Processes Affecting Carbon Storage in the Forest Floor and in Downed Woody Debris

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INTRODUCTION

Many forests differ from other types of ecosystems, such as grasslands or rangelands, in that they develop a thick horizon of decaying organic matter, together with highly heterogeneous accumulations of woody debris, on the soil surface. Particularly in temperate and boreal forests, foliar, root, and woody litter accumulate in all stages of decomposition from fresh litter to material that is highly decayed and partly stabilized. As litter decays, organic carbon in the surface organic horizon has several fates: some is mineralized to CO_2 through biotic respiration, some is stabilized and remains in place to form a humus layer, and some is converted to soluble decomposition intermediates

Table 9.1   Mean Simulated Values of Forest-Floor C Pools, Fluxes, and Turnover Rate at 60 Years Following Clear-Cutting in the White Mountain National Forest, NH

Cover	Area (ha)	DOC Flux (g m^{-2} year^{-1})	CO_2-C Flux (g m^{-2} year^{-1})	Forest-Floor C Pool Size (g C/m^2)	Forest-Floor C Turnover Rate (%/year)
Hardwood	217,550	24.6	242	3625	7.4
Coniferous	66,050	33.6	188	4460	5.0
Mixed	38,800	29.3	218	3850	6.4
Overall	322,400	27.0	228	3825	6.7

Note: Values are landscape-level means by forest cover type, calculated by a biogeochemical process model linked to a geographic information system (Currie and Aber, 1997).

and transported via soil solution to deeper soil horizons. The characteristics of the surface organic horizon (O horizon), or forest floor, depend on temperature and rainfall regimes, litter production rates, litter quality, and soil microbial and animal activities. Litter quality is determined largely by the tree species present, which in turn depend on elevation, climate, and land-use history.

The O horizon varies among forest types and climates from little more than a thin litter layer to very thick and well developed. Thin forest floors most often occur in systems where fire is frequent and in those humid forests in which earthworm activity is high and decomposing litter is well mixed into upper mineral soils. Thick forest floors, in contrast, are likely to occur in cool, moist forests where soils are acidic and decomposition is slow or incomplete. Litter accumulation and decay processes typically exhibit high variability at multiple scales: within forest stands, across heterogeneous landscapes, and among forest biomes. Land-management activities, including forest harvest, contribute to the temporal dynamics of the forest floor as forests respond to management and undergo succession over the following decades. Differing histories of land use and management in patches of forested landscapes also contribute to great spatial heterogeneity in forest-floor C stores. Still, some regional-scale patterns can be generalized. For example, in the absence of recent disturbance, forest floor masses in the humid forests of New Hampshire tend to be greater under coniferous vegetation than deciduous; cooler temperatures in the higher-elevation spruce-fir forests contribute to the already slow decay rates of the coniferous needle litter (Table 9.1).

Mineral soil horizons store most of the C in forest soils, though most litter inputs enter the forest floor. From the perspective of C budgeting and C sequestration in whole soils, forest floors are important as reservoirs of stored C, as intermediate pools that act as a source of much of the C that ultimately is stored in mineral soils, and as responsive ecosystem components that exhibit feedbacks from forest change. Globally, forests floors store approximately 68 Pg C in fine litter and humus, with perhaps another 75 Pg C in coarse woody detritus (Matthews, 1997). Although this amounts to only about 3–6% of the global C pool in the top 3 m of mineral soil (2344 Pg C; Jobággy and Jackson, 2000), C in the forest floor is more dynamic because the residence time of C is shorter there than in mineral soil. Forest-floor C stocks have the potential to rise or decline quickly in response to disturbance or to changes in management practices, tree species composition, or environmental conditions (Gaudinski et al., 2000; Trumbore, 2000). Processes taking place in the forest floor also affect the movement of C into mineral soil horizons in two ways. First, decomposition produces soluble C compounds (DOC, dissolved organic carbon) that are transported downward into mineral soils. Second, animal activities and forest disturbances, such as windthrow or logging, mix organic matter from the surface into the mineral soil.

THE FOREST FLOOR DEFINED AND MEASURED

In understanding forest-floor C storage and C fluxes, it is important to consider how forest floors are measured in field studies. The forest floor is usually synonymous with the organic or O

horizon, which is defined in the U.S. Soil Taxonomy as having greater than 20% organic carbon by mass (Soil Survey Staff, 1999). The distinction between the O horizon and the mineral soil can be unclear and somewhat subjective in the field, however (Federer, 1982). The O horizon can have up to three sub-horizons, which are defined by their rubbed fiber content. The Oi, or fibric layer, consists of relatively undecomposed litter. The Oe or hemic layer contains partially decomposed, highly fragmented material. The Oa or sapric layer contains humus, which is black and greasy feeling, not fibrous. In other systems of soil classification, these three layers have been referred to as the L (litter), F (fragmented) and H (humus) layers. Some researchers collect an A horizon and report this as part of the forest floor, sometimes as a fourth horizon (Federer, 1984) and sometimes as part of the Oa. The A horizon is an organic-rich horizon that technically comprises part of the mineral soil, because it contains less than 20% organic carbon by mass.

The degree to which downed woody debris, i.e., branches, logs, stumps, coarse roots, and other buried dead wood, enters definitions of the forest floor varies among field studies. Some researchers sieve the forest floor and exclude material larger than the mesh size of the sieve. This technique is standard for mineral soils, in which fragments greater than 2 mm are not considered part of the mineral soil. For the forest floor, there are three key factors that vary among field studies. First, many decayed organic fragments, unlike rock fragments, can be made to pass through a sieve with the application of force (some investigators use a rubber stopper to press matter through the sieve). In addition, sieves coarser than 2 mm are sometimes used, introducing variation between studies. Second, organic material excluded by sieving may or may not be weighed and reported as coarse organic fragments. Third, some investigators process forest-floor samples by grinding them in a mill rather than sieving. This technique includes small sticks, log fragments, and bark that would not pass through a sieve. This variation in how the forest floor is measured introduces uncertainty in generalizations about carbon storage in the forest floor and in coarse woody debris.

Accurate carbon accounting of the forest floor, fragmented woody debris, and roots is made difficult by the fact that these components are not generally separated in field studies. Live roots (fine and coarse) are usually excluded from *conceptual* definitions or model representations of the forest floor, which is defined as detrital material. However, live fine roots are almost always included in *operational* measurements of forest floor mass and C because distinguishing live roots from dead is difficult. Also problematic is that field studies often overlook woody debris buried within or beneath the forest floor, as well as entire organic horizons that have been buried as a result of severe disturbances such as windthrow and logging operations. Because these horizons lie beneath mineral soil horizons, they are not part of the forest floor, although they can be important in following the fate of forest-floor carbon following disturbance.

PROCESSES GOVERNING FOREST-FLOOR C DYNAMICS

One of the most well-studied aspects of litter decomposition is the rate of mass loss from foliar and fine-root litters incubated in the field under a variety of temperature and moisture regimes. Most decomposition studies emphasize decay rates in the first few years, the period when fine litter mass is lost most rapidly. However, several other terms are critical for C accounting or forecasting. These terms include the proportion of fine litter and wood that becomes stabilized as humus or mineral soil organic matter (SOM) (Alperin et al., 1995), as well as the decomposition rates of humus or soil organic matter. Another factor to recognize for accurate C accounting is that a significant fraction of the mass lost from field-incubated litter occurs through the production of DOC that is transported to lower soil horizons (Currie and Aber, 1997). The following sections will separately discuss the factors that determine decomposition rates in early and late stages of decay, those that influence the completeness of decay, and the factors that govern the production and leaching of DOC, as well as processes that mix O horizon material into upper mineral soils.

Early-Stage Decomposition

Early rates of decomposition are primarily controlled by climate and litter quality (chemical and physical properties of the litter; Swift et al., 1979; Lavelle et al., 1993) through their effects on the activities of soil organisms. Climate determines decay rates over very broad geographical scales, while litter quality influences rates within a region (Meentemeyer, 1978; Berg et al., 1993; Aerts, 1997). These factors tend to be positively related, in that climates that are unfavorable for decomposition also have vegetation that produces low-quality litter (Aerts, 1997). Decomposition is slow where litter moisture is below 30% or above 150% of litter dry weight (Haynes, 1986), such as in deserts, bogs, and swamps. If moisture conditions are adequate, decomposition rates generally increase with increasing temperature, with the greatest relative increase at low temperatures (Winkler et al., 1996; Peterjohn et al., 1993; Hobbie, 1996). Temperature and moisture interact in controlling decay rates: Temperature affects rates of evaporation and thus moisture, while accumulated detrital mass affects the thermal insulating property of the forest floor, and moisture content also affects the soil heat budget and temperature through increased heat capacity. Biogeochemical process models of C cycling often represent the temperature and moisture controls on decay rates simply and empirically, with regressions of field-measured decay rates across environmental gradients. For example, some models use actual evapotranspiration (AET) as a surrogate controlling variable that combines the positive effects of both temperature and moisture across a broad range of conditions in well-drained forest soils (Meentemeyer et al., 1978; Currie and Aber, 1997; Figure 9.1).

The chemical quality of litter is largely a function of the C chemistry of the litter, particularly sugars, cellulose, lignin, and phenols (Minderman, 1968). Lignin is a class of large-molecular-weight polyphenolic compounds that are difficult for microbes and fungi to decompose enzymatically. Typically, lignin is operationally defined as the acid-insoluble residue remaining after a process of extraction and acid hydrolysis of litter in the laboratory; as measured, this fraction actually includes tannins and cutin together with lignin (Preston et al., 1997). Rates of decay often correlate with indices of C chemistry such as litter lignin content (Meentemeyer, 1978; Tian et al., 1992; Van Vuuren et al., 1993) or lignin:N ratio (Melillo et al., 1982). The operationally defined lignin fraction correlates with slow decay because compounds in this fraction are poorer substrates for the microbial community. Early decay rates are sometimes related positively to the initial concentrations of N in litter (Witkamp, 1966; Taylor et al., 1989; Tian et al., 1992) or P in litter at
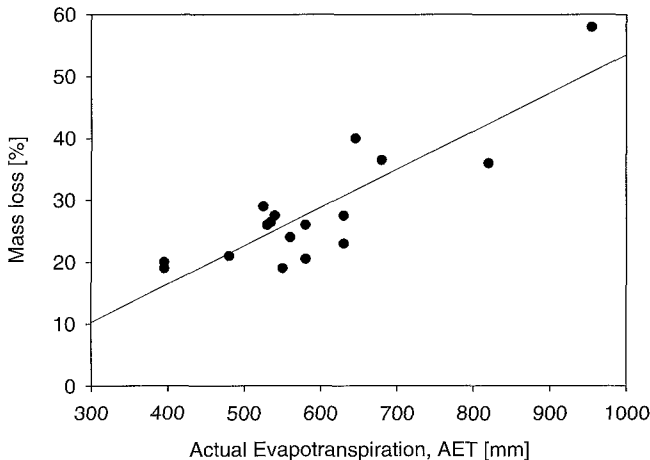
Figure 9.1   Percentage mass loss in decaying litter as a function of actual evapotranspiration (AET). (After Berg, B. et al., *Biogeochemistry*, 20: 127, 1993.)

sites with low P availability (Vitousek et al., 1994; Aerts and Decaluwe, 1989; Vesterdal, 1999). In some ecosystems, the concentrations of phenolic compounds or cutin may slow litter decomposition (Aerts and Decaluwe, 1989; Gallardo and Merino, 1993). Leaf toughness is sometimes negatively related to decomposition rate, probably through its influence on palatability and accessibility to decomposer organisms (Perez-Harguindeguy et al., 2000).

Late-Stage Decomposition

Through a complex set of processes including secondary (microbial) synthesis of C compounds and condensation of the intermediates of decomposition into polyfunctional macromolecules, a fraction of decomposing C becomes stabilized in humic substances in forest soils (Zech and Kogel-Knabner, 1994; Stevenson, 1994). Humification occurs both in the forest floor and in mineral soil horizons. Once litter has been transformed to humus or mineral SOM, the rate of decay is slow, constrained primarily by the recalcitrant chemical properties of the material (Johansson et al., 1995; Prescott et al., 2001; Giardina and Ryan, 2001). Humification is sometimes viewed as a convergent process that reduces differences among litter types (Melillo et al., 1989). Some differences in rates of C mineralization indicate, however, that there is variation in the recalcitrance of humus or mineral SOM within the range set by its low quality (Howard and Howard, 1993; Nadelhoffer et al., 1991). Rates of decay of late-stage material are influenced by temperature, moisture, soil texture, and availability of exogenous labile C and N (Melillo et al., 1989). Rates of soil respiration increased two-fold with each 10°C rise in temperature (i.e., Q_{10} = 2) (Katterer et al., 1998), and Q_{10} values greater than 2 have been reported at temperatures below 5°C (Kirschbaum, 1995; Niklinska et al., 1999; Grogan et al., 2000). Mineralization of soil organic matter generally increases with increasing moisture content up to field capacity but declines with greater moisture (Stanford, 1974; Howard and Howard, 1993; Paul and Clark, 1996). The influence of moisture on decomposition of soil organic matter appears to be greatest at high temperatures (Douglas and Tedrow, 1959; Zak et al., 1999).

Fine-textured soils are usually associated with high contents of organic matter and low rates of mineralization relative to coarse-textured soils (Burke, 1989; Paul and Clark, 1996; Koutika et al., 1999; Jobággy and Jackson, 2000). This has been attributed to the organic matter being physically protected from microbial decomposition by mineral particles (Oades, 1988; Van Veen and Kuikman, 1990). Alternatively, the greater C accumulation in fine-textured soils may be an indirect effect of greater productivity on these sites, as laboratory studies have provided no clear evidence of a direct effect of clay content on soil C mineralization rates (Giardina et al., 2001).

Completeness of Decay

A single-exponential model of decay, e^{-kt}, is often used to describe the early stages of decomposition (Olson, 1963; Jenny et al., 2001). However, there are several indications that mass loss from fine litter abruptly slows upon reaching the humus stage (Howard and Howard, 1974; Melillo et al., 1989; Aber et al., 1990; Berg, 1991). An alternative model includes a limit to decomposition, beyond which the rate of decay is almost immeasurably slow (Berg, 1991). The proportion of the original mass of litter that remains at this point varies among species (Berg and Ekbohm, 1983; Berg et al., 1996). It appears that the higher the initial quality of fine litter, the greater the proportion that becomes humus. This has been observed in N-fertilized vs. unfertilized foliar litter (Berg and Ekbohm, 1991; Prescott, 1995; Cotrufo et al., 2001), green vs. brown needles (Berg and Ekbohm, 1991), broadleaf vs. needle litter (Berg and Ekbohm, 1991; Prescott et al., 2001), and high quality (lignin C:N = 10) compared with low quality (lignin C:N = 35) roots (Van Vuuren et al., 1993). The decomposition limit may be related to N concentrations in litter, as some N compounds react with aromatic substances in the soil, yielding recalcitrant humic compounds (Berg et al., 1996). Thus higher initial N concentrations in fine litter may result in less complete decay and greater formation of humus.

Models of decay and stabilization typically characterize the fraction of fine litter that becomes humified as 15 to 20% of initial litter mass (Aber et al., 1990). We have little information on the fraction of woody litter that can be stabilized, although some models use the 20% result from fine litter to describe the humification of woody debris (Currie et al., 1999). This extrapolation provides simulated accumulations of humus that appear reasonable, though this rate of transfer to humus, together with the decay rates of humus, are some of the most poorly constrained aspects of models of C balance in the forest floor (Currie and Aber, 1997).

Leaching of Dissolved Organics to Mineral Soil Horizons

The transfer of C to mineral soils through the movement of DOC can comprise a significant term in the soil C budget and has long been recognized as a key factor in the formation of forest soils (Dawson et al., 1978). It is important to recognize that the fate of C lost in litter decomposition studies is not solely as CO_2 to the atmosphere. A significant fraction of litter C losses occurs as the leaching of soluble organics to lower soil horizons (Gosz et al., 1973; McClaugherty, 1983; Qualls et al., 1991). At the Harvard Forest in Massachusetts, fluxes of DOC leaching from the forest floor ranged from 22 to 40 g m^{-2} $year^{-1}$ (Currie et al., 1996), a transfer of C that would amount to 1700 to 3000 g C m^{-2} over the lifetime of a 75-year-old stand. The contribution that DOC ultimately makes to soil C storage depends on the production and leaching of DOC, the recalcitrance of DOC to mineralization, and the retention and stabilization of DOC in mineral soil horizons.

DOC in forest soils includes a wide range of compounds, from simple carbohydrates and amino acids to high-molecular-mass, polyfunctional organic acids, including soluble humic substances (McDowell and Likens, 1988; Vance and David, 1989; Qualls and Haines, 1991). DOC is typically defined and measured as the quantity of C present in solution and passing through a filter of a standard pore size (usually 0.45 to 0.7 μm). Operationally, this includes not only dissolved materials, but also macromolecular colloids, the solubilities of which tend to be strongly controlled by solution pH. Some fraction of DOC is composed of organic compounds that are labile to microbial decomposition, but most DOC is substances in intermediate stages of decay, including secondary and humic substances, that are not easily degradable (Qualls and Haines, 1992; Guggenberger and Zech, 1994).

The forest floor is the location of most DOC production in forest soils, although some DOC leaches from forest canopies in throughfall (Figure 9.2), and some is generated in the mineral soil (McDowell and Likens, 1988; Qualls and Haines, 1991). Because DOC is composed largely of decomposition products and intermediates, the seasonal timing and annual quantities of DOC fluxes may be associated with litter inputs and decay (Qualls et al., 1991; Currie et al., 1996; Kalbitz et al., 2000). Fluxes of DOC leaching from forest floors appear to be controlled by both biotic and abiotic factors. Biotic factors include litter quality parameters such as polyphenol content (McClaugherty, 1983) or floristic classes of litter. In some studies in the eastern United States, coniferous forests exhibited greater DOC leaching fluxes than deciduous forests (Cronan and Aiken, 1985; Currie et al., 1996). However, a recent analysis across 42 field studies in temperate forests worldwide indicated no such overall pattern (Michalzik et al., 2001). Abiotic factors, such as temperature, interact with biotic factors in complex ways. The simple abiotic effect of water movement, however, appears to exhibit a strong control over DOC leaching fluxes across a range of temperate forests (Kalbitz et al., 2000; Michalzik et al., 2001).

The solubility of C compounds affects the transfer of DOC from organic to mineral soil horizons. In mineral soil horizons, DOC concentrations are regulated by sorption and desorption processes that tend toward equilibrium between the sorbed and solution phases (Qualls and Haines, 1992). Soils and soil horizons differ in their capacities to adsorb DOC and in their equilibrium points of DOC sorption and desorption. These differences result from the nature of the DOC present, the solution pH, the presence and the ionic strength of inorganic acid anions, the soil texture, and the soil mineralogy (Evans et al., 1988; Jardine et al., 1989; Moore et al., 1992; Kaiser et al., 1996). Iron minerals are particularly important in the physical sorption of DOC in some soils. In Spodosols
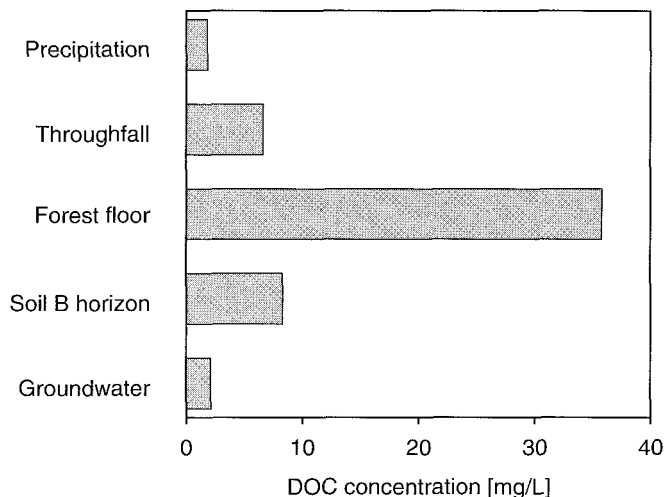
Figure 9.2   Mean DOC fluxes in different parts of the hydrologic pathway across a range of forest ecosystems. The highest fluxes from beneath the forest floor illustrate production of DOC in the forest floor; lower fluxes in mineral soil arise from sorption of DOC in lower soil horizons. (After Cronan, C.S., in *Organic Acids in Aquatic Ecosystems,* Perdue, E.M. and Gjessing, E.T., Eds., John Wiley & Sons, New York, 1990.)

in the northeastern United States, for example, the sorption or coprecipitation of DOC with iron and aluminum oxy-hydroxides (sesquioxides) produces diagnostic organo-mineral B horizons (McDowell and Wood, 1984). Depending on the particular soil, clays or sands can be associated with DOC sorption. In a South Carolina forest, sandy upper horizons retained most of the DOC before it reached the clay-rich Bt horizon (Dosskey and Bertsch, 1997).

Variation in the movement and sorption of DOC is explained primarily by physical factors across the entire range of mineral soils in the United States, including boreal, temperate, and tropical soils (Kalbitz et al., 2000; Neff et al., 2000; Michalzik et al., 2001). The more hydrophilic fractions of DOC that are not sorbed in soils percolate through to groundwater, streams, and lakes, though this typically comprises small percentages (ca. 5%) of the DOC produced in the forest floor (Figure 9.2). Since the majority of DOC in forest soils is composed of relatively recalcitrant compounds, the production and transport of DOC is important to long-term C storage in soils.

Natural Mixing of Forest-Floor Material into Mineral Soil

The mixing of organic matter into mineral soil can represent both an important loss of C from a forest floor and a significant gain of C for a mineral soil. Mixing occurs through a variety of mechanisms, some natural and some accelerated by forest management practices. We first address two mechanisms of mixing that do not depend on human activities; in a later section we consider mixing that results from anthropogenic disturbance.

Many soil organisms depend on detrital carbon, and some soil animals have the ability to move C between soil horizons. The mixing of organic matter by soil organisms is called bioturbation. In particular, earthworms, ants, and termites can be extremely effective at mixing organic material into mineral soil. Earthworms sometimes do so to the point that the forest floor can be eliminated, and litter falling on the soil surface is incorporated into the mineral soil before it can form an Oe or Oa horizon. The overall effect of mixing by soil animals is believed to be a reduction in C storage through heightened rates of decay related to animal activity, together with greater nutrient availability and turnover. At the same time, earthworm activity produces an increase in water-stable aggregates in mineral soil (Coleman and Crossley, 1996). Earthworms are present only in some forest soils. They are more likely to be present in base-rich soils forming from calcareous parent

material, and they are generally absent from soils with acidic pH regimes in the forest floor. The European earthworm, *Lumbricus terrestris,* can be found in forests that followed agriculture land uses. The spread of earthworms to other forested areas has a significant impact on C storage through the elimination of the forest floor.

Windthrow provides an additional mechanism for mixing forest floor material into mineral soil. When trees fall and their root crowns tip up, mineral material is often deposited on the surface of the forest floor. Pit and mound topography is a sign that forest soils have been disturbed by trees falling and burying some of the forest floor area under tip-up mounds. Even if a forest produces few tip-up mounds annually, over the timescale of soil formation, this process may result in the mixing of substantial amounts of carbon into mineral soil.

DOWNED WOODY DEBRIS

Dead wood is present in forests as standing dead trees, dead trees suspended off of the ground, attached dead wood on living trees, and downed wood. Here we consider downed woody debris resting on the forest floor or buried in soils. Pool sizes of downed woody debris are controlled by inputs and losses in the same manner as fine litter. There are major differences, however, in the temporal patterns of inputs and pool sizes. Inputs of large woody debris often result from large, infrequent disturbances, and legacies of these pulsed inputs are present in C stocks for decades or centuries. The long time periods and great spatial heterogeneity make woody litter inputs and decay more difficult to study than fine litter. As a result, we know much less about controls on decay rates, leaching of DOC to mineral soils, and rates of humification and stabilization, compared with the corresponding processes controlling fine litter decomposition.

Studies of woody debris typically measure wood volume or mass. Wood volume can be converted to mass if the specific gravities (or bulk densities) are quantified for material in each decay class. Detrital masses (oven-dry wt., usually 105°C) can then be converted to C stores through multiplication by an estimate of C concentration, typically approximated as 48 to 58%. Concentrations of C prior to decomposition were 47% in Douglas-fir wood in western Washington (Edmonds and Eglitis, 1989), 49–53% in silver fir, 48–51% in incense cedar, 52% in Jeffrey pine, and 50–55% in sugar pine, all species in Sequoia National Park (Harmon et al., 1987). Concentrations of C across all size classes and stages of decay averaged 51% in both pine and oak forests in central Massachusetts (Currie et al., 2002; Currie and Nadelhoffer, in press).

Inputs and Pool Sizes

Inputs to pools of downed woody debris depend not only on large, infrequent disturbances, but also on processes that occur both regularly and intermittently in the absence of disturbance. In a successional forest stand composed of a mix of species, pools of downed woody debris can be expected to vary during the lifetime of the stand as a result of developmental patterns in the stand such as stem exclusion and forest succession, and because individual species differ in productivity, mortality, and rates and processes of wood decay (Hely et al., 2000).

When forests experience widespread mortality and generation of woody litter, the temporal pattern of the summed mass of downed woody debris generally forms a U-shaped curve (Harmon et al., 1986; Spies et al., 1988). Woody litter inputs from the stand-initiating disturbance decay slowly over time, producing the first half of the curve. After a lag time that differs among forest types, inputs of woody detritus resume. The resumption of inputs produces the rise in woody detrital pools in the second half of the U-shaped curve. Depending on the forest type, wood production, and climate, a period of 80 to 500 years may elapse before pool sizes of downed woody debris again reach peak values (Spies et al., 1988; Boone et al., 1988; Sturtevant et al., 1997; Clark et al., 1998).

Forest types differ in the amount of C stored in downed woody debris (Table 9.2). Accumulations of coarse woody debris in the old-growth forests of coastal Oregon, Washington, and British Columbia are among the highest found in the world. Inputs of large-size material, together with the slow decay typical of cool climates, are responsible for these accumulations (Spies and Cline, 1989). Moisture, above a certain point, can also retard wood decomposition, particularly coupled with cool temperatures that reduce evaporation.

Managed forests have highly variable loads of woody debris, related primarily to thinning schedules (Duvall and Grigal, 1999) and to the amount of woody residues remaining after harvest. In general, because of wood removal, pools of coarse woody debris in managed forests are smaller than those in unmanaged forests (Krankina et al., 1998), although pool sizes can be quite high immediately following harvest. Pools of C in stumps (excluding coarse and fine roots) from a harvested 40-year-old Douglas-fir stand in western Washington ranged from 2 to 102 kg C per stump, in addition to 25 Mg C ha^{-1} in branches and unused stem portions (Piatek and Terry, unpublished data). In even-aged stands, a recognizable cohort of woody debris from the present stand is sometimes evident after the stand has passed through the stem-exclusion phase of development, as observed in a 73-year-old plantation of red pine in central Massachusetts (Currie and Nadelhoffer, in press). A chronosequence investigation of wave-regenerated mountain hemlock forests in Oregon found variation over 50 years of stand development in both the pool sizes and decay-class distributions of coarse woody debris (Boone et al., 1988).

Inputs of woody detritus result from a mix of natural disturbances, both large and infrequent disturbance events together with small and more frequent events. The hemlock-hardwood forests of the Great Lakes region, for example, can experience catastrophic windstorms and fire that result in large inputs that signal the end of the lifetime of a forest stand, while tree falls from smaller windstorms result in small inputs (Canham and Loucks, 1984; Mladenoff, 1990; Tyrrell and Crow, 1994; Duvall and Grigal, 1999). Another form of natural disturbance that can be large or small is insect-induced mortality; spruce-budworm outbreaks in the northeastern United States, for example, cause heavy mortality that is species-specific (Hely et al., 2000). A recent study estimated that volume of downed woody debris in the northern hardwood forests increased by 22% due to mortality from beech bark disease (McGee, 2000). A comparison of background and disturbance-related mortality in two old-growth systems revealed that the two sources of mortality produced approximately equal inputs of coarse woody debris for forests of an equivalent size (Harmon and Hua, 1991).

Losses from Woody Detrital Pools

Decay rates of woody debris are highly heterogeneous, due not only to differences in climate and litter quality but also to sizes of individual logs and their positions on or in the soil. Smaller diameter pieces of Douglas-fir and red alder generally decomposed faster than larger diameter pieces (Edmonds et al., 1986; Stone et al., 1998), whereas small-diameter residues decomposed more slowly than larger ones in Douglas-fir and hemlock ecosystems (Erickson et al., 1985) and in loblolly pine slash in South Carolina (Barber and Van Lear, 1984). The different relationships between size classes and decay rates among different species and climates may arise from several factors. Moisture is an important but complex factor because moisture in decaying logs depends on climate, log size, and the presence or absence of bark (Harmon et al., 1986). The physical breakdown and morphological changes in decaying logs vary due to white-rot vs. brown-rot fungi, insect activity, fragmentation patterns, and patterns of bark sloughing.

Wood generally decays more slowly than fine litter. Some representative values of the first-order decay rate k range from 0.0165 year^{-1} for 40- to 80-cm-diameter Douglas-fir wood on southern Vancouver Island (Stone et al., 1998), to 0.04 year^{-1} for old-growth maple and hickory wood in Indiana (MacMillan, 1988), 0.067 year^{-1} for loblolly pine wood in the South Carolina Piedmont (Barber and Van Lear, 1984), and 0.096 year^{-1} for northern hardwood boles at the Hubbard Brook

Table 9.2 Amounts of Woody Debris in Different Forest Ecosystems, with Associated Age and Stand Characteristics

Location	Age (years)	Stand Characteristics	Deadwood Mass (Mg/ha)	Source
South Carolina Piedmont	41-year-old plantation	predicted quantities of logging slash	61	Barber and Lear, 1984
Tennessee	—	*Fagus-Betula* forest	29	Harmon et al., 1986; Harmon and Hua, 1991
New Hampshire	—	*Fagus-Betula* forest	30–49	Gore and Patterson, 1986; Tritton, 1980 (as cited in Harmon and Hua, 1991)
Massachusetts	73-year-old plantation	*Pinus resinosa*	40	Currie and Nadelhoffer, in press
	61-year-old natural stand	*Quercus* spp.	27	
Indiana	old growth	*Quercus* spp.	15	MacMillan, 1988
		Carya spp.	2.3	
		Fagus grandifolia	0.2	
		Acer spp.	0.4	
Great Lakes	90 year	managed	6.6	Duvall and Grigal, 1999
		unmanaged	10	
Alberta	—	—	18–112	Hely et al., 2000
Western Oregon	old growth	—	215 ± 103	Sollins et al., 1980
Olympic National Park, Washington	—	—	537	Agee and Huff, 1987 (as cited in Harmon and Hua, 1991)
Sequoia National Park, California	mixed forest	chronosequence	28–383	Harmon et al., 1987

Location	Age (years)	Stand Characteristics	Deadwood Volume (m³/ha)	Source
Northern Michigan, Wisconsin	>350 years	mixed stand	>65	Tyrrell and Crow, 1994
Alberta	—	—	109–124	Lee et al., 1997; Hely et al., 2000
Pacific Northwest	—	clear-cut	280	Howard, 1981; Erickson et al., 1985
		preharvest	200	
Southern Vancouver Island, B.C.	—	65-year-old record	31–105	Stone et al., 1998
Sequoia National Park, California	mixed conifer forest	chronosequence	83–1105	Harmon et al., 1987
Lowland tropics	—	site topographically varied	96–154	Gale, 2000

Experimental Forest in New Hampshire (Arthur et al., 1993). In the case of loblolly pine in South Carolina, a k value of 0.067 year^{-1} yields a mass loss of 50% in about 10 years and 99% in 64 years (Barber and Van Lear, 1984). Species differences in decay rates are pronounced. Over a 14-year period, lodgepole pine log segments, for example, lost 2.1% of dry mass per year, while white spruce and subalpine fir lost on average 4.35% of dry mass per year (Laiho and Prescott, 1999). Red alder wood also decomposed faster than Douglas-fir wood in western Washington (Edmonds et al., 1986). Maple wood in an Indiana old-growth forest decomposed faster than hickory species, while oak and beech decomposed at the slowest rates (MacMillan, 1988). In contrast, beech decayed the fastest at Hubbard Brook, followed by maple, birch, and then ash (Arthur et al., 1993).

Decay rates of woody debris are measured most often as mass losses over time. For accurate C accounting, however, mass loss due to CO_2 mineralization must be distinguished from losses due to fragmentation or DOC leaching. Fragmentation and DOC leaching from wood do not result directly in CO_2 mineralization and have rarely been quantified. Where these have been studied in the United States, results suggest that about 25 to 50% of mass may be lost to fragmentation and 10% to DOC leaching (Mattson et al., 1987; Harmon and Hua, 1991). Fragmentation, together with advanced decay, eventually produces material that becomes mixed with other forest-floor material and thus subject to bioturbation or mixing into mineral soil pools through other means. DOC leaching, likewise, has the potential to add significant quantities of C to mineral SOM pools, as discussed above.

Removal of woody debris in managed forests constitutes another loss from woody detrital pools. Harvesting residues are removed to facilitate tree planting, reduce fire hazard, and to increase woody-fiber utilization. Recent trends in forest management in the Pacific Northwest, such as reduction in residue burning, management of riparian buffer zones for coarse woody debris inputs to streams (western Washington), and provision of woody debris for wildlife have the potential to increase stocks of woody debris in managed forests if these practices gain widespread use. However, the opposite management activities of harvesting younger stands and increasing the utilization of woody materials would most likely have the opposite effect.

DISTURBANCE, MANAGEMENT, AND SCALING UP TO LANDSCAPES

To scale biogeochemical pools and fluxes from intensive-study sites up to landscapes and regions, factors causing landscape heterogeneity must be adequately captured (Alperin et al., 1995). In many forested landscapes of the United States, forest management activities are a major cause of landscape heterogeneity in forest floor C storage. Intensive management affects forest floor pools and processes directly through site preparation and indirectly through selection of tree species, thinning, and repeated harvest. Harvest of unmanaged forests has direct effects through the disturbance associated with logging and indirect effects by altering species composition and population demographics, whether by partial cutting or by clear-cutting. In selecting management practices, managing forests for C storage must be weighed against other goals, for example managing forests to retain N deposition and mitigate N export to surface waters, and providing a continuing supply of forest products.

Disturbance and Subsequent Dynamics in Forest-Floor C Pools

Disturbances can affect both inputs and losses of C from forest floor pools. Modern harvesting operations that make use of heavy machinery can severely disturb the forest floor, creating mineral soil mounds and ruts, and mix forest-floor material with underlying mineral soil horizons. In the years following harvest, there is an immediate but temporary reduction in inputs of leaf litter and root litter. Both soil mixing and reduced litter production act to reduce the amount of carbon in the forest floor after harvest. Logging residues, however (stems, branches, foliage, roots, and stumps

left on the site), provide litter inputs to the forest floor. The combined effect can increase or decrease carbon storage in the forest floor during and immediately following forest harvest. Decomposition rates may increase or decrease after forest harvest, further increasing variation in the response of forest-floor carbon to forest management.

Mixing of the forest floor with mineral soil results in a loss of carbon from the forest floor but not necessarily from the soil to the atmosphere. In a commercial whole-tree harvest at the Hubbard Brook Experimental Forest in New Hampshire, logging operations disturbed 65% of the soil surface of the area, removing forest floors from 25% of the area and burying forest floors under mineral soil in 57% of the mineral-soil mounds produced at the surface (Ryan et al., 1992). The severity of soil disturbance depends in part on the intensity of harvest, increasing with the amount of skidding required. The nature of soil disturbance has also changed with changes in logging technology over time, with horse logging probably causing less disturbance than tractor logging or skidding. These changes in technology and the intensity of harvest make it difficult to compare recently cut stands with older stands (Yanai et al., in press), but such "chronosequence" comparisons are among the few methods available for estimating the long-term effects of logging on soil carbon storage.

Of the changes in inputs to the forest floor following forest harvest, aboveground litter production is the easiest to measure. Leaf litter is reduced in northern hardwoods for less than a decade; canopy closure occurs quickly and leaf production along with it (Covington and Aber, 1980). In an unfertilized loblolly pine plantation in the southeastern United States, canopy closure occurred within 8 years post-harvest, and a steady state was reached in foliar litter production within 15 years or earlier (Piatek and Allen, 2000). Inputs of carbon from roots are difficult to assess, but the values of production following harvest are likely to be similar to those of foliar production (Fahey and Hughes, 1994).

The production of forest-floor organic matter from slash is more difficult to assess than from leaf litter because of uncertainty in the amount of time it takes for slash to enter the forest floor and uncertainty in the residence time in the forest floor before it is respired, leached, or mixed into mineral soil. Clearly, silvicultural systems that remove more biomass, such as whole-tree harvest, leave less slash and will provide less carbon to the forest floor than those that are less intensive. Limbing trees before they are removed from the stand will provide more carbon return to soil than will slash piles concentrated at the landing. The burning of residues obviously reduces the carbon return to the forest floor and can directly consume upper layers of the forest floor (Little and Ohmann, 1988; Vose and Swank, 1993). As noted in previous sections, inputs of coarse woody debris, whether from logging slash or from tree mortality as stand development proceeds, drive the storage of C in downed woody debris (e.g., Laiho and Prescott, 1999; Tinker and Knight, 2000; Currie and Nadelhoffer, in press).

Changes in decomposition rates might be expected to follow forest harvest, because of changes in moisture and temperature regimes or changes in substrate quality during the transition. Studies using litterbags have found decomposition rates to be reduced in clear-cuts. In a southern Appalachian hardwood forest 8 years after clear-cutting, decomposition rates of leaves of three hardwood species were slower in a clear-cut than in an adjacent uncut site (Blair and Crossley, 1988). In a coastal montane coniferous forest on Vancouver Island, mass loss of needle litter was slower in harvested plots than in old-growth forest (Prescott et al., 2000). In these cases, investigators have attributed slower rates of litter decay to drier surface conditions. It remains possible that decomposition rates could increase lower in the soil profile, for example in the humus layer, but this possibility has not yet been studied in the field. Most rates of wood decay available in the literature derive from studies conducted under forest canopies. Wood decomposition may be altered after harvest, due to alteration of temperature and moisture regimes or to changes in log placement, such as burial or elevation (Edmonds et al., 1986).

Covington (1981) studied a chronosequence of forest floors in stands with a range of time periods since harvest in northern hardwood forests in New Hampshire. The chronosequence showed

an apparent decline in forest-floor mass, from a presumed landscape-averaged steady-state value, in the first 20 years. This finding was interpreted as evidence that 50% of forest floor organic matter was lost to decomposition within 20 years after clear-cutting (Covington, 1981). A similar chronosequence (Federer, 1984) was resampled after an interval of 15 years (Yanai et al., 1999); the predicted decline in young stands was not observed (Yanai et al., 2000). Some of the purported loss of organic matter in the Covington (1981) study is probably explained by mixing with mineral soil at the time of harvest, which does not result in an equivalent loss of carbon to the atmosphere (Yanai et al., in press).

Scaling to Landscapes

Measurements of forest floor and woody litter mass, nutrient, and C pools are typically made at single intensive-study sites or sometimes in multiple sites scattered across a landscape (for example chronosequence studies). These have been scaled up to landscapes, regions, and continents through extrapolation with simulation models (e.g., Currie and Aber, 1997) or by compiling measurements from multiple sites (e.g., Vogt et al., 1986; Harmon et al., 1986).

Matthews (1997) reviewed the methods used to scale up detrital pools and synthesized these and other data compilations for a combined set of measurements for over 1000 sites, located largely in the Northern Hemisphere. These data suggested that the global stock of C in fine litter amounts to 68 Pg C; previous measured and modeled estimates ranged from 50 to 200 Pg C (Matthews, 1997). By approximating coarse woody debris (CWD) pools from live biomass pools (Harmon and Hua, 1991), Matthews (1997) estimated the global C pool in CWD to be 75 Pg C. However, as both the modeled and data-based compilations are largely based on ecological study sites in relatively undisturbed ecosystems (i.e., often avoiding harvested or burned sites), they may overestimate the C stocks in heterogeneous landscapes made up of mosaics of disturbance and recovery. In order to consider the broader range of disturbance conditions, Birdsey and Heath (1995) and Heath and Smith (2000) developed a simple bookkeeping approach to estimate C stocks across the United States. They combined three resources: the Vogt et al. (1986) compilation of forest-floor mass in relatively undisturbed ecosystems (which excludes coarse woody debris), a series of prescribed curves of expected changes in forest floor mass over time after harvest or agricultural abandonment, and forest inventory information on the age-class structure of forests. This approach allows for the effects of past land uses on current carbon stocks, but it depends strongly on the accuracy of the prescribed response curves.

For woody debris, scaling pool sizes across the landscape is problematic. At a particular site, a steady state in woody litter pools is likely never achieved (Spies et al., 1988). This makes it necessary to sample a large number of sites to characterize a landscape and, at best, consider the landscape mosaic to comprise a larger-scale steady state. Pools of woody debris exhibit complex relationships with management and disturbance histories. This information is possible to gather at some intensively studied sites with historical records, such as the Harvard Forest in Massachusetts (Currie and Nadelhoffer, in press). However, detailed information concerning land use and disturbance history is difficult to collect in a quantitative and spatially explicit way across landscapes, making it problematic to scale up the results of studies conducted at particular sites. It can be collected, with great effort, in a stratified manner across a range of management activities in a given forest type, for example in a study of red pine plantations in the Great Lakes region (Duvall and Grigal, 1999).

GLOBAL CHANGE AND ECOSYSTEM-LEVEL FEEDBACKS

The C balances of forest ecosystems in the United States and elsewhere are likely to be altered by the results of human activities, including elevated CO_2, elevated N deposition, land-use change,
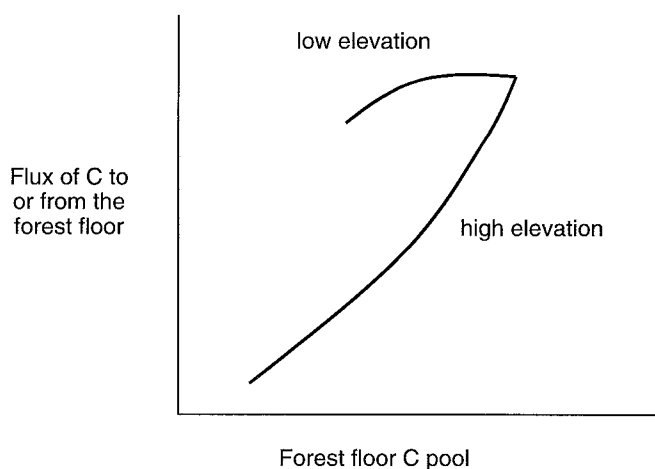
Figure 9.3   Schematic diagram depicting complexity in the relationships between forest floor C pool vs. fluxes of C into or out of the forest floor. Fluxes of C include litter inputs, CO_2 mineralization, and DOC leaching. The existence of two potential values of an input or output flux given one pool size arises from differing residence times for C in forest floors at different elevations. (After Currie, W.S. and Aber, J.D., *Ecology,* 78: 1844, 1997.)

species shifts and invasive species, and potential changes in climate (Vitousek, 1994). Although the forest floor arises through the accumulation of detritus, it exists as a functional component of forest ecosystems, strongly linked to production through complex feedbacks. The forest floor plays key ecological roles related to water infiltration, water-holding capacity, pH buffering, rooting medium, nutrient storage, and nutrient release for uptake by vegetation. Interactions and feedbacks among changes in forest composition, environmental conditions, and forest floor processes are complex. An illustration of these complex relationships is the hysteresis between forest floor C storage and C fluxes to or from the forest floor as expressed by a biogeochemical model (Figure 9.3). In these model results, which are consistent with field studies, two distinct relationships exist between C fluxes and pool sizes even within one forest type, corresponding to different residence times for C at lower and higher elevations in a montane landscape (Currie and Aber, 1997).

   Interactions among aspects of global environmental change will almost certainly impact forest-floor C storage and fluxes of DOC to mineral soils through effects on species interactions, quantities and qualities of litter inputs, and rates or end points of decomposition. Elements of global and regional change such as CO_2 fertilization, N deposition, and warming have all been hypothesized to increase litter quantity to varying degrees through increased plant production (e.g., Melillo et al., 1996; Houghton et al., 1998). Altered precipitation regimes could be expected to increase production in some locations as well. Increased litter production is expected to cause some short-term increases in C sequestration, particularly in surface detrital pool with rapid turnover times. However, heterotrophic respiration should increase rapidly in response and lead to minimal new C sequestration, except perhaps in boreal regions where decomposition is limited by cold temperatures (Schlesinger and Andrews, 2000). At the Duke Forest, North Carolina, doubling atmospheric CO_2 concentrations for three years did increase plant litter production, and forest-floor C sequestration increased in response by ca. 0.6 Mg C ha^{-1} $year^{-1}$ (Schlesinger and Lichter, 2001). However, the rapid turnover of this material indicates that this increased rate of C sequestration should persist for only a few years (Schlesinger and Lichter, 2001).

   Elevated N deposition is an aspect of global and regional change in the United States that might be expected to alter forest C balances at large scales, through increased C fixation or sequestration (Townsend et al., 1996; Schindler and Bayley, 1993). Whether N deposition is likely to have significant impacts on forest growth depends largely on the partitioning of N inputs between increased immobilization in soils vs. increased availability to plants (Nadelhoffer et al., 1999).

This partitioning, in turn, depends to a great extent on C and N interactions in forest soils, particularly in the forest floor, where nutrient cycling and immobilization are most active (Currie et al., 1999). Microbes consuming forest-floor material that is carbon-rich, including coarse woody debris, have the potential to compete with trees for N and other nutrients, thus potentially reducing production of live biomass in forests through an ecosystem-level feedback. For example, immobilization of limiting nutrients in woody residue in southwestern Alberta (Laiho and Prescott, 1999) and in forest floors in southeastern pine plantations (Piatek and Allen, 2001) may leave fewer nutrients available for trees to support growth of biomass. Such N immobilization is likely to differ among forest types or soils. In pine and oak forests in central Massachusetts, a long-term ^{15}N tracer study indicated that immobilization of N in fine woody debris on the forest floor was minor, and patterns of ^{15}N among forest types and treatments were instead related to plant N uptake (Currie et al., 2002).

The carbon balance of a forest depends not only on production but also on rates of decay and stabilization of detritus. Nitrogen availability has been traditionally considered to stimulate litter decay rates, but recent literature demonstrates a wide range of effects, including inhibition of decay or changes in the end point of decomposition. Some studies have observed either no effect or enhanced litter decomposition (e.g., Prescott et al., 1992; Hobbie, 2000) in response to N fertilization. Some evidence suggests that additional N may stimulate decomposition of low-lignin litters but may suppress decomposition of high-lignin litters (Carreiro et al., 2000). Enhanced N availability has been shown to reduce the decomposability of some litter types, perhaps due to reactions between litter N and lignin that tend to stabilize organic matter (Soderstrom et al., 1983; Berg et al., 1987; Nohrstedt et al., 1989; Wright and Tietema, 1995; Magill and Aber, 1998; Berg, 2000). Decreased decomposition of plant litter could ultimately lead to an increase in forest floor C stocks.

Foliage exposed to elevated atmospheric CO_2 often has a higher C:N ratio, thus resulting in litter of potentially poorer quality than that grown under ambient conditions (reviewed in Field et al., 1992; Mooney et al., 1999). This theoretically might lead to slowed decomposition; however, experimental efforts have demonstrated that CO_2 fertilization has almost no effect on litter C:N and litter decay (reviewed in Mooney et al., 1999). Changes in litter quality under elevated CO_2 or N availability within a litter type have generally resulted in much smaller effects on decay rates than effects due to differences among litter types. This suggests that some aspects of global change will result in large changes in decay rates of fine litter only when they are associated with a change in the species composition (Prescott, 1995; Hobbie, 1996).

Many forest floors of the United States have large accumulations of humus that decay at a slow rate; small changes to the rate of decay could yield large effects on the forest-floor C balance. There have been several indications that high availability of N may reduce rates of humus decomposition (Soderstrom et al., 1983; Magill and Aber, 1998; Berg et al., 1987; Nohrstedt et al., 1989). Berg et al. (1996) attributed the inhibitory effect of ammonium to lignolytic enzyme production by white-rot fungi, which are the only fungi that can degrade lignin completely (Keyser et al., 1978; Reid, 1983; Carreiro et al., 2000). Evidence to date suggests that N deposition or fertilization of ecosystems that have high-lignin litter will lead to greater accumulations of humus or soil organic matter and greater sequestration of C.

If soils are warmer under altered climate, litter is likely to decompose more quickly, although indirect effects of soil warming on soil moisture may confound this response, and the effects of soil warming are likely to vary with litter quality (Rustad et al., 2000). Experimental soil warming of 5°C over ambient increased decomposition of red maple litter at the Howland Forest, Maine, although warming effects disappeared after 30 months (Rustad and Fernandez, 1998) and had little effect on red maple litter at Huntington Forest, New York (McHale et al., 1998). Red spruce litter at Howland Forest showed little effect after 18 months of warming but had 19% less C than ambient plots at 30 months (Rustad and Fernandez, 1998). Similarly, American beech litter at Huntington Forest had 16 to 19% less C than ambient plots during the first and second years of litter decay (McHale et al., 1998). Data from the experiment at Howland Forest suggest that DOC production

in the forest floor and sorption in the mineral soil both increase in response to increased temperature (Rustad et al., 2000).

A direct short-term or decadal-scale effect of soil warming is likely to be decreases in forest-floor C stocks as a result of increased decomposition of relatively labile material (Shaver et al., 2000). However, this also increases N mineralization (Melillo et al., 1995; Rustad et al., 2000), which in turn can increase plant growth and litter production. The net effect of these processes may be a short-term decline in forest-floor carbon stocks followed by longer-term increases in response to increased litter inputs (Shaver et al., 2000). Ultimately, the net impact of warming on soil respiration is expected to be greater than stimulation of photosynthesis (Schlesinger and Andrews, 2000), but these predictions remain uncertain.

SUMMARY AND CONCLUSION

Surface organic horizons in forest soils (forest floors) are important as reservoirs of stored C, as intermediate pools that transfer fluxes of C to mineral soils through leaching of DOC and mixing, and as responsive ecosystem components that are likely to exhibit feedbacks from forest change. Globally, forests floors store only approximately 3 to 6% of the overall C pool in the top 3 m of soil. However, C pools in forest floors are more dynamic than C pools in mineral soils. The residence time of C is shorter in forest floors than in mineral soils, with the potential to rise or decline quickly in response to disturbance or to changes in management practices, tree species composition, or environmental conditions such as moisture and temperature. Pool sizes and dynamics of soil C in the forest floor result from the combined processes of litter production, losses to CO_2 mineralization, and losses through DOC transport to mineral soils. Rates of each of these processes are strongly controlled by moisture and temperature.

In many respects our knowledge of processes controlling C storage in forest floors is inadequately characterized or constrained by field data. In particular, we lack adequate knowledge of the rates of stabilization of fine litter and woody detritus and of what controls the turnover rates of the humified matter thus produced. Models that are used to assess sizes of, and changes in, stocks of forest-floor C use highly simplified representations of controls on decomposition, humification, and DOC transfer.

Rates and amounts of C storage in the O horizons of U.S. forests are highly variable among forest types and regions. This is exacerbated by strong spatial differences in histories of disturbance, land use, and management practice. Forest management practices affect both C stocks in forest floors and in downed woody debris. In litter and humus, steady states in C pool sizes can be achieved within several decades (longer, in colder climates) following logging, or other major disturbances, or following reversion to forest after agricultural abandonment. For downed woody debris, where inputs are much more variable in time and material takes much longer to decay, pool sizes essentially never reach steady state. Carbon stocks always retain the signature of past events that caused large inputs (or caused reductions in inputs) of logs, even over centuries.

Some potential for increases in C storage in forest floors could come through changes in land use or management goals to those that would promote C storage. For example, in areas that have reverted to forest after agricultural abandonment in the last century, or in forests that are currently logged for forest products, if woody detritus were allowed to fall and accumulate in the form of large logs, large increases in C storage could result. In many cases this goal would conflict with the goal of producing forest products, but it would not conflict with goals of managing for wildlife protection, stream protection, or recreational use. Similarly, significant storage of C might be achieved in areas where wet, bottomland forests existed previously but were cleared and drained for agriculture. Bottomland forests are among the most highly productive forests, and their wet soil conditions also inhibit decomposition. Although this conflicts with agricultural use of the land,

in terms of the goal of C storage, potential for the most rapid increases in forest floors probably occurs in areas that previously supported wet, bottomland forests.

Though the potential of forest floors to increase C storage are directly related to changes in litter inputs, they are mediated by complex interactions with other aspects of environmental change. The forest floor is not only a C storage pool but also a central, functional component of forest ecosystems. Forest floors release nutrients for biomass production and release DOC for transport downward in soil solution, contributing to C storage in mineral soils. We should expect differences in these and other processes among regions, forest types, and soils. Thus the long-term, interactive effects of multiple components of global change and land management on the dynamic linkages between the forest floor, living vegetation, and soil organic matter can be expected to be complex, variable among forest types, and potentially surprising.

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