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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.

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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

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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 km² (Anselman and Crutzen, 1989) to 8,800,000 km² (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, northtemperate forests in Minnesota, and in south-temperate forests in South Carolina, with MAT spanning from $-2 \circ C$ to $18 \circ C$ (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 CaCl₂ 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 NH₄Cl 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 airtight Mason jars with a rubber septum for gas sampling. Throughout the experiment, soils were maintained at constant moisture of $60\% \pm 5\%$ of WHC and at constant LIT (10 °C or $30 °C \pm 2 °C$). 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,

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