID, Poulton PR, and Evershed RP (1998) Organic geochemical studies of soils from the Rothamsted Classical Experiments: IV. *Preliminary results from a study of the effect of soil pH on organic matter decay. Org. Geochem.* 29(5–7): 1779–1795.
Van Gestel M, Merckx R, and Vlassak K (1993) Microbial biomass responses to soil drying and rewetting: the fate of fast- and slow-growing microorganisms in soils from different climates. *Soil Biol. Biochem.* 25(1): 109–123.
Van Veen JA and Kuikman PJ (1990) Soil structural aspects of decomposition of organic matter by microorganisms. *Biogeochemistry (Dordrecht)* 11(3): 213–234.
Van Veen JA, Ladd JN, and Amato M (1985) Turnover of carbon and nitrogen through the microbial biomass in a sandy loam and a clay soil incubated with uniformly carbon- 14-labeled glucose and nitrogen-15 ammonium sulfate under different moisture regimes. *Soil Biol. Biochem.* 17(6): 747–756.
Van Vuuren MMI, Berendse F, and De Visser W (1993) Species and site differences in the decomposition of litters and roots from wet heathlands. *Can. J. Botany* 71(1): 167–173.
Veeman WS (1998) Nuclear magnetic resonance, a simple introduction to the principles and applications. *Geoderma* 80(3–4): 225–242.
Vitousek PM and Sanford RL Jr. (1986) Nutrient cycling in moist tropical forest. *In Annual Review of Ecology and Systematics, Annual Reviews (ed. R. F. Johnston)* 17: 137–168.
Vitousek PM, Turner DR, Parton WJ, and Sanford RL (1994) Litter decomposition on the Mauna Loa environmental matrix, Hawaii: patterns, mechanisms, and models. *Ecology (Tempe)* 75(2): 418–429.
Vogt K (1991) Carbon budgets of temperate forest ecosystems. *Tree Physiol.* 9(1–2): 69–86.
Wagner GH and Wolf DC (1999) Carbon transformations and soil organic matter formation. In: Sylvia DM, Fuhrmann JJ, Hartel PG, and Zuberer DA (eds.) *Principles and Applications of Soil Microbiology*, pp. 218–258. Prentice Hall.
Waksman SA (1932) *Humus*. Williams and Wilkins.
Waksman SA and Tenney FG (1927) The composition of natural organic materials and their decomposition in the soil: I. *Methods of quantitative analysis of plant materials. Soil Sci.* 24: 275–283.
Waksman SA and Tenney FG (1928) Composition of natural organic materials and their decomposition in the soil: III. *The influence of nature of plant upon the rapidity of its decomposition. Soil Sci.* 27: 155–171.
Wallwork JA (1970) *Ecology of Soil Animals*. London: McGraw-Hill.
Walse C, Berg B, and Sverdrup H (1998) Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity. *Environ. Rev.* 6(1): 25–40.
Ward DM, Bateson MM, Weller R, and Ruff-Roberts AL (1992) Ribosomal RNA analysis of microorganisms as they occur in nature. In: Marshall KC (ed.) *Advances in Microbial Ecology*, pp. 219–286. Plenum.
Wasilewska L (1991) The role of nematode in the process of elemental recycling on drained fen differentiated by peat origin. *Polish Ecol. Stud.* 17: 191–201.
Weil RR (1992) *Inside the heart of sustainable farming*. The New Farm January, 43–48.
West AW, Grant WD, and Sparling GP (1987) Use of ergosterol, diaminopimelic acid and glucosamine contents of soils to monitor changes in microbial populations. *Soil Biol. Biochem.* 19(5): 607–612.
West AW, Sparling GP, Feltham CW, and Reynolds J (1992) Microbial activity and survival in soils dried at different rates. *Austral. J. Soil Res.* 30(2): 209–222.
Whipps JM and Lynch JM (1985) Energy losses by the plant in rhizodeposition. *Ann. Proc. Phytochem. Soc. Euro.* 26: 59–71.
White DL, Haines BL, and Boring LR (1988) Litter decomposition in southern appalachian black locust and pine hardwood stands-litter quality and nitrogen dynamics. *Can. J. Forest Res.: Revue Canadienne De Recherche Forestiere* 18(1): 54–63.
White G. (1789) The Natural History and Antiquities of Selborne, in the County of Southampton: With Engravings, and an Appendix. Printed by T. Bensley, for B. White and son.
Whitford WG (1989) Abiotic controls on the functional structure of soil food webs. *Biol. Fertility Soils* 8(1): 1–6.
Whitford WG, Meentemyer V, Seastedt TR, et al. (1981) Exceptions to the AET model: deserts and clear-cut forest. *Ecology* 62(1): 275–277.
Whitford WG, Steinberger Y, and Ettershank G (1982) Contributions of subterranean termites to the economy of Chihuahuan desert ecosystems. *Oecologia* 55: 298–302.
Whitman WB, Coleman DC, and Wiebe WJ (1998) Prokaryotes: the unseen majority. *Proceedings of the National Academy of Sciences of the United States of America* 95(12): 6578–6583.
Wilson MA (1989) Solid-state nuclear magnetic resonance spectroscopy of humic substances: basic concepts and techniques. In: Hayes MHB, MacCarthy P, Malcolm RL, and Swift MJ (eds.) *Humic Substances II: in Search of Structure*, pp. 309–338. Wiley.
Wilson MA (1990) Application of nuclear magnetic resonance spectroscopy to organic matter in whole soils. In: MacCarthy P, Clapp CE, Malcolm RL, and Bloom PR (eds.) *Humic Substances in Soil and Crop Sciences: Selected Readings*, pp. 221–260. American Society of Agronomy.
Wilson MA, Pugmire R, Zilm KW, Goh KM, Heng S, and Grant D (1981) Cross-polarization 13C NMR spectroscopy with "magic angle" spinning characterizes organic matter in whole soils. *Nature* 294: 648–650.
Witkamp M and Crossley DA (1966) The role of microarthropods and microflora in the breakdown of white oak litter. *Pedobiologia* 6: 293–303.
Witkamp M and Olson JS (1963) Breakdown of confined and nonconfined oak litter. *Oikos* 14: 138–147.
Woese CR (1987) *Bacterial Evolution. Microbiol. Rev.* 51(2): 221–271.
Wolters V (2000) Invertebrate control of soil organic matter stability. *Biol. Fertility Soils* 31(1): 1–19.
Wood TM and Garcia–Campayo V (1994) Enzymes and mechanisms involved in microbial cellulolysis. In: Ratledge C (ed.) *Biochemistry of Microbial Degradation*, pp. 197–231. Kluwer Academic.
Xu M and Qi Y (2001) Spatial and seasonal variations of Q(10) determined by soil respiration measurements at a Sierra Nevadan forest. *Global Biogeochem. Cycles* 15(3): 687–696.
Yu ZS, Dahlgren RA, and Northup RR (1999) Evolution of soil properties and plant communities along an extreme edaphic gradient. *Euro. J. Soil Biol.* 35(1): 31–38.
Zak JC, Willig MR, Moorhead DL, and Wildman HG (1994) Functional diversity of microbial communities: a quantitative approach. *Soil Biol. Biochem.* 26(9): 1101–1108.
Zarda B, Hahn D, Chatzinotas A, et al. (1997) Analysis of bacterial community structure in bulk soil by *in situ* hybridization. *Arch. Microbiol.* 168(3): 185–192.
Zech W, Johansson MB, Haumaier L, and Malcolm RL (1987) Cpmas carbon-13 Nmr and Ir spectra of spruce and pine litter and of the Klason lignin fraction at different stages of decomposition. *Zeitschrift fuer Pflanzenernaehrung und Bodenkunde* 150(4): 262–265.
Zech W, Ziegler F, Koegel-Knabner I, and Haumaier L (1992) Humic substances distribution and transformation in forest soils. *Sci. Total Environ.* 117–118: 155–174.
Zech W, Senesi N, Guggenberger G, et al. (1997) Factors controlling humification and mineralization of soil organic matter in the tropics. *Geoderma* 79(1–4): 117–161.
Zhang H and Schrader S (1993) Earthworm effects on selected physical and chemical properties of soil aggregates. *Biol. Fertility Soils* 15(3): 229–234.
Zogg GP, Zak DR, Ringelberg DB, MacDonald NW, Pregitzer KS, and White DC (1997) Compositional and functional shifts in microbial communities due to soil warming. *Soil Sci. Soc. Am. J.* 61(2): 475–481.