



Effects of flooding and warming on soil organic matter mineralization in *Avicennia germinans* mangrove forests and *Juncus roemerianus* salt marshes



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ABSTRACT

Under a changing climate, coastal wetlands experience sea level rise, warming, and vegetation change, all of which may influence organic matter mineralization. In coastal wetlands of subtropical west-central Florida (USA), we investigated how soil carbon (C) and nitrogen (N) mineralization respond to soil water, temperature, and ecosystem type (*Avicennia germinans* mangrove forest vs. *Juncus roemerianus* salt marsh). We evaluated how soil respiration and mineral N concentration varied along a soil moisture gradient, and whether these relationships differed between ecosystem types. Then, we manipulated soils in a 28-d laboratory incubation to evaluate how potentially mineralizable C and N respond to temperature (23 vs. 27 °C), soil hydroperiod (inundated 4 vs. 20 h/d), and soil source. Soil saturation and inundation suppressed short-term (minutes to weeks) C mineralization from near-surface soils. Soil CO₂ efflux declined by 65% as soil moisture increased from 75% to 85%, and potentially mineralizable C was 18% lower with a 20-h hydroperiod than with a 4-h hydroperiod. Organic C quality appears to be greater in *A. germinans* than in *J. roemerianus* soils, as *A. germinans* soils had higher field CO₂ efflux rates and greater mineralizable C:N (despite lower total C:N). Increasing incubation temperature from 23 to 27 °C elevated potentially mineralizable C by 40%, indicating that two symptoms of climate change (increased inundation from sea level rise, and warming) may have opposing effects on soil C mineralization. Temperature sensitivity of C mineralization was high for long-hydroperiod soils, however, suggesting that protection of soil organic matter (SOM) due to prolonged inundation will be undermined by warming. Potentially mineralizable N was greater in *J. roemerianus* soils, although *in situ* mineral N was not different between ecosystems, instead correlating positively with SOM. These results indicate that models forecasting soil elevation responses to climate change might include inundation effects on mineralization rates.

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1. Introduction

Organic matter is highly concentrated in the soils and sediments of coastal wetlands (Chmura et al., 2003; Duarte et al., 2005; Donato et al., 2011; Breithaupt et al., 2012). The mineralization of this abundant material can release large masses of carbon dioxide (CO₂) and nutrients to the atmosphere and adjacent waters (Boto and Wellington, 1988; Twilley et al., 1992; Childers et al., 2002; Bouillon et al., 2008). Organic matter mineralization also results in soil mass loss, thereby lowering wetland elevation and imperiling the resilience of these ecosystems to sea level rise (DeLaune and Pezeshki, 2003; Kirwan and Mudd, 2012; Morris et al., 2012).

However, organic matter mineralization is fundamental to the structure and function of coastal wetlands. Mineralization supplies a large amount of energy to productive detrital food webs (Teal, 1962; Robertson et al., 1992). Mineralization can likewise provide much of the nitrogen (N) needed to maintain high primary production in mangrove forests (Nedwell et al., 1994; Alongi et al., 2002) and salt marshes (Anderson et al., 1997), both of which are limited by available N (Valiela et al., 1982; Feller et al., 2003; DeLaune et al., 2005; Simpson et al., 2013).

Because organic matter mineralization regulates coastal ecosystem material fluxes, resilience, and productivity, it is important to identify sources of variation in this process. These sources of variation include soil inundation and water content, temperature, and plant community, which are themselves sensitive to climate change. Climate change possibly increases soil inundation and moisture content owing to sea level rise, causes warming,

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and results in vegetation shifts associated with woody plant (mangrove) encroachment into latitudes where herbaceous salt marshes have historically predominated. We therefore investigated how soil carbon (C) and N mineralization in subtropical mangrove forest and salt marsh ecosystems respond to variation in soil inundation and moisture content, temperature, and plant community.

Current evidence is inconsistent regarding how variation in soil inundation and moisture content affect mineralization rates. Coastal wetland soils often exhibit negative reduction-oxidation potentials (de la Cruz et al., 1989; Alongi et al., 1999; Matthijs et al., 1999), particularly during prolonged inundation (Nyman and DeLaune, 1991; Ferreira et al., 2007). Sulfate and iron reduction are thus common anaerobic respiratory pathways (Howarth and Teal, 1979; Nedwell et al., 1994; Kristensen et al., 2000; Alongi et al., 2001; Kristensen et al., 2011; Livesley and Andrusiak, 2012). These pathways have lower energy yields than does oxic respiration, which narrows the fraction of soil organic matter (SOM) that is energetically favorable to mineralize (Canfield, 1993). Based on these principles, it is expected that increased inundation will exacerbate anoxia, further suppressing mineralization rates. Indeed, mineralization is suppressed by experimentally raising the water table, inundating soil, and lowering soil redox potential (DeLaune et al., 1981; Nyman and DeLaune, 1991; Alongi et al., 2001; Miller et al., 2001; Gribsholt and Kristensen, 2003). However, decreased organic matter mineralization with increased inundation is not universally observed (Alongi et al., 2012). In temperate salt marshes, experimental increases in tidal inundation either had no effect or slightly increased decomposition in litter bags (Kirwan et al., 2013). This finding corroborates comparative studies, in which decomposition in litter bags at low intertidal positions was either similar to or even greater than decomposition at less-inundated higher positions within temperate salt marshes (Kruczynski et al., 1978; Valiela et al., 1982; Hackney, 1987; Christian et al., 1990; Blum, 1993; Blum and Christian, 2004).

Elevated temperatures increase mineralization rates by helping cellular respiration achieve required activation energies. The possibility that warming-induced increases in organic matter mineralization and soil CO₂ efflux will feed back positively on global temperatures has stimulated interest in understanding mineralization–temperature relationships (Fierer et al., 2006). In many coastal wetlands, organic matter mineralization rates are greater at warmer temperatures (Alongi et al., 2000), and exhibit a striking seasonal pattern with higher rates during summer (Howarth and Teal, 1979; Morris and Whiting, 1986; Middelburg et al., 1996; Miller et al., 2001; Alongi et al., 2005; Kirwan and Blum, 2011). The effect of temperature on mineralization in wetlands, however, can be masked by or confounded with other factors such as moisture and plant species composition (Davidson et al., 1998; Theodose and Martin, 2003). For instance, coastal wetland studies have found variable or no responses of mineralization to seasonality (Alongi et al., 1999; Pongparn et al., 2009), experimental warming (Charles and Dukes, 2009), and spatial variation in temperature (Lovelock, 2008).

Another constraint on SOM mineralization is vegetation assemblage. Plant-mediated factors such as litter chemistry, microclimate, and edaphic properties regulate the accessibility and net energetic value of organic matter. Coastal vegetation assemblages are reorganizing with rising sea levels, climate warming, and human-aided plant dispersal, lending urgency to understanding plant species effects on SOM dynamics. One important redistribution is the encroachment of tropical and subtropical woody vegetation (mangrove forests) into more temperate latitudes dominated by herbaceous salt marsh plants (Guo et al., 2013; Saintilan et al.,

2014). Side-by-side comparisons of mangrove and salt marsh biogeochemistry have become more common recently (Comeaux et al., 2012; Krauss et al., 2012; Bianchi et al., 2013), atop some early pioneering work (Patterson and Mendelssohn, 1991). All comparisons have been between mangrove forests dominated by black mangrove (*Avicennia germinans*) and salt marshes with monocultures of the grass *Spartina alterniflora*. Some studies indicate that mangrove and salt marsh biogeochemistries differ, suggesting that *A. germinans* replacement of *S. alterniflora* might alter ecosystem C and N dynamics. One study, for instance, found higher concentrations of soil organic matter, C, N, and moisture, as well as lower soil bulk density and sand content, in well-established black mangrove forests than in *S. alterniflora* marshes and mixed marsh-mangrove wetlands (Osland et al., 2012). Conversely, other studies have found no differences between *A. germinans* forests and *S. alterniflora* marshes in organic matter production, decomposition, C burial, soil bulk density, N content, or dissolved and gaseous N fluxes (Perry and Mendelssohn, 2009; Henry, 2012; Henry and Twilley, 2013). Thus, the first-order effects of plant species on organic matter dynamics, as with the effects of soil water and temperature, are inconsistent probably because multiple controls interact differently at different sites.

Avicennia germinans is abundant at the northern, subtropical extent of mangrove distribution in the Americas, and is sympatric with salt marshes along many subtropical coastlines. Consequently, a focus on the salt marsh ecotone with this particular mangrove species provides an opportunity to envision the biogeochemical consequences of climate-induced plant redistribution. Yet we are aware of no studies that compare mangrove biogeochemistry with that of rush marshes dominated by species such as *Juncus roemerianus* (a frequent sympatric neighbor of *A. germinans*), or that investigate how such differences might be mediated by other global change factors such as temperature and inundation.

We tested the hypothesis that organic matter mineralization in coastal wetlands is affected by interactions among soil water (moisture and inundation), temperature, and vegetation assemblage. First, using a comparative field survey, we evaluated how *in situ* soil respiration and mineral N concentration varied along a soil moisture gradient, and whether these relationships differed between *Avicennia germinans* mangrove forest and *Juncus roemerianus* salt marsh habitats. Second, we used a factorial laboratory experiment to evaluate whether C and N mineralization potentials (28-d lab incubations) respond to soil hydroperiod, temperature, and SOM source (mangrove forest vs. salt marsh).

2. Material and methods

2.1. Site description

The study area was the Salt Springs Run tidal estuary (28.2903° N, 82.7278° W) in peninsular west-central Florida, USA. The climate is subtropical with mean daily temperatures ranging from 18 °C in January to 28 °C in July, and annual precipitation of 1176 mm falling primarily between June and September. This region lies within the latitudinal transition between mangrove forests and salt marshes. Tides are semi-diurnal, with amplitudes between mean high and low water ranging from 0 m neap tides to 1.3 m spring tides (median 0.48 m) (U.S. NOAA National Ocean Service data). Sea level rise is 2.4 ± 0.8 mm per year (1973–2006 data, NOAA NOS, based on monthly mean sea level data collected at station 8726724, Clearwater Beach, Florida). Water over the soil surface at high tide has a salinity of 34–35. Mangrove forests in this estuary are dominated by *Avicennia germinans*, sometimes fringed on the seaward side by red mangrove (*Rhizophora mangle*). Salt marshes are landward of the mangrove forests, and are a monoculture of black needlerush

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