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The effect of increasing salinity and forest mortality on soil nitrogen and phosphorus mineralization in tidal freshwater forested wetlands

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Abstract Tidal freshwater wetlands are sensitive to sea level rise and increased salinity, although little information is known about the impact of salinification on nutrient biogeochemistry in tidal freshwater forested wetlands. We quantified soil nitrogen (N) and phosphorus (P) mineralization using seasonal in situ incubations of modified resin cores along spatial gradients of chronic salinification (from continuously freshwater tidal forest to salt impacted tidal forest to oligohaline marsh) and in hummocks and hollows of the continuously freshwater tidal forest along the blackwater Waccamaw River and alluvial Savannah River. Salinification increased rates of net N and P mineralization fluxes and turnover in tidal freshwater forested wetland soils, most likely through tree stress and senescence (for N) and conversion to oligohaline

marsh (for P). Stimulation of N and P mineralization by chronic salinification was apparently unrelated to inputs of sulfate (for N and P) or direct effects of increased soil conductivity (for N). In addition, the tidal wetland soils of the alluvial river mineralized more P relative to N than the blackwater river. Finally, hummocks had much greater nitrification fluxes than hollows at the continuously freshwater tidal forested wetland sites. These findings add to knowledge of the responses of tidal freshwater ecosystems to sea level rise and salinification that is necessary to predict the consequences of state changes in coastal ecosystem structure and function due to global change, including potential impacts on estuarine eutrophication.

Keywords Tidal freshwater wetland · Tidal forest · Mineralization · Nitrogen · Phosphorus · Salinification · Sea level rise

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Introduction

Tidal freshwater wetlands are sensitive to slight changes in sea level and river discharge that result in salinification due to their landscape position as an ecotonal ecosystem between uplands and aquatic systems and between non-tidal freshwater rivers and tidal saline estuaries (Odum 1988; Conner et al. 2007; Whigham et al. 2009). Recent and future projected

increases in sea level are expected to convert tidal freshwater wetlands to salt-impacted wetlands at their current locations with some degree of inland migration of tidal freshwater wetlands depending on the local topography and inputs of freshwater and sediment (Brinson et al. 1995). Some information on the response of tidal freshwater marsh ecosystems to salinification has been reported (summarized by Neubauer and Craft 2009). However, little is known about the response of tidal freshwater forested wetlands to sea level rise and salinification (Conner et al. 2007), despite the greater area of tidal freshwater forest compared to marsh in some regions (e.g., continental United States, Field et al. 1991). A static model of rising sea level predicts a net loss in area of tidal freshwater forested wetlands but little change in tidal freshwater marsh in the southeastern United States (Craft et al. 2009).

Salinification is known to alter nutrient cycling rates in freshwater ecosystems (Megonigal and Neubauer 2009). For example, Craft (2007) found faster decomposition of roots and slower accretion rates of soil N (N) with rising salinity along a freshwater to saline tidal marsh gradient. Krauss et al. (2009) also documented a decrease in soil N content associated with salinification and forest dieback in tidal freshwater forests. Several mechanisms could account for nutrient loss from salinified tidal freshwater soils. First, enhanced availability of sulfate in salt-impacted anoxic soils results in desorption of sediment phosphate through sulfide and Fe interactions as well as increased microbial metabolism and mineralization of N and phosphorus (P) by providing an alternative electron acceptor (Caraco et al. 1993; Portnoy and Giblin 1997; Lamers et al. 1998; Weston et al. 2006, 2011; Geurts et al. 2010). Second, increased ionic strength in porewater can desorb exchangeable soil and sediment ammonium (Rysgaard et al. 1999; Weston et al. 2010) and phosphate (Sundareshwar and Morris 1999). Finally, increases in the amount and nutrient content of detritus inputs associated with plant stress or mortality could stimulate microbial nutrient mineralization in soils (Scott and Binkley 1997), although this mechanism has not been documented in tidal freshwater wetlands.

Tidal freshwater forested wetlands typically occur at higher elevations and upstream from tidal freshwater or oligohaline marshes, at the edge of tidal influence (Whigham et al. 2009). In the United States, tidal freshwater forested wetlands are most extensive

in the southeastern Coastal Plain where sufficient river discharge, shallow land surface slope, and wide floodplains support extensive tidal freshwater systems (Conner et al. 2007). The attributes of floodplain forests generally differ between blackwater and alluvial rivers due to differences in water chemistry and sediment and nutrient availability (Wharton et al. 1982; Junk and Furch 1993; Hupp 2000; Schilling and Lockaby 2006; Anderson and Lockaby 2007; Noe 2013), but we are not aware of studies that have contrasted tidal freshwater forested wetlands occurring on blackwater and alluvial rivers. Furthermore, the presence of hummock and hollow microtopographic patterning has commonly been noted in tidal freshwater forested wetlands and is known to impact hydrology, plant diversity and growth, and soil chemistry (Conner et al. 2007; Day et al. 2007; Duberstein and Conner 2009; Courtwright and Findlay 2011). Sea level rise and salinification affect tidal freshwater forested wetlands by increasing tree mortality, reducing plant diversity, and eventually causing a state change to tidal freshwater or oligohaline marshes (Conner et al. 2007). However, too little is known about biogeochemical cycling in tidal freshwater forested wetlands to predict its response to salinification (Anderson and Lockaby 2007).

We hypothesize that salinification increases both N and P mineralization fluxes in the soils of tidal freshwater forested wetlands as they convert to oligohaline marsh. However, the magnitude of response is likely to vary among alluvial and blackwater tidal rivers. The goals of the study were to quantify changes in N and P soil mineralization (1) along a longitudinal river salinification gradient from continuously freshwater to heavily salt impacted tidal swamp to oligohaline marsh; (2) between a blackwater and an alluvial river; and (3) between microtopographic hummock and hollow locations; (4) as well as to compare the possible mechanisms associated with changes to N and P mineralization fluxes due to salinification of tidal freshwater forested wetland soils.

Methods

Site description

The longitudinal riverine transition from tidal freshwater forested to oligohaline marsh wetlands was

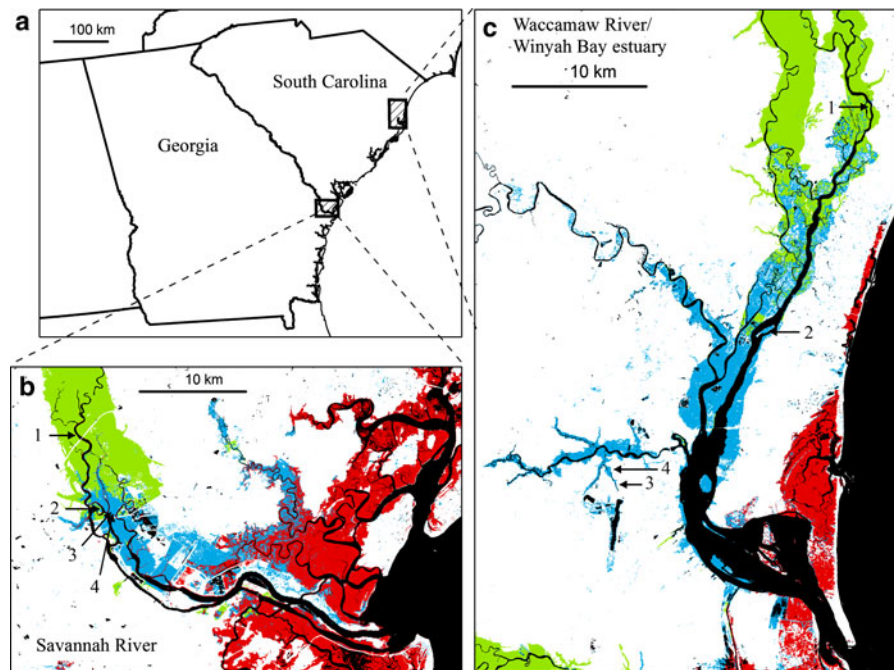


Fig. 1 Study site locations in the southeastern United States (a), on the Savannah River (b), and on the Waccamaw River and Winyah Bay estuary (c). Sites 1 through 4 are shown along both the Savannah and Waccamaw Rivers (1 continuously freshwater forest, 2 moderately salt impacted forest, 3 highly salt impacted forest, 4 oligohaline marsh). Colors represent tidal forest (green), freshwater and oligohaline marsh (blue), salt marsh

(red), open water (black), and uplands or other wetlands (white). Wetlands distribution based on Southeast GAP Regional Land Cover (McKerrow 2010; Tidal forest = Atlantic Coastal Plain Small Brownwater River Floodplain Forest; freshwater and oligohaline marsh = Atlantic Coastal Plain Central Fresh-Oligohaline Tidal Marsh; salt marsh = Atlantic Coastal Plain Central Salt and Brackish Tidal Marsh). (Color figure online)

studied along the floodplains of both the Waccamaw (South Carolina, USA) and Savannah rivers (Georgia and South Carolina, USA). The tidal forested wetland sites along these rivers follow those of Krauss et al. (2009), with the addition of an oligohaline (0.5–5 ppt salinity, Odum et al. 1984) marsh site on each river downstream from the forested wetlands. The four sites along each river ranged sequentially from continuously freshwater forest at the upstream end, moderately salt impacted forest (with moderate tree stress and mortality), highly salt impacted forest (with extensive tree mortality), and oligohaline marsh at the downstream end (Fig. 1). The dominant tree species in the tidal forests is *Taxodium distichum* [L.] L.C. Rich; however, *T. distichum* was a co-dominant with *Nyssa aquatica* L. on freshwater sites.

The Waccamaw River, a blackwater river with a watershed area of 1,981 km² within the Coastal Plain physiographic province, is part of the Winyah Bay estuary (46,620 km²) that includes inputs from the blackwater Sampit River (426 km²) and alluvial Pee

Dee River (Fig. 1). The longitudinal river transect includes a continuously freshwater forested wetland on Richmond Island along the Waccamaw River (soil porewater salinity of 0.1 ppt, June 2010 to 2011, updated from Krauss et al. 2009), a moderately salt impacted forest on Butler Island along the Waccamaw River (1.0 ppt), a highly salt impacted forest along the lower Sampit River (1.9 ppt), and an oligohaline marsh along the lower Sampit River (3.2 ppt). This longitudinal salinification gradient is hereafter referred to as the “Waccamaw River”.

The Savannah River is a large redwater alluvial river that has a total watershed area of 27,390 km² with a large portion within the Piedmont physiographic province. Discharge is affected by three dams upstream of the sites, constant dredging of the estuarine river, and historically by a one-way tidal flap gate installed along one of three channel braids to the Savannah River that caused wetland salinization (Pearlstone et al. 1993) but with only minor shifts in tidal swamp salinity (<1 ppt, Duberstein and Kitchens

2007). The longitudinal river transect includes a freshwater forest (0.1 ppt), a moderately salt impacted forest (1.4 ppt), a highly salt impacted forest (3.1 ppt), and an oligohaline marsh (3.5 ppt; Fig. 1).

Site layout

Three transects were established at each site, perpendicular to the channel and spaced 25 m apart. One mineralization measurement plot (0.25 m²) was chosen randomly from along each transect at a distance from 10 to 25 m from the channel. Each mineralization plot was subdivided into four quadrants that were each used once destructively for measuring mineralization using modified resin cores (see below, Noe 2011) every 3 months for 1 year. Hummock and hollow microtopography was present only at the continuously freshwater tidal forest site along each river. Each mineralization plot at those sites was split into nearby hummock and hollow sampling locations.

Mineralization method

Net mineralization of soil N and P was measured in situ using relatively open incubations of surficial (5 cm) soil using the DiStefano and Gholz (1986) resin core technique modified for use in hydrologically dynamic wetlands (Noe 2011). Modified resin cores allow for soil water and gas exchange and therefore track changes in the surrounding soil abiotic environment during incubation, as well as perform better than closed vessel incubations in wetland soils (Noe 2011). The method incubates in place a soil core with six mixed-media, ion-exchange resin bead bags, three placed above and three below the soil inside a PVC core tube. Net mineralization is quantified as the amount of inorganic nutrient at the end of incubation compared to an adjacent soil core collected at the beginning of incubation. The resin bags trap and quantify inorganic N and soluble reactive P (SRP) produced from inside the intact soil core (two inner resin bags located just above and below the 5 cm soil core) and prevent external inputs from entering the incubating soil core (two outer resin bags located at the top and bottom of the resin core). The two middle bags (located between each pair of inner and outer bags) serve as a quality control check to ensure that the inner and outer bags were not saturated with ions and

incapable of trapping nutrients. The resin bags are designed to trap all dissolved anions and cations, and thus also prevent loading of external salts and sulfate into the incubating soil. Therefore, modified resin cores measure the long-term mineralization response of soils to salinification gradients and not the response to concurrent inputs of ions. Preliminary testing identified that two modifications to the Noe (2011) method were necessary to limit loading to the two middle bags at our salt impacted sites: (1) increasing the mass of resin in the outer bags by 50 % and correspondingly increasing the length of the core tube to 11 cm; and (2) decreasing the duration of incubation from 4 weeks to 1–2 weeks.

Mineralization was measured quarterly, in September and December 2009, and March and June 2010. Each quarter, the surficial soil (0–5 cm) in each mineralization plot was sampled with two beveled, thin-walled, PVC core tubes, 7.8 cm in diameter and 11 cm in length. Each core tube was driven into the ground until the soil surface was 3 cm below the top of the tube. The modified resin core method severs roots inside the incubating core and prevents root uptake during incubation. The abundance of woody roots in the hummocks necessitated first cutting the hummock soil vertically with a pruning saw prior to inserting the coring tube. Cores were then removed, and the excess 3 cm of soil on the bottom of the core was removed, resulting in a soil core depth of 5 cm in the middle of the core tube. One core was processed as an initial core and analyzed within 48 h to yield initial 2 M KCl extractable soil NH₄⁺, NO₃⁻, and SRP concentrations (Keeney and Nelson 1982; Noe 2011).

The second core was processed as a modified resin core by placing 6 mixed-media resin bags around the soil in the core, 3 above and 3 below the soil. The two inner and two middle bags each contained 20 g of resin and the two outer bags each contained 30 g of resin (necessitated by the higher rate of ion capture by outer bags in a pilot study). The resin core was inserted back into the core hole and made flush with the surrounding soil surface. Resin cores were then incubated in situ for approximately 1–2 weeks and then processed the same as the initial core.

Areal net mineralization fluxes (*M*) were determined by comparing the amount of inorganic nutrients in the modified resin cores after field incubation to initial soil cores collected at the start of the incubation:

$$M = \frac{S_r + R_u + R_l - S_i}{AD}$$

where S_r , R_u , R_l , and S_i are the quantity of nutrient (mol) in the soil of the modified resin core, upper inner resin bag, lower inner resin bag, and initial soil core, respectively, representing the net production of nutrient. A is the area of the soil core (m^2) and D is the duration of the incubation (days). The production of SRP, NH_4^+ , and NO_3^- estimated fluxes of net P mineralization, net ammonification, and net nitrification, respectively. Net N mineralization is the sum of ammonification and nitrification. Due to variation in soil bulk density among plots, mineralization fluxes are expressed on an area basis ($\text{mol m}^{-2} \text{day}^{-1}$). Nitrogen and P turnover rates are calculated as the mineralization flux divided by the standing stock of TN and TP in the soil ($\text{mol mol}^{-1} \text{day}^{-1}$, or day^{-1}).

In addition to mineralization fluxes, inorganic nutrient loading fluxes to the soil surface were estimated from the amount of SRP, NH_4^+ , and NO_3^- captured by the outer bag on top of each incubating resin core. This upper outer resin bag was flush with the soil surface and exposed to air and surface water. Loading flux (L) was calculated as:

$$L = \frac{R_s}{AD}$$

where R_s is quantity of nutrient (mol) in the upper outer resin bag.

Soil characterization

A suite of soil attributes were measured that could describe the longitudinal river salinification, black-water versus alluvial, and microtopography gradients and have been shown to influence nutrient mineralization in other studies (Table 1). A subsample of soil from each initial and each incubated resin core was dried (60°C until constant mass) to estimate gravimetric ($[\text{wet mass} - \text{dry mass}]/\text{dry mass}$), volumetric ($[\text{gravimetric moisture}/\text{density of water}]$, assuming $1.0 \text{ g H}_2\text{O mL}^{-1}$), and water filled pore-space moisture content (WFPS; $\{\text{volumetric moisture}/[1 - (\text{bulk density}/\text{quartz parent material density})]\}$, assuming 2.65 g cm^{-3}). Bulk density was estimated from the dry weight of the soil and the volume of the soil. Dried soils from the resin cores were then ground and passed through a 1-mm porosity sieve; coarse organic matter

was preground with a Wiley mill (Thomas Scientific, Swedesboro, New Jersey, USA). Ground resin-core soils were each analyzed for TC, TN, and TS (Flash 2000 CHNS analyzer; Thermo Electron, Milan, Italy), followed by microwave-assisted acid digestion and measurement of total P, Fe, and Al (ICP-OES; Perkin-Elmer, Waltham, Massachusetts, USA) of the December 2009 incubation only. The remaining soil from initial and resin cores was air dried and then analyzed for pH using a 1:2 soil-to-DI water slurry (Robertson et al. 1999). The conductivity of soil extracts was measured by shaking 4 g dw equiv. mass of field moist soil with 40 mL of deionized water for 60 min, centrifuging, and analyzing the supernatant with a conductivity probe (Beckman Instruments, Fullerton, California, USA). Soil temperature was measured by an iButton[®] (Maxim Integrated Products, Sunnyvale, California, USA) attached mid-depth on the outside of each modified resin core during incubation. The iButton[®] collected a temperature reading every 15 min; only the concurrent data record among all sites for each incubation was included for further analysis. Water levels were recorded hourly at each site using a vented pressure transducer (Infinites USA, Port Orange, Florida, USA) placed at the bottom of a 1-m deep, 7.6-cm-diameter PVC well with gravel backfill located at a topographic low point. Transducer data and depth below the soil surface were used to calculate flood frequency and water table depth for the site.

Soil texture was measured for a single resin core incubation (December 2009) using a LISST-100X laser particle size analyzer (Sequoia Scientific, Inc., Bellevue, Washington, USA). A homogenized soil sample was first combusted at 550°C for 4 h to remove organics and then sieved to $\leq 250 \mu\text{m}$. A 0.02 g sample of material that passed through the sieve was added to 10 mL sodium hexametaphosphate solution (50 g NaHMP/L) and 90 mL deionized water, placed in an ultrasonic bath for 5 min, agitated on a shaker table at 100 rpm for 16 h in order to breakup soil aggregates, and then analyzed on the LISST-100X fitted with a stirring mixing chamber (Gee and Bauder 1986). The LISST-100X reported particle volume concentrations for 32 log-spaced size classes ranging in size from 1.2 to $250 \mu\text{m}$. Median particle size (d_{50}) was interpolated from the cumulative size distribution of LISST output. The percent clay ($< 2 \mu\text{m}$), silt ($2\text{--}50 \mu\text{m}$), and fine sands ($50\text{--}250 \mu\text{m}$) were

Table 1 Mean (one SE; $n = 3$ plots) attributes of surficial (0–5 cm) soils at sites along the Savannah (S) and Waccamaw (W) rivers for Sites 1 through 4, including the hummock (U) and hollow (L) microtopography subplots at Site 1

Measurement	SIU	SIL	S2	S3	S4	WIU	WIL	W2	W3	W4
Bulk density (g dw cm ⁻³)	0.26 (0.02)	0.27 (0.03)	0.25 (0.02)	0.39 (0.01)	0.30 (0.02)	0.21 (0.01)	0.18 (0.01)	0.24 (0.01)	0.32 (0.13)	0.28 (0.01)
WFPS (%)	93 (2)	97 (3)	100 (2)	111 (2)	110 (8)	87 (2)	90 (4)	95 (3)	96 (6)	105 (3)
Gravimetric moisture (%)	333 (23)	331 (45)	376 (24)	240 (5)	325 (4)	393 (2)	477 (16)	370 (14)	342 (100)	353 (21)
Volumetric moisture (%)	83 (1)	87 (3)	90 (1)	94 (1)	97 (6)	80 (1)	84 (3)	86 (2)	84 (2)	94 (3)
pH	5.2 (0.1)	5.2 (0.1)	5.0 (0.1)	5.0 (0.1)	4.7 (0.1)	5.3 (0.0)	5.3 (0.0)	4.7 (0.1)	4.6 (0.2)	4.0 (0.0)
Silt (%)	46 (5)	49 (0)	52 (2)	57 (2)	55 (1)	54 (1)	64 (4)	55 (1)	59 (3)	56 (2)
Clay (%)	45 (5)	41 (3)	41 (2)	29 (1)	39 (2)	29 (2)	25 (1)	29 (3)	22 (8)	27 (2)
Sand (%)	8 (2)	9 (3)	7 (1)	14 (2)	6 (2)	16 (3)	10 (5)	16 (2)	18 (6)	18 (3)
Conductivity (mS cm ⁻¹)	0.2 (0.1)	0.1 (0.0)	4.3 (1.0)	9.7 (1.0)	15.1 (0.9)	0.2 (0.0)	0.2 (0.1)	18.2 (0.9)	28.5 (6.8)	44.1 (5.8)
Water depth (cm)		-8.5	1.1	-2.3	1.6		0.1	3.5	7.5	13.4
Inundation frequency		0.22	0.31	0.34	0.30		0.29	0.35	0.42	0.54
Temperature										
P (μmol cm ⁻³)	17.5 (0.1)	17.7 (0.0)	18.3 (0.1)	18.9 (0.1)	18.7 (0.2)	17.5 (0.1)	17.6 (0.1)	18.4 (0.1)	18.1 (0.1)	18.2 (0.2)
C (mmol cm ⁻³)	12.0 (0.7)	10.7 (0.4)	8.0 (1.8)	19.8 (2.1)	9.8 (1.0)	8.2 (0.8)	6.4 (0.8)	6.9 (1.4)	6.9 (2.0)	7.3 (0.6)
N (mmol cm ⁻³)	3.4 (0.2)	2.9 (0.2)	3.8 (0.3)	2.1 (0.1)	2.8 (0.2)	3.9 (0.2)	3.3 (0.2)	4.1 (0.1)	4.2 (0.7)	3.0 (0.3)
S (mmol cm ⁻³)	0.13 (0.00)	0.12 (0.01)	0.12 (0.01)	0.10 (0.00)	0.09 (0.01)	0.12 (0.01)	0.10 (0.01)	0.11 (0.01)	0.10 (0.00)	0.09 (0.00)
Fe (mmol cm ⁻³)	0.04 (0.00)	0.04 (0.00)	0.05 (0.01)	0.10 (0.02)	0.13 (0.00)	0.04 (0.00)	0.03 (0.00)	0.07 (0.01)	0.14 (0.02)	0.29 (0.04)
Al (mmol cm ⁻³)	0.21 (0.02)	0.15 (0.03)	0.10 (0.03)	0.33 (0.00)	0.19 (0.01)	0.09 (0.01)	0.08 (0.01)	0.11 (0.02)	0.13 (0.02)	0.25 (0.02)
Microbial C (μmol cm ⁻³)	0.91 (0.19)	0.75 (0.11)	0.59 (0.16)	1.28 (0.18)	0.75 (0.13)	0.56 (0.07)	0.52 (0.09)	0.68 (0.06)	0.65 (0.10)	0.78 (0.11)
Microbial N (μmol cm ⁻³)	21.6 (2.2)	16.7 (1.4)	6.3 (0.7)	7.4 (0.8)	4.3 (1.1)	12.9 (1.0)	8.0 (1.2)	8.2 (1.8)	6.5 (2.4)	7.6 (1.0)
Microbial P (μmol cm ⁻³)	2.2 (0.5)	1.7 (0.3)	0.6 (0.0)	0.5 (0.1)	0.3 (0.0)	1.6 (0.1)	0.8 (0.1)	0.5 (0.1)	0.5 (0.2)	0.4 (0.1)
Extractable nitrate (μmol N cm ⁻³)	6.0 (0.3)	5.6 (1.1)	4.1 (0.6)	1.6 (1.6)	0.0 (0.0)	7.9 (1.3)	6.6 (0.6)	1.7 (0.2)	0.8 (0.1)	1.2 (0.6)
Extractable ammonium (μmol N cm ⁻³)	0.0091 (0.0022)	0.0105 (0.0044)	0.0005 (0.0003)	0.0059 (0.0011)	0.0012 (0.0009)	0.0064 (0.0007)	0.0094 (0.0008)	0.0016 (0.0008)	0.0010 (0.0007)	0.0054 (0.0021)
Extractable SRP (μmol P cm ⁻³)	0.055 (0.004)	0.070 (0.014)	0.055 (0.007)	0.136 (0.011)	0.079 (0.020)	0.079 (0.009)	0.061 (0.010)	0.069 (0.016)	0.066 (0.019)	0.058 (0.006)
Nitrate loading (μmol N m ⁻² day ⁻¹)	0.0045 (0.0011)	0.0037 (0.0004)	0.0040 (0.0003)	0.0054 (0.0007)	0.0055 (0.0015)	0.0022 (0.0001)	0.0024 (0.0001)	0.0020 (0.0003)	0.0022 (0.0000)	0.0054 (0.0007)
Ammonium loading (μmol N m ⁻² day ⁻¹)	110 (12)	160 (40)	111 (54)	62 (22)	18 (9)	122 (27)	222 (65)	251 (127)	87 (64)	44 (20)
SRP loading (μmol P m ⁻² day ⁻¹)	29 (14)	16 (7)	47 (23)	120 (35)	76 (14)	16 (7)	13 (3)	38 (15)	96 (11)	105 (17)
	58 (10)	50 (4)	99 (12)	86 (11)	109 (16)	44 (5)	60 (14)	56 (28)	18 (4)	56 (11)

Measurements from the quarterly incubations within each plot were first averaged, eliminating temporal variation prior to calculating spatial variability from the three replicate plots in each site. Water depth and inundation frequency were not measured on hummocks (SIU or WIU)

determined from their appropriate LISST-100X output size classes (Gee and Bauder 1986, U.S. Department of Agriculture definition), corrected for the amount of soil that was retained on the 250- μm sieve (coarse sand).

Soil from each resin core was analyzed for soil microbial biomass C, N, and P. Subsamples of soil for microbial biomass C and N were sieved through a #10 sieve to remove debris, then divided into nonfumigated and fumigated subsamples and weighed into glass flasks. Samples designated for fumigation were placed in vacuum desiccators containing wet paper towels, a container of soda lime, and beaker of ethanol-free chloroform with boiling chips. The vacuum desiccators were evacuated until chloroform boiled for 2 min. Samples were then incubated for 24 h in darkness (Joergensen 1995; Vance et al. 1987). After incubation, samples were shaken for 30 min with 0.5 M K_2SO_4 and then vacuum filtered. Filtrate was frozen, defrosted and filtered with 0.45 μm filter prior to analysis for C and N on the Shimadzu TOC-V analyzer (Shimadzu TOC-V, Columbia, MD). All nonfumigated samples were processed in the same manner with the exception of the use of chloroform. Microbial biomass C and N were calculated as the difference between element contents of fumigated versus nonfumigated samples.

Soils from the resin cores were analyzed for microbial biomass P only in June 2010. Subsamples of soils were sieved through #10 sieves to remove debris and then divided into three subsamples (non-fumigated control, nonfumigated recovery, and fumigated sample). The nonfumigated control sample was weighed into a glass flask, extracted with 200 mL 0.5 M NaHCO_3 by shaking for 30 min, centrifuged, then vacuum filtered. The nonfumigated recovery sample was treated in the same manner with the addition of a KH_2PO_4 spike. The fumigated samples were then treated as described for microbial biomass C and N. Immediately prior to analysis, samples were filtered again then analyzed using an ammonium molybdate, ascorbic acid method and read on a spectrophotometer at 882 nm following calibration. Microbial biomass P was calculated using the equation $\text{biomass P} = E_p/K_{EP}$, where $E_p = (F - U)/(Z - U) \times 25$. F represents the fumigated soil's $\text{PO}_4\text{-P}$, U the nonfumigated soil $\text{PO}_4\text{-P}$ and Z the $\text{PO}_4\text{-P}$ extracted from the spiked nonfumigated soil and the K_{EP} value as determined by Brooks et al. (1982).

Statistics

For all statistics, variables were transformed when necessary to best approximate a normal distribution and $\alpha = 0.05$. Spatial and temporal differences among rivers, sites, and seasons were tested using repeated measures analysis of variance. The model included the three main factors of river ($n = 2$), site ($n = 4$), and season ($n = 4$), and their two- and three-way interactions, with season as the repeated measure in each plot (SAS 9.1). Because hummocks were restricted to the continuously freshwater tidal forest sites, only the hollow plots were used to compare that site to the other salt impacted sites. Covariance structure was modeled using compound symmetry. Significant site effects were evaluated further using pairwise difference tests with Tukey's adjustment.

The effects of microtopographic position also were tested using repeated measures analysis of variance on data from hummocks and hollows at the upper freshwater tidal swamp site on each river, the only locations with hummock/hollow microtopography present. The model included the three main factors of microtopographic position ($n = 2$), river ($n = 2$), and season ($n = 4$), and their two- and three-way interactions, with season as the repeated measure in each plot (SAS 9.1).

Soil attribute data from each season in each plot was synthesized into multivariate gradients, using principal components analysis, that were then related to mineralization fluxes. Data from the initial soil cores were used for the soil attributes of gravimetric moisture, volumetric moisture, WFPS, conductivity, pH, bulk density, and extractable inorganic nutrient content, due to the potential artifact of incubation on soil conditions (Noe 2011), otherwise, data from the incubated soils inside modified resin cores were used. First, the 24 soil attribute variables (Table 1) were simplified using PCA with Varimax rotation and an eigenvalue significance threshold of 1.0 for components (SPSS 13; $n = 120$ with 30 plots and 4 seasons). For the few soil attributes that were only measured for a single season, those values were applied to the remaining seasons. Each of the resulting components was assigned a synthetic description based on the maximum loading of each soil attribute variable to the various components. Component scores for each plot were calculated using the regression method. Second, plot component scores were tested for differences

among rivers and sites using factorial two way analysis of variance for each component. Third, the correlations of each component with mineralization fluxes were evaluated using Pearson Product-Moment correlation. Finally, individual soil attribute variables related to the salinification gradients were directly correlated to the mineralization fluxes using Pearson Product-Moment correlation. These last correlation analyses permitted direct (univariate) tests of the effects of salinity, sulfur, and pH on mineralization fluxes.

Results

Spatial gradients in mineralization

Salinification gradients

Soil net P mineralization flux ($\mu\text{mol m}^{-2} \text{ day}^{-1}$), P turnover rate (day^{-1}), and extractable SRP concentration ($\mu\text{mol cm}^{-3}$) each significantly varied among sites along the riverine salinification gradients (Table 2). Along both rivers, net P mineralization flux, P turnover rate, and extractable SRP concentration were much greater in the downstream oligohaline marsh than in the continuously freshwater, moderately salt impacted, or highly salt impacted tidal forests (Fig. 2). In addition, mean P mineralization flux and extractable SRP concentrations in the Savannah River's highly salt impacted tidal forest were elevated compared to the moderately salt impacted or continuously freshwater tidal forest along that river (but not significantly different). However, P turnover rate at the Savannah River's highly salt impacted tidal forest site was more similar to the other tidal forested sites, indicating that elevated net P mineralization flux there was due to greater P content of soils (Table 1). The greatest P mineralization flux and turnover rates occurred during September in the oligohaline marsh along the Savannah River (River by Site by Season interaction). With the exception of the wide range in September, P mineralization metrics generally varied little among seasons.

Net nitrification flux also significantly differed among sites along the riverine salinification gradients (Table 2). The salt impacted tidal forested sites had greater nitrification flux than either the continuously freshwater tidal forest or oligohaline marsh sites

(Fig. 2). However, the pattern depended on the river and season (Table 2), with greatest nitrification at the moderately impacted tidal forest site on the Waccamaw River (in June) and the highly impacted tidal forest site on the Savannah River (in December; Fig. 2). Mean ammonification and net N mineralization (the sum of ammonification and nitrification) fluxes and N turnover rates were greatest in the highly salt impacted tidal forests than the other tidal forest or oligohaline marsh sites (Fig. 2), although differences among sites were not statistically significant (Table 2). This trend was more pronounced on the Savannah River than the Waccamaw River (Fig. 2). Specifically, mean N turnover rate was 30 and 99 % greater at the highly salt impacted compared to continuously freshwater tidal forest sites on the Waccamaw and Savannah Rivers, respectively. Nitrogen mineralization fluxes and turnover rates were generally lowest in March and December, intermediate in September, and greatest in June. Soil extractable ammonium concentrations were significantly greater at the highly salt impacted tidal forest on the Savannah River (Tables 1, 2). Soil extractable nitrate concentrations were significantly greatest at the continuously freshwater tidal forests, particularly during September. To summarize, P mineralization was greatest in the oligohaline marshes and N mineralization had a trend of being greatest in the highly salt impacted tidal forests.

Blackwater versus alluvial river

All measured soil N and P mineralization processes and extractable nutrient concentrations, with the exception of N turnover rate, differed between the blackwater Waccamaw River and alluvial Savannah River in the repeated measures ANOVAs (Table 2). Net P mineralization flux, P turnover rate, nitrification flux, and all three extractable nutrient concentrations were generally greater in the soils of Savannah River wetlands, whereas ammonification and net N mineralization fluxes and the ratio of N:P mineralized were generally greater in the Waccamaw River (Fig. 2; Table 1). Differences in P mineralization and soil extractable SRP concentration between rivers were more pronounced than for N mineralization and soil extractable DIN concentrations. However, as indicated by the large number of significant interaction terms in the ANOVAs (Table 2), most differences in

Table 2 Repeated measures ANOVA on mineralization measurements

Measurement	Statistic	River	Site	Season	River*Site	River*Season	Site*Season	River*Site*Season
	Num DF	1	3	3	3	3	9	9
	Den DF	16	16	48	16	48	48	48
P mineralization flux	<i>F</i>	26.55	4.48	11.02	1.87	13.33	1.15	2.9
	<i>P</i>	<0.001	0.018	<0.001	0.176	<0.001	0.350	0.008
P turnover rate	<i>F</i>	11.6	8.4	6.2	2.34	19.3	1.98	4.83
	<i>P</i>	0.004	0.001	0.001	0.113	<0.001	0.062	0.000
Ammonification flux	<i>F</i>	1.01	1.39	24.27	0.69	2.92	1.18	1.6
	<i>P</i>	0.330	0.281	<0.001	0.571	0.044	0.329	0.144
N mineralization flux	<i>F</i>	0.97	1.46	25.01	0.71	3.7	1.3	1.51
	<i>P</i>	0.338	0.262	<0.001	0.561	0.018	0.262	0.171
N turnover rate	<i>F</i>	0.57	1.89	22.01	0.81	1.6	1.02	1.19
	<i>P</i>	0.462	0.172	<0.001	0.506	0.203	0.436	0.321
% Nitrification	<i>F</i>	11.29	2.09	6.18	1.18	10.32	0.76	0.74
	<i>P</i>	0.004	0.141	0.001	0.346	<0.001	0.655	0.675
N:P mineralized	<i>F</i>	8.56	0.46	2.49	0.54	1.93	0.18	0.43
	<i>P</i>	0.010	0.713	0.071	0.660	0.137	0.995	0.912
Extractable SRP	<i>F</i>	26.91	11.02	21.7	7.13	8.93	6.97	2.58
	<i>P</i>	<0.001	0.000	<0.001	0.003	<0.001	<0.001	0.016
Extractable ammonium	<i>F</i>	1.63	3.21	6.49	3.31	8.44	1.61	0.63
	<i>P</i>	0.220	0.051	0.001	0.047	0.000	0.140	0.766
Extractable nitrate	<i>F</i>	0.34	20.76	7.42	4.26	13.58	2.36	1.66
	<i>P</i>	0.568	<0.001	0.000	0.022	<0.001	0.027	0.126

Model terms include River (Savannah and Waccamaw), Site (continuously freshwater forest, moderately salt impacted forest, highly salt impacted forest, and oligohaline marsh), the repeated measure of Season, and their interactions

DF degrees of freedom. Significant *P* values are highlighted in bold

rates between rivers depended on site or season. The greater rates of net P mineralization and P turnover on the Savannah River were more pronounced in September, greater extractable SRP concentration, and nitrification were more pronounced in December, and greater extractable ammonium and nitrate were more pronounced in March. Greater rates of ammonification, net N mineralization, and the ratio of N:P mineralized on the Waccamaw River occurred in September and March. To summarize, in general the blackwater river had more inorganic N production whereas the alluvial river had much more inorganic P production in wetland soils.

Hummock and hollow microtopography

Hummock and hollow microtopography was present at the continuously freshwater tidal forested wetland sites along each river. The mean elevation difference

between hummock and hollow was 4.2 cm at the Savannah River and 9.2 cm at the Waccamaw River. Soil nitrification flux was the only parameter significantly influenced by microtopography (Table 3). Net nitrification flux was 202 % greater in the higher hummocks than the lower hollows (Fig. 3). However, the difference in nitrification between hummock and hollows depended on the season, with hummocks having greater production of nitrate during December and June. Mineralization fluxes in hummocks or hollows did not differ between rivers (Table 3). To summarize, nitrification was more prevalent on higher elevation hummocks than lower elevation hollows of the continuously freshwater tidal forests.

Gradients in soil attributes

Principal component analysis identified seven significant multivariate gradients of soil attributes. These

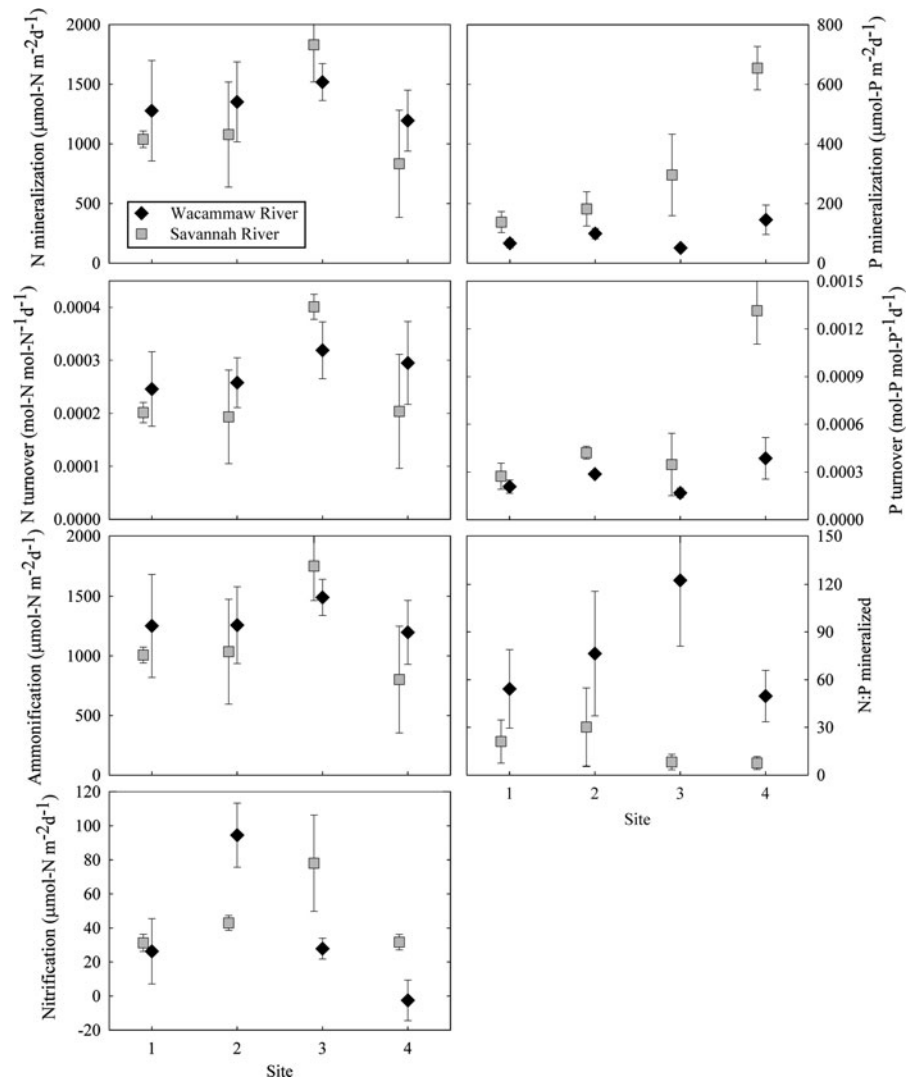


Fig. 2 Mean annual mineralization fluxes (mean of quarterly incubations \pm one SE, $n = 12$) along the longitudinal salinification gradients of the Savannah and Waccamaw Rivers. Site 1

continuously freshwater forest (hollows only), 2 moderately salt impacted forest, 3 highly salt impacted forest, 4 oligohaline marsh

principal components, in descending order of variance explained, are interpreted to describe gradients of salinification/microbes, mineral content, inundation, moisture, season, silt, and sand/clay (Table 4). The dominant gradient, the salinification/microbes component, included both total S and conductivity that were negatively loaded and microbial C, N, and P, total N, and pH that were positively loaded. The mineral content component included total P, Al, Fe, and bulk density that were positively loaded and total C and gravimetric moisture content that were negatively loaded. The inundation component

included positive loading of both inundation frequency and mean water depth. The moisture component was positively loaded by both volumetric moisture content and WFPS. The seasonality component was most influenced by soil temperature which was positively associated with ammonium loading to the soil surface and negatively with SRP loading to the soil surface. The silt component included negative loading of silt and nitrate loading to the soil surface. Finally, the sand/clay component included positive loading by sand as well as negative loading with clay.

Table 3 Repeated measures ANOVA on mineralization measurements showing the effects of microtopography in the continuously freshwater tidal forests

Measurement	Statistic	MT	River	Season	MT*River	MT*Season	River*Season	MT*River*Season
	Num DF	1	1	3	1	3	3	3
	Den DF	8	8	24	8	24	24	24
Ammonification flux	<i>F</i>	0.03	0.35	7.93	0.04	1.02	0.5	0.55
	<i>P</i>	0.864	0.571	0.001	0.845	0.400	0.687	0.655
Nitrification flux	<i>F</i>	5.79	0.12	1.71	0.22	5.37	19	0.04
	<i>P</i>	0.043	0.742	0.192	0.654	0.006	<0.001	0.989
N mineralization flux	<i>F</i>	0.15	0.3	9.24	0.03	1.04	1.21	0.56
	<i>P</i>	0.711	0.597	0.000	0.867	0.392	0.328	0.647
N turnover rate	<i>F</i>	0.03	0.88	12.44	0.01	0.98	0.69	0.6
	<i>P</i>	0.870	0.376	<0.001	0.932	0.419	0.567	0.622
P mineralization flux	<i>F</i>	0.52	1.25	9.03	2.96	0.37	3.5	0.69
	<i>P</i>	0.491	0.296	0.000	0.124	0.774	0.031	0.567
P turnover rate	<i>F</i>	1.62	0	8.06	1.44	0.32	2.95	0.56
	<i>P</i>	0.239	0.949	0.001	0.264	0.812	0.053	0.645
N:P mineralized	<i>F</i>	0.44	2.03	5.8	0.66	0.61	1.19	0.46
	<i>P</i>	0.524	0.193	0.004	0.442	0.617	0.337	0.711
Extractable ammonium	<i>F</i>	0.06	3.47	1.22	3.87	0.42	6.3	1.64
	<i>P</i>	0.817	0.100	0.324	0.085	0.741	0.003	0.205
Extractable nitrate	<i>F</i>	0.79	1.88	3.71	0.56	1.47	7.2	0.74
	<i>P</i>	0.399	0.208	0.025	0.477	0.249	0.001	0.541
Extractable SRP	<i>F</i>	0.19	11.76	22.85	0.64	0.51	0.9	1.09
	<i>P</i>	0.671	0.009	<0.001	0.447	0.682	0.458	0.374

Model terms include microtopography (MT, hummock and hollow), River (Savannah and Waccamaw), the repeated measure of Season, and their interactions

DF degrees of freedom. Significant *P* values are highlighted in bold

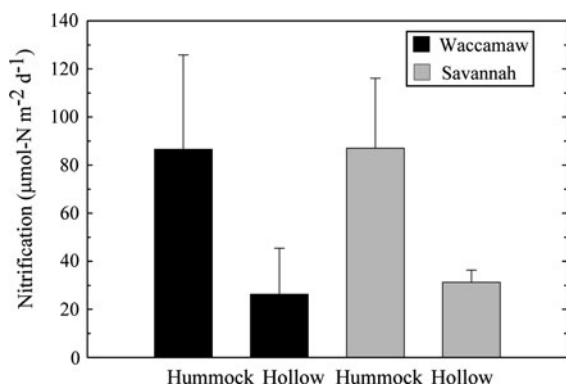


Fig. 3 Mean annual net nitrification flux (mean of quarterly incubations + one SE, $n = 12$) in hummocks and hollows of the continuously freshwater tidal forest (Site 1) on the Savannah and Waccamaw Rivers

Wetland soils significantly differed between the Savannah and Waccamaw rivers for all of the multi-variate gradients in soil attributes (ANOVA, all $P < 0.050$) except the seasonality component ($P = 0.214$). In general, the soils of the Waccamaw River were more salt impacted (and had lower pH), had less mineral content, were inundated more frequently and had deeper mean surface water, had less water volume, and were siltier (including more nitrate loading to the soil surface) and sandier with less clay than those of the Savannah River. Soils also differed among the four sites on both rivers for the salinification/microbes, mineral content, inundation, and sand/clay components (all $P < 0.021$) but not the moisture, seasonality, or silt components (all $P > 0.060$). Salt impacts increased along the gradient

Table 4 Principal component analysis of soil attributes from each mineralization incubation using Varimax rotation ($n = 120$)

Measurement	PC1	PC2	PC3	PC4	PC5	PC6	PC7
S	-0.82	0.14	0.12	0.03	0.04	0.11	0.19
Microbial P	0.82	-0.27	-0.15	-0.14	0.00	0.09	0.08
Conductivity	-0.79	0.16	0.22	0.16	0.11	-0.09	0.18
pH	0.72	0.14	0.24	-0.11	-0.34	-0.05	-0.17
Microbial N	0.69	0.17	-0.43	-0.14	0.15	0.19	0.11
Microbial C	0.57	0.20	-0.49	-0.01	0.44	0.17	0.12
N	0.55	0.06	0.51	-0.22	-0.14	0.46	-0.12
P	0.18	0.90	-0.05	0.06	-0.04	0.03	-0.14
Al	-0.06	0.87	0.06	-0.05	0.03	0.12	-0.09
Fe	-0.30	0.86	0.01	0.06	0.03	0.17	-0.04
Gravimetric moisture	0.04	-0.81	0.07	-0.16	-0.16	0.09	-0.19
Bulk density	-0.10	0.71	-0.03	0.55	0.15	-0.10	0.18
C	0.13	-0.50	0.39	-0.27	0.16	0.38	0.02
Inundation frequency	-0.16	0.05	0.87	0.06	0.06	-0.01	0.16
Water depth	-0.38	-0.14	0.75	0.03	0.13	-0.18	0.18
WPFS moisture	-0.17	0.21	0.02	0.95	0.06	0.03	-0.03
Volumetric moisture	-0.17	0.06	0.04	0.94	0.01	0.07	-0.12
Temperature	0.02	0.06	-0.13	0.09	0.85	-0.18	-0.13
Ammonium loading	-0.19	0.19	0.33	0.10	0.76	-0.01	0.03
SRP loading	0.08	0.08	-0.05	0.13	-0.60	-0.20	-0.38
Silt	-0.17	-0.02	0.20	-0.05	0.00	-0.80	0.10
Nitrate loading	0.41	-0.12	-0.14	-0.08	0.05	-0.53	0.06
Sand	-0.09	-0.01	0.11	-0.06	0.04	-0.09	0.93
Clay	0.17	0.01	-0.21	0.06	-0.03	0.60	-0.70
Description	Salinification/microbes	Mineral	Inundation	Moisture	Season	Silt	Sand/clay
% Variance explained	18	17	11	10	9	8	8

For each rotated principal component (PC), partial correlations with each soil attribute, a synthetic description of each component based on the dominant loading variables (partial correlations highlighted in bold), as well as the percent of total variance explained are provided

from continuously freshwater to moderately salt impacted to highly salt impacted tidal forest and to oligohaline marsh. The highly salt impacted tidal forest sites had the greatest mineral content and sand content, while the continuously freshwater tidal forest sites were inundated less frequently and had shallower mean surface water depth. Finally, differences between rivers depended on site for the mineral content, sand/clay, and silt components (significant interaction term, all $P < 0.001$).

Microtopographic differences in soil attributes were apparent at the continuously freshwater tidal forest sites on both rivers. Hummocks differed from hollows for the salinification/microbes component (ANOVA, $P = 0.032$), with greater microbial biomass nutrient content and total N content than

hollows. Hummocks also had greater mineral content ($P = 0.005$), specifically greater bulk density, C, P, Fe, and Al (Table 1), as well as less silt content and lower nitrate loading to the soil surface than hollows along the silt component ($P < 0.001$). Finally, hummocks had more sand along the sand/clay component ($P = 0.033$), although this trend was more evident on the Waccamaw River (interaction term, $P = 0.010$). To summarize, soils were substantially different between the alluvial Savannah and blackwater Waccamaw rivers, generally somewhat different among the salinification gradient sites but with large differences in salt content, S, pH, and microbial biomass, and finally hummocks had greater microbial biomass and mineral content than hollows.

Table 5 Pearson Product-Moment Correlations of mineralization measurements with the multivariate soil attribute principal components ($n = 120$)

Measurement	Statistic	PC1:Salinification/ microbes	PC2:Mineral	PC3:Inundation	PC4:Moisture	PC5:Season	PC6:Silt	PC7:Sand/ Clay
Ammonification flux	<i>r</i>	0.107	0.151	-0.017	-0.098	0.475	-0.217	-0.034
	<i>P</i>	0.246	0.100	0.857	0.285	0.000	0.017	0.714
Nitrification flux	<i>r</i>	0.160	0.030	0.070	-0.167	0.101	0.004	0.017
	<i>P</i>	0.081	0.748	0.444	0.069	0.274	0.966	0.857
N mineralization flux	<i>r</i>	0.119	0.145	-0.007	-0.111	0.472	-0.211	-0.031
	<i>P</i>	0.196	0.114	0.943	0.227	0.000	0.021	0.734
N turnover rate	<i>r</i>	-0.020	0.174	-0.115	-0.020	0.474	-0.283	0.006
	<i>P</i>	0.829	0.058	0.210	0.825	0.000	0.002	0.946
P mineralization flux	<i>r</i>	-0.082	0.203	0.259	0.148	-0.163	0.013	-0.283
	<i>P</i>	0.374	0.026	0.004	0.107	0.076	0.887	0.002
P turnover rate	<i>r</i>	-0.199	-0.013	0.258	0.144	-0.031	0.037	-0.256
	<i>P</i>	0.029	0.886	0.004	0.116	0.735	0.689	0.005
N:P mineralized	<i>r</i>	-0.125	-0.212	0.041	0.004	0.332	-0.031	0.044
	<i>P</i>	0.177	0.021	0.660	0.967	0.000	0.737	0.632

Significant *P* values are highlighted in bold

Correlates of mineralization

Net P mineralization flux and P turnover rate were each significantly positively correlated with the multivariate sand/clay component, increasing with more clay and less sand content, and the inundation component, increasing with frequency and depth of inundation (Pearson Product-Moment Correlations, $n = 120$; Table 5). In addition, P turnover rate was significantly negatively correlated with the salinification/microbes component, increasing with S and conductivity. Net P mineralization flux was also significantly positively correlated with the mineral content component. Finally, the ratio of N:P mineralized was significantly positively correlated with the seasonality component, increasing with temperature, and negatively correlated with the mineral content component, decreasing with P content. The significant correlations of P mineralization metrics with the multivariate soil attribute components all had low correlation coefficients ($r < |0.28|$).

Ammonification flux, net N mineralization flux, and N turnover rate were each significantly positively correlated with the seasonality component, increasing with temperature, and negatively with the silt component, increasing with silt content (Table 5). Seasonality had the strongest association with the N mineralization metrics ($r > |0.47|$) compared to any other multivariate correlates of mineralization.

The individual soil attribute variables that generated the multivariate salinification component also were each directly related to the mineralization metrics in order to identify their relative importance. In general, only weak relationships existed between the mineralization metrics and soil conductivity, S, and pH. Sulfur content was significantly negatively correlated to net nitrification flux ($r = -0.229$, $P = 0.012$). Phosphorus turnover rate was significantly positively related to soil conductivity ($r = 0.239$, $P = 0.009$), but not S ($r = 0.090$, $P = 0.327$), suggesting that the correlation between P turnover and the salinification/microbes component, which included both S and conductivity, was due to conductivity. Finally, higher pH was associated with greater P net mineralization flux ($r = 0.203$, $P = 0.026$), greater nitrification flux ($r = 0.183$, $P = 0.046$), and a smaller ratio of N:P mineralized ($r = -0.270$, $P = 0.003$). Notably, N turnover and P turnover were not related to soil total S content ($r = 0.017$, $P = 0.852$; and $r = 0.090$, $P = 0.327$; respectively) nor was N turnover related to soil conductivity ($r = 0.055$, $P = 0.551$). When the relationships between mineralization and individual soil attributes were evaluated along each river separately, there were no significant correlations involving S, conductivity, or pH with mineralization metrics along the Waccamaw River. Along the Savannah River,

S was positively correlated with P mineralization flux ($r = 0.295$, $P = 0.022$) and P turnover ($r = 0.339$, $P = 0.008$), but conductivity had stronger correlations with P mineralization flux and P turnover ($r = 0.423$, $P = 0.001$; and $r = 0.415$, $P = 0.001$; respectively).

Discussion

Salinification impacts on tidal freshwater ecosystems

Previous studies have found that increases in sulfate loading associated with salinification or pollution provides an alternative electron acceptor that stimulates anoxic microbial carbon respiration and nutrient release from freshwater wetland soils (Caraco et al. 1993; Portnoy and Giblin 1997; Lamers et al. 1998; Weston et al. 2006, 2011). However, we found little evidence that long-term enhanced sulfate availability increased microbial nutrient mineralization in tidal wetlands along our coastal freshwater to oligohaline salinification gradients. Soil total S increased 450 % from the continuously freshwater tidal forests to the oligohaline marshes, but S content in the incubated soil had no positive correlations with any mineralization flux or turnover rate. Along the Savannah River only, P mineralization and P turnover were positively correlated with S, but were more strongly correlated with salt content. Although we did not directly measure sulfate, sulfide, or sulfate reduction, soil total S provides a proxy for long-term sulfate availability in the modified resin cores that were used to measure mineralization. Salinification at our study sites has occurred for years (Cormier et al. 2012). Sulfate loading and reduction that occurred at the sites prior to core incubation would have generated sulfide, some of which would precipitate with Fe^{2+} and be measured as total S in the soil (Reddy and DeLaune 2008). It should be noted that no new sulfate would have entered soil incubating inside the modified resin cores due to the capacity of the resin bags to capture anions (Noe 2011). However, some of the soil total S inside the resin cores would likely be oxidized to sulfate during low tide and provide an internal source of sulfate for reduction during high tide inundation (Reddy and DeLaune 2008).

Net nitrification fluxes decreased with greater soil total S. Soils with higher total S also likely had greater

sulfide content, which has been shown to limit the activity of nitrifying bacteria (Joye and Hollibaugh 1995). Alternatively, there may be less oxygen available in the reducing soils that have higher total S. Reduced S may compete for limited soil oxygen available in these tidal wetland soils and limit nitrifying bacteria from oxidizing ammonium to nitrate. Although saltwater also can limit nitrification (Rysgaard et al. 1999), conductivity was not correlated with nitrification in this study.

We also found no evidence that saltwater increased the desorption of exchangeable soil ammonium. Net ammonification fluxes and soil extractable ammonium concentrations were not correlated with soil conductivity along the field salinification gradients of the Savannah and Waccamaw rivers. Many laboratory experiments have found that pulses of saltwater result in the desorption of exchangeable ammonium from tidal freshwater and oligohaline soils and sediments (Rysgaard et al. 1999; Weston et al. 2010). Although we do not know when salt pulses first reached our formerly continuously freshwater and now salt impacted sites, salinification at these sites has occurred at least since the beginning of the measurement of soil porewater salinity in 2005 (Cormier et al. 2012). It is likely that large pools of exchangeable ammonium would have been lost by salt desorption at salt impacted sites prior to measurement from 2009 and 2010 in this study. Similarly, the lack of a relationship between soil S and nutrient mineralization fluxes in this study could be due to loss of the labile pool of organic matter that could be oxidized by microbes using sulfate after years of chronic salinification at these sites.

Both soil net ammonification flux and ammonium concentrations peaked at the highly salt impacted tidal forest sites, which during this study had porewater salinities of 2.9 and 3.5 on the Waccamaw and Savannah rivers, respectively (unpublished data). Given the lack of a relationship between N fluxes and soil S or conductivity, the elevated N mineralization flux in the soils of the highly salt impacted tidal forested wetlands is likely due to inputs of labile detritus from the dead, dying, and stressed trees. Nitrogen turnover rates have the same pattern as net N mineralization flux, indicating that elevated mineralization is due to greater microbial activity and not a larger pool of total N substrate in surficial soils. Salt intrusion in tidal freshwater forests causes premature

leaf senescence resulting in elevated N concentrations in litterfall (Brinson et al. 1985). Cormier et al. (2012) also measured increased N content of litterfall at the highly salt impacted tidal forest site on the Savannah River. Alternatively, greater inputs of herbaceous biomass in the highly salt impacted tidal forests, which are converting to marsh, likely increased the lability of detritus inputs (Neubauer and Craft 2009). Inputs of detritus with greater nutrient content can stimulate faster turnover rates of soil N mineralization, perhaps by priming microbial activity (Scott and Binkley 1997). Thus, chronic salinification generated more labile detritus (tree litter or herbaceous) that may have caused a release of inorganic N from tidal freshwater forest wetland soils. This effect of salinification on the release of N from tidal freshwater ecosystems could lead to estuarine eutrophication (Neubauer and Craft 2009).

The oligohaline marshes on both rivers, as well as the highly salt impacted tidal forest on the Savannah River, had substantially greater P mineralization than the continuously freshwater tidal forested wetlands. Net P mineralization fluxes, P turnover rates, and extractable soil SRP concentrations were greatest where tidal forest converted to open oligohaline marsh. Soil P turnover rate was correlated with the multivariate salinification/microbes PCA component, with faster turnover of P associated with greater salinification. Specifically, faster turnover of soil P was positively correlated with increased soil conductivity. Rates of P turnover increased only when extractable soil conductivity exceeded 10 mS cm^{-1} . Sundareshwar and Morris (1999) also found that the increase in ionic strength along salinification gradients decreased the capacity of soils to sorb P and increased porewater SRP concentrations of salt impacted compared to freshwater tidal wetland soils. Phosphorus turnover rate was not correlated with soil S content in the incubated soil suggesting that phosphate release was not related to Fe reduction resulting in the formation of FeS. This finding is in contrast to some studies that have shown that greater sulfate availability results in greater soil and sediment P release (Caraco et al. 1993; Portnoy and Giblin 1997; Lamers et al. 1998; Geurts et al. 2010), although another study also did not support this relationship (Dierberg et al. 2011). However, the amount of phosphate released was typically four orders of magnitude less than the amount of Fe present in the soils of this study,

suggesting low sensitivity to detecting a pattern between P mineralization and FeS formation.

Net P mineralization flux and P turnover rate were positively correlated with the inundation component. As would be expected with the mechanism of lowered redox driving phosphate release from soil (Bridgman et al. 1998; Surridge et al. 2007), P mineralization increased with greater water depth and inundation frequency. However, the relationship was unimodal with greatest P mineralization at moderate-to-high inundation (5 cm deep on average) or inundated around 50 % of the time. Water depth relative to soil surface and the frequency of inundation of sites increased towards the coast. Because the salinification/microbes and inundation gradients were statistically independent output of the principal components analysis, water depth and inundation frequency also describe landscape gradients in the impact of sea level rise on tidal wetland soils that were separate from salinification in this study.

Finally, soil P mineralization fluxes and turnover rates increased with soil pH. Soil pH decreased with salinification along both rivers. However, the greater acidity of salt impacted soils is likely an artifact of the method used to measure soil pH. Soils were first air dried and then rewetted to measure pH according to standard methods (Robertson et al. 1999). Drying the soils likely oxidized the pool of reduced S in salt impacted soils and lowered measured pH upon rewetting. We measured no change in soil pH along the salinification gradients when we did not first dry the soils (June incubation, unpublished data). Although the greatest P mineralization fluxes and turnover rates occurred in oligohaline marshes, which had the most acidic dried soils, overall few high P mineralization rates were observed at low pH. Instead, the greater P mineralization rates occurred in the more basic soils of the Savannah River due to a fundamental difference in rivers associated with their catchment geochemical characteristics.

Blackwater versus alluvial rivers

The geologic characteristics of catchments have large influence on river and floodplain biogeochemistry and geomorphology (Wharton et al. 1982; Junk and Furch 1993; Hupp 2000; Schilling and Lockaby 2006; Anderson and Lockaby 2007; Noe 2013). Blackwater rivers draining Coastal Plains have less suspended

sediment load and inorganic material, less ionic strength, lower pH, and more organic matter than alluvial rivers draining Piedmont or montane physiographic provinces (Beck et al. 1974). Floodplains of blackwater rivers have among the lowest recorded sedimentation rates due to their low suspended sediment availability (Hupp 2000). Floodplain soils of blackwater rivers also are more organic, acidic, and N and P deficient and have lower cellulose and lignin decomposition than those of alluvial rivers (Stanturf and Schoenholtz 1998; Entry 2000). Differences in soil attributes influence plant chemistry, with more P and a lower ratio of N:P in floodplain litterfall that is closer to optimum for plant productivity on alluvial compared to blackwater rivers (Schilling and Lockaby 2006). Consequently, floodplains of alluvial rivers have greater vegetative productivity than blackwater rivers (Junk and Furch 1993; Lockaby and Walbridge 1998; Schilling and Lockaby 2006).

The tidal wetland soil attributes in this study differed greatly between an alluvial and a blackwater river. The tidal floodplain soils of the blackwater Waccamaw River had less mineral content, lower pH, coarser soil texture, and more nitrate and less phosphate loading to the soil surface than those of the alluvial Savannah River. These differences in soil attributes are typical of the lower mineral sediment availability of blackwater rivers reported in the literature. Similarly, Kroes et al. (2007) found that deposited sediment in a tidal freshwater forested wetland on a blackwater river had much higher organic content and greater C:P than an upstream non-tidal forested wetland that received enhanced sedimentation due to watershed disturbance. Furthermore, the blackwater soils in this study were more salt impacted (greater conductivity and S), were inundated more frequently, and had deeper mean surface water than alluvial soils. Sediment starved blackwater tidal floodplain soils would accrete more slowly than the alluvial soils and therefore be more impacted by salinity incursions and sea level rise (Conner et al. 2007; Kirwan et al. 2010).

Differences in blackwater versus alluvial soil physicochemistry resulted in different patterns of P and N mineralization in the tidal forested wetlands. Net P mineralization flux and P turnover rate were much greater in alluvial than blackwater floodplain soils (250 and 125 % higher, respectively), indicating greater inorganic P release and P lability. The alluvial

soils also had greater extractable SRP concentrations (55 % higher), and greater SRP loading to the soil surface (81 % higher), than blackwater soils. Greater net P mineralization fluxes were associated with the multivariate gradient in soil mineral content. This soil mineral component was positively associated with soil P, Fe, and Al. Greater rates of net P mineralization flux ($\mu\text{mol P m}^{-2} \text{ day}^{-1}$) are likely due to the elevated concentrations of mineralizable P substrate in alluvial soils, as measured by soil TP, due to the fact that the turnover rate of soil P ($\text{mol P mol P}^{-1} \text{ day}^{-1}$) was constant across the gradient of soil mineral content. The modified resin core method (Noe 2011) for measuring net P mineralization accounts for the production of extractable SRP from both organic matter decomposition as well as reduction of metals that results in SRP desorption. The strong correlation of soil TP and Fe in this study, and the correlation of both with net P mineralization flux, suggests that reductive dissolution of Fe–P minerals was a likely source of much of the mineralized P (Patrick et al. 1973). Net P mineralization flux as well as P turnover rate also were greater in the finer textured (more clay, less sand) alluvial soils compared to blackwater soils. This multivariate gradient in soil texture was statistically independent of soil metal and P gradient as well as the soil moisture gradient. The lower porosity of finer textured soils may have limited oxygen inputs to the wetland soils resulting in lower redox (Groffman and Tiedje 1991). Ammonification, nitrification, and net N mineralization fluxes differed between rivers for some seasons, and nitrification differed between rivers for some sites. Although not significantly different for all seasons, the blackwater soils had 12 % greater net N mineralization fluxes and turnover rates than alluvial soils.

Together, these differences in N and P mineralization resulted in substantially varying nutrient stoichiometry. The average molar ratio of net N:P mineralized was 76 in the blackwater soils compared to 17 in the alluvial soils, or a difference of 352 %. The deficiency in P mineralization in the blackwater soils of the tidal forested wetlands of the Waccamaw River basin could impact plant production and be a generality in other blackwater forested wetlands. Schilling and Lockaby (2006) found that litterfall production was likely limited by P in blackwater forested wetlands. However, litterfall production was greater at the Waccamaw than the Savannah River sites

(Cormier et al. 2012), suggesting that the stoichiometry of soil nutrient mineralization might not always be as predictive of production as is litterfall nutrient stoichiometry (e.g., Schilling and Lockaby 2006). Nonetheless, the N content of litterfall along the two rivers was generally greater on the Waccamaw than the Savannah sites (Cormier et al. 2012), suggesting the alluvial Savannah sites had sufficient soil P availability to drive N limitation of plant production that resulted in greater N resorption proficiency (and less N in litterfall).

Microtopography

Wetland microtopography is known to have large influences on ecosystem processes, from plant diversity to biogeochemistry (Werner and Zedler 2002; Bruland and Richardson 2005; Moser et al. 2007, 2009; Ahn et al. 2009; Wolf et al. 2011). Hummock and hollow microtopography is common in tidal freshwater forested wetlands (Day et al. 2007). This microtopography creates large heterogeneity in water-table elevation relative to the soil surface and frequency of inundation (Day et al. 2007), and is the dominant gradient controlling plant distribution and species richness in these frequently inundated tidal wetlands (Rheinhardt 2007). Tree and herbaceous species in tidal freshwater forests are preferentially found on hummocks (and likely help build and maintain hummocks) compared to hollows (Duberstein and Conner 2009; Courtwright and Findlay 2011). Little is known about the nutrient biogeochemistry of hummocks compared to hollows in tidal freshwater forested wetlands (Anderson and Lockaby 2007), although hummocks have been shown to be more oxidizing than hollows (Courtwright and Findlay 2011).

We measured higher rates of net nitrification flux in the soils of hummocks compared to hollows, but no other measured soil nutrient fluxes or turnover rates differed. Hummocks and hollows differed more in their soil attributes, including more microbial nutrients, more P and metals, more clay, less silt, and less nitrate loading to the soil surface in hummocks. The higher elevation of hummocks leads to less frequent inundation (Day et al. 2007; Rheinhardt 2007), likely increasing oxygen availability (Courtwright and Findlay 2011) to nitrifying soil bacteria. Enhanced production of nitrate in the soils of hummocks could be

meaningful given the apparently strongly reducing conditions in tidal freshwater forested wetlands that generally leads to little nitrification (only 3 % of total inorganic N production). Hotspots of nitrate production in hummock soils could lead to enhanced denitrification (Wolf et al. 2011) and root N uptake (Jones et al. 2000). Despite greater rates of nitrate production inside incubating resin cores (which sever roots) located in hummocks, inputs of nitrate to the soil surface of hummocks were less than hollows by an equal amount. As a result of equal inputs of nitrate to their soils, concentrations of soil extractable nitrate in ambient soils were similar in both hummocks and hollows. Nor did concentrations of ambient soil extractable ammonium differ, although the small amount of ammonium substrate needed for the elevated production of nitrate in hummocks relative to the large standing stock of ammonium would make detection of depleted ammonium difficult.

Although microtopographic heterogeneity is common in freshwater tidal forested wetlands, the landscape distribution of hummock/hollow patterning is not clear. Along both the Savannah and Waccamaw rivers, hummocks are present at the continuously freshwater tidal forested sites but are not present at forested sites that have had low level salinification (>1 ppt) nor adjacent oligohaline marshes. However, hummock/hollow microtopography is present in some mesohaline marshes associated with herbaceous tussock formation (Stribling et al. 2007). Hummocks also diminish in height and then are not present as tidal fluctuations diminish upstream near the limit of floodplain inundation by tides in many tidal freshwater rivers (Rheinhardt 2007, personal observations by the authors). The loss of hummocks due to salinity incursions into tidal freshwater forests would decrease the ecosystem services of coupled N processes that lead to enhanced denitrification as well as plant diversity.

Conclusions

First, long-term salinification increased rates of net N and P mineralization fluxes and turnover in tidal freshwater forested wetland soils, most likely through tree stress and senescence (for N) and conversion to oligohaline marsh (for P). Stimulation of N and P mineralization by salinification was apparently

unrelated to inputs of sulfate or direct effects of increased soil conductivity (for N). Second, the tidal wetland soils of an alluvial river mineralized more P relative to N than a blackwater river. These strong differences in soil N and P availability were associated with many differences in soil characteristics and likely had impacts on productivity and nutrient cycling in tidal river floodplains. Third, microtopography increased nitrification flux which could lead to enhanced N cycling and plant production. However, hummock and hollow patterning was not present at locations with low level salinification. These findings add to knowledge of the responses of tidal freshwater ecosystems to sea level rise and salinification. Very little information has been published on the biogeochemistry of tidal freshwater forested wetlands (Anderson and Lockaby 2007), although slightly more is known about tidal freshwater marshes (Megonigal and Neubauer 2009). These patterns of altered N and P mineralization along salinification gradients provide necessary information on the consequences of state changes in coastal ecosystem structure and function (Brinson et al. 1995) that is needed to project the change in tidal freshwater wetland characteristics and ecosystem services in response to global change (Craft et al. 2009; Neubauer and Craft 2009).

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