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Variable temperature sensitivity of soil organic carbon in North American forests

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Abstract

We investigated mean residence time (MRT) for soil organic carbon (SOC) sampled from paired hardwood and pine forests located along a 22 °C mean annual temperature (MAT) gradient in North America. We used acid hydrolysis fractionation, radiocarbon analyses, long-term laboratory incubations (525-d), and a three-pool model to describe the size and kinetics of the acid insoluble C (AIC), active and slow SOC fractions in soil. We found that active SOC was 2 ± 0.2% (mean ± SE) of total SOC, with an MRT of 33 ± 6 days that decreased strongly with increasing MAT. In contrast, MRT for slow SOC and AIC (70 ± 6% and 27 ± 6% of total SOC, respectively) ranged from decades to thousands of years, and neither was significantly related to MAT. The accumulation of AIC (as a percent of total SOC) was greater in hardwood than pine stands (36% and 21%, respectively) although the MRT for AIC was longer in pine stands. Based on these results, we suggest that the responsiveness of most SOC decomposition in upland forests to global warming will be less than currently modeled, but any shifts in vegetation from hardwood to pine may alter the size and MRT of SOC fractions.

Keywords: carbon quality, Q_{10}, radiocarbon, SOC decomposition, SOC fractionation, stable C, temperate forests

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Introduction

The impact of climate change on the carbon (C) balance of terrestrial ecosystems depends on changes in the total quantity and quality of detrital C entering soils as well as changes in the rate at which stable soil organic carbon (SOC) is decomposed by heterotrophic organisms and released back to the atmosphere as carbon dioxide (CO_2). If the heterotrophic decomposition rate of most SOC is enhanced by warming, then the CO_2 sink strength of soils may decline in a warmer world, resulting in a positive feedback to global temperatures (Jenkinson *et al*., 1991; Schimel *et al*., 1994). In contrast, if the decomposition of most SOC is negligibly responsive to temperature (Giardina & Ryan, 2000), forest soils may continue to act as a net sink for atmospheric CO_2, and thus provide a negative feedback to increased atmospheric CO_2 concentration (Holland *et al*., 2000). Critically, available information is inadequate to assess with confidence the likelihood of either outcome (Davidson & Janssens, 2006).

Studies have documented a wide range of SOC decomposition responses to temperature (Wedin & Pastor, 1993; Townsend *et al*., 1995; Giardina & Ryan, 2000; Fang *et al*., 2005; Davidson & Janssens, 2006; Conant *et al*., 2008). Short-term lab incubations indicate similar temperature sensitivity for both active and less active SOC (e.g., Fang *et al*., 2005), but these incubations are not sufficiently long to describe the decomposition responses of stable SOC. Mathematical models also based on short-term incubations have shown that it is theoretically possible to have an increase in the

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temperature sensitivity of stable SOC compared with active SOC (Knorr *et al*., 2005), but these models require important assumptions about the distribution and activation energies of SOC across fractions – assumptions that have yet to be validated. In contrast, some studies suggest that stabilization of SOC may increase with global warming (Dalias *et al*., 2001; Thornley & Cannell, 2001; Fissore *et al*., 2008). In line with these results, other modeling efforts point to a smaller than predicted temperature response of SOC decomposition (Ise & Moorcroft, 2006).

Indirect effects of climate change on SOC MRT may originate also from variations in tree species composition and distribution (Sykes & Prentice, 1996; Xu *et al*., 2007). Efforts to quantify the links between the chemical characteristics of inputs and accumulation of SOC with different MRT have yielded diverse outcomes (Melillo *et al*., 1989; Quideau *et al*., 2001). Based on evidence that litter mass loss is greater for simple substrates (Melillo *et al*., 1982), the C : N and lignin : N of inputs to soil have been used to predict SOC quality. However, inherent chemical recalcitrance of inputs to soil appears to correlate with only the initial phase of C decomposition (von Lützov *et al*., 2006), and the reciprocal role played by C and N in SOC stabilization may be more complex than previously suggested (as summarized by Sollins *et al*., 2007; see also Fog, 1988; Swanston *et al*., 2004; Kleber *et al*., 2007). Further, there is growing evidence that higher quality litter (e.g. low C : N or low lignin : N) may have long-term stabilizing effects on SOC, resulting in accumulation of SOC with low MRT (Giardina *et al*., 2001). For example, protein-like C compounds consistently are found in stable SOC (Lorenz *et al*., 2007), while lignin-like molecules represent only a minor component. Limited lignin accumulation in stable SOC fractions suggests a faster decomposition of lignin than previously hypothesized and the concomitant contribution to SOC of other organic molecules, such as alkyl-C compounds that are in part of microbial origin (Mikutta *et al*., 2006; Lorenz *et al*., 2007). Overall, evidence indicates that N has inhibitory effects on microbial enzymatic activity, reacts with C compounds to form stable organic matter, and can facilitate the binding of organic matter to soil clay minerals (Prescott *et al*., 2000; Berg & Meentemeyer, 2002; Russell *et al*., 2007), all of which can contribute to SOC stabilization (Magill *et al*., 1997). Clearly, the nature of the relationship between litter quality and SOC quality remains uncertain.

Uncertainty in controls over soil C process rates may also be compounded by unclear terminology. Throughout this paper we refer to three fractions of SOC: acid insoluble C (AIC), slow and active SOC. We define AIC as the residue that is insoluble in 6 N HCl following a series of physical and chemical fractionation steps. The resulting SOC fraction includes chemically recalcitrant substrates and C that is strongly stabilized by the mineral phase. The AIC fraction may be chemically or physically protected by mechanisms similar to those protecting the 'stable' C fraction isolated using similar approaches (e.g., acid hydrolysis of bulk soil, density fractionation). The CO_2 evolved during incubation studies under controlled conditions represents the biological fractionation of active and, depending on duration of the incubation, part of the slow SOC stored in soil (Townsend *et al*., 1997; Collins *et al*., 2000; Paul *et al*., 2001). Overall, extended lab incubations are consistent with other methods in isolating active SOC (McLauchlan & Hobbie, 2004), which is quantified through analysis of CO_2 efflux from incubated soils and is mathematically defined as the SOC released early in the incubation. The slow SOC fraction is less labile with mean residence times (MRT) intermediate between active and the AIC fraction, and is estimated by difference (see also 'Methods').

Despite complications relating to terminology, separation of SOC into conceptual fractions with different MRT is useful for both describing the dynamics of SOC (Paul *et al*., 2006), and also predicting the response of SOC to changing temperature (von Lützov *et al*., 2007). For these reasons, we relied on C fractionation and radiocarbon analysis, laboratory incubations, and a well-established three-pool first-order decomposition model (Paul *et al*., 2001, 2006) to provide a quantitative characterization of AIC, slow and active SOC fractions and their decomposition rates.

The MRT for stable SOC ranges from hundreds to even thousands of years (Trumbore *et al*., 1996; Torn *et al*., 1997). Hydrolysis in HCl isolates a residue that is measurably older than the hydrolysable material (Leavitt *et al*., 1997). This approach was used in agricultural and forest soils of North America to separate a fraction of SOC that was on average 1300-year older than total SOC (Paul *et al*., 2001). Chemical analyses showed that the SOC fraction that is insoluble in concentrated HCl is composed mainly of waxes and long-chain alkyl compounds (Rovira & Vallejo, 2002; Paul *et al*., 2006), lignin-like compounds (Collins *et al*., 2000), and other aromatic compounds that are resistant to degradation (Paul & Clark, 1996). Easily degradable compounds such as soluble carbohydrates, proteins, and amino acids are typically susceptible to solubilization in presence of acids (Barriuso *et al*., 1987).

Forests store large quantities of SOC (Jobbagy & Jackson, 2000) and continue to be a net sink of atmospheric C (Fan *et al*., 1998), yet few studies have examined the relationships between mean annual temperature (MAT), vegetation cover, and SOC MRT. Our

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study builds on pioneering work across elevation (Trumbore *et al*., 1996) and continental (Paul *et al*., 2001) gradients but relies on a highly controlled MAT gradient across North America (Fissore *et al*., 2008), where surface soil texture, growing season site water balance, vegetation cover (paired sites of *Pinus* or hardwood dominated forest), and stand maturity (well past canopy closure) were similar. We used this paired gradient to isolate the effects of temperature and vegetation on SOC fraction size and MRT and to test several hypotheses about SOC response to temperature.

Our first hypothesis was that despite higher decomposition rates for active SOC at warm sites, decomposition rates for AIC and slow SOC would not be temperature limited, and so the MRT of these SOC fractions would be insensitive to MAT. Further, we hypothesized that increasing MAT shifts the distribution of SOC from active to stable fractions because the temperature response of soil chemical–physical reactions are stronger than that of microbial enzymatic processes and so warming results in a net increase in the transfer of C compounds from unprotected to protected sites (Thornley & Cannell, 2001). Also, we used this MAT gradient to ask questions about how temperature interacts with contrasting surface litter types (pine vs. hardwood) to affect SOC fraction size and MRT. We hypothesized that, although high-quality hardwood litter initially decomposes more rapidly than low-quality pine litter, a higher proportion of stable SOC accumulates in hardwood than in pine soils because of the long-term inhibitory effects on SOC decomposition exerted by N (Berg, 2000; Giardina *et al*., 2001; Berg & Meentemeyer, 2002) and because N contributes to the formation of the structures of stable C compounds (Fog, 1988; Russell *et al*., 2007).

This study addresses a critical knowledge gap regarding how SOC fraction size and MRT respond to changes in MAT and vegetation by relying on a sampling design that represents a space for time substitution. By sampling along a gradient in MAT, our results highlight longer-term changes that integrate decades to centuries long climate effects on SOC process rates across sites. This approach provides less information on short-term responses to climate change. None-the-less, coupling this MAT gradient with radiocarbon analyses, we were able to estimate the size and MRT of the AIC fraction under field conditions, where resulting data integrate the *in situ* effects of MAT, substrate supply, and vegetation on SOC stabilization. We quantified the dynamics of active C using a lab-based approach with results scaled to the field using paired incubations at two temperatures to develop temperature response functions. The field-based AIC fraction data and the lab-based active SOC fraction data were combined to model the size and kinetics of AIC, slow and active SOC fractions along our continental-scale MAT gradient.

Methods

Site description and soil characteristics

Soils used in this study were sampled from 26 sites located in six bioclimatic regions spanning a 22 °C MAT gradient in North America (Table 1). Across regions, mean annual precipitation (MAP) increased with MAT. Higher evapotranspiration at warm sites resulted in relatively constant calculated growing season water balance across the gradient. All but the Michigan sites were located in Experimental Forests of the USDA National Forest Service or of Universities. Closed-canopy stands were mature for the region. Hardwood species composition was similar along the gradient, with the exception of the coldest Colorado site, where maple was not present. We sampled even-aged aspen stands in Colorado and also Minnesota, where we also sampled sugar maple dominated forests. Pine species composition varied in relation to climate. Stand history and climate data were available for all locations. Most sites have always been in forest, with two Michigan sites and two Georgia sites having a history of land clearing. For these sites, forest cover at the time of sampling had been in place for at least 70 years. Detailed site description is provided by Fissore *et al*. (2008) and is summarized in Tables 1 and 2.

We collected soils at fixed depth increments without consideration of soil horizons. We sampled the top 20 cm of the mineral soil after removing forest floor material by using a $\varnothing$ 10 cm soil auger. Immediately after sampling, soils were shipped overnight in coolers to the USDA Forest Service Lab in Houghton, MI where we separated roots and rocks from fresh soil (< 2 days from sampling) using a 2 mm-mesh sieve. Soils were then dried at 30 °C in a forced air oven and processed for chemical–physical characterization, incubation, and archiving.

Soils were coarse-textured with pH varying between 4.3 and 6.1 (Table 2). Proportion of expandable clay minerals, pH, cation exchange capacity (CEC), and SOC content were all negatively related to MAT. Soil texture was finer and SOC content was generally higher in hardwood than pine sites (Fissore *et al*., 2008).

Quantifying AIC

The AIC fraction was isolated from other fractions by chemical and physical fractionation including acid hydrolysis (Loya *et al*., 2003) followed by radiocarbon analyses (Torn *et al*., 2002). These methods allowed us

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Table 1 Sampling sites location and main characteristics

Sample	Location	MAT (°C)	MAP (mm yr^{-1})	Forest type	Main tree species	Soil type	Parent material
CO-P1	Colorado	−2	474	Pine	*Pinus contorta*	Entic Haplocryods	Slope wash, gneiss and schist
CO-P2	Colorado	−2	474	Pine	*P. contorta*	Mixed Typic Cryochrepts	Outwash, gneiss and schist
CO-A1	Colorado	−2	474	Hardwood	*Pinus tremuloides*	Entic Haplocryods	Slope wash, gneiss and schist
CO-A2	Colorado	−2	474	Hardwood	*P.tremuloides*	Mixed Typic Cryochrepts	Outwash, gneiss and schist
MN-P1	Minnesota	4	700	Pine	*Pinus resinosa*	Mixed frigid Typic Udipsamment	Glacial outwash plains
MN-P2	Minnesota	4	700	Pine	*P. resinosa*	Mixed frigid Typic Udipsamment	Glacial outwash plains
MN-A1	Minnesota	4	700	Hardwood	*P. tremuloides*	Mixed frigid Typic Udipsamment	Glacial outwash plains
MN-H1	Minnesota	4	700	Hardwood	*Acer* spp.	Mixed frigid Typic Udipsamment	Glacial outwash plains
MI-P1	Michigan	5	771	Pine	*P. resinosa*	Mixed Frigid Typic Haplorthods	Glacial outwash plains
MI-P2	Michigan	5	867	Pine	*P. resinosa*	Frigid Typic Haplorthods	Glacial outwash plains
MI-A1	Michigan	5	771	Hardwood	*P. tremuloides*	Mixed Frigid Typic Haplorthods	Glacial outwash plains
MI-H1	Michigan	5	771	Hardwood	*Acer* spp.	Typic Fragiorthods	Glacial outwash plains
MI-H2	Michigan	5	867	Hardwood	*Acer* spp.	Frigid Typic Haplorthods	Glacial outwash plains
KY-P1	Kentucky	12	850	Pine	*Pinus virginiana*	Mesic Typic Hapludults	Sandstone, shale, and siltstone
KY-H1	Kentucky	12	850	Hardwood	*Acer* spp.	Mesic Typic Hapludults	Sandstone, shale, and siltstone
KY-H2	Kentucky	12	850	Hardwood	*Acer* spp.	Mesic Umbric Dystrochrepts	Sandstone, shale, and siltstone
KY-H3	Kentucky	12	850	Hardwood	*Acer* spp.	Mesic Typic Dystrochrepts	Sandstone, shale, and siltstone
SC-P1	South Carolina	18	1332	Pine	*P. virginiana*	Thermic Glossaquic Hapludalfs	Marine sediments
SC-P2	South Carolina	18	1332	Pine	*P. virginiana*	Aquic Quartzipsamment	Sandy marine sediments
SC-P3	South Carolina	18	1332	Pine	*P. virginiana*	Aquic Quartzipsamment	Sandy marine sediments
SC-H1	South Carolina	18	1332	Hardwood	*Acer* spp.	Thermic Aeric Endoaquults	Marine sediments
SC-H2	South Carolina	18	1332	Hardwood	*Acer* spp.	Thermic Aeric Endoaquults	Marine sediments
SC-H3	South Carolina	18	1332	Hardwood	*Acer* spp.	Thermic Aeric Paleaquults	Clayey sediments
SC-H4	South Carolina	18	1332	Hardwood	*Acer* spp.	Thermic Aeric Alaquods	Sandy marine sediments
GA-P1	Georgia	20	1270	Pine	*Pinus taeda*	Thermic Typic Kanhapludults	High-grade metamorphic and igneous
GA-H1	Georgia	20	1270	Hardwood	*Acer* spp.	Thermic Typic Kanhapludults	High-grade metamorphic and igneous

For Colorado, samples were taken from Fraser Experimental Forest and Routt National Forest (USDA Forest Service); in Minnesota from Marcel and Cutfoot Experimental Forests (USDA Forest Service), in Michigan from industrial lands and from Michigan Technological University's Alberta Forestry Center; in Kentucky from the Daniel Boone National Forest (USDA Forest Service) and the University of Kentucky Robinson Forest; in South Carolina from Santee Experimental Forest and Francis Marion National Forests (USDA Forest Service); and in Georgia from the University of Georgia Agricultural Experiment Station.
MAT, mean annual temperature; MRT, mean residence time.

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Table 2 Main soil chemical and physical characteristics of soils sampled across the 22 °C MAT gradient

Sample	Texture	Clay (%)	pH	CEC (cmolc kg^{-1})	C (%)	*N* (%)
CO-P1	Sandy-loam	8.3	5.8	6.8	2.20	0.09
CO-P2	Sandy-loam	12.0	5.6	10.5	2.64	0.10
CO-A1	Sandy-loam	10.0	6.1	26.4	8.07	0.53
CO-A2	Sandy-loam	7.0	6.1	10.6	3.48	0.11
MN-P1	Sandy-loam	4.5	5.6	4.5	1.45	0.07
MN-P2	Loamy-sand	3.0	5.3	3.2	1.05	0.05
MN-A1	Sandy-loam	8.5	5.7	4.8	1.60	0.09
MN-H1	Sandy-loam	8.0	5.8	6.9	1.93	0.11
MI-P1	Sand	1.0	4.9	1.7	1.07	0.05
MI-P2	Sand	2.0	4.7	1.6	1.33	0.07
MI-A1	Loamy-sand	3.0	5.0	2.0	1.34	0.07
MI-H1	Sandy-loam	4.0	4.9	5.5	3.38	0.24
MI-H2	Sand	2.0	4.8	2.2	1.62	0.09
KY-P1	Sandy-loam	10.0	4.4	3.2	2.24	0.06
KY-H1	Loam	16.0	5.7	6.6	2.10	0.16
KY-H2	Loam	15.0	4.8	3.7	2.34	0.14
KY-H3	Sandy-loam	8.0	4.6	2.1	1.22	0.05
SC-P1	Loamy-sand	4.0	4.8	2.1	1.74	0.06
SC-P2	Sand	3.5	4.9	1.3	0.88	0.03
SC-P3	Sand	1.0	4.7	1.4	1.37	0.04
SC-H1	Loam	20	4.4	5.8	2.06	0.09
SC-H2	Loam	16	4.3	3.5	1.76	0.07
SC-H3	Sandy-loam	13	4.6	2.8	1.47	0.06
SC-H4	Sand	3.0	4.8	1.9	1.24	0.05
GA-P1	Sand	3.5	4.5	1.3	1.00	0.04
GA-H1	Sandy-loam	13	5.2	3.6	2.50	0.17

More details on site characteristics and soil analyses can be found in Fissore *et al*. (2008).

MAT, mean annual temperature; CEC, cation exchange capacity.

to quantify both the size and MRT of the AIC fraction. Due to the high cost of radiocarbon analyses, we limited analyses to a subset of 16 of the 26 soils samples from the MAT gradient.

Fractionation for AIC consisted of removing water-extractable SOC through agitation in DI water for 24 h, followed by filtration through a 0.45 μm glass filter membrane using a pump-vacuum system. The nonextracted soil material captured on the membrane was scraped off into specimen cups and dried at 60 °C. This material was then mixed with a solution of 1 M NaCl to float and remove particulate matter. The remaining soil was then rinsed several times though a fiber membrane with deionized water and then centrifuged to remove excess of salt (Loya *et al*., 2003). The separated soil material was again dried at 60 °C and then analyzed to assess %C (Costech Elemental Combustion System 4010 Mass Spectrometer, Costech, Valencia, CA, USA). Using 5 g of this soil residue for each of the 16 samples, we removed any identifiable fragments of plant material by hand under a microscope (× 20 magnification, and ~ 50 h per sample). Particular attention was paid to removing only identifiable plant material. Following microscope work, the soil was acidified in 6 N HCl for 12-h at 116 °C to separate acid-soluble and acid-insoluble SOC fractions. The solution of soil residue and acid was then allowed to cool overnight (approximately 12 h) to ambient temperature and subsequently rinsed with deionized water and then decanted into a pump–vacuum system that passed the water and soil mixture through a glass fiber membrane to isolate AIC. This was repeated until no remaining soil was observed. The glass fiber carrying the residue was then transferred into Al-tins of known weight and oven dried at 60 °C. The residue was then scraped off the fiber membrane and analyzed to assess %C that is AIC (Costech Elemental Combustion System 4010 Mass Spectrometer).

AIC fraction and the paired bulk soil (total SOC) for the 16 samples were analyzed for radiocarbon content by accelerator mass spectrometry at Lawrence Livermore National Laboratory. Sample preparation consisted of combustion in presence of CuO and Ag followed by reduction of CO_2 in presence of H_2 and a Fe catalyst to produce graphite (Vogel *et al*., 1984). The ^{14}C analysis was then conducted using graphite targets (Vogel, 1992). Radiocarbon data are reported as $\Delta^{14}C$, which refers to the deviation in parts per thousand from the $^{14}C/^{12}C$ of oxalic acid standard and samples were corrected for fractionation effects to a forest $\delta^{13}C$ value of −25‰ (Stuiver & Polach, 1977).

Quantifying active and slow SOC fractions

Long-term incubations (525 days) allowed us to quantify the kinetics of active SOC on soil samples used for the radiocarbon analyses plus an additional 10 soils samples from across the MAT gradient and vegetation types to improve our estimates of total loss and temperature sensitivity (Q_{10}) of SOC decomposition. These incubations were conducted on two identical sets of 26 soil samples at lab incubation temperatures (LIT) of 10 °C (LIT10) and 30 °C (LIT30). We selected LIT10 because this temperature corresponds to the average MAT across our sites and characterizes growing season soil temperatures at the coldest sites, while LIT30 represents growing season soil temperatures at the warm-end of the gradient, and is also a commonly used temperature in previous incubation studies (Winkler *et al*., 1996; Collins *et al*., 2000; Paul *et al*., 2006).

For each soil sample, 30 g of dry soil were placed into 120 mL specimen cups, brought to moisture corresponding to 60% of water holding capacity (WHC), and then incubated in 1-L mason jars. Each jar was

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provided with a lid and septum for gas collection. Throughout the incubation, samples were maintained moist at 60 ± 5% of WHC and at constant temperature (10 or 30 °C) in Precision 815 low temperature incubators (Winchester, VA). We determined soil WHC by saturating a known amount of 30 °C-dry soil that was previously brought to a specific bulk density of 1 mg m^{-3} (Elliott *et al*., 1994). The saturated soil, after free water was allowed to drain, represented 100% of WHC, while dry soil represented 0% of WHC.

During the 525 days incubation, we periodically measured the CO_2 efflux over a 24-h period for each soil sample. Before each gas sampling event, we flushed the samples with ambient air for 30-min, sealed the jars, and immediately sampled a subset of 5–10 samples for time zero head space gas measurements. Samples in the sealed jars were then incubated at the predefined LIT10 or LIT30 for 24-h and head space gas was sampled a second time for Gas Chromatograph (CO_2) analysis (Agilent 6890 Gas Chromatograph, Agilent Inc., Palo Alto, CA, USA). Gas sampling utilized a 50 mL gas-tight syringe by first drawing and plunging the syringe three times to guarantee homogeneous gas sampling. Each sample was injected into 4-mL gas-tight vials and analyzed within 8-h of collection. Time zero gas measurements were used as baseline ambient [CO_2] to be subtracted from head space [CO_2] at the end of the 24-h period to calculate efflux rates. Cumulative SOC loss was obtained from the conversion of CO_2 efflux rates into percent of the initial soil C lost during the incubation. An initial 30-day trial of our experiment showed high reproducibility ($r^2 = 0.96$, $P < 0.01$, $n = 34$), and analyses over 24 h showed strong linearity of efflux rates ($r^2 = 0.99$; $P < 0.01$; $n = 10$; Fissore *et al*., 2008). We calculated values of temperature sensitivity (Q_{10}) by comparing the two LITs as:

$$Q_{10} = \left(\frac{R_1}{R_2}\right) e^{\left(\frac{10}{LIT30-LIT10}\right)}, \quad (1)$$

where R_1 and R_2 equal SOC respiration rates at LIT30 and LIT10, respectively. For comparison and following Conant *et al*. (2008), we also calculated Q_{10} based on the time required for a known amount of SOC to decompose.

MRT and kinetics of SOC fractions

For a subset of 16 soil samples (Table 3), we evaluated the size and kinetics of the three SOC pools according to a three-pool first order decomposition model (Collins *et al*., 2000; Paul *et al*., 2001) as follows:

$$C_{t(t)} = C_a e^{-ka(t)} + C_s e^{-ks(t)} + C_r e^{-kr(t)}, \quad (2)$$

where $C_{t(t)}$ is the total SOC at time t; C_a, C_s, and C_r represent the C mass in the active, slow and AIC fractions, respectively; ka, ks, and kr are the rates of decomposition. We then solved for the corresponding model:

$$dC/dt = C_a ka\, e^{(-kat)} + C_s ks\, e^{(-kst)} + C_r kr\, e^{(-krt)}, \quad (3)$$

where C_a, ka, and ks were obtained through the analysis of the CO_2 efflux rates from the decomposition study by curve fitting, while C_s was constrained as $C_s = (C_{tot} - (C_a + C_r))$; C_r and kr were derived from acid hydrolysis (Leavitt *et al*., 1997) and radiocarbon analysis. Specifically, calculation of field-based radiocarbon-derived MRT of AIC was accomplished using a time-dependent steady-state model (Trumbore *et al*., 1995; Gaudinski *et al*., 2000; Torn *et al*., 2002). The MRT of active and slow SOC was obtained as $1/k$ from lab incubation curves. For lab-derived SOC fractions (active and slow), MRT values were scaled to field MAT by multiplying (lab) MRT by the following conversion factor:

$$Q_{10} \times e^{\left(\frac{LIT10-MAT}{LIT30}\right)}, \quad (4)$$

where MAT is site-specific. Hereafter active and slow MRT will always refer to field-scaled MRT. This adjustment allows comparison of ^{14}C-based MRT, which reflect field conditions, to incubation-based MRT. In contrast to earlier studies (Collins *et al*., 2000; Haile-Mariam *et al*., 2000; Paul *et al*., 2001), we did not rely on an assumed Q_{10} of 2.0 to scale lab results to the field, but instead adopted the average Q_{10} calculated from our incubation experiments ($Q_{10} = 1.5$). Using an assumed Q_{10} of 2 instead of the incubation-derived Q_{10} of 1.5 to scale MRT from the lab to the field results in on average a twofold increase in active SOC MRT (MRT = 70 ± 15 with $Q_{10} = 2$ vs. MRT = 33 ± 6 with $Q_{10} = 1.5$), with larger increases at cold sites and smaller at warm sites. Critically, these changes in relationship of active SOC MRT with MAT (with $Q_{10} = 2$, MRT active SOC = −6.5MAT + 134.4; $r^2 = 0.79$; $P < 0.05$; $n = 16$ vs. $Q_{10} = 1.5$, where MRT active SOC = −2.5MAT + 57.1; $r^2 = 0.82$, $P < 0.05$) do not alter our conclusions about the relationship between AIC MRT and MAT because the AIC MRT is derived from radiocarbon analyses. For the slow SOC fraction, using a Q_{10} of 2 in the model would actually dampen the effect of MAT on MRT.

Statistical analysis

In each of the six bioregions examined in this study, we sampled between two to six replicate stands, for a total of 26 sites. Each replicate stand sample was composed of three aggregated subsamples. Replicated stands were considered true replicates because of geographic location and vegetation type. Differences in vegetation type

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Table 3 SOC fractions and SOC mineralization kinetics determined using a three-pool model from long-term incubation, acid hydrolysis, and radiocarbon analysis

	Active SOC				Slow SOC				Acid insoluble SOC		
Sample	mg C g^{-1} soil	% Total SOC	(lab) MRT (days)	(scaled) MRT (days)	mg C g^{-1} soil	% Total SOC	(lab) MRT (days)	(scaled) MRT (years)	mg C g^{-1} soil	% Total SOC	MRT (years)
CO-P1	0.72	3.3	23	85	16.98	77.2	213	12	4.30	19.5	683
CO-P2	0.81	3.1	15	56	16.39	62.1	140	11	9.20	34.8	908
CO-A2	0.87	2.5	19	71	22.63	65.0	178	18	11.30	32.5	601
MN-P1	0.45	3.1	19	55	4.05	27.9	115	8	10.00	69.0	918
MN-H1	0.31	1.6	12	35	3.69	19.1	74	4	15.30	79.3	1188
MN-P2	0.29	2.7	17	47	9.61	91.6	100	10	0.60	5.7	1835
MI-P2	0.31	2.3	10	28	12.40	93.2	58	16	0.60	4.5	1682
MI-H2	0.34	2.1	12	32	15.66	96.6	66	27	0.20	1.2	5699
KY-P1	0.64	2.8	14	29	17.36	77.5	49	16	4.40	19.6	918
KY-H3	0.19	1.6	8	16	8.21	67.3	27	7	3.80	31.1	581
SC-H2	0.15	0.9	6	10	8.65	49.2	14	9	8.8	50.0	425
SC-P3	0.15	1.1	11	18	10.45	76.3	25	15	3.10	22.6	1606
SC-P2	0.09	1.0	6	10	8.51	96.7	14	6	0.20	2.3	2659
SC-H3	0.16	1.1	8	12	7.92	53.9	17	5	6.60	44.9	380
GA-P1	0.12	1.2	7	11	8.58	85.8	14	12	1.30	13.0	1442
GA-H1	0.71	2.8	9	14	21.89	87.6	18	7	2.40	9.6	1688
Average	0.39	2.1	12	33	12.06	70.4	70.2	11	5.13	27.5	1451
(± SE)	(0.07)	(0.2)	(1.3)	(5.8)	(1.45)	(5.9)	(15.7)	(1.4)	(1.15)	(5.9)	(323)*
Average pine	0.40[a]	2.3[a]	13.6[a]	38[a]	11.59[a]	76.5[a]	80.8[a]	12[a]	3.74[a]	21.2[a]	1436[a]
(± SE)	(0.09)	(0.3)	(1.9)	(8.3)	(1.52)	(7.1)	(22.4)	(1)	(1.23)	(6.9)	(201)
Average hardwood	0.39[a]	1.8[a]	10.6[a]	27[a]	12.66[a]	62.7[a]	56.5[a]	11[a]	6.91[a]	35.5[b]	1470[a]
(± SE)	(0.11)	(0.3)	(1.7)	(8.2)	(2.81)	(9.7)	(22.3)	(3)	(2.00)	(9.9)	(725)†

All values refer to the top 20 cm of mineral soil. Lab-derived active and slow SOC MRT was scaled to field MAT according to (scaling factor) = $Q_{10} \times e^{\left(\frac{LIT10-MAT}{LIT30}\right)}$. Same letters represent no significant difference within the same column assessed at the 5% level.

*Without the contribution of MI-H2 average MRT is 1168 (± 160).

†Without the contribution of MI-H2 average MRT is 765 (± 200). Pine and hardwood AIC MRT is significantly different when MI-H2 is excluded.

SOC, soil organic carbon; MAT, mean annual temperature; MRT, mean residence time.

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within each region (paired hardwood and pine) were used as a qualitative variable for the regression analyses. We used simple linear regression to evaluate the relationship between MAT and the size and MRT of AIC, slow and active SOC; multiple linear regression to investigate the relationship of different soil characteristics with SOC decomposition; and *t*-test analyses to assess differences in SOC loss and site characteristics between vegetation types. We relied on nonlinear regression to describe the relationship between AIC content and delta $\Delta^{14}C$ (SPSS 15.0, SPSS Inc., Chicago, IL, USA). In all cases significance was assessed by $\alpha = 0.05$. The three-pool SOC model was conducted through nonlinear regression of the SOC decomposition curve at LIT30 of soil samples (PROC NLIN METHOD = MARQUARDT, SAS 9.1, 1995).

Results

SOC quality across the MAT gradient

AIC. Size and MRT of the AIC fractions were obtained through chemical–physical fractionation and radiocarbon analysis of bulk sieved soils. Resulting information

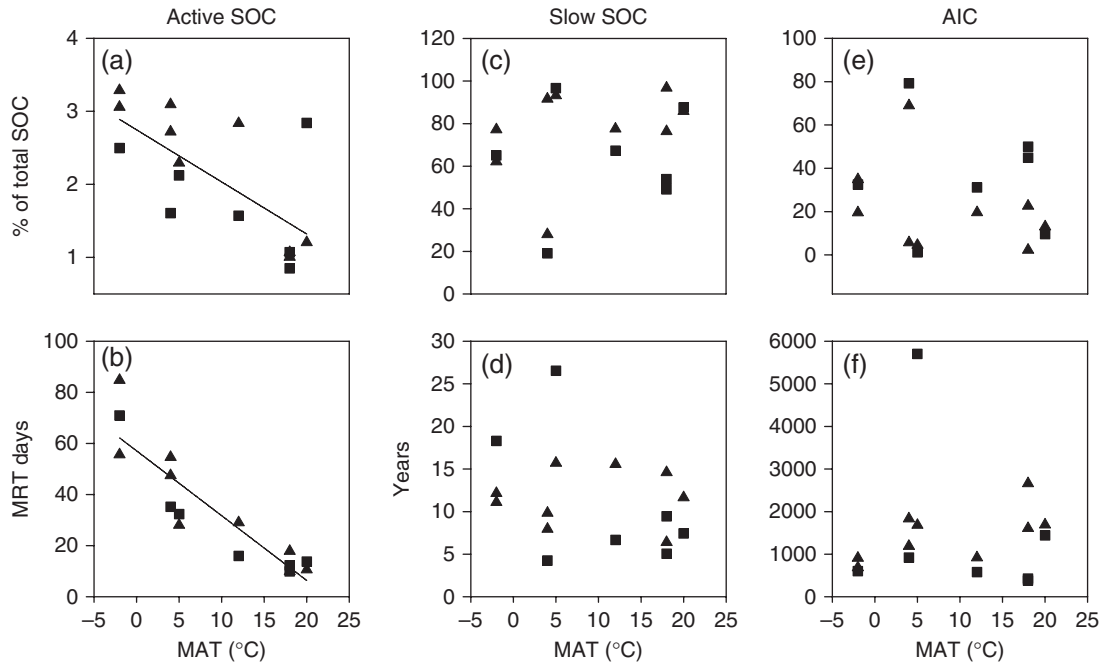

Fig. 1 Relationship between active, slow and acid insoluble SOC as isolated by the three-pool decomposition model and mean annual temperature (MAT) and mean residence time (MRT). In all panels, triangles represent pine stands and squares represent hardwood stands. Mean residence time of active and slow SOC refers here to field-scaled MAT according to (conversion factor): $Q_{10} \times e^{\left(\frac{LIT10-MAT}{LIT30}\right)}$. The effect of scaling MRT to field MAT did not affect the regression curves significantly. For instance, the effect of scaling reflects on the slope of the regression in 3b but not on the significance of the relationship (MRT = −2.3 MAT + 17.2; $r^2 = 0.68$, $P < 0.01$; $n = 16$). SOC, soil organic carbon.

Table 4 Regression analysis of the three SOC fractions (Fig. 1) that describes the effect of mean annual temperature (MAT) on size of each fraction (as % of total SOC) and mean residence time (MRT)

SOC fraction	*x*	*y*	*n*	Regression equation	r^2	*P* value
Active	MAT	% of total SOC	16	$y = -0.07\ x + 2.75$	0.48	<0.05
Active	MAT	MRT	16	$y = -2.54\ x + 57.11$	0.82	<0.01
Slow	MAT	% of total SOC	16	$y = 0.54\ x + 65.35$	0.04	0.48
Slow	MAT	MRT	16	$y = -0.22\ x + 13.50$	0.10	0.22
Acid insoluble	MAT	% of total SOC	16	$y = -0.47\ x + 31.91$	0.03	0.54
Acid insoluble	MAT	MRT	16	$y = -0.37 + 1454.25$	<0.01	0.99

SOC, soil organic carbon.

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represents MRT under field conditions, and integrates MAT, MAP, and substrate supply in the field over centuries. The proportion of total SOC that was AIC averaged 27% across MAT (Table 3), and AIC % increased with increasing total SOC. The size of the AIC fraction was variable but unrelated to MAT (Fig. 1e). Stepwise multiple linear regression analyses showed that only CEC was significantly related to AIC as a percent of total SOC (Fig. 2). AIC was unrelated to pH, clay content, and vegetation type, which were excluded from the final model.

The MRT of AIC was 1451 year (Table 3), which was consistently longer than the MRT for total SOC in bulk soil (average MRT of total SOC = 180 years, SE = 22, $n = 16$). The long MRT for AIC at one MI site (5670 years) clearly influenced MRT for this fraction across MAT (see footnote in Table 3). Soil $\Delta^{14}C$ and radiocarbon-based estimates of MRT for AIC were unrelated to MAT (Fig. 1f, Table 4). Notably, $\Delta^{14}C$ values were inversely but nonlinearly related to AIC content (Fig. 3). While $\Delta^{14}C$ of total SOC was unrelated to clay content ($r^2 = 0.07$, $P = 0.32$, $n = 16$), $\Delta^{14}C$ of AIC was negatively related to clay content ($r^2 = 0.40$, $P < 0.01$, $n = 16$) and both $\Delta^{14}C$ and AIC MRT were unrelated to CEC.

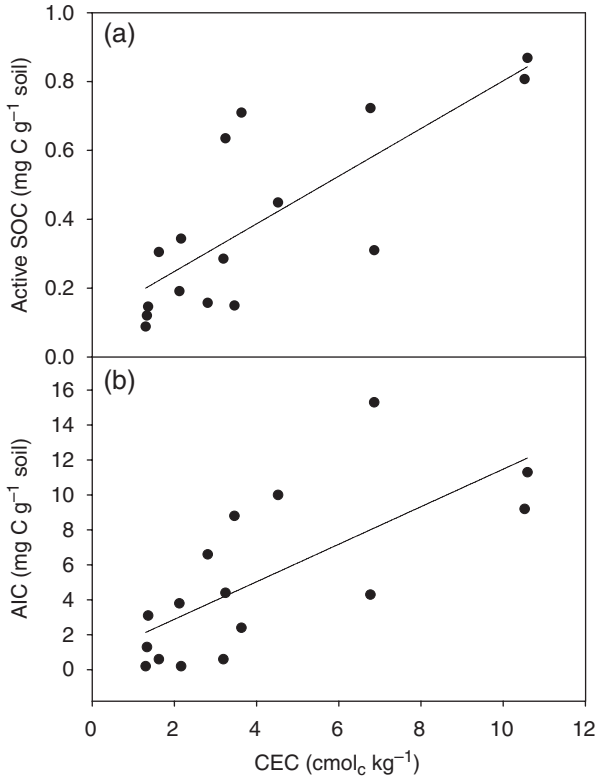

Fig. 2 Linear regressions showing the effect of CEC on (a) active SOC fraction ($r^2 = 0.56$, $P < 0.01$, $n = 16$) and (b) acid insoluble C (AIC) content ($r^2 = 0.51$, $P < 0.01$, $n = 16$). SOC, soil organic carbon; CFC, cation exchange capacity.

Active C. The rate of CO_2 efflux (mg C g^{-1} initial soil C day^{-1}) from soils incubated at LIT30 decreased from 1.98 (± 0.13, mean ± SE) mg C g^{-1} soil C day^{-1} at day 1 to 0.57 (± 0.05) mg C g^{-1} soil C day^{-1} at day 22. A more muted pattern was observed at LIT10, where CO_2 efflux rate declined from 0.38 (± 0.02) mg C g^{-1} soil C day^{-1} on day 1 to 0.25 (± 0.02) mg C g^{-1} soil C day^{-1} on day 22. In both cases, rates of respiration stabilized at low values in later stages of the incubation (Fig. 4a). The CO_2 efflux rates (μg C g^{-1} soil day^{-1}) obtained from LIT30 on a subset of 16 soil samples were used to quantify the size and kinetics of active SOC according to a three-pool decomposition model (Paul *et al.*, 2001, 2006) that utilizes curve fitting of the CO_2 efflux data per soil sample throughout the incubation. According to this three-pool model, the proportion of active SOC ranged between 0.1 and 0.9 mg C g^{-1} soil across sites, which represented between 0.9% and 3.3% of total SOC (Table 3) and was negatively related to MAT (Fig. 1a). The associated active SOC MRT varied across sites between 10 and 85 days, and was longer at cold than at warm sites (Fig. 1b). Among soil characteristics, only CEC was a good predictor of active SOC MRT ($r^2 = 0.56$; $P < 0.01$; $n = 16$).

Slow C. The size of slow SOC fraction was estimated in the model by subtracting active plus AIC from total SOC. Slow SOC represented between 19% and 97% of total SOC (Table 3) and was unrelated to MAT (Fig. 1c). The MRT for slow SOC ranged between 4 and 27 year, and also was unrelated to MAT (Fig. 1d) or other soil characteristics. Exclusion of the single site with longer than average MRT did not significantly affect our results.

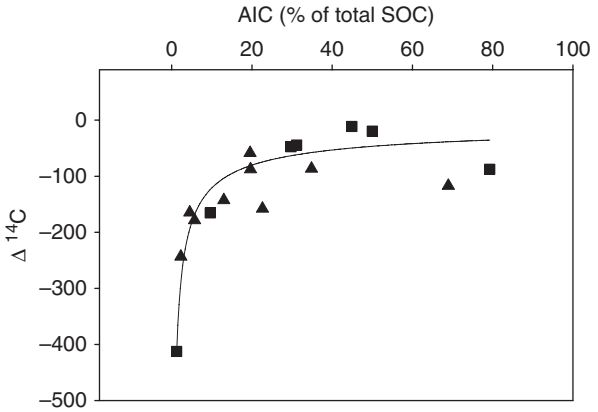

Fig. 3 Relative proportion of total SOC that is acid insoluble C (AIC) and correspondent values of $\Delta^{14}C$. Triangles represent pine stands while squares represent hardwood stands. The equation for the nonlinear regression fit was: $\Delta^{14}C = -471.9$ (AIC %) e (−0.59) ($r^2 = 0.94$, $P < 0.01$, $n = 16$). SOC, soil organic carbon.

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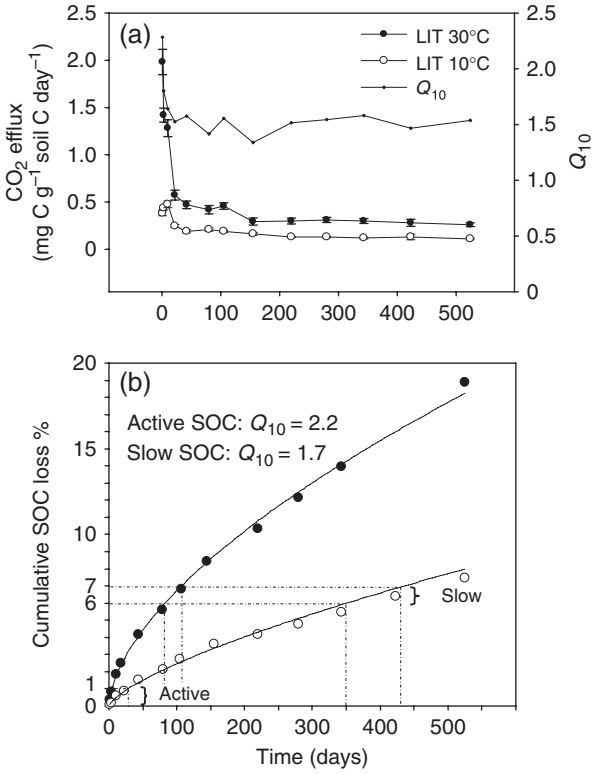

Fig. 4 (a) Carbon efflux rates and temperature sensitivity values (Q_{10}) from soils incubated at 30 and 10 °C for 525 days. Q_{10} was calculated by comparing CO_2 efflux rates at 10 and 30 °C at specific times during the incubation. (b) Cumulative SOC loss during the 525-day incubation at 30 and 10 °C. Q_{10} in this case was calculated based on the time required at each LIT to decompose 1% of SOC. Specifically, active SOC Q_{10} refers to the initial 1% of SOC being decomposed, while slow SOC Q_{10} refers to the time required to decompose 1% of SOC after the decomposition of 6% of SOC. SOC, soil organic carbon; LIT, lab incubation temperatures.

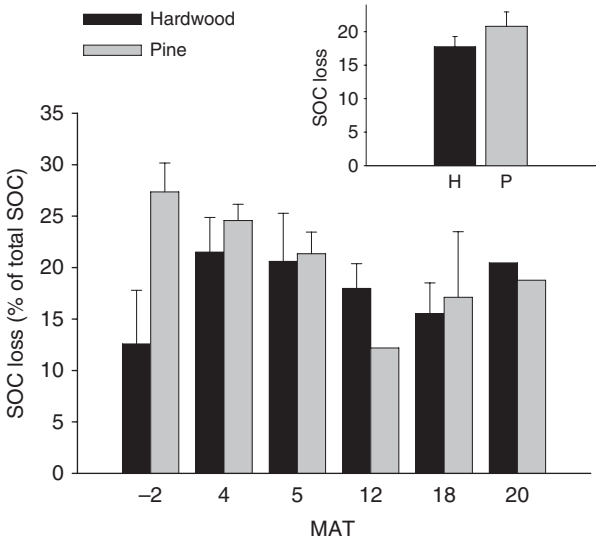

Fig. 5 Percent of total SOC lost during the 525-day incubation at 30 °C. Values are average per group of MAT + SE Regression analysis of these data showed $r^2 = 0.08$, $P = 0.16$, $n = 26$ for LIT30; $r^2 < 0.01$, $P = 0.96$, $n = 26$ for LIT10. The insert graph shows the overall average SOC loss (+ SE) across the MAT gradient for each vegetation type ($n = 15$ for hardwood, $n = 11$ for pine). *t*-Test analysis showed no significant difference between hardwood and pine sites (overall and for each MAT) and this lack of significance was in some cases due to limited sample size. SOC, soil organic carbon; MAT, mean annual temperature; LIT, lab incubation temperatures.

Results from the two LITs were used also to calculate Q_{10}, which ranged between 2.3 and 1.6 (average $Q_{10} = 1.9 \pm 0.19$) during the initial 10 days of incubation, and stabilized to an average value of 1.5 ($\pm$ 0.02) for the remainder of the incubation (Fig. 4a). Different approaches have been proposed to calculate Q_{10} that take into account the fact that after a certain amount of time, soils incubated at low LIT retain a higher amount of active SOC than similar soils incubated for the same amount of time at higher LIT (Conant *et al*., 2008). Across sites, we found similar results when Q_{10} was calculated based on the time required for a certain amount of SOC to decompose at two different LITs (Conant *et al*., 2008). Specifically, Q_{10} associated with the respiration of an initial 1% of SOC, which has been hypothesized to be representative of the active SOC fraction (Conant *et al*., 2008), was 2.2; Q_{10} of the 1% SOC respired after the first 6% had been respired, indicative of the slow SOC fraction, was 1.7 (Fig. 4b). Calculated total cumulative SOC loss (as % of total SOC) was significantly affected by LIT ($P < 0.01$, $n = 26$), but not by MAT. While C loss at LIT30 appeared to be more pronounced at cold sites than at warmer ones, especially in pine stands (Fig. 5), there was no significant relationship with MAT. Overall, the decline in Q_{10} with incubation time matches the *in situ*, radiocarbon-based estimates of AIC MRT, which showed no significant relationship with MAT.

SOC quality and forest type

For pine soils, there was a weak but nonsignificant decline in $\Delta^{14}C$ with increasing MAT ($r^2 = 0.33$, $P = 0.10$, $n = 9$), which suggests that MRT may actually increase with MAT. While not significant, this trend suggests that increased MAT does not result in reduced MRT for stable C forms. In contrast, there was no relationship between MAT and MRT of AIC for hardwood stands (Fig. 1). Pine soils had proportionally less AIC compared with hardwood soils, but while pine soils had lower % of AIC, the $\Delta^{14}C$ values for pine AIC were more negative than those in hardwood stands (Fig. 3). There was one exception of a very negative $\Delta^{14}C$ value ($\Delta^{14}C = -412‰$) observed for AIC in the MI

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hardwood site (Table 3), which represented only 1.2% of total SOC. Overall, MRT of AIC was longer in pine than hardwood soils when this MI hardwood site was excluded (see footnote in Table 3).

During 525-days incubations at LIT30, there was a small difference in SOC loss (% of total SOC derived from cumulative decomposition data) between pine and hardwood soils (Fig. 5). While the incubation showed weak evidence that MAT explained the variability in SOC loss (and hence the size of active SOC) in pine ($r^2 = 0.31$, $P = 0.07$, $n = 11$), this relationship was better described when incubation data were plotted in a three-pool decomposition model.

The three-pool decomposition model showed no significant difference in the proportion (expressed as % of total SOC) of active SOC between pine and hardwood, although pine soils had slightly more active SOC with longer MRT (Table 3). For both vegetation types there was significant decline in both proportion and MRT of active SOC with increasing MAT (Fig. 1a and b, Table 3). Specifically, MAT explained 82% and 84% of the variation in active SOC MRT in pine and hardwood soils, respectively. The proportion of slow to total SOC was similar in pine and hardwood across sites, with nearly identical MRT (Table 3).

Discussion

SOC fractions across the MAT gradient

The effects of warming on the net release of organic C from soils to the atmosphere depend fundamentally on how temperature regulates the decomposition of stable SOC. In line with previous results (Townsend *et al*., 1997; Collins *et al*., 2000), our study shows that only a small fraction of total SOC is active (<3.5% in our study) with an MRT that was highly sensitive to temperature. In contrast, we found that the slow and AIC fractions make up a much larger proportion of total SOC with both showing much longer MRT that are much less sensitive or insensitive to MAT. These results support our initial hypothesis that SOC decomposition rates are less sensitive to changes in MAT than currently modeled, and support the view that for upland forests within our range of MAT, SOC losses in response to global warming will be less than predicted (Giardina & Ryan, 2000).

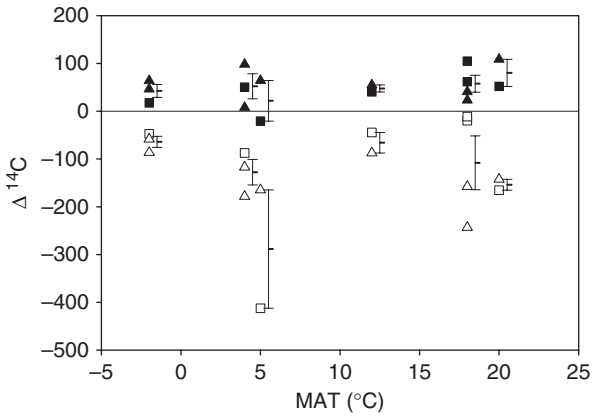

Fig. 6 Values of $\Delta^{14}C$ of total and acid insoluble SOC for a subset of 16 soil samples across the MAT gradient. Triangles represent pine stands, squares represent hardwood stands. For each vegetation type, full symbols represent total SOC and open symbols acid insoluble C. For both total SOC and acid insoluble C, single-line symbols represent the average $\Delta^{14}C$ (± SE) for each group of sites with similar MAT. Positive values of $\Delta^{14}C$ indicates dominance of modern ^{14}C, negative values of $\Delta^{14}C$ indicate dominance of older C. SOC, soil organic carbon; MAT, mean annual temperature.

Both the temperature sensitivity of active SOC and AIC and the methods used to estimate sensitivity are still highly debated. Calculation of temperature sensitivity of SOC fractions according to CO_2 efflux rates at two given LITs has recently received some criticism in favor of an alternative approach based on the time required for a known amount of SOC to decompose (Conant *et al*., 2008). This latter approach has shown higher Q_{10} for stable SOC in several grassland soils (Conant *et al*., 2008). However, similar calculations led to a different outcome in our study. We found substantially lower Q_{10} for older than younger SOC regardless of how sensitivity was calculated (Fig. 4). That our findings are directly in line with earlier incubation studies (e.g., Winkler *et al*., 1996; Holland *et al*., 2000) indicates that methodology cannot explain the difference between studies. Instead, variation may derive from soil chemical differences including higher amounts of total and active SOC in grassland soils compared with forest soils. Critically, both calculation approaches focus on the temperature sensitivity of <20% of total SOC that is lost during several hundred days of incubation. To examine the effects of MAT on the remaining 80% of total SOC, our combined fractionation and radiocarbon approach shows opposite trends in temperature sensitivity for active SOC and AIC fractions, with the MRT of the AIC fraction being weakly (pine) or not sensitive (hardwoods) to MAT. The use of fractionation techniques and radiocarbon analyses provides an *in situ* estimate of the size and MRT of AIC (i.e., SOC formation and loss under field conditions), and so integrates effects due to temperature, moisture, and priming that may be lost during long-term incubations due to a constant environment and elimination of labile C compounds inputs to soil (Dijkstra & Weixin, 2007).

If temperature had a strong positive effect on the decomposition of stable SOC (Fang *et al*., 2005; Knorr *et al*., 2005), we would expect $\Delta^{14}C$ values for AIC

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fraction to be less negative at warm sites of our MAT gradient than at cold sites. In contrast, $\Delta^{14}C$ values for the slow and AIC fractions were unrelated or very weakly related to MAT (Fig. 6), with Q_{10} values that ranged between 1 and 1.2 across MAT for these two fractions. Because the AIC fraction was ten times larger than the active C fraction across forest soils, our findings suggest that generalizations from short-term incubations may provide a highly misleading view of SOC sensitivity to temperature.

These results are in line with the findings of Trumbore *et al*. (1996), who found that stable SOC was insensitive to MAT in contrast to high sensitivity reported for active SOC. Further, in a comparison of temperate and tropical soils, Six *et al*. (2002) observed that tropical soils accumulate a greater proportion of SOC that is more stable compared with temperate soils. In the case of pine soils, our results suggest higher rates of SOC stabilization with increasing MAT. These collective findings support the hypothesis proposed by Thornley & Cannell (2001), who postulated stabilization of SOC is promoted at warm temperatures despite the positive effect of temperature on litter decomposition.

In soils rich in Al and Fe oxides (i.e., highly-weathered soils more typical of warmer sites) SOC stabilization may be further accentuated because of aggregation and complexation processes (Dalal, 2001; Jastrow *et al*., 2007). Similarly, greater SOC stabilization also has been hypothesized for fine-textured soils (Nichols, 1984), but the extent of this effect on SOC fractions across clay content is still not clear. In line with our findings, previous studies have shown mixed results between soil texture and SOC content (Percival *et al*., 2000; Plante *et al*., 2006) or decomposition rates (Giardina & Ryan, 2000; Giardina *et al*., 2001). Further, changes in mineralogy (shifts from high charge density clays to low charge density clays) and chemistry (lower pH and CEC) may exert opposing effects on SOC content and decomposition rates (Fissore *et al*., 2008).

Both the physical–chemical association of SOC with the mineral matrix (Jastrow *et al*., 2007; Rasmussen *et al*., 2007) and the specific exchange properties of the mineral phase affect SOC stabilization (Torn *et al*., 1997; Kleber *et al*., 2007). Across our field sites, the limited range of clay content of our soils did not correspond to a limited range in mineralogy, and the observed wide differences in clay mineral composition (Fissore *et al*., 2008) may in part explain variation in MRT across SOC fractions. Several lines of evidence indicate that mineralogy is a better predictor of SOC stabilization than soil texture alone (Torn *et al*., 1997; Rasmussen *et al*., 2006). To this end, we observed that the content of both AIC and active SOC was positively related to CEC, which is indicative of the negative charge of the mineral phase. This supports the view that a portion of active SOC also can be stabilized by clay minerals in the presence of exchangeable sites (Sørensen, 1972; Mikutta *et al*., 2006). While CEC – and hence the mineral phase – contributes to SOC stabilization, the mechanisms and interactions involved remain unclear (Ågren & Wetterstedt, 2007; Sollins *et al*., 2007) and that these mechanisms may have different effects on the MRT of AIC and active SOC.

Both MAT and CEC were good predictors of active SOC MRT, with longer MRT observed at cold sites where both lower temperature and higher CEC could contribute to higher stabilization rates. The AIC fraction showed a different pattern, with ^{14}C-based MRT of AIC being inversely related to the fraction of total SOC that was acid insoluble (Fig. 3). At the same time, AIC, as a percent of total SOC, increased with CEC, but MRT of the AIC fraction was not related to CEC. We speculate that less SOC is stabilized when few binding sites are available because of low clay content or clay with limited surface charge, but this SOC is more resistant to degradation, resulting in longer MRT. Conversely, abundance of reactive surface charges and other binding characteristics of the mineral phase can stabilize SOC across a wide range of MRT through cation bridging of negatively charged organic groups, interactions with hydrous oxides and Al and Fe groups and other organominerals interactions (Oades, 1988). For these reasons, reduced SOC decomposition in presence of highly charged clay minerals occurs across soil types (Torn *et al*., 1997; Rasmussen *et al*., 2006, 2007) and involves both labile and recalcitrant organic compounds (Jastrow *et al*., 2007).

Across large scales, MAT and mineralogy ultimately may be useful parameters in predicting the size and MRT of different SOC fractions and may help explain the observed divergence among short-term laboratory studies and long-term field studies. Critically, if substrate supply controls the influence of temperature on soil C decomposition rates, then cold climate soils or currently water-logged soils, where soil C substrate supply is high, may release more C than anticipated from standard model Q_{10} values (Giardina & Ryan, 2000; Davidson & Janssens, 2006).

Previous studies have found stable SOC to be either a small (Trumbore *et al*., 1996) or large (Paul *et al*., 2001) fraction of total SOC across sites in North America. We suggest that differences in vegetation type, soil, and site characteristics may explain this apparent discrepancy. Paul *et al*. (2001) found that approximately 50% of total SOC is stable in mixed hardwood forests, consistent with our findings for several hardwood soils sharing similar bioclimatic regions. Finer-textured soils may explain the slightly higher MRT found by Paul *et al*. (2001) where greater clay content and CEC might have

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contributed to higher rates of SOC stabilization. In contrast, Trumbore *et al*. (1996) reported that stable SOC accounted for 15% or less of total SOC in coarse-textured oak and pine sites. In line with these findings, AIC accounted for 20% or less of total SOC for the majority of our pine sites. The 12-year time span between soil sampling and analysis in our study and the study of Paul *et al*. (2001) and Trumbore *et al*. (1996) prevents us from making direct radiocarbon comparisons. However, our results do suggest that conclusions about the distribution of SOC fractions and sensitivity to a changing climate appear to depend strongly on the sites selected.

The presence of a very old (5670 years) AIC at one of our sandy soils from Michigan is unusual, considering the shallow depth: previous findings of a 13 000 old nonhydrolysable fraction were for a deep horizon soil from Wisconsin (Paul *et al*., 2001). A combination of factors, including SOC chemical recalcitrance, soil texture, and soil depth may contribute to the stabilization of extremely old SOC. However, the relative importance of these factors for surface soils remains uncertain, and may or may not explain the long MRT of the AIC in this Michigan soil sample.

SOC fractions and MRT in relation to forest type

The interaction between plant species composition and microbial communities is hypothesized to affect ecosystem processes such as C and nutrient cycling across ecosystems (Hobbie, 1992; Binkley & Giardina, 1998; Lorenz *et al*., 2007). In the long-term, climate change may also affect C allocation belowground (Litton & Giardina, 2008) as well as changes in tree species composition that together with allocation can affect SOC formation and storage (Giardina *et al*., 2005). We found that the effects of tree species were more complex than we originally hypothesized. Our results suggest that the active and slow C fractions in our pine forest soils have a shorter MRT than in the paired hardwood forest soils. Also in line with our hypotheses, these pine soils store a smaller AIC fraction than hardwood forest soils, although this fraction appears to be older. In a subtropical study examining natural mixed forests and pine plantations, differences in SOC fractions have been related to changes in litter chemistry, with a vegetation conversion into a plantation resulting in a decrease in total SOC and a 17.7% decrease in water-soluble organic C (Chen *et al*., 2004). In temperate forests in North America, SOC accumulated at a greater rate in hardwood than conifer stands (Morris *et al*., 2007), whereas at high latitude sites, active SOC content was found to be lower in hardwood than pine soils (Smolander & Kitunen, 2002). Terrestrial ecosystem models incorporate a strong control of litter chemistry on long-term SOC stabilization, but effects of initial litter chemistry, such as lignin : N and lignin concentration, on litter decomposition may disappear after just a few years (Prescott *et al*., 2004) or even reverse in the long-term (*sensu* Berg & Meentemeyer, 2002). The concomitant effects of climate and litter chemistry on litter and SOC decomposition likely affect SOC accumulation and MRT across forest types, but our understanding of the mechanisms involved is far from complete. For example, the relationship between belowground litter quality and quantity and aboveground litter quality and quantity and their relative contributions to SOC formation remain poorly quantified.

In our study, a larger fraction of total SOC was active in pine forest soils, and in both pine and hardwood soil the decomposition of active SOC increased with increasing MAT, probably because of greater C accumulation and slower decomposition of active C at cold sites. This finding suggests that all else being equal, if MAT increases, greater losses of active SOC will occur from pine forests than hardwood soils and overall this loss will be greater in cold ecosystems. In contrast, AIC accumulation was greater in hardwood than pine sites, and modeled SOC decomposition rates were independent of MAT. These findings suggest that for our coarse texture soils, MAT is a driver of active SOC decomposition but not of AIC. This finding also supports the view that initial decomposition is related to climatic conditions across extended geographical areas (Liski *et al*., 2003), but that other factors such as soil structure, texture, and mineralogy affect long-term SOC stabilization across forest types.

Higher clay content in hardwood than pine soils (Fissore *et al*., 2008) could explain vegetation-type differences in total SOC. One could argue that the effect of clays may have obscured the effect of vegetation not only for SOC accumulation but also for SOC stabilization. Rasmussen *et al*. (2007) found that SOC stabilization was related to the mineral assemblage in various conifer stands, with greater stabilization occurring in the presence of highly charged minerals. Across forest types in our study, CEC did not predict MRT of AIC. Conversely, the MRT of active SOC was positively related to CEC. The complex potential interactions between mineral assemblage and vegetation type clearly need further investigation, and highlight the difficulty of identifying trends from naturally occurring stands compared with common garden type studies (Binkley & Giardina, 1998; Hobbie *et al*., 2006).

Microbial community function and structure also likely contributes to differences in SOC quality and decomposition across our sites, though we have not yet addressed this potential source of variation. Pre-

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sence of fungal communities specialized in decomposition of low quality substrates may be responsible for limited accumulation of stable SOC in conifer soils (Giardina *et al*., 2001). In contrast, the microbial communities generally found in hardwood forests preferentially decompose active C substrates, leaving behind more stable compounds. Recent studies have pointed to the complexity of the processes involved in SOC stabilization and to the importance of biologically derived C compounds in forming stable SOC (Lorenz *et al*., 2007; von Lützov *et al*., 2007). However, microbial factors are likely to covary with vegetation, soil and site characteristics, complicating interpretation of findings. As changes in tree and forest ecosystems distribution have been predicted as a consequence of climate change (Hughes, 2000; Hansen *et al*., 2001), our results, which integrate these covarying factors, suggest that SOC stabilization will also be modified. Clearly, interactions with other ecological variables such as moisture (Davidson & Janssens, 2006), atmospheric pollutants (Loya *et al*., 2003), or altered allocation patterns (Litton & Giardina, 2008) may have dominant affects on belowground processes, and so will be important to consider in the next generation of terrestrial ecosystem models.

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