

## CHAPTER 7

# Forest Soil Ecology and Soil Organic Carbon

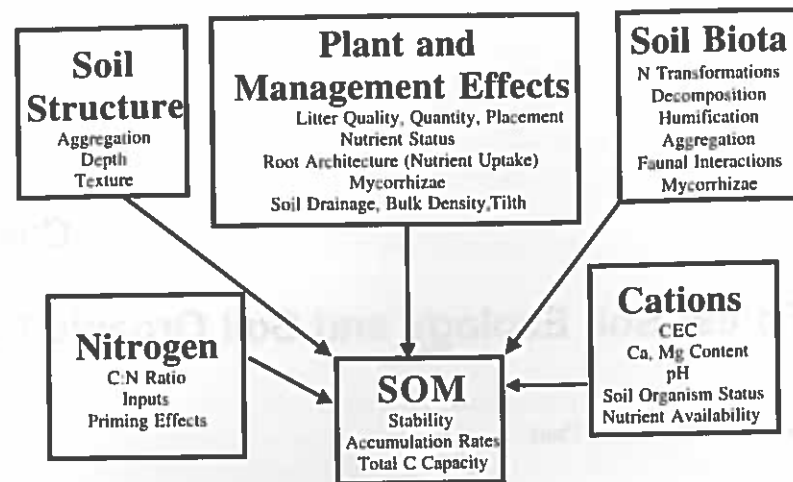
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### INTRODUCTION

Storage of C in forest soils is dependent on plant production rates, allocation of C, decomposition rate of products entering the soil, and stabilization within the soil by aggregation, absorption, and humification. The largest contributions to soil C pools are roots and litter. Estimates of litter are available for many ecosystems, but values for roots and fine-root production are difficult to obtain (Nadelhoffer and Raich, 1992) and pose an obstacle for understanding physiological activities of soil organisms (Zak and Pregitzer, 1998). Litter contributes cellulose, hemicellulose, lignins, pigments, water-soluble sugars, amino acids, aliphatic acids, and alcohol- and ether-soluble constitu-



**Figure 7.1** Biological and chemical controls on C sequestrations in forest soils.

ents including fats, oils, waxes, and resins. While roots contain a number of the same components, they also contribute to the soil C pool by providing, to depth, a diet with rapid turnover of dead tissue, mucilage, and cells sloughed off the growing root tip as it moves through soil (Ulrich et al., 1981). Before roots enter the detrital pool they also contribute root-derived substrates that fuel rhizosphere communities and stimulate the initiation of symbiotic relationships such as mycorrhizae. Regardless of the source, plant materials and the biomass produced from consumption of live plant materials contribute to detrital pools that support the complex food webs that in part regulate C sequestration in soils.

The controls that regulate soil properties and therefore C accumulations in a given ecosystem are, as delineated by Dukochaev (Brady and Weil, 1999) more than 100 years ago, climate, biota (including both organisms and vegetation), topography, parent material, and time. Management practice is expressed primarily through impact on biota and cannot be overemphasized, especially when global change, N pollution, and land-use alterations are altering ecosystem structure and function in nearly all ecosystems. Underlying these broadscale factors that regulate C are a set of fine-scale biological and chemical controls that regulate C sequestration in forest soils (Figure 7.1). The amount of soil organic matter in a system tends to reach a steady-state value as dictated by the factors listed above (Vitousek and Reiners, 1975; Baldock and Nelson, 2000), but changes occur quickly with alterations to vegetation or to the soil physical, chemical, or microbial community structure.

Soil organic matter results from the protection of a small portion of annual net plant productivity (NPP) from decomposition by the soil biota, aggregates, clay surfaces, and humification. Decomposition rates can vary widely depending on the quality and quantity of the material that enters soil and as a consequence of chemical or physical protection and abiotic controls. Belowground community processes such as aggregation and humification can result in resistant forms of C, as can chemical processes such as association of C with clay particles or metal ligands. The soil biota and their enzymes mediate decomposition and are therefore a critical part of the carbon cycle.

#### SOIL ORGANISMS IMPORTANT IN FOREST-SOIL C TRANSFORMATIONS

The number of species involved with C transformations in forest soils is truly staggering. There are representatives from every kingdom, and the rates and products of decomposition are intimately related to the diversity present. The primary organisms involved with the dissolution or reassociation

of C compounds are the bacteria and the fungi, but soil animals and protozoa have essential support roles in litter breakdown and in regulating decomposer population size. The complexity of the detrital food web limits our ability to isolate individual organisms and identify the processes that each regulates. The concept of genetic redundancy — the capacity of a number of organisms (species) to carry out some general processes, such as decomposition — is much discussed in ecology. This is, to some extent, supported by the success of models utilizing a series of first-order reactions to describe soil organic matter (SOM) dynamics. If specific biota were controlling decomposition, more-complex models would be required. A number of texts on soil ecology describe the organisms and processes involved with organic matter dynamics in soil (Killham, 1994; Coleman and Crossley, 1996; Paul and Clark, 1996; Sylvia et al., 1999). Only the organisms essential for C transformations are described here in context of their contribution to storage of C in forest soils. We describe only a few organisms from each group that are key to the quality, quantity, or residence time of C in forest soils.

#### Prokaryotes

The smallest and most numerous organisms in the soil (other than viruses) are the prokaryotes, bacteria, and archaea (van Elsas et al., 1997), which have great complexity and diversity. Whether this diversity is due to the heterogeneous, spatial soil environment or is an historic artifact of the great genetic diversity relative to the speed of colonization of microhabitats or both is not known. Most are chemoorganotrophs, which are heterotrophs acquiring both energy and C from breakdown of organic materials. Some are lithotrophic heterotrophs, using organic materials for C and rock dissolution for energy. Some organisms are strictly chemoautotrophic, using  $\text{CO}_2$  for C and inorganic sources of energy. These include the organisms involved with N and S transformations, the nitrifiers, such as *Nitrosospira*, *Nitrosomonas*, and *Nitrobacter* and sulfur oxidizers such as *Thiobacillus* and *Sulfobolus*. Most soil microbes, due to their long evolutionary history, are uniquely adapted to oligotrophic environments and have adapted strategies for nutrient-poor habitats. The sulfur oxidizers are considered especially important. They are thought to have been involved in the decomposition that occurred 3 to 3.5 billion years ago, before the advent of photosynthesis (Des Marais, 2000). Others such as the rhizobia have formed symbiotic relationships with plants that allow acquisition of C compounds from the plant in exchange for fixed atmospheric N.

Soil bacteria are primarily decomposers of simple carbohydrates, organic acids, and amino acids. Substrate selectivity varies greatly from one bacterial species to another. Studies using plate counts suggest that the genera involved in C turnover include *Pseudomonas* (plant pathogens, oxidative sugar metabolizers, a few humic acid utilizers), *Bacillus*, and *Arthrobacter*. In contrast, genetic analysis finds four main lines of descent, including those falling into the  $\alpha$  subphylum of the *Proteobacteria*, the planctomycetes, the actinomycetes, and one containing *Verrucomicrobium* (Liesack et al., 1997). The genes for free-living N fixation are distributed throughout numerous genera, as are those for denitrification. Cyanobacteria are photosynthetic bacteria that contribute to primary productivity as well as N fixation in forest soils. While a large number of bacteria and soil fauna are involved in the conversion of organic N to  $\text{NH}_4$ , there are relatively few genera of organisms such as *Nitrosospira*, *Nitrosomonas*, and *Nitrobacter* involved in transformations of  $\text{NH}_4$  to  $\text{NO}_3$ . These organisms are found in low numbers in soils, often having only one or two distinct species present in most soils (Phillips et al., 2000), and have been found active at  $\text{pH} < 5$ , such as are found in acid forest soils.

Bacterial community structure has been examined using a number of techniques, including classical plate counts, phospholipid analysis, and nucleic acid analysis in soils. Both microscopic (Liu et al., 2001) and DNA analysis (Blackwood and Paul, in preparation) indicate great morphological and genetic diversity, with only a small percentage of organisms being culturable (Bakken, 1997). Differences among bacterial communities have been identified based on forest types and soil chemistry. Species identification currently does little to further our understanding of process-level detail, but generalizations have allowed researchers to further mechanistic understanding of soil

food webs. Priha et al. (2001) found greater numbers of gram-negative organisms such as pseudomonads associated with birch and greater numbers of gram-positive organisms such as bacillus and arthrobacter associated with pine and spruce. The suggested community differentiation based on the organism's physical structure (the gram stain that is indicative of cell-wall type) may become more important in acidic forest soils. Studies that aim to link changes in community structure with functional differences will do much to improve our understanding of process-level events.

The actinomycetes are grouped with the bacteria. They differ from the rest of the bacteria in that they have a filamentous form reminiscent of the fungi, yet their size and chemical and nucleic acid components place them firmly in the bacteria. They are important in C and N transformations, especially of fats and waxes, and they produce antimicrobial compounds that can inhibit the growth of bacteria. They include plant pathogens, which can alter the type and amount of material in the detrital pool, and have enzymes that are involved in oxidative coupling and degradation of chitin, cellulose, and hemicellulose. Actinomycetes are also important in symbiotic relationships as nitrogen fixers with forest tree species (Thorn, 2000). These organisms tend to be acid-sensitive, so they are not common in acidic forest soils.

### Protozoa

The kingdom Protozoa contains small unicellular, phagotrophic microorganisms with mitochondria. They fulfill a number of roles in soil C cycling. Ciliates are consumers of soil bacteria and fungi. Flagellates include bacterial feeders as well as organisms that play a role in wood digestion as symbionts of termites and cockroaches. Testacea feed on humus and thrive in forest soils (Coleman and Crossley, 1996). They were identified early on as diagnostic species for identifying mull- and mor-type humus. Amoebae play important roles as consumers of bacteria, fungi, and algae as well as small particles of organic matter (Coleman and Crossley, 1996), and they have been found to be important in N mineralization (Bamforth, 2000). Amoebae are sufficiently small that they can access organisms within soil pores that exclude larger organisms. Overall, these groups of organisms enhance microbial and plant growth with their excretions and regulate size and composition of microbial communities.

### Chromista

The organisms of the kingdom Chromista include phototrophic and saprotrophic unicellular and multicellular eukaryotes. The most important groups for forest C cycling are the algae, phototrophs that contribute to primary productivity in ecosystems. Algae can be quite numerous, with numbers ranging from 5000 cells per gram soil in the lower horizon to 650,000 per gram soil in the upper horizons (Steubing, 1970), and growth is strongly influenced by season (Hunt et al., 1979). Algae contribute as primary producers to forest ecosystems, providing a food source for soil animals including the protozoa and nematodes (Albrecht, 1999).

Algae and the prokaryotic cyanobacteria can each form symbiotic mutualisms with fungi called lichens. Lichens play a role in primary productivity, increasing detrital materials on the forest floor and providing food for animals, yet they also participate in rock weathering. In forests, lichens contribute significantly to N budgets by fixing atmospheric N that is then moved to soils (Killham, 1994). Lichens increase interception of rainfall, resulting in increased nutrient deposition in through-fall and slower decomposition rates on the forest floor (Knops et al., 1996). This also makes them sensitive to atmospheric pollutants, and they often are used as indicators of forest health.

### Fungi

Fungi often exceed the bacteria in biomass and carry out the decomposition of most of the structural components of plant residues in aerobic environments. They provide enzyme systems for breakdown of compounds from the simplest sugar to the most complex compounds, such as

lignin, as well as being able to penetrate new environments and translocate nutrients such as N from the soil to the litter layer (Hart et al., 1993). Fungi have a multitude of roles in food webs ranging from pathogens to saprotrophs to symbiotic mutualists. Some fungi produce organic acids that provide nutrition for soil organisms such as bacteria but are also key to solubilizing nutrients such as P. In addition to motile groups, three main fungal nonmotile groups involved in decomposition are the organisms in the phyla Zygomycota, Ascomycota, and Basidiomycota (Thorn, 2000).

The first group includes the Zygomycetes or sugar fungi that utilize relatively labile sugar compounds. This group is not known to produce extracellular enzymes and can utilize sugars that have already been solubilized by other organisms. This group also includes one of the most important groups of fungi, the Glomales. These are the endomycorrhizal fungi, symbiotic mutualists with the roots of many plant species, including a large number of deciduous forest trees and understory plants. The final important organisms in the phylum Zygomycota for C storage are the Zoopagales and Entomophthorales, which increase detritus pools as parasites on insects and other fungi.

The Ascomycota — with 46,000 species, some of which are asexual — includes a number of fungi that are important in decomposition and plant nutrition. They are important in decomposition, with enzyme systems capable of degrading celluloses and hemicelluloses. They form lichens with algae, are parasites of plants and animals, and inhabit dung. They are also important for plant nutrition through their ectomycorrhizal or ectendomycorrhizal relationships with forest species (Klironomos, 2000).

The Basidiomycota are also important in the soil food web through their roles in decomposition and plant nutrition. The basidiomycetes include two of the most important groups of forest fungi. The first group, often defined as white rots, have enzyme systems capable of degrading lignin, hemicellulose, cellulose, and soil humics. The second group forms ectomycorrhizae with forest trees, including conifers and a limited number of deciduous trees such as oaks and poplar.

Fungal decomposition processes have been discussed in terms of succession since first described by Garrett (1951), where specific fungi colonize a substrate, alter its chemical composition and nutrient availability, and are replaced by organisms better able to utilize the emerging compounds. Initial fungal colonization is by airborne ascomycetes and Fungi Imperfecti, which may be weak pathogens, and occurs before leaves or needles are lost from the tree (Richards, 1987). The sugar fungi, such as the Mucorales, also early colonizers, use the easily metabolized compounds including simple soluble sugars and amino acids. Ascomycetes and basidiomycetes replace the earlier fungi when simple compounds are no longer available or waste products cause growth to cease. This is, of course, a gross oversimplification of a very complex process.

The diversity of decomposers on litter is very large and changes very slowly as substrates are exhausted. There has been a great deal of research to determine the order and relationship of decomposers as it has become clear that there is no clear-cut relationship between physiological groups of fungi and substrate composition (Richards, 1987). There has been some speculation that the early-stage fungi outcompete the latter-stage fungi, whereas recent studies suggest that the enzyme systems of these organisms are more highly specialized for the plant tissue compounds they utilize (Cox et al., 2001). Regardless of the relationships or order of appearance, the latter-stage fungi, such as the white-rot fungi, can have very large impacts on litter decomposition rates. McLaugherty et al. (1985) found that litter decomposition rates increased twofold in forests with white-rot fungi compared with those without the fungi, even under similar climatic conditions. This should have large implications for models that utilize climate and litter content to predict long-term decomposition rates for forests. Soil organisms can be managed indirectly by methods that include zero tillage in agriculture or managing for mycorrhizal fungi in restoration efforts. Indeed, increasing decomposition rates of forest residues for more rapid decay has been attempted as a technique of plantation management (Blanchette and Shaw, 1978). Methods for managing complex ecosystem parameters such as C cycling in forests to increase C sequestration might include implementing pH control, altering tree species composition and residue inputs, etc., but our understanding of belowground interactions is currently too primitive for this type of manipulation.

## Animals

Forest soils house a multitude of different animal species. Their biomass increases by a factor of six from boreal to tropical forests (Waring and Running, 1998). Of the soil macrofaunal communities (2 mm to 20 mm), the earthworms have greater biomass than other animals in forests, followed by myriapods, termites and coleopterans, ants, arachnids, and others. Reports on the amount of litter tissue consumed by these organisms vary. Most suggest that the amount of plant C consumed by animals ranges from 7% (Waring and Running, 1998) to 10–20% (Satchell, 1974). Satchell (1974) suggested that the example most often cited for demonstrating the importance of animals in litter decomposition is that of Edwards and Heath (1963). Oak and beech disks were placed in litterbags with openings of 0.5- and 7-mm mesh and buried 2.5-cm deep in a freshly plowed field. The area lost for the planted disks was reported at the end of 9 months, and the greatest loss was reported for the litterbags with the largest openings. While the results support the importance of animals in decomposition processes, there are other mechanisms important for litter breakdown that could account for the observed results (Satchell, 1974):

- Weight loss occurred without a noticeable loss in volume
- The number of disks per bag would affect the relative nitrogen uptake
- The litter material was subjected to irregular treatment:
  - Litter left on the surface would have tannins leached prior to breakdown by fungi
  - Buried litter would be in a microclimate influenced by the burier, e.g., earthworm, which would alter decomposition rates

Regardless of these arguments, both the experiment and its critical appraisals highlight the fact that there are multiple mechanisms important for decomposition of litter. Understanding the role of animals in detrital food webs is limited by our inability to separate the role of animals from interactions across trophic levels and substrates from the processes of the microbes.

Soil and canopy animals impact ecosystem food webs through a variety of chemical, physical, and biological processes. The larger animals are responsible for the physical and chemical processes. These include fragmenting organic matter on the surface, mixing litter through the profile, transporting bacterial and fungal propagules, and leaving open channels for water, air, and nutrient movement that serve as "hot spots" of microbial activity (Hendrix, 2000). These organisms are also involved with chemical and biological processes such as transforming organic matter into decay-resistant materials lining the channels; encapsulating organic matter in feces, making it more resistant; and releasing immobilized nutrients from microbial biomass. Grazing by animals can also serve to regulate the composition and metabolic activity of microbial populations (van Vliet, 2000). Finally, soil animals play an active role in converting plant residues to humus, selective decomposition of organic matter, making organic matter more invadable by microbes, and enhancing soil aggregation (Edwards et al., 1970).

There are a number of animal groups important in the regulation of C in forest soils through the processes described above. These animals include the nematodes, microarthropods, macroarthropods, enchytraeids, earthworms, and vertebrate animals that occupy soils. Canopy animals also impact the nutrient status of soils by abrading plant tissues and producing frass, which increases nutrient throughfall to the soils. While these animals in the canopy are as important as the ones below, our discussion focuses on the animals involved in the soil food web.

## Nematodes

Nematodes are small soil animals ranging in size from 0.5 to 2 mm and are thus often included in the soil microbiota. They participate in food webs as bacterivores, fungivores, herbivores (plant parasites, root feeders, etc.), and predators (on other nematodes or insects) (McSorley, 2000). They

moderate C storage in forests by increasing decomposition rates by inoculating new substrates with bacteria and increasing CO<sub>2</sub> release. Nematodes are also important in N cycling in forests because they consume prey with a lower C:N ratio, resulting in the excretion of NH<sub>4</sub>. Nematodes have been found to be particularly abundant in coniferous forests (Waring and Running, 1998) but are also important in deciduous forest food webs. Blair et al. (1990) found higher litter decomposition rates to be associated with litter from a mix of three deciduous forest species than for litterbags with individual species. These higher rates were associated with greater nematode biomass and lower microbial and microarthropod densities. While resource heterogeneity is the likely cause, the mechanism for increased decomposition involves complex species interactions that are not currently understood.

## Microarthropods

Microarthropods, the multisegmented-body-and-limb insects and arachnids with a chitinous skeleton, include organisms that range in size from 0.2 to 10 mm. Springtails and mites represent 90% of the microarthropods important in soil food webs. Springtails (Collembola) are for the most part either fungivores or detritivores, and mites (Acari) are either fungivores, detritivores, or predators on small fauna. The density of microarthropods is higher in temperate forests than tropical forests and higher in coniferous forests than deciduous forests (Waring and Running, 1998). In forests, the collembola provide a link between organic-matter decomposition and the predators that are active on the surface of the litter. In coniferous forests this is a particularly important link in food webs (Butterfield, 1999). They can also change fungal community dynamics by selective grazing on specific fungal species, altering decomposition rates (Crossley and Coleman, 2000a). Mites have been found to increase decomposition rates and wood breakdown by tunneling into wood to get fungi.

## Macroarthropods

The macroarthropods are large enough to be sampled as individuals. They are important in soil physical structure because, unlike the microarthropods, they are capable of restructuring or moving large amounts of soil. Macroarthropods important in forest soils include millipedes, which function as detritivores and play a role in Ca cycling (Crossley and Coleman, 2000b), and spiders and beetles that are both predators on smaller soil organisms. Macroarthropods are more numerous in deciduous than coniferous forests. They are important in forest C dynamics due to their role as detritivores and predators. Termites, which are more common in warm temperate and tropical forests, redistribute soil mineral fractions and organic matter by nest building, feeding on wood, plant, and humus, and growing their own fungi (Coleman and Crossley, 1996; Crossley and Coleman, 2000b). Ants, which are found in nearly all ecosystems, bring soil up from lower horizons and redeposit it, exposing buried C and enhancing mineralization rates.

## Enchytraeids

Enchytraeids are oligochaetes that are smaller than earthworms, ranging from 5 cm to less than 1 mm. They consume microbially digested leaves to graze on bacteria and fungi. The result is encapsulation of organic materials into fecal pellets providing protection from decomposition and serving as building blocks for macroaggregates. Enchytraeids are believed to replace earthworms in acid forest soils in temperate latitudes (Killham, 1994). They impact C storage in forest soils through microbial grazing, altering microbial species composition, and release of nutrients, especially nitrogen (van Vliet, 2000; Šimek et al., 1991). They may also retard decomposition rates by decreasing microbial populations and incorporating C into soil and soil aggregates.

## Earthworms

Earthworms are large oligochaetes that range in length from a few millimeters to 1.4 m. Their abundance and biomass establish them as major players in the soil (Coleman and Crossley, 1996). Earthworms are nonselective feeders on soil. The mineral and organic soil materials are consumed, and nondigestible intake is excreted after enrichment with Ca as casts. Earthworms contain some enzymes capable of decomposing chitin and oligosaccharides, and the gut milieu may promote decomposition of other C constituents of litter. They are abundant in temperate deciduous forest soils but absent from acid conifer soils (Waring and Running, 1998). The impact of earthworms on forest-soil C is greater than that of any other group of animals. Earthworms alter soil physical structure, the chemical composition of C compounds, density of microbes on fragmented organic matter, and location of organic matter (Hendrix, 2000). They concentrate Ca content of soil and produce decay-resistant casts that allow for the movement of water and nutrients deeper into the profile. Finally, they concentrate cations and bury soil organic carbon (SOC) lower in the profile, resulting in slower decomposition rates than would be expected for surface material. Earthworms are also important in the development of humus-rich mull horizons relative to the poorly decomposed, acidic mor horizons often found in nonearthworm soils.

## SOIL PROCESSES IMPORTANT IN FOREST-SOIL C TRANSFORMATIONS

The storage of C in forest soils is dependent on the organisms described above and on the processes performed through the interaction of these organisms. These include mycorrhizae, which increase biomass and nutrient uptake; promote transformations of N such as N mineralization; facilitate decomposition and humification; and alter the soil physical structure through mixing and aggregation and food web interactions. The organisms in these interactions are considered ecosystem engineers (Hooper et al., 2000) due to their influence on plant productivity and ecosystem structure.

### Mycorrhizal Relationships

Mycorrhizal fungi form symbiotic relationships with nearly all tree species. Many of the ancient families such as the redwoods, and cypress, as well as many tropical trees are endomycorrhizal. The oaks and conifers of temperate forests tend to be ectomycorrhizal. Others such as the poplars and willows have endomycorrhizal colonization as young trees and have ectomycorrhizal colonization as the trees mature. The differences between ecto- and endomycorrhizae are the groups of fungi involved, as described earlier, and the actual location of the fungal hyphae in the plant root. Ectomycorrhizal fungi have exchange structures external to cortical cells of the host plant, while endomycorrhizal fungi have exchange organs that are located within the cortical cell wall but do not penetrate the cell membrane (Allen, 1991). In both relationships the fungi provide plants with nutrients including P, N, micronutrients, and water, and the plants supply the fungi with photosynthate. They have also been shown as capable of mediating intertree C transfers (Smith and Read, 1997). The primary contribution of mycorrhizae to forest-soil C is through their impact on net primary productivity.

The fungi provide services in addition to direct access to nutrients, which enhances host productivity and contributes to SOC formation. These services include altering decomposition rates, accessing alternative nutrient sources for improved host nutrition, increasing soil aggregation, providing defense against fungal pathogens for the host, and direct contributions to soil C by altering sink strength, biomass, and exudates.

Mycorrhizal fungi have the potential to impact the rate at which decomposition occurs. Controversy has surrounded the "Gadgill effect" of lower decomposition rates in litter with mycorrhizae

than without, due to interaction of mycorrhizal fungi with decomposer populations (Smith and Read, 1997). While the research that demonstrated this effect has not been successfully repeated, there is a great deal of evidence that decomposition rates are altered by mycorrhizal fungi, and there is evidence that ectomycorrhizal fungi possess the enzymes necessary for the decomposition of C compounds such as lignin (Leake and Read, 1997). Mycorrhizal fungal species may also undergo succession as forests age in response to alterations in C inputs, moving from species with enzyme systems that are suitable for the inorganic substrates in young forests, to species capable of degrading the more-complex organic C compounds found in older stands (Dighton, 1995). Mycorrhizal alterations to nutrient cycling provide a direct route for plant nutrition from decomposed materials to plants without losses due to leaching or immobilization by other organisms.

Mycorrhizal fungi also access nutrients from other soil organisms. Klironomos and Hart (2001) demonstrated that ectomycorrhizal fungi could access N directly from collembola. The fungus excreted enzymes into the soil that killed the collembola, followed by enzymes that broke the collembola down structurally. N was harvested and transferred directly to the plant. Under experimental conditions, nearly 25% of the N in the plant was from the collembola.

Mycorrhizal fungi can also limit access to organisms pathogenic to or parasitic on mycorrhizal host roots. Gange et al. (1994) demonstrated that the presence of mycorrhizae on the roots of *Taraxacum officinale* decreased the number of black-pine-weevil larvae feeding on the roots. Both ecto- and endomycorrhizal species have been reported to protect plant hosts from pathogenic attack (Azcón-Aguilar and Barea, 1992). Protection of hosts increases NPP in forests, thus increasing the amount entering detrital pools and SOC.

Mycorrhizal fungi can make direct contributions to soil C by altering sink strength, improving aggregation, producing exudates, and contributing fungal biomass to detrital pools. Mycorrhizal fungi impact soil aggregation by producing polysaccharides as well as by directly interacting with soil particles with hyphae. Soil particles bound to fungal hyphae enhance aggregation, which protects SOC. Furthermore, mycorrhizal fungi may contribute to C found in those aggregates (Allen, 1991). A great deal of research is currently focusing on the glycoprotein glomalin that is produced by endomycorrhizal fungi, and the results suggest that glomalin plays a role in aggregate stability (Wright and Upadhyaya 1996, 1999; Wright and Anderson, 2000). Glomalin can be found in large quantities in forest soils and has relatively slow turnover times. Rillig et al. (2001) detected glomalin in quantities of up to 60 mg/cm<sup>3</sup>, representing 4–5% of soil C and N in tropical forest soils and with turnover times ranging from 6 to 42 years. Glomalin in temperate forests has been poorly studied. Preliminary results suggest large pools in temperate forest soils and increases in soils that have been returned to forests from agriculture (Rillig et al., 2003).

Mycorrhizal fungi also alter sink strength in plants by creating a sink for C in roots. Increases in root C demand result in the higher net photosynthetic rates associated with heavily colonized roots (Smith and Read, 1997). The increased photosynthate results in greater biomass for mycorrhizal plants, even with the drain that the fungi represent (Paul and Kucey, 1981). Mycorrhizal fungi also exude a variety of organic acids into the soil (Sollins et al., 1981). These acids, used for mineral liberation and chemical weathering (Jurinak et al., 1986), also provide easily consumed C compounds for maintaining microbial populations (Morris and Allen, 1994).

A final source of SOC added by the mycorrhizal fungi is in the hyphal biomass. Mycorrhizal biomass is difficult to determine for forest soils, but it is estimated that up to 20% of the total photosynthate goes to the fungi for respiration, nutrient acquisition, and maintenance. Nutrient acquisition requires extension of a hyphal network. One estimate put the biomass production of an ectomycorrhizal hyphal network at 830 kg biomass/ha per annum for sheath, mycelium, and sporophore production in the FH horizon of a pine forest (Smith and Read, 1997). This would make a reasonably large contribution to the soil detrital pool. Ultimately, mycorrhizal symbioses have a number of direct and indirect mechanisms by which they increase SOC pools and provide a larger contribution to forest-soil C storage than would be obvious through their simple role in nutrient uptake.

## N Transformations

Nitrogen is the most common limiting factor for growth in forest soils after water. Tree growth is closely related to the demand for N (Melillo and Gosz, 1983), and N in excess of plant maintenance is necessary for photosynthetic production to exceed plant demand. The amount of N that entered ecosystems through processes other than biological N fixation was a fraction of that which was needed to support ecosystems prior to anthropogenic deposition. Even with deposition, N-fixing organisms continue to play an important role in ecosystem dynamics. In forests, N fixers are found as symbiotic partners with trees and herbs, as symbiotic partners with fungi, and as free-living soil organisms. The amount of N that enters forest systems varies greatly, depending on the source. For example, asymbiotic fixation is reported to range from 1.5 to 38 kg/ha/year, and symbiotic fixation with alder can range from 40 to 325 kg/ha/year (Marshall, 2000), although total fixation is more often reported to range from 5 to 10 kg/ha/year for forests and woodlands (Knowles and O'Toole, 1975; Brady and Weil, 1999). Cyanophycophilous lichens in forest canopies in an old-growth Douglas-fir ecosystem in Oregon produced 2.8 kg/ha/year, which is lower than the 8 kg/ha/year reported by others under optimal conditions (Sollins et al., 1980).

Nitrogen that enters the ecosystem through fixation is bound in organic forms and must be mineralized for plant uptake. The organisms involved with N mineralization range from the smallest bacteria to some of the larger macroscopic animals. In N-limited systems, microorganisms can immobilize large quantities of N, which will further limit plant growth. In N-rich systems, in contrast, the turnover of organisms is rapid and plant growth is not limited. Initial research suggested that N turnover was more rapid in young forest stands than it was in older forest stands. More recent research suggests that this is not the case. In fact, the N cycle in forest soils is so tight that N released through mineralization will be taken up quickly by organisms, and only through tracer work, using  $^{15}\text{N}$ , can the N turnover be detected (Davidson et al., 1992). This inhibits  $\text{N}_2\text{O}$  pollution of the atmosphere by leakage in both the process of nitrification as well as in denitrification. The N is therefore retained in these systems through rapid recycling to microbial or vegetative biomass.

Nitrogen deposition has altered the availability of N in ecosystems. Nitrogen is currently accumulating at rates greater than previously recorded, and increased N availability will impact C storage in ecosystems. Melillo and Gosz (1983) report average retention rates of fertilized N to be 60%, with the rest lost through leaching and/or denitrification. Elsewhere, Melillo (1996) predicted that increased N deposition would result in an additional C sequestration of 0.9 Pg C for boreal and temperate system forests based on N retention efficiency of 100%. Nitrogen storage rates across four afforested deciduous sites in the eastern U.S. region ranged from 23 kg/ha/year to 45 kg/ha/year when compared with current agriculture on the same soil type (Paul et al., 2002; Morris et al., in preparation). Increases in soil N were greater in all sites than would have been expected based on atmospheric deposition rates as determined by National Atmospheric Deposition Program (NADP) data (NADP/NTN, 2000) or N fixation (Knowles and O'Toole, 1975). This would indicate that N-stimulated C sequestration on deciduous afforested sites is a great deal higher than predicted by Melillo (1996).

The greatest C storage will occur if additional N entering systems is maintained in tree biomass, which has a C:N ratio of 150:1 (Melillo and Gosz, 1983) rather than the 8:1 C:N ratio characteristic of humified organic material in most soils. Further work is necessary to determine whether the soils are a better sink than vegetative biomass, as was found by  $^{15}\text{N}$  tracer studies on a beech-maple-red spruce forest in Maine (Nadelhoffer et al., 1993, 1995). Sink strength may be related to the efficiency with which vegetation can take up different forms of N. As vegetation may provide a stronger sink than soils depending on depositional  $\text{NH}_4^+:\text{NO}_3^-$  ratios (Nadelhoffer et al., 1999).

Nitrogen retention in a southern Michigan afforested site 60 years after planting was 33% greater than for adjacent agriculture on the same soil type (Morris et al., in preparation). The N is accumulating, with approximately 60% in aboveground biomass and 40% in soil at a C:N ratio of approximately 10:1. Disregarding the ability of forests to absorb larger amounts of N (and therefore

more soil C) can lead to errors in global C models. Finally, interactions of N deposition and global change may have effects not previously investigated.

Nitrogen availability may also control the decomposition rate of litter in forest soils. Increased N retention in soils will result in decreased C:N ratios. This is apparent in afforested systems compared with the native forest systems (Morris et al., in preparation). Nitrogen additions can increase C turnover where N deficiency is slowing down decomposition. In other soils, however, it can decrease decomposition rates (Fog, 1988). This can be attributed to two factors: available N inhibits lignin decomposition (Boominathan and Reddy, 1992), and N is required as a component of SOM, which often has a C:N ratio of 8:1 in its humified form and helps build stable organic matter (Haider, 1992). In contrast, Prescott (1995) found no change in decomposition rates when N was added to a coniferous forest exogenously as fertilizer or endogenously as litter with higher N. Her conclusion was that higher N must be accompanied by greater amounts of microbially metabolizable C for decomposition rates to change. Alternatively for C storage, increased productivity through N fertilization may increase litter quantity, which in the end will result in more litter C and thus more C ultimately entering SOC pools without alterations to decomposition rates. There is concern that N saturation may eventually occur in the afforested systems, resulting in ecosystem health problems from concomitant soil acidification and Al solubility problems, as described in the acid-forest-soil literature (Aber et al., 1989).

## Production and Decomposition of Humus

Decomposition rates affect C sequestration in forest soils. Slow decomposition rates result in the accumulation of organic matter in litter and modified plant materials, slowing the return of nutrients for plant uptake. Fast decomposition, in contrast, may result in high steady-state losses of  $\text{CO}_2$  and rapid recycling of nutrients. For C storage in forest systems, the products of decomposition/humification will control the sequestration and are a great deal more important than the rate of decomposition. Carbon storage is dependent on materials entering the detrital pool, but long-term storage is the result of resistant C compounds being produced in conjunction with physical and chemical protection.

Evaluation of SOC for relative residence times and/or resistance to degradation has been done using a number of fractionation schemes. Chemical analyses break SOC into fulvic and humic acids and humin. The most ecologically relevant fractionation schemes rely on partitioning of SOC by biological fractionation, which is dependent on the *in situ* microbial and microarthropod communities (Robertson and Paul, 2000). The biological fractionation includes partitioning of soil C pools into active, slow, and resistant materials based on first-order kinetics, with results in pools varying in turnover times from 50 to 100 days for the active, 10 to 100 years for the slow, and in the 1000s of years for the resistant (Collins et al., 2000; Haile-Mariam et al., 2000). Carbon accumulations must be in the slow or resistant pools for long-term storage.

Plants produce a number of compounds that decay slowly. Lignin makes up a relatively small amount of green plant material but comprises 15–35% of the wood of most trees (Käärik, 1974). Lignin is composed of aromatic polymers with high molecular weights. The structure of lignin makes it resistant to microbial decay. The resulting products of decomposition are  $\text{CO}_2$ , organic acids used as energy compounds to a limited extent, and molecules formed through coupling reactions. Up to 70% of the lignin is initially stabilized in the soil pool (Haider, 1992), although reports elsewhere suggest that only 0.1% of NPP is found as humus in any year (Waring and Running, 1998). Dunbar and Wilson (1983) report that the majority of oxygen in humics is derived from carbohydrates, suggesting a lack of understanding of the complexity of the processes involved.

The coupling reactions that result from lignin degradation produce humic substances that are even less well-defined structurally than lignin. The organisms responsible for the production of humic substances include fungi, actinomycetes, and a limited number of bacteria, i.e., a "synergistic consortia of microbes" (Haider, 1992). These organisms produce enzymes such as monophenol

**Table 7.1** Pool Sizes for Total ( $C_t$ ), Active ( $C_a$ ), Slow ( $C_s$ ), and Resistant ( $C_r$ ) Soil C Pools in the A Horizons at Russ Forest, MI, Using a Three-Pool Constrained Model<sup>a</sup>

A Horizon <sup>b</sup>	$C_t$ (mg/kg)	$C_a$ (mg/kg)	$C_s$ (mg/kg)	$C_r$ (mg/kg)
Agriculture	10,249	308	5325	4617
Afforested land	14,138	726	6933	6481
Native forest	29,722	1761	13,491	14,469

<sup>a</sup>  $C_t = C_a k_a e^{(-k_a \cdot \text{days})} + (C_{\text{SOC}} - C_r - C_s) k_s e^{(-k_s \cdot \text{days})} + C_r k_r e^{(-k_r \cdot \text{days})}$  = rate of C evolution per unit time [ $d(\text{CO}_2) dt^{-1}$ ];  $C_{\text{SOC}}$  = SOC measured at time 0;  $C_r$  = resistant C (nonhydrolyzable C);  $k_r$  = 1/MRT when using carbon dating or 1/1000 year when using an assumed MRT (Mean Residence Time);  $C_a$  = active C;  $k_a$  = turnover rate for active pool;  $C_s$  = slow C ( $C_{\text{SOC}} - C_r - C_a$ );  $k_s$  = turnover rate for slow pool.

<sup>b</sup> The depth of the A horizon was 23 cm in agriculture, 31 in afforested land, and 11 in the native forest.

Source: Data from Morris, S.J. et al., in preparation.

monooxygenases or peroxidases, which incorporate products of lignin breakdown with other plant compounds (such as flavonoids and waxes) or with bacterial products (such as phenols and amino acids) to produce large molecules of unique structure (Sjogblad and Bollag, 1981; Dagley, 1967; Haider, 1992). The result is humic material that provides buffering capacity, CEC, water-holding capacity, nutrient reserves, and a long-term storage pool of C in forest soils.

The SOC pools in forests and areas returned to forest from agriculture or by invasion of grasslands can be quite large. Measurements using long-term incubations and curve fitting (Paul et al., 2001) showed that an afforested deciduous forest on former agriculture soil and an agricultural soil in a southern Michigan site had 45 to 50% of total soil C in the resistant or recalcitrant C pool and a similar amount in the slow C pool (Table 7.1). These pools represent an increase in total C, with increases in both the slow and resistant pools in the afforested site over the agriculture site as a result of alterations in litter quantity, quality, and decomposition products. Forest soils on the same soil type as the one sampled in Michigan were found to have a mean residence time of 1435 years for the resistant fraction vs. 656 for the total soil C (Collins et al., 2000).

The organisms specifically involved in the decomposition process can play a role in the type of humus formed. While soil formation is principally dependent on multiple biological and non-biological factors that are chiefly long-term processes dictated by climate and vegetation (Wilding et al., 1983; Brady and Weil, 1999), there are other short-term processes that influence soil formation on the local scale such that the forest floor on the same soil type may have significantly different characteristics (Handley, 1954; Minderman, 1960). This phenomenon has been most keenly observed in the mull-type forest floor and mor-type forest floor that forms most notably under beech and often under many coniferous trees.

It has been suggested that the impact of mor vs. mull formation is a fundamental difference in the processes involved in SOM turnover and resynthesis rather than simply a change in the rate of turnover between the two systems (Handley, 1954). The difference between the formation of a mull forest floor and a mor is entirely due to the organisms processing the material. The mor form includes three layers identified as fresh litter, partially decomposed but recognizable litter, and homogeneous humus. Mull in contrast has litter mixed into the mineral soil by animals. The mull results in a more nutrient-rich site, and NPP benefits from the rapid release of nutrients not necessarily from more rapid decomposition but, rather, decomposition resulting from animal interactions that shred litter for bacterial degradation (Prescott et al., 2000). In contrast, mor is the result of fungal attack on litter, resulting in incomplete decomposition and nutrient immobilization. The formation of the two distinctly different forest floors has been attributed to the presence or absence of disturbance by earthworms, burrowing animals such as moles, or litter incorporation into soil. Formation of mull may also be related to Ca and the relationship of microorganisms, fungi, or

earthworms to Ca. This is believed to be a reversible system (Handley, 1954), so management to promote development of Ca-rich mull forest scenarios could increase soil C and N sequestration. Further research is necessary to determine the degree to which physical disturbance and Ca results in one forest floor type over the other.

### Soil Mixing and Aggregation

Physical protection is provided to SOC through processes that limit degradation, usually by limiting oxygen, moisture, or temperatures necessary for microbial decomposition. Aggregation is the formation of organomineral complexes that are the basic component of soil physical structure. Abiotic forces such as compaction, freeze-thaw, etc., can aid in aggregate formation, but the organisms involved with soil mixing and nutrient acquisition are also involved in the formation of aggregates.

Aggregate formation may be the result of fungal and plant roots binding and joining soil mineral particles. Alternatively, fungal and bacterial polysaccharides excreted during activities may bind particles, or plant particles may become encrusted by mineral deposits, resulting in aggregate formation (Kay and Angers, 2000). Regardless of the method, SOC is greater in highly aggregated soils, either resulting in or as a consequence of aggregation. Soil organisms that bind mineral particles together contribute fecal materials or produce polysaccharides that mix with organic matter. Humic substances also play a role in aggregate stability. Forest soils contain very high numbers of aggregates and large amounts of aggregate-bound C. Agricultural soils returned to forest increase in aggregate number and C content. Six et al. (2002) found that up to 20% of the difference in whole-soil SOC stocks could be accounted for by differences in microaggregate-protected C in these soils. The position of C within the microaggregate provides longer-term storage for C in the forest and afforested soils because organic materials within soil aggregates have lower decomposition rates than those located outside of aggregates.

### Soil Food Web Diversity

Soil food webs represent the most diverse and complicated food webs of those in any terrestrial ecosystem. Studies of relationships of belowground diversity to aboveground diversity often fail to show correlation at the local scale, but they are more robust at the landscape scale (Hooper et al., 2000). While this might suggest that the relationships are not dictated by local conditions, this actually reflects the difference in scale between aboveground and belowground ecosystems. As described above, the key to C storage in forest ecosystems is the interaction of organisms in multiple trophic levels.

Current ecological theory suggests that diversity is essential for stability (defense against disturbance) and resilience (recovery from disturbance). Soil microorganisms have been discussed as "functionally redundant," meaning that many organisms perform similar tasks so that they are buffered against loss of function with loss of species. Recent research investigating the impacts of disturbance on soil bacteria suggests that soils with low catabolic diversity in bacterial populations are less resistant to stress than systems with high catabolic diversity (Degens et al., 2001). Our understanding of the function of microbes, especially those involved in complex multispecies interactions, is limited. Management for C storage must include maintenance of microbial diversity and buffering against disturbances that will alter or decrease diversity within soil food webs.

### CONCLUSION

Sequestration of C in forest soils is dependent on the interaction of soil organisms with each other and their environment. Management for C sequestration in forest soils must include an

understanding of these interactions and the factors that control the growth and maintenance of these organisms.

Sequestration of C in soil is the result of incomplete decomposition, and long-term C storage is achieved through alterations to organic materials through processes such as humification and movement of materials lower in the soil profile. Forests have great potential for soil C storage because the inputs are rich in compounds such as lignins, which are difficult to decompose even under optimal conditions, and rich in organisms that can optimize forest net primary productivity while maintaining belowground C stocks.

Considerations of C sequestration in forest soils should include mention of the consequences of climate change, because temperature and moisture most often limit the processes described above. Predicting the impact of future climate change on ecosystem dynamics is complex because of interactive impacts on tree health, soil biota, and tree growth relative to soil C humification and decomposition. Increased temperatures should increase decomposition, however the added CO<sub>2</sub> should increase tree growth rates. If increased net primary productivity due to CO<sub>2</sub> is greater than the decomposition due to warming, there should be a higher net C storage in forest soils. Unfortunately, research to date has provided evidence for both increases and decreases in decomposition rates resulting from climate change, largely as a consequence of the relationship between moisture and temperature. Impacts of climate change on the organisms that mediate soil C dynamics will ultimately determine C sequestration under these conditions.

The potential for forest soils to store C will be affected by alterations to the structure and function of belowground forest communities. Research is currently needed to evaluate the controls on C sequestration and the impact that specific management strategies and disturbances have on these systems. This includes a more comprehensive mechanistic understanding of the role of microbial community structure in organic matter turnover, as well as an understanding of the role of nutrients such as Ca, Mg, and N in C cycling. Ultimately, forest soils can provide large C pools that have very long mean residence times, but optimizing these pools and protecting them once formed requires an understanding of C dynamics that is currently incomplete.

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