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Comparison of soil organic matter dynamics at five temperate deciduous forests with physical fractionation and radiocarbon measurements

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Abstract Forest soils represent a significant pool for carbon sequestration and storage, but the factors controlling soil carbon cycling are not well constrained. We compared soil carbon dynamics at five broadleaf forests in the Eastern US that vary in climate, soil type, and soil ecology: two sites at the University of Michigan Biological Station (MI-Coarse, sandy; MI-Fine, loamy); Bartlett Experimental Forest (NH-BF); Harvard Forest (MA-HF); and Baskett Wildlife Recreation and Education Area (MO-OZ). We quantified soil carbon stocks and measured bulk soil radiocarbon to at least 60 cm depth. We determined surface (0–15 cm) soil carbon distribution and turnover times in free light (unprotected), occluded light (intra-aggregate), and dense (mineral-associated) soil fractions. Total soil carbon stocks ranged from 55 ± 4 to 229 ± 42 Mg C ha^{-1} and were lowest at MI-Coarse and MO-OZ and highest at MI-Fine and NH-BF. Differences in climate only partly explained differences in soil organic matter ^{14}C and mean turnover times, which were 75–260 year for free-light fractions, 70–625 year for occluded-light fractions, and 90–480 year for dense fractions. Turnover times were shortest at the warmest site, but longest at the northeastern sites (NH-BF and MA-HF), rather than the coldest sites (MI-Coarse and MI-Fine). Soil texture, mineralogy, drainage, and macrofaunal activity may be at least as important as climate in determining soil carbon dynamics in temperate broadleaf forests.

Keywords 14C · Carbon cycle · Soil carbon · Soil fractionation · Soil fauna · Terrestrial carbon cycle

Abbreviations

SOM	Soil organic matter
MA-HF	Harvard Forest
NH-BF	Bartlett Forest
UMBS	University of Michigan Biological Station
MO-OZ	Missouri Ozark
fLF	Free light fraction
oLF	Occluded light fraction
DF	Dense fraction
MF	Mobilized fraction

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NEE Net ecosystem exchange of carbon
DOM Dissolved organic matter

Introduction

The development of robust and predictive climate models requires the inclusion of fully coupled carbon dynamics (Friedlingstein et al. 2001; Cox et al. 2000). Soils play a significant role in the global carbon cycle as a substantial reservoir of carbon, an important component of the terrestrial carbon sink for atmospheric CO_2 (US Climate Change Science Program 2007; Sabine et al. 2004), and a source of biospheric CO_2 flux into the atmosphere (Schlesinger and Andrews 2000). However, soil carbon dynamics have been difficult to model and detailed understanding of how soil carbon pools are likely to change in the future remains elusive (Heimann and Reichstein 2008; Jones et al. 2005).

Numerous factors have been identified as controls of soil carbon storage and dynamics including climate; plant cover type; ecosystem productivity; and soil texture, mineralogy, and structure (e.g., De Deyn et al. 2008; Homann et al. 2007; Amundson 2001; Baldock and Skjemstad 2000; Paul 1984; Post et al. 1982). These factors control soil carbon storage and dynamics by influencing the balance of carbon inputs (through plant productivity) and losses (through decomposition and leaching), and can be effectively studied using natural gradients (e.g. Fissore et al. 2008; Schuur et al. 2001; Trumbore et al. 1996).

Separation of bulk soil carbon into pools of varying stability, often accomplished through physical fractionation, allows for investigation into the effects of these variables on labile and stabilized soil carbon pools independently (Trumbore et al. 1996). Fractionation schemes may be designed to separate soil organic matter (SOM) into fractions that represent pools that are more or less stable or stabilized via different mechanisms. For example, the method described in Golchin et al. (1994) yields an unprotected free light fraction (fLF), an occluded light fraction (oLF) physically protected within aggregates, and a mineral-associated dense fraction (DF). This method, and modifications of it, allow for investigation of factors influencing physical protection and organo-mineral interactions, two mechanisms for SOM stabilization (Lützow et al. 2006). Modeling turnover times of bulk SOM or soil fractions allows for examination of the influence of these controlling factors on carbon turnover (Torn et al. 2005; Townsend and Vitousek 1995).

The influence of climatic factors on soil carbon storage at global and continental scales has been well documented through observations made across large climate gradients and biomes. These trends are driven by climatic controls on plant productivity and decomposition rates and include increasing soil carbon stocks with increasing precipitation (especially in warm climates) and with decreasing temperature when moisture is held constant (Guo et al. 2006; Post et al. 1982). Increasing mean residence times (MRTs)of active SOM pools with decreasing temperature have been reported for gradients spanning differences in mean annual temperature (MAT) of 10 °C or more, also resulting from slower decomposition in cooler climates (Fissore et al. 2009; Trumbore et al. 1996; Townsend and Vitousek 1995).

Large variability in soil carbon stocks is observed even within biomes and bioclimatic zones, resulting from site-specific edaphic and topographic factors (Jobbágy and Jackson 2000; Post et al. 1982). These factors are clearly important when considering variation within a region or in local studies with narrower ranges of MAT or mean annual precipitation (MAP). Moreover, temperature and precipitation interact to affect soil carbon cycling through effects on microbial activity (Leirós et al. 1999), plant productivity (Alvarez and Lavado 1998), soil fertility (Posada and Schuur 2011; McFarlane et al. 2010; Torn et al. 2005), and soil texture and mineralogy (Fissore et al. 2009).

Comparisons of sites within the same vegetation type or biome, help in identifying and understanding environmental factors (such as soil texture and mineralogy, hydrology, and macrofauna), including how these factors shape variation within the landscape and may interact with climate. Clay content has been found to be positively correlated to soil carbon stock, the portion of soil carbon in stabilized (mineral-associated) fractions, and turnover times of stabilized SOM (McFarlane et al. 2010; Homann et al. 2007; Telles et al. 2003), in part a result of high adsorption of dissolved organic matter (DOM) to clay particle surfaces (Silver et al. 2000). Soil mineralogy may be more important than, or explain the patterns seen with, texture in stabilizing soil carbon, considering demonstrated increases in soil carbon storage and turnover time with increasing amounts of poorly crystalline minerals (Rasmussen et al. 2006;

Rasmussen et al. 2005; Masiello et al. 2004; Torn et al. 1997). Macrofauna, particularly earthworms, can have great influence over litter decomposition, soil and litter mixing, and soil aggregate formation (Coleman et al. 2004; Bossuyt et al. 2004; Swift et al. 1979), all of which influence soil carbon storage and cycling.

In this paper, we analyze soil carbon storage, distribution, and turnover times at five temperate broadleaf forests in the eastern U.S. with similar vegetation but with differing climate and soil characteristics. We compare deep soil carbon stock and soil ^{14}C inventories, the first such to be published for four of these sites (Gaudinski et al. 2000 reports soil carbon dynamics at Harvard Forest). In addition to the bulk soil inventory, we provide a more detailed analysis of SOM near the surface (top 15 cm), where the most dynamic soil carbon pools are found (Paul et al. 1997; Trumbore et al. 1996). We also compare carbon distribution and ^{14}C-based turnover times of surface soil density fractions amongst our five sites.

We hypothesized that if the trends observed in large-scale gradients and used to parameterize models, including increasing soil carbon stocks and slower soil carbon turnover with decreasing temperature, increasing moisture, and increasing clay content, hold across the eastern deciduous forest ecoregion, we would find larger carbon stocks at sites with cooler and wetter climate and finer soil texture (MI-Fine and NH-BF) and smaller carbon stocks at sites with warmer climate (MO-OZ) and coarser soil texture (MI-Coarse). We also expected to find slower soil carbon turnover at sites with cooler and wetter climate and finer soil texture (MI-Fine and NH-BF) and faster soil carbon turnover at sites with warmer climate (MO-OZ) and coarser soil texture (MI-Coarse).

Methods

Study sites

We collected soil from five deciduous broadleaf forests across the eastern deciduous forest zone in the U.S. that were chosen to cover the range of the

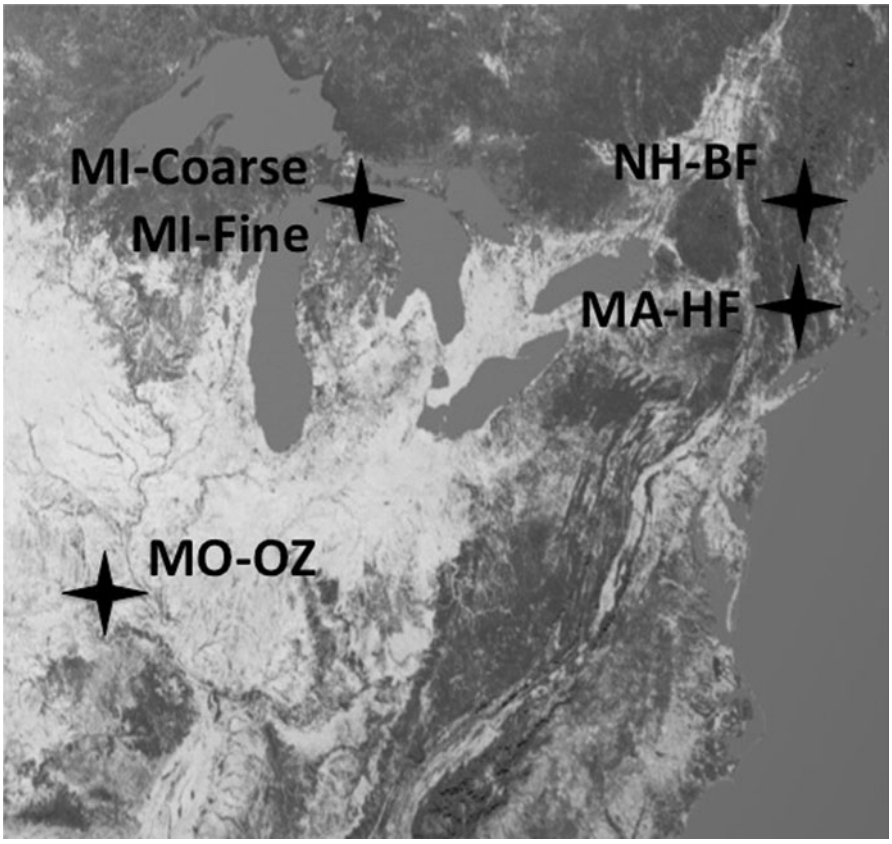

Fig. 1 Location of study sites mapped on tree cover (Base: NASA/University of Maryland)

Table 1 Study site characteristics[a]

	MI-Coarse UMBS	MI-Fine Colonial Point	NH Bartlett Forest	MA Harvard Forest	MO Ozark BREA
Latitude (°N)	45.5598	45.4846	44.0647	42.5377	38.7441
Longitude (°W)	84.7138	84.6843	71.2880	72.1715	92.2000
Elevation (m)	235	206	269	343	232
Dominant species	*Populus grandidentata*, *Populus tremuloides*, *Pinus strobus*, Quercus rubra	*Fagus grandifolia*, *Acer saccharum*, *Populus grandidentata*, *Quercus rubra*	*Quercus rubra*, *Fagus grandifolia*, *Betula papyrifera*, *Tsuga canadensis*	*Quercus rubra*, *Acer rubrum*, *Betula lenta*, *Pinus strobus*, *Tsuga canadensis*	*Quercus alba*, *Quercus velutina*, *Carya ovata*, *Acer saccharum–Tilia americana*, *Juniperus virginiana*, *Fraxinus quadrangulata*, *Quercus muehlenbergii*[b]
Soil type[c]	Rubicon series Entic Haplorthod or Blue Lake series Lamellic Haplorthod	Rudyard series Aquic Glossudalf	Berkshire series Typic Haplorthods	Gloucester series Dystrochrept	Weller series Hapludalf or Clickenbeard series Arguidoll
Mean stand age (years)	79	N/A	99	81	77
Parent material	Glacial till and lake deposits	Lake plain deposits	Glacial till derived from granite and gneiss[c]	Glacial till	Loess over limestone
Textural class	Sand	Loam	Coarse loam	Coarse loam	Silt loam
Mean annuala air T (°C)[e]	6.8	Approximately same as MI-Coarse	7.3	8.2	13.0
January mean air T (°C)[e]	−6.6	Approximately same as MI-Coarse	−6.5	−4.5	0.2
July mean air T (°C)[e]	18.8	Approximately same as MI-Coarse	19.7	19.9	24.5
MAP (mm)[e]	608	Approximately same as MI-Coarse	1,300	1,141	1,037
Mean annual soil T (°C)[f]	7.9	8.0	7.7	8.6	12.0
Mean annual volumetric SWC (%)[f]	16.6	34.4	27.9	31.0	24.9
Soil texture (% sand/silt/clay)[f]	89/9/1	48/33/19	62/26/12	65/26/9	4/75/21
Aboveground litterfall (Mg C ha^{-1} $year^{-1}$)[f]	1.24 ± 0.07	1.12 ± 0.10	0.97 ± 0.04	1.06 ± 0.10	1.65 ± 0.07

[a] From AmeriFlux website (see http://public.ornl.gov/AmeriFlux/site-select.cfm), unless otherwise noted, except for MI-Fine which is either the same as MI-Coarse or is from Jim Le Moine, personal communication (2010). For additional information on Harvard Forest see Urbanski et al. (2007) and Barford et al. (2001)

[b] See Belden and Pallardy (2009) and Pallardy et al. (1988)

[c] Soil type from soil survey documentation and personal communication with Dave Hollinger (2010), Steve Pallardy (2009), and Jim Le Moine (2010)

[d] From NH-BF website (http://www.fs.fed.us/ne/durham/4155/bartlett.htm)

[e] Calculated from AmeriFlux L2 data available on web or from data provided by site collaborators. UMBS air temperature was measured at 46 m height and both air temperatures and MAP were calculated from datasets provided by Bob Vande Kopple for 2004–2009. NH-BF air temperatures were calculated from datasets provided by Dave Hollinger for 2004–2009 and measured at 23 m height. NH-BF precipitation from AmeriFlux L2 data, 2004–2007. All MA-HF from AmeriFlux L2, 1992–2007 with air temperature measured at 28 m height. All MO-OZ from AmeriFlux L2, 2005–2009 with air temperature measured at 27 m height

[f] Measured in this study

ecoregion from northern cold, wet forests to southern warm, dry forests (Fig. 1). Four of these forests are AmeriFlux sites where net ecosystem exchange of carbon (NEE) has been measured with the eddy covariance technique. At these sites, our plots were located in the eddy-flux tower footprint, allowing us to use meteorological data collected at the towers to characterize climate at the sites.

The two coldest sites were located at the University of Michigan Biological Station (UMBS) in Northern Michigan (Table 1). The coarse-textured Michigan site (MI-Coarse) is located in the UMBS AmeriFlux tower footprint. Soils are very deep, well drained, and derived from deep lake plain sand deposits. They are classified as Rubicon or Blue Lake series Haplorthods and are coarse textured (Soil Survey Staff 2009). The fine-textured Michigan site (MI-Fine) is located about 9 km from MI-Coarse and provides a site of similar climate but contrasting soil type and drainage to MI-Coarse. This site is the only one of our sites not located at an eddy-flux tower site. It has very deep, somewhat poorly drained soils formed in clayey lake plain deposits classified as Rudyard series Haplorthods (Soil Survey Staff 2009). Rudyard soils commonly include C horizons that contain thin lenses and veins of calcium carbonate deposits, which provide an inorganic source of soil carbon with an unknown age, possibly ^{14}C-free. Soils from MI-Fine were tested for the presence of calcium carbonates (US Salinity Laboratory Staff 1954). Calcium carbonate accounted for less than 1 % of the total carbon in the top 15 cm.

Two sites were located in the northeastern U.S. The Bartlett Experimental Forest in northern New Hampshire (NH-BF) has well drained soils that were formed in glacial till derived from granite and gneiss that have a coarse-loamy texture and are classified as Berkshire series Haplorthods (Soil Survey Staff 2009). Harvard Forest in Massachusetts (MA-HF) has soils that were formed in glacial till with sandy loam texture that are classified as Gloucester series Dystudepts (Soil Survey Staff 2009).

The warmest and southern-most site is located at the Baskett Recreation and Education Area in the Missouri Ozarks (MO-OZ). Soils at this site include two soil types: Weller series Hapludalfs with a silt loam texture derived from loess deposits and Clinkenbeard series Argiudolls with a clay loam texture derived from limestone colluvium and residuum (Soil Survey Staff 2009). Soil samples from MO-OZ were tested for the presence of carbonates, which if derived from limestone bedrock would add an inorganic and ^{14}C-free source of carbon to the soil. Soil carbonate concentration was determined quantitatively using acid titration with phenolphthalein indicator (Loeppert and Suarez 1996). For all plots, carbonate concentration was below 0.01 % and inorganic carbon was less than 0.5 % of total soil carbon for surface mineral soils above 15 cm. The greatest contribution of carbonate to total soil carbon occurred at 60–75 cm depth where 1.3 % of total carbon was from carbonates.

At each site, samples were collected from five 2 m × 2 m square plots and the location and distribution of study plots were chosen by local site managers and their understanding of site variability and the existing tower footprints. Study plots were established and soils sampled in November–December 2007 from the four AmeriFlux sites and in November 2008 from MI-Fine.

Soil microclimate

To provide detailed microclimate information for our sites, we installed one soil moisture and one temperature probe (Soil Moisture Smart Sensor and Temperature Smart Sensor, Onset Computer Corporation, USA) at each plot at the time of soil sampling. Soil temperature probes were installed in the O-horizon and at 10 cm depth in the mineral soil. Moisture probes were installed in the top 10 cm of the O-horizon surface for each of the five plots at each site. Observations recorded hourly from fall 2007 (or 2008 for MI-Fine) through 2009 are shown in Table 1.

Macroinvertebrate surveys

Earthworms have been observed at our Michigan and Missouri sites, but not at the northeastern sites. To have a more quantitative understanding of the soil fauna present, we conducted macro invertebrate surveys at our four AmeriFlux sites. Macroinvertebrate surveys were conducted adjacent to each of the five plots at MI-Coarse, NH-BF, MA-HF, and MO-OZ in June and September 2010. Leaf litter was collected from two 50 cm × 50 cm sub-plots. Directly beneath these, two 30 cm × 30 cm soil pits were manually excavated to 30 cm depth, which included Oa and mineral soil material. Leaf litter, O horizon, and mineral soil were placed on a plastic sheet for hand

sorting in the field. Large roots (>2.5 cm diameter) were left intact in the pits while fine roots, soil clods, and aggregates were broken into pieces smaller than 5 cm diameter. All macro invertebrates were collected, placed into 70 % ethanol solution, and returned to the laboratory for identification at the USDA-FS Forestry Sciences Laboratory in Athens, Georgia.

Soil sampling

Organic and mineral soil samples were collected from each plot at each site at vertical intervals to a depth of 90 cm, or to the depth at which impenetrable rocks were encountered. For O horizons, a 27 cm diameter circular sampling frame (576 cm^2) was used for sampling and Oi material was separated from Oe/Oa. Current year litter was collected on a 2 m^2 tarp, which was placed over existing Oi material prior to leaf fall (September or October), and collected after leaves had fallen (November or December). Mineral soil samples were collected at 0–5 and 5–15 cm, and at 15 cm intervals to depth. Soil sampling was conducted by extraction of 10 cm diameter (81.7 cm^2) cores using a gasoline powered hole saw for samples to 30 cm depth and diamond bit coring tools for deeper soils. Samples were collected to 90 cm depth at MI-Coarse, 75 cm depth at MI-Fine and NH-BF, and to 60 cm depth at MA-HF and MO-OZ. One sample of each horizon or depth was collected from each plot. Samples were taken back to the laboratory and frozen until processing when samples were thawed, sieved to 2 mm, hand-picked to remove roots, and dried at 70 °C.

Density fractionation

Sieved soil samples from 0–5 and 5–15 cm depth of each plot were fractionated into three density fractions using a modification of the methods of Swanston et al. (2005). This procedure yields three physical fractions that represent unprotected SOM (fLF), SOM physically protected within the soil structure (oLF), and mineral associated SOM (DF). Our modifications were intended to minimize physical alteration of the sample matrix during ultrasonic disruption of aggregates. Samples were separated by density in low C/N sodium polytungstate (SPT-0, TC Tungsten Compounds) adjusted to a density of 1.65 g cm^{-3}. The density was chosen after conducting density fractionation of these soils with SPT adjusted to several densities and selecting the density that produced light fractions with the highest carbon concentration.

50 ml of SPT was added to 20 g of oven-dry equivalent soil in a centrifuge bottle. The bottle was gently inverted to wet all of the soil. After sitting for 1 h, the soil and SPT solution were centrifuged at 3,500 rpm (4,710×g) in a swinging bucket rotor at 25 °C. The floating material (fLF) was aspirated and rinsed extensively with Nanopure Low TOC Reagent Grade H_2O to remove residual SPT. To disrupt aggregates, sediment remaining at the bottom of the bottle was mixed in SPT for 1 min at 1,700 rpm using a benchtop mixer (G3U05R, Lightnin, New York, NY) and sonified in an ice bath for a total input of 100 J ml^{-1} (Branson 450 Sonifier, Danbury, CT). The mixture was centrifuged as before and then allowed to sit overnight for particles to settle. The oLF was then aspirated and rinsed in the same manner as the fLF. The remaining sediment, the DF, was rinsed of residual SPT with Nanopure H_2O. When rinsing DF from MO-OZ, 30 ml of 1 M $CaCl_2$ in 3 ml of 1 M HCl was used to flocculate suspended material to ensure complete sample recovery. After rinsing, all fractions were transferred to pre-weighed Al tins and dried at 55 °C until standing water had evaporated at which point they were dried at 105 °C for 48 h. Fractions were then weighed, ground, and prepared for isotopic and chemical analysis.

Sample analysis

Organic horizon and bulk soil samples used for calculation of carbon stock were analyzed for carbon concentration using a LECO TruSpec CN analyzer at Oak Ridge National Laboratory. Bulk soil pH for 0–5 and 5–15 cm depths was measured in water and 0.01 M $CaCl_2$ at a1:1 soil:solution ratio (Thomas 1996). Soil texture for 0–5 and 5–15 cm depths was measured using the micropipette method (Burt et al. 1993; Miller and Miller 1987). Bulk soil and density fractions were analyzed for C and N concentration, $\delta^{13}C$, and $\Delta^{14}C$. Some oLF yields were too small to analyze for C and N using the LECO analyzer that was used for bulk measurements to calculate C stocks. Therefore, carbon and nitrogen concentrations of all fractions were determined using a Costech ECS 4010 Elemental Analyzer (EA) at Lawrence Berkeley National Laboratory. Carbon and nitrogen

concentrations in bulk soils from 0–5 and 5–15 cm depths were also measured with the Costech EA for calculations of mass balances so that any differences between carbon recovered in the fractions and in the bulk soil samples before fractionation could be attributed to loss or gain during fractionation rather than from discrepancies between the LECO and EA instruments.

Radiocarbon values were measured on the Van de Graaff FN accelerator mass spectrometer (AMS) at the Center for AMS at Lawrence Livermore National Laboratory. No samples were treated to remove carbonates. Samples were prepared for ^{14}C measurement by sealed-tube combustion to CO_2 in the presence of CuO and Ag and then reduced onto iron powder in the presence of H_2 (Vogel et al. 1984). Aliquots of CO_2 were analyzed for $\delta^{13}C$ at the Department of Geological Sciences Stable Isotope Laboratory, University of California Davis (GVI Optima Stable Isotope Ratio Mass Spectrometer). $\delta^{13}C$ values are reported relative to V-PDB. Measured $\delta^{13}C$ values were used to correct for mass-dependent fractionation and ^{14}C isotopic values are reported in $\Delta^{14}C$ notation, had an average AMS precision of 3 ‰, and were corrected for ^{14}C decay since 1950 (Stuiver and Polach 1977).

Data analysis

Soil C turnover

Mean turnover times were calculated for O horizons, bulk soils for all depths sampled (except where there were significant amounts of $CaCO_3$), and for density fractions (0–15 cm). Reported turnover times are means of the five plots at each site and are for total soil carbon. To determine turnover times, we used the time-dependent steady-state model described below, which calculates the $\Delta^{14}C$ of a given pool over time and varies turnover times to match measured $\Delta^{14}C$ (Torn et al. 2002; Gaudinski et al. 2000). Samples with a significant (≥5 %) contribution of inorganic carbon to total carbon were excluded because the model assumes all carbon is organic in origin. For density fractions, a three-pool model was used to determine turnover times of all three fractions simultaneously and using the mass balance of carbon and the amount of ^{14}C in bulk soil as additional constraints (Torn et al. 2009; Marín-Spiotta et al. 2008). Turnover times were determined using the following equation (Torn et al. 2009):

$$F'_{\mathrm{SOM}(t)} = \left[I \times F'_{\mathrm{atm}(t-1)} + C_{(t-1)} F'_{\mathrm{SOM}(t-1)} (1-k-\lambda)\right] \Big/ \left[C_{(t)}\right] \tag{1}$$

where $F' = (\Delta^{14}C \times 1000^{-1}) - 1$ (or absolute fraction modern); I = Inputs of carbon to a given SOM pool or fraction (g C m^{-2} y^{-1}); C = Stock of C for the given SOM pool (g C m^{-2}); k = Decomposition rate constant of the given SOM pool ($year^{-1}$), equal to the reciprocal of turnover time, or τ^{-1}; F'_{atm} = the ^{14}C value of atmospheric CO_2; F'_{SOM} = the ^{14}C value of the given carbon pool; λ = radioactive decay rate of ^{14}C ($year^{-1}$); t = year in which calculation is being performed.

This model has several important assumptions. First, it assumes steady state, thus, inputs equal losses, or I = k × C. The ^{14}C signature (F'_{SOM}) at any time depends on the ^{14}C signatures of the atmosphere (F'_{atm}) and of the given carbon pool in previous years (F'_{SOM}). Second, we used a time-lag of 1 year between the ^{14}C value of the atmosphere and new inputs ($F'_{atm(t-1)}$) to a given pool because these are deciduous systems that shed leaves each year. Although this is likely an appropriate time lag for leaf inputs to O horizons, root inputs in these forests may be slightly older (Gaudinski et al. 2010). In addition, inputs to a given SOM fraction or pool, particularly mineral-associated fractions and deep soils, probably have a longer lag time between fixation and incorporation and carbon may cycle from one fraction or depth to another as organic compounds are assimilated and transformed by microbes. Thus, calculated turnover times are most accurately interpreted as indicating the residence time of carbon in the ecosystem rather than in the given fraction or pool. Third, this turnover time model assumes that all carbon in a given pool has an equal probability of exiting the pool (i.e., normal distribution of turnover times within a pool) and that the given pool is homogenous with regards to ^{14}C signature.

With the assumptions of well mixed pools and steady state met, the turnover time for a given fraction or pool is equal to the MRT and thus estimates both the average time carbon atoms spend in a given pool before leaving that pool and the average age of material in the pool (Trumbore 2000; Rodhe 1992). The assumptions are better met for an individual

fraction, but poorly met for bulk soil carbon given its heterogeneity. We have estimated turnover times for bulk soil, commonly referred to as mean soil age, because we believe they will help our readers in interpreting bulk ^{14}C data and identifying trends across depths and horizons and between sites. Unlike for $\Delta^{14}C$ values, turnover times, residence times, or mean ages do not depend on the year sampled or current atmospheric $\Delta^{14}C$ value. However, because the model assumptions with which they are calculated are never perfectly held for bulk soil carbon, they should be treated as a relative indicator of ecosystem residence time rather than precise estimate of MRT (see Torn et al. 2009 for detailed discussion).

Atmospheric $\Delta^{14}C$ (used to calculate F'_{atm}) was compiled from multiple sources. Annual atmospheric $^{14}CO_2$ values measured from North American tree rings were taken from Stuiver et al. (1998) up to and including 1954. Annual values for the Northern Hemisphere for 1955–1996 and 1999 were taken from Hua and Barbetti (2004) with Zone 1 values used for all sites except MO-OZ for which Zone 2 values were used. Atmospheric $^{14}CO_2$ values for 1997–1998 and 2000–2003 were taken from Levin and Kromer (2004). Values for after 2003 are calculated global mean $^{14}CO_2$ taken from Graven et al. (2012).

During the 20th century, the amount of ^{14}C in the atmosphere increased drastically and then declined as a result of atmospheric weapons testing during the 1950s and 1960s. In some cases, ^{14}C values allowed for two modeled solutions for turnover time, one corresponding to the increasing (older) side of the atmospheric ^{14}C bomb curve, and one corresponding to the decreasing (more recent) side of the curve (Trumbore 2000; Marín-Spiotta et al. 2008). In these cases, the most likely solution was identified using information about carbon cycling at the site. Specifically, we relied on aboveground litterfall rates and carbon stock in the given carbon pool, and calculated input rates to the given carbon pool ($I = \tau^{-1} \times C$ at steady-state). For example, a $\Delta^{14}C$ value of 97 ‰ for the NH-BF Oe/Oa horizon yields one solution for turnover time of 9 years and one solution for a turnover time of 91 years. Based on calculations of what input rates would need to be for an Oe/Oa horizon turnover time of 9 years (about four times annual aboveground litterfall) or 91 years (about one-third annual aboveground litterfall), 91 years can be identified as the most likely solution. In some cases only some plots for a given horizon or soil depth at a given site yielded two solutions for turnover time. When only one or two plots provided a second solution, we assumed the solution closest to the singular solution for turnover time of the plots with one solution was correct.

Statistical analyses

We determined carbon stocks in O horizons, bulk mineral soil, and surface soil fractions. Differences in total carbon stocks to 15 cm and to depth sampled between sites were determined using analysis of variance (ANOVA) with depth treated as a repeated measure with SYSTAT 12. Differences among surface soil fractions were tested using ANOVA with depth treated as a repeated measure and fractions as split-plots for a given depth. When significant interaction effects were observed, multiple comparisons tests with a Tukey HSD or ANOVA was done by site to describe depth and fraction effects (the case for C recovery and ^{14}C of density fractions). Statistical significance for ANOVA and multiple linear comparisons were tested at $\alpha = 0.05$.

Results

Site characteristics: microclimate, macrobiota, and edaphic factors

In addition to site characterization data available through the AmeriFlux archives and site mentors, we added measurements of soil temperature and moisture, soil macro invertebrates, litterfall, and soil pH and texture. Mean annual soil temperature in 2008 and 2009 was similar at all sites except MO-OZ, which was considerably warmer than the other sites (Table 1), consistent with the trend across the sites in mean air temperature. The coldest winter soil temperatures occurred at MI-Coarse (data not shown). Soil moisture in 2008 and 2009 varied more seasonally at MO-OZ and MI-Coarse than at NH-BF and MA-HF, and Michigan was substantially drier than the north-eastern sites. However, recent data suggest these patterns may reflect drier than normal years in Michigan and Missouri (data not shown).

We used litterfall as a proxy for net primary productivity (NPP) and input of plant carbon to soil.

Estimates of belowground primary productivity are not currently available for our sites, but syntheses suggest that belowground carbon allocation in forests is two or more times greater than aboveground litterfall (Davidson et al. 2002; Raich and Nadelhoffer 1989). Litterfall rates were similar at the Michigan and northeastern sites, 1.0–1.2 Mg C ha^{-1} $year^{-1}$, but was higher at MO-OZ (1.6 Mg C ha^{-1} $year^{-1}$) (Table 1, $p < 0.01$) suggesting forest productivity and the rate of carbon inputs to soil may be higher at the warm site.

In our macrobiotic surveys, we found earthworms at MI-Coarse and MO-OZ, but not at NH-BF or MA-HF consistent with previous, non-quantitative observations at the sites. We did not conduct macro invertebrate surveys at MI-Fine, but European earthworms have been observed at the site (Lehr et al. 2009) and could be present in greater numbers than at MI-Coarse, as earthworm densities tend to be higher in finer-textured soils (Nordström and Rundgren 1974). Earthworm densities were much higher at MO-OZ than at MI-Coarse (Table 2). Epigeic earthworm species, which consume and physically break down fresh plant litter in organic horizons, were present at both MO-OZ (*Lumbricus rubellus*) and MI-Coarse (*L. rubellus* and *Dendrobaena octaedra*). Very high densities of endogeic earthworms, which live and feed on organic matter in the mineral soil, were found in mineral soil at MO-OZ (*Aporrectodea caliginosa*, and *Octolasion tyrtaeum*, Table 2), but they were rare at MI-Coarse. A few anecic earthworms, which bring surface litter into burrows or middens in the mineral soil, were found in mineral soil at MI-Coarse (*Lumbricus terrestris*), but they were not observed at MO-OZ. Millipedes (*Diplopoda* sp.) were found at MI-Coarse, MA-HF and NH-BF, but not at MO-OZ. Millipedes were more abundant at MA-HF and NH-BF (0.45 and 0.70 individuals m^{-2}, respectively), where worms were not present, than at MI-Coarse (0.2 individuals m^{-2}). At MA-HF and NH-BF, it is likely that millipedes are largely responsible for the initial breakdown of fresh litter, although mixing of new carbon inputs and mineral soil by millipedes is likely less than that attributed to earthworms (Snyder et al. 2009).

All sites had acidic soils and soil pH did not change between 0–5 and 5–15 cm. Surface soil pH measured in water was 4.4 at MI-Coarse, 3.8 at NH-BF, 4.2 at MA-HF, and 4.8 at MO-OZ. Differences amongst these sites were not statistically significant. The pH of MI-Fine was 6.0, significantly higher than that measured for the other four sites ($p = 0.01$). pH measured in 0.01 M $CaCl_2$ was consistently 0.4 pH units lower than pH measured in water.

Surface soil textural analysis showed MI-Coarse soils have the coarsest texture, followed by NH-BF, MA-HF, and MI-Fine, with soils at MO-OZ having the finest texture (Table 1). Textures at NH-BF and MA-HF were similar, with MA-HF having slightly more clay than NH-BF. Clay contents were similar at MI-Fine and MO-OZ (about 20 %), but MI-Fine had substantially more sand than MO-OZ.

Profile bulk soil carbon stocks and ^{14}C

Across the five eastern deciduous forests sites, we observed a four-fold variation in total soil carbon storage (to the deepest depth sampled), with the smallest stock (55 Mg C ha^{-1}) at MI-Coarse (also where soil was sampled to the deepest depth) and the largest stock (229 Mg C ha^{-1}) found at the poorly drained MI-Fine ($p < 0.01$, Fig. 2). All plots at MO-OZ and MI-Fine and one plot at MI-Coarse lacked an Oe/Oa horizon, consistent with observations of earthworms at these sites. In contrast, thick Oe/Oa horizons at NH-BF and MA-HF contributed 30 and 20 Mg C ha^{-1} to soil carbon stocks respectively. The top 15 cm of mineral soil accounted for approximately 25 % of total mineral soil carbon stock at MI-Coarse; 35 % at NH-BF, 45 % at MO-OZ, and 50 % of total mineral soil carbon stock at MI-Fine and MA-HF. Mineral soil carbon stocks to 15 cm, as with the whole profile were larger at MI-Fine (114 Mg C ha^{-1}) than at the other sites ($p < 0.05$, Fig. 2).

At all sites, $\Delta^{14}C$ of litterfall and Oi horizon were similar to the previous year's atmospheric value, indicating the carbon was recently photosynthesized (Fig. 3). Relatively high $\Delta^{14}C$ values in Oe/Oa horizons, and 0–5 cm soil at MO-OZ where no Oe/Oa is present, indicated the retention of bomb ^{14}C and resulted in estimated mean turnover times of 9–90 years (Table 3). Bulk mineral soil $\Delta^{14}C$ values differed amongst sites and declined with depth, a pattern observed in other soil profiles where ^{14}C has been measured (Gaudinski and Trumbore 2003; Torn et al. 2002; Trumbore 2000). $\Delta^{14}C$ values in surface bulk soil were lowest at NH-BF and MA-HF and highest at MO-OZ ($\alpha = 0.01$). In soils of 0–5 cm

Table 2 Earthworm densities in surface litter/organic horizons and mineral soil at MI-Coarse and MO-OZ in individuals m^{-2}

	MI-Coarse		MO-OZ	
	June	September	June	September
Organic horizons/litter				
Epigeic	0.8 ± 0.6	4.0 ± 1.9	14.4 ± 5.2	4.0 ± 1.4
Endogeic	0 ± 0	0.4 ± 0.5	0.8 ± 0.6	3.6 ± 1.9
Total	0.8 ± 0.6	4.4 ± 1.8	15.2 ± 5.4	7.6 ± 3.0
Mineral soil				
Epigeic	6.7 ± 4.5	1.1 ± 1.2	69.9 ± 18.9	15.54 ± 4.6
Endogeic	0	4.4 ± 5.0	256.4 ± 41.7	131.0 ± 18.5
Anecic[a]	<2	<1	0	0
Total	~7	~6	326.3 ± 57.6	146.5 ± 20.8

Values are means followed by standard errors

[a] Because anecic species (e.g. *L. terrestris*) could not be reliably sampled by the pit digging method (see Callaham and Hendrix 1997), we used a chemical extractant (mustard solution) on a limited number of sites to confirm their presence, but this did not give a good estimate of their abundance at all sites

depth, ^{14}C values ranged from 6 to 100 ‰ at 0–5 cm, corresponding to bulk soil carbon turnover times of 83 to 312 years. At 45–60 cm depth (the deepest interval sampled at all sites), ^{14}C values ranged from −14 (Mi-Coarse) to −129 ‰ (NH-BF), corresponding to bulk soil carbon turnover times at depth of 427 to 1,243 years. The decline in mineral soil $\Delta^{14}C$ with depth was less pronounced at MI-Coarse than at the other sites (Fig. 3), suggesting little stabilization of SOM with depth in this coarse textured soil relative to the other sites.

Surface SOM

SOM chemistry

We investigated surface SOM content, distribution, and turnover time for the 0–5 and 5–15 cm mineral soil depths. Bulk soil carbon and nitrogen concentrations decreased with depth (Table 4, $\alpha = 0.01$), but C:N ratios did not change with depth. Specifically, bulk SOM chemistry differed amongst sites and these differences were consistent across depths (no interaction of site and depth effects). Bulk soil carbon concentrations were lower at MI-Coarse and MO-OZ than at MA-HF and MI-Fine (Table 4, $\alpha = 0.05$) and nitrogen concentrations were higher at MI-Fine than the other sites (with the exception of MA-HF, $\alpha = 0.01$). In addition, C:N ratios were narrower at MI-Fine and MO-OZ than at the other sites (Table 4, $\alpha = 0.01$). At all sites, the two light-density fractions had higher C and N concentrations and wider C:N ratios than DF ($p < 0.01$). As with bulk soil, oLF at MI-Fine had higher N concentrations and lower C:N ratios than did most oLF's from the other sites ($\alpha = 0.01$, exceptions are 0–5 cm depth MO-OZ for % N and MA-HF for C:N ratio).

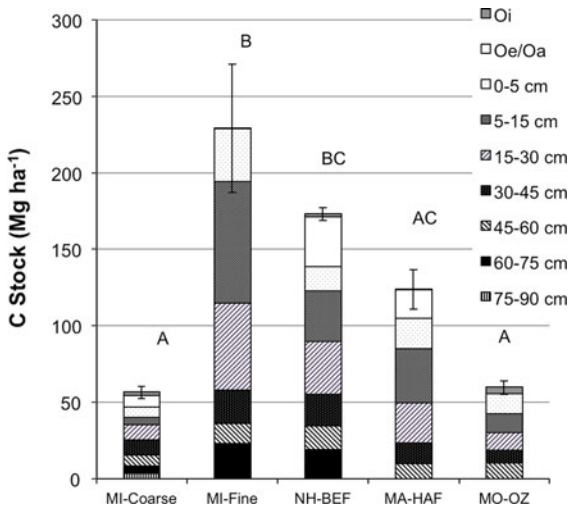

Fig. 2 Soil carbon stocks by horizon or depth and total carbon stocks (Mg C ha^{-2}) for five study sites. *Error bars* are standard errors on mean total soil C stock ($n = 5$). *Letters* indicate statistically significant differences in total soil C stock between sites, alpha = 0.05

Soil carbon distribution among density fractions

During soil fractionation, some amount of bulk soil carbon is lost via dissolution in SPT solution or water rinses (McFarlane et al. 2010; Crow et al. 2007). This SPT- or water-mobilized fraction (MF) represented on average 2 % of bulk soil carbon at MI-Coarse, 9 % at MI-Fine and NH-BF, 11 % at MA-HF, and 12 % at MO-OZ. No bulk soil N was mobilized during fractionation for soils from MI-Coarse, but the MF averaged 3 % of bulk soil N at MI-Fine, 8 % at NH-BF, and 13 % at MA-HF and MO-OZ. Results below are calculated as a proportion of the total C and N recovered following density fractionation.

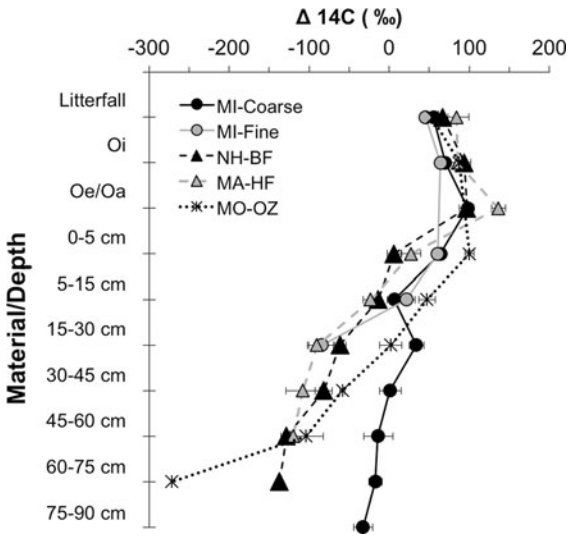

Fig. 3 $\Delta^{14}C$ of litterfall, organic horizons, and bulk mineral soil by site and depth. Values are means with standard errors. Note that there is no data for Oe/Oa horizons at MI-Fine and MO-OZ because this horizon is not present at those sites or for below 30 cm at MI-Fine because of the presence of $CaCO_3$

At all sites except MI-Coarse, DF contained most of the soil carbon (60 % of bulk soil carbon on average, Fig. 4, $\alpha = 0.01$). The proportion of soil carbon in fLF or oLF varied with the fLF containing 10, 26, 28, and 20 % and the oLF representing 33, 8, 19, and 19 % of the recovered soil carbon at MI-Fine, NH-BF, MA-HF, and MO-OZ, respectively (Fig. 4). In contrast, at MI-Coarse site over half of the bulk soil carbon was recovered in the unprotected fLF and only 37 % was recovered in the mineral-associated DF. Similar patterns were observed for N distribution across fractions. Patterns in soil C and N distribution amongst fractions were consistent across depths, although the proportion of soil carbon (NH-BF, $\alpha = 0.01$) or nitrogen (MA-HF, $\alpha = 0.01$) in the DF increased with depth at some sites.

Surface soil and density fractions C isotopes

There was a general trend of higher $\delta^{13}C$ values for DFs than for light fractions (Table 4), a trend observed by others (Sollins et al. 2009). This trend was most pronounced at MO-OZ and NH-BF and not statistically significant at the other sites ($\alpha = 0.05$). $\delta^{13}C$ values of density fractions varied among sites with no apparent pattern or trend.

Table 3 Mean turnover times (years) for bulk litterfall, O horizon, and mineral soil

Horizon/depth	MI-coarse	MI-fine	NH-BF	MA-HF	MO-OZ
Litterfall	3 ± 1 (151 ± 13)	1 ± 1 (173 ± 13)	4 ± 2 (132 ± 23)	7 ± 5 (111 ± 38)	2 ± 1 (151 ± 15)
O_i	5 ± 1 (125 ± 15)	4 ± 2 (136 ± 19)	8 ± 2 (94 ± 20)	7 ± 4 (106 ± 31)	6 ± 3 (97 ± 8)
$O_e + O_a$	9 ± 2 (88 ± 14)	NA	91 ± 23 (9 ± 2)	53 ± 17 (16 ± 4)	NA
0–5 cm	137 ± 24 (4 ± 2)	144 ± 37 (5 ± 1)	312 ± 93	238 ± 94	83 ± 13 (9 ± 2)
5–15 cm	310 ± 90	256 ± 94	400 ± 50	463 ± 118	173 ± 49
15–30 cm	210 ± 62	NC[b]	723 ± 136	962 ± 203	337 ± 49
30–45 cm	339 ± 129	NC[b]	888 ± 206	1139 ± 385	689 ± 164
45–60 cm	427 ± 172	NC[b]	1315	1243 ± 292	1101 ± 51
60–75 cm	394 ± 149	NC[b]	1404	NA[c]	3084 ± 396
75–90 cm	488 ± 202	NC[b]	NA	NA[c]	NA[c]

Where two solutions for turnover time are shown, the solution above is believed to be correct and the alternate solution is provided to the right in parentheses

[b] Not calculated as $CaCO_3$ ≥5 % of total soil carbon

[c] Not available as no soil sample was collected from this depth

Table 4 Surface bulk soil and fraction chemistry, isotopes, and turnover time

Site	Depth (cm)	Fraction	C (%)	N (%)	C:N	δ^{13}C (%)	Δ^{14}C (‰)	τ (year)
MI-Coarse	0–5	Bulk	1.9 ± 0.3	0.08 ± 0.01	26 ± 1	−26.9 ± 0.2	64 ± 6	NA
		fLF	44 ± 9	1.3 ± 0.3	36 ± 2	−27.2 ± 0.2	60 ± 12	150 ± 26
		oLF	47 ± 1	1.4 ± 0.1	35 ± 2	−26.8 ± 0.4	38 ± 9	197 ± 25
		DF	0.9 ± 0.2	0.04 ± 0.1	20 ± 2	−26.6 ± 0.4	58 ± 5	147 ± 8
	5–15	Bulk	0.5 ± 0.1	0.02 ± 0.00	24 ± 1	−26.3 ± 0.1	6 ± 9	NA
		fLF	37 ± 2	0.8 ± 0.9	48 ± 5	−26.7 ± 0.2	22 ± 21	271 ± 72
		oLF	44 ± 2	1.0 ± 1.2	43 ± 11	−26.7 ± 0.1	−33 ± 12	516 ± 75
		DF	0.2 ± 0.1	0.02 ± 0.00	12 ± 2	−25.9 ± 0.1	28 ± 11	226 ± 36
MI-Fine	0–5	Bulk	8.4 ± 2.0	0.6 ± 0.1	15 ± 1	−27.3 ± 0.2	61 ± 7	NA
		fLF	29 ± 1	1.3 ± 0.2	23 ± 1	−27.9 ± 0.2	69 ± 7	129 ± 11
		oLF	32 ± 1	1.8 ±	18 ± 1	−27.7 ± 0.2	62 ± 5	141 ± 9
		DF	4.3 ± 1.1	0.32 ± 0.09	14 ± 1	−26.7 ± 0.2	56 ± 5	150 ± 10
	5–15	Bulk	6.4 ± 2.5	0.44 ± 0.16	14 ± 1	−26.6 ± 0.2	21 ± 11	NA
		fLF	30 ± 1	1.1 ± 0.1	27 ± 2	−27.3 ± 0.5	40 ± 10	192 ± 24
		oLF	33 ± 2	1.8 ± 0.1	18 ± 2	−27.1 ± 0.2	37 ± 11	202 ± 31
		DF	4.0 ± 2.7	0.32 ± 0.22	12 ± 1	−26.2 ± 0.4	17 ± 16	281 ± 60
NH-BF	0–5	Bulk	4.1 ± 0.6	0.16 ± 0.02	25 ± 1	−26.7 ± 0.1	6 ± 9	NA
		fLF	30 ± 2	0.85 ± 0.04	36 ± 1	−28.8 ± 0.5	22 ± 12	258 ± 61
		oLF	44 ± 4	1.4 ± 0.2	32 ± 2	−27.2 ± 0.3	−6 ± 24	340 ± 145
		DF	1.9 ± 0.4	0.10 ± 0.02	18 ± 1	−28.3 ± 0.2	−4 ± 8	399 ± 42
	5–15	Bulk	3.8 ± 0.7	0.15 ± 0.02	24 ± 2	−26.3 ± 0.3	−14 ± 4	NA
		fLF	31 ± 1	0.89 ± 0.01	35 ± 1	−27.1 ± 0.1	22 ± 8	244 ± 29
		oLF	35 ± 4	1.1 ± 0.1	32 ± 3	−26.8 ± 0.1	−20 ± 12	446 ± 67
		DF	2.8 ± 0.5	0.12 ± 0.02	23 ± 1	−25.7 ± 0.1	−29 ± 5	482 ± 28
MA-HF	0–5	Bulk	10 ± 4	0.38 ± 0.12	26 ± 1	−26.9 ± 0.2	27 ± 13	NA
		fLF	36 ± 1	1.1 ± 0.1	34 ± 2	−28.5 ± 0.3	67 ± 9	134 ± 17
		oLF	42 ± 1	1.39 ± 0.08	31 ± 2	−27.2 ± 0.2	12 ± 9	285 ± 36
		DF	4.1 ± 0.5	0.18 ± 0.02	23 ± 3	−27.2 ± 0.4	13 ± 11	284 ± 49
	5–15	Bulk	6 ± 1.5	0.23 ± 0.04	25 ± 2	−26.3 ± 0.1	−23 ± 10	NA
		fLF	35 ± 1	0.91 ± 0.08	40 ± 2	−27.0 ± 0.3	33 ± 14	221 ± 41
		oLF	43 ± 1	1.06 ± 0.11	42 ± 4	−26.7 ± 0.5	−47 ± 16	626 ± 113
		DF	3.6 ± 0.5	0.17 ± 0.02	21 ± 1	−26.1 ± 0.3	−37 ± 13	553 ± 82
MO-OZ	0–5	Bulk	2.8 ± 0.1	0.19 ± 0.01	15 ± 1	−26.8 ± 0.1	100 ± 6	NA
		fLF	30 ± 1	1.06 ± 0.1	29 ± 1	−28.4 ± 0.2	108 ± 6	75 ± 6
		oLF	38 ± 1	1.44 ± 0.1	27 ± 1	−28.7 ± 0.2	112 ± 4	72 ± 3
		DF	1.5 ± 0.1	0.13 ± 0.01	11 ± 1	−26.3 ± 0.2	94 ± 5	90 ± 5
	5–15	Bulk	1.2 ± 0.1	0.09 ± 0.01	13 ± 1	−25.9 ± 0.1	37 ± 11	NA
		fLF	32 ± 1	0.85 ± 0.05	39 ± 3	−28.0 ± 0.1	111 ± 8	74 ± 7
		oLF	39 ± 2	0.98 ± 0.07	40 ± 1	−27.8 ± 0.2	56 ± 18	165 ± 37
		DF	0.7 ± 0.1	0.07 ± 0.01	10 ± 1	−25.3 ± 0.1	34 ± 11	209 ± 29

Density fractions are: *fLF* free light fraction, *oLF* occluded light fraction, *DF* dense fraction

As with bulk soil, Δ^{14}C for each fraction declined with depth ($p < 0.05$, Table 4); the exception of fLF at MO-OZ (Table 4) likely the result of earthworms mixing surface litter into mineral soil. Δ^{14}C values were higher for fLF than oLF and DF ($p < 0.05$), except at MI-Fine where no differences in Δ^{14}C

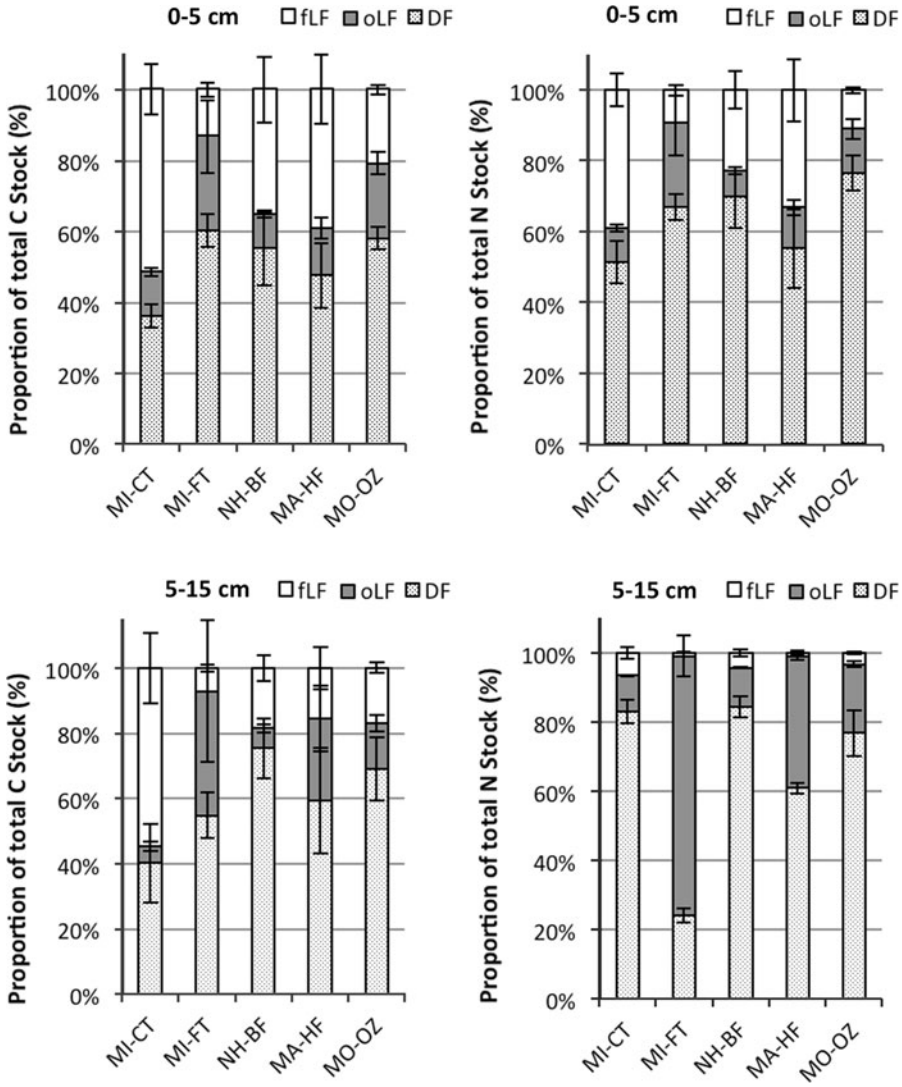

Fig. 4 C and N stocks in surface soil density fractions. Density fractions are: *fLF* free light fraction, *oLF* occluded light fraction, *DF* dense fraction

amongst soil fractions were observed. In general, $\Delta^{14}C$ values of oLF and DF were similar with the exception of the 5–15 cm depth at MI-Coarse, where oLF was more depleted than DF. For a given fraction, $\Delta^{14}C$ values were lowest at NH-BF and MA-HF and highest at MO-OZ with a few exceptions, including similar oLF $\Delta^{14}C$ at MO-OZ and MI-Fine and DF $\Delta^{14}C$ at MO-OZ and both Michigan sites.

SOM turnover times

Soil carbon distribution and ^{14}C data were used to calculate ^{14}C-based turnover times (τ) of density fractions with a three-pool steady-state model in which τ approximates MRT (Table 4). Trends in turnover times across sites were similar to those for bulk soil mean turnover times for surface soils, although turnover times of fLF were shorter and oLF and DF longer than bulk soil mean turnover time.

The shortest turnover times were found at MO-OZ, the warmest site, where they ranged from about 75 years for fLF to roughly 200 years for oLF and DF (5–15 cm depth). Turnover times at MO-OZ were two-thirds those at NH-BF and MA-HF (statistically significant for NH-BF at both depths and MA-HF for the 5–15 cm depth only, $\alpha = 0.05$) and those at MI-Coarse (statistically significant for 5–15 cm depth ($\alpha = 0.05$). The longest turnover times were at NH-BF and MA-HF, not at the coldest (MI-Coarse and MI-Fine) or most poorly drained (MI-Fine) sites, and were roughly 250 years

for fLF at NH-BF and as high as 625 and 550 years for oLF and DF at MA-HF. Turnover times at MI-Fine were about half as long as those at NH-BF (both depths) and MA-HF (5–15 cm depth only, $\alpha = 0.05$). Turnover times were not different between MI-Coarse and MI-Fine in surface soils despite large differences in soil carbon stocks, in soil texture and drainage.

Turnover times increased with depth from 0–5 to 5–15 cm by about 150 years for the DF and 175 years for the oLF, but not for fLF ($\alpha = 0.05$). In addition, differences in turnover times between the fLF and protected fractions (DF and oLF) were more pronounced with depth. As suggested by $\Delta^{14}C$ values, fLF had the shortest turnover times at all sites, ranging from about 70 years at MO-OZ to roughly 260 years at NH-BF, and indicating that this unprotected SOM pool was the most labile of the three pools. At MI-Coarse, however, fLF and DF turnover times were similar, roughly 200 years, while the longest turnover times were found in oLF ($\alpha = 0.05$). This suggests that what little carbon stabilization occurs at MI-Coarse is through physical protection. At NH-BF and MA-HF, oLF and DF had similar turnover times to one another, roughly 400 years at NH-BF and 300 or 600 years at MA-HF 0–5 and 5–15 cm depths, respectively ($\alpha = 0.05$), suggesting the two fractions are similarly stable.

To determine if MF carbon represented a distinct carbon pool, we estimated the $\Delta^{14}C$ of MF for each plot at each site using a mass balance approach and determined τ for this fraction using the same model described above. Calculated $\Delta^{14}C$ values and modeled turnover times were highly inconsistent across plots within a site with turnover times ranging from 1 to nearly 6,000 years if solutions on either side of the bomb curve were considered (data not shown). These results suggest that there is not one consistent type or age of soil carbon mobilized during density fractionation. Losing a mixture of carbon recently fixed from the atmosphere and older carbon is consistent with findings of another study using this method in a temperate broadleaf forest in Pennsylvania (Crow et al. 2007).

Discussion

Factors controlling soil carbon stocks and turnover

The variability in soil carbon stocks, distribution, and turnover times at our sites suggests that the relative importance of different factors controlling soil carbon dynamics differs among sites. Some of our results are consistent with expected differences in soil carbon storage and turnover at sites with varying climate and soil texture. For example, cold and poorly drained MI-Fine had the largest soil carbon stocks, while sandy MI-Coarse and warm MO-OZ had smaller carbon stocks. In addition, the warmest site, MO-OZ, had the shortest turnover times (i.e., fastest decomposition). Unexpectedly, the longest turnover times for protected soil fractions (oLF and DF) were found at MA-HF, not at the coldest sites. Also surprisingly, turnover times in surface bulk soil and fractions at MI-Fine and MI-Coarse were similar, despite large differences in carbon stocks and soil texture.

Longer turnover times imply slower decomposition rates and could result from direct limitations on microbial activity, such as freezing or dessication; or the state of the organic matter at the site, including its mineral association or protection within aggregates. Climate cannot explain longer turnover times at MA-HF as this site is warmer than MI-Coarse and NH-BF. Differences in turnover between these sites cannot be explained by differences in the molecular structure or plant-residence time of inputs as these forests are dominated by similar tree species with similar physiology and litter chemistries.

We suspect that differences in stabilization of SOM through physical protection or association with minerals explain observed differences in turnover times between MA-HF and MI-Coarse. The relatively large amount of soil carbon in unprotected fLF, high ^{14}C values, and short turnover times for bulk soil and protected fractions at MI-Coarse suggest less effective stabilization of soil carbon at this site than at MA-HF. These results suggest that the sandy site has a lower capacity for longterm carbon storage and stabilization than the other sites, consistent with trends reported in the literature and incorporated into soil carbon models (e.g., Schimel et al. 1994; Oades 1988) of decreasing soil carbon storage with increasing sand or decreasing clay contents. However, differences in texture alone are unlikely to explain short turnover times at MI-Coarse compared to MA-HF for two reasons. First, turnover times at MA-HF were slightly longer than those at NH-BF despite similar texture and warmer temperatures. Second, turnover times at MI-Fine were similar to those at MI-Coarse despite large differences in texture. Soil mineralogy and the presence of

reactive Fe- or Al-oxides have been observed to influence SOM stabilization and soil carbon storage (Heckman et al. 2009; Spielvogel et al. 2008; Kleber et al. 2005), and organo-mineral interactions may vary considerably among our sites.

Alternatively, it is possible that earthworm invasions at MI-Coarse and MI-Fine have enhanced decomposition and soil carbon loss at these sites relative to MA-HF and NH-BF where earthworms are not present. These effects have been observed at sites where earthworms have invaded that had no prior earthworm activity (Bohlen et al. 2004; Alban and Berry 1994) and might contribute to short turnover times at the MI sites. However, differences in macrobiotic activity cannot explain differences in carbon dynamics between MA-HF and NH-BF.

Also surprisingly, despite large differences in soil carbon stocks between MI-Fine and MI-Coarse, no difference in soil carbon turnover times was observed. These sites are within 10 km of one another, have similar macroclimate, vegetation, and parent materials, but differ in landscape position, hydrology, soil texture, and likely mineralogy. Hydrology and DOM transport may exert strong influence on soil carbon dynamics at MI-Fine. Local heterogeneity in subsurface hydrology such is difficult to represent in land surface models. Alternatively, it is possible that short turnover times at MI-Fine are a result of soil carbon saturation as described by Six et al. (2002). SOM at MI-fine also had higher nitrogen concentrations and lower C:N ratios in bulk soil, oLF, and DF, indicating a different source, different decomposition stage, or larger fraction of microbial biomass-products in SOM at this site.

The variability in $\Delta^{14}C$ values and turnover times at our sites suggests that the relative importance of different SOC stabilization mechanisms differs among sites. For example, ^{14}C values and turnover times at MO-OZ suggest greater mixing of fresh OM into oLF at the surface (0–5 cm), most likely through earthworm activity. Below 5 cm at MO-OZ and at other sites, microbiota, soil mineralogy, or hydrology may influence aggregate formation and physical protection more than bioturbation by macrofauna. Heckman et al. (2009) found that the dominant stabilization mechanism for soil carbon in *Pinus ponderosa* forests in Arizona differed among sites with different soil acidity and parent materials, with metal-humus complexation and chemical recalcitrance dominating stabilization in acidic sites with rhyolitic and granitic parent materials, and mineral adsorption the dominant mechanism for stabilization of carbon in basic sites with limestone and basalt parent materials. It is likely that the dominant mechanism for carbon stabilization, physical protection or association with minerals through adsorption or formation of metal-humus complexes, differs across our sites as well.

Our findings indicate that edaphic, hydrological, and biological factors are at least as important as climate in controlling soil carbon storage and turnover within the temperate broadleaf forest biome. This is not the only study to find that site-specific factors contribute to soil carbon storage and turnover in ways that may be important for explaining variability in soil carbon dynamics across the landscape. For example, a study of soil carbon turnover in forests along an elevation gradient in the Italian Alps found that differences in soil acidity and clay content caused a confounding effect on the sensitivity of turnover time to mean annual soil temperature (Hakkenberg et al. 2008). In a study of 26 North American forests across a 22 °C gradient in MAT, MRTs for active SOM pools increased with decreasing temperature while MRTs for slowly cycling SOM pools were not affected by MAT or forest type, but perhaps by clay mineralogy (Fissore et al. 2009). Numerous studies have found that soil mineralogy, particularly of sub surface soils, has very high influence on the turnover and amount of carbon in mineral-associated soil carbon pools (e.g., Spielvogel et al. 2008; Mikutta et al. 2006).

Relevance of physical fractions to soil carbon cycling

We selected the fractionation scheme used in this study because it provides physical fractions for chemical and isotopic analysis that approximate an unprotected pool (fLF); a physically protected pool (oLF); and a mineral-associated, stable pool (DF). Chemical analysis of density fractions has shown an increasing degree of decomposition with increasing degree of mineral association across density fractions (Marín-Spiotta et al. 2009; Golchin et al. 1994). Previous studies have also shown that fLF tends to consist of plant materials with a visible structure, sometimes coated in mineral particles (Wagai et al. 2009); while oLF tends to contain highly fragmented plant debris, char, pollen and fungal spores, and

unrecognizable, partially decomposed organic matter (Wagai et al. 2009; Golchin et al. 1994). DF consists of minerals and mineral-associated organic matter (Wagai et al. 2009). Observations using light microscopy of our fractions are consistent with these observations, although we saw char in all of our soil fractions.

At each site and across sites, turnover times of fLF were shorter than of the other fractions, especially DF, demonstrating that carbon in this pool was more readily decomposed, or labile, than SOM in the physically protected and mineral-associated fractions. Turnover times increased with depth, but were more pronounced with oLF and DF than fLF, a trend also found at a deciduous forest in Tennessee (Swanston et al. 2005). We found a greater range in $\Delta^{14}C$ values and turnover times for oLF than the other two fractions. oLF is assumed to be SOM that is weakly associated with minerals or protected by aggregates because it is released by physical disruption (Rasmussen et al. 2005; Swanston et al. 2005; Golchin et al. 1994). In one of the few studies to compare oLF characteristics across more than a few sites, Marín-Spiotta et al. (2008) observed a greater variability in chemistry of oLF than fLF and DF in tropical secondary forests based on ^{13}C-nuclear magnetic resonance (NMR) spectroscopy. They also observed a larger range in $\Delta^{14}C$ values in oLF than the other fractions, consistent with our findings, and concluded that oLFs from different sites include materials at different stages of decay.

As mentioned previously, we observed black carbon in the form of char in soil fractions from all of our sites. We did not quantify the amount of char or analyze isolated char pieces for ^{14}C, so we cannot quantitatively assess the influence of char on SOM turnover times reported in this paper. However, it is unlikely that the presence of char explains long turnover times of some oLF's, particularly those at NH-BF and MA-HF. Our sites are forests that were harvested in the past, have regrown since the late 1800s, and have had fires suppressed for the last 120 years or longer. Efforts at reconstructing fire histories for our sites suggest that historically MO-OZ had more frequent fires than the other sites, followed by MI-Coarse and MI-Fine. Fires were probably less frequent, but a part of the pre-European settlement landscape history, at MA-HF and NH-BF. It is possible that estimated turnover for fractions with high char content represents an average of two significant and distinct pools, with the char turning over more slowly than the rest of the organic matter in the fraction. This effect would be most pronounced in sites with higher fire frequency such as MO-OZ, where oLF turnover times are relatively short and thereby do not seem to be highly impacted by the presence of old black carbon. In sites and plots with lower fire frequency, such as MA-HF and NH-BF where the longest turnover times are found, older char should not greatly affect the estimated turnover time since it requires substantial mass addition to lower a radiocarbon value through dilution. Finally, when the oLF is considered functionally, physical protection is likely the primary driver of stabilization, so the active turnover of char and other organic matter in oLF may be quite similar regardless of biochemical properties (Schmidt et al. 2011).

Comparisons of carbon stocks, distribution, and turnover to other studies

Although our data are the first published for MI-Coarse, MI-Fine, NH-BF, and MO-OZ, comparable studies have been conducted previously at MA-HF about 30 m south of our plots (Gaudinski et al. 2000) and at other sites. We report carbon stocks for our sites that are within one standard deviation of the world averages reported by Post et al. (1982) for temperate warm moist (60 ± 26 Mg C ha^{-1}), cool moist (121 ± 82 Mg C ha^{-1}), and cool wet (139 ± 88 Mg C ha^{-1}) forests. Previous work at MA-HF reported much lower total soil carbon stocks (88 Mg C ha^{-1}) than we do (123 Mg C ha^{-1}). We sampled about 10 cm deeper, accounting for about 10 Mg C ha^{-1}. Also, they used quantitative pits ($n = 2$) whereas we used cores ($n = 5$). Total carbon stock at Walker Branch, a temperate broadleaf forest in eastern Tennessee that is slightly warmer than MO-OZ, sampled to comparable depth was 46–57 Mg C ha^{-1} (Gaudinski and Trumbore 2003), on the low end of the range observed at our sites.

Not surprisingly, carbon concentration declined with depth at all our sites and except at MI-Coarse most soil carbon was in the top 30 cm of mineral soil. $\Delta^{14}C$ also declined with depth and the rate of decline differed amongst sites. $\Delta^{14}C$ values and turnover times in the subsurface at all of our sites were higher than those reported for similar depths from Russian steppe (Torn et al. 2002) and tropical forest (Trumbore 1993)

and may reflect bioturbation, disturbance or glaciation history, or simply faster cycling of deep soil carbon in these temperate forests.

Previous studies also reported turnover times for Oi and Oe/Oa and density fractions at MA-HF (Gaudinski et al. 2000) and for Walker Branch (Gaudinski and Trumbore 2003). The first study found similar turnover times for MA-HF O horizons as we report in this study. The second found turnover times at Walker Branch for Oi that were similar to those we report for our sites and for Oe/Oa of 6–13 years, slightly longer than what we report for MI-Coarse (5 years). Similar to our findings, these studies reported that over half of mineral soil carbon was in DF (Swanston et al. 2005; Gaudinski et al. 2000). We found similar turnover times for density fractions from MA-HF as did Gaudinski et al. (2000). Turnover times for a broadleaf forest in Pennsylvania (Crow et al. 2007) and Walker Branch (Gaudinski and Trumbore 2003) were also within the range of turnover times we found, although turnover times reported for light density fractions by these studies are more similar to those at MO-OZ than our northeastern sites. Relatively long turnover times for fLF at MA-HF and NH-BF could be related to the large O horizons at these sites.

The variation in turnover times among fractions and with depth at our sites demonstrate the importance of representing multiple soil carbon pools in carbon cycle models. A new forest-specific version of the DayCent model for ecosystem carbon cycling, ForCent, allows for separate modeling of organic horizons and mineral soil carbon pools (Parton et al. 2010). As with similar models, ForCent uses three discrete soil carbon pools: an active, slow, and passive pool. Our soil fractions most closely approximate the slow (fLF) and passive (oLF + DF) pools described in these models. Larger scale models should consider accommodating a similar structure for soil carbon pools that cycle on different timescales and allowing them to be driven by different factors at different sites depending on edaphic factors, hydrology, and macrobiota.

Conclusion

We observed differences in soil carbon stock, distribution, and turnover at five temperate broadleaf forests. Some of these differences could be explained by well-documented trends in soil carbon storage and dynamics across gradients of climate or soil texture that are often included in carbon models. For example, cooler sites with finer soil texture tended to have larger soil carbon stocks than warmer or coarse textured sites. In addition, the shortest turnover times were observed at the warmest site where decomposition should occur more quickly. However, we found a fourfold increase in soil carbon stocks across sites that is not explained by climate but by edaphic factors or hydrology. In addition, the longest turnover times were not found at the coolest sites or the sites with the finest soil texture, but at sites without earthworms and perhaps with soil mineralogy favorable for stabilization via organo-mineral interactions.

Our observations lead us to conclude that site-specific factors other than climate significantly contribute to soil carbon storage, distribution, and turnover in temperate broadleaf forests. Factors, such as soil macrobiotic activity, texture and mineralogy, and hydrology may be important in determining soil carbon dynamics of a given ecosystem and the inclusion of these factors may be required to improve the sensitivity and accuracy of carbon models provided model resolution allows for variation in these parameters at scales relevant to soil carbon cycling. Future soil carbon studies that explicitly consider the role of macrofauna, soil hydrology, and mineralogy as factors influencing soil carbon storage, distribution, and turnover are necessary for improving our ability to capture variability in soil carbon cycling within biomes in predictive carbon models.

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