

Controls on Soil Organic Carbon Stocks and Turnover Among North American Ecosystems

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ABSTRACT

Despite efforts to understand the factors that determine soil organic carbon (SOC) stocks in terrestrial ecosystems, there remains little information on how SOC turnover time varies among ecosystems, and how SOC turnover time and C input, via plant production, differentially contribute to regional patterns of SOC stocks. In this study, we determined SOC stocks (gC m^{-2}) and used soil radiocarbon measurements to derive mean SOC turnover time (years) for 0–10 cm mineral soil at ten sites across North America that included arctic tundra, northern boreal, northern and southern hardwood, subtropical, and tropical forests, tall-grass and shortgrass prairie, mountain grassland, and desert. SOC turnover time ranged 36-fold among ecosystems, and was much longer for cold tundra and northern boreal forest and dry desert (1277–2151 years) compared to other warmer and wetter habitats (59–353 years). Two measures of C

input, net aboveground production (NAP), determined from the literature, and a radiocarbon-derived measure of C flowing to the 0–10 cm mineral pool, I , were positively and SOC turnover time was negatively associated with mean annual evapotranspiration (ET) among ecosystems. The best fit model generated from the independent variables NAP, I , annual mean temperature and precipitation, ET, and clay content revealed that SOC stock was best explained by the single variable I . Overall, these findings indicate the primary role that C input and the secondary role that C stabilization play in determining SOC stocks at large regional spatial scales and highlight the large vulnerability of the global SOC pool to climate change.

Key words: carbon turnover; climate change; radiocarbon; soil carbon; terrestrial ecosystems; terrestrial production.

INTRODUCTION

The response of the global soil organic carbon (SOC) pool to increasing temperature and changing moisture regimes will play a major role in determining how terrestrial systems will respond to cli-

mate change (IPCC 2007). Factors that control the dynamics and size of the relatively small SOC pool that turns over within a few years have been extensively studied and are relatively well understood (for example, Nadelhoffer 1990; Hart and others 1994; Frank and Groffman 1998; Fissore and others 2008; Craine and others 2010). Considerably less is known about the dynamics of the much larger pool of SOC that turns over at decadal to millennial time scales (Trumbore 2009). Because the dynamics of this older SOC pool largely determines soil carbon (C) stocks of ecosystems and will

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predominately dictate the direction and strength of the terrestrial feedback on climate change, there is great interest in documenting these long time-scale SOC dynamics and understanding the factors that control the size of this relatively old soil C pool. Recently developed radiocarbon methods have been used to examine long time-scale SOC processes in temperate broadleaf and tropical forest, temperate cropland, and arctic tundra (for example, Trumbore and Harden 1997; Torn and others 1997; Paul and others 2001; Horwarth and others 2008; Trumbore 2009; Tipping and others 2010; Posada and Schuur 2011). However, we are unaware of a radiocarbon study that has compared pedologically similar soil C sampled at the same depth from a wide range of ecosystem types. Such a study would contribute to a general understanding of how SOC processes, particularly turnover time, vary among habitats and how SOC turnover rates contribute to regional-scale patterns of soil SOC stocks.

The SOC pool is primarily determined by the long-term difference between the C assimilated by plants and C lost in metabolism. At the regional scale, plant production is principally a function of climate (Rosenzweig 1968). The residence time of soil C varies widely according to four inter-related processes (Trumbore 2009): (1) climatic stabilization, which is a function of thermal energy and/or moisture control on decomposition (Meentemeyer 1978; Fissore and others 2008; Posada and Schuur 2011), (2) chemical stabilization (that is, recalcitrance) that influences resistance to decomposition (Krull and others 2006; Lützow and others 2006 2006), (3) physical stabilization, which is a result of a diverse array of physical associations between organic matter (OM) and clay surfaces and the inhibiting effects of soil particle aggregation on decomposition (Oades 1984; Jastrow 1996; Torn and others 1997; Baldock and Skjemstad 2000; Masiello and others 2004, Rasmussen and others 2005; Mikutta and others 2006), and (4) stabilization due to the size, composition, and spatial distribution of the decomposer community (Ekschmitt and others 2005; Briones and others 2010). Although considerable attention has been paid to different factors that control ecosystem C assimilation and the stabilization of SOC, we are unaware of any study that has explored the relative importance of C input versus soil C stability in controlling soil C stocks that have accumulated under a wide range of environmental conditions.

The overall goal of this study was to examine regional-scale controls on mineral SOC turnover times and stocks among arctic tundra, grassland,

desert, and boreal, temperate, subtropical, and tropical forest ecosystems across North America. Soil C stocks and radiocarbon measurements were used to model SOC turnover times and calculate C input rates to the mineral soil C pool among habitats. We had two specific objectives. The first was to examine how SOC turnover time was associated with mean annual temperature (MAT), moisture (MAP), and evapotranspiration (ET), a climatically derived water budget variable, and soil clay content among ecosystem types. The second was to determine the relative contributions of SOC turnover time and C input in determining mineral soil SOC stocks among ecosystems across North America.

MATERIAL AND METHODS

Soil Collection

Soil was collected in ten different ecosystem types across North America and Puerto Rico in 2005 (Table 1) to determine SOC turnover times and stocks (gC m^{-2}). The 0–10 cm depth interval of mineral soil was collected at each site. At two sites, where mineral soil was overlain by a well-developed organic layer (northern boreal forest, northern hardwood forest), the organic layer also was collected. An arctic tundra site (Toolik Lake) was an exception, where the top approximately 20 cm of organic soil was collected and separated into O_e (dark brown, fibrous) and O_a (black, well decomposed) horizons by color. Three replicate samples of soil were collected at each site using a soil corer, shovel, or trowel. Each of the replicate soil samples was examined separately, except at four of the sites (shortgrass plains, tallgrass prairie, subtropical hammock, southeastern hardwood forest), where samples were combined and measurements were made on the pooled sample.

Mineral soil samples were passed through a 2-mm sieve to remove coarse stones and large roots. Clumps of soil were broken apart to homogenize the samples as much as possible. The soil was then passed through a 250- μm sieve, which removed most of the remaining detectable root material. All remaining visible root fragments were removed from an approximately 200 cm^3 subsample that was collected from the re-homogenized soil. Soil texture was determined on the subsample using standard methods (Elliot and others 1999) and bulk density measurements were obtained from the literature (see Table 1 for references). All visible roots were removed from the organic layers with forceps. Mineral soil and organic layer percent C was determined on a CE Instruments NC 2100 soil

Table 1. A Description of the Study Sites

Ecosystem	Location	Community Description	Latitude Longitude	MAT (°C)	MAP (mm)	ET (mm)	NAP (g m ⁻² y ⁻¹)	Clay (%)	C stock (gC m ⁻²)	References
Arctic Tundra	Toolik Lake, AK	Moist acidic tussock	68°N 150°W	-8.5	328	319	141	-	-	http://www.lternet.edu/sites/arc/
Arctic Tundra	Thule Air Base, Greenland	Dwarf shrub, high arctic	76°N 68°W	-11.2	128	128	32	8	680	Wein and Rencz (1976), Horwarth and others (2008), Czimczik and Welker (2010)
Northern Boreal Forest	~30 km SW of Fairbanks, AK	<i>Picea mariana</i> floodplain	64°N 147°W	-2.8	269	263	162	15	2140**	Ruess and others (2003), Vogel and others (2008)
Mountain grassland	Yellowstone National Park	Dry, upland	44°N 110°W	4.9	360	335	116	16	2245 (163)	Frank and Groffman (1998)
Northern Hardwood Forest	Hubbard Brook LTER site, NH	Mesic, slope-bottom <i>Acer saccharum</i> , <i>Fagus grandifolia</i> mixed hardwood	44°N	5.7	1334	516	705	22	2331 (208)	Bohlen and others (2001), http://www.lternet.edu/sites/hbr/
Shortgrass Plains	Central Plains Experimental Range, CO	Upland	72°W 41°N	9.5	333	331	117	18	1142	Knapp and Smith (2001), http://www.lternet.edu/sites/sgs/
Tallgrass prairie*	Konza Prairie LTER, KS	<i>Bouteloua agracilis</i> , <i>Aristida purpurea</i> grassland	39°N 97°W	13.0	861	704	398	37	2647	Knapp and others (1998), http://www.lternet.edu/sites/knzn/
Southern Hardwood Forest	Great Smoky Mountains National Park	<i>Liriodendron tulipifera</i> mixed hardwood	35°N 83°W	12.4	1148	700	2408	20	4330 (280)	Whittaker (1966)
Desert	Sevilleta LTER site, NM	<i>Bouteloua eriopoda</i> grassland	34°N 107°W	13.5	263	257	50	10	465 (24)	Kieft and others (1998), Muldavin and others (2008), http://www.lternet.edu/sites/sev/
Subtropical hammock	MacArthur Agro-ecology Research Center, FL	<i>Quercus virginiana</i> hammock	27°N 81°N	22.2	2131	1015	1660	12	3422	Schmalzer and Hinkle (1996), http://www.lternet.edu/sites/luq/
Tropical Forest	Luquillo Experimental Forest LTER site, Puerto Rico	<i>Dacryodes excels</i> , <i>Sloanea berteriana</i> mixed forest	18°N 66°W	23.3	3563	1093	1197	55	4089	Sanford and others (1991) Johnston (1992), Wang and others (2002), http://www.lternet.edu/sites/luq/

Clay and C stock refers to 0–10 cm mineral soil. Standard error is in parentheses for each site that replicate soil samples were analyzed.

*Burned every 20 years.

**Value from Ruess and others (2003).

analyzer (CE Elantech Inc., Lakewood NJ, USA). Mineral SOC stock (gC m^{-2}) was calculated by multiplying the proportion soil C by bulk density (g soil cm^{-3}), then scaling up to 1 m^2 .

Soil Radiocarbon

$\Delta^{14}\text{C}$ (‰) measurements were made on a 1 g homogenized subsample of soil that had all visible root material removed under a dissecting scope. Soil organic radiocarbon values were derived as the deviation from a 1950 standard representing isotopic composition in 1950, prior to bomb-generated increases in atmospheric $^{14}\text{CO}_2$, where

$$\Delta^{14}\text{C} = [F - 1] \times 1000 \quad (1)$$

and where

$$F = \frac{(^{14}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{14}\text{C}/^{12}\text{C})_{\text{standard}}} \quad (2)$$

The more positive the soil $\Delta^{14}\text{C}$ value, the greater the proportion of the soil C was represented by bomb-produced ^{14}C . Negative $\Delta^{14}\text{C}$ values represented C that was predominantly comprised of C assimilated before 1950. A sample with a $\Delta^{14}\text{C}$ equal to zero has the same isotopic composition as that of atmospheric CO_2 in 1950. Radiocarbon values were corrected for (1) isotopic fractionation by adjusting $\Delta^{14}\text{C}$ measurements to a common $\delta^{13}\text{C}$ value of -25‰ and (2) radioactive decay of the standard after 1950. All samples were acid pre-treated to remove mineral C and radiocarbon measurements were determined at the Arizona AMS Laboratory (Tucson, AZ).

Stable C Turnover Rates

We calculated the turnover time (years) of the soil C pool among ecosystems with a soil C stock modeling approach described in detail elsewhere (Trumbore 1993; Torn and others 2005; Frank and others 2011). In brief, this method derived the historic record of $\Delta^{14}\text{C}$ content of two soil C pools, active and stable, at an annual time step. We assumed steady state dynamics, so that the size of the two pools did not change over time, and that the $\Delta^{14}\text{C}$ value of the C assimilated by plants was determined by the atmospheric $\Delta^{14}\text{C}$ value of CO_2 for that year (<http://www.radiocarbon.org/IntCal04.htm>; Levin and Kromer 2004; Graven 2008). The $\Delta^{14}\text{C}$ value for C metabolized and lost from the stable pool was equal to the radiocarbon value of the C pool the previous year. For each pool, the C input and output equaled the C pool size divided by turnover time (years). The size of

the active pool was set at 3% of the total SOC pool, similar to other studies (Parton and others 1987; Torn and others 2005; Frank and others 2011), and the $\Delta^{14}\text{C}$ value of that pool was the atmospheric value for the previous year. (Varying the size of the labile pool from 1–5% was found not to change derived stable turnover rates by more than 5 years). The stable C pool (soil C–active C) and the turnover time of the active pool were known. To determine the turnover time of the stable pool, we found the value for stable C turnover time that resulted in the correct soil $\Delta^{14}\text{C}$ value for the soil collected in 2005.

Other Site Measurements

We added a Greenland arctic site, for which 0–10 cm soil radiocarbon and soil property characteristics were known (Horwarth and others 2008; Czimczik and Welker 2010), to include arctic mineral soil in our analyses. Monthly temperature and precipitation values were gathered directly from webpages of LTER sites (arctic tundra [Toolik Lake], northern hardwood forest [Hubbard Brook], shortgrass plains [Shortgrass Steppe], tallgrass prairie [Konza Prairie], desert [Sevilleta], tropical forest [Luquillo Experimental Forest]) or records from municipal weather stations located 10–15 km (mountain grassland, southern hardwood forest, subtropical hammock), 30 km (northern boreal forest), or approximately 120 km (tundra [Thule]) from the site using the National Climatic Data Center climate records (<http://www.ncdc.noaa.gov/oa/ncdc.html>). Thirty- to 40-year records were used to calculate MAT and MAP for the sites; the length of the record depended on the length of the sequence of uninterrupted or nearly uninterrupted data (mean monthly values were used for rare missing values). The two exceptions were the Greenland arctic and southern hardwood forest sites, for which MAT and MAP values were calculated from 10-year nearly uninterrupted weather records. Monthly temperature and precipitation data were used to run a water-balance model (McCabe and Markstrom 2007) to generate mean ET rates at each site. This model estimated biologically available moisture accounting for precipitation and temperature regimes and the rooting depth and soil texture at each of the sites.

Annual net aboveground production (NAP) and soil bulk density values were obtained from the literature (see Table 1 for references). We derived I , the annual rate of C flowing to the 0–10 cm mineral soil C pool, using the steady state relationship, $I = (s\text{CS}/t) + a\text{CS}$, where $s\text{CS}$ was the stable SOC

pool (gC m^{-2}), which equaled $0.97 \cdot \text{SOC}$, t was the stable SOC pool turnover time (years), and $a\text{CS}$ was the active SOC pool that turned over annually, which equaled $0.03 \cdot \text{SOC}$.

Statistical Analyses

Values for the two topographic positions in mountain grassland and tallgrass prairie were averaged to provide a single sample for each of the grassland types. Likelihood ratio tests (Burnham and Anderson 2002) were used to select the best bivariate linear or nonlinear relationship between pairs of several variables: MAT, MAP, ET, C turnover time, percent clay (for mineral soils only), and soil C stock. The one exception was the relationship of stable SOC turnover time with MAP. In this case, there was no significant difference between two and three parameter decay functions, which would have normally required the selection of the least complex, two-parameter model. We chose the more complex model, however, because the two-parameter model yielded unrealistic negative SOC turnover times for high MAP ecosystems.

We also built two separate models with the best combination of variables to describe soil C turnover times and SOC stocks. We performed these analyses on standardized data to better assess the relative importance of each independent parameter included in the models (Sokal and Rohlf 1995). We used the small sample Akaike information criterion (c-AIC) for model selection (Burnham and Anderson 2002). All statistical analyses were performed in R version 2.10.1.

RESULTS

Mean $\Delta^{14}\text{C}$ values and turnover rates of 0–10 cm mineral soil C varied widely among North American ecosystem types (Table 2). Stable SOC turnover times ranged from 59 years in subtropical hammock to 2151 years in Greenland high arctic tundra. For the three sites where more than a single soil layer was examined, the rate of SOC turnover declined with depth (Table 2). The period required for stable SOC turnover in the overlying organic soil layer was 895 and 233 years shorter than the mean turnover period for SOC in the 0–10 cm mineral soil at the northern boreal forest and northern hardwood forest, respectively. At the Toolik Lake arctic tundra site, the stable SOC turnover time for the surface O_e organic layer was 686 years shorter than the subsurface O_a organic layer (Table 2).

Stable SOC turnover time declined exponentially with the three climatic parameters, MAT, MAP,

and ET (Figure 1A–C), indicating that the metabolic loss of SOC sped up among warmer and wetter climates. The relationships were predominantly or entirely determined by the much longer SOC turnover times for arctic tundra, northern boreal, and desert ecosystems that experienced extreme cold or dry conditions. Remarkably, SOC turnover times varied relatively little (59–353 years) among the remaining ecosystems that experienced a larger variation in climatic conditions. An exception to the relationships was that stable mineral SOC turnover time for desert soil was significantly longer than predicted by the SOC turnover–MAT relationship derived from other ecosystems (Figure 1A), due to extreme moisture limitation in that habitat. The qualitatively similar functions of SOC turnover with the three climatic variables, MAT, MAP, ET, was due to a positive correlation between MAT and MAP among ecosystems included in the study ($r = 0.66$, $P = 0.036$). SOC turnover also exponentially declined with clay content (Figure 1D); a counterintuitive result considering reports of clay stabilizing SOC (for example, Oades 1984; Mikutta and others 2006). However, the relationship between SOC turnover and clay content was due to both biological (that is, decomposition) and geochemical (that is, chemical weathering) processes increasing with warmer and wetter conditions. The partial correlation coefficient between SOC turnover and ASIN percent clay when the effect of ET was held constant was non-significant ($r_p = 0.22$). Thus, when the effect of climate on the two processes was removed, SOC turnover was unrelated to soil clay content among our study sites. AIC comparisons of models including all permutations of the independent variables MAT, MAP, ET, and clay to describe stable C turnover time yielded a model with just the single variable ET.

The 0–10 cm mineral SOC stock (gC m^{-2}) was exponentially related to NAP (Figure 2A). The exponential shape of the function was due to the relatively low soil C stocks for three low productive ecosystems, that is, desert, arctic, and shortgrass plains. There was a positive, quadratic relationship between SOC stock and the derived steady state rate of C flowing to the mineral C pool (I), based on C stock and turnover time measures (Figure 2B). The function reflected an increasing SOC pool as I increased, but a declining stabilization of C flowing to the mineral C pool among the most productive, warm, and moist ecosystems. There also was a weak, positive linear relationship between soil SOC stock and soil clay content (Figure 2C). SOC stock and stable SOC turnover time were negatively related (Figure 2D), indicating, a bit

Table 2. Soil $\Delta^{14}\text{C}$, Radiocarbon-derived Stable SOC Turnover Time, and Annual C Input (I) Values among Ecosystems

Ecosystem	Soil layer	Soil $\Delta^{14}\text{C}$ (‰)	Stable SOC turnover (years)	Annual carbon input (I) ($\text{gC m}^{-2} \text{y}^{-1}$)
Tundra (Toolik)	Top organic	38 (14)	185 (34)	–
	Bottom organic	–101 (27)	871 (315)	–
Tundra (Thule)	Mineral	–895	2151	21
Northern boreal forest	Organic	–8 (17)	382 (98)	–
	Mineral	–121 (10)	1277 (106)	69*
Mountain grassland/ dry, upland	Mineral	32 (20)	235 (72)	77 (7)
Mountain grassland / mesic, slope-bottom	Mineral	42 (15)	208 (27)	109 (17)
Northern hardwood forest	Organic	71 (6)	120 (9)	–
	Mineral	–5 (5)	353 (25)	76 (9)
Shortgrass plains	Mineral	49	162	41
Tallgrass prairie/upland	Mineral	51	158	96
Tallgrass prairie/bottomland	Mineral	16	260	106
Southern hardwood forest	Mineral	92 (9)	95 (10)	174 (16)
Desert	Mineral	–146 (19)	1388 (197)	14 (3)
Subtropical hammock	Mineral	130	59	159
Tropical forest	Mineral	87	99	163

Standard error is in parentheses for each site that replicate soil samples were analyzed.

*Standard error could not be derived because of the single SOC stock value obtained from Ruess and others (2003).

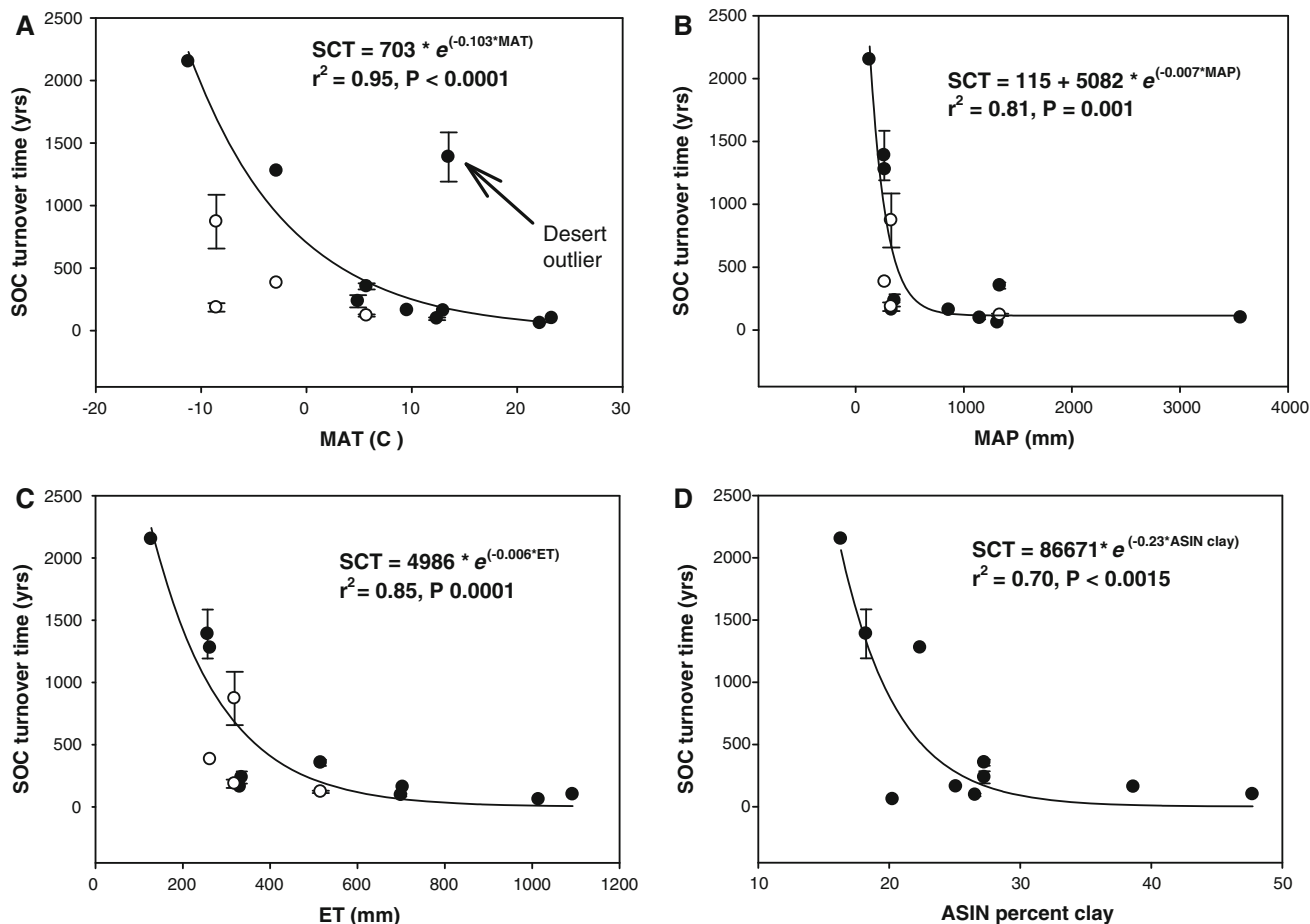


Figure 1. The relationships of stable SOC turnover times with three climatic variables: **A** mean annual temp (MAT), **B** mean annual precipitation (MAP), **C** evapotranspiration (ET), and **D** arc sine-transformed percent clay for 0–10 mineral SOC among 10 North American ecosystems. The *filled circles* are mineral SOC turnover times for which functions were derived and *open circles* represent turnover times for organic layers at northern hardwood, northern boreal, and arctic tundra sites.

counterintuitively, that faster turnover of the large stable pool equivalent to 97% of SOC was associated with greater SOC stocks. The positive and negative associations of the two measures of C input (NAP, I) and SOC turnover with SOC stocks, respectively (Figure 2), was a function of both plant growth and SOC decomposition being primarily under climatic control. Comparisons of all permutations of functions describing the variation in SOC stocks among ecosystems from the pool of independent variables examined in this study (MAT, MAP, ET, clay content, NAP, I) revealed that the best fit model was the polynomial function with the single variable, I (Figure 2B).

DISCUSSION

There were two principal goals of this study. The first was to determine the variation in stable SOC turnover time among a wide range of North

American terrestrial ecosystems and environmental conditions. SOC turnover ranged by 36-fold (59–2151 years) among ecosystems, indicating the markedly different periods of time that assimilated C resided in the soil among terrestrial habitats. This large variation in stable SOC turnover time was closely associated with mean ET, an index of the biologically available moisture in a system. Previous studies have reported associations of ET with regional-level variation in NAP (Rosenzweig 1968; Sala and others 1988; Knapp and Smith 2001), also found in this study, and litter decomposition rate (Meentemeyer 1978). There appeared to be a threshold level of ET of about 300 mm, above which turnover was relatively unresponsive to ET and below which turnover time increased exponentially (Figure 1B). Qualitatively similar functions were found for the relationships of MAT and MAP with stable SOC turnover time. The phase

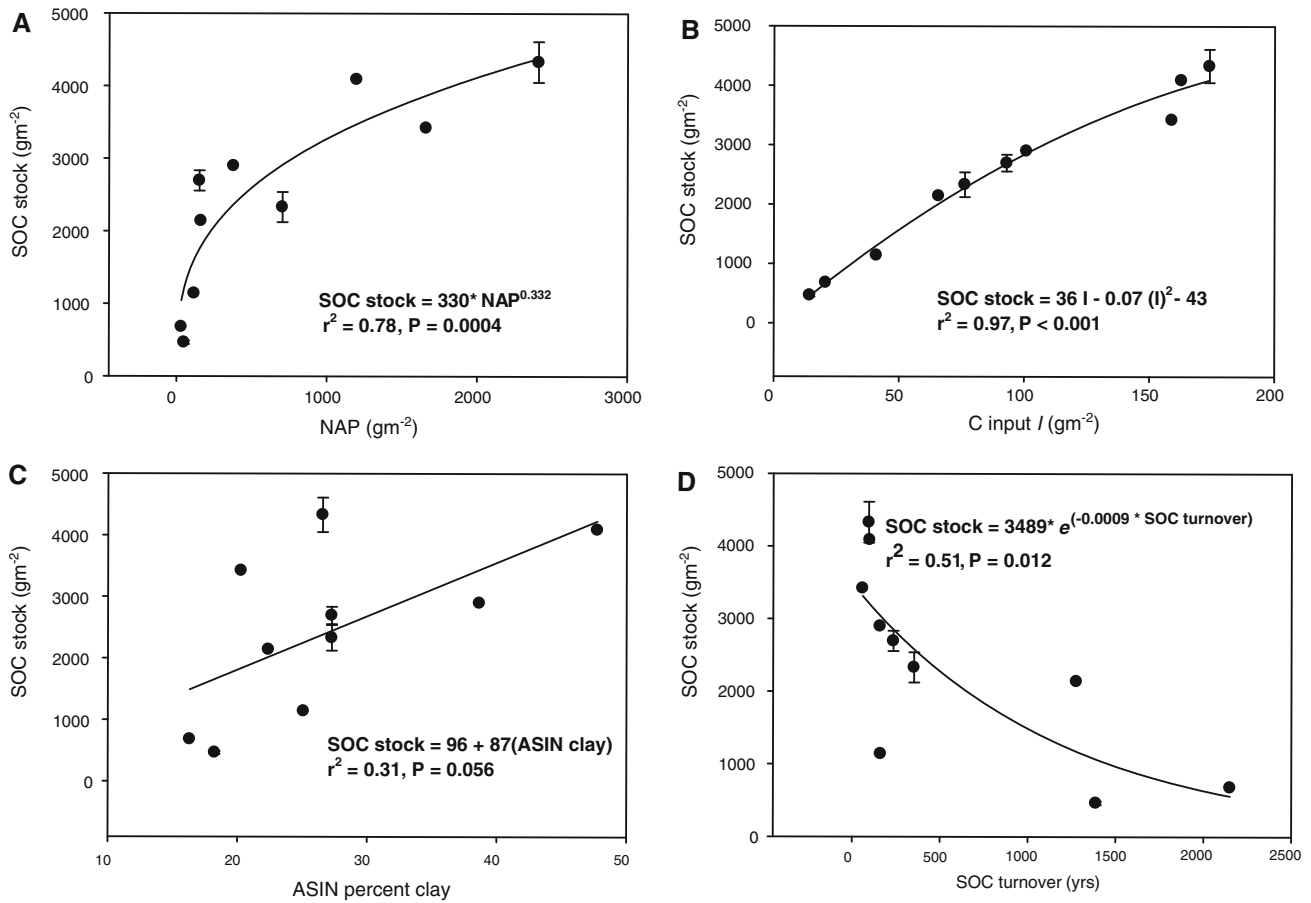


Figure 2. The relationships of SOC stock (gC m^{-2}) with **A** NAP, **B** the derived C input to the 0–10 mineral SOC pool (I), **C** arc sine-transformed percent clay, and **D** SOC turnover.

change from liquid to ice that occurs at 0°C is a threshold at which microbial activity declines by several orders of magnitude (Monson and others 2006; Schuur and others 2008). This effect of ice formation on decomposition is likely responsible for the relatively steep increase in SOC turnover time below zero MAT (Figure 1A) among high northern latitude habitats. SOC turnover time exhibited an even steeper increase among sites receiving less than 330 mm precipitation in the relationship between SOC turnover time and MAP (Figure 1B), suggesting a particularly sharp moisture limitation threshold on SOC turnover that occurs in very dry habitat.

Although focusing on the properties of mineral SOC was the primary objective of this study, C turnover time also was measured for organic soil layers at three of the ecosystem sites. The shorter SOC turnover times for the organic layer versus mineral soil (northern hardwood, northern boreal forests) and the top versus bottom organic layer (Toolik arctic site) were likely due to the (1) deposition of recently

assimilated, relatively labile C on the soil surface compared to lower layers that received older inputs from above, and (2) lack of physical stabilization forces between OM and clay surfaces in the organic layers. Turnover times for the organic layer C also were faster than the predicted mineral soil values when controlling for ambient temperature (Figure 1A). In contrast, organic layer SOC turnover times did not seem to differ from the functions describing relationships of mineral SOC turnover with MAP (Figure 1B) and ET (Figure 1C), suggesting that moisture limitation operated on the decomposition of labile (organic layer) and more stable (mineral soil) C in the same manner.

The second goal of this study was to examine factors associated with 0–10 cm mineral SOC stocks. Previous meta-analyses of global datasets have found that SOC stocks increased with MAP and clay content and declined with MAT (Post and others 1982; Jobbágy and Jackson 2000). One difference between previous studies and this one is that we also were able to examine how SOC stocks

were associated with the flow of C directly into the mineral SOC pool (I) versus factors such as harsh climatic conditions and soil clay content that can stabilize SOC. We found that differences in SOC stocks at this very large continental scale were best described by a model that included the single variable, C input (I), which explained 97% of the variation in SOC stocks among ecosystems. Lengthening the SOC turnover time, that is, increasing stabilization, would be expected to increase SOC stocks. However, we found that SOC stock declined with increasing stabilization among the widely variable ecosystems we examined (Figure 2D). This latter rather counterintuitive finding was due to the opposite effects that ET had on C input versus SOC turnover, increasing the former and reducing the latter. The positive relationship between SOC stock and I (Figure 2B) reflects warmer and wetter climatic conditions increasing I more than they reduce SOC stabilization.

We found that the derived annual C input (I) was much lower than annual NAP. If one assumes that 55% of aboveground tissue is C (Sturner and Elser 2002), C input to the 0–10 cm mineral soil (I) averaged only 54% (SE 38%) of the C in NAP (C_{NAP}) among ecosystems. Considering that C_{NAP} does not include root C that also flows to the mineral soil C pool, the actual percentage of the relevant pool of plant-assimilated C that makes its way via leaf and root pathways to the mineral soil is markedly less than 54%. Such results indicate the importance of herbivory and leaf and root litter decomposition, in addition to plant production, in determining the flow of C to the soil and the size of SOC stocks.

Clay was defined in this study on the basis of particle size and, given the wide range of climatic conditions and thus chemical weathering conditions, the study systems included a diverse array of morphological types of clay. Weathered clays usually have a plate morphology and can render OM unavailable when organic material penetrates the pores between stacks of plates and forms bonds with the negatively charged mineral surfaces (Oades 1988). The stabilizing effects of secondary minerals on SOC stabilization has been demonstrated in a number of studies. In controlled laboratory experiments, slower decomposition has been observed in soils with higher clay content (Ladd and others 1977, 1981) and for OM associated with mineral surfaces (Miltner and Zech 1998; Van Hees and others 2003; Kalbitz and others 2005; Mikutta and others 2006). In addition, field studies have found the amount and the mineral properties of a weathered clay (for example, the crystalline phase) (Torn and others 1997; Masiello and others 2004; Kleber and others

2005) can influence SOC sequestration. In northern latitude habitats included in this study, clay particles likely were represented by finely ground primary minerals, and thus likely had negligible effects on SOC stabilization. The combination of the relatively unweathered clay material in arctic tundra and northern boreal forest and the low amount of clay in the arctic (8%) and desert (9%) soils suggests that the very long SOC turnover times for those three habitats (Table 2) were not due to clays stabilizing SOC, but instead a function of climatic SOC stabilization.

Global warming is expected to increase the net flow of soil-stored SOC to the atmosphere. The response of high latitude soils to climate change has received considerable attention because of the relatively large 7–8°C increase in MAT forecasted for high latitudes by the end of the twenty-first century (IPCC 2007) and the large vulnerable pool of C stored in permafrost soil, estimated to be as much as 50% of terrestrial C (Schuur and others 2008; Tarnocai and others 2009). Using the function between stable SOC turnover time and MAT of Figure 1A, an 8°C increase for arctic tundra from –10 to –2°C would result in mean stable SOC turnover time declining from 1969 to 863 years. It is still unclear how increasing thermal energy will differentially influence OM that ranges in age and recalcitrance (Briones 2009). However, there is some empirical evidence that climatic warming may stimulate decomposition of recalcitrant SOC more than labile SOC (Frierer and others 2005; Conant and others 2008). If correct, warming would result in a marked increase in stable SOC turnover rates, particularly across high latitude habitats that possesses old C that has been up to now stabilized by extreme cold conditions. Of course, the resulting SOC stock for a habitat will not be singularly determined by the effects of increasing temperatures on decomposition, but also on the influence that climate warming will have on ecosystem production (Luo and others 2011). A recent lowering of Alaskan forest production due to warmer and drier conditions (Beck and others 2011) suggests that climate change is also reducing C input among northern ecosystems. Thus, global climate change may have a two-pronged effect on SOC stocks at northern latitudes by reducing C inputs and releasing old, previously stabilized SOC.

We can think of three important caveats for interpreting the results of this study. First, we only examined the SOC down to 10 cm in the soil. Although that SOC pool receives all of the aboveground C and is an interval that supports dense root growth and turnover in the majority of habitat

types (Nadelhoffer and Raich 1992), most SOC is found below 10 cm among ecosystems, with properties differing markedly from surface OM (Jobbágy and Jackson 2000). Consequently, further work is required to determine how closely the results of this study for 0–10 cm mineral SOC may reflect the dynamics of deeper and whole-soil C. Second, turnover times and C inputs reported here were derived for steady state conditions. Modeling studies suggest that even in harsh climates, SOC stocks will reach equilibrium during primary succession within 2000 years (Horwarth and others 2008). Nevertheless, it is unclear how fire (Thornicke and others 2008), forest harvesting practices (Whittaker and others 1974), fluctuating grazing at the grassland sites (Houston 1982; Knapp and others 1998; Hart and Ashby 1998), and recent disruption in climate may have produced non-equilibrium dynamics and confounded our analyses. Third, the relationships of stable SOC turnover time and 0–10 cm mineral SOC stocks with environmental conditions and C input estimates were derived from a single sample per habitat type. Clearly, additional samples will be required to flesh out the variation around these climatically driven regional-scale relationships.

The results of this study include several important conclusions. Variation in C residence time in the top 10 cm of mineral soil ranges by as much as 36-fold and is largely a function of climatic stabilization that occurs in extreme cold and dry habitats. SOC stocks were best explained by C inputs, and not by the stabilization of soil C among ecosystems across North America. These findings indicating how climate plays the preeminent role in controlling SOC stocks, by determining both C inputs, through controlling plant production, and stabilization, through inhibiting decomposition in harsh climates, highlight the probable large changes in SOC dynamics and stocks that will occur in response to climate change.

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