Ecosystems (2009) 12: 672–685
DOI: 10.1007/s10021-009-9250-8

ECOSYSTEMS

Carbon Mineralization and Labile Organic Carbon Pools in the Sandy Soils of a North Florida Watershed

Mi-Youn Ahn,[1]* Andrew R. Zimmerman,[2] Nick B. Comerford,[1] James O. Sickman,[3] and Sabine Grunwald[1]

[1]Soil and Water Science Department, University of Florida, P.O. Box 110290, Gainesville, Florida 32611, USA; [2]Department of Geological Sciences, University of Florida, 241 Williamson Hall, P.O. Box 112120, Gainesville, Florida 32611-2120, USA; [3]Department of Environmental Sciences, University of California, Riverside, Riverside, California 92521, USA

Abstract

The large pool of actively cycling carbon (C) held in soils is susceptible to release due to changes in land-use, management, or climate. Yet, the amount and distribution of potentially mineralizable C present in soils of various types and the method by which this soil C fraction can best be quantified, are not well established. The distribution of total organic C (TOC), extractable C pools (hot-water-extractable and acid-hydrolyzable), and in vitro mineralizable C in 138 surface soils across a north Florida watershed was found to be quite heterogeneous. Thus, these C quality parameters could not statistically distinguish the eight landuses or four major soil orders represented. Only wetland and upland forest soils, with the largest and smallest C pool size, respectively, were consistently different from the soils of other landuse types. Variations in potential C mineralization were best explained by TOC (62%) and hot-water-extractable C (59%), whereas acid-hydrolyzable C (32%) and clay content (35%) were generally not adequate indicators of C bioavailability. Within certain landuse and soil orders (Alfisol, Wetland and Rangeland, all with $>3\%$ clay content), however, C mineralization and clay content were directly linearly correlated, indicating a possible stimulatory effect of clay on microbial processing of C. Generally, the sandy nature of these surface soils imparted a lack of protection against C mineralization and likely resulted in the lack of landuse/soil order differences in the soil C pools. If a single parameter is to be chosen to quantify the potential for soil C mineralization in southeastern U.S. coastal plain soils, we recommend TOC as the most efficient soil variable to measure.

Key words: hot-water-extractable carbon; acid-hydrolyzable carbon; carbon mineralization; coastal plain; Florida; Santa Fe River Watershed.

Introduction

More than two to three times as much organic carbon (C) is held in soils worldwide as is in terrestrial biomass (Jacobson and others 2000). Soil organic matter (SOM) can, therefore, be regarded as a potentially important C sink, mitigating global warming by sequestering C removed from the atmosphere by plants (Bolin and Sukumar 2000). Conversely, soils can be a source of CO_2, with

Received 21 May 2008; accepted 12 March 2009;
published online 5 May 2009

Author Contributions: Conceived of or designed study: Sabine Grunwald, Nick Comerford, and James Sickman—Performed research: Mi-Youn Ahn—Analyzed data: Mi-Youn Ahn, Andrew Zimmerman, and Nick Comerford—Contributed new methods or models: Andrew Zimmerman, Nick Comerford, and James Sickman—Wrote the paper: Mi-Youn Ahn, Andrew Zimmerman, and Nick Comerford.

**Corresponding author; e-mail:* mahn@ufl.edu

microbes and other soil organisms annually releasing 50–75 Pg of CO_2–C to the atmosphere, about 10 times the annual emissions from the burning of fossil fuels (IPCC 1996; Raich and Tufekcioglu 1992; Schlesinger and Andrews 2000). Because any net increase in soil CO_2 emissions, perhaps in response to environmental changes, can influence global climate, identification of the factors that regulate soil respiration is critical in predicting ecosystem responses to global change.

Soil microorganisms play a dominant role in SOM mineralization (Tate 2000; Tufekcioglu and others 2001) and soil microbial community respiration is usually limited by the bioavailability of organic substrates (Raich and Tufekcioglu 2000). The bioavailability of SOM is determined by two, possibly interrelated factors, chemical and physical availability. Chemical availability, often referred to as lability, is determined by the chemical composition of SOM in relation to the ability of microbial exoenzymes to break organic polymers into smaller units that can, in dissolved form, pass through microbial cell walls. Such compound classes as carbohydrates and proteins are thought of as extremely labile, whereas lipids, lignin and humic substances are relatively chemically refractory. Physical availability refers to the physical location of SOM. If bound within mineral aggregates or sorbed within small pores, SOM may be protected from enzymatic attack and therefore be essentially biologically nonavailable (Jastrow and Miller 1997; Kaiser and Guggenberger 2000). Thus, soil structure and mineralogy (soil types) will be an important determinant of soil C storage and dynamics.

Soil organic matter (SOM) content, composition, and soil structure are known to vary with landuse type and soil management (for example, Bridgham and others 1998; Ghani and others 2003; Lorenz and others 2006; Paul and others 2002; Post and Kwon 2000; Pouyat and others 2007; Pulleman and others 2000; Shrestha and others 2007; Walter and others 2003). Thus, it is likely that landuse will, at least in part, be a determinant of C release from soils. Landuse change, for example, can modify long-term soil C stocks by ±50% (Guo and Gifford 2002; Searchinger and others 2008; Woodbury and others 2007). Some of the greatest soil C losses that accompany a landuse change have been observed during the transition from forest or pasture to annual crops, with the largest C increases attending the converse landuse transformations (Guo and Gifford 2002).

Correct identification of the ''mineralizable'' soil C pool is essential as it is an important component in modeling soil C dynamics and ecosystem responses to changing environmental factors (Buchmann 2000; IPCC 1996; Schlesinger and Andrews 2000; Stewart and others 2008). Various methods have been used to quantify mineralizable soil C (Bremer and others 1994). Two common methods are water extraction and acid-hydrolysis. Some evidence does exist that these extractable C pools represent chemically labile C, whereas other evidence suggests C biological availability. The water-soluble C (SC) component of soil originates, in part, from microbial biomass and soluble carbohydrates (Ghani and others 2003; Sparling and others 1998). SC quantity has been correlated with the soil's low-density fraction, microbial biomass, and total enzyme activity (Haynes 2000; Landgraf and others 2003, 2005; Tirol-Padre and others 2005). SC has been used as a proxy for soil mineralizable C (Leinweber and others 1995) and, in specific circumstances, has been correlated with basal soil respiration (Tirol-Padre and others 2005), and has been found to be sensitive to soil management (Haynes 2005). It has been proposed as an indicator of soil quality (Ghani and others 2003).

Acid-hydrolyzable C (HC) has also been proposed as an indicator of mineralizable SOM (Stout and others 1981). For example, HC was used in forest litter decomposition models to represent the C fraction lost during early decomposition (Zhang and others 2007a). HC has also been found to decrease during in vitro microbial incubations (Pare and others 1998). Soil HC quantity has been found to be positively correlated with microbial biomass, light fraction C, size of stable aggregates and 12-day soil organic C mineralization (C_{min}) rates (McLauchlan and Hobbie 2004).

Soil incubations are a more direct approach to quantifying mineralizable soil C than various procedures using chemical extraction or organic compound class analysis. Measured C_{min} rates have ranged from less than 0.007 to 35.6% of total soil C using varying incubations times (12–800 days) and soil temperature and moisture conditions (Alvarez and Alvarez 2000; Collins and others 2000; Giardina and others 2001; Haile-Mariam and others 2000; McLauchlan and Hobbie 2004). However, they are, by nature, short-term measurements, and must, therefore, measure only a subset of the total potential mineralizable soil C (Minderma and Vulto 1973; Paul and and others 2001a, 2006). Further, laboratory incubation conditions are generally optimized for temperature and moisture. Thus in vitro C_{min} can only serve as a proxy for total potential mineralizable soil C.

Only a few studies have combined the measurement of extractable soil C pools such as SC and HC and laboratory incubations to better understand soil organic C dynamics (Paul and others 2006) and access the relative value of these techniques and data derived by these methods. The studies that exist in the literature have been limited to one or only a few landuse or soil types and to a relatively small sample size (Alvarez and Alvarez 2000; Collins and others 2000; Giardina and others 2001; Haile-Mariam and others 2000; McLauchlan and Hobbie 2004). Thus, there is a lack of documentation that allows us to assess the relationship between soil C storage and C_{min} at the landscape scale, and across soil and landuse types. Therefore, the first goal of this research was to investigate the distribution of various organic C pools across and within a range of landuse and soil orders in the Santa Fe River Watershed in north Florida. We hypothesize that, because of differences in the type and amount of organic matter inputs, soil management and mineralogy, landuse, and soil orders will be distinguishable by their distribution of extractable soil C and C_{min} fractions. However, we recognize the high sand content of this watershed's surface soils may dampen soil C protection mechanisms, thus obscuring differences between landuse and soil orders. A second objective was to investigate relationships between measurements of in vitro total C_{min} and C_{min} rate and those of soil C pools (TOC, SC, and HC) and soil texture. This goal was motivated by a need to determine the most effective tool for evaluating long-term versus short-term soil C storage parameters which can be used to model soil C dynamics and the future effects of environmental change.

Materials and Methods

Sampling locations were chosen using a stratified-random sampling plan designed to sample soil type/landuse combinations proportional to their aerial extent in the 3,585 km^2 Santa Fe River Watershed, FL (Grunwald and others 2006). Soil samples were collected from 138 sites (Figure 1) encompassing eight landuse/land-cover types with the following areal coverages: semi-mature to mature Pine Plantations and Pine Plantation Regeneration (28%), Improved Pasture (15%), Upland Forest (14%), Wetlands (13%), Urban areas (11%), annual Crops (10%) and Rangeland (9%). The number of samples obtained from multiple locations within each landuse type was: Pine Plantations 27, Crops 12, Pine Plantation Regeneration 12, Improved Pasture 20, Rangeland 13, Upland Forest 20, Urban areas 16, and Wetlands 18. Although we have no detailed history of landuse change within the study area, this region of north Florida is not experiencing rapid development and sites were chosen that showed no evidence of recent disturbance. The soil order Ultisols made up 36% of the samples collected, Spodosols 28%, and Entisols 22%. Other soil orders accounted for the remaining 14% of the samples and included Alfisols (11%), Mollisols (2%), and Inceptisols (1%). Among the major soil Great Groups represented were Alaquods, Paleudalfs, Quartzipsamments, Paleaquults, and Paleudults. Additional information on the Santa Fe Watershed and distribution of landuse and soil types can be found in Grunwald and others (2006).

Soil samples, integrated from the uppermost 0–30 cm of the mineral soil column, were collected during 2004 (mostly during spring). All samples were collected by soil auger (5 cm diameter × 1 m), air-dried, homogenized, and passed through a 2-mm sieve prior to chemical analysis. TOC was measured using a Thermo-Finnigan Flash EA1112 elemental analyzer after the soil samples had been oven-dried at 70°C for 72 h and ground in a ball mill. This analysis is assumed to represent TOC here, as inorganic C content in north Florida soils was found by us and others (Guo and others 2006) to represent less than 2% of total soil C. Soil clay content was measured by the ''pipette method'' (Day 1965).

Hot-water-extractable or ''soluble'' C (SC) was determined by a modified version of the method of Gregorich and others (2003) and Sparling and others (1998). Ten milliliters of distilled water were added to 1 g soil samples and shaken end-over-end for 30 min at 30 rpm. The tubes were then capped and placed in a hot water bath at 80°C for 16 h. At the end of this period, each tube was shaken for another 10 min. Following centrifugation (20 min at 8000 rpm), the supernatant was filtered through 0.7-μm filter membranes and the filtrate analyzed for dissolved C using a Shimadzu TOC-5050 analyzer.

Acid-hydrolyzable soil C (HC) was determined following the methods of Sollins and others (1999). Briefly, 1 g of soil was refluxed for 16 h in digestion tubes with 10 ml of 6 M HCl. The solid residue (with unhydrolyzable C) was recovered after centrifugation, washed with 100 ml of deionized water, dried overnight at 80°C, and weighed prior to TOC analysis as described above. A correction was made for mineral mass loss during the hydrolysis and acid-hydrolyzable C was calculated as TOC less the unhydrolyzable C. All C pools were measured in duplicate.

The microbial mineralization rate was determined by measuring in vitro CO_2 production in soil incubations. Dry soil samples (1 g) were wetted to field capacity with 0.5–0.8 ml distilled water in 12-ml borosilicate vials. Sample and control vials (with no

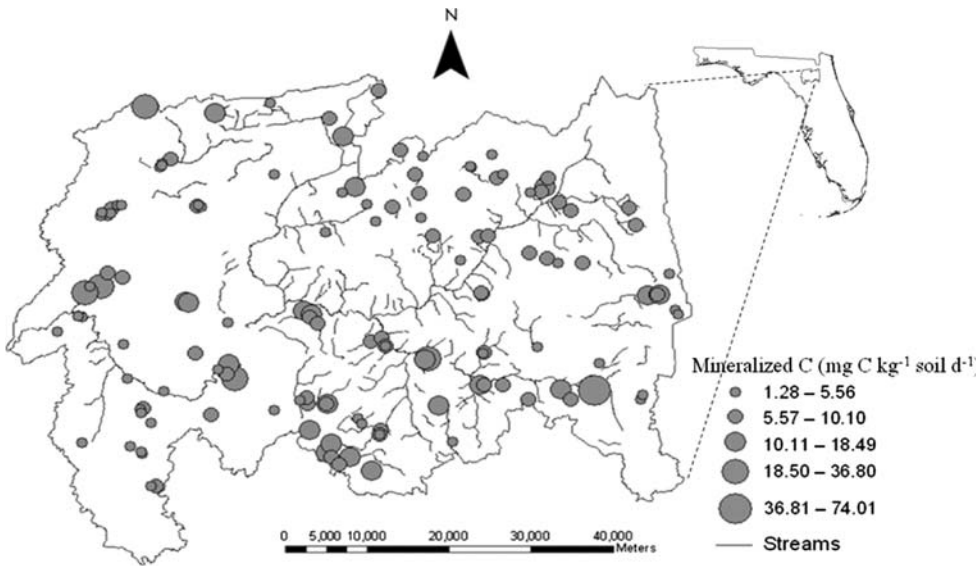

Figure 1. Location map of sampling/carbon mineralization rates (mg C kg^{-1} soil d^{-1}) in the Santa Fe River Watershed, FL.

soil) were filled with CO_2-free air, sealed with rubber septa, and incubated at 35°C in the dark. Duplicate vials were prepared for each soil. The evolved CO_2 in the headspace was measured using a modified CO_2 coulometer (UIC Inc., Joliet, IL) with CO_2-free air as a purge and carrier gas (sample running time of 5 min). After CO_2 analysis, each vial was flushed with CO_2-free air prior to another incubation period. The analytical detection limit for CO_2, determined using acidification of $CaCO_3$ standards was 0.1 µg C. The first two CO_2 measurements were made after 3 and 8 days incubations, then at weekly intervals for a period of 36 days. A final analysis was performed after 87 days incubation.

Statistical analyses were conducted using Statistica® version 8.0 (StatSoft Inc., Tulsa Oklahoma, USA). When the population distribution of a variable was not normal, $\log_{10}$ transformations were made to comply with assumptions of normality. Population distributions of TOC, SC, HC, and C_{min} rate were found to be lognormal. C pool and mineralization comparisons were made among landuses using analysis of variance with landuse or soil order as the sole main effect. Post-hoc mean separations were made among landuse or soil order based on Tukey's Honest Significant Difference unequal sample size separation technique (StatSoft 2007). Means presented in all tables, where the statistical analysis was performed on transformed data, are the back-transformed means using the equation:

$$z = \exp\left[y * \ln 10 + 0.5\sigma^2 * (\ln\ 10)^2\right]$$

where z is the back-transformed value, y is the $\log_{10}$ value and σ is the variance of the $\log_{10}$ value (Webster and Oliver 2001).

Regressions between C_{min} rate and C pools for all sites were evaluated with the General Regressions Model (StatSoft 2007) using a randomly selected learning subset of the data (99 of the sites). Regression validation was performed on the remaining 39 sites. Landuse was subsequently added into the regressions as binary encoded variables for each landuse or soil order to determine if the strength of the relationship could be improved.

A comprehensive suite of soil-landscape and C_{min} rate was assembled using local geographic information system (GIS) (geographic data: x coordinates, m; y coordinates, m) and ArcGIS version 9.0 (Environmental System Research Institute, Redlands, CA). Landuse data were derived from a supervised classification of Landsat ETM + 2003 imagery with an overall classification-accuracy of 82%. Spatial modeling was conducted using the ISATIS software (Geovariances Americas Inc., Houston, TX) for semivariogram modeling. The prediction quality consists of two components: map precision that measures the residual variability in prediction, and map accuracy that measures the closeness of the predictions to true conditions (Mueller and others 2001).

Results

Organic Carbon Pools

More than 96% of the 138 watershed soils sampled (uppermost 30 cm) were classified as sandy. Soils at 76% of the sites had less than 4% clay by weight and 93% of the sites had less than 8% (data not shown). TOC in the uppermost 30 cm of soil ranged 0.3–20.2 wt%. In all soils, HC was greater than

SC. HC and SC ranged from 0.2–9.0 to 0.001–0.07 g C kg^{-1}, respectively. Therefore, HC always represented a greater portion of TOC than did SC, 23.7 ± 12.7% (range of 7–98%) and 6.4 ± 1.9 (range of 2–11%), respectively. Similar C pool fraction sizes have been reported previously for HC as a percent of TOC (%HC/TOC of 30–80%: Paul and others 2006; Plante and others 2006) and for SC as a percent of TOC (for example, 0.7–10%; Pouyat and others 2007; Wang and Wang 2007; Zhang and others 2006; Zhao and others 2008).

The average TOC concentration, when grouped by landuse, ranged from 7.6 g C kg^{-1} for Upland Forest soils to 31.8 g C kg^{-1} for Wetland landuse (Table 1). Upland Forest soils contained significantly less TOC than soils of Pine Plantation Regeneration and Wetland landuses. The mean TOC concentrations of all other landuses, however, were not significantly different from each other (Table 1). The average SC and HC content within each landuse ranged from 0.52–1.4 to 2.1–6.4 g C kg^{-1}, respectively. As with TOC, SC, and HC generally showed large variations within each landuse in the watershed, with coefficients of variation ranging from 19 to 113%. However, SC in Upland Forest and Crop landuse soils were significantly less than in Pine Plantation Regeneration and Wetland landuse soils (Table 1). All other landuses had intermediate SC values that were not statistically distinguishable. The ability of HC content to differentiate soils of various landuses was similar to that of SC. Upland Forest showed the lowest HC content, that was significantly different only from that of the Pine Plantation Regeneration and Wetland soils (Table 1).

Representatives of four major soil orders, Spodosols, Ultisols, Entisols, and Alfisols, were found among all landuses of the watershed. Spodosols were the dominant soils in Pine plantation (44%) and Pine plantation regeneration (64%). Ultisols were dominant in Crop (77%), Improved pasture (50%), Rangeland (50%), and Urban (63%) landuses, Entisols in Upland Forest (55%), and Alfisols in both Upland forest and Wetland (59%). Wetland soils showed the most diversity of soil orders and included Mollisols and Inceptisols. Average TOC, SC, and HC concentrations were greatest in Mollisols (data not shown), however, only three soil samples were classified as Mollisols. Of the four most common soil orders, Spodosols contained the greatest average TOC, SC, and HC content, whereas Ultisols contained the lowest. The only significant differences in soil order-grouped average TOC, SC, or HC values were between Spodosols and Ultisols (Table 2).

When expressed as a percent of TOC, variability (CV%) of SC and HC within landuse and soil orders was generally reduced, with the exception of %HC/TOC within soil orders (Table 3 and 4). Average %SC/TOC and %HC/TOC ranged from 4.8 to 7.1 and from 20.8 to 35.6%, respectively, when grouped by landuse (Table 3). Although SC content in the Wetland soil was greatest on a soil weight basis, on a TOC basis it was the lowest, and was significantly lower than %SC/TOC in Pine Plantations and Upland Forest soils. On a TOC basis, HC was also lowest in the Wetland soil and was significantly less than in Pine Plantation Regeneration and Rangeland soils (Table 1 and 3). SC represented a similar proportion of the TOC in each of the four major soil orders (6.0–6.8%). However, HC represented a significantly greater portion of TOC in Ultidols than in Entisols, even though variability in the former was quite high (Table 4).

Table 1. Mean Total and Extractable Carbon, Mineralization Rates and Clay-Size Particle Weight Percent in Soils of Each Landuse in the Santa Fe River Watershed

Landuse	TOC g C kg^{-1} soil	SC g C kg^{-1} soil	HC g C kg^{-1} soil	C mineralization rate mg C kg^{-1} soild^{-1}	Clay %
Pine plantations(n = 24)	9.6 (57)^{ab}	0.65 (50)^{ab}	2.7 (58)^{ab}	3.8 (28)^{a}	1.8 (64)^{a}
Crop (n = 12)	9.4 (24)^{ab}	0.54 (34)^{a}	3.1 (19)^{abc}	4.4 (36)^{ab}	4.1 (72)^{b}
Pine plantation reg. (n = 12)	15.8 (38)^{b}	1.04 (31)^{bc}	5.6 (32)^{bc}	5.3 (47)^{ab}	2.0 (64)^{a}
Improved pasture (n = 18)	12.2 (36)^{ab}	0.74 (33)^{ab}	3.5 (41)^{abc}	5.1 (33)^{ab}	2.7 (71)^{ab}
Rangeland (n = 11)	13.5 (31)^{ab}	0.73 (39)^{ab}	4.6 (48)^{abc}	6.0 (40)^{ab}	3.0 (66)^{ab}
Upland forest (n = 20)	7.6 (68)^{a}	0.52 (56)^{a}	2.1 (48)^{a}	4.0 (72)^{a}	2.4 (72)^{ab}
Urban (n = 16)	11.8 (54)^{ab}	0.68 (52)^{ab}	3.5 (53)^{ab}	5.8 (54)^{ab}	4.3 (123)^{b}
Wetland (n = 18)	31.8 (118)^{c}	1.40 (113)^{c}	6.4 (93)^{c}	7.7 (102)^{b}	7.6 (140)^{c}
Total (n = 138)	14.9 (57)	0.80 (50)	3.7 (58)	5.3(52)	3.4 (143)

Notes: Column values are the mean for the landuse along with the coefficient of variation (%) in parentheses. Similar letters in each column indicate that the means are not significantly different at the $P < 0.05$ level using an unequal N HSD technique. The C mineralization rate was calculated from the 15 to 29 day incubation time period. TOC = Total organic C, SC = hot water extractable C, HC = acid hydrolyzable C.

Table 2. Mean Total and Extractable Carbon, Mineralization Rates and Clay-Size Particle Weight Percent in Each Soil Order in the Santa Fe River Watershed

Soil classes	TOC g C kg^{-1} soil	SC g C kg^{-1} soil	HC g C kg^{-1} soil	C mineralization rate mg C kg^{-1} soil d^{-1}	Clay %
Entisols (n = 30)	12.9 $(128)^{ab}$	0.64 $(80)^{ab}$	3.2$(46)^{ab}$	6.7 $(77)^{a}$	2.4 $(94)^{a}$
Spodosols (n = 37)	13.8 $(43)^{a}$	0.89 $(32)^{b}$	4.3 $(46)^{b}$	7.0 $(51)^{a}$	2.6 $(143)^{ab}$
Ultisols (n = 48)	10.1 $(40)^{b}$	0.60 $(48)^{a}$	2.9 $(50)^{a}$	6.9 $(51)^{a}$	2.8 $(59)^{ab}$
Alfisols (n = 16)	12.3 $(56)^{ab}$	0.77 $(45)^{ab}$	2.5 $(61)^{a}$	8.3 $(52)^{b}$	4.4 $(74)^{b}$

Notes: Column values are the mean for the soil class along with the coefficient of variation (%) in parentheses. Similar letters in each column indicate that the means are not significantly different at the $P < 0.05$ level using an unequal N HSD technique. The C mineralization rate was calculated from the 15 to 29 day incubation time period. TOC = Total organic C, SC = hot water extractable C, HC = acid hydrolyzable C.

Table 3. Mean Relative Abundance of Extractable Carbon Fractions (SC and HC) in TOC, and Total Mineralized C as a Percent of Extractable Carbon Fractions in Soils of Each Landuse in the Santa Fe River Watershed

Landuse	%SC/TOC	%HC/TOC	Total 87 day C mineralization (C_{min})		
			%C_{min}/TOC	%C_{min}/SC	%C_{min}/HC
Pine plantations (n = 24)	7.0 $(23)^{b}$	31.1 $(44)^{ab}$	3.7 $(35)^{bc}$	55.1 $(36)^{abc}$	15.3 $(88)^{ab}$
Crop (n = 12)	6.1 $(31)^{ab}$	33.4 $(27)^{ab}$	4.2 $(33)^{bc}$	70.8 $(28)^{bc}$	13.3 $(38)^{ab}$
Pine plantation reg. (n = 12)	6.7 $(16)^{ab}$	35.2 $(19)^{b}$	2.9 $(34)^{ab}$	45.3 $(35)^{a}$	8.6 $(32)^{a}$
Improved pasture (n = 18)	6.4 $(28)^{ab}$	30.3 $(35)^{ab}$	3.8 $(37)^{bc}$	60.4 $(33)^{bc}$	14.6 $(59)^{ab}$
Rangeland (n = 11)	5.6 $(21)^{ab}$	35.6 $(30)^{b}$	4.0 $(35)^{bc}$	75.1 $(47)^{bc}$	14.0 $(78)^{ab}$
Upland forest (n = 20)	7.1 $(24)^{b}$	31.8 $(48)^{ab}$	4.6 $(28)^{c}$	67.0 $(30)^{bc}$	24.6 $(113)^{b}$
Urban (n = 16)	6.0 $(20)^{ab}$	27.0 $(40)^{ab}$	4.5 $(46)^{bc}$	79.5 $(38)^{c}$	17.5 $(59)^{ab}$
Wetland (n = 18)	4.8 $(45)^{a}$	20.8 $(35)^{a}$	2.1 $(33)^{a}$	50.3 $(44)^{ab}$	11.1 $(35)^{ab}$
Overall	6.4 (30)	30.7 (54)	3.8 (45)	63.1 (44)	14.9 (63)

Notes: Columns values are the means for the landuse along with the coefficient of variation (%) in parentheses. Similar letters in each column indicate that the means are not significantly different at the $P < 0.05$ level using an unequal N HSD technique.
TOC = Total organic C, SC = hot water extractable C, HC = acid hydrolyzable C.

Table 4. Mean Relative Abundance of Extractable Carbon Fractions (SC and HC) in TOC, and Total Mineralized C as a Percent of Extractable Carbon Fractions in Soils of Each Soil Order in the Santa Fe River Watershed

Soil class	%SC/TOC	%HC/TOC	Total 87 day C mineralization (C_{min})		
			%C_{min}/TOC	%C_{min}/SC	%C_{min}/HC
Entisols (n = 30)	6.5 $(31)^{a}$	20.9 $(39)^{a}$	3.9 $(39)^{ab}$	60.1$(30)^{ab}$	12.5 $(44)^{a}$
Spodosols (n = 39)	6.8 $(25)^{a}$	28.1 $(119)^{ab}$	3.3 $(42)^{a}$	49.9 $(40)^{a}$	13.0 $(99)^{a}$
Ultisols (n = 50)	6.0 $(27)^{a}$	39.5 $(305)^{ab}$	4.0 $(40)^{ab}$	71.1 $(44)^{b}$	25.5$(287)^{ab}$
Alfisols (n = 16)	6.7 $(26)^{a}$	39.5 $(80)^{b}$	4.2 $(38)^{b}$	63.3 $(36)^{ab}$	27.7 $(107)^{b}$

Notes: Columns values are the means for the soil type along with the coefficient of variation (%) in parentheses. Similar letters in each column indicate that the means are not significantly different at the $P < 0.05$ level using an unequal N HSD technique.
TOC = Total organic C, SC = hot water extractable C, HC = acid hydrolyzable C.

Organic Carbon Mineralization

The total amount of C released from surface soil samples during the 87-day incubation (total C_{min}) ranged from 0.1 to 3.7 g C kg^{-1} (0.5 ± 0.4). Expressed as a percent of TOC, total C_{min} ranged from 1.1 to 9.6% and averaged 3.8 ± 1.6%. The amount of C mineralized was more comparable to that of the extractable C pools with %total C_{min}/SC and %total C_{min}/HC, ranging from 17.4 to more than 100% (63.1 ± 27.9) and 3.4–93.3% (14.9 ± 9.4), respectively. With the exception of the low-value for Wetland soils (2.1%) and high-value for Upland Forest soils (4.6%), %C_{min}/TOC was not significantly different among landuses (Table 3). Values of %C_{min}/SC were higher for Urban than for two other landuses, whereas values for Pine Plantation Regeneration were lower than for five other landuses. In comparison, %C_{min}/HC differentiated landuse to a lesser degree, showing only the Pine Plantation Regeneration and Upland Forest soils to be significantly different (Table 3). Similarly, total C_{min} expressed as a percent of C pool size did not greatly differentiate soil orders (Table 4). But there were significant differences in %C_{min}/TOC between Spodosols (3.3%) and Alfisols (4.2%), between the %C_{min}/SC of Spodosols (49.9%) and Ultisols (71.1%), and between the %C_{min}/HC of Entisols (12.5%) and Spodosols (13.0%) and that of Alfisols (27.7%).

After an initial incubation period of 3 days, during which CO_2 release rate (C_{min} rate) was relatively high, C_{min} rate stabilized and was constant in each soil during the remainder of the 87-day incubation. Therefore, we can conclude that a transition from mineralization of an active to a slowly cycling C pool was not reached (Paul and others 2001b). Plots of CO_2 released versus time were mathematically modeled using linear regression and had an overall average correlation coefficient of $R^2 = 0.978 \pm 0.036$ (data not shown). Here, the 15–29-day incubation time period was chosen for examination of C_{min} rate, though there was no significant difference in rates calculated using other incubation periods.

Carbon (C) mineralization rates, which were strongly correlated with total C_{min} ($R^2 = 0.901$), ranged from 1.3 to 74 mg C kg^{-1} soil d^{-1} and averaged 5.3 ± 2.8 mg C kg^{-1} soil d^{-1}. The spatial distribution of measured aerobic C_{min} rates was shown in Figure 1. Although there appear to be relatively high values in the southern and eastern portions of the field site, there was no significant correlation between rates and either longitude or latitude. To investigate spatial autocorrelation, a spherical semivariogram model (data not shown) was fitted with the parameters of range (2,150 m), partial sill (38.35), and nugget (3.98). It indicated a positive spatial correlation between C_{min} rate at each sampling site and proximal sampling sites. In other words, within a range of 2,150 m, similar values tend to be near each other.

The average C_{min} rate, when grouped by landuse, ranged from 3.8 to 7.7 mg C kg^{-1} soil d^{-1} (Table 1). Soil C_{min} rate in the forest soils, Pine Plantation and Upland Forest, were significantly lower than that of Wetland soils. In addition, Wetland soils showed the greatest coefficients of variation (102%), with C_{min} rates ranging from 2.7 to 74 mg C kg^{-1} soil d^{-1}. There were no other significant differences in soil C_{min} rates among landuses. When grouped by soil order, average soil C_{min} rates ranged from only 6.7 to 8.3 mg C kg^{-1} soil d^{-1} and showed high variability within each soil order (Table 2). Only Alfisols, with the highest average C_{min} rate, were significantly different from other soil orders.

Carbon Pools and Mineralization Rate and Soil Texture Relationships

Relationships between C_{min} rate and SOM quality indicators such as TOC, HC, and SC and grain-size parameters were examined using linear correlation techniques. The strength of these relationships across all soils of this study is indicated by the square of the Pearson correlation coefficients (R^2: Table 5). All ''strong'' relationships between two variables (those with $R^2 > 0.25$ listed in Tables 5 and 6) have positive slopes and indicate ''direct'' relationships. The strongest relationships with C_{min} rate were found with TOC ($R^2 = 0.62$, $P < 0.001$) and SC ($R^2 = 0.59$, $P < 0.001$). For the whole data set, C_{min} rate showed a stronger linear relationship with clay content ($R^2 = 0.35$, $P < 0.001$) than with sand and silt ($R^2 = 0.25$ and 0.14, respectively) though all these relationships were significant. Interestingly, the C_{min} rate was significantly cor-

Table 5. The Squares of the Pearson Correlation Coefficients for the Linear Regressions Between Log-Normalized Carbon Mineralization Parameters and Log-Normalized Indices of Soil Organic Carbon Quality and Quality and Grain Size

Log-normal	Log-normalized mineralization parameters	
	C_{min} rate	C_{min} rate/TOC
TOC	0.62**	0.24**
SC	0.59**	0.11**
HC	0.32**	0.15**
%SC/TOC	0.10**	0.25**
%HC/TOC	<0.01	<0.01
Clay	0.35**	0.06**
Sand	0.25**	<0.01
Silt	0.14**	<0.01

All linear regression had a positive slope, when $R^2 > 0.15$.
Notes: TOC = Total organic C, SC = hot water extractable C, HC = acid hydrolyzable C. Data includes all sites (N = 138) from the Santa Fe River Watershed.
** = Significant P < 0.05; ** = Very significant: P < 0.005.*

Table 6. The Squares of the Pearson Correlation Coefficients for the Linear Regressions between Log-Normalized Carbon Mineralization Rates and Log-Normalized Total and Extractable Organic Carbon Fractions and Grain and Clay Contents or Soil Order in the Santa Fe River Watershed

Log-normalized C_{min} rate	Log-normal			
	TOC	SC	HC	Clay
Landuse				
Pine plantation	0.71**	0.58**	0.19	0.26*
Crop	0.61*	0.78**	0.39	0.20
Pine plantation reg.	0.89**	0.82**	0.74**	0.17
Improved pasture	0.24	0.60*	0.10	0.06
Rangeland	0.59	0.50	0.21	0.57*
Upland Forest	0.82**	0.88**	0.31	0.29*
Urban	0.67**	0.64*	0.45	0.47**
Wetland	0.94**	0.88**	0.91**	0.49**
Soil class				
Entisol	0.84**	0.86**	0.77**	0.32**
Spodosol	0.69*	0.56*	0.35*	0.22**
Ultisol	0.62**	0.62**	0.39*	0.11*
Alfisol	0.72**	0.74**	0.47	0.59**

All linear regression had a positive slope, when $R^2 > 0.10$.
Notes: TOC = Total organic C, SC = hot water extractable C, HC = acid hydrolyzable C.
** = Significant: $P < 0.05$; ** = Very Significant: $P < 0.005$.*

related to the proportion of soluble C in each sample as indicated by %SC/TOC ($R^2 = 0.1$), but not to the proportion of hydrolizable C (%HC/TOC, $R^2 < 0.01$). The C_{min} rate was also significantly correlated to the proportion of TOC mineralized in each sample (%TOC_{min}, $P < 0.001$).

Stronger relationships were observed between C_{min} rate and C forms in soils within certain landuses and soil orders (Table 6). For example, R^2 values were generally greater than 0.70 and very significant for the C_{min}-TOC and the C_{min}-SC relationship within Pine Plantation, Pine Plantation Regeneration, Upland Forest and Wetland soils and within Entisols and Alfisols. The C_{min}-HC relationship was generally weaker than that of C_{min}-TOC or C_{min}-SC both overall, and within landuse and soil types. The C_{min}-HC relationship was only strong (>0.70) within Pine Plantation Regeneration, Wetland, and Entisol soils.

C mineralization (C_{min}) rate was generally less strongly correlated with clay content than TOC or SC within each landuse or soil type. However, strong and significant C_{min}-clay content relationships were found for Rangeland, Wetland soils, and Alfisols ($R^2 = 0.57$, 0.49, and 0.59, respectively). Overall, C_{min} displayed the strongest linear relationships with measurements of C pool size (TOC, SC, and HC) within forest and Wetland landuse and within Entisol and Alfisol soils. These relationships were weakest for Improved Pasture and Rangeland soils.

Discussion

Extensive measurements of the chemical lability (SC and HC) and bioavailability (C_{min}) of soil C across a north Florida watershed, including a range of landuse and soil types, revealed relationships that can be used to shed light on the nature of these soil C fractions and the dominant C sequestration mechanisms and soil C dynamics in these sandy soils.

Objective 1. Organic C Pools and Total C_{min} Across Landuse and Soil Orders

The average TOC, SC, and HC concentrations of Santa Fe watershed soils were 14.9, 0.8, and 3.7 g C kg^{-1}, respectively, and lower than the corresponding values of 1–208, 1–11, and 6–34 g C kg^{-1}, respectively, found in other recent studies (Boyer and Groffman 1996; Ghani and others 2003; Schwendenmann and Pendall 2006; Tan and others 2004; Wang and Wang 2007; Zhang and others 2006). The sandy nature of the Santa Fe River watershed also distinguishes the surface soils of this study from those of many other published reports. In fact, soils from most of these previous studies had relatively greater clay contents (up to 60% more) than soils from our study sites. Thus, it is likely the low-clay content of our soils is a major reason for their overall low TOC, SC and HC concentrations (Sarkhot and others 2007b). Sorption of C to clay is known to stabilize C against enzymatic attack (Stewart and others 2008). Aggregation also protects soil C from mineralization (Stewart and others 2008). Although larger macro-aggregates (>2 mm diameter) are weak or absent in these sandy soils, small macro and microaggregates (<2 mm diameter) do occur and have been shown to hold approximately 50% of the total SOC (Sarkhot and others 2007b). However, the ability of these aggregates in the coastal plain sandy soils to protect C from mineralization is poorly understood (Sarkhot and others 2007a).

Many have noted the influence of landuse type/change on soil TOC and extractable organic C content (including SC and HC: Gerzabeck and others 2006; Ghani and others 2003; Lorenz and others 2006; Paul and others 2002; Schwendenmann and Pendall 2008; Zhang and others 2006). Although most of these studies have examined soil C pools before and after landuse change, a few have contrasted the soil C pool characteristics of a number of current and stable landuses. For example, forest soils showed 6 and 8% more TOC than crop (Zhang and others 2006) and tree plantation soils (Wang and Wang 2007), respectively. Improved pasture and urban soils were found to contain 8 and 12% more TOC than tree plantation soils (Cohen and others 2008). In contrast, this study found greater TOC in Wetland and Pine plantation soils than Upland Forest soils but few other significant differences. Similarly, a study conducted in a nearby (north Florida) pine plantation forest found that, even when organic C inputs are increased by a factor of four, there were no discernible differences in TOC in these sandy surface soils (Harding and Jokela 1994; Shan and others 2001). The capacity and major mechanism used by these coastal plain soils to hold and protect C remain to be determined, as is the influence of landuse on aggregate stability and subsequent protection from mineralization.

In general, the relative proportions of extractable C of the TOC in these north Florida soils (%SC/TOC and %HC/TOC) were similar to those of previous reports (Paul and others 2006; Pouyat and others 2007; Wang and Wang 2007; Zhang and others 2006; Zhao and others 2008). However, both the amount of extractable soil C and the proportion of SC and HC to TOC could not differentiate soils of different current landuses, with the exception of Wetland (discussed below). Even larger landuse groupings such as forest (including Pine plantation, Pine forest regeneration, and Upland forest) and non-forest (including Crop, Improved pasture, Rangeland, and Urban) showed statistically similar proportions of SC or HC to TOC. The same heterogeneity in each soil order's soil C pool size and relative proportion of extractable C generally resulted in a lack of statistical differentiation.

Examples of both similar and dissimilar findings regarding the labile fraction in different soil types can be found in the literature. Zhao and others (2008) found no significant difference in %SC/TOC between crop and forest soils within the top 20-cm (0.8 and 0.7%, respectively). In contrast, Zhang and others (2006) found that cultivated soil contained a significantly higher %SC/TOC (8.1%) than other landuse types (5.7, 5.3 and 3.4% for abandoned cultivated soil, wetland and forest soils, respectively, in the top 30-cm on average). Boyer and Groffman (1996) also reported a significantly greater SC fraction in a crop soil (~6%) than forest soil (~1.5%) in the top 30-cm. However, in both of these latter two studies, each landuse type was only sampled in triplicate from the same plots.

Tan and others (2004) reported a significant difference between the %HC/TOC in the top 20-cm of crop and forest soils (63 vs. 47%, respectively). As in our study, however, Schwendenmann and Pendall (2006) found there was no significant difference in the average %HC/TOC in the top 0–40 cm of forest and grassland soils (49 and 50%, respectively). Interestingly, they did find that the %HC/TOC of forest and grassland soils was significantly different in the top 0–5 cm. These comparisons with other studies highlight the importance of sampling statistics and sample depths in reaching conclusions as to the influence of landuse and soil type on C quality.

Wetland soils contained the largest C pool sizes (TOC, SC, and HC), but had proportions of SC and HC relative to TOC that were significantly smaller than some of the forest and non-forest soils. Similarly, Zhang and others (2006) found that wetland soils had larger TOC and SC pool sizes than other landuse types (forest and crop) but relatively lower proportions of SC to TOC. The finding that Wetland SOM contains larger proportions of refractory soil C is unexpected in that wetlands typically accumulate large stocks of organic C because, due to waterlogging and resulting anoxic conditions, microbial decomposition of SOM is suppressed. Thus, one might expect SOM to be relatively more labile, reflecting little degradation. It may be that an additional result of the absence of oxygen in wetland soils is the suppression of polyphenol oxidase enzyme activity which breaks down plant-produced biopolymers (Freeman and others 2004; McLatchey and Reddy 1998). Thus, refractory organic polymers may be more likely to persist, resulting in lowered proportions of SC and HC.

To compare our C mineralization rates and proportions with that of others, C_{min} rates of previous studies were converted to a standard unit of C_{min} after a 87-days incubation. The total C_{min} after 87-days was quite variable, ranging from 0.1 to 3.7 g C kg^{-1}. Others have found similar mineralizable pool sizes (<0.1–5.4 g C kg^{-1} in crop, forest, grassland, or paddy soils) for cross-landuse studies (normalized here to an 87-day-incubation period: Alvarez and Alvarez 2000; Giardina and others 2001; Schwendenmann and Pendall 2006; Zhang and and others 2007b; Zhao and others 2008). The proportion of soil TOC, SC, and HC that was mineralized during the 87-day incubation was also quite variable both within and across landuse types and soil orders. Although this resulted in landuse-grouped means that were statistically similar, differences, besides those for Wetland soils, were still found. For example, the average proportion of TOC mineralized in Crop, Rangeland, Upland forest, and Urban soil was about one-third greater than that of Pine Plantation Regeneration forest and Improved Pasture soils. Previous studies have reported similar C mineralization proportions (normalized here to an 87-day-incubation period) to those found in this study. For example, an average of 3.5% of TOC was mineralized in Minnesota wetland soils (Bridgham and others 1998) compared to 1.1–3.7% for Santa Fe watershed wetland soils. Similar fractions of TOC were mineralized in incubations of forest, grassland, and crop soils (3.0–7.7, 2.9 and 3.5–6.0%, respectively: Alvarez and Alvarez 2000; Giardina and others 2001; Schwendenmann and Pendall 2008; Zhao and others 2008) compared to 2.9–4.6, 3.8–4.0 and 4.2% for the Santa Fe watershed forest (Pine plantation, Pine plantation regeneration, Upland forest), grassland (Rangeland, Improved pasture), and crop soils.

The high degree of spatial heterogeneity in total C_{min} and C_{min} rates found in this large watershed might be expected given previous reports of similar heterogeneity in soil respiration rates for some relatively small wetlands, forests, grasslands, and farmlands (Bridgham and others 1998; Franklin and Mills 2003; Han and and others 2007; Xu and Qi 2001). However, it should be noted that most published soil respiration rates are collected either in the field or on intact soils columns. These rates, therefore, may reflect variations in soil temperature and soil moisture which are certainly influential environmental factors controlling soil respiration (Han and others 2007; Wiseman and Seiler 2004). However, the in vitro incubations used in this study allow temperature and moisture to be controlled and constant. Therefore, only differences in the amounts, types and physical location (for example, structure or mineralogical association) of organic C fractions or native microbial populations can be considered as possible causes of variation in total C_{min} and C_{min} rates.

Despite the apparent SOM heterogeneity, the spatial autocorrelation analysis revealed that soil C quality distributions still retained some order. It seems that, in these sandy soils, gross landuse-related factors, such as OM input type, and soil order-related factors, such as parent material and climate, have less importance than sub-landscape scale factors and perhaps longer-term history and management factors. For example, crop soil C quality could vary with tillage system, time since tillage, crop rotation, and nutrient amendments. For forest soils, additional factors could include site preparation or pre-planting management, species composition and age.

Objective 2. Relationship Between Measurements of in vitro C_{min} Rate and Soil C Pools

As microbes can utilize only dissolved organic constituents, one would expect a close relationship between C_{min} rates and measures of extractable C such as SC or HC. However, the presence of extractable OM does not guarantee the physical accessibility of that OM to soil microbes. In addition, SC and HC measure the ''extractability'' of SOC and do not necessarily provide information on the ability of microbes to utilize the extracted substrate (that is, chemical bioavailability: Helfrich and others 2007; Poirier and others 2006).

Some have found direct correlations between the non-acid hydrolyzable C fraction and soil C age (Collins and others 2000; Paul and others 2001a). However, this does not necessarily produce a relationship between HC and mineralizability as the HC pool is a complex one that may include both labile and slowly degrading components. Our results showed that HC was a poor indicator of mineralization rate, both in the overall data set and within most data subsets (landuse and soil orders). However, C_{min} rate exhibited statistically significant linear relationships with both TOC and SC. Although this was true for the data set as a whole, both the strongest and the weakest C_{min}-TOC and C_{min}-SC relationships were found for soils within certain landuse and soil orders. For example, C_{min} was strongly related to TOC and SC in Wetland and most of the forest soils and Entisols and Alfisols. But these relationships were weaker for non-forest soils such as Rangeland, Crop, Urban, and

Improved Pasture. It may be that the soil C pool-mineralization potential relationships are less well-developed in soils that have been subjected to recent disturbance, such as pastures and urban landuse, which may have introduced spatial heterogeneity in C lability.

Because of the known ability of clays to sorb and protect OM from degradation (Jardine and others 1989; Keil and others 1994; Stewart and others 2008), one might expect to find a positive relationship between TOC and extractable C pools and clay, and a negative relationship between C_{min} rate and clay content. On the contrary, we found only weak correlations between TOC and clay content (R^2 = 0.16) and between SC or %SC/TOC and clay content (overall as well as within landuse and soil orders). Even more surprising was the significant direct relationship between overall C_{min} rate and clay content (R^2 = 0.35). This relationship was even stronger in soils within landuse and soil order groups with average clay contents that exceeded 3% (Wetland, Urban, Rangeland landuses, and Alfisols). One possible explanation is that, in predominantly sandy soils such as these, a small amount of clay is of benefit to microbial soil communities. Positive correlations have been found between soil microbial biomass and clay content (Franzluebbers 1999; Gregorich and others 1991; Ladd and others 1996). Clay-sized particles may provide a necessary surface area for stable microbial colonization. It may also be that the small amounts of clay did not exceed some lower threshold needed for an OM protection mechanism to operate effectively.

The ability of TOC and SC to predict soil C mineralization rates was evaluated with a stepwise General Regressions Model (StatSoft 2007) using a randomly selected learning subset of the data (99 samples). This is a standard and well-accepted method for using regression as a predictive tool and should be carried out whenever one has enough observations that allow this independent testing procedure. Best-fit linear equations of the learning data set normalized C_{min} against TOC and SC yielded R^2 values of 0.67 and 0.59, respectively (plotted in Figure 2). Then regression validation was performed using the remaining 39 samples. The validation data sets exhibited smaller R^2 values (0.48 and 0.45, respectively) that were highly significant ($P < 0.05$). Landuse was subsequently added into the regressions as binary encoded variables for each landuse class to determine if including landuse improved the relationship. Under these conditions the sample size constrained the use of both learning and validation approaches; thus C_{min} was regressed against C pools with no validation component. Adding a Wetland landuse factor explained an additional 7% of the variability in the ability of TOC to predict C_{min} and adding a Pine Plantation Regeneration factor explained an additional 10% of the variability in the C_{min}-SC regression. Other than these, landuse and soil order increased the predictive power of these regressions to only a minor degree.

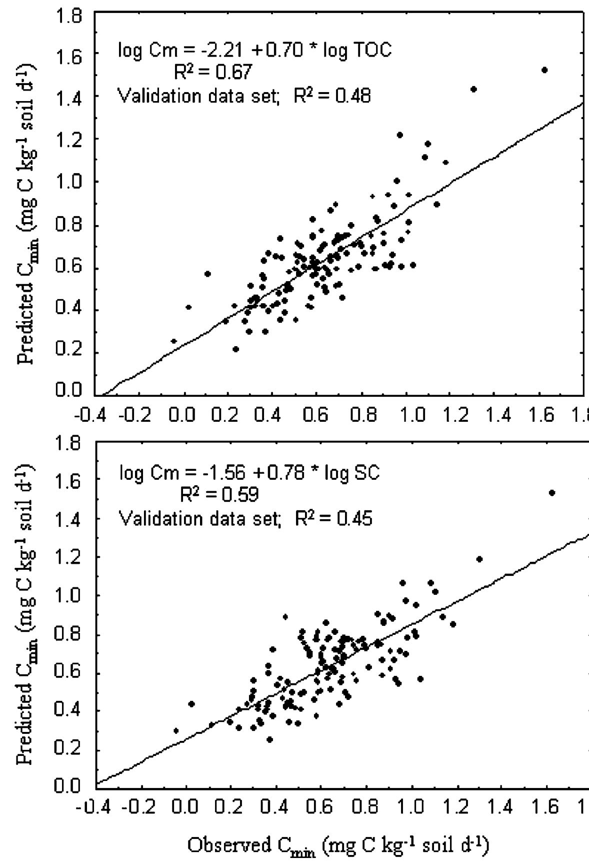

Figure 2. Observed soil carbon mineralization rates (mg C kg^{-1} soil d^{-1}) plotted against mineralization rate predicted by stepwise multiple linear regression of this variable against (**A**) total soil organic carbon (TOC; mg kg^{-1} soil) and (**B**) hot water extractable soil carbon (SC). The data points plotted are from the learning data set and the equation provided was used to calculate the predicted values.

Measurements of the chemical lability of soil C are often made to serve as indicators of C quantity likely to be preserved over the long-term (sequestered), or conversely, released to the atmosphere (mineralized). The results presented here suggest that, at the multi-use landscape scale, both TOC and SC were robust predictors of the amount of potentially mineralizable soil organic C. Our results imply that HC is not an appropriate proxy for microbial bioavailability of C in mineral soil systems, even though it has been shown to be an effective extraction technique for some forest soils (Rovira and Vallejo 2007; Silveira and others 2008). Moreover, HC extraction is time-consuming and generally has a higher measurement uncertainty than TOC or SC (Paul and others 2006).

Conclusion

Our analyses of organic C pools and C_{min} in a large number of soils within a Florida watershed indicated significant heterogeneity in the chemical and biological lability overall and within the soils of individual landuses and soil orders. Thus C quality, as measured by TOC, C extraction (SC and HC), and C bioavailability (in vitro total C_{min} and C_{min} rate), was statistically indistinguishable in most of the forest and non-forest landuse soils and four major Florida soil orders. An exception was Wetland soils which, though rich in TOC had a relatively low fraction of bioavailable C. The sandy soils of this region may lack the OM protection mechanisms present in other soils and, therefore, may result in the limited landuse or soil order differences in C_{min} observed. We recommend that if a single C fraction measurement must be chosen to reflect the heterogeneity of C_{min} rate in sandy coastal plain soils, TOC rather than extractable C fractions (SC or HC) is the most efficient. With TOC, one can consistently predict the potential for C mineralization and it has the advantage of ease of measurement.

Acknowledgments

We acknowledge Chunhao Xu and Yu Wang for laboratory analyses. Funding was provided through the Cooperative Ecosystem Service Unit, Natural Resources Conservation Service, U.S. Department of Agriculture and the large-scale project ''Geo-temporal estimation and visualization of nitrogen and other soil properties in the mixed-use Santa Fe River Watershed'' United States Department of Agriculture (USDA)—Nutrient Science for Improved Watershed Management Program. We also appreciate the helpful comments provided by two anonymous reviewers.

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