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Relations of mineral-soil C and N to climate and texture: regional differences within the conterminous USA

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Abstract Soil is a prominent component of terrestrial C and N budgets. Soil C and N pools are influenced by, and may reciprocally influence, many environmental factors. Our objective was to determine the quantitative relations of surface mineral-soil organic C, N, and C/N ratios to climate and soil texture across seven ecological regions that make up the conterminous USA. Up to 608 soil profiles per region and their corresponding climates were evaluated with regression analysis. The organic C pool (kg C m^{-2}) in the upper 20 cm of mineral soil was positively related to mean annual precipitation, evapotranspiration and clay content in all regions. It was negatively related to a temperature/precipitation index in all regions and negatively related to mean annual temperature, except in the northwest temperate forest region. Soil C/N ratios were negatively related to clay or silt content in all regions. These relations are consistent with concepts of moisture and temperature controls on detrital production, differential effects of temperature on detrital production and decomposition, and stabilization of organic matter by clay and silt. Differences in quantitative relations among regions may be related to vegetation-composition effects on soil organic matter processes, clay mineralogy, and faunal mixing of surface organic horizons with mineral soil. Regional differences also occurred in the importance of climate vs. soil texture in explaining the variability in soil C. The regional differences indicate the importance of using region-specific, rather than generalized, equations for projecting long-term soil responses to climate change and for conducting ecosystem-model calibration or validation.

Keywords Carbon pools · Mineral soil · Soil organic carbon · Soil organic nitrogen

Abbreviations

AET	Actual evapotranspiration
MAP	Mean annual precipitation
MAT	Mean annual temperature
SOC	Mineral-soil organic carbon
USA	United States of America

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Introduction

Soil is an important global organic C and N pool (Batjes 1996) and contains ~70% of the organic C and ~95% of the N in terrestrial ecosystems (Schlesinger 1997). The interaction between soil organic C and soil N influences plant-available N, thereby affecting ecosystem productivity and the terrestrial C cycle. Process-based numerical models that incorporate both vegetation and soil allow projection of C- and N-cycle responses to climatic, atmospheric and land-use changes (Homann et al. 2000; Kirschbaum 2000; Parton et al. 1987; Pepper et al. 2005; VEMAP Members 1995). Empirical relations among soil organic C, soil N and the factors that influence them allow calibrating and testing these models, as exemplified for the central Great Plains of the USA (Burke et al. 1989). Reducing uncertainties in model projections of global, continental, and subcontinental C and N cycles requires expanded and refined assessment of empirical soil data from expansive geographic areas under broad climatic regimes.

Jenny (1941) synthesized and summarized relations among mineral-soil C, N, climate and soil texture. His examples illustrated several key points for the central and eastern USA: soil N increased with increased moisture in grasslands, and to a lesser extent in forests; soil N increased with decreased temperature; sandy soils contained less mineral-soil organic C (SOC) and soil N than loamy soils; and sandy soils had higher soil C/N ratios than loamy soils. Similar trends have been observed in intensive studies within the central USA (Burke et al. 1989; Franzmeier et al. 1985; Sims and Nielsen 1986), as well as in other regions of the USA (Conant et al. 1998; Grigal and Ohmann 1992; Homann et al. 2004) and in other countries (Hontoria et al. 1999; Paruelo et al. 1998). However, there have been notable contrasting exceptions to these trends. SOC decreased, rather than increased, with decreasing temperature in forests of western Oregon (Homann et al. 1995) and Finland (Liski and Westman 1997). SOC and soil N decreased, rather than increased, with increasing precipitation in Australian rainforests (Spain 1990). The contrasting trends may occur because of the inherently different environmental conditions among the areas, such as magnitudes and ranges of the climatic regimes, seasonality of weather, and confounding but unknown environmental variables. Alternatively, different methods of sampling, data synthesis, and data analysis may contribute to the discrepancies. Whether the contrasting results among these studies are due to actual differences in environmental processes, or differences in research methodologies, remains unclear.

The objective of this study was to determine quantitative relations of SOC, soil N, and soil C/N ratios to climatic indicators and soil texture across the conterminous USA. We addressed the following questions:

Do ecological regions differ in their relations of SOC and soil N to climate and soil texture?
Do regional differences observed with annual temperature and precipitation disappear when seasonal interactions of moisture and temperature are considered?
Do regions differ in the relative importance of climate and soil texture in explaining SOC variability?

Our evaluation expands previous pedon-based research by encompassing the entire continental USA. We used a single soil database and a standard set of methods to allow rigorous comparison among seven ecological regions.

Methods

Data acquisition and synthesis

We examined the relation of soil C and N properties to climate and soil textural properties for pedons within the conterminous USA. We analyzed four dependent variables:

$\log SOC_{20}$ and $\log SOC_{100}$—$\log_{10}$ of Walkley-Black soil organic carbon mass in surface 20 or 100 cm of mineral soil (kg C m^{-2})
$\log N_{20}$—$\log_{10}$ of Kjeldahl N mass in upper 20 cm of mineral soil (kg N m^{-2})
C/N_{20}—the ratio of SOC_{20} to N_{20} (kg C kg^{-1} N)

We evaluated their relations to the following independent variables:

logMAP—$\log_{10}$ of mean annual precipitation (cm $year^{-1}$)
MAT—mean annual temperature (°C)
logAET—$\log_{10}$ of actual evapotranspiration (AET, cm $year^{-1}$; Homann et al. 1995)
T/P Index—a temperature/precipitation index calculated as

$$[10^{\text{monthly temperature }(^\circ\text{C})/100}]/[10^{\text{monthly precipitation (cm)}/100}],$$

and averaged over all months

$\log\text{Clay}_{20}$ or $\log\text{Clay}_{100}$—$\log_{10}$ of clay mass in surface 20 or 100 cm of mineral soil (kg clay m^{-2}) $\log\text{Silt}_{20}$ or $\log\text{Silt}_{100}$, which are $\log_{10}$ of silt mass in surface 20 or 100 cm of mineral soil (kg silt m^{-2})

Soil data were from the Natural Resources Conservation Service's Soil Survey Laboratory Characterization Data on CD-ROM (September 1997 version) (National Soil Survey Center, Lincoln, NE), which includes pedons sampled through 1992. Analytical procedures used by Natural Resources Conservation Service are reported in Soil Survey Laboratory Staff (1992). To include a pedon in our analysis, we required the following information: (i) a location specified in latitude and longitude or USA Public Land Survey System coordinates; (ii) clay, silt, organic C and N concentrations and rock content for the surface mineral-soil horizon and for at least 80% of the soil depth under consideration, either 20 or 100 cm.

We calculated contents (kg m^{-2}) of SOC, soil N, silt and clay constituents as follows:

$$\begin{aligned}\text{SOC or soil N}\ (\text{kg m}^{-2}\ \text{to a 20 or 100 cm depth})\\ &= \Sigma[\text{C or N concentration}\ (\%)/100\%\\ &\times \text{bulk density}\ (\text{g cm}^{-3})\\ &\times \text{horizon depth}\ (\text{cm})\\ &\times (1 - \%\text{rock volume}/100\%)\\ &\times 10^{4}\ \text{cm}^{2}\ \text{m}^{-2}\\ &\times 10^{-3}\ \text{kg g}^{-1}]\end{aligned}$$

$$\begin{aligned}\text{Clay or Silt}\ (\text{kg m}^{-2}\ \text{to a 20 or 100 cm depth}) =\\ &\Sigma[\%\text{clay or silt}/100\%\\ &\times \text{bulk density}\ (\text{g cm}^{-3})\\ &\times (1 - \%\text{C}/58\%)\\ &\times \text{horizon depth}\ (\text{cm})\\ &\times (1 - \%\text{rock volume}/100\%)\\ &\times 10^{4}\ \text{cm}^{2}\ \text{m}^{-2}\\ &\times 10^{-3}\ \text{kg g}^{-1}]\end{aligned}$$

where the summations are over the horizons, or portions of horizons, within the depth under consideration. The inclusion of the (1 − %C/58%) term in the clay and silt calculation adjusts for the presence of organic matter in the soil. Bulk density values from the Natural Resources Conservation Service database were obtained by the clod method (Soil Survey Laboratory Staff 1992). Missing bulk density values were interpolated between measurements of adjacent horizons or calculated from organic C concentration and horizon-specific equations presented by Manrique and Jones (1991) and Homann et al. (1995). Other missing data were interpolated between measurements of adjacent horizons.

Monthly temperatures and precipitation, MAT and MAP for pedon locations were obtained from the Oregon Climate Service (Corvallis, OR), which uses the Parameter-elevation Regression on Independent Slopes Model (PRISM) to generate climate layers (Daly et al. 1994). PRISM generates 4-km^2 gridded estimates of climate variables using 1961–1990 point data from US Historical Climate Network Weather Stations. To assess the suitability of PRISM for our purposes, we obtained 1961–1990 30-year averages for MAT and MAP from 47 US Weather Service stations located in separate states across the USA (National Oceanic and Atmospheric Administration's US Divisional and Station Climate Data and Normals, on CD-ROM, December, 1994). These stations were not part of the US Historical Climate Network, and therefore, were independent of the data used by PRISM. PRISM estimates and the independent weather station data values were highly correlated (r = 0.99) for both MAP and MAT, thereby substantiating the use of PRISM values for our study.

We divided the conterminous USA into seven general ecological regions (Fig. 1) based on geographic location and dominant natural vegetation by combining 76 major ecoregions of the US Environmental Protection Agency. The general regions were NWF, northwest coniferous forests; WMF, western mountain forests; WDS, western desert, shrub, steppe, chaparral, and grassland; NPG, northern plains and grasslands; SPG, southern plains and grasslands; NEF, northeastern deciduous and coniferous forests; SEF, southeastern deciduous and coniferous forests. Actual vegetation of pedons within a region may differ from the general regional vegetation, but information to identify pedon-specific vegetation and land-use history was limited. Soil C and N characteristics for these regions are given in Table 1.

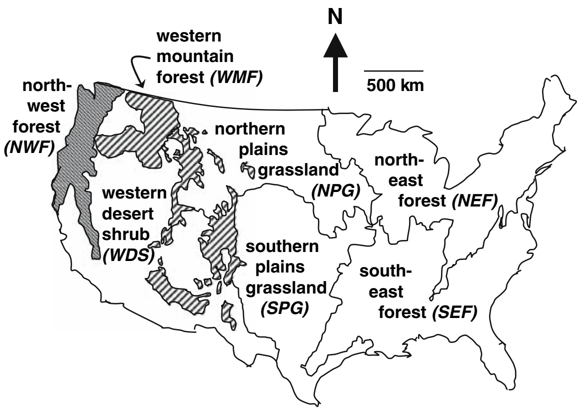

Fig. 1 Geographic extent of seven general ecological regions within the conterminous USA

Statistical analyses

For the conterminous USA and for each region individually, we conducted forward stepwise regression analysis (Statistix, Analytical Software, Tallahassee FL, USA) of each dependent variable ($\log SOC_{20}$, $\log SOC_{100}$, $\log N_{20}$, C/N_{20}) with four independent variables ($\log MAP$, MAT, $\log Clay_{20}$ or $\log Clay_{100}$, $\log Silt_{20}$ or $\log Silt_{100}$), using a criterion of $P < 0.05$ to enter variables into or remove variables from a regression equation. We also conducted an analysis with $\log SOC_{20}$ vs. logAET, T/P Index, $\log Clay_{20}$, and $\log Silt_{20}$. Other transformations of variables and more complex equations containing polynomial and interaction terms were evaluated, too; but they were not pursued because but they did not consistently yield greater explanatory capability. To assess multicolinearity of independent variables (Zar 1999), Pearson correlation coefficients were monitored; only the correlation between logMAP and MAT in the NEF region, and logAET and T/P Index in NEF and SEF regions, exceeded the guideline of $|r| < 0.7$ used in previous soil–climate analyses (Grigal and Ohmann 1992; Homann et al. 1995). To represent the conterminous USA, we randomly selected 165 pedons from each region for the C analyses and 120 pedons from each region for the N analyses; this precluded regions with high number of pedons from biasing the results.

To assess differences between regions, we calculated the least significant difference (LSD) between regression coefficients of different regions as follows:

$$\mathrm{LSD} = 2^{0.5} \times \mathrm{SE}_{\mathrm{pooled}} \times t$$

where $\mathrm{SE}_{\mathrm{pooled}}$ is the standard error of the regression coefficient, pooled across all regions having significant ($P < 0.05$) regression coefficients, and t is the two-tailed t-value for $\alpha = 0.05$ and df associated with $\mathrm{SE}_{\mathrm{pooled}}$. To assess the relative importance of an independent variable in explaining the variation in SOC, we calculated the difference between adjusted r^2 of the regression models with and without the variable of interest.

Results and discussion

Soil C and climate

For the conterminous USA, SOC_{20} was positively related to MAP (Table 2). A positive relation also occurred in each region, but the quantitative relation differed among some regions (Table 2, Fig. 2). Except for NWF, logMAP regression coefficients were lower for SOC_{100} than SOC_{20} (Tables 2 and 3), supporting the concept that the relative influence of precipitation on SOC decreases with greater soil depth (Jobbágy and Jackson 2000).

The increases of SOC_{20} and SOC_{100} with MAP in most USA regions are consistent with the numerous studies that have found SOC to increase with precipitation. This relation has been observed previously in the NPG and SPG regions and some of their subregions (Burke et al. 1989; Sims and Nielsen 1986), and in subregions of the NWF (Homann et al. 1995; Sun et al. 2004), NEF (Grigal and Ohmann 1992), and WMF (Conant et al. 1998). In an evaluation of the conterminous USA using generalized soil properties from STATSGO, the state geographic soils database, Guo et al. (2006) found SOC increased up to 85 cm MAP, then fluctuated with further increases in MAP. In contrast, our analysis (Tables 2 and 3) shows SOC increases with MAP both above and below 85 cm MAP, based on responses in NWF, NEF, and SEF, which tend to have higher MAP than other regions (Fig. 2). Similar positive relations of SOC with MAP have been observed in other countries, including the Swiss Alps (Perruchoud et al. 2000), Spain (Hontoria et al. 1999), Sri Lanka (Somaratne et al. 2005.), India (Miller et al. 2004), and China (Xie et al. 2004; Dai and Huang

Table 1 Soil C and N characteristics for the upper 20 cm and upper 100 cm of mineral soil in the regions of the conterminous USA

Region	Number of pedons	Mean	SD	Min	Median	Max
SOC_{20} (kg C m^{-2})						
NWF	165	5.8	2.9	1.0	5.4	14.7
WMF	193	4.3	2.4	0.3	3.9	14.0
WDS	608	2.7	2.0	0.2	2.2	13.2
NPG	386	4.4	1.9	0.9	4.0	12.0
SPG	523	3.5	1.9	0.2	3.1	13.1
NEF	292	4.7	2.0	1.0	4.4	12.8
SEF	296	4.0	2.4	0.7	3.4	13.0
SOC_{100} (kg C m^{-2})						
NWF	165	13.3	8.7	1.4	11.2	48.5
WMF	193	9.3	6.1	1.3	7.6	43.8
WDS	608	7.0	4.7	0.6	5.9	31.8
NPG	386	10.5	4.9	2.2	9.7	32.6
SPG	523	9.0	4.7	1.0	8.5	37.0
NEF	292	8.8	4.0	1.9	7.8	33.4
SEF	296	7.7	4.8	2.1	6.4	35.0
N_{20} (kg N m^{-2})						
NWF	120	0.34	0.20	0.03	0.29	0.96
WMF	121	0.30	0.18	0.03	0.25	1.03
WDS	376	0.23	0.14	0.01	0.20	1.00
NPG	139	0.39	0.15	0.11	0.37	0.77
SPG	325	0.31	0.17	0.06	0.29	1.22
NEF	125	0.40	0.16	0.13	0.39	0.94
SEF	211	0.27	0.17	0.04	0.23	0.91
C/N_{20} (kg C kg^{-1} N)						
NWF	120	19.3	5.7	9.8	18.6	33.5
WMF	121	16.2	5.1	8.3	15.8	32.2
WDS	376	11.5	3.1	7.0	10.9	33.6
NPG	139	10.9	1.6	7.1	10.7	18.4
SPG	325	11.4	2.1	7.3	11.1	26.0
NEF	125	13.4	4.2	8.4	12.3	31.5
SEF	211	16.0	5.5	7.5	15.2	34.6

2006), and in subglobal (Jobbágy and Jackson 2000) and global evaluations (Miller et al. 2004 based on the data of Post et al. 1982).

The positive relation of SOC with precipitation is not universal, however. In Nordic soils, SOC is not related to precipitation in fine textured soils, although it is positively related in coarse-textured soils (Callesen et al. 2003). In the Australian rain forest, SOC is negatively related to precipitation (Spain 1990).

For the conterminous USA, SOC_{20} was negatively related to increasing temperature (Table 2). A negative relation also occurred in each region except the NWF, where no relation was observed (Table 2, Fig. 3); similar results were obtained when concentrations (g kg^{-1}) of C, clay, and silt were used instead of masses (kg m^{-2}) (data not shown). Except for WMF, MAT regression coefficients were lower for SOC_{100} than SOC_{20} (Tables 2 and 3), supporting the concept that the relative influence of temperature on SOC decreases with greater soil depth (Jobbágy and Jackson 2000). The decrease in SOC with increased temperature in most USA regions is consistent with similar patterns previously found in the NPG and

Table 2 Regression coefficients and their standard errors (SE) for log(SOC_{20}, kg C m^{-2} in upper 20 cm of mineral soil) in conterminous USA and its regions, with MAP and MAT as explanatory climatic variables

Region	Intercept[a]	Coefficients[a]				Adj r^2	n
		logMAP	MAT	$logClay_{20}$	$logSilt_{20}$		
USA	−0.70	0.57	−0.021	0.15	0.10	0.37	1155
SE	0.06	0.03	0.001	0.02	0.03		
NWF	−0.46[b]	0.49		0.14		0.30	165
WMF	−0.92	0.27[c]	−0.012[c]	0.18	0.44	0.23	193
WDS	−1.48	0.63	−0.016	0.24	0.35	0.52	608
NPG	−0.70	0.85	−0.055	0.17		0.28	386
SPG	−1.00	0.66	−0.029	0.40		0.45	523
NEF	−1.92	1.35	−0.039	0.14		0.21	292
SEF	−2.42	1.56	−0.026	0.06[c]		0.23	296
SE_{pooled}	0.23	0.12	0.004	0.03	0.06		
LSD[d]		0.32[e]	0.011[e]	0.09[e]	0.16		

[a] Regression equations are of the form: log(SOC_{20}, kg C m^{-2} in upper 20 cm of mineral soil) = intercept + coefficient × log(MAP, cm $year^{-1}$) + coefficient × (MAT, °C) + coefficient × log($Clay_{20}$, kg m^{-2} in upper 20 cm of mineral soil) + coefficient × log($Silt_{20}$, kg m^{-2} in upper 20 cm of mineral soil)

[b] $P < 0.01$ and [c]$P < 0.05$. For other coefficients and intercepts, $P < 0.001$. Coefficients with $P > 0.05$ are not shown and not included in equations

[d] LSD, least significant difference ($P < 0.05$) within a column between regions

[e] There is a difference between at least two regions with non-zero coefficients

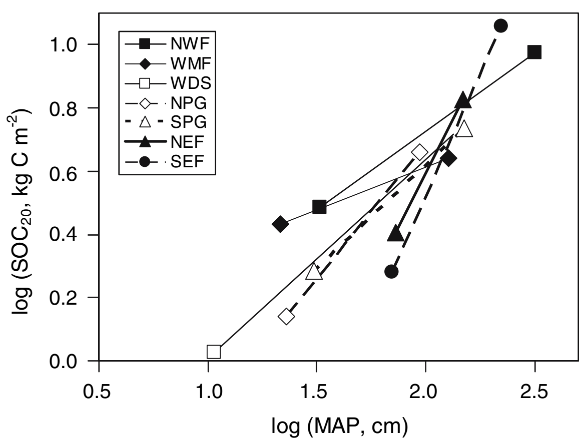

Fig. 2 Soil organic C in the upper 20 cm of mineral soil (SOC_{20}) as related to mean annual precipitation (MAP) in seven ecological regions within the conterminous USA. Lines span the range of MAP in each region. Values are for MAT = 10°C, $Clay_{20}$ = 30 kg m^{-2}, and $Silt_{20}$ = 80 kg m^{-2}

SPG (Burke et al. 1989), a subregion of WMF (Conant et al. 1998), southern Spain (Hontoria et al. 1999; Ganuza and Almendros 2003), Alaska (Kane et al. 2005), India (Miller et al. 2004), Australian rain forest (Spain 1990) and subglobally and globally (Jobbágy and Jackson 2000; Miller et al. 2004).

In contrast, the NWF region SOC showed no relation with temperature. This may be the result of subregions that have contrasting relations. Previous studies in subregions of NWF found either negative (Douglas et al. 1998; Homann et al. 2004) or positive relations (Homann et al. 1995). A positive relation of SOC with temperature has also been observed in Finland forests (Liski and Westman 1997). In an evaluation of the conterminous USA using generalized soil properties from STATSGO, SOC did not exhibit a consistent upward or downward trend with MAT, but fluctuated over the range of MAT (Guo et al. 2006). Further, in a reassessment of Post's (1982, 1985) data set, Kirschbaum (2000) found some moisture-determined biomes showed SOC decreased with increased temperature, while other biomes had inconsistent trends of SOC with increased temperature.

Causes of regional differences

The negative relation of SOC to MAT in six of the seven regions (Tables 2 and 3) suggests increased

Table 3 Regression coefficients and their standard errors (SE) for log(SOC_{100}, kg C m^{-2} in upper 100 cm of mineral soil) in conterminous USA and its regions

Region	Intercept[a]	Coefficients[a]				Adj r^2	n
		logMAP	MAT	$logClay_{100}$	$logSilt_{100}$		
USA	−0.29	0.33	−0.016	0.08	0.22	0.25	1155
SE	0.07	0.03	0.002	0.02	0.03		
NWF	−0.70[b]	0.52		0.27		0.27	165
WMF	−0.43[b]		−0.014[b]	0.16	0.43	0.32	193
WDS	−1.14	0.41	−0.014	0.22	0.37	0.53	608
NPG	−0.59	0.55	−0.041	0.26	0.12[c]	0.30	386
SPG	−0.53	0.37	−0.026	0.45		0.51	523
NEF	−1.27	1.05	−0.020		0.10[b]	0.12	292
SEF	−1.67	1.34	−0.021			0.18	296
SE_{pooled}	0.22	0.11	0.004	0.04	0.04		
LSD[d]		0.31[e]	0.011[e]	0.10[e]	0.12[e]		

[a] Regression equations are of the form: log(SOC_{100}, kg C m^{-2} in upper 100 cm of mineral soil) = intercept + coefficient × log(MAP, cm $year^{-1}$) + coefficient × (MAT, °C) + coefficient × log($Clay_{100}$, kg m^{-2} in upper 100 cm of mineral soil) + coefficient × log($Silt_{100}$, kg m^{-2} in upper 100 cm of mineral soil)

[b] $P < 0.01$ and [c] $P < 0.05$. For other coefficients and intercepts, $P < 0.001$. Coefficients with $P > 0.05$ are not shown and not included in equations

[d] LSD, least significant difference ($P < 0.05$) within a column between regions

[e] There is a difference between at least two regions with non-zero coefficients

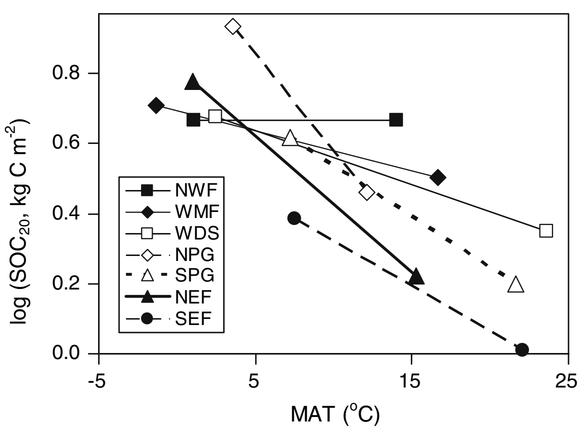

Fig. 3 Soil organic C in the upper 20 cm of mineral soil (SOC_{20}) as related to mean annual temperature (MAT) in seven ecological regions within the conterminous USA. Lines span the range of MAT in each region. Values are for MAP = 75 cm, $Clay_{20}$ = 30 kg m^{-2}, and $Silt_{20}$ = 80 kg m^{-2}

temperature generally enhances decomposition more than detrital production, thereby causing decreased SOC. In the coniferous forests of the NWF region, however, temperature-sensitive faunal processes may moderate the negative SOC–MAT relation. Specifically, native fauna stimulate forest floor turnover and mixing of surface organic matter into the mineral soil (Reich et al. 2005). But limited mixing by native fauna in cold areas (Eisenhauer et al. 2007) may effectively suppress detrital input into the mineral soil. In warmer areas, a greater fraction of the surface detritus becomes mixed with the mineral soil, balances the enhanced decomposition from higher temperature, and results in no response of SOC to MAT (Tables 2 and 3).

Alternatively, the different SOC–MAP–MAT relations among regions may occur because the annual climatic values do not adequately represent the influence of climate on production and decomposition processes. In landscapes with minor erosion and sediment deposition, SOC occurs from a long-term imbalance between detrital production by plants and detrital decomposition by microorganisms (Sollins et al. 1996). Seasonal interactions of temperature and moisture, which are not reflected in MAP and MAT, are the specific conditions to which plants and microorganisms respond. Seasonalities of temperature and precipitation are likely to result in different SOC in spite of the same mean annual values; e.g., the magnitude of change in SOC in response to change in MAT depends on the seasonal amplitude of temperature (Kirschbaum 2000).

We hypothesized that climate variables that incorporate the seasonal interactions of temperature and precipitation would yield a single SOC–climate relation across regions, in contrast to the different relations among regions when MAP and MAT are used (Tables 2 and 3). We used AET and a monthly based temperature/precipitation index to aggregate the seasonal interactions. AET reflects biological activity as both net primary production and decomposition are related to it (summarized by Schlesinger 1997). The temperature/precipitation index may reflect a greater response of decomposer microorganisms to temperature increases, but a greater response of plant producers to moisture increases.

Although SOC_{20} was positively related to AET and negatively related to temperature/precipitation in all regions (Table 4), a single SOC–climate relation did not occur across all regions. Instead, the differences in coefficients between some regions caused a rejection of our hypothesis and indicate the importance of other soil forming factors in differentiating the regions. For example, vegetation composition affects detrital production, above- and belowground partitioning of detrital deposition, decomposability of detritus, and soil microclimate impacts on decomposition rates; cumulatively these result in different amounts of SOC under the same climate (Cole et al. 1995; Ganuza and Almendros 2003; Homann and Grigal 1996; Kulmatiski et al. 2004; Jobbágy and Jackson 2000; Rothe et al. 2002). Under the different climates within and between regions, varying climate-induced vegetation composition and the corresponding C-influencing attributes may result in the different SOC–climate relations among regions.

These interpretations assume that the regional differences are real, rather than statistical artifacts caused by different ranges of the independent variables. The NWF region did not show a relation of SOC_{20} with temperature, whereas all other regions had a negative relation (Table 2). We reassessed pedons from the zone where the other regions overlapped with the NWF climatic envelope, roughly 1–14°C and 1.6 to 2.2 log(MAP, cm/year). For the 131 NWF pedons in this zone, SOC_{20} was not related to MAT ($P = 0.4$), whereas for 131 pedons from the other regions in this zone, there was a negative relationship with MAT ($P = 0.03$). These different regional responses under a constrained climatic zone suggest the differences between regions are not a statistical artifact, but are due to inherently different relations with climate.

Soil N and climate

Comparison of the N_{20} and SOC_{20} regression coefficients for the conterminous USA and individual regions indicated N_{20} was less responsive than SOC_{20} to logMAP but equally responsive to MAT (Tables 2 and 5). The greater responsiveness of SOC_{20} than N_{20} to logMAP resulted in C/N_{20} being positively related to MAP in four of the regions and across the entire USA (Table 6). In contrast, MAT regression coefficients were similar for N_{20} and SOC_{20} in all regions except NEF, resulting in limited relation of C/N_{20} to MAT (Table 6). The increase in C/N with precipitation and decrease with temperature we observed over the conterminous USA has been observed in subregions of the NWF (Jenny 1980), NPG and SPG (Honeycutt et al. 1990; Miller et al. 2004), India (Miller et al. 2004), and globally (Miller et al. 2004).

Texture relations

For the conterminous USA, SOC_{20} was positively related to both clay and silt (Table 2). A positive relation with clay occurred within each region (Table 2, Fig. 4). Highest regression coefficients occurred in the warm, dry WDS and SPG regions and the lowest in the warm, moist SEF region. Differences among regions may be related to clay mineralogy. The low proportions of illite and smectite in the SEF region (Birkland 1999), and conversely presence of less reactive clay minerals (Richter et al. 1999), may suppress the clay influence on organic matter accumulation and stability. SOC_{20} was also related to silt in three dry regions. The texture relations with SOC_{100} were similar to those for SOC_{20}, with the exception that SOC_{100} was not related to clay in NWF and SEF (Table 3).

Comparison of the N_{20} and SOC_{20} regression coefficients for the conterminous USA indicated N_{20} was more responsive than SOC_{20} to clay and silt (Tables 2 and 5). This was also reflected in many of the regional coefficients. The more positive responsiveness of N_{20} than SOC_{20} results in C/N_{20} being

Table 4 Regression coefficients and their standard errors (SE) for log(SOC_{20}, kg C m^{-2} in upper 20 cm of mineral soil) in conterminous USA and its regions, with AET and T/P Index as explanatory climatic variables

Region	Intercept[a]	Coefficients[a]				Adj r^2	n
		logAET	T/P Index	$logClay_{20}$	$logSilt_{20}$		
USA	0.85	0.34	−1.11	0.11	0.10	0.37	1155
SE	0.10	0.04	0.05	0.02	0.03		
NWF	0.16[d]	0.77	−0.81	0.10[c]		0.37	165
WMF	−1.00[c]	0.86[b]	−0.68	0.21	0.34	0.26	193
WDS	−0.80	0.57	−0.59	0.23	0.35	0.49	608
NPG	1.91	0.49	−2.17	0.16		0.28	386
SPG	0.46[c]	0.43	−1.16	0.40		0.46	523
NEF	1.01[b]	1.21[b]	−2.61	0.14		0.18	292
SEF	0.96[c]	0.86[c]	−1.87	0.05[c]		0.20	296
SE_{pooled}	0.30	0.21	0.23	0.03	0.06		
LSD[e]		0.59[f]	0.64[f]	0.09[f]	0.17		

[a] Regression equations are of the form: log(SOC_{20}, kg C m^{-2} in upper 20 cm of mineral soil) = intercept + coefficient × log(AET, cm $year^{-1}$) + coefficient × (T/P Index) + coefficient × log($Clay_{20}$, kg m^{-2} in upper 20 cm of mineral soil) + coefficient × log($Silt_{20}$, kg m^{-2} in upper 20 cm of mineral soil). T/P Index = [$10^{\text{monthly temperature (oC)/100}}$]/[$10^{\text{monthly precipitation (cm)/100}}$], averaged over all months

[b] $P < 0.01$, [c] $P < 0.05$, [d] $P > 0.05$ (intercept only). For other coefficients and intercepts, $P < 0.001$. Coefficients with $P > 0.05$ are not shown and not included in equations

[e] LSD, least significant difference ($P < 0.05$) within a column between regions

[f] There is a difference between at least two regions with non-zero coefficients

Table 5 Regression coefficients and their standard errors (SE) for log(N_{20}, kg N m^{-2} in upper 20 cm of mineral soil) in conterminous USA and its regions

Region	Intercept[a]	Coefficients[a]				Adj r^2	n
		logMAP	MAT	$logClay_{20}$	$logSilt_{20}$		
USA	−1.76	0.39	−0.021	0.33	0.10	0.43	840
SE	0.07	0.03	0.002	0.02	0.03		
NWF	−2.24	0.37			0.52	0.31	120
WMF	−1.64		−0.012[c]	0.33	0.35[b]	0.30	121
WDS	−2.26	0.39	−0.019[c]	0.22	0.41	0.52	376
NPG	−2.01	0.83	−0.040	0.27		0.47	139
SPG	−1.82	0.60	−0.036	0.50	−0.10[c]	0.49	325
NEF	−0.40[b]		−0.009	0.26	−0.18[c]	0.19	125
SEF	−2.50	0.95	−0.035	0.27		0.38	211
SE_{pooled}	0.25	0.13	0.005	0.04	0.07		
LSD[d]		0.36[e]	0.013[e]	0.12[e]	0.19[e]		

[a] Regression equations are of the form: log(N_{20}, kg N m^{-2} in upper 20 cm of mineral soil) = intercept + coefficient × log(MAP, cm $year^{-1}$) + coefficient × (MAT, °C) + coefficient × log($Clay_{20}$, kg m^{-2} in upper 20 cm of mineral soil) + coefficient × log($Silt_{20}$, kg m^{-2} in upper 20 cm of mineral soil)

[b] $P < 0.01$ and [c] $P < 0.05$. For other coefficients and intercepts, $P < 0.001$. Coefficients with $P > 0.05$ are not shown and not included in equations

[d] LSD, least significant difference ($P < 0.05$) within a column between regions

[e] There is a difference between at least two regions with non−zero coefficients

Table 6 Regression coefficients and their standard errors (SE) for C/N$_{20}$ (kg C kg^{-1} N in upper 20 cm of mineral soil) in conterminous USA and its regions

Region	Intercept[a]	Coefficients[a]				Adj r^2	n
		logMAP	MAT	logClay$_{20}$	logSilt$_{20}$		
USA	14.8	6.5	−0.07[c]	−5.9	−1.6[c]	0.41	840
SE	1.3	0.5	0.03	0.4	0.6		
NWF	38.7				−10.9	0.24	120
WMF	4.3[d]	11.1		−5.9		0.44	121
WDS	8.3	4.7		−2.4		0.12	376
NPG	17.2			−3.5		0.20	139
SPG	2.4[d]	6.2		−1.3		0.22	325
NEF	32.6		−0.23[c]	−4.3	−5.2	0.32	125
SEF	−15.0[d]	19.0[b]		−6.1		0.22	211
SE$_{pooled}$	5.2	2.8	0.10	0.7	1.6		
LSD[e]		7.8[f]		1.8[f]	4.6[f]		

[a] Regression equations are of the form: C/N$_{20}$ (kg C kg^{-1} N in upper 20 cm of mineral soil) = intercept + coefficient × log(MAP, cm year^{-1}) + coefficient × (MAT, °C) + coefficient × log(Clay$_{20}$, kg m^{-2} in upper 20 cm of mineral soil) + coefficient × log(Silt$_{20}$, kg m^{-2} in upper 20 cm of mineral soil)

[b] $P < 0.01$, [c] $P < 0.05$, [d] $P > 0.05$ (intercept only). For other coefficients and intercepts, $P < 0.001$. Coefficients with $P > 0.05$ are not shown and not included in equations

[e] LSD, least significant difference ($P < 0.05$) within a column between regions

[f] There is a difference between at least two regions with non-zero coefficients

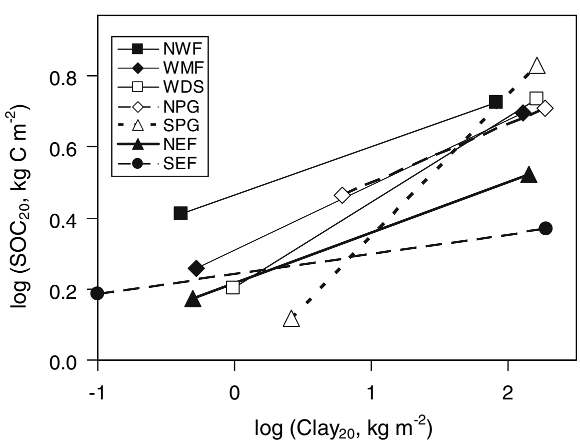

Fig. 4 Soil organic C in the upper 20 cm of mineral soil (SOC$_{20}$) as related to clay in the upper 20 cm of mineral soil (Clay$_{20}$) in seven ecological regions within the conterminous USA. Lines span the range of clay in each region. Values are for MAT = 10°C, MAP = 75 cm, and Silt$_{20}$ = 80 kg m^{-2}

negatively related to clay in six regions and to silt in two regions (Table 6).

The positive relations of SOC and N with clay have been observed previously in subregions of NEF (Grigal and Ohmann 1992), NPG and SPG (Burke et al. 1989; Franzmeier et al. 1985; Nichols 1984), Australian rainforest (Spain 1990), Denmark (Sorensen 1981), and the Netherlands (Hassink et al. 1993). The relations are not universal, however. In New Zealand grasslands, clay, temperature and precipitation explained little of the variation in SOC; in contrast, allophane and extractable aluminum explained more than half of the variability (Percival et al. 2000). The negative relation of C/N with increased clay and silt (Table 6; Hassink et al. 1993; Jenny 1941) is consistent with C/N ratios of separated particle-size fractions decreasing from sand to silt to clay (Amelung et al. 1998; Hassink et al. 1993).

Across the entire USA, clay and silt made minor contributions to explaining SOC variability compared with precipitation and temperature (Fig. 5). However, the relative importance of climatic and soil textural variables in explaining SOC varied substantially among regions (Fig. 5). Clay was as important as climate in SPG, and clay plus silt were more important than climate in WMF.

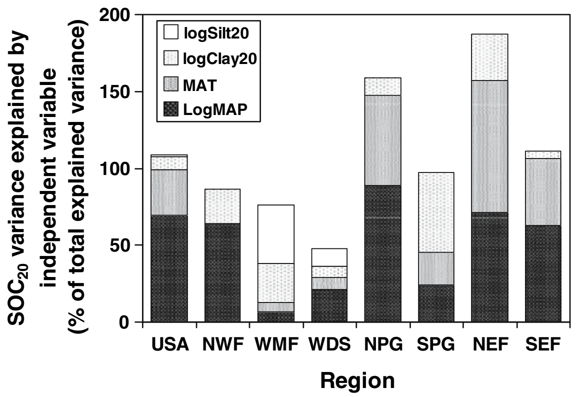

Fig. 5 Contribution of individual explanatory variables to explaining variance of soil organic C in the upper 20 cm of mineral soil (SOC_{20}). Values do not add to 100% because of interactions among explanatory variables

Application of relations

Our regional relations allow a preliminary projection of long-term mineral–SOC response to climate change. As an example, we used a climate change scenario presented by Smith et al. (2005). This scenario was based on the University of Illinois at Urban Champagne general circulation model, a global mean temperature increase of 2.5°C, IS92a forcing assumptions, and a pattern scaling method to produce regional change patterns of both temperature and precipitation, which are presented for our regions in Table 7. This scenario in combination with the region-specific SOC equations (Table 3) indicate an increase in SOC_{100} in two regions, a decrease in three regions, and minimal change in the two remaining regions (Table 7). Similarly, in addressing whether soils will store more or less C in response to global warming and increased carbon dioxide, Kirschbaum (2000) concluded there are likely to be important differences among global regions. In addition, our assessment indicates the importance of considering region-specific responses versus applying generalized relations. Compared with the regional relations, the application of a general USA equation (Table 3) or global equation (Miller et al. 2004) results in different directions and magnitudes of SOC change in many of the regions (Table 7). Thus, the use of a generalized SOC equation, or extrapolation from one area to another, may yield misleading results in projecting long-term SOC change.

The C/N relations may be useful for other investigations of environmental change. In an assessment of recent C sequestration, De Vries et al. (2006) used soil C/N ratios and soil N retention estimates to calculate soil C changes across European forests. A model incorporating variable soil C/N ratios explains inter-regional variation in stream nitrate in the United Kingdom (Evans et al. 2006). Similar assessments in the USA may make use of our soil C/N equations to estimate soil properties over broad areas and their influence on water quality. The integration of regional C/N equations with spatial data bases of soil C (Guo et al. 2006; Johnson and Kern 2003) and climate (Kittel et al. 2004) will allow the spatial distribution of surface soil N to be mapped and compared with coarser scale assessments (Batjes 1996; Post 1985).

Table 7 Projected regional change of SOC_{100} in response to climate change, based on regional, USA, and global soil–climate equations

Region	Increase in MAP[a] (cm year^{-1})	Increase in MAT[a] (°C)	% Change in SOC_{100}, regional equations[b]	% Change in SOC_{100}, USA equation[b]	% Change in SOC_{100}, global equation[b]
NWF	30	2.5	12	−2	−4
WMF	30	2.3	−7	4	−4
WDS	30	2.3	21	14	26
NPG	15	2.0	−4	2	−2
SPG	20	1.7	0	3	4
NEF	10	2.0	1	−4	−6
SEF	5	2.2	−5	−6	−6

[a] Climate change scenario derived from Smith et al. (2005)

[b] Regional and USA equations from Table 3; global equation from Miller et al.'s (2004) Holdridge analysis

The influence of land-use change on SOC is not addressed in our equations and requires additional consideration. The SOC loss as a result of cultivation increases with increased precipitation, although the relation is highly curvilinear (Burke et al. 1989; Miller et al. 2004). Burke et al. (1989) found cultivation-induced SOC loss to increase with silt and decrease with clay. Given that both silt and clay differ among general soil texture categories, cultivation-induced SOC loss may not differ among some categories.

The soil–climate–texture relations provide a context for considering mechanisms and processes that determine soil C and N pools, such as soil respiration associated with soil C pools and intra-annual climate patterns (Conant et al. 1998), multiple mechanisms by which organic matter is stabilized by clays (Hassink et al. 1993; Plante et al. 2006), and relations of different soil organic fractions to climate and particle-size fractions (Amelung et al. 1997, 1998; Franzluebbers et al. 2001). However, as with other broad-area statistical studies of controls on SOC and soil N (Burke et al. 1989; Dai and Huang 2006; Grigal and Ohmann 1992; Homann et al. 1995), our relations do not necessarily indicate direct cause-and-effect associations. Factors correlated with our independent variables may influence SOC and soil N. For example, within the NEF and SEF regions, a high-elevation forest that received approximately twice as much precipitation as other forests also received three times as much atmospheric N deposition (Johnson and Lindberg 1992). Enhanced N inputs may increase soil N and the stability of soil organic matter (Homann et al. 2001; Swanston et al. 2004).

Our regional relations provide a basis to expand application of dynamic soil organic models throughout the conterminous USA, by providing information against which to calibrate and test the models. This has been accomplished in the combined NPG and SPG regions, for which Burke et al. (1989) demonstrated agreement of observed soil–climate relations with those generated by the Century model of soil organic matter dynamics (Parton et al. 1987). The models incorporate multiple processes that influence SOC and soil N, and allow investigation of interacting variables, such as rising carbon dioxide, temperature and N inputs on grassland and forest C-budgets (Pepper et al. 2005).

Conclusions

Using a consistent methodology, we found differences among seven USA regions in the relation of mineral-soil C and N to temperature, precipitation, clay and silt. Contrary to our hypothesis that relations of C to process-related climatic variables would be consistent across the regions, we also found regional differences in C relations with evapotranspiration and a temperature/precipitation index. The specific causes for the regional differences remain to be determined, although differential faunal mixing of surface organic horizons with mineral soil, clay mineralogy, and vegetation composition are likely contributing factors. Over the entire USA, climate was more important than soil texture in explaining the variability in soil C, but distinct differences occurred among regions.

Our study complements recent broad-area studies that found SOC–climate relations differ among regions of China (Dai and Huang 2006) and between vegetation types in the conterminous USA (Guo et al. 2006). Our study differs from the conterminous-USA evaluation of Guo et al. (2006) by using pedon data rather than generalized soil data, and by considering soil N and soil C/N, in addition to SOC. The continental-USA scale of our evaluation fills a gap between regional- and global-scale assessments of soil–climate–texture relations (Burke et al. 1989; Grigal and Ohmann 1992; Homann et al. 1995; Jenny 1941; Miller et al. 2004; Post et al. 1982, 1985).

Compared with generalized global or continental equations, the region-specific quantitative relations produce refined estimates of potential changes in soil C and N in response to environmental change. This is particularly important given that soil is the largest terrestrial C and N pool, and soil responses to climate change may vary among regions. In addition, the relations may be applied to ecosystem model calibration, testing, or development. They may be used in investigations of the spatial distribution of soil N within the USA and its consequences on landscape-scale biogeochemical processes.

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References

Amelung W, Flach KW, Zech W (1997) Climatic effects on soil organic matter composition in the Great Plains. Soil Sci Soc Am J 61:115–123

Amelung W, Zech W, Zhang X, Follett RF, Tiessen H, Knox E, Flach K-W (1998) Carbon, nitrogen, and sulfur pools in particle-size fractions as influenced by climate. Soil Sci Soc Am J 62:172–181

Batjes NH (1996) Total carbon and nitrogen in the soils of the world. European J Soil Sci 47:151–163

Birkland PW (1999) Soils and geomorphology, 3rd edn. Oxford University Press, New York

Burke IC, Yonker CM, Parton WJ, Cole CV, Flach K, Schimel DS (1989) Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils. Soil Sci Soc Am J 53:800–805

Callesen I, Liski J, Raulund-Rasmussen K, Olsson MT, Tau-Strand L, Vesterdal L, Westman CJ (2003) Soil carbon stores in Nordic well-drained forest soils—relationships with climate and texture class. Global Change Biol 9:358–370

Cole DW, Compton JE, Homann PS, Edmonds RL, Van Miegroet H (1995) Comparison of carbon accumulation in Douglas fir and red alder forests. In: McFee WW, Kelly JM (eds) Carbon forms and functions in forest soils. Soil Science Society of America, Madison, WI

Conant RT, Klopatek JM, Malin RC, Klopatek CC (1998) Carbon pools and fluxes along an environmental gradient in northern Arizona. Biogeochemistry 43:43–61

Dai W, Huang Y (2006) Relation of soil organic matter concentration to climate and altitude in zonal soils of China. Catena 65:87–94

Daly C, Neilson RP, Phillips DL (1994) A statistical-topographic model for mapping climatological precipitation over mountainous terrain. J Appl Meteor 33:140–158

De Vries W, Reinds GJ, Gundersen P, Sterba H (2006) The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. Global Change Biol 12:1151–1173

Douglas CL Jr, Rasmussen PE, Collins HP, Albrecht SL (1998) Nitrogen mineralization across a climosequence in the Pacific Northwest. Soil Biol Biochem 30:1765–1772

Eisenhauer N, Partsch S, Parkinson D, Scheu S (2007) Invasion of a deciduous forest by earthworms: Changes in soil chemistry, microflora, microarthropods and vegetation. Soil Biol Biochem 39:1099–1110

Evans CD, Caporn SJM, Carroll JA, Pilkington MG, Wilson DB, Ray N, Cresswell N (2006) Modelling nitrogen saturation and carbon accumulation in heathland soils under elevated nitrogen deposition. Environ Pollut 143:468–478

Franzluebbers AJ, Haney RL, Honeycutt CW, Arshad MA, Schomberg HH, Hons FM (2001) Climatic influences on active fractions of soil organic matter. Soil Biol Biochem 33:1103–1111

Franzmeier DP, Lemme GD, Miles RJ (1985) Organic carbon in soils of north central United States. Soil Sci Soc Am J 49:702–708

Ganuza A, Almendros G (2003) Organic carbon storage in soils of the Basque Country (Spain): the effect of climate, vegetation type and edaphic variables. Biol Fertil Soils 37:154–162

Grigal DF, Ohmann LF (1992) Carbon storage in upland forests of the Lake States. Soil Sci Soc Am J 56:935–943

Guo Y, Gong P, Amundson R, Yu Q (2006) Analysis of factors controlling soil carbon in the conterminous United States. Soil Sci Soc Am J 70:601–612

Hassink J, Bouwman LA, Zwart KB, Bloem J, Brussaard L (1993) Relationships between soil texture, physical protection of organic matter, soil biota, and C and N mineralization in grassland soils. Geoderma 57:105–128

Homann PS, Caldwell BA, Chappell HN, Sollins P, Swanston CW (2001) Douglas-fir soil C and N properties a decade after termination of urea fertilization. Can J Forest Res 31:2225–2236

Homann PS, Grigal DF (1996) Below-ground organic carbon and decomposition potential in a field-forest glacial-outwash landscape. Biol Fertil Soils 23:207–214

Homann PS, McKane RB, Sollins P (2000) Belowground processes in forest-ecosystem biogeochemical simulation models. Forest Ecol Manage 138:3–18

Homann PS, Remillard SM, Harmon ME, Bormann BT (2004) Carbon storage in coarse and fine fractions of Pacific Northwest old-growth forest soils. Soil Sci Soc Am J 68:2023–2030

Homann PS, Sollins P, Chappell HN, Stangenberger AG (1995) Soil organic carbon in a mountainous, forested region: relation to site characteristics. Soil Sci Soc Am J 59:1468–1475

Honeycutt CW, Heil RD, Cole CV (1990) Climatic and topographic relations of three Great Plains soils. II. Carbon, nitrogen, and phosphorus. Soil Sci Soc Am J 54:476–483

Hontoria C, Rodríguez-Murillo JC, Saa A (1999) Relationships between soil organic carbon and site characteristics in peninsular Spain. Soil Sci Soc Am J 63:614–621

Jenny H (1941) Factors of soil formation. McGraw Hill, New York

Jenny H (1980) The soil resource. Springer-Verlag, New York

Jobbágy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Applic 10:423–436

Johnson DW, Lindberg SE (eds) (1992) Atmospheric deposition and forest nutrient cycling. Springer-Verlag, New York

Johnson MG, Kern JS (2003) Quantifying the organic carbon held in forested soils of the United States and Puerto Rico. In: Kimble JM, Heath LS, Birdsey RA, Lal R (eds) The potential of U.S. forest soils to sequester carbon and mitigate the greenhouse effect. CRC Press, New York

Kane ES, Valentine DW, Schuur EAG, Dutta K (2005) Soil carbon stabilization along climate and stand productivity gradients in black spruce forests of interior Alaska. Can J Forest Res 35:2118–2129

Kirschbaum MUF (2000) Will changes in soil organic carbon act as a positive or negative feedback on global warming? Biogeochemistry 48:21–51

Kittel TGF, Rosenbloom NA, Royle JA, Daly C, Gibson WP, Fisher HH, Thornton P, Yates DN, Aulenbach S, Kaufman C, McKeown R, Bachelet D, Schimel DS (2004) VEMAP phase 2 bioclimatic database. I. Gridded historical (20th century) climate for modeling ecosystem dynamics across the conterminous USA. Climate Res 27:151–170

Kulmatiski A, Vogt DJ, Siccama TG, Tilley JP, Kolesinskas K, Wickwire TW, Larson BC (2004) Landscape determinants of soil carbon and nitrogen storage in southern New England. Soil Sci Soc Am J 68:2014–2022

Liski J, Westman CJ (1997) Carbon storage in forest soil of Finland. 1. Effect of thermoclimate. Biogeochemistry 36:239–260

Manrique LA, Jones CA (1991) Bulk density of soils in relation to soil physical and chemical properties. Soil Sci Soc Am J 55:476–481

Miller AJ, Amundson R, Burke IC, Yonker C (2004) The effect of climate and cultivation on soil organic C and N. Biogeochemistry 67:57–72

Nichols JD (1984) Relation of organic carbon to soil properties and climate in the southern Great Plains. Soil Sci Soc Am J 48:1382–1384

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci Soc Am J 51:1173–1179

Paruelo JM, Jobbágy EG, Sala OE, Lauenroth WK, Burke IC (1998) Functional and structural convergence of temperate grassland and shrubland ecosystems. Ecol Applic 8:194–206

Pepper DA, Del Grosso SJ, McMurtrie RE, Parton WJ (2005) Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO_2], temperature and nitrogen input. Global Biogeochem Cycles 19:GB1004, DOI 10.1029/2004GB002226

Percival HJ, Parfitt RL, Scott NA (2000) Factors controlling soil carbon levels in New Zealand grasslands: is clay content important? Soil Sci Soc Am J 64:1623–1630

Perruchoud D, Walthert L, Zimmermann S, Lüscher P (2000) Contemporary carbon stocks of mineral forest soils in the Swiss Alps. Biogeochemistry 50:111–136

Plante AF, Conant RT, Stewart CE, Pautian K, Six J (2006) Impact of soil texture on the distribution of soil organic matter in physical and chemical fractions. Soil Sci Soc Am J 70:287–296

Post WM, Emmanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones. Nature 298:156–159

Post WM, Pastor J, Zinke PJ, Stangenberger AG (1985) Global patterns of soil nitrogen storage. Nature 317:613–616

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol Lett 8:811–818

Richter DD, Markewitz D, Trumbore SE, Wells CG (1999) Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400:56–58

Rothe A, Cromack K Jr, Resh SC, Makineci E, Son Y (2002) Soil carbon and nitrogen changes under Douglas-fir with and without red alder. Soil Sci Soc Am J 66:1988–1995

Schlesinger WH (1997) Biogeochemistry, an analysis of global change, 2nd edn. Academic Press, New York

Sims ZR, Nielsen GA (1986) Organic carbon in Montana soils as related to clay content and climate. Soil Sci Soc Am J 50:1269–1271

Smith SJ, Thomson AM, Rosenberg NJ, Izaurralde RC, Brown RA, Wigley TML (2005) Climate change impacts for the conterminous USA: an integrated assessment. Part 1. Scenarios and context. Climatic Change 69:7–25

Soil Survey Laboratory Staff (1992) Soil survey laboratory methods manual. Soil survey investigations report no. 42, version 2.0. National Soil Survey Center, Lincoln, NB, USA

Sollins P, Homann PS, Caldwell B (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74:65–105

Somaratne S, Seneviratne G, Coomaraswamy U (2005) Prediction of soil organic carbon across different land-use patterns: a neural network approach. Soil Sci Soc Am J 69:1580–1589

Sorensen LH (1981) Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. Soil Biol Biochem 13:313–321

Spain AV (1990) Influence of environmental conditions and some soil chemical properties on the carbon and nitrogen contents of some tropical Australian rainforest soils. Aust J Soil Res 28:825–839

Sun OJ, Campbell J, Law BE, Wolf V (2004) Dynamics of carbon stocks in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. Global Change Biol 10:1470–1481

Swanston C, Homann PS, Caldwell BA, Myrold DD, Ganio L, Sollins P (2004) Long-term effects of elevated nitrogen on forest soil organic matter stability. Biogeochemistry 70:227–250

VEMAP Members (1995) Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochem Cycles 9:407–437

Xie XL, Sun B, Zhou HZ, Li AB (2004) Soil organic carbon storage in China. Pedosphere 14:491–500

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River, NJ, USA