Biogeochemistry **45:** 115–145, 1999.

Forest soil carbon inventories and dynamics along an elevation gradient in the southern Appalachian Mountains[1,2]

C.T. GARTEN Jr., W.M. POST, III, P.J. HANSON & L.W. COOPER
Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, TN 37831-6038, USA

Accepted 17 July 1998

Key words: climate, C/N ratios, light-fraction organic matter, particulate organic matter, soil C turnover

Abstract. Soil organic carbon (SOC) was partitioned between unprotected and protected pools in six forests along an elevation gradient in the southern Appalachian Mountains using two physical methods: flotation in aqueous $CaCl_2$ (1.4 g/mL) and wet sieving through a 0.053 mm sieve. Both methods produced results that were qualitatively and quantitatively similar. Along the elevation gradient, 28 to 53% of the SOC was associated with an unprotected pool that included forest floor O-layers and other labile soil organic matter (SOM) in various stages of decomposition. Most (71 to 83%) of the C in the mineral soil at the six forest sites was identified as protected because of its association with a heavy soil fraction (> 1.4 g/mL) or a silt-clay soil fraction. Total inventories of SOC in the forests (to a depth of 30 cm) ranged from 384 to 1244 mg C/cm^2.The turnover time of the unprotected SOC was negatively correlated ($r = -0.95$, $p < 0.05$) with mean annual air temperature (MAT) across the elevation gradient. Measured SOC inventories, annual C returns to the forest floor, and estimates of C turnover associated with the protected soil pool were used to parameterize a simple model of SOC dynamics. Steady-state predictions with the model indicated that, with no change in C inputs, the low- (235–335 m), mid- (940–1000 m), and high- (1650–1670 m) elevation forests under study might surrender ≈ 40 to 45% of their current SOC inventory following a 4 °C increase in MAT. Substantial losses of unprotected SOM as a result of a warmer climate could have long-term impacts on hydrology, soil quality, and plant nutrition in forest ecosystems throughout the southern Appalachian Mountains.

Introduction

Soil organic matter (SOM) has a potentially important role in the Earth's carbon (C) cycle because it is the largest terrestrial C pool. It is estimated that, globally, SOM (including surface detritus) contains ≈ 1580 Gt of C as compared to ≈ 610 Gt C in terrestrial vegetation and ≈ 750 Gt C in the atmosphere (Schimel 1995). Approximately 40% of the global soil C inven-

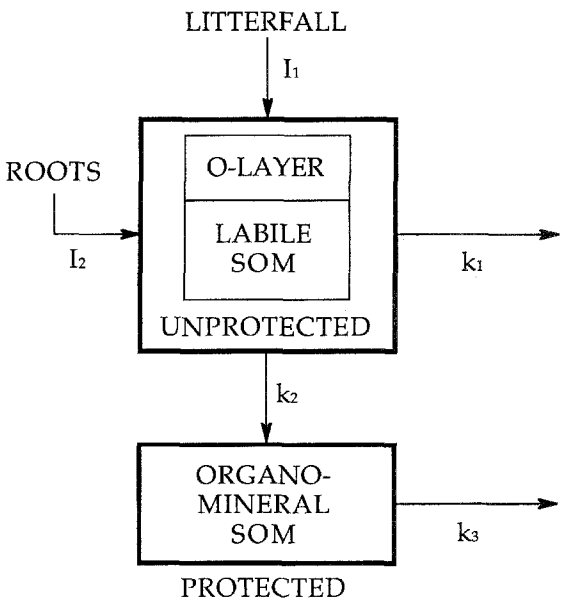

Figure 1. A simple model of soil organic carbon (SOC) dynamics in forest ecosystems. Annual aboveground and belowground C inputs to the unprotected soil C pool are represented by parameters I_1 and I_2, respectively. The unprotected pool is comprised of forest floor O-layers and labile organic matter in the mineral soil (SOM). Rate constants k_1 and k_3, respectively, represent annual decomposition losses from unprotected and protected soil C pools. Parameter k_2 is the annual fractional transfer of unprotected SOC to the protected soil pool.

tory resides in forest ecosystems (Hudson et al. 1994). A relatively small change in forest soil C inventories could have important implications for the global C budget. It is important that we understand how the dynamics of forest soil organic carbon (SOC) may influence both atmospheric CO_2 concentrations and soil quality following large-scale changes in climate or land use.

Several approaches have been used to investigate factors affecting the dynamics of SOC, including soil chronosequence studies (Schlesinger 1990; Torn et al. 1997), long-term experimental manipulations at field sites (Jenkinson & Rayner 1977; Balesdent et al. 1988; Balesdent 1996), and use of bomb carbon-14 as a tracer for calculating SOC turnover (Harrison et al. 1993; Trumbore et al. 1996; Harrison 1997). The former studies have been a valuable resource to parameterize and test predictions from theoretical models of SOC dynamics (e.g., Parton et al. 1988; Jenkinson 1990; Harrison 1997). These models typically simulate SOC dynamics by assuming C transfers between a small number of discrete conceptual pools.

In this work, we have defined two principal pools of forest SOM (Figure 1). The first pool consists of the forest floor O-layers as well as labile SOM within the mineral soil. The second pool is organomineral SOM. Forest floor O-layers and labile SOM consist mainly of organic matter in various stages of decomposition, thus these pools have been aggregated and are collectively referred to as "unprotected". Within the mineral soil, SOC that is associated with primary soil particles through organomineral complexes is referred to as "protected". Physical protection resulting from interactions between SOM and primary soil particles (silt and clay) plays an important role in determining the accumulation of SOC and its turnover time (Oades 1988; Balesdent et al. 1988; Balesdent 1996). In some models, 25 to 50% of the SOC is assumed to be associated with a physically or chemically stabilized fraction of SOM (Jenkinson & Rayner 1977; Parton et al. 1987; Van Dam et al. 1997). However, it is unprotected SOC that has the greatest potential to respond to changes in land use or climate and to thereby influence the global C cycle over a time scale of decades to centuries (Harrison et al. 1993; Harrison 1997).

Temperature is an important factor controlling both the amount and turnover time of unprotected SOC. From an analysis of bomb carbon-14 data in archived and contemporary soil samples, Trumbore et al. (1996) reported relatively long turnover times (7 to 65 years) for fast-cycling, low-density SOM in the upper 20 cm of soil along an elevation gradient in the California Sierra Nevada. Turnover times for SOM in forests and pastures also vary as a function of temperature along altitudinal gradients on the island of Hawaii (Townsend et al. 1995). From these, and other studies (Kirschbaum 1995), it can be concluded that temperature is a primary controller of SOC dynamics at regional and global scales.

Regional differences in forest SOC inventories and turnover rates exist because of natural variability in climate, soil types, rates of aboveground and belowground C inputs, different rates of transfer between various SOC pools, and differing rates of SOM decomposition. Temperate and boreal forests are distinguished from grasslands, deserts, and agro-ecosystems by having relatively large inventories of unprotected SOC in the form of forest floor organic matter. Estimates of decomposition rate constants for forest floor organic matter vary widely depending upon forest type, location, and climate. For example, the turnover time of forest floor C in the California Sierra Nevada is four times longer than that in forests from the eastern United States (Olson 1963). Such differences might also readily extend to pools of labile mineral soil C and give rise to large geographic differences in the turnover time of SOC within the temperate forest biome.

The extent of C storage in forest soils is important for understanding the interrelationships between increasing atmospheric CO_2 concentrations, the global C cycle, and climate change. In the present study, different pools of forest SOC have been quantified along an elevation gradient in the southern Appalachian Mountains in eastern Tennessee. Our objectives were to better understand the distribution of SOC between different soil pools and to determine how inventories and turnover times of forest SOC vary as a function of mean annual temperature. In addition, empirical measurements related to climate, litterfall C returns, and C inventories in different soil pools, along with a limited set of assumptions, have been used to parameterize a two compartment model of SOC dynamics at six forest sites. Climate change assessments forecast that mean annual global temperature will increase by 1 to 3.5 °C over the next 200 years (IPCC 1998), but predictions for the southeastern United States suggest that regional warming might be much higher. For east Tennessee, predictions suggest that average annual temperature will increase by 4 to 5 °C (Cooter 1998). Our model was used to predict changes in forest SOC inventories following a 4 °C increase in mean annual temperature.

Site descriptions

Low-elevation sites

The low elevation forests were located on the Oak Ridge Reservation near Oak Ridge National Laboratory (35°54′N, 84°20′W). Both low-elevation forests were aggrading and had not been disturbed for more than 50 years.

Site 1LP was located at an elevation of 235 m and was used during the Integrated Forest Study (Johnson & Lindberg 1992). It had a loblolly pine (*Pinus taeda*) overstory with some mixed deciduous understory comprised mostly of yellow-poplar (*Liriodendron tulipifera*) and red maple (*Acer-rubrum*). The basal area was 37.0 m^2/ha. The alluvial silt-loam soil was classified as a fluventic dystrochrept and the soil depth was ≈ 80 cm (Johnson & Lindberg 1992).

Site 2WB was located at an elevation of 335 m on Walker Branch Watershed. The overstory was mainly red maple and yellow-poplar with some loblolly pine and sourwood (*Oxydendrum arboreum*). The basal area was 19.8 m^2/ha. The silt-loam soil was classified as a typic paleudult and the soil depth was ≈ 190 cm (Lietzke 1994).

Mid-elevation sites

The mid-elevation forests were located off the Roaring Fork Motor Trail in the Great Smoky Mountains National Park (35°41′N, 83°28′W). The presence of numerous large trees indicated that the mid-elevation forests were mature. It was estimated that both sites had not been disturbed for more than 60 years.

Site 3SB was located at an elevation of 940 m on a gentle slope. The overstory was mainly Carolina silverbell (*Halesia carolina*) and eastern hemlock (*Tsuga canadensis*). The basal area was 56.3 m^2/ha. The sandy silt-loam soil appeared to be derived from an ancient alluvium. There was a mull-type humus layer.

Site 4MH was located at an elevation of 1000 m on the top of a ridge. The mixed deciduous hardwood overstory was mostly oak (*Quercus* spp.) and maple (*Acer* spp.) with some birch (*Betula* spp.) and sourwood. The basal area was 44.9 m^2/ha. Eastern hemlock was prevalent in the understory and may have once been a more dominant species at this site. The silt-loam soil was covered by a fibrous, mor-type humus layer.

High-elevation sites

The high elevation forests were located along the Appalachian Trail between Mount Collins and Newfound Gap (35°36′N, 83°28′W) in the Great Smoky Mountains National Park. The high-elevation forests were undergoing canopy decline due to Fraser fir (*Abies fraseri*) mortality caused by an insect infestation (balsam woolly adelgid). Based on previous studies (Nicholas et al. 1992), it was estimated that the high elevation forests had not been disturbed for more than 100 years. The soils were tentatively classified as umbric dystrochrepts based on classifications at similar nearby sites (Johnson et al. 1991; Johnson & Lindberg 1992). Soil depth was estimated at $\approx$ 60 to 65 cm; also based on previous studies (Johnson & Lindberg 1992).

Site 5BB was located at an elevation of 1650 m at the top of a steep slope. The overstory was dominated by red spruce (*Picea rubens*) and beech (*Fagus grandifolia*) and included standing dead Fraser fir. The understory was mostly maple (*Acer pensylvanicum* or *A. spicatum*) and birch. The basal area was 42.2 m^2/ha. The poorly drained, loam soil contained numerous rock fragments. There was a mull-type humus layer. There were indications that, following heavy storms, this site was subject to overland flow which could wash away freshly fallen leaf litter.

Site 6SP was located at an elevation of 1670 m on a gentle slope. The overstory was principally comprised of very old, mature red spruce among standing dead Fraser fir. The understory was mainly birch, mountain ash (*Sorbus americana*), and maple (*A. pensylvanicum or A. spicatum*). The basal

area was 40.1 m^2/ha. The soil was a sandy loam, derived from sandstone parent material, with a mor-type humus layer.

Methods

Climate measurements

Air temperature ($\approx$ 2 m above the ground) and soil temperatures ($\approx$ 10 cm deep) were measured at each site at 2 hour intervals over a two year period and recorded on a Li-Cor LI-1000 data logger (Li-Cor, Inc., Lincoln, NE). Data from each site were averaged over time to calculate mean monthly air temperatures. Soil temperatures (from two sensors at each site) were averaged over space and time to calculate the mean monthly soil temperatures. Mean monthly temperatures were estimated from sites at the same elevation or from data in a prior year whenever monthly means could not be calculated due to data logger malfunction or, more commonly, disturbance of the equipment by wildlife. Throughfall was measured from September 1995 to September 1996 using open funnels that drained into plastic bottles (2 per site). Sample volumes were recorded on each visit to a site and the volumes were converted to cm of throughfall. Cumulative throughfall was used as an indicator of the annual amount of wet deposition reaching the forest floor.

Soil properties

The pH of the O-layer and the mineral soil (0–20 cm) from each site were measured in 0.01 M $CaCl_2$ using a dry solid:solution (w/w) ratio of 1:20 and 1:6, respectively. Mixtures were vigorously stirred for 5 minutes, or until the sample was completely wetted, and allowed to settle overnight prior to the pH measurement. Soil texture was determined from two soil samples (0–20 cm depth) collected at each site. Air dried soil (40 grams) was dispersed by shaking overnight in a solution of sodium hexametaphosphate (35.7 g/L) and wet sieved through a 2 mm, 0.425 mm, and a 0.053 mm sieve. Sand content was equivalent to the air dry fraction $>$ 0.053 mm. Percentage silt and clay were determined by the hydrometer method (Gee & Bauder 1986) on soil that passed the 0.053 mm sieve. Sand, silt and clay content was corrected for gravel and rocks (coarse fraction $>$ 2 mm).

Soil C inventories

Concentrations and inventories of SOC were determined from 18 composite soil samples collected at each site over a period of 20 months. Soil samples

were collected from each site on 3 occasions in 1995 (October, November, December), 5 occasions in 1996 (February, May, July, September, November), and 1 occasion in 1997 (May). During the first four sampling occasions, two to four soil cores were collected at each site and the same depth increments from each core were composited. On the following five sampling occasions, three soil cores were collected from three (in 1996) or two (in 1997) randomly located 1-m^2 plots at each site. The same depth increments from each plot were composited.

Soils were collected with a stainless steel soil recovery probe with hammer attachment and 2.4 cm diameter butyrate plastic liners (AMS Soil Sampling Equipment). In the laboratory, each soil core was extruded from the plastic liner and divided into four depth increments. The first increment consisted of the forest floor O-horizon (O_i+O_e+O_a) which was carefully removed from the top of the mineral soil. The mineral soil core was then cut into the remaining three depth increments: 0–5, 5–20, and 20–30 cm. On a few occasions, the last depth increment was not complete and the entire increment was discarded. Forest floor O-layers and mineral soil samples from the 2.4 cm diameter cores were air dried to a constant weight at room temperature (20 °C) in a laboratory equipped with a continuously operating room dehumidifier.

High spatial variability in measures of O-layer dry mass were expected in the six forests, therefore two additional sampling methods were used to check forest floor C inventories. The second method involved sampling the forest floor by excavating the O-layers under plates with a known surface area (145 cm^2). Seven estimates of the forest floor C inventory were obtained at each site with this method (later referred to as method 2) between June 1995 and August 1997. The third method involved estimates of forest floor mass obtained by driving a 5 cm diameter PVC pipe into the soil. The O-layers were carefully removed from the top of the soil core extruded from each pipe. Eight estimates of the forest floor C inventories were obtained at each site with this method (later referred to as method 3) between May and November 1996. Forest floor samples were air dried to a constant weight at room temperature (20 °C) in a laboratory equipped with a continuously operating room dehumidifier. The dry samples were ground to a fine powder in a sample mill and analyzed for C concentrations.

The moisture content of mineral soil samples from the 2.4 cm diameter cores was determined gravimetrically. The air dried mineral soil samples were crushed inside a plastic bag using a rubber mallet and sieved through a 2 mm sieve to remove coarse debris (rocks and gravel). The coarse fraction (debris > 2 mm) was weighed. The dry mass of the sieved soil (< 2 mm) was calculated by subtracting the weight of the coarse fraction (> 2 mm) from the total soil dry mass. Percentage coarse fraction was calculated as: 100 × [(dry

mass > 2 mm) / ((dry mass < 2 mm) + (dry mass > 2 mm))]. Mineral soil samples were ground with a mortar and pestle to pass a 0.425 mm sieve and analyzed for C concentrations.

Carbon inventories (mg C/cm^2) in the forest floor O-layers were calculated from concentration (mg C/g dry mass) and dry mass (g dry mass/cm^2) data. Carbon concentrations were determined using a Carlo-Erba NA 1500 analyzer. Organic C inventories (mg C/cm^2) in the mineral soil were calculated by multiplying the SOC concentration (mg C/g soil) in the sieved (< 2 mm) soil fraction by the areal density (g soil/cm^2) of that fraction. The areal density of the sieved soil was calculated as the product of the bulk density (g soil/cm^3) for the sieved soil fraction and the increment depth (cm). The coarse fraction (> 2 mm) was excluded from all calculations of SOC concentrations and inventories. It was assumed that rocks and gravel (the principal constituents of the coarse fraction) made no appreciable contribution to amounts of SOC. Coarse roots (>2 mm) were also not included in our estimates of SOC inventories in the mineral soil.

Inventories of SOC were expressed as mg C/cm^2 because this unit is more appropriate to our soil sampling procedures; mg C/cm^2 can be converted to g/m^2 by multiplying by 10. Scaling the data to larger areas (e.g., hectares) would be unwarranted, however, because we have no estimates of soil bulk density on scales that make allowances for stumps, large roots, large rocks, and boulders present at each study site. Extrapolating the data to larger scales without such estimates could lead to serious overestimates of SOC inventories at scales larger than 1-m^2.

Litterfall C and N

Litterfall was collected whenever the sites were visited in 1995, 1996, and 1997. Litterfall samplers at each site included two plastic trays (47 cm × 38 cm) and a stainless steel screen (122 cm × 122 cm) placed in close proximity to the area where soil samples were collected. Litterfall was oven dried (65 °C) and sorted into three fractions: (1) wood and seed, (2) coniferous, and (3) deciduous. Each fraction was weighed and samples from the same site at a particular time were composited by litter type and analyzed for C and nitrogen (N) concentrations using a Carlo-Erba NA 1500 Analyzer. Litterfall C return to the forest floor (mg C/cm^2) was calculated as the product of concentration (mg C/g) and litterfall dry mass per unit area (g/cm^2). Annual C return was then calculated as the sum of C returns over the year.

Root C and N

Belowground litter inputs at each site were not measured, however coarse roots (> 2 mm) were recovered from 8 soil cores (6.5 cm diameter and 20 cm deep) collected periodically between December 1995 and October 1996 at each site. Roots were recovered by shaking a fresh soil sample overnight in a solution of Na-hexametaphosphate (35.7 g/L) and filtering the mixture through a 2 mm sieve. Roots were oven dried (65 °C), weighed, and analyzed for C and N concentrations using a Carlo-Erba NA 1500 analyzer.

Density separations

Soil organic matter was separated into a light and a heavy fraction by flotation in aqueous $CaCl_2$ (1.4 g/mL). Separations were performed on 20 increment samples from each site: 10 samples from the 0–5 cm increment and 10 samples from the 5–20 cm increment of mineral soil. Two increment cores were selected from 1995 (October and December samples), 6 increment cores from 1996 (February, May, September, November samples), and 2 increment cores from 1997 (May samples) for the density separations.

Five grams (± 0.0001 g) of oven dry (65 °C) soil that had been ground to pass a 0.425 mm sieve were shaken overnight with 25 mL of solution and allowed to settle. The light fraction organic matter (LF-OM) floating on the solution was removed with a pipet and recovered by filtration (Whatman #541). In order to maximize recovery of the LF-OM, the separation was repeated at least 3 times, or until no material floated on the solution. The pooled LF-OM from each sample was thoroughly washed with distilled water to remove excess $CaCl_2$ and was oven dried (65 °C). The heavy fraction organic matter (HF-OM) was recovered by centrifugation, washed 3 times with distilled water to remove excess calcium chloride, oven dried (65 °C), and weighed. No attempt was made to account for losses of soluble C because such losses probably would not affect the weight of the light and heavy fractions. The LF-OM mass was determined by difference between the initial soil dry mass and the HF-OM dry mass. Both LF-OM and HF-OM were analyzed for C and N concentrations using a Carlo-Erba NA 1500 Analyzer.

Soil C in the LF-OM (mg LF-OM C/g soil) or HF-OM (mg HF-OM C/g soil) was calculated by multiplying the fractional mass (g fraction/g soil) by the respective C concentration (mg C/g fraction). The fraction of SOC in LF-OM from each increment sample was one measure of labile C in the mineral soil and was calculated as: LF = (mg LF C/g soil) / (mg LF C/g soil + mg HF C/g soil). The fraction of SOC in HF-OM in each sample was equivalent to 1 – (LF).

Separations by wet sieving

Soil organic matter was also separated into a particulate organic matter (POM) and an organomineral fraction (SiCl) by wet sieving (Cambardella & Elliot 1992, 1993). Replicate soil cores were collected from each site on four occasions in 1996 (May, July, September, and November) and one occasion in 1997 (May). In the laboratory, each soil core was cut into three depth increments: (1) O-layers, (2) 0–5 cm mineral soil, and (3) 5–20 cm mineral soil. Separations by wet sieving were performed on 20 mineral soil increments from each site: 10 samples from the 0–5 cm increment and 10 samples from the 5–20 cm increment.

Twenty grams of air dry soil were dispersed by shaking overnight in a 100 mL solution of Na-hexametaphosphate (5 g/L). The mixture was wet sieved through a 0.053 mm sieve. The POM fraction (> 0.053 mm) was weighed after oven drying (65 °C). No attempt was made to remove sand from the POM fraction because it contributed little to the SOC content of this fraction. The SiCl fraction that passed the 0.053 mm sieve was also weighed after oven drying (65 °C). Both the POM and the SiCl fractions were ground to pass a 0.425 mm sieve and analyzed for C and N concentrations with a Carlo-Erba NA 1500 Analyzer.

Soil C in the POM (mg POM C/g soil) or SiCl (mg SiCl C/g soil) fraction was calculated by multiplying the fractional mass (g fraction/g soil) by the respective C concentration (mg C/g fraction). The POM fraction of SOC from each increment sample was another measure of labile C in the mineral soil and was calculated as: POM fraction = (mg POM C/g soil) / (mg POM C/g soil + mg SiCl C/g soil). The SiCl fraction of SOC in each sample was equivalent to 1 – (POM fraction).

Statistical analysis

One-way analysis of variance (ANOVA) was used to test for significant differences among site means. Measurements were averaged over space or time, depending upon the particular comparison that was undertaken. Comparisons between individual site means were made using Fisher's Least Significant Difference when the F-value in the ANOVA was statistically significant. Unless otherwise stated, each null hypothesis was rejected at a probability < 0.05.

Modeling forest SOC dynamics

A model of forest SOC dynamics (Figure 1) was parameterized on the basis of data from the six study sites and several simple assumptions. The two

state variables in the model were unprotected (U) and protected (P) SOC. The model was formulated based on first-order differential equations of the general form: dx/dt = fluxes into a compartment – fluxes from a compartment. An annual time step was used for each simulation. The units for the state variables and fluxes were mg C/cm^2 and mg C/cm^2 per year, respectively.

Unprotected SOC was equivalent to the sum of C inventories in the forest floor O-layer and the labile C pool in the mineral soil. Labile SOC was calculated by multiplying the C inventory in the upper 30 cm of mineral soil by a fraction which was determined by density separations (LF-OM) and wet sieving (POM fraction) methods (see Results). Protected SOC was calculated by multiplying the C inventory in the upper 30 cm of mineral soil by the protected fraction which was also determined by density separations (HF-OM) and wet sieving (SiCl fraction). It was assumed that labile and protected fractions determined from samples of the upper 20 cm of mineral soil were representative of those same respective fractions over the upper 30 cm of mineral soil.

The process of modeling forest SOC dynamics first involved calibration of the model to fit predicted SOC inventories to measured SOC inventories at the six forest sites and calculation of the annual loss rate constant for unprotected SOC (k_1). Inputs to the unprotected soil pool included C in aboveground and belowground litter (Figure 1). Belowground litter C inputs to soil (I_2) at each site were assumed to equal aboveground litterfall C inputs (I_1), and total annual C inputs (I) to unprotected SOC were calculated as: $I = 2\ (I_1)$.

The turnover time for protected SOC (TT_p) was arbitrarily set at 100 years, and the rate constant for loss from the protected SOC pool (k_3) was calculated as $1/TT_p$. Thus, a key assumption is that losses from the protected SOC pool are temperature independent, or at least much more insensitive to temperature than unprotected SOC (see Discussion). Given values for the inputs and parameter k_3, parameters k_1 and k_2 (Figure 1) were derived from the following set of formulae using measured values for the state variables (U and P). The rate constant for C transfer from the unprotected to the protected soil pool (k_2) was calculated as:

$$k_2 = P/(TT_p \times U),$$

where P and U were the measured SOC inventories in the protected and unprotected pool, respectively, and TT_p was the turnover time of protected SOC.

The rate constant for C loss from the unprotected soil pool (k_1) was calculated as:

$$k_1 = (I/U) - k_2.$$

Parameters k_1 and k_2 were fitted to yield values for the state variables that would correspond to measured SOC inventories at equilibrium. According to the preceding set of formulae, turnover times TT_u and TT_p did not necessarily covary. The turnover time of unprotected SOC (TT_u) was equivalent to $1/(k_1 + k_2)$.

Finally, the effect of a 4 °C increase in mean annual air temperature (MAT) on steady-state inventories of SOC was modelled following adjustment of the decomposition rate constant for unprotected SOC (k_1) to a new value (k_1') using site specific Q_{10} values and the following formula:

$$Q_{10} = (k_1'/k_1)^{[10/(T_2-T_1)]}$$

where T_1 is the initial MAT and T_2 is the new MAT. The Q_{10} values for SOM decomposition decrease with increasing temperature (Kirschbaum 1995), and the following Q_{10} values (in parenthesis) were used to solve for k_1' following a 4 °C increase in MAT at each study site: 1LP (3.9), 2WB (3.8), 3SB (4.5), 4MH (4.4), 5BB (5.6), and 6SP (5.6). Site specific Q_{10} values were derived from Kirschbaum's previously described relationship between temperature and CO_2 efflux from soil or litter in laboratory studies (see Figure 1; Kirschbaum 1995).

Results

Climate and soil properties

Site differences in climate and soil properties are summarized in Table 1. Mean annual air and soil temperatures declined along the elevation gradient by ≈ 0.5 °C with every 100 m increase in elevation. Seasonal changes in mean monthly air and soil temperatures at the low-, mid-, and high-elevation sites are shown in Figure 2. In July, mean monthly soil temperature at the low- and high-elevation sites differed by 7 °C. In January, the low- and high-elevation sites differed by 4 °C. Annual throughfall was $\approx$ 50% greater at the high-elevation sites compared to the low-elevation sites. Dry mass to fresh mass ratios for samples collected at different depths indicated that low elevation soils (sites 1LP and 2WB) were significantly drier than those at mid- and high-elevations (Table 1). The data in Table 1 indicated that high-elevation forests (5BB and 6SP) were both cooler and wetter than the mid- and low-elevation forests. High elevation forest soils were also more sandy and more acidic than soils at lower elevations (Table 1). The coarse fraction (small rocks and gravel > 2 mm) was highest in soils from sites 4MH, 5BB, and 6SP. The coarse fraction content was significantly less in alluvial soils at sites 1LP and 3SB (Table 2).

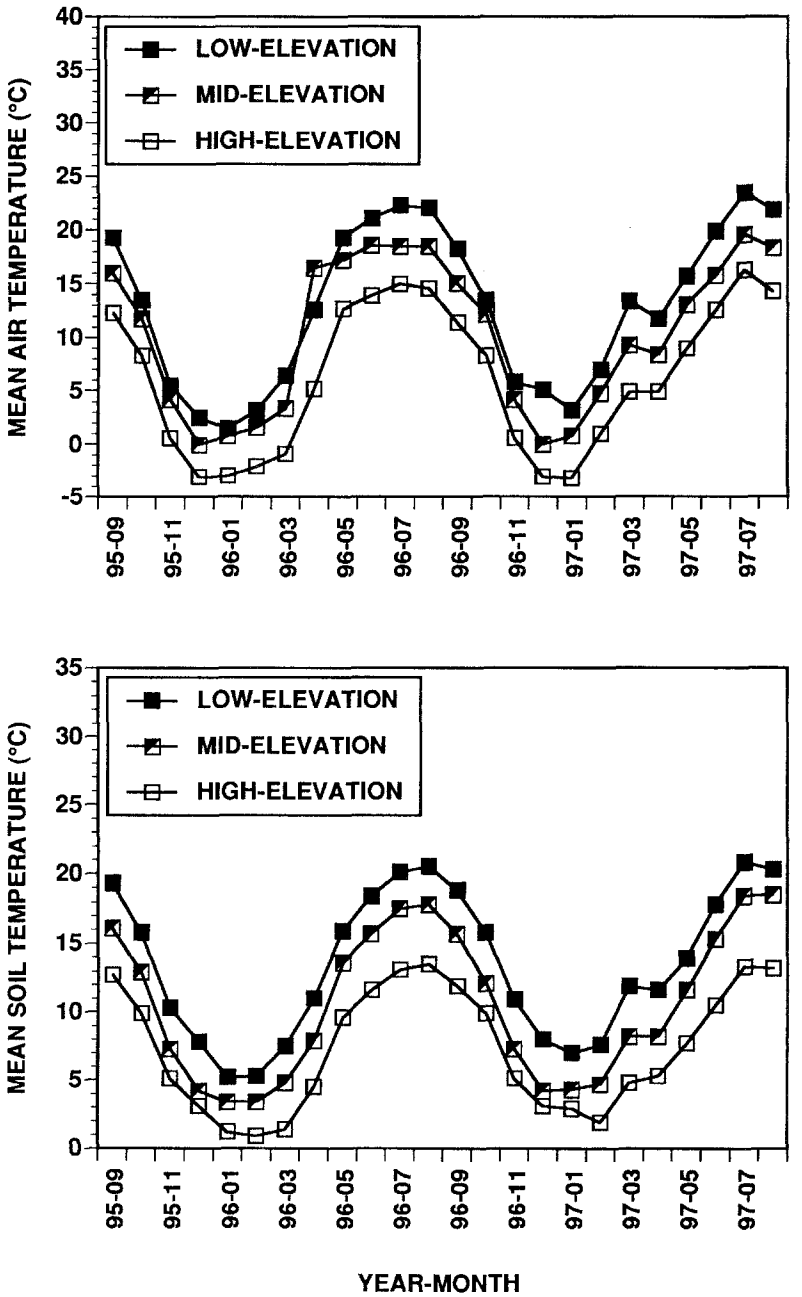

Figure 2. Mean monthly air and soil (≈ 10 cm deep) temperatures over a two year period at low- (235–335 m), mid- (940–1000 m), and high-elevation (1650–1670 m) forest ecosystems in the southern Appalachian Mountains.

Table 1. Climate and soil properties at the six forest sites along an elevation gradient in the southern Appalachian Mountains. Mean annual air and soil temperatures were calculated from data over a 2 year period (1995–1997). Throughfall measurements at site 4MH were discontinuous due to periodic disturbance by bears. Mean dry mass:fresh mass (DM/FM) ratios were based on 18 soil samples per site. Coefficients of variation are shown in parenthesis. Means in the same row that do not share the same alphabetic superscript are significantly different ($p < 0.05$).

Site variable	1LP	2WB	3SB	4MH	5BB	6SP
Elevation (m)	235	335	940	1000	1650	1670
Temperature (°C)						
Annual Mean (Air)	12.6	13.1	10.3	10.5	6.2	6.4
Annual Mean (Soil)	13.4	13.5	10.6	10.6	7.4	7.3
Throughfall (cm/year)	117	124	113	—	191	175
pH O-Layer	3.9	4.5	4.0	3.2	3.1	3.1
pH Soil (0–20 cm)	4.5	4.2	3.8	4.0	3.4	3.5
Sand (%)	0.13	0.33	0.33	0.21	0.40	0.52
Silt (%)	0.73	0.57	0.55	0.63	0.45	0.36
Clay (%)	0.14	0.10	0.12	0.16	0.15	0.12
DM/FM Ratio						
Soil 00–05 cm	0.82 [a]	0.82 [a]	0.62 [c]	0.68 [b]	0.67 [b]	0.59 [d]
	(0.04)	(0.03)	(0.04)	(0.07)	(0.07)	(0.10)
Soil 05–20 cm	0.84 [b]	0.86 [a]	0.70 [e]	0.76 [c]	0.76 [c]	0.74 [d]
	(0.03)	(0.02)	(0.03)	(0.04)	(0.03)	(0.02)
Soil 20–30 cm	0.85 [b]	0.87 [a]	0.75 [e]	0.81 [c]	0.77 [d]	0.78 [d]
	(0.02)	(0.02)	(0.04)	(0.05)	(0.03)	(0.04)

Litterfall C returns

Site differences in annual C return to the forest floor in litterfall, averaged over three years, were not statistically significant (Table 3). Over all sites and years, the mean (± SE) annual aboveground litterfall C input was 23.0 ± 2.4 mg C/cm^2. However, each year there was less annual C return in litterfall at site 5BB than at the other five forest sites (the range was 22 to 64% less C return at site 5BB). The grand mean for annual litterfall C return at the six study sites was similar to a previously reported regional mean annual litterfall input for southern Appalachian forests (Sharpe et al. 1980). Sharpe et al., in a regional analysis of litter dynamics, found no significant differences among forest types in aboveground litterfall and calculated a regional mean annual litterfall input equivalent to 20 mg C/cm^2. Carbon concentrations in litterfall

Table 2. Areal density (g/cm^2) of the coarse fraction (rocks and gravel > 2 mm) in different mineral soil increments at the six study sites. Each mean is based on 18 samples. Coefficients of variation are shown in parenthesis. Means in the same row that do not share the same alphabetic superscript are significantly different.

Soil zone	1LP	2WB	3SB	4MH	5BB	6SP
00–05 cm	0.18 ^{a}	0.54 ^{cd}	0.26 ^{ab}	0.70 ^{de}	1.06 ^{e}	0.43 ^{bc}
	(1.27)	(0.89)	(1.09)	(0.60)	(0.51)	(1.04)
05–20 cm	0.41 ^{a}	1.62 ^{b}	0.70 ^{a}	3.39 ^{c}	2.68 ^{c}	1.55 ^{b}
	(1.47)	(0.87)	(0.71)	(0.55)	(0.40)	(0.64)
20–30 cm	0.27 ^{a}	1.16 ^{bc}	0.62 ^{ab}	2.93 ^{d}	1.72 ^{c}	1.45 ^{bc}
	(1.52)	(0.68)	(0.76)	(0.78)	(0.70)	(1.16)

Table 3. Mean annual C return to the forest floor in aboveground litterfall and mean C/N ratios in litterfall and coarse roots at the six forest sites. Means for litterfall are based on data from three years (1995, 1996, and 1997). Means for coarse roots are based on 8 soil samples per site. Coefficients of variation are shown in parenthesis. Means in the same row that do not share the same alphabetic superscript are significantly different.

Variable	1LP	2WB	3SB	4MH	5BB	6SP
C Return (mg C/cm^2)	29.8 ^{a}	23.9 ^{a}	22.3 ^{a}	26.6 ^{a}	13.2 ^{a}	22.3 ^{a}
	(0.37)	(0.26)	(0.52)	(0.67)	(0.09)	(0.16)
C/N Ratios						
Litterfall	60.7 ^{b}	65.8 ^{b}	43.3 ^{a}	63.9 ^{b}	34.1 ^{a}	42.3 ^{a}
	(0.07)	(0.20)	(0.04)	(0.13)	(0.04)	(0.18)
Coarse roots	72.7 ^{b}	91.9 ^{b}	46.3 ^{a}	99.1 ^{b}	49.2 ^{a}	56.1 ^{a}
	(0.37)	(0.27)	(0.29)	(0.15)	(0.10)	(0.13)

were $\approx$ 500 mg C/g dry mass; thus, litterfall dry mass can be approximated as 2 times the litterfall C return (Table 3).

Litterfall C/N ratios at sites 1LP, 2WB, and 4MH were significantly greater than litterfall C/N ratios at sites 3SB, 5BB, and 6SP (Table 3). Site differences in C/N ratios were not clearly related to litterfall composition (Table 4). For example, two sites on opposite ends of the elevation gradient (1LP and 6SP) differed from other study sites by having a higher percentage of coniferous litterfall (Table 4), but the litterfall C/N ratio at

Table 4. Litterfall composition at the six forest sites based on data over three years (1995, 1996, and 1997). Coefficients of variation are shown in parenthesis. Means in the same row that do not share the same alphabetic superscript are significantly different.

Variable	1LP	2WB	3SB	4MH	5BB	6SP
% Deciduous	40 ^{a}	94 ^{c}	74 ^{c}	81 ^{c}	73 ^{bc}	49 ^{ab}
	(0.19)	(0.06)	(0.13)	(0.13)	(0.30)	(0.41)
% Coniferous	54 ^{b}	1 ^{a}	9 ^{a}	3 ^{a}	1 ^{a}	36 ^{b}
	(0.07)	(0.43)	(0.45)	(0.43)	(1.15)	(0.27)
% Wood or seed	6 ^{a}	5 ^{a}	17 ^{a}	17 ^{a}	26 ^{a}	15 ^{a}
	(1.07)	(1.22)	(0.78)	(0.70)	(0.82)	(0.67)

the low-elevation site (1LP) was significantly higher than that at the high-elevation site (6SP). There were also significant differences in litterfall C/N ratios at sites with similar elevations and similar litterfall composition (3SB and 4MH). The C/N ratios in coarse roots covaried with litterfall C/N ratios (Table 3). A positive correlation between mean C/N ratios in litterfall and coarse roots across the six study sites was statistically significant ($r = +0.92$, $p < 0.01$).

C inventories in forest floor O-layers

Despite considerable within site variation, there were significant differences among study sites in forest floor C inventories (Table 5). Different methods for estimating C inventories in the O-layer gave similar results at three (1LP, 2WB, 3SB) of the six study sites. Forest floor C inventories at the latter three sites were based on estimates from 2.4 cm diameter soil cores (Method 1). Method 1 appeared to significantly underestimate C inventories in the O-layer at site 4MH which had a fibrous mor-type litter layer. Carbon inventories in the forest floor at site 4MH were based on an average of methods 2 and 3 which gave similar results (Table 5). Forest floor C inventories at site 5BB were estimated from the two methods that gave the most similar results (method 1 and 2). At site 6SP, methods 1 and 2 significantly underestimated O-layer C inventories compared to method 3. Although methods 1 and 2 were in good agreement at the latter site, estimates of forest floor C inventories at site 6SP were based on results from method 3. Previously published data from spruce and fir forests near site 6SP (Johnson & Lindberg 1992) indicate that expected O-horizon C inventories in this forest type are in the range of 440

Table 5. Mean forest floor (O-layer) C inventories (mg C/cm^2) at six different sites in the southern Appalachian Mountains as determined by three different methods (see text). Coefficients of variation are shown in parenthesis. Means in the same row that share the same alphabetic superscript are not significantly different. Means in the same column that share the same numeric superscript are not significantly different.

Method	N	1LP	2WB	3SB	4MH	5BB	6SP
1	18	78 ^{a1}	66 ^{a1}	96 ^{a1}	144 ^{b1}	168 ^{b1}	246 ^{c1}
		(0.34)	(0.45)	(0.40)	(0.26)	(0.48)	(0.29)
2	7	59 ^{a1}	44 ^{a1}	90 ^{a1}	254 ^{c2}	157 ^{b1}	306 ^{c1}
		(0.37)	(0.21)	(0.67)	(0.22)	(0.36)	(0.28)
3	8	64 ^{a1}	48 ^{a1}	90 ^{a1}	241 ^{b2}	235 ^{b1}	538 ^{c2}
		(0.41)	(0.36)	(0.63)	(0.51)	(0.58)	(0.46)

to 670 mg C/cm^2. Reasons for the apparent underestimation of forest floor C inventories by methods 1 and 2 are unknown.

C inventories in the mineral soil

Areal density of the soil fraction < 2 mm, C concentrations, and SOC inventories at different soil depths on an area basis are presented in Table 6. Soil organic C inventories in the low-elevation forests were significantly less than those in the mid- and high-elevation forests (Table 6), but there were no significant correlations across the six forest sites between air or soil temperature and SOC inventories in the mineral soil.

Soil organic C concentrations declined 79 to 92% from the 0–5 cm layer to the 20–30 cm layer of mineral soil at 5 of the 6 study sites (Table 6). Concentrations followed a more gradual decline with depth at site 3SB, declining by only 67% over the upper 30 cm of mineral soil. At each study site, the decline in mean SOC concentration with soil depth was described by a logarithmic relationship of the form $\ln(Y) = a + b(X)$, where Y = concentration (mg C/g soil) and X = soil depth (cm). The exact depth of the soil at each site is unknown, but based on logarithmic declines in SOC concentrations with soil depth it was estimated that the upper 30 cm of mineral soil contained 81 to 93% of the SOC inventory at sites 1LP, 2WB, 4MH, 5BB, and 6SP and $\approx$ 70% of the total SOC inventory at site 3SB.

Table 6. Mean areal densities, SOC concentrations, and SOC inventories at different depths from six forest sites in the southern Appalachian Mountains. Means are based on 18 soil samples per site. Coefficients of variation are in parenthesis. Within each soil depth, means in the same column that do not share the same alphabetic superscript are significantly different.

Soil depth	Site	Areal density g soil/cm^2	SOC concn mg C/g soil	SOC inventory mg C/cm^2
00–05 cm	1LP	5.57 ^{c} (0.11)	19.1 ^{a} (0.17)	106 ^{a} (0.18)
	2WB	4.63 ^{b} (0.13)	26.9 ^{a} (0.14)	125 ^{a} (0.19)
	3SB	2.91 ^{a} (0.14)	76.7 ^{b} (0.12)	222 ^{bc} (0.15)
	4MH	2.68 ^{a} (0.24)	90.7 ^{c} (0.26)	235 ^{cd} (0.24)
	5BB	2.79 ^{a} (0.26)	76.1 ^{b} (0.28)	203 ^{b} (0.23)
	6SP	2.94 ^{a} (0.22)	92.6 ^{c} (0.31)	258 ^{d} (0.19)
05–20 cm	1LP	19.6 ^{c} (0.04)	8.6 ^{a} (0.11)	169 ^{a} (0.10)
	2WB	18.4 ^{c} (0.09)	8.2 ^{a} (0.25)	149 ^{a} (0.25)
	3SB	12.1 ^{b} (0.07)	41.9 ^{c} (0.15)	506 ^{d} (0.15)
	4MH	11.5 ^{b} (0.13)	25.6 ^{b} (0.23)	292 ^{b} (0.23)
	5BB	13.9 ^{a} (0.10)	26.8 ^{b} (0.45)	362 ^{c} (0.35)
	6SP	14.6 ^{a} (0.08)	22.8 ^{b} (0.21)	332 ^{bc} (0.20)
20–30 cm	1LP	14.5 ^{c} (0.09)	3.5 ^{a} (0.18)	51 ^{a} (0.20)
	2WB	13.9 ^{c} (0.08)	3.2 ^{a} (0.17)	44 ^{a} (0.13)
	3SB	10.1 ^{a} (0.10)	25.0 ^{e} (0.30)	246 ^{d} (0.24)
	4MH	9.2 ^{a} (0.25)	7.2 ^{b} (0.38)	65 ^{a} (0.41)
	5BB	10.0 ^{a} (0.12)	16.0 ^{d} (0.20)	159 ^{c} (0.21)
	6SP	11.3 ^{b} (0.12)	10.9 ^{c} (0.34)	120 ^{b} (0.28)

SOC in LF-OM and HF-OM

The partitioning of SOC between LF-OM and HF-OM was relatively similar across the six sites. At every site, HF-OM contained most of the C in the mineral soil. In the 0–5 cm depth increment, there were no significant differences among sites in the fraction of SOC associated with LF-OM or HF-OM (Table 7). The mean fraction of SOC associated with LF-OM and HF-OM in the 0–5 cm increment of mineral soil, over all study sites, was 31 and 69%, respectively.

There were significant site differences in the fraction of SOC associated with LF-OM and HF-OM in the 5–20 cm depth increment. Site 6SP had

Table 7. Mean fractional distribution of SOC between LF-OM and HF-OM in two mineral soil increments at six forest sites. Coefficients of variation are shown in parenthesis. Each mean is based on 10 samples. Means in the same row that share the same alphabetic superscript are not significantly different.

Soil depth	Part	1LP	2WB	3SB	4MH	5BB	6SP
00–05 cm	LF-OM	0.30 [a]	0.34 [a]	0.28 [a]	0.33 [a]	0.28 [a]	0.30 [a]
		(0.22)	(0.10)	(0.25)	(0.25)	(0.26)	(0.42)
	HF-OM	0.70 [a]	0.66 [a]	0.72 [a]	0.67 [a]	0.72 [a]	0.70 [a]
		(0.10)	(0.05)	(0.10)	(0.12)	(0.10)	(0.18)
05–20 cm	LF-OM	0.24 [bc]	0.29 [c]	0.23 [b]	0.27 [bc]	0.21 [b]	0.14 [a]
		(0.42)	(0.36)	(0.10)	(0.21)	(0.21)	(0.39)
	HF-OM	0.76 [a]	0.71 [a]	0.78 [a]	0.73 [a]	0.79 [a]	0.86 [b]
		(0.13)	(0.15)	(0.03)	(0.08)	(0.06)	(0.06)

Table 8. Mean fractional distribution of SOC between POM and SiCl fractions in two mineral soil increments at six forest sites. Coefficients of variation are shown in parenthesis. Each mean is based on 10 samples. Means in the same row that share the same alphabetic superscript are not significantly different.

Soil depth	Part	1LP	2WB	3SB	4MH	5BB	6SP
00–05 cm	POM	0.27 [a]	0.33 [a]	0.28 [a]	0.30 [a]	0.24 [a]	0.43 [b]
		(0.19)	(0.17)	(0.36)	(0.28)	(0.60)	(0.30)
	SiCl	0.73 [b]	0.67 [b]	0.72 [b]	0.70 [b]	0.76 [b]	0.57 [a]
		(0.07)	(0.09)	(0.14)	(0.12)	(0.19)	(0.23)
05–20 cm	POM	0.15 [b]	0.25 [d]	0.16 [b]	0.21 [c]	0.10 [a]	0.11 [a]
		(0.23)	(0.16)	(0.19)	(0.22)	(0.38)	(0.58)
	SiCl	0.85 [c]	0.75 [a]	0.84 [c]	0.79 [a]	0.90 [d]	0.89 [d]
		(0.04)	(0.05)	(0.04)	(0.06)	(0.04)	(0.07)

significantly more SOC in HF-OM and significantly less SOC in LF-OM than the other five sites. Although there were other statistically significant differences between sites in LF-OM, five of the six sites (1LP, 2WB, 3SB, 4MH, and 5BB) were similar with 71 to 79% of SOC in the HF-OM and the balance (21 to 29%) in LF-OM (Table 7).

SOC in POM and SiCl fractions

Wet sieving methods for characterizing C in the mineral soil yielded results that were, in many respects, similar to those obtained with density separations. Most of the C in the mineral soil at each site was associated with the SiCl fraction (Table 8). In the 0–5 cm soil increment, there were no significant differences among five of the six study sites in the fraction of SOC associated with POM and SiCl. Site 6SP contained significantly more SOC in the POM fraction and significantly less SOC in the SiCl fraction than the other forest sites (Table 8).

There were significant site differences in the distribution of SOC between POM and SiCl fractions in the 5–20 cm increment of mineral soil. The high elevation forest soils contained significantly more SOC in the SiCl fraction ($\approx$ 90%) than the low- and mid-elevation sites which contained between 75 to 85% of the SOC in the SiCl fraction (Table 8).

Considering data from both depth increments (0–5 and 5–20 cm) and all six study sites, the mean fraction of POM soil C was correlated with the mean fraction of soil C in LF-OM ($r = +0.82$, $p < 0.01$). Mean C/N ratios in LF-OM were significantly correlated with the mean C/N ratios in the POM fraction, and the mean C/N ratios in HF-OM were significantly correlated with the mean C/N ratios in the SiCl fraction (Figure 3). These correlations indicated agreement between density separations and wet sieving methods for distinguishing different pools of mineral SOC.

Labile and protected mineral soil C

The fractional distribution of SOC between LF-OM and HF-OM or between POM and SiCl fractions in the upper 20 cm of mineral soil at each study site (Table 9) was calculated as a weighted average based on data from Tables 6, 7, and 8. Density and wet sieving separations produced similar results for classifying C in the mineral soil, thus LF-OM and POM fractions were averaged to yield estimates of the labile fraction and HF-OM and SiCl fractions were averaged to yield estimates of the protected fraction of SOC. Most (71 to 83%) of the C in the mineral soil at the six forest sites was identified as protected because of its association with HF-OM or the SiCl fraction. The labile C in the mineral soil ranged from 17 to 29% of the total SOC.

Unprotected and protected SOC inventories

Carbon inventories summed over the upper 30 cm of mineral soil (Table 6) were multiplied by labile and protected fractions calculated for the upper 20 cm of mineral soil (Table 9) to arrive at the respective estimates of unprotected and protected pools of SOC (Table 10). Unprotected SOC ranged from

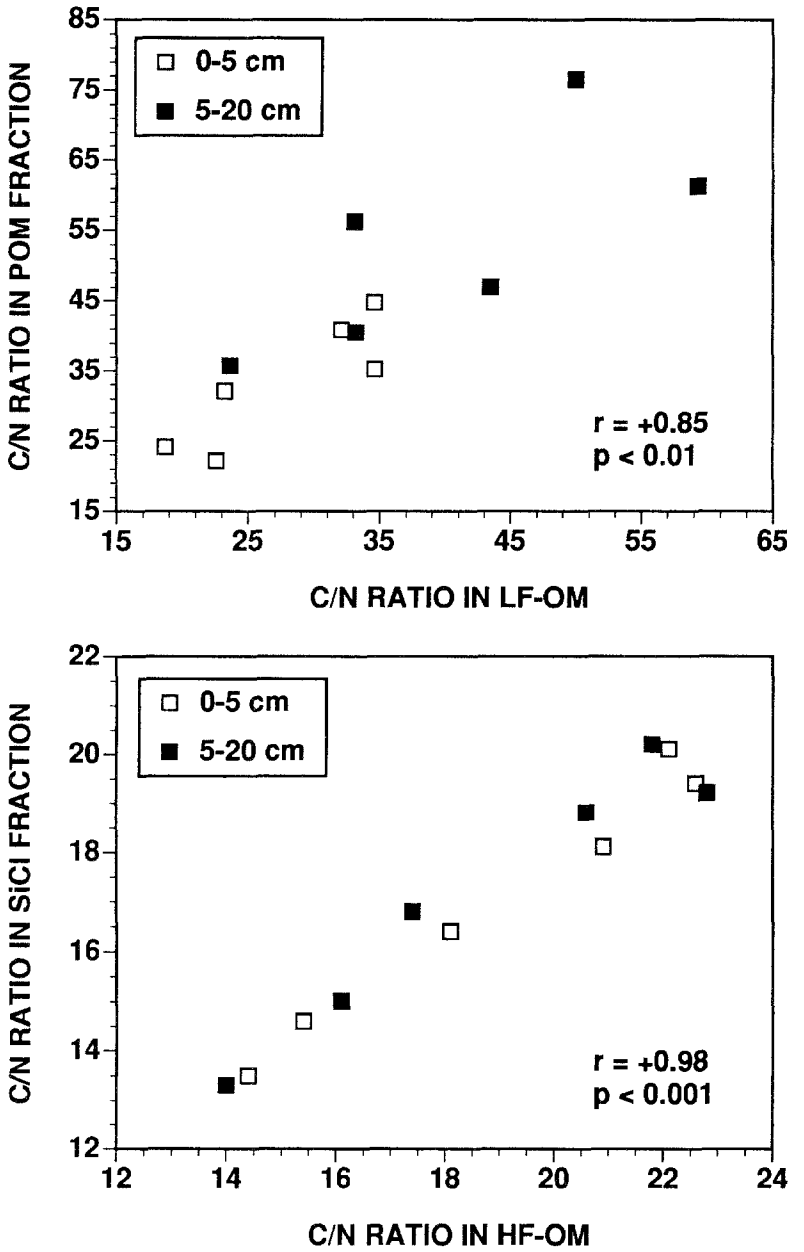

Figure 3. Top panel: Correlation between mean C/N ratios in LF-OM (determined by density separations) and mean C/N ratios in POM fractions (determined by wet sieving) from mineral soils collected at six forest sites in the southern Appalachian Mountains. Each mean was based on 10 samples. Open squares are for samples taken at 0 to 5 cm soil depth and closed squares are for samples taken at 5 to 20 cm soil depth. Bottom panel: Correlation between mean C/N ratios in HF-OM and mean C/N ratios in SiCl fractions from the same mineral soil samples.

Table 9. Distribution of SOC between LF-OM and HF-OM or between POM and SiCl fractions in the upper 20 cm of mineral soil. The LF-OM and POM fractions were averaged to yield a labile fraction of mineral soil C. The protected fraction was calculated as an average of SOC associated with the HF-OM and SiCl fractions.

Part	1LP	2WB	3SB	4MH	5BB	6SP
LF-OM	0.25	0.30	0.24	0.28	0.22	0.17
POM	0.18	0.27	0.18	0.23	0.12	0.16
Labile fraction	0.22	0.29	0.21	0.26	0.17	0.17
HF-OM	0.75	0.70	0.76	0.72	0.78	0.73
SiCl	0.82	0.73	0.82	0.77	0.88	0.84
Protected fraction	0.78	0.71	0.79	0.74	0.83	0.83

Table 10. Carbon inventories (mg C/cm^2) in unprotected and protected soil pools at the six forest sites in the southern Appalachian Mountains. Total SOC was calculated to a depth of 30 cm. Unprotected and protected SOC inventories were calculated using labile and protected fractions of SOC from Table 9.

Soil pool	Component	1LP	2WB	3SB	4MH	5BB	6SP
Unprotected (U)	O-layer	78	66	96	248	168	538
	Mineral Soil	72	92	205	156	123	120
	Total U	150	158	301	404	291	658
	% Total SOC	37	41	28	48	33	53
Protected (P)	Mineral soil	254	226	769	444	603	586
	% Total SOC	63	59	72	52	67	47
Total SOC	U + P	404	384	1070	848	894	1244

28 to 53% of the total SOC inventory, and protected SOC ranged from 47 to 72% of the total SOC inventory. Inventories of SOC at the low-elevation forests (1LP and 2WB) were $\approx$ 30 to 50% as large as those estimated for more mature forests at mid- and high-elevations in the Great Smoky Mountains National Park. Forests with mor-type humus layers (4MH and 6SP) had a higher percentage of unprotected SOC than other sites. This latter difference was caused by the large contribution of O-layer C to inventories of unprotected SOC (Table 10).

Table 11. Derived annual fractional transfers from unprotected SOC at six forest sites in the southern Appalachian Mountains (see Figure 1). Parameter k_1' is the decomposition rate adjusted for a 4 °C increase in mean annual temperature.

Parameter	1LP	2WB	3SB	4MH	5BB	6SP
k_1	0.2897	0.2768	0.1273	0.1029	0.0583	0.0610
k_1'	0.5015	0.4732	0.2321	0.1868	0.1161	0.1213
k_2	0.0169	0.0143	0.0255	0.0110	0.0207	0.0089

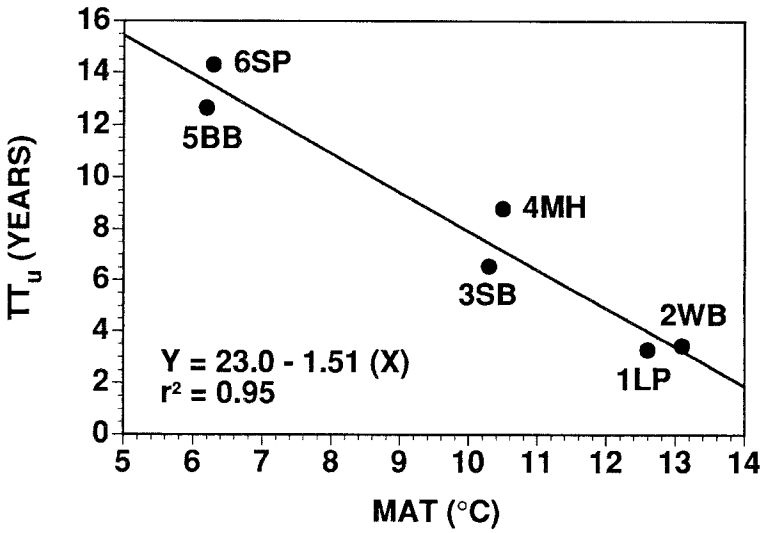

Figure 4. Relationship between derived turnover times of unprotected SOC (TT_u) and mean annual air temperature (MAT) at six forest sites along an elevation gradient in the southern Appalachian Mountains. Codes next to symbols correspond to site locations.

Modelling forest SOC dynamics

Derived annual loss rates (k_1 and k_2) from unprotected SOC at the six forest sites are presented in Table 11. An annual litterfall C return of 23 mg C/cm^2 was used as the best estimate of long-term aboveground C inputs to soils, except at site 5BB where the value was reduced by 50%. Across the elevation gradient, estimates of parameter k_1 increased (Table 11) and the derived turnover times for unprotected SOC (TT_u) decreased with increasing MAT (Figure 4). Calculated values for k_1' at the six forest sites following a 4 °C increase in MAT are also presented in Table 11. Simulations with the model to predict the change in steady state SOC inventories following a 4 °C increase in MAT indicated that low-, mid-, and high-elevation forest soils

Table 12. Predicted unprotected (U), protected (P), and total SOC inventories (mg C/cm^2), at steady-state and to a depth of 30 cm, at six forest sites following a 4 °C increase in mean annual air temperature (MAT). The percent reduction in current total SOC inventories (see Table 10) that accompanies a 4 °C increase in MAT is shown in the last row.

Variable	1LP	2WB	3SB	4MH	5BB	6SP
Unprotected (U)	89	93	179	233	168	353
Protected (P)	150	133	455	256	348	315
Total SOC (U + P)	239	226	634	489	516	668
Reduction (%)	41	41	41	42	42	46

would give up ≈ 40 to 45% of their current SOC inventory (to a depth of 30 cm) (Table 12). The simulations assumed that aboveground and belowground C inputs to the soil did not change over time. Soil C inputs would need to increase by ≈ 70 to 85% to offset predicted losses of SOC at the higher MAT.

Discussion

There are both advantages and disadvantages to using elevation gradients as an approach for testing the effect of environmental variables on the dynamics of forest SOC. One advantage is that the state of soil C present at an undisturbed site is the product of natural change that includes the adaptation of biological and nonbiological components to an existing climate. Undisturbed forest ecosystems along elevation gradients have a much greater probability of being adapted to prevailing climates than ecosystems that are manipulated through short-term experiments. Unlike experimental manipulations of systems, which include more or less instantaneous and discrete changes in one or several variables, studies along elevation gradients reflect the outcome of multiple interacting environmental factors over long time periods. Short-term responses that normally accrue over a period of several years in field experiments may not be the same as responses that accrue in nature from complex interactions between soil, plant, and microbial systems over a period of decades to centuries. Gradient studies may yield useful data for modelling changes in SOC storage because undisturbed natural ecosystems are more likely to approximate steady-state conditions than experimentally manipulated systems.

Understanding the present state of forest SOC inventories allows us to qualitatively predict how soil C storage will change with climate, but there are several important limitations to studies along elevation gradients. First, there are no formal controls and all comparisons among ecosystems at different points along the gradient are relative. Second, the range of environmental differences along elevation gradients may be too narrow for making confident predictions to other ecosystems through extrapolation. Third, it may be impossible to determine cause and effect relationships from studies along elevation gradients because of the many potentially confounding factors that accompany changes in elevation.

The third limitation is especially important because elevation gradients are often accompanied by natural changes in climate (both MAT and moisture), vegetation type, soil properties (chemistry, texture, and parent material), and soil nutrient availability. For example, along elevation gradients in the southern Appalachian Mountains, N deposition increases from $\approx$ 10 kg N/ha per year at low elevations to $\approx$ 28 kg N/ha per year at high elevations due to greater dry deposition and greater fog and cloud water deposition in high-elevation forests (Lovett & Lindberg 1993). Lower C/N ratios in litterfall and coarse roots at sites 5BB and 6SP on our elevation gradient are probably explained, in part, by elevated N availability in these high-elevation forest ecosystems (Johnson et al. 1991). Although factors affecting soil formation and SOM accumulation (such as mineralogy, vegetation, and topography) may vary dramatically along elevation gradients, MAT is unquestionably one of the most important factors controlling SOC accumulation and turnover (Trumbore et al. 1996).

Rates of SOM decomposition are strongly affected by prevailing MAT because soil microbial processes are a function of temperature (Insam 1990; Kirschbaum 1995; Winkler et al. 1996). Across the sites examined in the southern Appalachian Mountains, differences in MAT can account for a high percentage of the variation in calculated turnover times of unprotected SOC. Precipitation and soil moisture also covary with temperature along our elevation gradient (Table 1), but there is no pronounced seasonality to precipitation in this region and rarely does soil moisture decline to levels that are insufficient to sustain soil microbial activity for extended periods of time. Thus, we assume that soil moisture is less of a limiting factor to SOM decomposition along the elevation gradient than is MAT.

A significant limitation to current models of SOC dynamics is the lack of correspondence between conceptual soil C pools and experimentally verifiable fractions (Christensen 1996). We have used previously described methods for the separation of POM (Cambardella & Elliott 1992) and LF-OM (Spycher et al. 1983) from organomineral matter in order to quantify

the SOC inventories in different forest soil pools. Departing from methods used by other authors (e.g., Spycher et al. 1983; Trumbore et al. 1996), LF-OM was floated in solutions of relatively low density. The soils were also not dispersed by sonification prior to density separations because such techniques may redistribute SOC from organomineral to labile mineral soil fractions (Elliott & Cambardella 1991). These separations yielded LF-OM that was almost certainly free of organomineral matter, which generally has a density > 1.7 g/cm^3 (Sollins et al. 1984; Janzenet al. 1992). Our estimates of labile SOC based on density separations could be regarded as minimum estimates due to the low density of the solution used to separate LF-OM and HF-OM. Nonetheless, amounts of SOC associated with LF-OM ranged from 17 to 30% of the total SOC (to a depth of 20 cm) at the six forest sites. The latter range is comparable to the percentage of SOC associated with LF-OM (< 1.65 g/cm^3) in surface soils from a variety of other forests (Christensen 1992).

Despite some uncertainties, the different methods used to separate labile and protected fractions of SOC appeared to characterize similar pools of forest SOM. Separations of forest SOM at a density of 1.4 g/cm^3 resulted in a LF-OM pool that was similar in quality (i.e., C/N ratio) and quantity to POM isolated by wet sieving methods. Correlations between the C/N ratios in similar fractions (LF-OM versus POM and HF-OM versus SiCl) obtained by different methods suggest that it is valid to partition SOC at these forest sites between a labile and an organomineral pool. The labile pool (LF-OM or POM) is comprised of partially decomposed organic debris. Cambardella and Elliott (1992) have also suggested that POM isolated from grassland soils is the same as LF-OM isolated by density separations. In absolute amounts, more SOC was associated with the organomineral pool. The organomineral fraction represents SOC that is relatively more protected from microbial decomposition through physicochemical mechanisms. There was a tendency for cooler and wetter soils in high-elevation forests to have more SOC in the organomineral fraction than in the labile mineral soil fraction, but the differences were small.

Through modeling it was possible to derive a relationship between the turnover time of unprotected forest SOC and MAT. The modeling approach assumed that (1) SOC inventories were near steady-state, (2) belowground C inputs were equal to aboveground litterfall C inputs, (3) the annual transfer of SOC from the unprotected to the protected soil pool was site specific, and (4) the turnover of protected SOC was described by a single rate constant which is independent of MAT.

Concerning the first model assumption, we do not know the long-term (i.e., centuries) history of the six study sites, but the sites are located on government lands that have been subject to minimal or no disturbance for more

than 50 years. Furthermore, broadleaf and needleleaf forests are the natural potential vegetation of this region; thus, the assumption of near steady state forest SOC inventories is reasonable. Concerning the second model assumption, summaries of data on root biomass and annual production in different temperate forest ecosystems (Hendrick & Pregitzer 1993) indicate that fine root production is balanced by fine root mortality on an annual time-scale (i.e., turnover = annual production/fine root biomass = 1 year). Therefore, organic C recycling to the unprotected soil pool by way of root mortality will be nearly equal to fine root production. Furthermore, summaries of C returns in annual aboveground forest litterfall, belowground C allocation, and fine root production (as estimated by the N budget method) indicate that the ratio of aboveground litterfall C return to fine root production is near unity in many forest ecosystems (Raich & Nadelhoffer 1989; Nadelhoffer & Raich 1992). In the absence of any data to the contrary, the assumed equality between inputs of aboveground and belowground C to the unprotected SOC pool was considered reasonable.

With respect to the last two model assumptions, both unprotected and protected SOC (as defined in Figure 1) may include some intraaggregate SOM because the methods we used to distinguish these two pools involved minimal soil dispersion. Transfers of C into and out of the protected soil pool are controlled by processes that create and destroy, respectively, physicochemically protected SOC. These processes may depend more on site specific edaphic factors than on prevailing temperature conditions (see e.g., Torn et al. 1997). Soil aggregates are continuously created and destroyed through physical and chemical mechanisms, and one result of soil aggregate formation is that SOC becomes protected from decomposition (Jastrow 1996). Protected SOC may or may not be chemically recalcitrant. Although there can be differences in the turnover of SOC associated with silt and clay size soil fractions (Bonde et al. 1992; Buyanovsky et al. 1994; Gregorich et al. 1995), no distinction was made in the present study between the smaller primary soil particles. Recent studies indicate that the turnover of protected SOC (defined as that fraction of SOC associated with soil particle sizes < 0.050 mm) can be described by a singe rate constant (Balesdent 1996). We are not saying that the turnover of protected SOC is completely independent of temperature; only that TT_p is probably less influenced by MAT than TT_u. Clearly additional studies are needed to resolve exactly how the turnover of protected SOC is affected by differences in soil properties and climate.

Observed differences in forest SOC inventories along the elevation gradient (Table 10) were not a straightforward function of elevation or MAT because of the many interacting environmental factors that affect SOC storage. Despite the probable importance of other factors, MAT was a reasonable

predictor of the turnover time of unprotected SOC in model results that were derived by fitting the measured distribution of SOC between unprotected and protected soil pools. Simulations with the model suggest that, if all other factors remain constant, a warming climate will significantly impact SOC inventories in forests of the southern Appalachian Mountains. After reaching a new steady state (with no change in inputs of C to the unprotected soil pool), forest SOC inventories were predicted to decline by $\approx$ 40 to 45% following a 4 °C increase in MAT (Table 12). This conclusion is unaffected by assumptions related to the turnover time of protected SOC. Due to the way in which model transfers were derived, increasing the turnover time of protected SOC by a factor of 10 (from 100 to 1000 years) has little effect on the estimated turnover time of unprotected SOC. Therefore, the predicted declines in unprotected SOC as a result of regional warming remain approximately the same even if there are appreciable errors in the estimation of TT_p.

Carbon inventories in the forest floor O-layers are a substantial contributor to the amount of unprotected SOC at each of the six forest sites along the elevation gradient. It is assumed that the turnover of C in the forest floor O-layers and the turnover of labile SOC are sufficiently similar that these two components of unprotected soil C can be combined and described by a single rate constant (i.e., k_1 in Figure 1). However, there may be differences in the decomposition rate of forest floor O-layers and labile C in the mineral soil (due to soil aggregate formation) that could be accentuated in a changing climate. For example, if the forest floor was frequently drier than the underlying mineral soil, then the decomposition rate of forest floor O-layers could be slower than that of labile SOC due to moisture limitations on microbial activity. Based on data available from studies along the elevation gradient, we are unable to make distinctions such as this between the turnover times of these two very different pools of SOC (Figure 1). Tracer experiments using additions of enriched carbon-13 labelled compounds to the forest floor are underway at all six forest sites in an attempt to determine what differences exist between the turnover time of C in the forest floor O-layer and labile organic C in the mineral soil.

Even though each fraction exists in a different soil horizon, both forest floor C and labile C in the mineral soil are more vulnerable to microbial decomposition and the effects of climate change than protected SOC. The loss of unprotected SOC from forest ecosystems following regional warming could diminish the beneficial effects that O-layers and stores of labile SOC impart to forest soils. Those benefits include reduced evaporation, greater water holding capacity, and essential nutrients (like N, P, and Ca) that are made available for plant growth through the mineralization of unprotected SOM. Substantial losses of unprotected SOM as a result of a warmer cli-

mate could have long-term adverse impacts on hydrology, soil quality, and plant nutrition in forest ecosystems throughout the southern Appalachian Mountains.

Acknowledgements

Research sponsored by the Terrestrial Carbon Processes Program, Office of Health and Environmental Research, U. S. Department of Energy under contract DE-AC05-960R22464 with Lockheed Martin Energy Research Corporation. We thank the following persons currently or formerly affiliated with Oak Ridge National Laboratory for their technical contributions to this research: Scott Dolvin, Bonnie Lu, Tracy Misek, Rhonda Webster, and Tom Stephens (deceased). Stan Wullschleger and Bob Luxmoore, both with the Environmental Sciences Division at Oak Ridge National Laboratory, provided us with constructive and helpful reviews of the draft manuscript. We also wish to thank anonymous referees who contributed to further improvements in the draft manuscript through their very thoughtful and critical reviews. Publication No. 4807, Environmental Sciences Division, ORNL.

Notes

1. Research sponsored by the Terrestrial Carbon Processes Program, Office of Health and Environmental Research, U. S. Department of Energy under contract DE-AC05-96OR22464 with Lockheed Martin Energy Research Corporation.
2. Publication No. 4807, Environmental Sciences Division, ORNL.

References

Balesdent J, Wagner GH & Mariotti A (1988) Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. Soil Science Society America Journal 52: 118–124

Balesdent, J (1996) The significance of organic separates to carbon dynamics and its modelling in some cultivated soils. European Journal of Soil Science 47: 485–493

Buyanovsky GA, Aslam M & Wagner GH (1994) Carbon turnover in soil physical fractions. Soil Science Society America Journal 58: 1167–1173

Bonde TA, Christensen BT & Cerri CC (1992) Dynamics of soil organic matter as reflected by natural ^{13}C abundance in particle size fractions of forested and cultivated oxisols. Soil Biology and Biochemistry 24: 275–277

Cambardella CA & Elliott ET (1992) Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Science Society America Journal 56: 777–783

Cambardella CA & Elliott ET (1993) Methods for physical separation and characterization of soil organic matter fractions. Geoderma 56: 449–457

Christensen BT (1992) Physical fractionation of soil and organic matter in primary particle size and density separates. In: Stewart BA (Ed) Advances in Soil Science, Vol. 20 (pp 1–90). Springer-Verlag, New York

Christensen BT (1996) Matching measurable soil organic matter fractions with conceptual pools in simulation models of carbon turnover: revision of model structure. In: Powlson DS, Smith P & Smith JU (Eds) Evaluation of Soil Organic Matter Models, NATO ASI Series, Vol. I 38 (pp 143–159). Springer-Verlag, Berlin

Cooter EJ (1998) General circulation model scenarios for the southern United States. In: Mickler RA & Fox S (Eds) The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment (pp 15–54). Springer, New York

Elliott ET & Cambardella CA (1991) Physical separation of soil organic matter. Agriculture, Ecosystems, and Environment 34: 407–419

Gee GW & Bauder JW (1986) Particle-size analysis. In: Klute A (Ed) Methods of Soil Analysis, Part I. Physical and Mineralogical Methods (pp 383–411). Soil Science Society of America, Madison, Wisconsin

Gregorich EG, Ellert BH & Monreal CM (1995) Turnover of soil organic matter and storage of corn residue carbon estimated from natural ^{13}C abundance. Canadian Journal of Soil Science 75: 161–167

Harrison, KG, Broecker WS & Bonani G (1993) The effect of changing land use on soil radiocarbon. Science 262: 725–726

Harrison KG (1997) Using bulk soil radiocarbon measurements to estimate soil organic matter turnover times. In: Lal R, Kimble JM, Follett RF & Stewart BA (Eds) Soil Processes and the Carbon Cycle (pp 549–559). CRC Press, Boca Raton, Florida

Hendrick RL & Pregitzer KS (1993) The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. Canadian Journal of Forest Research 23: 2507–2520

Hudson RJM, Gherini SA & Goldstein RA (1994) Modeling the global carbon cycle: nitrogen fertilization of the terrestrial biosphere and the "missing" CO_2 sink. Global Biogeochemical Cycles 8: 307–333

Insam H (1990) Are the soil microbial biomass and basal respiration governed by the climatic regime? Soil Biology and Biochemistry 22: 525–532

IPCC (The International Panel on Climate Change) (1998) Summary for policymakers – The regional impacts of climate change: An assessment of vulnerability, In: Watson RT, Zinyowera MC & Moss RH (Eds) A Special Report of IPCC Working Group II, International Panel on Climate Change, Geneva, Switzerland

Janzen HH, Campbell CA, Brandt SA, Lafond GP & Townley-Smith L (1992) Light-fraction organic matter in soils from long-term crop rotations. Soil Science Society America Journal 56: 1799–1806

Jastrow, JD (1996) Soil aggregate formation and the accrual of particulate and mineral-associated organic matter. Soil Biology and Biochemistry 28: 656–676

Jenkinson DS 1990. The turnover of organic carbon and nitrogen in soil. Philosophical Transactions of the Royal Society of London, Series B – Biological Sciences 329: 361–368

Jenkinson DS & Rayner JH (1977) The turnover of soil organic matter in some of the Rothamsted classical experiments. Soil Science 123: 298–305

Johnson DW & Lindberg SE (1992) Atmospheric Deposition and Forest Nutrient Cycling: A Synthesis of the Integrated Forest Study. Springer-Verlag, New York

Johnson DW, Van Miegroet H, Lindberg SE, Todd DE & Harrison RB (1991) Nutrient cycling in red spruce forests of the Great Smoky Mountains. Canadian Journal of Forest Research 21: 769–787

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

Lietzke DA (1994) Soils of Walker Branch Watershed, ORNL/TM-11724. Oak Ridge National Laboratory, Oak Ridge, TN

Lovett GM & Lindberg SE (1993) Atmospheric deposition and canopy interactions of nitrogen in forests. Canadian Journal of Forest Research 23: 1603–1616

Oades JM (1988) The retention of organic matter in soils. Biogeochemistry 5: 35–70

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322–331

Nadelhoffer KJ & Raich JW (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73: 1139–1147

Nicholas NS, Zedaker SM & Eagar C (1992) A comparison of overstory community structure in three southern Appalachian spruce-fir forests. Bulletin of the Torrey Botanical Club 119: 316–332

Parton WJ, Schimel DS, Cole CV and Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society America Journal 51: 1173–1179

Parton WJ, Stewart JWB & Cole CV (1988) Dynamics of C, N, P, and S in grassland soils: a model. Biogeochemistry 5: 109–131

Raich JW & Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems: global trends. Ecology 70: 1346–1354

Schimel DS (1995) Terrestrial ecosystems and the carbon cycle. Global Change Biology 1: 77–91

Schlesinger WH (1990) Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature 348: 232–234

Sharpe DM, Cromack K, Jr., Johnson WC & Ausmus BS (1980) A regional approach to litter dynamics in southern Appalachian forests. Canadian Journal of Forest Research 10: 395–404

Sollins P, Spycher G & Glassman CA (1984) Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. Soil Biology and Biochemistry 16: 31–37

Spycher G, Sollins P & Rose S (1983) Carbon and nitrogen in the light fraction of a forest soil: vertical distribution and seasonal patterns. Soil Science 135: 79–87

Torn MS, Trumbore SE, Chadwick OA, Vitousek PM & Hendricks DM (1997) Mineral control of soil organic carbon storage and turnover. Nature 389: 170–173

Townsend AR, Vitousek PM & Trumbore SE (1995) Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. Ecology 76: 721–733

Trumbore SE, Chadwick OA & Amundson RR (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science 272: 393–396

Van Dam D, Veldkamp E & Van Breemen N (1997) Soil organic carbon dynamics: variability with depth in forested and deforested soils under pasture in Costa Rica. Biogeochemistry 39: 343–375

Winkler JP, Cherry RS & Schlesinger WH (1996) The Q_{10} relationship of microbial respiration in a temperate forest soil. Soil Biology and Biochemistry 28: 1067–1072