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Soil organic carbon quality in forested mineral wetlands at different mean annual temperature

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ABSTRACT

Forested mineral soil wetlands (FMSW) store large stocks of soil organic carbon (SOC), but little is known on: (i) whether the quality of SOC stored in these soils (proportion of active versus more resistant SOC compounds) differs from SOC in upland soils; (ii) how the quality of SOC in FMSW varies with mean annual temperature (MAT); and (iii) whether SOC decomposition rates in these environments respond to warming and drying more strongly than those observed in upland soils. To address this substantial knowledge gap, we identified nine FMSW and fifteen paired upland forest sites across three bioregions in North America (sub-alpine in Colorado; north-temperate in Minnesota; and south-temperate in South Carolina) to test the following three hypotheses. First, FMSW store a higher proportion of active SOC compared with upland systems because long anaerobic periods favor the accumulation of labile substrates. Second, in FMSW, SOC quality decreases from cold to warm bioregions because high quality detritus accumulates preferentially at cool sites where decomposition is slow. Finally, decomposition of SOC in FMSW will respond more strongly to warming under aerobic conditions than SOC from upland forest soils because of higher accumulation of active SOC in FMSW. To test these hypotheses, we incubated FMSW and upland forest soils at two constant temperatures (10 and 30 °C) for 525-d under aerobic conditions and constant moisture. In contrast to our first hypothesis, we observed similarly rapid depletion of active SOC compounds at initial stages of incubation across FMSW and upland sites, and across the 525-d incubations we observed overall lower SOC decomposition rates in our FMSW soils. In line with our second hypothesis, and across FMWS and upland soils, we found greater SOC loss in the sub-alpine bioregion than both temperate regions. In contrast to our last hypothesis, we found no difference in the temperature sensitivity (Q_{10}) of SOC decomposition in FMSW and upland forest soils. Critically, total SOC loss (g SOC per g soil) was larger in FMSW because of the large amount of SOC stored in these ecosystems, indicating that despite a lack of difference between FMSW and upland responses, the total release of C from FMSW that could result from global warming may be large.

1. Introduction

The great capacity of wetland soils to store carbon (C) derives from the slow rate at which decomposition occurs under anaerobic conditions of poor drainage (Gorham, 1991; Hobbie et al., 2000). This vast soil organic C (SOC) stock may be susceptible to rapid decomposition if environmental conditions are altered, as in the case of increased temperature or altered hydrology (Billings et al., 1983; Savage and Davidson, 2001). Resulting SOC losses from wetland ecosystems could then result in a large positive feedback to climate change (Davidson and Janssens, 2006).

Despite the important role attributed to wetland ecosystems in the global C cycle, little information exists on soil C quality and sensitivity of SOC decomposition to climate change for most types of wetlands (Hill and Cardaci, 2004; Bridgham et al., 2006) including forested mineral soil wetlands (FMSW). In contrast to organic soil wetlands, mineral soil wetlands are characterized by the presence of a generally thin organic horizon overlying the mineral soil. High plant productivity has been measured in these environments (Campbell et al., 2000) and typically, as with other wetlands, FMSW store large quantities of SOC (Cui et al., 2005). Forest vegetation covers as much as 50% of the wetland area in North America (Dahl, 2000), and spans across a wide range of soil types (Soil Survey Staff, 1999). Globally, approximately 20% of the

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total SOC in wetlands resides in hydric mineral soils (Eswaran et al., 1995; Kirk, 2004). Mineral soil wetlands are estimated to extend over 2,300,000 km^2 (Anselman and Crutzen, 1989) to 8,800,000 km^2 (Eswaran et al., 1995) in North America for an estimated SOC pool of 36 Pg C (Bridgham et al., 2006). This enormous stock of SOC is particularly sensitive to global changes because small changes in forest hydrology due to rising temperatures or reduced precipitation could greatly alter the annual period that these soils are anaerobic (Davidson and Janssens, 2006).

Despite the magnitude of this C stock, surprisingly little is known about SOC quality in FMSW, which can be defined as the availability of organic substrates (with high availability corresponding to high quality) to soil decomposers and decomposability by soil microorganisms (Ågren and Bosatta, 1996; Rovira and Vallejo, 2002). According to this broadly accepted definition of SOC quality, the relative proportion of active and resistant SOC that accumulates in soil may be a good predictor of SOC quality and turnover (Ågren and Bosatta, 1996). As microbial decomposition of labile C substrates is temperature-dependent (Fierer et al., 2006), high accumulation of active SOC is expected at cold sites, while enhanced decomposition with increasing temperature may lead to the depletion of active SOC at warm sites (Hart and Perry, 1999). Because of preferential microbial utilization of structurally simple C compounds (Paul and Clark, 1996), decomposition rates for more resistant C substrates are slower and may be constrained more by substrate quality than temperature (Giardina and Ryan, 2000). Despite recent evidence that resistant SOC may show higher temperature sensitivity than labile SOC in grassland and agricultural ecosystems (Conant et al., 2008), incubation studies of high latitude wetland soils have shown that high quality SOC has higher temperature responses than more resistant SOC (Updegraff et al., 1995). In temperate upland forests in North America, Fissore et al. (2008) found that SOC quality decreases with increasing MAT and this process is driven by both the temperature sensitivity of active SOC and the temperature insensitivity of resistant SOC (Fissore et al., in press). This later finding is supported by a radiocarbon study of SOC across elevation sequences (Trumbore et al., 1996).

Our ability to predict the response of terrestrial C storage to climate change relies on improving our understanding of how SOC quality in ecosystems that store large quantities of SOC, such as FMSW, varies in relation to biophysical variables. We anticipated that there should be large differences between FMSW and upland systems in the size and sensitivity of these biogeochemical processes, as these processes in FMSW proceed under conditions that differ substantially from those in upland soils. Soils in FMSW experience much longer periods of anoxia, with impacts on soil chemistry, especially soil redox potential but also nutrient cycling, microbial community composition, temperature regimes, and thus decomposition rates (Groffman et al., 1996; Baker et al., 2001). However, current biogeochemical models do not distinguish FMSW from upland forests (Trettin et al., 2001), and remarkably, we are aware of no studies that have investigated SOC quality in FMSW across a climate gradient, or that have examined how SOC quality in FMSW compares with SOC in adjacent upland forests.

To begin to address this information gap, we quantified SOC quality in FMSW and upland forest soils in three bioregions in North America: a sub-alpine forest bioregion, a north-temperate forest bioregion, and a south-temperate forest bioregion. We used long-term lab incubation experiments to test three hypotheses: (i) FMSW store a higher proportion of active SOC compared with upland systems (i.e., SOC quality in FMSW is higher than upland forests) because long anaerobic periods favor the accumulation of labile substrates; (ii) SOC quality in FMSW declines with mean annual temperature (MAT); (iii) under aerobic conditions, decomposition of SOC in FMSW is more sensitive to changes in temperature than upland forest SOC because FMSW soils contain more active SOC, and the sensitivity of less decomposed, higher quality substrates to increased temperature under aerobic conditions is greater than for resistant, lower quality substrates (Giardina and Ryan, 2000).

2. Methods

2.1. Site and soil characterization

We sampled 9 FMSW and 15 upland forests across three bioregions in North America for a total of 24 soil samples. Sampling sites were located in sub-alpine forest ecosystems in Colorado, north-temperate forests in Minnesota, and in south-temperate forests in South Carolina, with MAT spanning from −2 °C to 18 °C (Table 1). In the summer of 2004 we sampled the top 20 cm of the mineral soil after removing any forest floor. Sampling was conducted by depth with a 10 cm diameter soil auger without separation into soil horizons. Each replicate soil sample results from the homogeneous combination of three sub-samples collected at the same sampling site. Vegetation type varied across sites, in particular across bioregions and typically upland forests included paired hardwood and pine forest type (Table 1; see also Fissore et al., 2008). Soil samples were stored in plastic bags and shipped immediately after sampling (time between sampling and delivery was less than 2-d) in cooler with blue ice to the USDA Forest Service Forestry Laboratory in Houghton, MI, USA, for analysis and incubations.

Soils were air-dried at 30 °C in a forced-air oven until constant weight was reached. We conducted laboratory analyses on soil samples after separating roots and rocks through a 2 mm mesh. We determined soil water holding capacity (WHC) by saturating a known amount of sieved and oven dried (30 °C) soil that was packed into a funnel to a specific bulk density of 1 Mg m^{-3} (Elliott et al., 1994). Dry soil represented 0% of WHC, while saturated soil, after free water was allowed to drain, represented 100% of WHC. The time required to water to drain varied among soils, but was typically between 1 h and 5 h.

We measured soil texture using the hydrometer procedure (Carter, 1993). Soil pH was measured with a Corning 440 pH meter (Corning Inc., NY, USA) by mixing 20 g of soil with 20 ml of H_2O, and 200 μl of 1 M $CaCl_2$ solution. Total C and N estimates for air-dry soils were obtained using dry combustion (LECO TruSpec CHN Analyzer, LECO Corporation, St. Joseph, MI, USA). Exchangeable cations (Al, Ca, K, Mg, Na) were extracted using a 1 M NH_4Cl solution in a 1:10 soil to solution ratio, shaken for 30 min on a reciprocating shaker, filtered through 8 μm ash-less filter paper and analyzed with ICP-OES (Thermo Elemental IRIS Intrepid, Thermo Scientific, Waltham, MA, USA). The sum of charge equivalent of exchangeable ions was used to obtain values for effective cation exchange capacity (Amacher et al., 1990).

2.2. Incubation and SOC efflux

We incubated our soil samples at two temperatures (lab incubation temperature, LIT) of 10 °C and 30 °C (see Fissore et al., 2008 for details). Briefly, the incubation experiment involved placing 120 ml specimen cups, each containing 30 g of dry soil, into 1 l air-tight Mason jars with a rubber septum for gas sampling. Throughout the experiment, soils were maintained at constant moisture of 60% ± 5% of WHC and at constant LIT (10 °C or 30 °C ± 2 °C). Between sampling events, jars were not sealed to avoid anoxia; to minimize water loss each Mason jar contained a 10 ml vial with water.

Estimates of CO_2 efflux were conducted on a 24-h basis, where 24-h before each gas sampling event, the Mason jars were opened under a fume hood to assure exchange with free air, then sealed,

Table 1
Location and soil and site characteristics of the forested mineral soil wetlands and upland forests at three bioregions in North America.

Bioregion	Site	Sample ID	MAT, °C	Dominant forest type	Main tree species	pH	Clay, %	C, %	N, %	CEC, $cmol_c\ kg^{-1}$
Colorado	Wetland	CO1W1	−2	Conifer	*Picea*, *Abies* spp.	6.1	43.8	9.98	0.34	38.6
	Wetland	CO2W1	−2	Conifer	*Picea*, *Abies* spp.	6.4	18.2	1.99	0.07	11.9
	Upland	CO1A1	−2	Hardwood	*P. tremuloides*	6.1	10.0	8.07	0.53	26.4
	Upland	CO2A1	−2	Hardwood	*P. tremuloides*	6.1	7.0	3.48	0.11	10.6
	Upland	CO2P1	−2	Conifer	*P. contorta*	5.6	12.0	2.64	0.10	10.5
	Upland	CO1P1	−2	Conifer	*P. contorta*	5.8	8.3	2.20	0.09	6.8
Minnesota	Wetland	MN1W1	4	Conifer	*P. resinosa*	4.6	29.9	4.31	0.21	8.8
	Wetland	MN1W2	4	Hardwood	*Alnus* spp; *F. nigra*	4.9	19.2	2.82	0.10	4.2
	Wetland	MN3W1	4	Hardwood	*Alnus* spp; *F. nigra*	4.8	24.6	2.40	0.12	5.9
	Wetland	MN3W2	4	Hardwood	*Alnus* spp; *F. nigra*	4.8	24.6	4.05	0.27	8.4
	Upland	MN1A1	4	Hardwood	*P. tremuloides*	5.7	8.5	1.60	0.09	4.8
	Upland	MN1H1	4	Hardwood	*Acer* spp.	5.8	8.0	1.93	0.11	6.9
	Upland	MN1P1	4	Conifer	*P. resinosa*	5.6	4.5	1.45	0.07	4.5
	Upland	MN2P1	4	Conifer	*P. resinosa*	5.3	3.0	1.05	0.05	3.2
South Carolina	Wetland	SC_W1	18	Hardwood	*Quercus* spp.	4.8	22.5	4.05	0.19	10.8
	Wetland	SC_W2	18	Hardwood	*Quercus* spp.	5.0	60.2	3.29	0.15	25.3
	Wetland	SC_W3	18	Hardwood	*Quercus* spp.	4.7	9.1	4.23	0.23	12.6
	Upland	SC_H1	18	Hardwood	*Acer* spp.	4.4	20.0	2.06	0.09	5.8
	Upland	SC_H2	18	Hardwood	*Acer* spp.	4.3	16.0	1.76	0.07	3.5
	Upland	SC_H3	18	Hardwood	*Acer* spp.	4.6	13.0	1.47	0.06	2.8
	Upland	SC_H4	18	Hardwood	*Acer* spp.	4.8	3.0	1.24	0.05	1.9
	Upland	SC_P1	18	Conifer	*P. virginiana*	4.8	4.0	1.74	0.06	2.1
	Upland	SC_P2	18	Conifer	*P. virginiana*	4.9	3.5	0.88	0.03	1.3
	Upland	SC_P3	18	Conifer	*P. virginiana*	4.7	1.0	1.37	0.04	1.4

and head-space gas samples measured as a baseline for subsequent CO_2 measurements (Agilent 6890 Gas Chromatograph, Agilent, Inc., Palo Alto, CA, USA). Jars were brought back to their designated LIT and head-space gas samples were collected after 24-h for CO_2 analysis. At each sampling event we used a 50 ml gas-tight syringe by drawing and plunging the syringe three times for homogeneous gas sampling. Gas samples were stored in 4 ml gas-tight vials and analyzed by gas chromatography for CO_2 within 8 h from sampling. Head-space CO_2 measurements were taken on day 1, 3, 10, 22, 42, 80, 105, 155, 220, 280, 342, 423, and 525. The CO_2 data were converted from a percent basis into $\mu g\ C\ g^{-1}$ soil $C\ d^{-1}$, which we define as SOC decomposition rate, expressed on a 24-h basis. This daily rate was utilized to calculate %SOC loss for the entire incubation period. To quantify total loss of SOC from soils, we also expressed CO_2 efflux as $\mu g\ C\ g^{-1}$ soil d^{-1}.

2.3. Soil organic carbon quality

We utilized measured SOC decomposition rates to evaluate the size of the active SOC fraction and then to estimate the contribution of the less readily decomposable "slow" SOC fraction to C loss during the 525-d incubation, as described in Townsend et al. (1997). Briefly, the rapid decline in SOC decomposition rate that typically takes place when soils are incubated is interpreted as the decomposition of active SOC. This approach assumes that when the decomposition curve reaches an asymptote all active SOC has been decomposed and further decomposition is due to slow SOC, with slow SOC decomposition rate being relatively constant during lab incubation for years.

To quantify the amount of SOC that was decomposed during the 525-d incubation at 30 °C, we fitted a non-linear curve to the SOC decomposition rate data for each soil sample according to $y = y_0 + a^*\exp(-bt)$, which in our case represented the best fit when compared to other possible curves. Percent SOC loss (SOC decomposition rate for the entire incubation period) was obtained as the integral under the fitted curve. The curve fitting calculates the decomposition rate of slow SOC as y_0, which corresponds to the asymptote of the decomposition rate curve and this rate was multiplied by 525 (duration of incubation) to obtain the size of slow SOC. Active SOC (as % of total SOC) was then calculated as follows:

$$\text{Active SOC}\,\% = \frac{\text{Total SOC decomposed} - (\text{slow SOC dec. rate}^*525)}{\text{Total initial SOC}} \cdot 100 \quad (1)$$

To validate our findings based on this approach, we also estimated % slow SOC as the mean of SOC decomposition rates of days 155–525 (corresponding to the asymptote in the CO_2 efflux curves for each sample) and then used this mean value to cross-check the results from curve fitting. For 5 samples the exponential decay curve resulted in a low r^2, and likely underestimated % slow SOC. Therefore we relied on the calculated total SOC decomposition and slow SOC as described above. This decision is reasonable because for the other soils, there was a highly significant correspondence between calculated slow SOC efflux rate and y_0 obtained through curve fitting ($r^2 = 0.95$, $P < 0.01$, $n = 24$).

We used data from both LITs to calculate and compare the temperature sensitivity (Q_{10}) of SOC decomposition rate and %SOC loss in both FMSW and upland sites according to the following:

$$Q_{10} = (R_1/R_2)\exp\left[10/(\text{LIT}_1 - \text{LIT}_2)\right] \quad (2)$$

where R_1 and R_2 indicate CO_2 efflux at LIT of 30 °C (LIT_1) and LIT of 10 °C (LIT_2). For comparison, we also calculated Q_{10} based on the time required for a known amount of CO_2 to evolve (*sensu* Conant et al., 2008).

2.4. Statistical analysis

For each of the three bioregions, we sampled two to four replicate sites for both FMSW and upland sites, for a total of 9

FMSW and 15 upland forests. We considered each site to represent a true replicate because of dispersed geographical locations, vegetation characteristics and soil type. We consider our wetland and upland sites as pairs because they were sampled within 1 km of each other.

We used 2-way ANOVA to describe the distribution of pH, clay content, total SOC content across bioregion and forest types (i.e., wetland versus upland forests) and *t* tests to assess difference within each bioregion between upland and wetland pH, clay content, SOC content, and SOC loss (SAS JMP 4.0.2, SAS Institute). We used linear regression to investigate the relationship between bioregion MAT and pH, clay content, CEC and to investigate the effect of clay content and CEC on SOC content and that of clay content on CEC and the effects of CEC on SOC loss. We used non-linear regression, specifically a three-parameter exponential decay curve to fit the CO_2 efflux rate in upland and wetland soils (SigmaPlot 8.0, SPSS Inc., Chicago, IL, USA). In all cases significance was assessed by $\alpha = 0.05$.

3. Results

3.1. Soil chemical–physical characteristics

Across FMSW, soil texture varied from sandy-loam to clay, with clay content varying between 9% and 60%, but there was no pattern between clay content and bioregion MAT ($P = 0.85$), and variation in clay content was as high within regions as across regions. Soil pH ranged between 4.6 and 6.4 across FMSW sites (Table 1), with the highest pH values for sub-alpine sites. Across upland forest soils, soil texture varied from sand to loamy sand, soil clay content was variable across sites ranging from 1% to 20%, and soil pH varied between 4.3 and 6.1 (Table 1). Regression analysis indicated that bioregion MAT had an inverse relationship with pH ($r^2 = 0.88$, $P < 0.01$, $n = 15$).

Across FMSW and upland sites, there was no significant effect of bioregion on total SOC content ($P = 0.60$) despite a trend for more SOC in the sub-alpine bioregion (Fig. 1). Total SOC was higher in FMSW than in upland forests: $4.1\% \pm 0.8$ (mean ± s.e.) and $2.2\% \pm 0.5$, respectively. One of the sub-alpine upland sites had three times more C than the mean across bioregions. Reanalysis of soil samples indicates that there was not an error in analyzing soils (see also Fissore et al., 2008). Soils are typically heterogeneous, therefore we did not exclude this sample from our analyses. Overall, FMSW had higher clay content (Table 1) and significantly higher %SOC than upland forests in the north and south-temperate sites analyzed here (Fig. 1). Across and within bioregions, however, there was no significant effect of clay content on SOC content (Fig. 2a). For FMSW, cation exchange capacity (CEC) varied across sites (Table 1), but CEC did not show a significant pattern across bioregions ($P = 0.88$), although it was positively related to %SOC (Fig. 2b). In contrast, for upland soils, CEC declined from sub-alpine to south-temperate ecoregions ($P < 0.01$). Similar to FMSW, in upland forest we did find that across all sites %SOC and CEC were positively related (Fig. 2b), and CEC increased with increasing clay content ($r^2 = 0.49$, $P = 0.04$, $n = 15$).

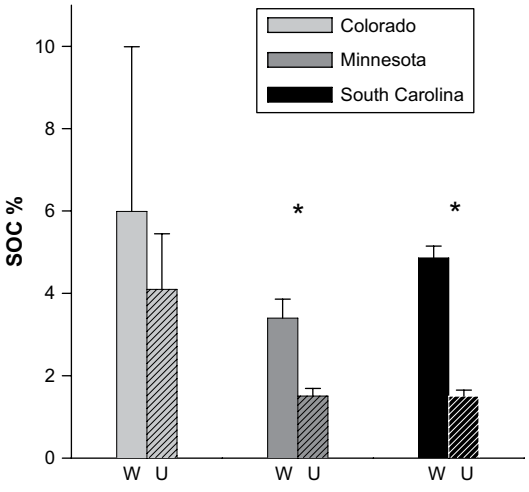

Fig. 1. (a) Initial soil organic carbon (SOC) content in wetland and upland soils by bioregions. *W* = forested mineral soil wetland, *U* = upland forests. Values are mean + s.e., $n = 2$ (Colorado-W), $n = 4$ (Minnesota-W), $n = 3$ (South Carolina-W), $n = 4$ (Colorado-U), $n = 4$ (Minnesota-U), $n = 7$ (South Carolina-U). Asterisks represent significant difference between forested mineral soil wetland and upland forests within a specific bioregion.

3.2. SOC quality across forest types and bioregions

On day 1 of the incubation, SOC decomposition rate for FMSW was 1.6 mg C g^{-1} soil C d^{-1} at high LIT and 0.3 mg C g^{-1} soil C d^{-1} at low LIT. During the initial stage of the incubation, we observed rapid decline in SOC decomposition rate at high LIT, while the decline at LIT 10 °C was more muted. At high LIT, decomposition rate stabilized in late stages of the incubation from average values of 1.0 mg C g^{-1} soil C d^{-1} for the first 22 days to 0.2 mg C g^{-1} soil C d^{-1} from day 22 to day 525 (Fig. 3, Table 2). A slightly higher decomposition rate was observed for upland forest sites, where at day 1 decomposition rate was 1.7 mg C g^{-1} soil C d^{-1} at high LIT. Subsequently, SOC decomposition rates averaged 1.2 mg C g^{-1} soil C d^{-1} during the first 22 days and 0.3 mg C g^{-1} soil C d^{-1} from day 22 to day 525 of the incubation (Fig. 3, Table 2).

By the end of the 525-d incubation we observed a significant effect of LIT on %SOC loss in both wetlands (11.8 ± 1.0, mean ± s.e., $n = 9$ for LIT 30 °C; 4.9 ± 0.4, $n = 9$ for LIT 10 °C) and in upland soils (19.0 ± 2.0, $n = 15$ for LIT 30 °C; 7.4 ± 0.7, $n = 15$ for LIT 10 °C). A two-way ANOVA showed higher %SOC loss from upland soils than FMSW at LIT 30 °C ($P = 0.01$). Within bioregions %SOC loss was significantly different between FMSW and upland forests only at north-temperate sites (Fig. 4a) and total SOC loss (g C per g of soil basis) was positively related to CEC in both FMSW ($r^2 = 0.73$, $P = 0.01$, $n = 9$) and upland forests ($r^2 = 0.49$, $P = 0.01$, $n = 15$), and showed a trend of being higher in FMSW than upland forests (Fig. 4b).

Percent active SOC in FMSW, calculated by curve fitting, was significantly greater in sub-alpine bioregions, while no significant differences were found between north and south-temperate

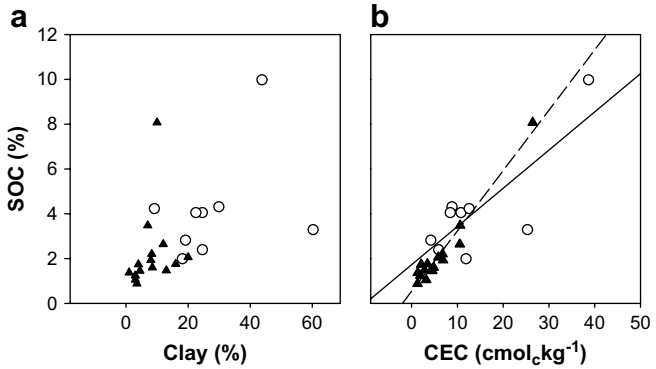

Fig. 2. Linear regression showing the relationship between clay (a) and CEC (b) with initial SOC content. Black symbols represent forested mineral soil wetland sites, white symbols represent upland forests. Wetlands SOC % = 0.07 (Clay %) + 1.59; $r^2 = 0.05$, $P = 0.42$. Upland SOC % = 0.06 (Clay %) + 2.59; $r^2 = 0.13$, $P = 0.35$. Wetland SOC % = 0.18 (CEC) + 1.73, $r^2 = 0.64$, $P = 0.01$. Upland SOC % = 0.27 (CEC) + 0.54, $r^2 = 0.95$, $P < 0.01$.

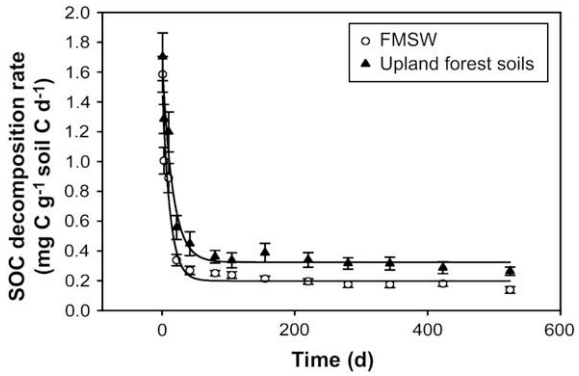

Fig. 3. Soil CO_2 efflux rate in forested mineral soil wetland (FMSW) and upland forest soils during the 525-d incubation at 30 °C. White circles represent FMSW, black triangles represent upland forest soils. Values are averages across samples for the day of sampling ± s.e. ($n = 9$ for FMSW, $n = 15$ for upland forest sites).

bioregions (Fig. 5, Table 3). In upland forest soils, % active SOC was not significantly different across bioregions (Fig. 5). The lack of pattern could have resulted from a single very high value for south-temperate sites (SC-P2 SOC% = 7.9%; Table 3). If this value is excluded, MAT explained 73% of the variation in % active SOC. Because no analysis error explained the high value, however, this value was retained in our analysis. There was an effect of forest type on % active SOC, with active SOC making up a larger fraction of total SOC in upland forests (Fig. 5, Table 3).

During the initial stage of the incubation, Q_{10} varied for wetland soils between 1.8 and 2.5 (average $Q_{10} = 2.1$), while from day 22 and through the remainder of the 525-d incubation Q_{10} stabilized between 1.3 and 1.6 (average $Q_{10} = 1.5$). In upland forests, Q_{10} ranged between 2.3 and 1.5 from day 1 to day 22 of the incubation (average $Q_{10} = 1.8$) and subsequently stabilized at values also between 1.3 and 1.6 (average $Q_{10} = 1.5$). Over the entire incubation, values for Q_{10} were lower in wetland than upland soils (Fig. 6). When Q_{10} was expressed in terms of the time required for a fixed amount of SOC to decompose (Conant et al., 2008), we observed Q_{10} values of 2.6 and 2.2 corresponding to the initial loss of 1% of SOC in FMSW and upland forest, respectively. At later stages of the incubation, the loss of 1% of SOC, between 3% and 4% in FMSW, showed a Q_{10} of 2.0, while at similar late stage upland soils had a Q_{10} of 1.8, corresponding to a SOC loss between 6% and 7%.

4. Discussion

In this study, we tested the following three hypotheses: (i) the proportion of active versus more resistant SOC compounds is higher in FMSW than in upland forests; (ii) SOC quality in FMSW declines with MAT; and (iii) the temperature sensitivity of SOC decomposition rate in FMSW is higher than in upland systems. Our results did not support our first or third hypotheses, but did support our second hypothesis that SOC quality in FMSW is higher in sub-alpine than in north and south-temperate bioregions.

4.1. Comparison between wetland and upland forest soils

The biogeochemical processes governing SOC accumulation in FMSW differ from those of upland forest soils due to differences in soil chemical and physical properties and hydrologic conditions characterizing wetland sites (Cui et al., 2005). Our comparison of FMSW and adjacent upland forest sites from three bioregions indicates that substantially more SOC accumulates in surface soils of wetland ecosystems than those in upland forests – in line with many previous studies of wetland ecosystems (e.g. Davidson and Janssens, 2006).

Although clay content did not significantly affect %SOC within wetland sites, fine textured soils have higher capacity to chemically and physically protect SOC from decomposition (Oades, 1988) than coarse textured soils such as those of our upland sites, which average a clay content of 8.1%. Hence, the difference in %SOC between FMSW and upland surface soils may relate to the finer texture of FMSW soils, as clay content is often positively correlated with %SOC (Jastrow et al., 2007). Clay increases soil surface area and associated increased in CEC can increase the density of SOC binding sites (Sørensen, 1972). Further, increased clay can enhance protection of SOC through the formation of aggregates (Jastrow et al., 2007). In fact, we identified a strong relationship between %SOC and CEC, which in turn was positively related to clay content.

Other factors may have contributed to SOC stabilization in FMSW sites such as litter chemistry and soil chemical characteristics (e.g. redox potential). For example, the tissue chemistry of vegetation often found in wetlands is characterized by low nutrient concentration and high concentrations of C compounds resistant to decomposition (Heal et al., 1981; Hobbie, 1996; Hobbie et al., 2000). Limited phenol oxidase activity under anaerobic conditions may further hinder the degradation of resistant C compounds in wetlands regardless of the temperature regime (Freeman, 2001a,b). Therefore, warm and wet sites should accumulate more resistant SOC than cold and dry sites (McTiernan et al., 2003). Our finding of lower active SOC content and lower SOC loss in FMSW than in upland forest soils supports the conclusion that a greater fraction of SOC in FMSW is resistant to decomposition – even under aerobic conditions. If the decomposition of active SOC is more sensitive to temperature than decomposition of resistant SOC (Giardina and Ryan, 2000), then SOC decomposition rates in FMSW may show lower responses to warming than those in upland forests. Critically, the magnitude of total SOC loss from FMSW, that is g C per g of soil, was higher than in upland forests and this difference could still drive substantial SOC losses from FMSW in a warmer world. While FMSW sites may generally accumulate more clay than adjacent upland sites, the confounding role of higher clay content in the FMSW complicates this interpretation.

4.2. SOC content and quality in forested mineral soil wetlands

For FMSW soils, we did not observe a clear pattern between %SOC and MAT across the three bioregions. Despite a trend of higher %SOC in sub-alpine sites, variability across sites was high. Clay content can directly affect C stabilization in soil (Parton et al., 1987; Giardina et al., 2001), but we also did not observe a clear relationship between %SOC and clay content across sites. Previous studies have shown that intrinsic characteristics of soil clay minerals (surface charge, surface area) are more highly correlated with SOC than clay content (Torn et al., 1997; Rasmussen et al., 2006). Across our sites, patterns in %SOC may have contributed to patterns in soil CEC, in part explaining the strong relationship between %SOC and soil CEC observed for FMSW sites. However, this relationship can also indicate stabilization of SOC by the mineral assemblage, as previously observed for some of these upland soils (Fissore et al., 2008).

Both resistant and active SOC can be stabilized by the mineral phase (Jastrow et al., 2007); however active SOC is more readily available and decomposes rapidly in presence of conditions favorable for microorganisms, as those provided under controlled

Table 2
Exponential decay function parameters and statistics for the CO_2 efflux rates in FMSW and upland soils during the 525-d incubations.

	y_0	a	b	r^2	P
FMSW	0.199	1.356	0.088	0.96	<0.001
Upland soils	0.324	1.372	0.064	0.97	<0.001

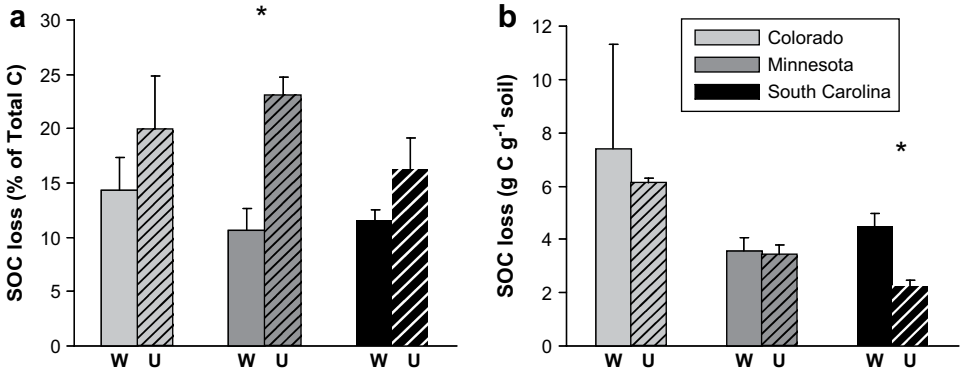

Fig. 4. Soil organic carbon loss during 525-d incubation at 30 °C across bioregions and forest types, (a) % SOC loss, (b) SOC loss on a per g soil basis. W = forested mineral soil wetland, U = upland forests. Values are mean + s.e., $n = 2$ (Colorado-W), $n = 4$ (Minnesota-W), $n = 3$ (South Carolina-W), $n = 4$ (Colorado-U), $n = 4$ (Minnesota-U), $n = 7$ (South Carolina-U). Asterisks represent significant difference between forested mineral soil wetland and upland forests within a specific bioregion.

incubations. Indication of the size of the active SOC fraction can be obtained from incubation studies by curve fitting SOC decomposition rate data to discriminate between different SOC fractions, with higher SOC loss indicating decomposition of higher quality SOC. The inverse situation, that is the accumulation of high quality SOC at cold FMSW sites, may relate to slower decomposer activity at these sites such that both resistant and labile compounds are retained in soil. A similar but stronger pattern emerged for total SOC loss (g C per g of soil), which relates to the high SOC accumulation in FMSW, especially in sub-alpine ecosystems. Constant incubation conditions and absence of new detrital inputs impact soil microbial activity (Hart et al., 1994). While this approach is valuable to describe and compare SOC quality across sites (Townsend et al., 1997; Conant et al., 2008; Steinweg et al., 2008), rates of SOC decomposition in the lab will differ from *in situ* rates.

Higher %SOC loss from FMSW in sub-alpine than in north or south-temperate bioregions despite higher (albeit not significant) SOC content in these soils points to the possibility that a change to aerobic conditions may shift soil carbon balance to one where loss is favored over stabilization processes. Under anaerobic conditions, higher SOC content in the cool climate soils may relate in part to the more acidic soil conditions at the warmer sites, which can constrain the accumulation of SOC due to low concentrations of divalent bonding sites (Oades, 1988; Webster et al., 2000). In fact, we did observe a significant positive relationship between SOC content and extractable Ca and Mg concentrations across FMSW sites (SOC% = 0.0008 Ca (ppm) + 2.36, $r^2 = 0.59$, $P = 0.02$; SOC% = 0.0257 Mg (ppm) + 0.63, $r^2 = 0.50$, $P = 0.03$). Further, while circum-neutral pH is optimal for microbial activity (Webster et al., 2000), this favorable condition may be suppressed because of anaerobic conditions. Similarly, while the low soil pH of the temperate sites may not negatively affect decomposers under anaerobic conditions, this effect could be expressed under aerobic

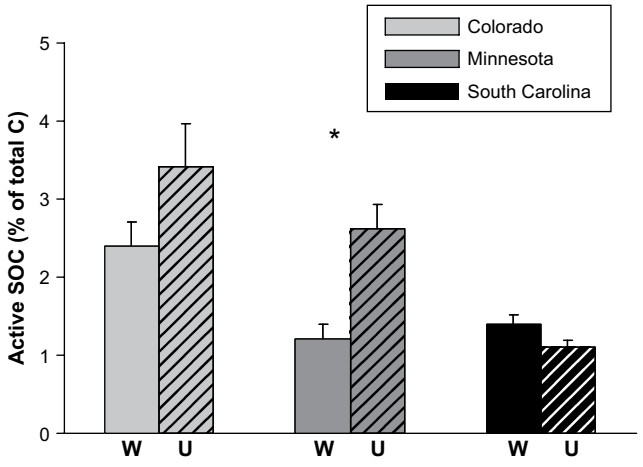

Fig. 5. Distribution of active SOC (as % of total SOC) across forest types and bioregions. Active SOC % was calculated after fitting a three-parameter exponential decay curve to the CO_2 efflux data from incubated soils at 30 °C and by then solving for Eq. (1) in the text. W = forested mineral soil wetland, U = upland forests. Values are mean + s.e., $n = 2$ (Colorado-W), $n = 4$ (Minnesota-W), $n = 3$ (South Carolina-W), $n = 4$ (Colorado-U), $n = 4$ (Minnesota-U), $n = 7$ (South Carolina-U). Asterisks represent significant difference between forested mineral soil wetland and upland forests within a specific bioregion.

Table 3
Total initial SOC, total SOC that has decomposed during the 525-d incubations at 30 °C, and calculated % of total SOC that is active across FMSW and upland forest soils. Total SOC decomposed and slow SOC were obtained by fitting CO_2 efflux values with a three-parameter exponential decay curve. Active SOC % was calculated according to equation (1).

Sample	Total initial SOC	Total SOC decomposed	Slow SOC	Active SOC
Wetlands	μg C g^{-1} soil	μg C g^{-1} soil	μg C g^{-1} soil	%
CO1W1	99,800	11,796	9718	2.08
CO2W1	19,900	3314	2777	2.70
MN1W1	43,100	4720	4220	1.16
MN1W2	28,200	3968	3473	1.75
MN3W1	24,000	2281	2026	1.06
MN3W2	40,500	3283	2949	0.82
SC_W1	40,500	5867	5387	1.19
SC_W2	32,900	3146	3152	1.54[a]
SC_W3	42,300	4537	3908	1.49
Mean	41,244	4768	4307	1.53
s.e.	7842	946	804	0.19
CO1P1	22,000	6624	5613	4.59
CO1A1	80,700	6233	4504	2.14
CO2A1	34,800	6336	5323	2.91
CO2P1	26,400	6752	5697	3.99
MN1P1	14,500	2209	1758	3.11
MN1A1	16,000	4011	3604	2.55
MN1H1	19,300	3182	2844	1.75
MN2P1	10,500	3656	3334	3.07
SC_H1	20,600	2076	1801	1.34
SC_H2	17,600	2090	1951	0.79
SC_H3	14,700	3268	3096	1.16
SC_H4	12,400	1885	1888	0.92[a]
SC_P1	17,400	1331	1334	1.29[a]
SC_P2	8800	2690	2695	7.89[a]
SC_P3	13,700	1615	1618	1.14[a]
Mean	21,960	3597	3137	2.58
s.e.	4521	504	391	0.48

[a] Active SOC calculated from lab incubation data and the slow SOC decomposition rate and fraction size as the mean between SOC decomposition rates of days 155–525 (corresponding to the asymptote in the C decomposition curves for each sample) as described in the text.

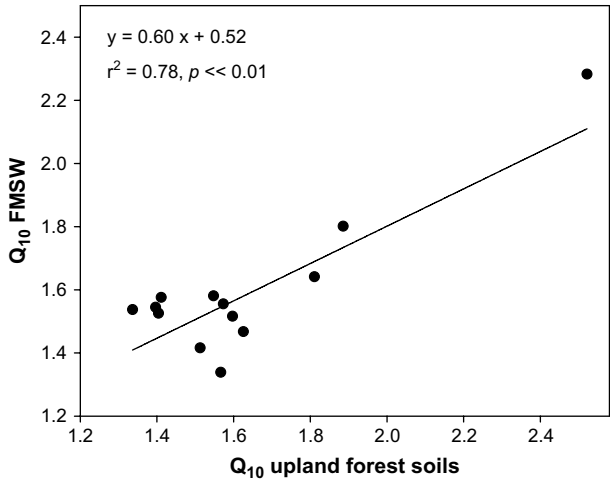

Fig. 6. Correlation between Q_{10} in forested mineral soil wetlands (FMSW) and Q_{10} in upland soils (both pine and hardwood) located at similar bioregions in North America. Each point refers to the Q_{10} at a specific time during the 525-d incubation and was calculated as in equation (2). Line represents 1:1 relationship between FMSW and upland forests Q_{10}.

conditions (Hobbie et al., 2002). Because wetland SOC balance depends on both stabilization and loss, and soil pH and CEC have different effects on these processes, it remains largely unknown how SOC balance will be affected by climate change related changes in wetland hydrological regimes.

While SOC decomposition rates showed that FMSW in the sub-alpine bioregion accumulated more high quality SOC, possibly because of inhibited decomposition and higher accumulation of detrital C, SOC quality was similar for north and south-temperate bioregions, despite large climatic differences. It is possible that differences between these two regions did not emerge because decomposition is not limited significantly by temperature. In contrast, for the sub-alpine sites, water saturated (oxygen-limited) soils or soils frozen for extended periods (temperature limited) may result in the accumulation of litter because of inhibited phenol oxidase activity, with potential for high SOC decomposition rates if periods of saturation are reduced or temperature constraints exceed threshold values (Nadelhoffer et al., 1991; Freeman et al., 2001a,b). Our findings indicate that the active fraction of SOC can be depleted rapidly if temperature and hydrologic conditions change in FMSW.

The rapid loss of active SOC, especially for the coldest sites, is in line with previous efforts that have suggested high temperature responses for SOC decomposition for wetlands worldwide. Giardina and Ryan (2000) emphasized high temperature sensitivity while Davidson and Janssens (2006) emphasized large stocks in soils with a hydrology that could change rapidly with warming. Our limited lab-based test of this hypothesis indicates that at least in the case of our FMSW sites, SOC losses from FMSW when oxygen is not limiting may be equally sensitive to rising temperatures as upland systems, though because of larger C densities, the total loss of SOC per unit area may exceed that from upland systems. Because few studies have examined these questions for FMSW, more research is clearly needed.

Two-pool decomposition models based solely on curve fitting of incubation data have been criticized because they may overestimate the size SOC fractions (Paul et al., 2001). For our samples, this approach provided values of active SOC that were similar to those of a three-pool constrained model, against which a subsample of soils was tested. We found rapid decline in SOC efflux at the initial stage of the incubation, similarly to previous incubation studies across a broad range of ecosystems (Winkler et al., 1996; Collins et al., 2000) and this is indicative of fast microbial utilization of easily decomposable (high quality) SOC compounds (Townsend et al., 1997; Paul et al., 2006).

4.3. Temperature sensitivity of SOC decomposition rates

Our third hypothesis postulated that the decomposition of SOC in FMSW under aerobic conditions would be more sensitive to changes in temperature than for SOC for upland forest soils. We based this hypothesis on the expectation that FMSW would contain a higher proportion of active SOC compared with upland forest soils. However, this expectation was not supported by our findings. High clay content for FMSW soils may explain why the temperature response of SOC decomposition was similar for FMSW and upland forest soils. Elevated values of Q_{10} have been hypothesized for modeling the temperature responses of anaerobic or frozen soils due to the large accumulation of labile SOC (Clein and Schimel, 1995). However, these values are typically restricted to Histosols or, more generally, to soils with high C accumulation in organic horizons (Goulden et al., 1998). The differences in results between those we observed for FMSW and those previously observed for organic wetlands could relate to longer aerobic periods for FMSW, which may prevent the formation of a thick organic horizon. The accumulation of slow SOC in our wetlands also could explain the limited responses to temperature observed in this study – reduced availability of SOC may relate to associations with the mineral soil matrix.

Similar temperature responses between FMSW and upland forest soils were obtained during the early stage of the incubation when Q_{10} was calculated based on the time required to the initial 1% of SOC to decompose. While FMSW showed weakly higher temperature responses than upland sites, this difference was not significant. At late stages of the incubation, this calculation approach resulted in higher Q_{10} values, with Q_{10} in FMSW being higher than those for upland soils. However, this observed difference could relate to the fact that Q_{10} is based on losses of SOC between a 3% SOC loss to 4% SOC loss (as a % of initial SOC) in FMSW versus losses of 6% to 7% in upland sites. When both soil types are compared for a common range of %SOC loss (3%–4%), differences were largely eliminated. It is also possible that higher clay content in FMSW soils conferred higher physically protection to SOC, and reduced its sensitivity to temperature later in the incubation.

Despite lower than anticipated temperature responses for SOC decomposition in FMSW, warming and associated reductions in anaerobic periods may result in larger losses of SOC in FMSW than in upland forests soils because decomposition rates are similar between the two forest types while %SOC is larger in FMSW. Critically, the net effect of warming on the C balance of FMSW will also depend on how warming affects forest productivity and the quality and quantity of belowground detrital inputs to soil (Giardina et al., 2005). More research is needed to investigate multiple factors that may affect SOC cycling in these ecosystems. Overall, as suggested by others (Trettin et al., 2001; Giardina et al., 2005; Cui et al., 2005), hydrology plays a critical role in belowground carbon allocation, the fate of belowground detrital inputs, and SOC decomposition in these ecosystems, and these remain poorly understood in FMSW ecosystems.

5. Conclusions

Whether wetlands become a large net source of C to the atmosphere in a warmer world depends on the quality of SOC currently stored in these ecosystems, the temperature sensitivity of that SOC to decomposition, the quality and quantity of forest detrital inputs returned to soils, and that stabilization of that

detritus as new SOC. Although FMSW represent highly productive ecosystems that are widely distributed across North America, there is very limited information on how these systems will be altered by climate change. Our findings show that FMSW in subalpine bioregions accumulate more active SOC than in warmer regions, indicating that with warming, this larger fraction of active SOC may be lost from colder sites. Across bioregions, FMSW accumulate significantly more SOC than upland forest soils from similar locations, indicating that with drying, these systems could lose large quantities of C. Critically, soils in our FMSW sites were dominated by resistant SOC, and were of finer texture than upland sites, and so *in situ* responses to warming and drying are highly uncertain. Retention of SOC could be related to the intrinsic resistance of the C substrate that typically accumulates in wetlands, but also to the physical and chemical protection exerted by clay minerals at wetland sites. Despite lower SOC quality, large losses of SOC are expected from FMSW if exposed to warm and dry conditions because of the large size of the SOC pool in these ecosystems. Lack of comparable data from previous studies prevents us from making generalizations beyond our own study, and so more experiments examining SOC process rates in FMSW are clearly needed to elucidate the role of FMSW in terrestrial C cycling.

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