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Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes

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Abstract. Temperate forests of North America are thought to be significant sinks of atmospheric CO₂. We developed a below-ground carbon (C) budget for well-drained soils in Harvard Forest Massachusetts, an ecosystem that is storing C. Measurements of carbon and radiocarbon (¹⁴C) inventory were used to determine the turnover time and maximum rate of CO₂ production from heterotrophic respiration of three fractions of soil organic matter (SOM): recognizable litter fragments (L), humified low density material (H), and high density or mineral-associated organic matter (M). Turnover times in all fractions increased with soil depth and were 2–5 years for recognizable leaf litter, 5–10 years for root litter, 40–100+ years for low density humified material and >100 years for carbon associated with minerals. These turnover times represent the time carbon resides in the plant + soil system, and may underestimate actual decomposition rates if carbon resides for several years in living root, plant or woody material.

Soil respiration was partitioned into two components using ¹⁴C: recent photosynthate which is metabolized by roots and microorganisms within a year of initial fixation (Recent-C), and C that is respired during microbial decomposition of SOM that resides in the soil for several years or longer (Reservoir-C). For the whole soil, we calculate that decomposition of Reservoir-C contributes approximately 41% of the total annual soil respiration. Of this 41%, recognizable leaf or root detritus accounts for 80% of the flux, and 20% is from the more humified fractions that dominate the soil carbon stocks. Measurements of CO₂ and ¹⁴CO₂ in the soil atmosphere and in total soil respiration were combined with surface CO₂ fluxes and a soil gas diffusion model to determine the flux and isotopic signature of C produced as a function of soil depth. 63% of soil respiration takes place in the top 15 cm of the soil (O + A + Ap horizons). The average residence time of Reservoir-C in the plant + soil system is 8±1 years and the average age of carbon in total soil respiration (Recent-C + Reservoir-C) is 4±1 years.

The O and A horizons have accumulated 4.4 kgC m⁻² above the plow layer since abandonment by settlers in the late-1800's. C pools contributing the most to soil respiration have short enough turnover times that they are likely in steady state. However, most C is stored as humified organic matter within both the O and A horizons and has turnover times from 40 to

100+ years respectively. These reservoirs continue to accumulate carbon at a combined rate of 10–30 gC m⁻² yr⁻¹. This rate of accumulation is only 5–15% of the total ecosystem C sink measured in this stand using eddy covariance methods.

Introduction

Well drained temperate forest soils in the northeastern United States have accumulated carbon (C) over the past century as forest has regrown over former fields and pastures. The rate at which mid-latitude forest vegetation and forest soils are still accumulating C and can act to ameliorate future anthropogenic inputs of CO₂ to the atmosphere is still uncertain. The capacity for ecosystems to store CO₂ depends both on their productivity and the residence time of C (Thompson et al. 1996). Hence, the average time between fixation of C by photosynthesis and its return to the atmosphere by respiration or decomposition is an important parameter for determining the timing and magnitude of C storage or release in response to disturbances like climate or land use change (Fung et al. 1997).

Eddy flux tower measurements made since 1990 in a temperate deciduous forest in central Massachusetts (Harvard Forest) show consistent net ecosystem uptake of C averaging nearly 200 gC m⁻² yr⁻¹ (Wofsy et al. 1993; Goulden et al. 1996). Interannual variability in the rate of net C storage has been linked to climate (Goulden et al. 1996). The Harvard Forest is growing on land used for agriculture or pasture in the 19th century and was damaged by a hurricane in 1938. Net carbon storage in a forest recovering from these disturbances is not surprising. However, the partitioning of C storage among vegetation and soils at this site is unknown, as is the potential for C storage rates to change in the future as recovery from disturbance progresses.

The goal of this work is to quantify the below ground carbon cycle in well drained soils that dominate the footprint of the eddy flux tower at the Harvard Forest. We use radiocarbon (¹⁴C) measurements in soil organic matter (SOM) and CO₂ to quantify the residence time of C in the plant + soil system and to determine the contribution of well-drained soils to the net sink measured by Wofsy et al. (1993) and Goulden et al. (1996). We also partition total soil respiration into two components using ¹⁴C: (1) root respiration and microbial metabolism of recent photosynthate within a year of initial fixation (Recent-C), and (2) CO₂ derived from microbial decomposition of SOM that resides in the soil longer than a year (Reservoir-C).

Radiocarbon measurements of SOM and CO₂ are an extremely useful tool to determine the dynamics of soil carbon. ¹⁴C produced by atmospheric weapons testing in the early 1960's (i.e. 'bomb C') is used as an isotopic

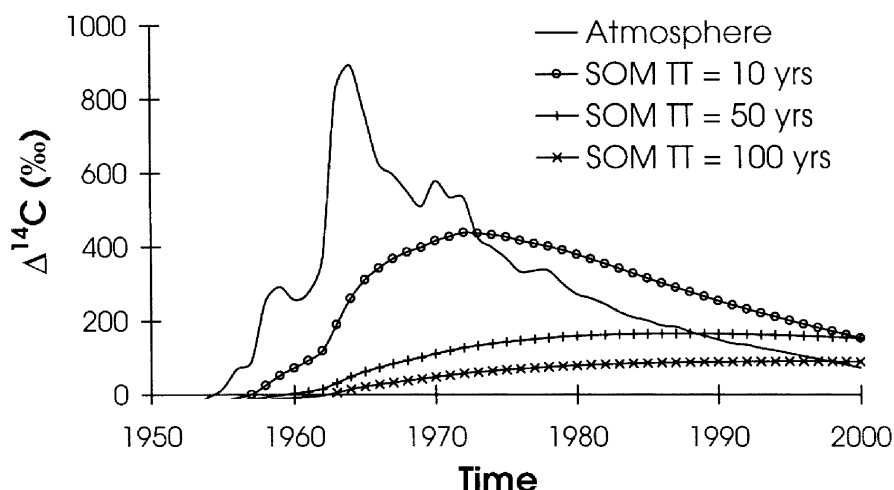


Figure 1. The time record of ^{14}C in the atmosphere (Northern Hemisphere) based on grapes grown in Russia (Burchuladze et al. 1989) for 1950–1977 and direct atmospheric measurements for 1977–1996 (Levin & Kromer 1997). We express radiocarbon data here as $\Delta^{14}\text{C}$, the difference in parts per thousand (per mil or ‰) between the $^{14}\text{C}/^{12}\text{C}$ ratio in the sample compared to that of a universal standard (oxalic acid I, decay-corrected to 1950). All samples are corrected for mass-dependent isotopic fractionation to -25‰ in $\delta^{13}\text{C}$. Expressed in this way, $\Delta^{14}\text{C}$ values greater than zero contain bomb-produced radiocarbon, and those with $\Delta^{14}\text{C}$ less than zero indicate that carbon in the reservoir has, on average, been isolated from exchange with atmospheric $^{14}\text{CO}_2$ for at least the past several hundred years. The ^{14}C content of a homogeneous, steady state C reservoir with turnover times of 10, 50 or 100 years is compared with that of the atmosphere through time.

tracer for C cycling on decadal time-scales. Carbon reservoirs such as SOM that exchange with the atmosphere reflect the rate of exchange through the amount of ‘bomb’ ^{14}C incorporated (Figure 1). ^{14}C in atmospheric CO_2 is currently decreasing at a rate of about 8‰ per year (Levin & Kromer 1997) because of uptake by the ocean and dilution by burning of ^{14}C -free fossil fuels. The ^{14}C content of a homogeneous C reservoir in any given year since 1963 may be predicted from the turnover time and the known record of atmospheric $^{14}\text{CO}_2$. Utilization of bomb-produced ^{14}C as a continuous isotopic label has advantages over other isotopic methods because it can be used in undisturbed ecosystems and can resolve dynamics that operate on annual to decadal time scales.

Soil organic matter is made up of C fractions that cycle on a continuum of time scales ranging from days to millennia. Because of this complexity, ^{14}C measurements of bulk SOM at a single point in time do not yield useful information about the rate of SOM cycling (Trumbore, in press). At the Harvard Forest, we separated SOM into distinct pools with different characteristic

Organic Horizons

Oi → Whole Sample → L_L Leaf Litter

Oe+Oa → Hand Picking → L_R Recognizable root litter
 → H Humified Material

Mineral Horizons

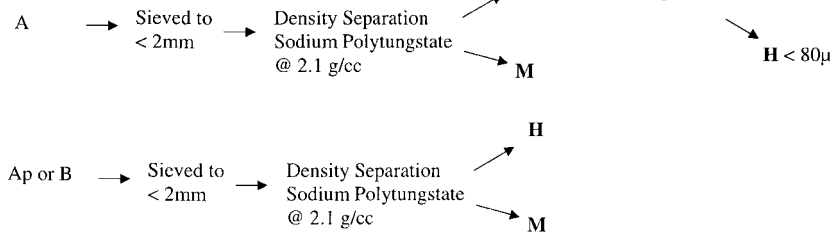


Figure 2. Schematic representation of soil sample processing into the homogeneous soil organic matter pools as defined in this paper; L_L or L_R (recognizable leaf or root litter respectively), H (undifferentiable SOM which is considered to be microbially altered or *humified*), and M (organic matter associated with *mineral* surfaces). All L_L, L_R and H components are low density (i.e. <2.1 g/cc) while the M components are considered high density (i.e. >2.1 g/cc).

turnover times (see Figure 2): recognizable leaf (L_L) and recognizable fine (<2 mm) root litter (L_R), organic matter that has been transformed by microbial action or humified, but is not stabilized by interactions with mineral surfaces (H), and organic matter that is associated with soil minerals and thus is separable by density (M). These four pools collectively comprise Reservoir-C as defined for this paper and represent detrital C that remains in the soil for one year or more. Carbon pools in SOM that cycle on timescales of less than one year are included in our definition of Recent-C.

Carbon dynamics derived from measurements of ¹⁴C in SOM fractions alone tend to underestimate the flux of CO₂ from soils. Heterotrophic respiration is dominated by decomposition of C with short turnover times and small reservoirs that are difficult to measure. The majority of easily measurable SOM stocks represent slowly cycling material with relatively long turnover times. Measurements of ¹⁴C in CO₂ can be used to determine the relative contributions of the recalcitrant C, which dominates SOM stocks, and the more rapidly cycling C, which dominates heterotrophic and autotrophic respiration. To derive a below-ground C budget that includes soil respiration, we combined measurements of CO₂ and ¹⁴CO₂ surface fluxes and soil

atmosphere profiles with a model of soil gas diffusion to determine the rate and ^{14}C signature of CO_2 production in soil by horizon. This, combined with the predicted production of CO_2 and $^{14}\text{CO}_2$ derived from the L_L , L_R , H and M fractions of SOM, allowed us to partition soil respiration into Recent-C and Reservoir-C.

Site description

The Harvard Forest is a mixed deciduous forest located near the town of Petersham in central Massachusetts. The study area is located on the Prospect Hill Tract (42.54° N, 72.18° W). The terrain is moderately hilly (average elevation 340 m) and currently about 95% forested (Wofsy et al. 1993). The soils are developed on glacial till deposits which are predominantly granitic. Drainage varies from well-drained uplands, which make up most of the area in the flux tower footprint, to very poorly drained swamps. The data reported here are for well drained soils with very low clay content and mapped as Canton Series (coarse-loamy over sandy or sandy skeletal, mixed mesic Typic Dystrachrepts). We sampled soils, soil respiration and soil gas profiles within 100 meters of the eddy flux tower where a multi-year record of soil respiration measured by flux chambers is maintained (Davidson et al. 1998). The sites are within a mixed deciduous stand, dominated by red oak (*Quercus rubra*) and red maple (*Acer rubrum*) with some hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*). The area comprising our study site was cleared in the mid-1800's, plowed and used primarily for pasture. The pasture was abandoned between 1860 and 1880 (Foster 1992). The regrowing forest was largely leveled by a hurricane in 1938 but has been growing undisturbed since that time.

Methods

Field

We sampled soils using the quantitative pit methodology as discussed by Huntington et al. (1989) and Hamburg (1984). This method involves sampling a large volume of soil to allow calculation of horizon-specific bulk densities. Two 0.5×0.5 m quantitative pits were dug in 1996 to a depth of about 80 cm. Pit locations were selected to be similar to those where Davidson et al. (1998) are monitoring soil respiration and soil CO_2 concentrations and are within 20 meters of their soil respiration collars. In each pit excavation proceeded downward to the base of each pedogenic horizon, which was differentiated

by color and textural changes. In order to minimize sampling errors due to repeated grid placement and removal, the top of each pedogenic horizon was calculated by taking a weighted mean of 25 measurements from within the 0.5×0.5 m grid. This system weights the center nine measurements 4×, the sides of the grid (not including the corners) 2× and the corners 1×. Additional samples which integrated each soil horizon were collected for radiocarbon and total C and N analyses from one of the pit faces. Samples of the forest floor (0.15×0.15 m squares), core samples of A horizons and grab samples of Ap and B horizons were collected in order to analyze the abundance and ¹⁴C of roots. During the summer of 1997, a third, shallower (0.17 m × 0.37 m) pit was dug to obtain more data for the O and A horizons. Samples were taken in approximately 2 cm vertical increments to the base of the Ap horizon.

Collars sampled were the same as those used by Davidson et al. (1998) to monitor soil respiration fluxes. Closed dynamic chambers were used for sampling isotopes in soil respiration, as shown in Figure 3. First, atmospheric CO₂ initially inside the chamber cover was removed by circulating air at flow rates of ~0.5 L min⁻¹ from the chamber headspace through a column filled with soda lime. Scrubbing continued until the equivalent of two to three chamber volumes had been passed over the soda lime. Then the air flow was switched and flowed through a molecular sieve trap (mesh size 13×). Molecular sieve 13× traps CO₂ quantitatively at room temperatures and then releases it when baked at 475 °C (Bauer et al. 1992). CO₂ was trapped from circulating chamber air until the amount required for isotopic (¹³C and ¹⁴C) measurements (~2 mg of C) was collected. Trapping times varied from about 10 minutes to an hour, depending on the soil CO₂ emission rate. To achieve 100% yields of CO₂ from the molecular sieve traps we have found that it is important to put a desiccant in-line (Drierite) in order to minimize the amount of water getting to the molecular sieve

To measure CO₂ and its ¹⁴C signature in the soil atmosphere we collected soil gas samples from stainless steel tubes (3 mm OD) inserted horizontally into soil pit walls (the soils pits were subsequently backfilled). The air within the tubing was first purged by extracting a 15 ml syringe sample through a fitting with a septum. Two more 5 ml samples were then withdrawn from each tube, the syringes were closed with a stopcock, and the CO₂ concentrations of the syringe samples were analyzed the same day in a LiCor infrared gas analyzer as described by Davidson and Trumbore (1995). For the ¹⁴C analysis, we filled evacuated stainless steel cans (0.5–2.0 L volume) by attaching them to the buried stainless steel tubes. A flow restrictor was used to fill the cans slowly during a 4 hour period so as to minimize disturbance of the concentration gradient. The soil gas tubes were installed along with

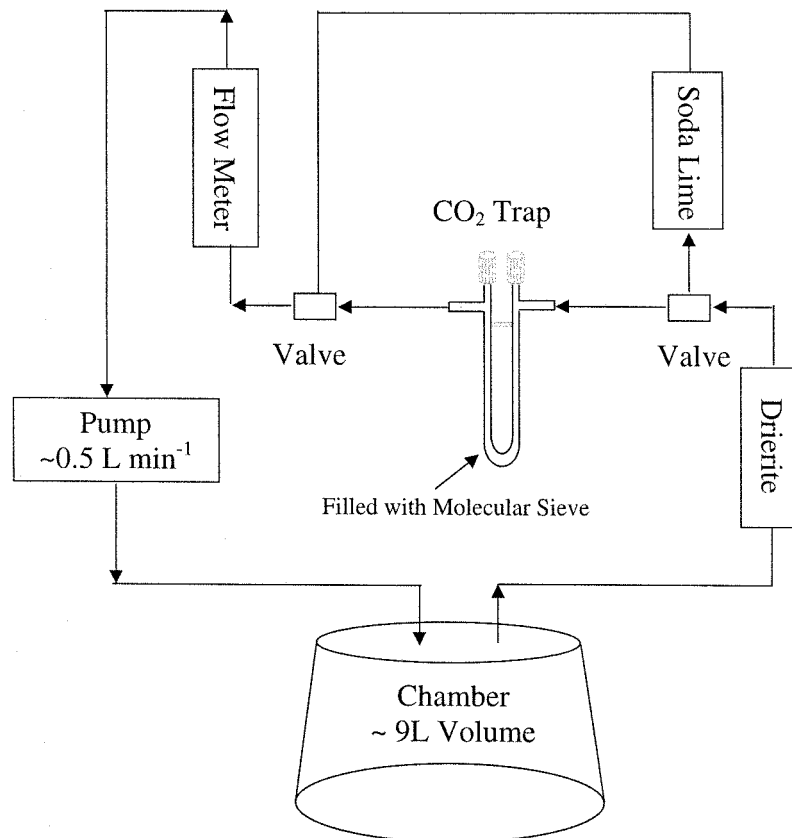


Figure 3. Sampling scheme for trapping CO₂ on molecular sieve (mesh size 13×) using a closed dynamic chamber system. Molecular sieve 13× traps CO₂ quantitatively at room temperatures and then releases it when baked at 475 °C (Bauer et al. 1992). The evolved CO₂ is purified cryogenically.

TDR and temperature probes in one pit in 1995 (not dug quantitatively for bulk density) and in a second pit dug in 1996 (dug quantitatively as discussed above). All pits were located within a few meters of each other. The concentrations of CO₂, water content, and temperature were measured weekly during the summer, once every two weeks during the autumn and spring, and once per month during the winter.

Aboveground litter inputs were collected in six 0.41 by 0.41 m baskets. Each basket was screened at the base and nailed into the ground. Samples were collected, dried and weighed, once in the spring and then on a biweekly basis from late September through early November 1996.

Laboratory

Prior to C and ^{14}C analyses, soil samples were separated into different SOM fractions as defined for this paper (L_L , L_R , H and M) according to procedures outlined in Figure 2. For mineral samples, material that was less than 2.1 g/cc was primarily humified material (H). Fine roots (L_R) were a significant component of low density organic matter only in the A horizon samples. To test for the importance of L_R in determining bulk low density ^{14}C values, after density separation, one A horizon sample was sieved to 80 μ and then hand picked to separate H from L_R components for ^{14}C analysis. The A_p , $Bw1$ and $Bw2$ horizons had such a small proportion of fine root material this additional processing was not performed. Once a soil C fraction was isolated, it was split and half the sample was archived while the other half was ground or finely chopped and analyzed for carbon and nitrogen content in a Fisons 5200 Elemental Analyzer. Grinding was done with an air cyclone sampler for the O_i horizon. $O_e + O_a$ samples and root samples were chopped finely with scissors and mineral samples were ground by hand with a mortar and pestle.

In order to quantify fine root biomass, samples were taken by coring or from subsamples dug from our quantitative pits. Samples were frozen immediately after collection, then stored and processed at the Woods Hole Research Center. $O_e + O_a$ horizons were thawed, a sub-sample removed (approximately 8 cm³) and quantitatively picked for fine roots (<2 mm in diameter). Mineral soils were thawed, sieved through a 5.6 mm sieve and the fine roots that did not pass through the sieve were weighed. In order to pick live versus dead fine roots, a sub-sample of the sieved soil was used (approximately 8 cm³). Graphite targets of all SOM fractions and soil gas (CO_2) were prepared at UCI using sealed tube zinc reduction methods (Vogel et al. 1992). The ^{14}C analyses of these targets were made by accelerator mass spectrometry (AMS) at the Center for AMS, Lawrence Livermore Laboratory, Livermore, California (Southon et al. 1992). Radiocarbon data are expressed as $\Delta^{14}\text{C}$, the per mil deviation from the $^{14}\text{C}/^{12}\text{C}$ ratio of oxalic acid standard in 1950, with sample $^{14}\text{C}/^{12}\text{C}$ ratio corrected to a $\delta^{13}\text{C}$ value of -25‰ to account for any mass dependent isotopic fractionation effects (Stuiver & Polach 1977). The precision for radiocarbon analyses prepared using the zinc reduction technique in our laboratory is $\pm 7\text{‰}$ for values close to modern (0‰).

We measured ^{13}C in a subset of our SOM samples to determine the proper ^{13}C correction for calculating $\Delta^{14}\text{C}$ values. Low density samples had $\delta^{13}\text{C}$ values which ranged between -24.78 and -27.57‰ . Low density H fractions averaged 0.38‰ higher in ^{13}C than the M fractions (density $> 2.1 \text{ gC m}^{-3}$). Because the overall variation in $\delta^{13}\text{C}$ was greater than the difference between

fractions, we used the same correction (-26%) for all SOM. The maximum error introduced to our ^{14}C determination by this assumption (5.1%) is less than the analytical uncertainty of 7% .

Measurements of ^{13}C for surface CO_2 flux samples were used to correct for mass dependent fractionation as well as to correct for incomplete stripping of atmospheric CO_2 in the chamber system during CO_2 trapping. The $\delta^{13}\text{C}$ value for CO_2 in air ($\delta^{13}\text{C}_{\text{atmosphere}}$) is $\sim -8.5\%$, whereas the $\delta^{13}\text{C}$ of soil respiration should be close to that of SOM ($\delta^{13}\text{C}_{\text{soil}} = -26\%$). The fraction of air (X) in our sample is then:

$$X = \frac{\delta^{13}\text{C}_{\text{measured}} - \delta^{13}\text{C}_{\text{soil}}}{\delta^{13}\text{C}_{\text{atmosphere}} - \delta^{13}\text{C}_{\text{soil}}}, \quad (1)$$

and we calculate the $\Delta^{14}\text{C}$ of the soil respiration:

$$\Delta^{14}\text{C}_{\text{soil}} = \frac{\Delta^{14}\text{C}_{\text{measured}} - X \times \Delta^{14}\text{C}_{\text{atmosphere}}}{(1 - X)}. \quad (2)$$

The value of $\delta^{13}\text{C}_{\text{atmosphere}}$ at the level of the respiration collars ($\sim 5\text{--}10$ cm) can become as light as $\sim -11\%$ due to atmospheric inversion which traps plant respired CO_2 and any fossil fuel derived CO_2 (particularly in winter) near the surface. Therefore, during each sampling event we trap one air sample and analyze this for $\delta^{13}\text{C}$. The resulting $\delta^{13}\text{C}$ is then used for $\delta^{13}\text{C}_{\text{atmosphere}}$ in calculation of equations 1 and 2 for that suite of samples. Values of X ranged between 0.09 and 0.61. The highest values of X are associated with the samples taken in May, 1996, when no attempt was made to strip the initial chamber of atmospheric CO_2 (values in May were 0.61, 0.49, 0.40 and 0.34). For the July, September and December sampling events when 2–3 chamber volumes were stripped prior to sampling, values of X were all below 0.31 with an average of 0.17.

Modeling

Our methods for data analysis involve four modeling components: 1) determination of CO_2 production by horizon, 2) estimation of $\Delta^{14}\text{C}$ of CO_2 produced within each horizon, 3) calculation of the amount of CO_2 derived from decomposition of Reservoir-C sources and 4) partitioning of soil respiration into Recent- versus Reservoir-C sources based on a C and ^{14}C mass balance approach. Each modeling component is discussed in turn below.

(1) CO_2 production within each horizon

The production of CO_2 within each horizon was calculated by combining estimates of diffusivity with measured CO_2 concentration gradients. Effective

diffusivity was estimated for each soil horizon using the model of Millington and Quirk (1961), modified for the presence of rocks and for temperature:

$$\frac{D_s}{D_o} = \alpha^{2x} \left(\frac{\alpha}{\varepsilon} \right)^2 \times \frac{(100 - \%RF)}{100} \times \left(\frac{T}{273} \right)^{1.75}, \quad (3)$$

where D_s is the diffusion coefficient in soil, D_o is the diffusion coefficient of CO_2 in air ($0.139 \text{ cm}^2 \text{ s}^{-1}$ at $273 \text{ }^\circ\text{K}$ at standard pressure), α is the total air-filled porosity, ε is the total porosity, %RF is the percent rock fraction, and T is the soil temperature ($^\circ\text{K}$). As described by Collin and Rasmuson (1988) and by Davidson and Trumbore (1995), the exponential term, $2x$, is usually close to $4/3$, and can be approximated by the polynomial

$$x = 0.477\alpha^3 - 0.596\alpha^2 + 0.437\alpha + 0.564 \quad (4)$$

The first term in the Millington and Quirk (1961) equation estimates diffusivity in the wet porous soil medium. The second term, which we have added here, adjusts for rock content of these glacial soils, assuming that diffusion of gases through rocks is negligible. The third term, adjusts for the effect of temperature on gaseous diffusion (Hendry et al. 1993). Total porosity is estimated as

$$\varepsilon = 1 - \left(\frac{BD}{PD} \right), \quad (5)$$

where BD is bulk density of the $<2 \text{ mm}$ soil fraction measured in our quantitatively sampled soil pits, and PD is a weighted average of particle density, assuming that organic matter has a PD of 1.4 g cm^{-3} and soil minerals have a PD of 2.65 g cm^{-3} . Air filled porosity (α) was calculated as the difference between total porosity and volumetric water content measured by time domain reflectometry (TDR) probes, as described by Davidson et al. (1998).

The soil CO_2 concentration profile was fitted to an exponential function (Figure 4):

$$[\text{CO}_2]_z = \text{CO}_{2\infty}(1 - e^{-\beta z}) + 0.04, \quad (6)$$

where $[\text{CO}_2]_z$ is the concentration of CO_2 at depth z in percent, $\text{CO}_{2\infty}$ is the fitted asymptotic CO_2 concentration at infinite depth, z is soil depth in cm, β is a fitted parameter, and 0.04 is an adjustment for the approximate concentration of CO_2 at the soil surface (i.e., about $400 \text{ } \mu\text{L CO}_2 \text{ L}^{-1}$ air). The first derivative of this equation is used to estimate the diffusion gradient as a function of depth:

$$\frac{d\text{CO}_2}{dz} = \text{CO}_{2\infty} \times \beta \times e^{-\beta z}. \quad (7)$$

CO₂ Flux and Production Estimates

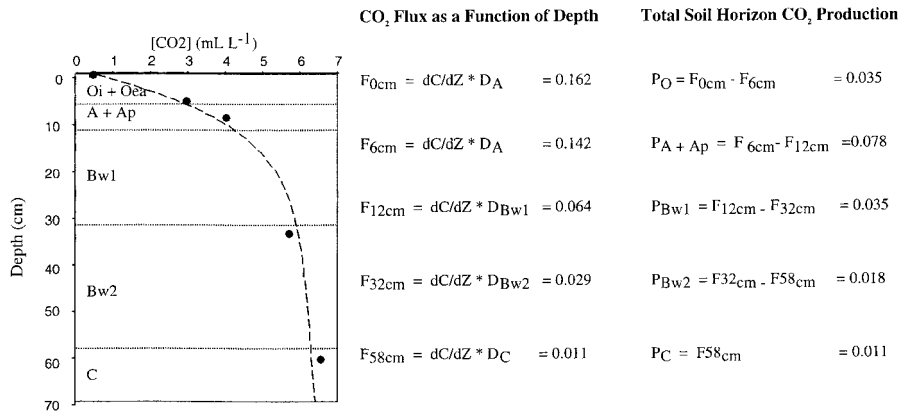


Figure 4. Calculation of CO₂ flux estimates by depth (F_z , where z indicates the profile depth) and CO₂ production estimates by soil horizon (P_h , where h indicates the specific soil horizon) in $\text{gC m}^{-2} \text{hr}^{-1}$. The values shown here are from measurements made on 25 August 1997. Interpolations among similar measurements made throughout the year were summed to obtain annual estimates. These estimates are for well drained soils within the footprint of the eddy flux tower at Harvard Forest.

Applying Fick's first law and combining equations, the flux of CO₂ at a given depth (F_z) can be calculated from the product of the diffusion gradient and the effective diffusivity:

$$F_z = \frac{d\text{CO}_2}{dz} \times D_s \times \frac{52700}{T} = \text{CO}_{2\infty} \times \beta \times e^{-\beta z} \times \alpha^{2x} \left(\frac{\alpha}{\varepsilon}\right)^2 \times \frac{(100 - \%RF)}{100} \times \left(\frac{T}{273}\right)^{1.75} \times D_o \times \left(\frac{52700}{T}\right), \quad (8)$$

where F_z has units of $\text{gC m}^{-2} \text{hr}^{-1}$, and where $52700/T$ is the factor needed to convert to these units.

Using this equation, the flux at the top of each mineral soil horizon (see Figure 4) was calculated for each sampling date in each of the two instrumented soil pits. Our approach to calculating diffusivity differs from many others (e.g., de Jong and Schappert 1972; Johnson et al. 1994; Mattson 1995), in which the flux was calculated from an assumed linear diffusion gradient between two points where CO₂ concentrations were measured. The exponential fit used here for characterizing the CO₂ profiles (Figure 4), while imperfect, appears more appropriate.

Finally, estimation of the production of CO₂ within each genetic horizon (P_h) was calculated from the difference between the flux at the top and bottom of a given soil horizon such that

$$P_h = F_{h-out} - F_{h-in}, \quad (9)$$

where F_{h-out} and F_{h-in} correspond to the appropriate F_z (Figure 4). Production within the O horizon was estimated by the difference between the mean of the six surface chamber flux measurements and the calculated flux at the top of the A horizon. This approach avoids the difficult problem of estimating diffusivity in the O horizons, where small differences in measured bulk density and water content (both of which are difficult to measure well) would have a large effect on our estimate, and where diffusion may not always be the dominant mechanism of gas transport.

(2) *Δ¹⁴C of CO₂ produced within each horizon*

The total CO₂ and ¹⁴CO₂ flux leaving a soil horizon results from a mixture of the CO₂ that is diffusing through that horizon and that which is produced within the horizon. Therefore, based on horizon specific estimates of CO₂ production (P_h) and measurements of the ¹⁴C in CO₂ coming into (ΔF_{h-in}) and going out (ΔF_{h-out}) of a subset of the soil horizons (in this notation, Δ refers to ¹⁴C of F in ‰ units, and not “change in F”), we can use a simple mixing equation to calculate the ¹⁴C of CO₂ produced within that horizon (ΔP_h) from both Recent- and Reservoir-C sources. The equations used to calculate ΔP_h (in ‰ units) from CO₂ production rates and fluxes (in gC m⁻² yr⁻¹) are Equation 9 and

$$(F_{h-in} + P_h) \times \Delta F_{h-out} = F_{h-in} \times \Delta F_{h-in} + P_h \times \Delta P_h \quad (10)$$

In this approach chamber measurements of ¹⁴C in CO₂ from the surface efflux serve as ΔF_{h-out} for the O horizon and are used to calculate ΔP_h for the entire O horizon. We lumped O, A and Ap horizons (representing the top ~15 cm) because of the large variability in the ¹⁴CO₂ data available for constraining the O/A and A/Ap transitions.

(3) *Decomposition of Reservoir-C*

We calculate decomposition of Reservoir-C fluxes by first calculating turnover times for each SOM component using its ¹⁴C signature and then calculating a decomposition flux based on that turnover time.

(3.1) *SOM turnover times from ¹⁴C*

We used two approaches to determine turnover times for SOM fractions from radiocarbon measurements. For organic matter in the Oi and mineral horizons

(Ap and B), we used a time-dependent, steady state model as presented in Trumbore et al. (1995):

$$C_{(t)} \times R_{\text{som}(t)} = I \times R_{\text{atm}(t)} + C_{(t-1)} \times R_{\text{som}(t-1)} - k \times C_{(t-1)} \times R_{\text{som}(t-1)} - \lambda \times C_{(t-1)} \times R_{\text{som}(t-1)}, \quad (11)$$

collecting terms:

$$R_{\text{som}(t)} = \frac{I \times R_{\text{atm}(t)} + (C_{(t-1)} \times R_{\text{som}(t-1)} \times (1 - k - \lambda))}{C_{(t)}}, \quad (12)$$

where:

- C = Stock of carbon for the given C pool in gC m^{-2}
- I = Inputs of C above and below ground in $\text{gC m}^{-2} \text{yr}^{-1}$
- k = Decomposition rate of SOM in yr^{-1}
- R = $\left(\frac{\Delta^{14}\text{C}}{1000}\right) - 1$
- R_{atm} = The ratio of ^{14}C in the atmosphere normalized to a standard.
- R_{som} = The ratio of ^{14}C in the given SOM pool: L, H or M, normalized to a standard.
- λ = radioactive decay constant for $^{14}\text{C} = 1/8267$ years.
- t = time (year) for which calculation is being performed

I and k are adjusted to match both observed C inventory and ^{14}C content for the fraction in 1996. Note that the R_{som} at any time t, depends not only on the $R_{\text{atm}(t)}$ but on both C inventory and R_{atm} of previous years.

For the Oe + Oa and A horizons that have accumulated above the plow layer since abandonment between 1860 and 1880, we used a nonsteady state model that matches both the total amount of C and ^{14}C in 1996. We assumed zero initial C in 1880. Assuming constant I and k, the amount of carbon initially added in each year j (since 1880) that remains and can be measured in 1996 (C_j) will be

$$C_j = I \times e^{-k(1996-j)}, \quad (13)$$

The ^{14}C signature of C_j will be $R_{\text{atm}(j)}$. Therefore the total amount of carbon and radiocarbon measured in 1996 is shown by Equations 14 and 15, respectively:

$$C_{1996} = \sum_{j=1880}^{j=1996} C_j, \quad (14)$$

$$R_{\text{som}(1996)} = \frac{\sum_{j=1880}^{j=1996} R_{\text{atm}(j)} \times C_j}{\sum_{j=1880}^{j=1996} C_j}. \quad (15)$$

Again, I and k were adjusted until they matched observations of C and ^{14}C for each fraction in Oe + Oa and A horizons. The rate of accumulation of carbon for a given fraction in 1996 is the difference in C inventory calculated for 1995 and 1996.

Both steady state and nonsteady state accumulation models assume (1) all carbon within a given SOM fraction (L_L , L_R , H, or M) is homogenous with respect to decomposition; (2) the time lag between photosynthetic fixation and addition of fixed C to SOM is one year or less (i.e. the $\Delta^{14}\text{C}$ of C added to each SOM fraction each year is equal to $R_{\text{atm}(j)}$) and (3) radiocarbon does not fractionate during respiration. We have already corrected for mass-dependent fractionation effects when calculating $\Delta^{14}\text{C}$ values. Any time lag that does exist between photosynthetic fixation and addition of fixed C to SOM (contrary to Assumption 2) will cause an overestimation of turnover time (TT) equal to this lag (Thompson & Randerson 1999). Assumption 2 holds for the majority of aboveground litter inputs (deciduous leaves) which are fixed and fall to the ground within one year. Effects of this assumption with respect to other SOM inputs will be discussed later in the text. Figure 5 shows the $\Delta^{14}\text{C}$ of a SOM fraction as a function of turnover times in 1996 for both the steady-state and nonsteady state models. Significant differences between approaches appear only for fractions with turnover times greater than about 25 years. This is because the assumption of zero initial carbon in 1880 in the accumulation model limits the amount of pre-bomb ^{14}C in the SOM that is available to dilute the post-bomb carbon that has accumulated since 1963.

(3.2) Calculating SOM decomposition fluxes

Decomposition fluxes for the L_L , H and M components of SOM are determined as the inventory in each fraction divided by the turnover time derived from ^{14}C . Since the turnover times for fine roots are too uncertain (as will be discussed in the results section), we treat the flux from L_R as an unknown and solve for it in the C and ^{14}C mass balance section.

The turnover times derived from ^{14}C data may represent the time scales for C loss via several mechanisms, including (1) decomposition loss of CO_2 to the atmosphere; (2) C transfer to another SOM fraction (for example litter to humified material, i.e., L_L or L_R to H or M); or (3) loss by leaching. Data

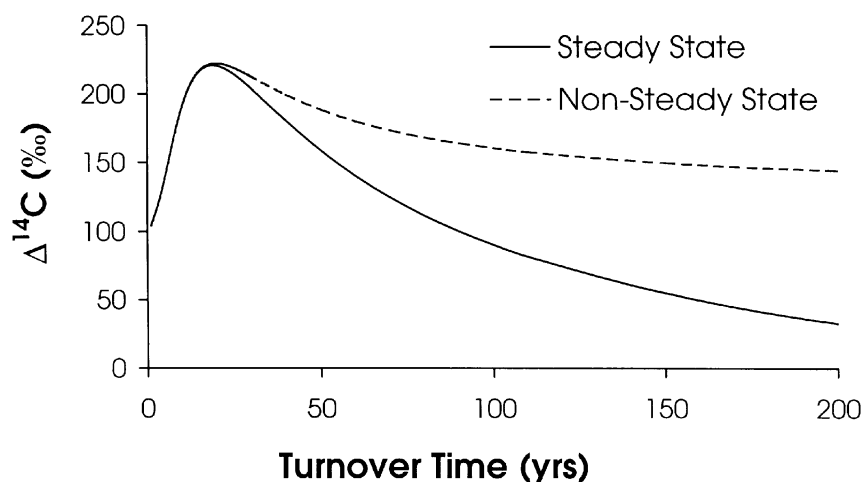


Figure 5. The predicted $\Delta^{14}\text{C}$ value in 1996 for homogeneous C reservoirs as a function of turnover times. The curves represent results for our steady state and nonsteady state (accumulation) models.

for dissolved organic carbon (DOC) transport from similar stands in Harvard Forest are available from Currie et al. (1996), and show leaching losses to be minor compared to the other fluxes, except in the O horizon where DOC loss is approximately $20 \text{ gC m}^{-2} \text{ yr}^{-1}$. This loss is only a few percent of the total annual CO_2 flux, hence we have excluded it from consideration here. Consequently, we assume all loss to be from decomposition or transfer from one C fraction to another.

We model the litter components L_L and L_R as having two fates: decomposition to CO_2 or transfer to the H or M fractions. For the H and M fractions we assume that their source of C is transfer from L_L and L_R fractions and that their most important loss process is decomposition to CO_2 . The flux of CO_2 derived from decomposition of leaf litter (F_{LL}) is the inventory of leaf C divided by its turnover time, corrected for the fraction of L_L that is transferred to the H + M pools. Since we cannot independently partition the flux of L_L into either CO_2 or a transfer flux, we bracket our estimates by assuming two extreme cases in which all of the H + M inputs come from either (1) L_L or (2) L_R .

(4) Partitioning of soil respiration sources

The total amount of radiocarbon in soil respiration equals the amount of CO_2 derived from Recent-C sources (root respiration and C metabolized within one year of original fixation; R), plus that derived from Reservoir-C (decomposition of L_L , L_R , H and M fractions that reside in the soil for longer than

one year). If the $\Delta^{14}\text{C}$ signatures of these components differ significantly, we may use a mass balance approach to determine the relative contribution of each to total soil respiration. We use an isotopic mass balance based on estimates of CO_2 production, the $\Delta^{14}\text{C}$ in CO_2 and ^{14}C -derived estimates of decomposition fluxes from the SOM fractions. For the whole soil profile, equations of mass balance for C and ^{14}C are

$$P = F_R + F_{LL} + F_{LR} + F_H + F_M \quad (16)$$

and

$$P \times \Delta P = F_R \times \Delta R_{\text{atm}(1996)} + F_{LL} \times \Delta L_L + F_{LR} \times \Delta L_R + \\ + F_H \times \Delta H + F_M \times \Delta M. \quad (17)$$

In Equations 16 and 17, P is the total annual soil respiration flux and F_R is the flux of CO_2 derived from Recent-C. F_{LL} , F_{LR} , F_H and F_M are fluxes of CO_2 derived from their respective Reservoir-C sources. The Δ values required for the ^{14}C mass balance are either measured (for ΔL_L , L_R , ΔH and ΔM), assumed to equal $\Delta R_{\text{atm}(1996)}$ (for Recent-C), or calculated from CO_2 and $^{14}\text{CO}_2$ fluxes (ΔP). For the soil profile as a whole, P and ΔP are the measured surface flux and its $\Delta^{14}\text{CO}_2$ signature respectively.

We then solved Equations 16 and 17 for the remaining unknowns, F_R and F_{LR} . Since C stocks and rates of C turnover vary vertically within the soil profile, the relative proportions of CO_2 from F_R versus the SOM fractions will vary with soil depth and horizon. Equations 16 and 17 may also be written and solved for each individual soil horizon. However, because of difficulties in characterization of the O/A horizon transition, and uncertainties in the production of roots as a function of depth, we have combined the O + A + Ap horizons and performed the ^{14}C mass balance on only three layers: the O + A + Ap (uppermost 15 cm of soil), B and C horizons.

Results

Carbon inventory

Average carbon stocks are shown in Table 1 by pedogenic horizon. Carbon stocks decrease rapidly with depth at all sites, from 470 gC Kg⁻¹ dry soil in the O horizons to less than 10 gC Kg⁻¹ dry soil for the Bw2 horizon. We report carbon inventories only to the bottom of the Bw2 horizon because the presence of large boulders limited our ability to measure bulk densities below this depth. The total C stock averages 8.8 kgC m⁻², with the majority of C

Table 1. Carbon stocks by soil horizon.

Horizon	Bulk density ^{1,2} (g cm ⁻³)	Soil carbon ³ (gC Kg ⁻¹ soil)	Bottom depth ⁴ (cm)	Total C stock ^{5,6} (gC m ⁻²)	Low density SOM			High density SOM
					Leaf litter L _L ^{7,8} (gC m ⁻²)	Fine root detritus L _R ^{7,8} (gC m ⁻²)	Humified H ^{8,9} (gC m ⁻²)	Mineral associated M ⁸ (gC m ⁻²)
Oi	0.06 (0.01)	450 (20)	2 (1)	380 (110)	380 (110)	0	–	NA
Oea	0.1 (0.02)	470 (10)	6 (1)	1640 (750)	–	230 (40)	1410 (750)	NA
A	0.35 (0.03)	270 (30)	10 (2)	2400 (820)	–	60 (25)	1780 (630)	560 (200)
Ap	0.54 (0.13)	60 (1)	16 (2)	2620 (660)	–	70	790 (200)	1760 (450)
Bw1	0.85 (0.07)	20 (1)	32 (4)	1245 (190)	–	4	40 (10)	1200 (180)
Bw2	0.93 (0.04)	6 (1)	59 (3)	510 (110)	–	1 (1)	5 (1)	500 (110)
Total				8800 (1310)	380 (110)	360 (70)	4030 (1000)	4020 (540)

¹ Gravel free bulk density (i.e. less than 2 mm).

² For Oi, Oe + Oa and A horizons $n = 3$, standard error in parenthesis; $n = 2$ for all other horizons; range in parenthesis.

³ For all horizons $n = 2$; range in parenthesis.

⁴ For Oi, Oe + Oa and A and Ap horizons $n = 3$, standard error in parenthesis; $n = 2$ for all other horizons; range in parenthesis.

⁵ Includes live root mass below the Oi horizon; total error in parenthesis.

⁶ C stock calculated using a z value (not shown) that accounts for waviness of horizon boundary and rocks.

⁷ On a dry weight basis; error term includes extrapolation from subsample to whole soil where subsample $n = 3$ to 5, otherwise $n = 1$ and no error is shown.

⁸ Low density means $\rho < 2.1$ g/cc, high density $\rho > 2.1$ g/cc.

⁹ Calculated by subtracting total roots from the total low density SOM.

(80%) in the upper 15 cm, which make up the organic and A + Ap horizons. Measured litterfall inputs to the O horizon were $150 \text{ gC m}^{-2} \text{ yr}^{-1}$ in 1996.

The fraction of soil volume taken up by rocks is spatially variable. In two of the three pits the O and A horizons were much less rocky (0–2% rocks) than the B horizons (10–35% rocks). However, one of our three pits had no less than 15% rocks in all horizons down to 60 cm. Spatial heterogeneity in soil C stocks has been studied in rocky forest soils similar to those found at Harvard Forest. Fernandez et al. (1993) show that between 73 and 455 samples are required to quantify C stocks to within 10% depending on soil depth. Huntington et al. (1988) were able to quantify C stocks to within 20% only after digging 60 $0.74 \times 0.74 \text{ m}$ pits. Therefore in this study instead of quantifying variability within a site we focus on the C dynamics for specific profiles and assume C dynamics will be the same even if the inventory of a given SOM fraction varies spatially for sites with similar drainage.

The four rightmost columns of Table 1 show the inventory of the isolated soil C fractions L_L or L_R , H and M. Carbon in low density fractions decreases rapidly with soil depth, from 100% in O horizons to <1% in B horizons. Low density carbon ($L_L + L_R + H$) makes up 54% of the total soil carbon stock, but is 87% of the carbon in O + A horizons.

Quantitative picking of roots showed they make up 7–19% ($n = 5$) and 1–4% ($n = 5$) of the dry mass in the Oe + Oa and A horizons, respectively. Assuming roots are 50% C by weight, the fraction of carbon in live and dead roots make up $\sim 14\%$ of the total C stocks in the Oe + Oa horizon, decreasing to $\sim 0.2\%$ in the Bw2 horizon. Our estimate of total fine root mass of 360 gC m^{-2} (live + dead) is lower than that of McClaugherty et al. (1982), who found 525 gC m^{-2} (live + dead) in well-drained mixed hardwood soils at a neighboring study area within the Harvard Forest. Fahey and Hughes (1994), found ~ 320 and 350 gC m^{-2} (live + dead) in June and October respectively in a mature northern hardwood forest. Our values also decrease more rapidly with depth than those of McClaugherty et al. (1982) who found 70, 55, and 15 gC m^{-2} for 15–30, 30–45 and $>45 \text{ cm}$ respectively for live + dead fine roots. In addition, our ratio of live:dead fine roots (data not shown) at all depths are significantly greater than those reported by McClaugherty et al. (1982), suggesting either differences in procedures for distinguishing live from dead roots or that we sampled during a seasonal maximum in live root abundance. Technically, it is the dead roots, not the live roots, that are decomposing and contributing to CO_2 fluxes. Therefore, live roots should not be considered part of the SOM. However, because we were not able to reliably distinguish live from dead with confidence, we report them together as L_R .

CO₂ production estimates

Total soil respiration as determined from chamber measurements in 1996 was $840 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Davidson & Savage, unpublished data). Production rates for CO₂ (Figure 4) by soil horizon were 190, 340, 235 and $75 \text{ gC m}^{-2} \text{ yr}^{-1}$ for the O, A + Ap, B and C horizons respectively. The estimates of CO₂ production within each soil horizon include uncertainties associated with the diffusion model, the exponential fit of the CO₂ concentration profiles, and, in particular, measures of rock content. We used the average rock content of two quantitatively sampled soil pits dug in 1996. One had almost no rocks in the O and A horizons while the other had 20–30% coarse fragments. Repeating the calculations assuming either no rocks or the higher estimate of rock content, changed CO₂ production rates for the A horizons by roughly $50 \text{ gC m}^{-2} \text{ yr}^{-1}$.

Radiocarbon in SOM fractions

The average radiocarbon content and the range of values measured in the isolated SOM fractions are plotted by horizon in Figure 6. $\Delta^{14}\text{C}$ values for the low density SOM (L_L or H) fractions increase from the Oi horizon (L_L) where values are $132 \pm 8\%$ to a maximum in the Oe + Oa horizon (H) of $200 \pm 19\%$. Humified material in the A horizon is 121% , and its ¹⁴C signature decreases rapidly in the Ap and B horizons. Within all mineral horizons, the low density carbon, which is primarily humus (H), has consistently higher $\Delta^{14}\text{C}$ values than mineral-associated (M) carbon, with the largest difference (55%) in the Ap horizon. Large negative $\Delta^{14}\text{C}$ values in both H and M fractions in the Bw1 and Bw2 horizons indicate the majority of soil carbon at these depths has not exchanged with the atmosphere since 1950 and has, in fact, remained in the soil long enough for significant radioactive decay to occur (half life = 5730 years).

The $\Delta^{14}\text{C}$ content of live and dead fine roots by horizon are also shown in Figure 6. All roots have $\Delta^{14}\text{C}$ values between 134 and 238‰, significantly higher than the atmosphere or live deciduous leaves sampled during 1996 ($97 \pm 7\%$). Live roots on average have lower $\Delta^{14}\text{C}$ values than dead roots, and $\Delta^{14}\text{C}$ values for both increase with soil depth. The $\Delta^{14}\text{C}$ values we measure for live fine roots are surprisingly high, as fine roots in this size class (<2 mm diameter) are thought to have annual or faster turnover based on studies that calculate turnover from the ratio of fine root biomass to production (see review by Vogt et al. 1986) and on direct measurements from rhizotrons, minirhizotrons or root screens (Burke & Dudley 1994; Hendrick & Pregitzer 1992; Hendrick & Pregitzer 1993; Fahey & Hughes 1994). There are three possible interpretations to explain our data. First, the bulk of the fine root mass may live for significantly longer than one year. Second, carbon in roots

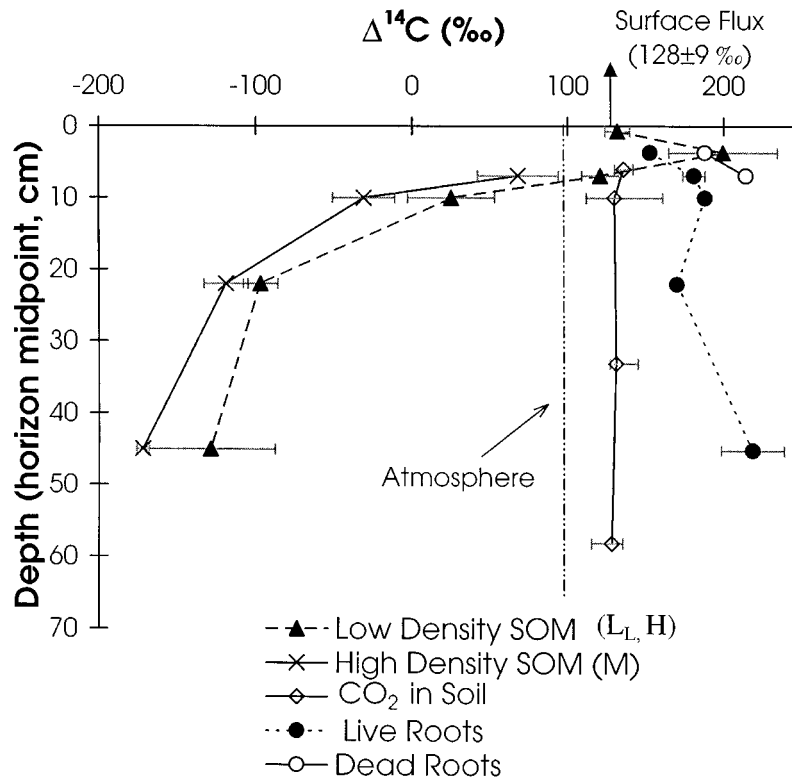


Figure 6. $\Delta^{14}\text{C}$ of below ground soil organic matter fractions and CO₂ by depth. All values except the $\Delta^{14}\text{C}$ of CO₂ are plotted at the midpoint of the soil horizon. For the soil organic matter fractions L_L, H and M, the error bars represent the range ($n = 2$) or the standard error of the mean ($n = 3$). For live and dead roots, the error bars where present, represent the error of the mean ($n = 3$) otherwise $n = 1$. For the soil CO₂ profiles values are an annual concentration weighted mean ($n = 3$ or 4) with error bars showing the entire range of values measured. The surface flux represents a flux weighted annual average from four sampling events. The $\Delta^{14}\text{C}$ for the atmosphere for 1996 ($97 \pm 1\text{‰}$) is also shown.

may be allocated from elsewhere in the plant, i.e., the roots may live for only a short time, but the carbon from which its tissues are constructed was fixed some time ago and was translocated from storage reservoirs when the root grew. Third, roots may take up SOM (Simard et al. 1997) either directly or via mycorrhizal associations, and incorporate it into their tissues. It is possible our root picking procedure may have mistaken dead roots for live ones, which could potentially be the cause of the elevated ^{14}C in live roots. To address this, we sampled one obviously living fine root in 1997. The main stem (1mm in diameter) had $\Delta^{14}\text{C}$ of 134‰ while a smaller growth off that stem had $\Delta^{14}\text{C}$ of 116‰. While these values are lower than the 1996 root numbers they are

still significantly higher than the atmosphere in 1997 ($92 \pm 7\%$), confirming that at least this one live root contained relatively “old” carbon. This one root may not be representative of all species and growth forms, which were averaged during the 1996 quantitative root picking.

The 1997 root data show that different parts of the same root have C that differs in age by 2 years. Thus, if longer turnover is the explanation for elevated ^{14}C , fine roots even 1 mm in diameter and less may not be acting as a single pool with one TT. The data would then imply that the tips (a small part of the mass) may turn over significantly faster than the rest of the root (the bulk of the mass). In a manner analogous to SOM stocks, the most recalcitrant root biomass pool is the largest fraction of the total root biomass pool and is the portion most easily separated from a soil sample for analyses.

Presently, we do not know which of the three above hypotheses for explaining high $\Delta^{14}\text{C}$ values in root biomass is correct, and additional research is being conducted to address this important issue. We can however, proceed with our mass balance approach without calculating any turnover times for fine roots based on their $\Delta^{14}\text{C}$ values. We instead solve for F_{LR} as one of the unknowns. However, even without an understanding of the mechanism, our $\Delta^{14}\text{C}$ data show that live fine roots, upon their death, are adding carbon to SOM that averaged roughly 165‰ in 1996 and that must have been fixed on average 7 ± 1 years previously.

Figure 7 shows the distribution of C and ^{14}C among the different low density components in O and A horizons. In the O horizon (Figure 7(A)), deciduous leaf parts had $\Delta^{14}\text{C}$ values that increased with depth, from 113‰ in the Oi to 132‰ in the Oe + Oa, where leaves became difficult to recognize. Radiocarbon in fine roots, which represent 14% of O horizon C (Table 1), ranged from 153‰ (live roots) to 188‰ (dead roots). The remaining, undifferentiable, material (H) had a $\Delta^{14}\text{C}$ value of $201 \pm 19\%$ ($n = 2$). Visual inspection shows H, which contained 63% of C in this O horizon sample, consisted of extremely fine root fragments (< 0.5 mm), and dark, humified material that could not be identified.

Figure 7(B) shows the distribution of C and $\Delta^{14}\text{C}$ for the A horizon low density fraction, which was sieved to 80μ and hand picked to remove roots. The measured components range in value from 48‰ to 266‰. The $> 80\mu$ material makes up 82% of this low density sample and has a $\Delta^{14}\text{C}$ of 130‰. Roots (live + dead) are 7% of the carbon with a weighted average $\Delta^{14}\text{C}$ of 256‰ ($n = 2$). The $< 80\mu$ fraction had the lowest measured ^{14}C value (48‰). The inventory-weighted average $\Delta^{14}\text{C}$ for all four components was 132‰. To calculate a flux for the H component alone, we take a stock weighted ^{14}C for the two components greater and less than 80μ (Figure 7(B)) which equals 121‰ ($0.82 * 130\% + 0.09 * 48\%$)/0.91.

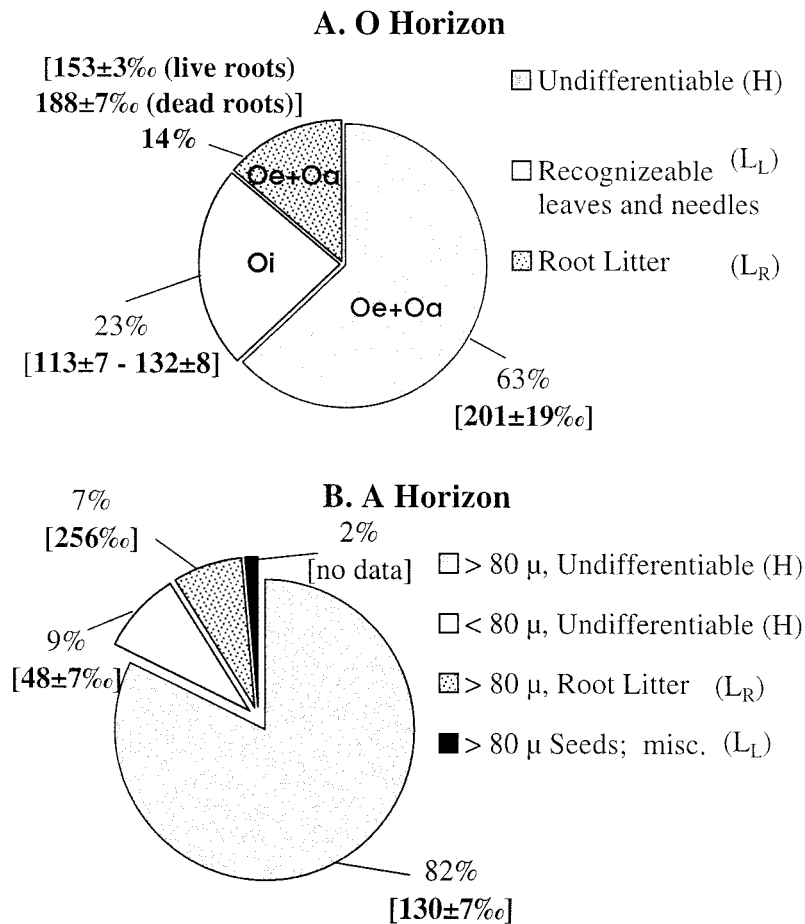


Figure 7. Heterogeneity of the O (top, Figure 7(A)) and A (bottom, Figure 7(B)) horizons. An error of 7‰ indicates analytical error, as $n = 1$. Errors other than 7‰ indicate either a range ($n = 2$) or standard error of the mean ($n = 3$). Values for the O horizon (Figure 7(A)) represent a composite of several samples and are representative of an average O horizon. Values for the A horizon in Figure 7(B) represent the results of quantitative sieving and picking one sample as outlined in Figure 2. The roots in the A horizon represent a stock weighted mean of two samples representing roots of two morphological types with values of $231 \pm 7\%$ and $266 \pm 7\%$.

Radiocarbon in the 1996 atmosphere at Harvard Forest

Partitioning of soil respiration using isotopic mass balance requires that we know the $\Delta^{14}\text{C}$ of CO_2 for the atmosphere in 1996 (variable $\Delta R_{\text{atm}(1996)}$ in Equation 17). For 1996, this value was obtained from two measurements of air within the Prospect Hill Tract on 11 July 1996, and one measurement of

a live deciduous leaf collected on the same date. The three values are 98 ± 7 , 96 ± 6 and 97 ± 7 ‰, averaging 97 ± 1 ‰. We assume the C lost within a year of being fixed by photosynthesis, including root respiration and decomposition of labile SOM, will have this value in 1996. We support this assumption with two lines of evidence. First, Horwath et al. (1994) performed a whole tree labeling study on two year old, three meter tall tulip poplar trees. They found that respiration of labeled C from the roots occurred within 12 hours of labeling, the peak activity in respiration was measured after two days and within two weeks the activity of root respiration was less than 5% of the maximum value. Second, three fruiting bodies of the genus *Boletus*, a mycorrhizal fungal symbiont, collected in 1996 at Harvard Forest had $\Delta^{14}\text{C}$ of 97, 99 and 98‰. The fact that their $\Delta^{14}\text{C}$ signature is the same as the 1996 atmosphere, indicates they are living off of Recent-C substrates, namely root exudates, and not the relatively ^{14}C enriched Reservoir-C of the O horizon in which they are rooted. Since root exudates are Recent-C it follows that maintenance metabolism by trees in this ecosystem must also be respiring Recent-C.

Radiocarbon in soil CO₂

Figure 8(A) and (B) shows CO₂ fluxes and measured $\Delta^{14}\text{C}$ in CO₂ of the surface flux for four sampling periods in 1996. The CO₂ fluxes shown in Figure 8(A) range between 40 and 200 mgC m⁻² hr⁻¹. The largest values measured were in the early summer and the lowest in the winter (see Davidson et al. (1998) for more complete seasonal CO₂ flux data). All flux measurements were made within 1–2 days of ^{14}C sampling, except for the late September sampling event when fluxes were measured 8 days previously. Measured $\Delta^{14}\text{C}$ in CO₂ values for 1996 in Figure 8(B) range from 103–176‰ and are all higher than the atmospheric $\Delta^{14}\text{CO}_2$ for 1996 (97 ± 1 ‰). Hence, decomposition of organic matter in the L_L, L_R and H fractions, primarily in the O and A horizons, and which have $\Delta^{14}\text{C}$ values greater than 100‰, must contribute significantly to the total soil CO₂ flux. In 1996, the highest $\Delta^{14}\text{C}$ values in soil respiration were observed in the spring and summer with values of 138 and 149‰ respectively. The lowest values were in fall and winter where $\Delta^{14}\text{C}$ drops to 111 to 121‰ respectively. The data from Figure 8(A) and (B) were used to calculate an annual flux weighted mean $\Delta^{14}\text{C}$ in soil respiration for 1996 of 128 ± 9 ‰ ($n = 11$).

The concentration-weighted annual average $\Delta^{14}\text{C}$ in CO₂ for soil air (by depth) is shown in Figure 6 and Table 2. $\Delta^{14}\text{C}$ values range from 128 to 136‰, all significantly greater than the 1996 atmosphere (97 ± 1 ‰). Temporal variability in measured $\Delta^{14}\text{C}$ values are greatest at 10 cm (the A horizon) where the values used for averaging ranged from 113 to 161‰. At all other

Table 2. Calculation of high and low density decomposition fluxes with associated $\Delta^{14}\text{C}_{\text{CO}_2}$ and measured profile $\Delta^{14}\text{C}_{\text{CO}_2}$.

Horizon	Stock (g C m ⁻²)	$\Delta^{14}\text{C}$ of SOM ¹ (‰)	Turnover time ² (years)	CO ₂ flux (g C m ⁻² -yr ⁻¹)	Flux horizon total (g C m ⁻² -yr ⁻¹)	$\Delta^{14}\text{C}$ of SOM horizon total (‰)	Measured profile ¹⁴ CO ₂ ³ (‰)
Oi (L _L)	380	132 (8)	4	25–95 ⁴	85–160	146	136
Oe + Oa (L _R)	230	188 ⁵	NA	NA			
Oe + Oa (H)	1410	201 (19) ⁶	40	35	35		
A (L _R)	60	216 ⁵	NA	NA	<22	115	130
A (H)	1780	121 ⁷	73 to >100 ⁸	<18			
A (M)	560	68 (26)	130 to >200 ⁸	<4			
Ap (H)	790	24.5 (28)	220	4	8	15	–
Ap (M)	1760	–31(20)	480	4			
Bw1 (H)	40	–97 (18)	990	0.04	<2	–118	131
Bw1 (M)	1200	–119 (17)	1200	1			
Bw2 (H)	5	–129 (40)	1300	0.004	<1	–171	128
Bw2 (M)	500	–172 (4)	1760	0.3			

NA = Not applicable, see text for details.

– = no data.

¹ Values are the average for two pits with range in parenthesis.

² A nonsteady state model is used for the Oe + Oa and A horizons and a steady state model used for Oi, Ap and deeper horizons.

³ Represents an annual concentration weighted average of the measured $\Delta^{14}\text{C}$ in CO₂ at the boundary with the horizon below.

⁴ Represents a range based on assuming all loss is as CO₂ or that 100% of inputs to the H + M fractions are from leaf litter.

⁵ Represents the $\Delta^{14}\text{C}$ samples picked for dead roots ($n = 1$).

⁶ Represents the humified organic material after quantitative root picking for the Oe + Oa ($n = 2$).

⁷ Represents a weighted $\Delta^{14}\text{C}$ value for the two humified (H) components shown in Figure 7(B), also text for discussion.

⁸ Range reflects that the $\Delta^{14}\text{C}$ values may include pre-disturbance C. The minimum represents the steady state case.

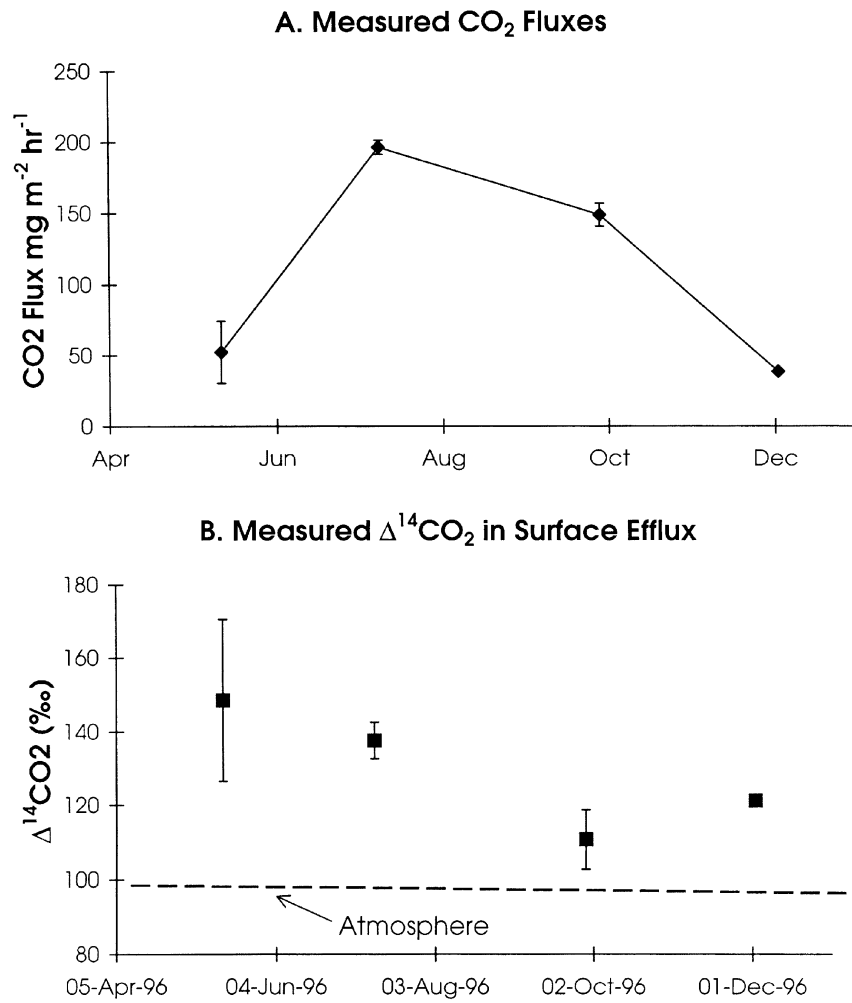


Figure 8. CO₂ fluxes for 1996 (top, Figure 8(A)). Error bars represent standard error ($n = 6$). $\Delta^{14}\text{CO}_2$ of soil CO₂ efflux (bottom, Figure 8(B)) Error bars where present represent standard error ($n = 3$) except in December 1996 where $n = 1$.

depths the annual variation was 20‰ or less. The fact that the $\Delta^{14}\text{C}$ in CO₂ is greater than either atmospheric CO₂ or H and M carbon in the mineral Ap and B horizons shows decomposition fluxes must be dominated by root litter (F_{LR}) which has much higher $\Delta^{14}\text{C}$ values.

Fluxes and turnover time of C in SOM fractions

Table 2 shows the turnover times for SOM fractions as derived from their radiocarbon content and the functions shown in Figure 5. Modern $\Delta^{14}\text{C}$

values ($>100\%$) have two possible turnover times for each $\Delta^{14}\text{C}$ value. For example, the $\Delta^{14}\text{C}$ of H in the Oe + Oa horizon is 201‰ which corresponds to turnover times of either 9 or 40 years (Figure 5, nonsteady state model). Based on the requirements for total CO_2 and $^{14}\text{CO}_2$ production in each horizon, we chose the longer turnover time for the H fraction in this and other horizons. We did not calculate turnover times for root litter (L_R) because of the potential for a significant lag time to affect the $\Delta^{14}\text{C}$ values measured in 1996. The time lag would also affect the TT for undifferentiable (H) material that is derived from both leaf litter and fine roots. In each case, failure to correct for any lag will cause overestimation of turnover times by as much as the inferred ^{14}C -derived lifetime of live roots (7 ± 1 years). Failure to account for time lags if roots are the principal source for more recalcitrant organic matter would result in turnover times for H and M fractions that are ~ 7 years too long.

The flux of CO_2 derived from decomposition of L_L , H and M fractions is calculated in Table 2 from the C inventory and turnover time. Again, no flux is calculated for fine root decomposition (F_{LR}); instead we use the CO_2 and $^{14}\text{CO}_2$ mass balance to calculate this below.

Partitioning of soil respiration

Equations 16 and 17 contain three unknowns: F_{LL} , F_{LR} and F_R . We therefore introduce an additional constraint so that we may solve for all three fluxes. As we have defined them, L_L and L_R pools represent the detrital root and leaf material that take longer than one year to decompose and are identifiable in SOM. From the inventory of detrital leaf litter (L_L ; 380 gC m^{-2}) measured in the soil, and its turnover time (4 years; Table 2), we calculate the annual flux of C into the L_L pool as $95 \text{ gC m}^{-2} \text{ yr}^{-1}$. The fate of leaf detritus is either to decompose directly to CO_2 (this is the flux F_{LL}) or to be incorporated into soil humus and mineral pools (H + M). We do not know this partitioning; however, based on C and ^{14}C inventory and our nonsteady state model, we assume the the annual rate of input to the H + M pools equals the decomposition flux from these pools ($\sim 70 \text{ gC m}^{-2} \text{ yr}^{-1}$, see Table 2). We then consider the two extreme cases, where all humus and mineral C is derived from leaf detritus, or all of it is derived from root detritus. F_{LL} is thus constrained to be between 25 and $95 \text{ gC m}^{-2} \text{ yr}^{-1}$. In Table 3, we use these minimum and maximum values for F_{LL} and solve for the two remaining fluxes, F_{LR} and F_R . Table 3 also shows cases for using the minimum and maximum values for observed $\Delta^{14}\text{C}$ of detrital leaf (113 and 132‰) and root (180 and 214‰) pools. The ranges and means of this approach are shown in Figure 9.

Our results from partitioning soil respiration for the entire soil profile using CO_2 and $^{14}\text{CO}_2$ mass balance are summarized in Table 3 and Figure 9. Approximately 41% (34%–51%) of CO_2 produced annually is derived from

Table 3. Parameters used and results of respiration partitioning for the whole soil profile based on eight scenarios.

Case	Parameters	Leaf litter F_{LL}^1 (gC m ⁻² yr ⁻¹)	Leaf litter ΔL_L^2 (‰)	Fine root litter F_{LR} (gC m ⁻² yr ⁻¹)	Fine root litter ΔL_R^3 (‰)	Recent-C F_R (gC m ⁻² yr ⁻¹)	Reservoir-C $F_{LL} + F_{LR} + F_{H+M}$ (gC m ⁻² yr ⁻¹)	Recent-C fraction	Reservoir-C fraction
Case 1	Min L_L , min ΔL_L , min ΔL_R	25	113	277	180	470	370	0.56	0.44
Case 2	Min L_L , min ΔL_L , max ΔL_R	25	113	197	214	550	290	0.66	0.34
Case 3	Min L_L , max ΔL_L , min ΔL_R	25	132	272	180	475	365	0.57	0.43
Case 4	Min L_L , max ΔL_L , max ΔL_R	25	132	193	214	554	286	0.66	0.34
Case 5	Max L_L , min ΔL_L , min ΔL_R	95	113	264	180	413	427	0.49	0.51
Case 6	Max L_L , min ΔL_L , max ΔL_R	95	113	187	214	490	350	0.58	0.42
Case 7	Max L_L , max ΔL_L , min ΔL_R	95	132	242	180	435	405	0.52	0.48
Case 8	Max L_L , max ΔL_L , max ΔL_R	95	132	172	214	505	335	0.60	0.40
Average		60		219		493	347	0.59	0.41
Minimum				172		413	286	0.49	0.34
Maximum				277		554	427	0.66	0.51

For all scenarios, $\Delta^{14}C$ of the atmosphere (ΔR) = 97‰, the $\Delta^{14}C$ of total soil respiration (ΔP) = 128‰, the flux of H + M is 70 gC m⁻² yr⁻¹ with a $\Delta^{14}C$ of 135‰. We combine the fluxes and their associated ^{14}C values of the H and M pools because their combined fluxes are relatively low (less than 10% of the annual total). Nonbold face values are parameters used in Equations 16 and 17, while bold faced values are the resulting calculations.

¹ Range reflects the two cases where either none or all of the inputs to H + M fractions are derived from leaf litter.

² Range is for the lowest and highest measured values of recognizable leaf parts.

³ Range reflects a mass weighted ^{14}C average of all dead roots (180‰) and the highest measured dead root value (214‰).

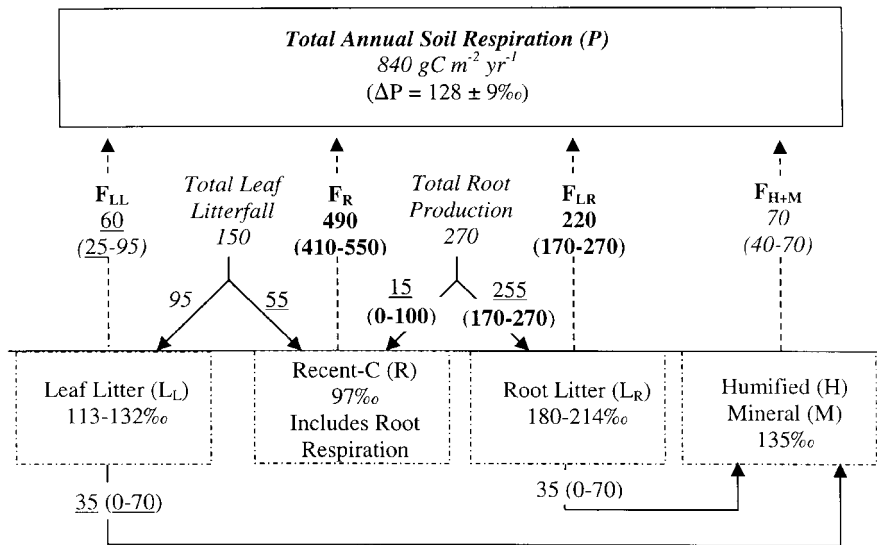


Figure 9. Results of isotopic mass balance approach to partitioning soil respiration into Recent- versus Reservoir-C sources. Solid arrows represent fluxes of organic C, while dashed arrows represent fluxes of CO₂. All units are in $\text{gC m}^{-2} \text{ yr}^{-1}$ with the average (and range). Production of litter (leaf and root) is assumed to have the isotopic composition of the atmosphere (97‰) in 1996. Bold numbers represent direct results from isotope mass balance model. Italicized numbers are independent measurements or calculated values used to constrain the model (see text for details) and underlined numbers are the resultant fluxes and transfers due to the model results and its constraints.

decomposition of low density SOM with TT greater than one year (L_L , L_R , H and M, i.e., Reservoir-C). The decomposition of H and M fractions with turnover times >40 years contributes only 8% of the total annual respiration flux, with the remaining 33% (26%–43%) from root and leaf litter decomposition (with plant + soil residence times of 2 to 10 years). The fluxes into and out of the H + M pools are constrained by their ¹⁴C-derived TT and reservoir size (Table 2) and represents an average over decadal time scales. The average flux of $70 \text{ gC m}^{-2} \text{ yr}^{-1}$ shown in Figure 9 implies the H + M pool to be in steady state. The uncertainty of $40\text{--}70 \text{ gC m}^{-2} \text{ yr}^{-1}$ is an estimate based on accumulation rates discussed in the following section.

Note that the flux of C into and out of the L_L pool is less than the total annual measured leaf litterfall ($150 \text{ gC m}^{-2} \text{ yr}^{-1}$; Figure 9). We infer that $55 \text{ gC m}^{-2} \text{ yr}^{-1}$ (1/3rd) of the freshly deposited litter is decomposed in <1 year (and hence is not detected from leaf detritus collected the following summer). Similarly, comparing the range of fluxes of C out of the L_R pool ($170\text{--}270 \text{ gC m}^{-2} \text{ yr}^{-1}$, which is equal to F_{LR} + the flux of root C transformed to humus) with annual root production estimates by McClaugherty et al. (1982) of 270

Table 4. Summary of respiration partitioning results.

Horizon	Total respiration (gC m ⁻²)	Fraction total respiration	Fraction produced that is Reservoir-C	Min	Max
Whole Soil	840	1.00	0.41	0.34	0.51
O + A + Ap	530	0.63	0.44	0.35	0.54
B	235	0.28	0.39	0.32	0.45
C	75	0.09	0.37	0.31	0.43

gC m⁻² yr⁻¹ indicates that 0–100 gC m⁻² yr⁻¹ of root litter is decomposed in less than one year.

Depth-dependence

Figure 4 and Table 4 show that 310 gC m⁻² yr⁻¹ or 37% of the total annual soil respiration is produced below 15 cm within the B and C horizons. Comparison of isotopic data for the SOM fractions in these horizons in Figure 6 and Table 2 clearly demonstrates that the two main sources must be root decomposition and Recent-C, because the decomposition of H + M reservoirs accounts for <2 gC m⁻² yr⁻¹ (with F_{LL} = 0). Application of C and ¹⁴C mass balance to the B and C horizons shows that 39% and 37% respectively, of the respiration comes from Reservoir-C (Table 4) and that essentially all of this flux is decomposition of roots with high $\Delta^{14}\text{C}$ values relative to the atmosphere. In the upper 15 cm of the soil profile (O + A + Ap) we estimate that 44% is Reservoir-C, with 32% from the decay of leaves and roots with TT of 2–10 years, and 12% from H and M fractions with TT >40 years. More frequent measurements of ¹⁴C in total soil respiration and within the vertical profile will allow for more detailed calculation of depth dependence of the make-up of soil respiration. Our measurement of root biomass in the B horizon (Table 1) is insufficient to support the approximately 90 gC m⁻² yr⁻¹ of decomposition required by the mass balance approach, if fine root mass is homogenous with respect to turnover.

Discussion

Rate of carbon accumulation in SOM

The O and A horizons have accumulated 4.4 kgC m⁻² above the plow layer (Ap horizon) since the late-1800s. This is roughly half the carbon in the soil profile. Carbon pools with turnover times that are less than several decades

(leaf and root litter), which make up 15% of the soil carbon in these horizons, must have achieved steady state with vegetation inputs by 1996. Most of the C in the O and A horizons, however, is in the form of altered, humified (H) material not associated with minerals. The rate of turnover of these fractions is slow enough (40 to 100+ years) that the annual C inputs (I in Equations 11–13) required to support the inventory and ^{14}C observed in 1996 are small (20–50 $\text{gC m}^{-2} \text{yr}^{-1}$ in the Oe + Oa and 10–30 $\text{gC m}^{-2} \text{yr}^{-1}$ in the A horizon. The rate of C accumulation in 1996 estimated using our accumulation model is 2–7 $\text{gC m}^{-2} \text{yr}^{-1}$ for the Oe + Oa and 8–23 $\text{gC m}^{-2} \text{yr}^{-1}$ for the A horizon. The ranges reported bracket the values obtained for different model runs representing mean, low and high values (i.e. ± 1 standard deviation) of both C stocks (Table 1) and their ^{14}C values (Table 2). Also included in the range are runs done using the specific C inventories and $\Delta^{14}\text{C}$ values for each of the two pits (data not shown). Variability in rock content between the two pits affected the overall C stock calculated for each pit and thus the pit with the most rocks had the smallest rates of C accumulation.

While these rates are large compared to storage rates in soils over longer timescales (e.g. Schlesinger 1990; Harden et al. 1992), they are less than the annual net C uptake measured for this ecosystem of $\sim 200 \text{ gC m}^{-2} \text{yr}^{-1}$ (Goulden et al. 1996). Overall C accumulation rates by the well drained soils which dominate the area within the tower footprint account for 5–15% of this net ecosystem uptake. The predominant wind directions at the tower site are southwesterly and northwesterly. A small area of poorly drained soils close to the tower to the southwest and a swamp 500 m from the tower to the northwest could be larger sinks per unit area than are the well drained soils.

We have assumed the leaf and root litter pools, which have TTs < 10 years, are at steady state. However, if net primary productivity has been increasing as a result of CO_2 or N fertilization, then leaf and root litter pools may be sequestering C. As discussed earlier, annual inputs to L_L and L_R pools are 150 and 270 $\text{gC m}^{-2} \text{yr}^{-1}$ (see Figure 9). Assuming a 1% per year increase in NPP between 1991 and 1996 and correcting for the inputs respired during the same year then the L_L and L_R pools could also be storing a combined $\sim 20 \text{ gC m}^{-2} \text{yr}^{-1}$ $((270 - 15) + (150 - 55)) \text{ gC m}^{-2} \text{yr}^{-1} * 0.01 \text{ yr}^{-1} * 5 \text{ yr}$ through this period. Combined with the accumulation in the humic fractions of the O and A horizons this could account for as much as 25% of the net ecosystem uptake.

Partitioning of soil respiration

We estimate from our radiocarbon studies that 59% of the soil respiration was derived from C that resided in the plant + soil system for less than one year. Using trenched plots to exclude roots, Bowden et al. (1993) estimate that

root respiration (plus decomposition of roots killed during trenching) was 33% of the total soil respiration at a nearby study site at the Harvard Forest. Using litterfall exclusion and addition manipulations, these authors estimate that 11% of the total soil respiration was from above-ground litterfall less than one year old. Hence, Bowden et al. (1993) estimated a total of 44% of the respiration was derived from C with a residence time in the *soil* system of less than one year. Both radiocarbon measurements and root and litter manipulations have uncertainties, and the best interpretation is probably that these two very different approaches yield estimates that about $50\pm 10\%$ of the soil respiration is derived from C that is less than one year old. Bowden et al. (1993) also estimate that 30% of soil respiration was from root litter that had resided in the soil more than one year, which is consistent with our radiocarbon data that show somewhat surprisingly long mean residence times for live and dead roots.

Time lags in the soil C reservoir – potential for interannual variability

The measured $\Delta^{14}\text{C}$ of total soil respiration is $128\pm 9\text{‰}$ for 1996 which corresponds to a mean residence time for C in the plant + soil system of 4 ± 1 years. This represents the time an average C atom spends in the plant + soil system since original photosynthetic fixation and includes both root respiration and all decomposition sources. We also calculate the average value for $\Delta^{14}\text{C}$ of heterotrophic respiration is 167‰ which corresponds to an average age of 8 ± 1 years. Thus a significant time lag exists between initial C fixation and ultimate respiration by heterotrophs. Therefore, variations in C storage or loss in any one year must partially reflect the net ecosystem uptake of previous years. (Schimel et al. 1997; Fung et al. 1997).

The age of C respired from soil can be used to predict the ^{13}C isotope disequilibrium for Harvard Forest. The ^{13}C isotope disequilibrium is the difference between the ^{13}C signature of atmospheric CO_2 being fixed by plants and the ^{13}C respired from soils. A difference is expected because the ^{13}C in the atmosphere has been decreasing with time due to the addition of ^{13}C -depleted fossil fuels to the atmosphere (e.g. Ciais et al. 1995; Fung et al. 1997). Using the $\delta^{13}\text{C}$ trend of -0.02‰ per year (Fung et al. 1997), and an average age of 8 ± 1 years for heterotrophic respiration, we estimate the ^{13}C isotope disequilibrium at the Harvard Forest to be $-0.16\pm 0.02\text{‰}$. This is less than that predicted using the CASA model for temperate deciduous forests (Thompson & Randerson 1999; Fung et al. 1997), largely due to the influence of woody debris in the CASA model. Woody debris is relatively small at the Harvard Forest floor, because of clearing of downed wood following the 1938 hurricane. However, Johnson and Todd (1998) note that woody debris does not seem to be an important source of humified SOM in a deciduous forest

at Oak Ridge, TN. Further work should place more emphasis on measuring radiocarbon in CO_2 respired from decomposing logs to assess the importance of this component to total soil respiration.

Heterogeneity issues

Comparison of the bulk SOM $\Delta^{14}\text{C}$ with the $\Delta^{14}\text{C}$ in CO_2 at depth (Figure 6) clearly demonstrates that the $\Delta^{14}\text{C}$ signature of the SOM alone is not enough to estimate C dynamics. Even with density separations into low and high density pools, $\Delta^{14}\text{C}$ of SOM is usually biased toward recalcitrant C stocks. This is particularly true in the mineral horizons where the vast majority of C stocks are hundreds of years old and have large negative $\Delta^{14}\text{C}$ values. The small pools of fast cycling SOM (fine roots) with significant amounts of 'bomb C' are effectively diluted beyond isotopic recognition. Our technique of respiration partitioning, which accounts for decomposition via $^{14}\text{CO}_2$ measurements, is particularly robust in the mineral horizons where the respiration sources are so isotopically different and have less spatial and temporal heterogeneity.

Methods of estimating bulk soil turnover rates by taking soil C stock divided by CO_2 flux also do not account for soil profile heterogeneity. Particularly in temperate forest soils with significant O and A horizon carbon stocks, this approach will yield poor estimates of the response time of soils to climate change scenarios. Figure 10 shows differences in soil C increase in response to a 10% increase in C inputs for a one-pool model with a turnover time of 25 years versus a multi-pool model representing the well drained soil at Harvard Forest. The one pool model overestimates the amount of C sequestered both in the short and long term. After 100 years, the one-pool model over predicts C storage by almost 600 gC m^{-2} .

Similarly, bulk SOM radiocarbon measurements may also cause an overestimation of decadal scale SOM response. For example, had we not partitioned the low-density carbon in the A horizon into different components (fine roots, undifferentiable material $>80 \mu$ and $<80 \mu$), the bulk ^{14}C value would have been 132‰ with a TT of 66 years. Instead, Figure 7B shows the sample to be composed of components with ^{14}C -derived TTs ranging from ~ 8 to >100 years. Analogous to taking an average TT for the whole soil, the response of SOM would be overestimated if the $\Delta^{14}\text{C}$ signatures of the low-density C sample components were represented using the bulk radiocarbon value (see Figure 10).

The turnover times we derive from modeling the ^{14}C content of SOM fractions are averages over several years to decades. Actual decomposition rates in any given year may deviate from these averages. For example soil respiration measured in Harvard Forest well-drained soils in 1997 (a dry year

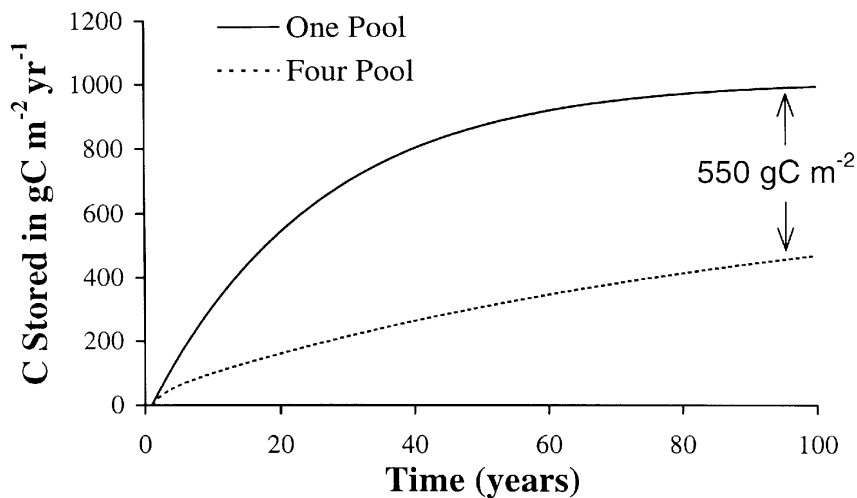


Figure 10. Increase in C storage associated with a 10% increase in NPP for two non-steady state models based on a one pool or four pool representation of soil organic matter stocks. In the one pool case the TT is 25 years and is equivalent to the total soil carbon stocks (8800 gC m^{-2}) divided by the total soil respiration ($840 \text{ gC m}^{-2} \text{ yr}^{-1}$) multiplied by the amount of decomposition from Reservoir-C (41%). In the four pool case stocks and TTs are modeled after those for the Harvard Forest well drained soils with TTs of 1, 4, 80 and 500 years. Both systems are not at steady state; the increases are relative to a nonsteady state run for each case.

relative to 1996) was $660 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Davidson & Savage, unpublished data), compared to $840 \text{ gC m}^{-2} \text{ yr}^{-1}$ for 1996. Monitoring of soil respiration isotopic composition should shed light on whether the reduction in soil respiration in future years is caused by changes in decomposition, changes in root respiration, or both. The power of coupling this approach to measuring soil profiles of CO_2 and $^{14}\text{CO}_2$ will allow determination of where in the soil profile changes occur in response to climate.

Conclusions

- SOM pools are accumulating C in well-drained Harvard Forest soils as they recover from historic disturbance. However, the rates of accumulation we infer, $10\text{--}30 \text{ gC m}^{-2} \text{ yr}^{-1}$, are only 5–15% of the $200 \text{ gC m}^{-2} \text{ yr}^{-1}$ observed by the eddy flux tower. More poorly drained soils also in the tower footprint may be accumulating larger amounts of C per square meter area, although they are far more limited in areal extent.
- Measurements of ^{14}C in soil organic matter emphasize organic matter fractions with longer turnover times (TT) which dominate soil carbon inventory. Calculations of TT derived by dividing total C inventory

by estimated heterotrophic respiration are not good predictors of the response time of soils because soil organic matter (SOM) is not homogeneous.

- Measurements of $\Delta^{14}\text{C}$ in CO_2 are required to correctly model the C that is actually respiring and to fully understand below ground C dynamics.
- Interpretation of ^{14}C data in SOM at Harvard Forest are complicated by fine root inputs with ^{14}C elevated by $\sim 65\%$ relative to the atmosphere, implying that the fine root C was fixed on average 7 ± 1 years ago. We do not currently understand the mechanism behind this lag in radiocarbon input.
- We estimate 41% of total soil respiration comes from decomposition of SOM that decomposes on timescales of 1–100+ years. Of this, 80% involves direct decomposition of leaf and root litter with TT of 2–10 years and 20% represents low density humified C pools and C associated with minerals (H and M respectively) which have TTs on the order of several decades or greater.
- About two-thirds of total soil respiration is produced within the O and A horizons. These organic rich horizons are comprised of (1) small pools of live roots and recent leaf and root litter that have residence times in the plant + soil system of ~ 1 –10 years and (2) relatively large pools of humified root and leaf litter which reside in the plant + soil system for 40–100+ years.
- Radiocarbon measurements of total below ground respiration measure the average time C spends in the plant + soil system from original photosynthetic fixation until respiration by autotrophs or heterotrophs. We estimate this time to be 4 ± 1 years for total soil respiration and 8 ± 1 years for heterotrophic respiration in well-drained soils at Harvard Forest, MA.

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References

- Bauer J, Williams PM & Druffel ERM (1992) Recovery of sub-milligram quantities of carbon dioxide from gas streams by molecular sieve for subsequent determination of isotopic natural abundance. *Anal. Chem.* 64: 824–827
- Bowden RD, Nadelhoffer KJ, Boone RD, Melillo JM & Garrison JB (1993) Contributions of aboveground litter, below ground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can. J. For. Res.* 23: 1402–1407
- Burchuladze AA, Chudy M, Eristavi IV, Pagava SV, Povinec P, Sivo A & Togonidze GI (1989) Anthropogenic ^{14}C variations in atmospheric CO_2 and wines. *Radiocarbon* 31: 771–776
- Burke MK & Raynal DJ (1994) Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. *Plant and Soil* 162: 135–146
- Collin M & Rasmuson A (1988) A comparison of gas diffusivity models for unsaturated porous media. *Soil Sci. Soc. Am. J.* 52: 1559–1565
- Currie WS, Aber JD, McDowell WH, Boone RD & Magill AH (1996) Vertical transport of dissolved organic C and N under long-term N amendments in pine hardwood forests. *Biogeochemistry* 35: 471–505
- Davidson EA, Belk E & Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4: 217–227
- Davidson EA & Trumbore SE (1995) Gas diffusivity and production of CO_2 in deep soils of the eastern amazon. *Tellus Ser. B Chem. Phys. Meteorol.* 47: 550–565
- De Jong E & Schappert HJV (1972) Calculation of soil respiration and activity from CO_2 profiles in the soil. *Soil Sci.* 113: 28–333
- Fahey TJ & Hughes JW (1994) Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *J. Ecol.* 82: 533–548
- Fernandez IJ, Rustad LE & Lawrence GB (1993) Estimating Soil mass, nutrient content, and trace metals in soils under a low elevation spruce-fir forest. *Can. J. Soil Sci.* 73: 317–328
- Foster DR (1992) Land-use history (1730–1990) and vegetation dynamics in central New England, USA. *J. Ecol.* 80: 753–772
- Fung I, Field CB, Berry JA, Thompson MV, Randerson JT, Malmstrom CM, Vitousek PM, Collatz GJ, Sellers PJ, Randall DA, Denning AS, Badeck F & John J (1997) Carbon 13 exchanges between the atmosphere and biosphere. *Global Biogeochemical Cycles* 11(4): 535–560
- Goulden ML, Munger JW, Fan Song-Miao, Daube BC & Wofsy SC (1996) Measurements of carbon sequestration by long-term eddy covariance: Methods and a critical evaluation of accuracy. *Global Change Biol.* 2: 169–182
- Hamburg SP (1984) Effects of forest growth on soil nitrogen and organic matter pools following release from subsistence agriculture. In: Stone EL (Ed) *Forest Soils and Treatment Impacts. Proceedings of the Sixth North American Forest Soils Conference* (pp 145–158). University of Tennessee
- Harden JW, Sundquist ET, RF Stallard RF & Mark RK (1982) Dynamics of soil carbon during deglaciation of the Laurentide Ice Sheet. *Science* 258: 1921–1924

- Hendrick RL & Pregitzer KS (1992) The demography of fine roots in a northern hardwood forest. *Ecology* 73(3): 1094–1104
- Hendrick RL & Pregitzer KS (1993) The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Can. J. For. Res.* 23: 2507–2520
- Horwath WR, Pregitzer KS & Paul EA (1994) ^{14}C Allocation in tree-soil systems. *Tree Physiol.* 14: 1163–1176
- Hendry MJ, Lawrence JR, Zanyk BN & Kirkland R (1993) Microbial production of CO_2 in unsaturated geologic media in a mesoscale model. *Water Resour. Res.* 29: 973–984
- Huntington T, Johnson CE, Johnson AH, Siccama TG & Ryan DF (1989) Carbon, organic matter and bulk density relationships in a forested spodosol. *Soil Sci.* 148(5): 380–386
- Huntington TG, DF Ryan & SP Hamburg (1988) Estimating soil nitrogen and carbon pools in a northern hardwood forest ecosystem. *Soil Sci. Soc. Am. J.* 52: 1162–1167
- Johnson D, Geisinger D, Walker R, Newman J, Vose J, Elliot K & Ball T (1994) Soil pCO_2 , soil respiration, and root activity in CO_2 -fumigated and nitrogen-fertilized ponderosa pine. *Plant and Soil* 165: 129–138
- Johnson DW & Todd DE (1998) Effects of harvesting intensity on forest productivity and soil carbon storage in a mixed oak forest. In: Lal R, Kimble JM, Follet RF & Stewart BA (Eds) *Management of Carbon Sequestration in Soil*. CRC Press, Boca Raton, Florida
- Levin I & Kromer B (1997) Twenty years of atmospheric $^{14}\text{CO}_2$ observations at Schauinsland Station, Germany. *Radiocarbon* 39: 205–218
- Mattson KG (1995) CO_2 efflux from coniferous forest soils: Comparison of measurement methods and effects of added nitrogen. In: Lal R, Kimble J, Levine E & Stewart BA (Eds) *Soils and Global Change* (pp 329–342). Lewis Publishers, Boca Raton, Florida
- McClagherty CA, Aber JD & Melillo JM (1982) The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology* 63: 1481–1490
- Millington RJ & Quirk JP (1961) Permeability of Porous Solids. *Trans. Farad. Soc.* 57: 1200–1207
- Schimel DS, Braswell BH & Parton WJ (1997) Equilibration of the terrestrial water, nitrogen, and carbon cycles. *Proceedings of The National Academy of Sciences of The United States of America* 94(16): 8280–8283
- Schlesinger WH (1990) Evidence from chronosequence studies for a low carbon – storage potential of soils. *Nature* 348: 232–234
- Simard SW, Perry DA, Jones MD, Myrold DD, Durall DM, & Molina R (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388: 579–582
- Southon JR, Vogel JS, Trumbore SE, Davis JC, Roberts ML, Caffee MW, Finkel RC, Proctor ID, Heikkinen DW, Berno AJ & Hornady RS (1992) Progress in AMS measurements at the LLNL spectrometer. *Radiocarbon* 34(3): 473–477
- Stuiver M & Polach H (1977) Reporting of ^{14}C data. *Radiocarbon* 19: 355–363
- Thompson MV, Randerson JT, Malmstrom CM & Field CB, (1996) Change in net primary production and net heterotrophic respiration: How much is necessary to sustain the terrestrial carbon sink? *Global Biogeochemical Cycles* 10(4): 711–726
- Thompson MV & Randerson JT (1999) Impulse response functions of terrestrial carbon cycle models: method and application. *Global Change Biol.* 5(4): 371–394
- Trumbore SE (in press) The average age of soil organic matter and soil respiration: Constraints on below-ground carbon dynamics from radiocarbon. *Ecological Applications*
- Trumbore S & Torn MS (in press) Soils and the global carbon cycle. In: Holland EA (Ed) *Notes from the Underground*. Publication of a NATO/ASI Workshop

- Trumbore SE, Davidson EA, de Camargo PB, Nepstad DC & Martinelli LA (1995) Belowground cycling of carbon in forests and pastures of Eastern Amazonia. *Global Biogeochemical Cycles* 9: 515–528
- Vogel JS (1992) A rapid method for preparation of biomedical targets for AMS. *Radiocarbon* 34: 344–350
- Vogt KA, Grier CC & Vogt DJ (1986) Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Advances Ecol. Res.* 15: 303–377
- Wofsy SC, Goulden ML, Munger JW, Fan S-M, Bakwin PS, Daube BC, Bassow SL & Bazzaz FA (1993) Net exchange of CO₂ in a mid latitude forest. *Science* 260: 1314–1317

