

# Biogeochemical effects of simulated sea level rise on carbon loss in an Everglades mangrove peat soil

Lisa G. Chambers · Stephen E. Davis ·  
Tiffany Troxler · Joseph N. Boyer ·  
Alan Downey-Wall · Leonard J. Scinto

Received: 31 July 2013 / Revised: 15 November 2013 / Accepted: 21 November 2013  
© Springer Science+Business Media Dordrecht 2013

**Abstract** Saltwater intrusion and inundation can affect soil microbial activity, which regulates the carbon (C) balance in mangroves and helps to determine if these coastal forests can keep pace with sea level rise (SLR). This study evaluated the effects of increased salinity (+15 ppt), increased inundation (−8 cm), and their combination, on soil organic C loss from a mangrove peat soil (Everglades, Florida, USA) under simulated tides. Soil respiration (CO<sub>2</sub> flux), methane (CH<sub>4</sub>) flux, dissolved organic carbon (DOC) production, and porewater nutrient concentrations

were quantified. Soil respiration was the major pathway of soil organic C loss (94–98%) and was approximately 90% higher in the control water level than the inundated treatment under elevated salinity. Respiration rate increased with water temperature, but depended upon salinity and tidal range. CH<sub>4</sub> flux was minimal, while porewater DOC increased with a concomitant, significant decline in soil bulk density under increased inundation. Porewater ammonium increased (73%) with inundation and soluble reactive phosphorus increased (32%) with salinity. Overall, the decline in soil organic C mineralization from combined saltwater intrusion and prolonged inundation was not significant, but results suggest SLR could increase this soil's susceptibility to peat collapse and accelerate nutrient and DOC export to adjacent Florida Bay.

Handling editor: K. W. Krauss

L. G. Chambers (✉)  
Earth and Atmospheric Sciences, Saint Louis University,  
104D O'Neil Hall, 3672 Lindell Blvd, Saint Louis,  
MO 63108, USA  
e-mail: chamberslg@slu.edu

S. E. Davis  
Everglades Foundation, Palmetto Bay, FL, USA

T. Troxler · L. J. Scinto  
Southeast Environmental Research Center, Florida  
International University, Miami, FL, USA

J. N. Boyer  
Center for the Environment, Plymouth State University,  
Plymouth, NH 03264, USA

A. Downey-Wall  
Department of Life Sciences,  
Texas A&M University - Corpus Christi, 6300 Ocean  
Drive, Corpus Christi, TX 78412, USA

**Keywords** Soil carbon · Sea level rise ·  
Everglades · Mangrove · Saltwater intrusion ·  
Greenhouse gas production

## Introduction

Mangroves, a type of forested coastal wetland found in the tropics, have higher rates of net primary production and carbon (C) sequestration than most forested ecosystems, with global estimates of 882,200 and 102,300 Mg C km<sup>−2</sup>, respectively (Bouillon et al., 2008; Donato et al., 2011). In addition to functioning

as a sink for atmospheric C, mangroves provide vital ecosystem services such as preventing shoreline erosion, transforming, degrading, and sequestering nutrients and pollutants, and serving as nursery habitat for many commercially important fisheries (e.g., Marshall, 1994; Rivera-Monroy & Twilley, 1996). Despite their ecological importance, mangroves have been lost globally at a rate of 0.7–2.1% annually due to human activities (e.g., shoreline development, wood harvest, and mariculture) and environmental stressors, such as sea level rise (SLR) (Valiela et al., 2001; Spalding et al., 2010). Global climate change could result in the loss of 10–15% of total mangrove area due to the cumulative impacts of SLR, and changes in atmospheric CO<sub>2</sub> concentration, temperature, storm frequency and intensity, and precipitation patterns (Alongi, 2008).

Global sea level is currently rising at a rate of 2.8–3.1 mm year<sup>-1</sup>, causing many coastal ecosystems to be exposed to saltwater intrusion and prolonged tidal inundation (IPCC, 2007). Coastal wetlands (including mangroves) have a natural feedback mechanism, which allows them to “keep pace” with SLR. The increasing height of the ocean enhances the transport and deposition of tidal sediments and nutrients, which accelerates above and belowground primary production and organic matter accumulation. This ultimately facilitates vertical accretion of wetland soils and helps maintain an optimal elevation relative to sea level (Morris et al., 2002; McKee et al., 2007; McKee, 2011). Local abiotic factors, such as tidal range and nearshore sediment supply, and the rate of SLR may be used to predict whether this feedback mechanism will be successful at preventing the submergence and loss of a coastal wetland (Nicholls et al., 1999; Alongi, 2008; Kirwan et al., 2010). However, vertical accretion ultimately hinges upon the ability of a wetland to accumulate and store soil C, a function of the balance between C inputs (primary production and deposition/accretion) and C loss (microbial respiration and export). One study indicates that approximately 60% of organic C inputs to mangroves are retained in the sediments (Alongi et al., 2001), but increases in salinity and inundation associated with SLR have the potential to alter both C inputs and losses.

Organic C inputs can be altered by SLR as a result of mangrove species’ tolerance and growth response to changes in salinity (e.g., Naidoo, 1985; Aziz & Khan,

2001; Sherman et al., 2003) or general shifts in plant community composition (Saha et al., 2011). In some mangroves, C inputs are compensating for SLR through soil accretion, which is meeting or exceeding the current rate of SLR (Gaiser et al., 2006; Smoak et al., 2012). However, acceleration in rate of SLR could reduce the resiliency of all coastal wetlands (Moorhead & Brinson, 1995; FitzGerald et al., 2008; Kirwan et al., 2010). Few studies have investigated how SLR affects the rate of C loss from the soil, especially the organic carbon (OC) pool. According to a laboratory study, >97% of soil OC losses in coastal wetlands result from microbial respiration (CO<sub>2</sub> flux), while export of dissolved OC (DOC) and methanogenesis (CH<sub>4</sub> flux) account for <3% of OC losses (Chambers et al., 2013). This makes understanding the response of soil microbial activity to changes in salinity and inundation critical to predicting how soil C storage is impacted by SLR.

Increasing salinity introduces two opposing chemical regulators on microbial activity. First, greater ionic strength may cause non salt-adapted microbial species to experience osmotic stress, interruptions in cellular function, and cell lysis (e.g., Rietz & Haynes, 2003; Wichern et al., 2006). Coastal wetland soils unaccustomed to high ionic strength exhibit a short-term suppression of CO<sub>2</sub> flux following salt additions (Chambers et al., 2011). However, microbial populations also appear to have a high capacity to adapt to salinity as the identity and abundance of individual species can shift rapidly in response to salt tolerance, substrate type, and nutrient availability (Capone & Kiene, 1988; Ikenaga et al., 2010).

Conversely, the abundance of sulfate (SO<sub>4</sub><sup>2-</sup>) in seawater has been shown to stimulate CO<sub>2</sub> flux in coastal wetland soils due to its ability to function as an alternative electron acceptor during anaerobic respiration (Weston et al., 2006; Chambers et al., 2011). Several studies have shown sulfate reduction to be the dominant pathway of microbial respiration in saline wetlands (Howarth, 1984; Weston et al., 2006; Kristensen et al., 2008). The higher energy yield of sulfate reducers, compared to methanogens, serves to promote anaerobic respiration, thereby reducing CH<sub>4</sub> flux in coastal wetlands (Jakobsen et al., 1981; DeLaune et al., 1983). The reduction in CH<sub>4</sub> emissions with increasing salinity is beneficial from the perspective of greenhouse gas emissions as CH<sub>4</sub> has a global warming potential ~25× greater than CO<sub>2</sub> (IPCC, 2007).

However, it is the net sum of all soil OC losses that will influence the sustainability of mangroves during SLR.

Prolonged inundation may enhance the rate of the initial leaching phase of mangrove litter decomposition, but the heterotrophic hydrolysis of more complex OC compounds tends to be slower under anaerobic conditions, compared to aerobic conditions (Kristensen et al., 1995, 2008). In coastal wetland soils, inundation and dry-down are linked to tidal cycles (lunar and wind) and the rate of CO<sub>2</sub> loss during low tide can be 50–300% greater than during high tide (Chambers et al., 2013). Extended periods of inundation in coastal wetlands are also correlated with the accumulation of hydrogen sulfide (HS<sup>-</sup>), a by-product of sulfate reduction that is known to reduce plant growth and inhibit key microbial processes such as nitrification (Koch et al., 1990; Joye & Hollibaugh, 1995). This suggests deeper, more prolonged periods of tidal inundation could reduce soil OC loss by slowing microbial respiration and disrupting other biogeochemical processes (e.g., N cycling) that are tightly coupled with OC mineralization rates.

Despite a growing understanding of the effects of salinity (Weston et al., 2006; Edmonds et al., 2009; Chambers et al., 2011; Weston et al., 2011) and inundation (Neubauer et al., 2000; Chambers et al., 2013) on coastal wetland OC loss, there is still a significant gap in discriminating between the individual and interactive effects of increases in salinity and inundation. This is of special concern in the Everglades (Florida, USA) where SLR is combined with past and proposed changes in the quantity of freshwater delivery to coastal areas, which could decouple the simultaneous increases in salinity and inundation normally anticipated with SLR (Harvey & McCormick, 2009). The goal of this study was to expose mangrove peat soils to increases in salinity, inundation, or both, in mesocosms that simulated tidal conditions and quantify the effect on soil OC losses through microbial respiration (CO<sub>2</sub> flux), methanogenesis (CH<sub>4</sub> flux), and porewater DOC production. Porewater nutrient concentrations were measured to assess the potential impact of the treatment conditions on N and P availability, which also influence microbial activity, and thus the rate of mineralization. Based on previous studies, we hypothesized that increasing salinity would accelerate soil OC loss through greater sulfate reduction, while increasing inundation would reduce OC loss by creating longer period of anaerobiosis; the combined

effects of increasing both salinity and inundation would be additive and result in no significant change in the rate of soil OC loss.

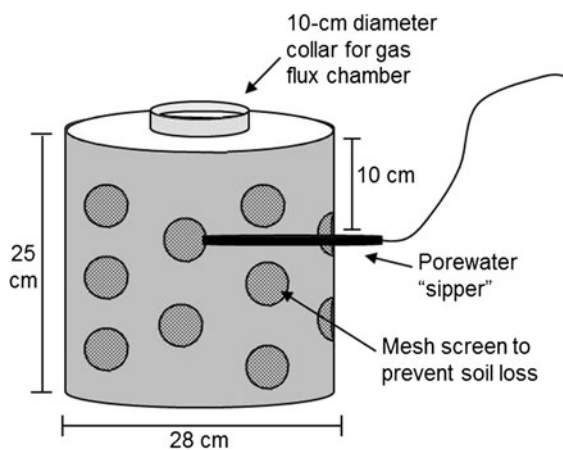
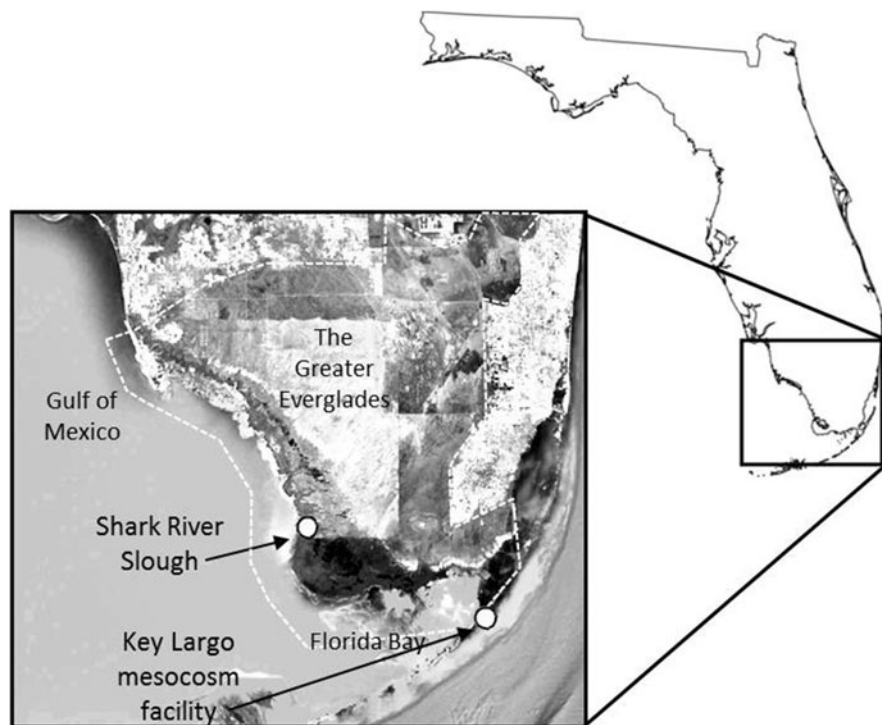
## Methods

### Study area and experimental facilities

In August 2011, 24 peat monoliths were collected from a mature mangrove forest adjacent to lower Shark River (Fig. 1; Florida Coastal Everglades Long-Term Ecological Research (LTER) site SRS 6) in the SW Everglades. The collection area is approximately 4 km inland from the Gulf of Mexico and experiences semi-diurnal tides (mean range of 1 m) and seasonally driven (June–October) freshwater inputs (Rivera-Monroy et al., 2007). The forest is composed of *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans* of large stature (10–14 m tall) (Chen & Twilley, 1999). The peat monoliths (approximately 25 cm deep × 28 cm diameter) were removed from the ground intact, and carefully placed in perforated buckets (Fig. 2). This was achieved by a team of three people using shovels to excavate an area of soil slightly larger than the size of the bucket, and then carrying the monolith to a platform where it was shaved-down to the exact diameter and height of the bucket, and placed inside. Once all 24 samples were collected, they were transported by boat and car to the experimental facility. At the time of collection, ambient salinity at Shark River Slough was ~17 ppt, a typical salinity for this site during the wet season (Chen & Twilley, 1999).

The monoliths were taken to an outdoor tidal mesocosm facility located at the Florida Bay Inter-agency Science Center (Key Largo, Florida USA). The Key Largo mesocosm facility consists of 12 large rectangular tanks (0.7 m D × 0.8 m W × 2.2 m L), each equipped with a water inflow, a standpipe with a ball-valve spigot to manipulate high tide and low tide water levels, and an outflow drain. Four 2,500 gal (9.46 m<sup>3</sup>) head tanks are located on an adjacent earthen mound and deliver water via gravity flow through a system of PVC pipes to a manifold. The manifold allowed for the manual mixing of water from multiple head tanks, and the delivery of water to individual mesocosms.

**Fig. 1** Location map (Florida, USA) and aerial photograph indicating where the peat monoliths were collected [Shark River Slough (25°21'52.7"N, 81°4'40.6 W)] and where the experiment took place [Florida Bay Interagency Science Center (25°5'9.21"N, 80°27'6.9"W)]. The white dashed line represents an unofficial approximation of the extent of the greater Everglades ecosystem



**Fig. 2** Schematic of the peat monolith design. Standard window screen mesh was wrapped around the sides of the monolith to prevent soil loss through the bucket perforation, but the soil surface was not covered. A porewater “sipper” was inserted into the center of the peat monolith (−10 cm depth) from the side of the bucket and a 10-cm diameter collar was centrally located

### Experimental design

The experiment consisted of a randomized split-plot design with repeated observations. The two manipulated factors were salinity (the whole-plot factor with

two nested blocks) and inundation (the subplot factor). Water temperature (°C) in each mesocosm was recorded twice daily and during CO<sub>2</sub> flux measurements as a potentially important covariant. The study ran for 10 weeks, which included a 3-week acclimation period, 1-week salinity ramp, and a 6-week experimental period.

Upon arrival of the monoliths at the mesocosm facility, standard window screen mesh was affixed to the outside of the buckets to allow for water exchange through the perforations, while preventing the loss of soil material (Fig. 2). If pneumatophores (modified mangrove root structures) were present, they were clipped at the soil surface, and any identifiable fresh litter was removed to leave a bare soil surface. The 24 monoliths were randomly assigned to one of four mesocosms (six monoliths in each) and one of two water levels nested within each mesocosm (three subplot water level replicates in each mesocosm). The monoliths assigned to the “control” water level treatment were placed on 8 cm tall risers, while those assigned to the “inundated” treatment were placed directly on the mesocosm floor. At these elevations, the soil surface of the control water level monoliths was approximately halfway between the high and low tide water levels (with roughly 13 cm of soil exposed

at low tide), while the soil surface of inundated treatments was 8 cm lower within the tidal range, having ~5 cm of soil exposed at low tide.

A 10-cm diameter polyvinyl chloride (PVC) collar (10 cm height) was inserted near the center of each peat monolith and left for the duration of the experiment. Collars were used for placement of a portable 10-cm diameter gas chamber used to collect CO<sub>2</sub> and CH<sub>4</sub> flux measurements. The centralized placement of the collars reduced the likelihood of any soil profile disturbance within the gas flux sampling area. A porewater sipper was also inserted through the side bucket perforations into the center of each peat monolith at a depth of -10 cm from the soil surface. The sipper consisted of a 5 cm long air stone (1 cm diameter) attached to a 1-m long sample tube. Oxidation–reduction probes were also installed in a subset of ten soil cores at a depth of -10 cm. Once the monoliths were placed in the mesocosms at their respective inundation heights, all four tanks were initially filled with “ambient” salinity surface water (15–20 ppt; see description of salinity treatments below). Semi-diurnal tides (every 6 h), with a 20-cm tidal range, began immediately and continued throughout the entire study. During each ebb tide, water flowed through the mesocosms and was discharged into Florida Bay, with new water added during the rising tide. The monoliths were allowed to acclimate at ambient salinity for 3 weeks; this acclimation period allowed any live root biomass severed during soil collection to degrade, minimizing collection effects during the experimental phase. During the acclimation phase, CO<sub>2</sub> flux measurements were collected every 3 days, allowing us to document a peak in C mineralization directly following the initial collection, which slowly declined and reached a steady state between 2 and 3 weeks.

To apply the salinity treatments, two head tanks were designated as “saltwater,” and were filled with surface water pumped directly from adjacent Florida Bay (~60 m away). Salinities in Florida Bay vary seasonally, ranging from 24 to 42 ppt (Kelble et al., 2007). The other two head tanks were designated as “freshwater,” and were regularly filled with surface water trucked from a nearby canal (C-111) that feeds freshwater to the coastal Everglades. Due to the challenge of maintaining constant head pressure in the tanks during the filling of the mesocosms, a double Hartford Loop was

constructed using two of the unused mesocosms, two raised water barrels equipped with stand-pipe drains, and multiple aquarium pumps to circulate the water between the holding reservoirs. This piping arrangement insured water flowed at the same rate into each of the mesocosms. Following the 3-week acclimation period, the two mesocosms assigned to the elevated salinity treatment were gradually ramped-up (~2 ppt day<sup>-1</sup>) to between 30 and 35 ppt for the remainder of the study. The remaining two mesocosms continued to receive ambient salinity (15–20 ppt) surface water. All mesocosms were partially shaded with three layers of mesh window screen. This was done to simulate natural conditions under a canopy of full-size trees where the peat soils are rarely exposed to full sunlight or full shade.

#### Soil and water properties

Oxidation–reduction potential was measured once a week approximately 1 h after low tide and high tide water levels were reached during a single tidal cycle. Soil properties were determined for five initial soil cores (5 cm diameter × 25 cm deep) collected at the same place and time as the peat monoliths. At the conclusion of the 10-week study, all 24 peat monoliths were destructively sampled for analysis of soil properties. Intact soil cores were collected at the soil collar locations using a 10-cm diameter, 25-cm long PVC core tube. The soils were divided into three depth increments (0–5, 5–15, and 15–25 cm) and analyzed for percent moisture, bulk density, percent organic matter, total C, and total N. Moisture content and bulk density were determined after drying a subsample at 70°C until constant weight. Organic matter (%) was estimated by mass loss on ignition (LOI) where dry soils were combusted at 550°C for 5 h and final weight was subtracted from initial weight. Total C and N content were determined using a Carlo-Erba elemental analyzer (CE Elantech, Inc., Lakewood, NJ, USA). Surface water salinity and temperature in the mesocosms was recorded twice daily at high tide and during CO<sub>2</sub> flux measurements using a handheld YSI (YSI Inc., Yellow Springs, OH, USA). General water quality parameters [NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, soluble reactive phosphorus (SRP), and DOC] of the source water were gathered from near-by long-term monitoring stations (see Table 1 caption).



**Table 1** Properties of the fresh source water and salt source water mixed to achieve the desired salinities in the mesocosms during the 10-week study

	Freshwater	Saltwater
Salinity (ppt)	<0.5 <sup>a</sup>	38.20 ± 2.50 <sup>b</sup>
NO <sub>3</sub> <sup>-</sup> (mg l <sup>-1</sup> )	5.76 ± 3.51 <sup>a</sup>	0.02 ± 0.01 <sup>b</sup>
NH <sub>4</sub> <sup>+</sup> (mg l <sup>-1</sup> )	2.41 ± 0.71 <sup>a</sup>	0.11 ± 0.08 <sup>b</sup>
SRP (mg l <sup>-1</sup> )	0.02 ± 0.001 <sup>a</sup>	0.001 ± .001 <sup>b</sup>
DOC (mg l <sup>-1</sup> )	7.15 ± 0.42 <sup>a</sup>	6.71 ± 0.32 <sup>a</sup>

Values represent mean ± standard deviation. Different letters represent significantly different means based on a one-way ANOVA ( $P < 0.05$ ). Saltwater data from DB Hydro ([www.sfwmd.gov](http://www.sfwmd.gov)) site FLAB24; freshwater data courtesy of T. Troxler (Florida International University) site JB (25°13'57.7"N, 80°31'28.4"W)

SRP soluble reactive phosphorus, DOC dissolved organic carbon

### CO<sub>2</sub> and CH<sub>4</sub> flux

Soil respiration (CO<sub>2</sub> flux) was measured ~3 times per week at daytime low tide for all 24 monoliths using a portable infrared gas analyzer (Li-Cor 8100, Lincoln, NE, USA) equipped with a 10-cm diameter chamber. Each flux rate was collected for 75 s before manually moving the chamber to another sample collar. Nighttime CO<sub>2</sub> flux was measured weekly on all monoliths at low tide using the same procedure in order to isolate respiration from the possible confounding effects of photosynthesis during the daytime measurements. Rising and falling tide CO<sub>2</sub> flux measurements were also obtained weekly on a subset of 12 soils (three from each treatment condition) for the 3 h immediately before and after daytime low tide. This involved 3–6 consecutive flux readings on each soil as the tide was rising and falling while concurrently measuring and recording the exact height of soil exposed above the water line at the time of each reading. This was conducted to determine if the physical movement of the water level within the soils was influencing CO<sub>2</sub> flux rates.

Methane (CH<sub>4</sub>) flux was measured once a week on a subset of monoliths using the 10-cm diameter chamber and 8100-664 Trace Gas Sampling Kit (Li-Cor, Lincoln, NB), which allowed in-line gas extraction. This type of sampling captured all CH<sub>4</sub> emitted from the soil to the atmosphere (e.g., diffusive and ebullition fluxes). The chamber was sealed for 20 min and 5 ml gas samples were extracted at 5 min intervals and

transferred to a 5 ml glass vial (previously capped with a butyl stopper and aluminum crimp-cap and evacuated to -75 kPa). Within 48 h of collection, CH<sub>4</sub> gas samples were run on a gas chromatograph (Shimadzu Scientific Instruments GC 8A, Columbia, MD, USA) fitted with a flame ionization detector (FID). CH<sub>4</sub> flux was calculated as the slope of CH<sub>4</sub>-C concentration over time.

### DOC and porewater nutrients

60 ml of porewater was extracted once per week during high tide from each of the monoliths by applying suction to the airstone in the center of the soil with a plastic syringe. Water was field-filtered through 0.45 µm membrane filters, transferred to a 60-ml acid-washed HDPE bottle, and stored at -20°C until analysis (within 30 days). Porewater was analyzed for NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup> (collectively DIN), SRP, and DOC at the Southeast Environmental Research Center, Nutrient Analysis Laboratory. SRP and DIN parameters were analyzed on a four-channel Alpkem RFA 300 auto-analyzer (OI Analytical, College Station, TX, USA) and DOC using a Shimadzu 5000 TOC (Shimadzu Scientific Instruments, Columbia, MD, USA).

### Data analysis

Statistical analysis was performed using SAS 9.3 software (SAS Institute Inc., Cary, NC, USA). Generalized mixed models (Proc GLIMMIX) were used to examine the relationship among day CO<sub>2</sub>, night CO<sub>2</sub>, CH<sub>4</sub>, redox, DOC, NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, and SRP and the independent variables of salinity, inundation, time, and temperature within the 24 soil core samples. Due to the fact that time and temperature were highly correlated (spearman's  $\rho > 0.75$ ,  $P < 0.001$  for all outcomes) we examined time and temperature in separate models. The presentation of results focuses on the outcomes for time, with the separate outcomes for temperature only presented if they deviated significantly from those of time. For the non-repeated variables, organic matter content, total C, total N, and bulk density, the same mixed model was used excluding the time and temperature variables. A two-way ANOVA (Proc GLM) was used to determine differences in total OC cycling and a one-way ANOVA evaluated differences between source water parameters. To investigate differences in the

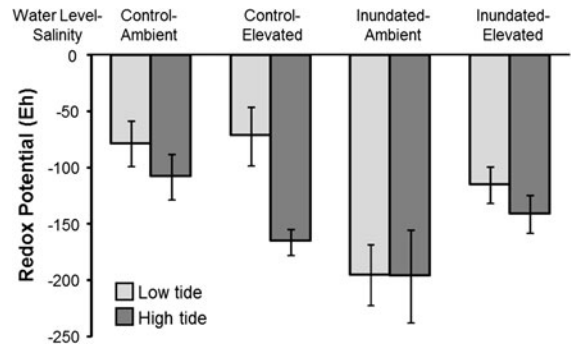
rate of CO<sub>2</sub> flux based on the amount (cm) of exposed soil during rising and falling tides, a linear regression was used to estimate the slope, and a two-way ANOVA model applied to determine differences among treatments. ANOVA models were used only when missing data points prevented the use of the full mixed model to analyze non-repeated measures. Pearson's Product correlations were performed to determine correlation coefficients among CO<sub>2</sub> flux, DOC production, porewater nutrients, and environmental variables. All analyses used a significance factor of  $\alpha = 0.05$ .

## Results

### Soil and water properties

Surface water salinity in all four mesocosms was  $17.4 \pm 0.9$  ppt (mean  $\pm$  standard deviation) for the first 3 weeks of the study (the acclimation period). Following the salinity ramp-up in the elevated salinity mesocosms, salinities were  $16.6 \pm 0.8$  and  $32.6 \pm 1.1$  ppt in the ambient and elevated salinity treatments, respectively, for the remaining 6-week study period. Nutrient concentrations were significantly higher in the fresh source water (Table 1), but were always diluted by mixing with seawater to achieve the ambient (15–20 ppt) and elevated (30–35 ppt) salinities used in the experiment. The control water level treatment had some portion of the soil exposed to the air approximately 12 h each day, while the inundated treatment soils were exposed to the air  $\sim 7$  h each day.

Soil redox potential at  $-10$  cm indicated all soils were under reduced conditions, ranging from  $-171$  to  $-588$  Eh (Fig. 3). The outcome redox for full mixed model analysis with time indicated tide (i.e., whether the redox measurement was recorded at high tide or low tide) was the only significant effect ( $P = 0.002$ ) with high tide redox values ( $-388.2 \pm 76.9$  Eh) being lower than low tide values ( $-352.3 \pm 86.2$  Eh) (Table 2). The final soil bulk density was significantly higher in the control water level treatments ( $0.20 \pm 0.04$ ), compared to the inundated treatments ( $0.18 \pm 0.02$ ;  $P = 0.009$ ) and was greater at 0–5 cm, compared to deeper in the soil profile ( $P < 0.001$ ). Raw data (according to depth) are presented in Table 3 and full mixed model results are available in Table 2.



**Fig. 3** Soil oxidation reduction (redox) potential readings taken at a depth of  $-10$  cm are presented according to treatment condition (control water level =  $-13$  cm low tide; inundated water level =  $-5$  cm low tide; ambient salinity = 15–20 ppt; elevated salinity = 30–35 ppt) and tidal condition. Bars represent mean ( $n = 11$ ); error bars represent standard error

Average organic matter content in the peat soils was  $53 \pm 7\%$ , total N averaged  $1.3 \pm 0.3\%$ , and total C averaged  $22 \pm 4\%$ . All three properties were significantly lower ( $P < 0.001$ ) in the surface soil (0–5 cm) compared to deeper in the soil profile and were not affected by inundation or salinity treatment. Soil pH was between 7.8 and 8.0.

### CO<sub>2</sub> and CH<sub>4</sub> flux

Within the elevated salinity condition, daytime low tide CO<sub>2</sub> flux rate was significantly higher at the control water level ( $1,189 \pm 699$  mg CO<sub>2</sub>-C m<sup>-2</sup> day<sup>-1</sup>), compared to the inundated water level ( $625 \pm 484$  mg CO<sub>2</sub>-C m<sup>-2</sup> day<sup>-1</sup>;  $P < 0.001$ ), but the main effect of salinity was not significant (Table 2). Time also had a significant effect on daytime CO<sub>2</sub> flux ( $P < 0.001$ ) that was confounded with temperature ( $r = -0.887$ ,  $P < 0.001$ ; Fig. 4). When temperature was considered instead of time in the model, there was a significant interaction among salinity, inundation, and temperature ( $P = 0.043$ ), such that within the elevated salinity condition, the polynomial relationship between temperature and the control water level treatment was different than the relationship with the inundated water level treatment (Fig. 5).

Nighttime CO<sub>2</sub> flux was significantly higher at the control water level ( $1,268 \pm 693$  mg CO<sub>2</sub>-C m<sup>-2</sup> day<sup>-1</sup>), compared to the inundated water level ( $802 \pm 462$  mg CO<sub>2</sub>-C m<sup>-2</sup> day<sup>-1</sup>;  $P = 0.027$ ). Time also had a significant effect on nighttime CO<sub>2</sub> flux ( $P < 0.001$ ) that was confounded

**Table 2** Full statistical results for the generalized mixed model run with time as an independent variable

	Day CO <sub>2</sub> flux	Night CO <sub>2</sub> flux	CH <sub>4</sub> flux	Redox	DOC	NO <sub>3</sub> <sup>-</sup>	NO <sub>2</sub>	NH <sub>4</sub> <sup>+</sup>	SRP
Salinity	$F(1,20) = 1.8$ $P = 0.189$	$F(1,20) = 1.24$ $P = 0.278$	$F(1,9) = 0.00$ $P = 0.958$	$F(1,6) = 1.02$ $P = 0.349$	$F(1,20) = 1.43$ $P = 0.246$	$F(1,20) = 4.37$ $P = 0.038$	$F(1,20) = 0.86$ $P = 0.357$	$F(1,20) = 1.48$ $P = 0.237$	<b><math>F(1,20) = 4.53</math></b> <b><math>P = 0.046</math></b>
Inundation	$F(1,20) = 9.20$ $P = 0.007$	<b><math>F(1,20) = 5.71</math></b> <b><math>P = 0.027</math></b>	$F(1,9) = 0.69$ $P = 0.427$	$F(1,6) = 3.77$ $P = 0.098$	<b><math>F(1,20) = 8.93</math></b> <b><math>P = 0.007</math></b>	$F(1,20) = 0.55$ $P = 0.460$	$F(1,20) = 0.52$ $P = 0.472$	<b><math>F(1,20) = 12.33</math></b> <b><math>P = 0.002</math></b>	$F(1,20) = 3.26$ $P = 0.086$
Time	<b><math>F(13,231) = 9.93</math></b> <b><math>P &lt; 0.001</math></b>	<b><math>F(6,113) = 17.06</math></b> <b><math>P &lt; 0.001</math></b>	$F(5,17) = 0.84$ $P = 0.541$	$F(4,61) = 1.92$ $P = 0.119$	<b><math>F(6,116) = 21.25</math></b> <b><math>P &lt; 0.001</math></b>	$F(6,116) = 8.65$ $P < 0.001$	$F(6,116) = 16.89$ $P < 0.001$	<b><math>F(6,116) = 5.32</math></b> <b><math>P &lt; 0.001</math></b>	$F(6,116) = 2.26$ $P = 0.042$
Salinity*inundation	<b><math>F(1,20) = 4.62</math></b> <b><math>P = 0.044</math></b>	$F(1,20) = 1.52$ $P = 0.232$	$F(1,9) = 0.29$ $P = 0.605$	$F(1,6) = 3.00$ $P = 0.132$	$F(1,20) = 0.36$ $P = 0.554$	$F(1,20) = 0.10$ $P = 0.748$	$F(1,20) = 0.10$ $P = 0.756$	$F(1,20) = 1.44$ $P = 0.244$	$F(1,20) = 0.49$ $P = 0.492$
Salinity*time	$F(13,231) = 1.42$ $P = 0.149$	$F(6,113) = 2.00$ $P = 0.072$	$F(5,17) = 0.53$ $P = 0.749$	$F(4,61) = 1.30$ $P = 0.279$	$F(6,116) = 0.07$ $P = 0.999$	<b><math>F(6,116) = 2.33</math></b> <b><math>P = 0.036</math></b>	$F(6,116) = 0.32$ $P = 0.925$	$F(1,116) = 0.32$ $P = 0.891$	$F(6,116) = 0.38$ $P = 0.891$
Inundation*time	$F(13,231) = 0.51$ $P = 0.919$	$F(6,113) = 1.90$ $P = 0.086$	$F(5,17) = 0.99$ $P = 0.455$	$F(4,61) = 1.00$ $P = 0.415$	$F(6,116) = 1.14$ $P = 0.345$	$F(1,116) = 0.94$ $P = 0.469$	$F(6,116) = 0.45$ $P = 0.845$	$F(6,116) = 1.96$ $PP = 0.077$	<b><math>F(6,116) = 2.98</math></b> <b><math>P = 0.010</math></b>
Salinity*inundation*time	$F(13,231) = 0.92$ $P = 0.536$	$F(6,113) = 1.08$ $P = 0.382$	$F(5,17) = 0.44$ $P = 0.776$	$F(4,61) = 0.98$ $P = 0.423$	$F(6,116) = 1.08$ $PP = 0.381$	$F(6,116) = 0.21$ $P = 0.972$	$F(6,116) = 0.21$ $P = 0.975$	$F(6,116) = 0.56$ $P = 0.759$	$F(6,116) = 1.11$ $P = 0.360$
Tide <sup>a</sup>				<b><math>F(1,61) = 10.35</math></b> <b><math>P = 0.002</math></b>					

Interpreted results are in bold. Note that time and temperature were highly correlated ( $P < 0.001$  for all outcomes) and were therefore examined in separate models. Outcomes for temperature produced the same significant results, unless otherwise noted in the text. Data presented as:  $F(\text{numerator degrees of freedom, denominator degrees of freedom}) = F \text{ value}, P = P \text{ value}$

<sup>a</sup> Interactions among tide and salinity, inundation, and time were also analyzed for Redox, but yielded no significant effects

SRP soluble reactive phosphorus, DOC dissolved organic carbon



**Table 3** Properties of the peat soils ( $t = \text{final}$ ) used in this study according to soil depth

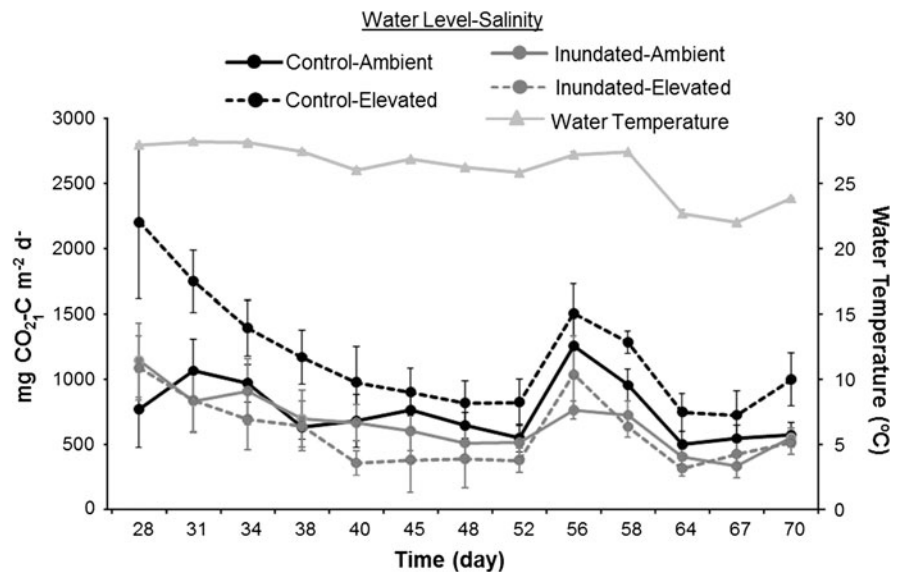
Soil depth	Bulk density ( $\text{g cm}^{-3}$ )	Organic matter (%)	Total N (%)	Total C (%)
0–5	$0.22 \pm 0.04$	$45.4 \pm 5.7$	$1.0 \pm 0.2$	$19.9 \pm 3.3$
5–15	$0.18 \pm 0.03$	$55.3 \pm 6.7$	$1.5 \pm 0.2$	$23.5 \pm 2.9$
15–25	$0.18 \pm 0.02$	$56.9 \pm 3.3$	ND	ND
Mixed model results <sup>a</sup>				
Salinity	$F(1,60) = 0.66$ $P = 0.421$	$F(1,60) = 1.25$ $P = 0.269$	$F(1,20) = 2.59$ $P = 0.123$	$F(1,20) = 3.82$ $P = 0.065$
Inundation	<b><math>F(1,60) = 7.28</math></b> <b><math>P = 0.009</math></b>	$F(1,60) = 1.30$ $P = 0.258$	$F(1,20) = 0.00$ $P = 0.970$	$F(1,20) = 0.00$ $P = 0.955$
Depth	<b><math>F(2,60) = 11.99</math></b> <b><math>P &lt; 0.001</math></b>	<b><math>F(2,60) = 31.3</math></b> <b><math>P &lt; 0.001</math></b>	<b><math>F(1,20) = 78.6</math></b> <b><math>P &lt; 0.001</math></b>	<b><math>F(1,20) = 32.17</math></b> <b><math>P &lt; 0.001</math></b>

Values represent mean  $\pm$  standard deviation. Mixed model data presented as:  $F(\text{numerator degrees of freedom, denominator degrees of freedom}) = F$  value,  $P = P$  value; interpreted results are bold

ND no data

<sup>a</sup> The mixed model also included terms for salinity\*inundation, salinity\*time, inundation\*time, and salinity\*inundation\*time, but produced no significant results

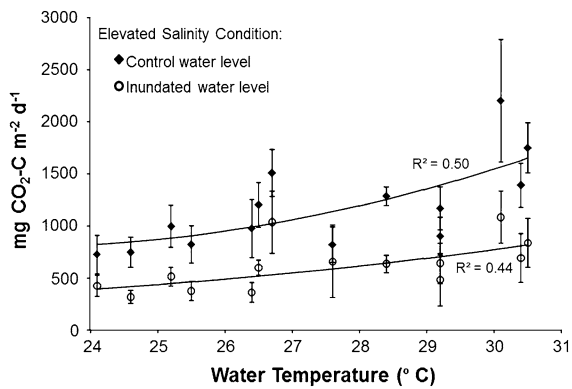
**Fig. 4** Relationship among daytime  $\text{CO}_2\text{-C}$  flux, water temperature, and time (experimental phase only) according to treatment condition. Points represent means; error bars represent standard error



with temperature ( $r = -0.855$ ,  $P < 0.001$ ), similar to the response of daytime  $\text{CO}_2$  flux. On average, nighttime  $\text{CO}_2$  flux rate was  $\sim 20\%$  higher than daytime flux rate, indicating the presence of photosynthetic activity on the soil surface during the experiment.

Rising and falling tides did not result in significant differences in the response of  $\text{CO}_2$  flux rate. The average slope (change in  $\text{CO}_2$  flux rate/change in cm of soil exposed above the waterline) was highest in the control

water level treatments ( $93\text{--}121 \text{ mg CO}_2\text{-C m}^{-2} \text{ day}^{-1}$ ) and lowest in the inundated-elevated salinity treatment ( $42\text{--}51 \text{ mg CO}_2\text{-C m}^{-2} \text{ day}^{-1}$ ), but was not significantly different when the tide was rising versus falling (Table 4). The full mixed model indicated no significant differences in  $\text{CH}_4$  flux between treatment conditions, time, or temperature (Table 2). On average, the inundated-ambient salinity treatment had the highest flux rate ( $27 \pm 77 \text{ mg CH}_4\text{-C m}^{-2} \text{ day}^{-1}$ ), followed by the inundated-elevated salinity treatment



**Fig. 5** Relationship between daytime  $\text{CO}_2\text{-C}$  flux and water temperature ( $^{\circ}\text{C}$ ) in the elevated salinity condition according to water level treatment. Points represent means; error bars represent standard error. Trend lines are polynomial fits with regression coefficients ( $R^2$  values) indicated

**Table 4** Relationship between  $\text{CO}_2\text{-C}$  flux rate ( $\text{mg m}^{-2} \text{day}^{-1}$ ) and cm of soil exposed above the water line during rising and falling tides; data presented according to treatment and tidal condition

Water level–salinity	Tide	Slope $\Delta \text{mg CO}_2\text{-C m}^{-2} \text{day}^{-1} / \Delta \text{cm soil exposed}$	Difference Rising – falling
Control–ambient	Rising	121.1	26.3
	Falling	94.8	
Control–elevated	Rising	93.0	–23.4
	Falling	116.4	
Inundated–ambient	Rising	74.4	–42.6
	Falling	117.0	
Inundated–elevated	Rising	41.8	–8.9
	Falling	50.7	

( $16 \pm 29 \text{ mg CH}_4\text{-C m}^{-2} \text{day}^{-1}$ ), the control water level–elevated salinity treatment ( $7 \pm 10 \text{ mg CH}_4\text{-C m}^{-2} \text{day}^{-1}$ ), and the control water level–ambient salinity treatment ( $0.2 \pm 0.7 \text{ mg CH}_4\text{-C m}^{-2} \text{day}^{-1}$ ). All soils had high within treatment variance that led to standard deviations greater than mean values.

#### DOC and porewater nutrients

Dissolved organic C concentration in the porewater was significantly higher ( $P = 0.007$ ) in the inundated condition ( $18.0 \pm 1.8 \text{ mg l}^{-1}$ ) compared to the

control water level condition ( $13.5 \pm 4.8 \text{ mg l}^{-1}$ ), and varied significantly with time ( $P < 0.001$ ; Table 2). DOC was also positively correlated with SRP and  $\text{NH}_4^+$  ( $P < 0.001$ ) concentrations. Porewater  $\text{NO}_3^-$  and  $\text{NO}_2^-$  both showed a significant salinity\*time interaction ( $P = 0.003$  and  $0.036$ , respectively). For  $\text{NO}_3^-$ , the ambient salinity treatment had higher concentrations on days 41 and 56, but lower concentrations than the elevated salinity treatment on day 62. For  $\text{NO}_2^-$ , the elevated salinity treatment was higher than the ambient salinity treatment on day 62. Ammonium concentrations were higher in the inundated condition ( $250.3 \pm 122.5 \text{ mg l}^{-1}$ ) than the control water level condition ( $144.4 \pm 67.0 \text{ mg l}^{-1}$ ;  $P = 0.002$ ) and also varied with time ( $P < 0.001$ ). Soluble reactive P was the only independent variable studied showing a significant main effect of salinity, with the elevated salinity treatment having higher porewater SRP ( $10.4 \pm 6.7 \text{ mg l}^{-1}$ ) than the ambient salinity treatment ( $7.9 \pm 4.2 \text{ mg l}^{-1}$ ). There was also a significant inundation\*time interaction for SRP, with earlier times (days 29 and 35) having higher SRP in the inundated condition, but no difference in SRP after day 35. Mean ( $\pm$ standard deviation) values for porewater nutrients according to the four treatment combinations are presented in Table 5.

#### Carbon budget

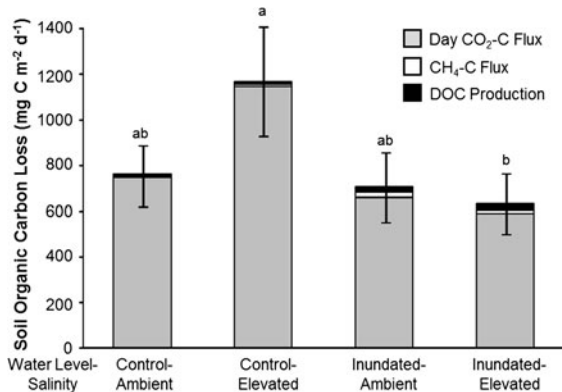
Combining the three pathways of soil OC loss (mean daily  $\text{CO}_2$  flux,  $\text{CH}_4$  flux, and DOC production  $\text{m}^{-2} \text{soil}$ ), indicates within the elevated salinity treatment, the control water level had higher rates of OC loss than the inundated water level (two-way ANOVA,  $P < 0.001$ ; Fig. 6). The majority (94–98%) of OC loss occurred through soil respiration, with  $\text{CH}_4$  flux and DOC production accounting for 0–4 and 1–4% of the total loss, respectively. Soil total C content in this peat soil averaged  $2,094 \pm 307 \text{ g C m}^{-2}$  in the top 0–5 cm, and  $6,332 \pm 1,198 \text{ g C m}^{-2}$  from 5 to 25 cm. Assuming active C cycling is confined to the upper 5 cm of soil, the three pathways measured in this study represent an average mass loss of  $3.1 \pm 1.4\%$  of the total soil C between 0 and 5 cm during the study period. The control water level–elevated salinity treatment had a significantly higher (two-way ANOVA,  $P = 0.016$ ) % total C mineralization over the study (4.5%), compared to the other three treatments (2.6%). However, these predictions of C mineralization may be significantly

**Table 5** Summary of soil porewater concentrations of DOC and various nutrients according to treatment condition

Water level–salinity	DOC (mg l <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> (mg l <sup>-1</sup> )	NO <sub>2</sub> <sup>-</sup> (mg l <sup>-1</sup> )	NH <sub>4</sub> <sup>+</sup> (mg l <sup>-1</sup> )	SRP (mg l <sup>-1</sup> )
Control–ambient	14.8 ± 1.6	1.65 ± 0.27	0.26 ± 0.05	141.6 ± 57.0	7.2 ± 2.3
Control–elevated	12.0 ± 2.9	1.29 ± 0.13	0.27 ± 0.06	140.9 ± 67.1	8.6 ± 3.7
Inundated–ambient	18.4 ± 4.2	1.51 ± 0.23	0.27 ± 0.08	211.7 ± 89.9	8.5 ± 3.0
Inundated–elevated	17.5 ± 5.0	1.26 ± 0.22	0.32 ± 0.13	287.7 ± 78.5	12.0 ± 3.0

Data indicates mean ± standard deviation; see mixed model results (Table 2) for significant differences

SRP soluble reactive phosphorus, DOC dissolved organic carbon



**Fig. 6** Mean rate of soil organic carbon loss via the three pathways measured, according to treatment condition. Bars represent means for daytime CO<sub>2</sub> flux ( $n = 310$ ), CH<sub>4</sub> flux ( $n = 44$ ), and DOC production ( $n = 163$ ); error bars represent standard error. Different letters represent significantly different means based on two-way ANOVA ( $P < 0.05$ )

underestimated because atmospheric CO<sub>2</sub> flux does not include the lateral transport of inorganic C (DIC), which can exceed DOC export by a factor of 3–10 (Bouillon et al., 2008).

## Discussion

### Soil and water properties

Sulfate reduction is normally the dominant pathway of anaerobic soil respiration in saline marshes and mangroves, accounting for 40–99% of total C mineralization and typically occurring at redox potentials between –100 and –150 mV (Patrick & DeLaune, 1977; Howarth, 1984; Kostka et al., 2002; Kristensen et al., 2008). The peat soils of this study were poised for sulfate reduction, with the inundated-ambient salinity treatment also being reduced enough to

support the highest rate CH<sub>4</sub> flux among the four treatment combinations (<–150 mV; Patrick & DeLaune, 1977). At a depth of –10 cm, the redox probes were above the elevation of the waterline in the control water level treatment during low tide, but below the waterline in the inundated treatment during low tide. However, the fact that all soils remained under reducing conditions during low tide suggests a relatively low soil hydraulic conductivity. The ability of highly decomposed peat to retain water against the pull of gravity has been demonstrated previously, and may decrease the importance of tidal fluctuations in coastal wetlands by continuing to promote anaerobic conditions even during low tides (Boelter, 1965). In this study, the average increase in CO<sub>2</sub> flux rate between high and low tide was 83 ± 10% in the control water level treatment and 57 ± 19% in the inundated treatment. The magnitude of this tidal effect on soil respiration rate is similar to that observed in a freshwater tidal marsh soil with a similar tidal range, but significantly lower than that of a brackish and salt marsh soil (Chambers et al., 2013). The low hydraulic conductivity exhibited by these mangrove peat soils may diminish the impact of slight changes in the duration of inundation caused by SLR on the rate of soil OC loss.

Initial soil bulk density was highest in the surface soils (0–5 cm), which is likely an artifact of a large quantity of storm-induced sediment deposition associated with hurricane Wilma in 2005 (Castaneda-Moya et al., 2010). A significant decrease in soil bulk density in the inundated treatment was observed during the study, which could be an indicator of soil's susceptibility to peat collapse, whereby the loss of soil C (through root death, erosion, etc.) compromises the soil structure and leads to rapid compaction and submergence (Portnoy & Giblin, 1997; Kool et al., 2006; Stagg & Mendelsohn, 2010). Past studies have

suggested the role of saltwater intrusion in promoting peat collapse (Davis et al., 2005), but our results indicate increased inundation may actually contribute more to changes in soil bulk density in this mesohaline mangrove. The removal of vegetation in the present study may have reduced the structural integrity of the soil, but does not explain why the decline in bulk density was only seen in the inundated treatment. Abiotic processes such as increased shear stress due to a deeper water column or the leaching of certain soil elements from excessive water-logging may have accelerated the loss of soil material in the inundated treatment (Craft et al., 2002; Stagg & Mendelsohn, 2010; Fagherazzi et al., 2012). With 20–30% of coastal wetlands predicted to be lost by 2100 as a result of SLR (Nicholls et al., 1999; IPCC, 2007), the possible role of inundation in initiating peat collapse warrants further investigation. Current rates of SLR are already expected to cause erosion of the seaward edge of Everglades' mangroves (Wanless et al., 1994) and a loss of bulk density under increased inundation could increase the susceptibility of the soil platform to break-up, especially during extreme events such as hurricanes.

#### CO<sub>2</sub> and CH<sub>4</sub> flux

Within the elevated salinity treatments, the average daytime CO<sub>2</sub> flux in the control water level condition was 90% higher than in the inundated condition. The alleviation of electron pressure (i.e., increased O<sub>2</sub> diffusion) during the lengthier period of low tide soil exposure in the control water level treatment, relative to the inundated treatment, likely contributed to this higher CO<sub>2</sub> flux rate (DeBusk & Reddy, 1998; Wright & Reddy, 2001). However, a similar inundation effect was not observed under ambient salinity, indicating the combination of a large tidal range and high salinity (i.e., high SO<sub>4</sub><sup>2-</sup> availability) can accelerate soil respiration. It is well established that higher seawater concentrations can increase the rate of sulfate reduction and enhance soil respiration (e.g., Chambers et al., 2011), while the byproducts of sulfate reduction (HS<sup>-</sup> and S<sup>2-</sup>) can be toxic to plants and microorganisms (Koch et al., 1990; Joye & Hollibaugh, 1995). Tidal flushing is critical to removing deleterious sulfide compounds (King et al., 1982) and wetland soils with low flushing often develop microzones where SO<sub>4</sub><sup>2-</sup> is depleted and methanogenesis becomes the dominant pathway for C mineralization

(King & Wiebe, 1980). Therefore, the combination of abundant SO<sub>4</sub><sup>2-</sup> to support sulfate reduction and high tidal flushing may provide an ideal condition for microbial respiration and C mineralization.

Time and water temperature were also significant predictors of CO<sub>2</sub> flux rate in this study. The control water level-elevated salinity treatment showed a notable decline in CO<sub>2</sub> flux during the beginning of the study that was not seen in other treatments. The response of soil microbes to elevated salinity is thought to be short term, with increases in the rate of sulfate reduction eventually being moderated by limitations of other nutrients (e.g., N and P) or the lability of C substrates (Chambers et al., 2011), but why a similar response was not observed in the inundated-elevated salinity treatment is unclear. Time was strongly correlated with temperature and likely contributed to the observed spike in CO<sub>2</sub> flux rate seen in all treatments around day 57. Higher temperatures accelerate microbial activity, which results in faster respiration (Smith et al., 1983; Neubauer, 2011; Krauss & Whitbeck, 2012) and higher decomposition rates (Sangiorgio et al., 2008; Kirwan & Blum, 2011) in wetland soils. However, the relationship between CO<sub>2</sub> flux and temperature was influenced by water level under elevated salinities. A similar response has been observed in forested wetlands where temperature had a greater influence on soil CO<sub>2</sub> flux under non-flooded conditions, compared to flooded conditions (Krauss et al., 2012). This study indicates the CO<sub>2</sub> flux rate accelerates more with temperature when the soils are exposed for a longer time period (i.e., the control water level treatments), and the response is most pronounced at water temperatures exceeding ~26°C. With global sea surface temperatures on the rise (IPCC, 2007), our data suggest that the impact of temperature on soil respiration might be greater in coastal systems with high salinities and larger tidal ranges, though in situ field studies are needed to confirm this finding.

This study also sought to understand if the physical process of a tide rising, versus falling, has an impact on CO<sub>2</sub> flux rate (i.e., does the upward momentum of a rising tide push additional CO<sub>2</sub> out of the pore space and therefore accelerate the rate of CO<sub>2</sub> flux?). Quantifying the relationship between the instantaneous CO<sub>2</sub> flux rate and the exact height of soil above the waterline during rising and falling tides revealed no significant effect of rising and falling tides on CO<sub>2</sub>

flux rate.  $\text{CH}_4$  flux rates were low (between 0.2 and 27  $\text{mg CH}_4\text{-C m}^{-2} \text{ day}^{-1}$ ), as expected due to the abundant  $\text{SO}_4^{2-}$  in seawater favoring the more energy efficient process of sulfate reduction over methanogenesis (Jakobsen et al., 1981). The average  $\text{CH}_4$  flux rate in mangrove sediments ranges from 0 to 60  $\text{mg CH}_4\text{-C m}^{-2} \text{ day}^{-1}$  (Kristensen et al., 2008), which is comparable to our findings. However, mangrove pneumatophores are thought to contribute significantly to  $\text{CH}_4$  flux by providing labile C substrates; the removal of pneumatophores from this study may have caused a 12–50% underestimation of  $\text{CH}_4$  flux rates (Laanbroek, 2010).

#### DOC and porewater nutrients

It is estimated that wetlands account for  $\sim 20\%$  of all DOC export to the ocean (Lugo et al., 1989) and the greater the tidal range, the greater the proportion of C lost to the ocean (Twilley et al., 1992). Porewater DOC in this study ranged from 12 to 18  $\text{mg l}^{-1}$ , which is slightly higher than reported for other mangroves (e.g., 5–10  $\text{mg DOC l}^{-1}$  for a mangrove forest in Tanzania; Bouillon et al., 2007). DOC was significantly greater in the inundated treatment, compared to the control water level treatment, which is contrary to past studies that found higher DOC concentrations in high marsh (less inundated) areas, than in low marsh areas (Cao et al., 2008) and higher porewater DOC during low tide than high tide (Bouillon et al., 2007). However, ours is the first study to investigate differences in porewater DOC as a function of SLR. Salinity did not result in any change in DOC, as was the case in a similar study testing the effects of saltwater intrusion on a tidal freshwater floodplain forest soil (Jun et al., 2012). It is estimated that  $\sim 30\%$  of porewater DOC is advected and exported during the ebb tide (Bouillon et al., 2007). If this figure is applied to the current data, an increase in relative water level of 8 cm will cause the average export of porewater DOC to Shark River Slough to increase from 4 to 5.2  $\text{mg l}^{-1}$ . Past in situ estimates of total mangrove DOC export to Shark River Slough during the summer months range from 8 to 11  $\text{mg l}^{-1}$  (Romigh et al., 2006), which included both litter and soil derived DOC.

The impact of salinity and inundation on N cycling in coastal wetland soils is of growing interest due to the importance of N in coastal eutrophication and the role of nitrate as an alternative electron acceptor

during C cycling. Salinity increases between 0 and  $\sim 10$  ppt are known to cause the release of significant amounts of  $\text{NH}_4^+$  from the soil cation exchange complex into the porewater, but once the salinity has passed a threshold of  $\sim 10$  ppt, the influence of this abiotic process is believed to be greatly diminished (Rysgaard et al., 1999; Baldwin et al., 2006; Weston et al., 2006). This is corroborated by the present study, which saw no significant increase in porewater  $\text{NH}_4^+$  with elevated salinity. However, this study did find evidence of increased  $\text{NH}_4^+$  concentrations under increased inundation. Prolonged inundation can cause  $\text{NH}_4^+$  to accumulate in the porewater because anaerobic conditions prevent nitrification (the oxidation of  $\text{NH}_4^+$  to  $\text{NO}_3^-$ ). This study also found that porewater  $\text{NO}_3^-$  in the elevated salinity treatment increased over time, relative to the ambient salinity treatment. High chloride concentrations associated with salinity can inhibit denitrification (Hale & Groffman, 2006; Seo et al., 2008), which may have caused  $\text{NO}_3^-$  to accumulate over time in the elevated salinity treatment. Soluble reactive P in the porewater was significantly higher in the elevated salinity treatment compared to the ambient salinity treatment. Previous studies have found no significant relationship between salinity and P availability (Weston et al., 2011), or have found increases in SRP adsorption as a result of saltwater intrusion (Jun et al., 2012). Our results for SRP are surprising, especially considering the low P availability in the salt source water, and warrants further study to understand the mechanism.

#### Implications for Everglades mangrove peat soils

A goal of this study was to enhance the mechanistic understanding of how SLR may impact biogeochemical processes in coastal Everglades mangrove peat soil, especially the loss of soil OC through microbial mineralization. The current mesohaline salinity and low topography of the study region suggests Shark River Slough will probably be subjected to simultaneous increases in both salinity and inundation as sea level rises. If this is the case, the rate of atmospheric  $\text{CO}_2$  flux from the soil can be expected to decline minimally over time.  $\text{CH}_4$  flux and DOC production will increase, but represents such a small portion of the OC budget ( $\sim 6\%$ ) that the affect on the soil OC balance will be negligible. Based on this mesocosm



study, the availability of  $\text{NH}_4^+$  and SRP in the porewater could increase substantially, which may contribute to greater export of these nutrients from the mangroves to Shark River Slough and the adjacent Florida Bay. The increase in inundation could also reduce the soil bulk density through increased leaching and material loss, but under current SLR rates, an increase in tidally deposited sediments may compensate for this decrease. Additional research and field studies are necessary to determine how C assimilation rates might be impacted by increases in salinity and inundation in mangroves, and if the natural feedback mechanism of vertical soil accretion could decouple SLR impacts, such that salinity increases while the accumulation of soil material compensates for increases in inundation. Recent evaluations of soil accretion rates near the study site suggest high ecosystem resilience to SLR, with combined OC burial and sediment deposition rates meeting or exceeding the current local rate of SLR (Smoak et al., 2012).

## Conclusion

The Everglades contain the largest mangrove forest in the contiguous USA, which overlies deep, carbon-rich peat soils that are highly vulnerable to rising sea levels. This study represents the first attempt to disentangle the effects of increasing salinity, increasing inundation, and the combination thereof, on the loss of Everglades soil OC through three major pathways ( $\text{CO}_2$  flux,  $\text{CH}_4$  flux, and DOC production) using experimental tidal mesocosms. Results indicate microbial respiration ( $\text{CO}_2$  flux) accounts for the majority (94–98%) of soil OC loss from this mangrove peat soil. Increasing tidal inundation from a low tide water depth of  $-13$  cm to a depth of  $-5$  cm decreased the average rate of  $\text{CO}_2$  flux by 35–37%. Increasing salinity from ambient (15–20 ppt) to 30–35 ppt increased the rate of  $\text{CO}_2$  flux by an average of 17–21%, and the combination of these two variables (increased inundation and elevated salinity) resulted in a synergistic decline in the rate of  $\text{CO}_2$  flux, 19–26% less than in the control treatment. The mean daytime  $\text{CO}_2$  flux in the control water level treatment was significantly higher (90%) than the inundated treatment under elevated salinity.  $\text{CO}_2$  flux was positively correlated with water temperature and did not differ

significantly whether the tide was rising or falling.  $\text{CH}_4$  flux was low in all treatments, and porewater DOC increased with greater inundation.

In addition to the observed changes in soil OC cycling, this study also identified other potentially important biogeochemical responses to simulated SLR. Most notably, porewater  $\text{NH}_4^+$  concentrations were approximately 73% higher with increased inundation, and porewater SRP concentrations were about 32% higher under increased salinity. If these nutrients are exported on the ebb tide into Florida Bay, they could contribute to algal blooms and coastal eutrophication. In addition, a significant decrease in soil bulk density was observed as a result of increased inundation within the short-time span of the study (10 weeks). Further research is needed to determine if this decline in bulk density may increase the soil's susceptibility to peat collapse. In order to fully understand the implications of SLR on Everglades' mangrove peat, field studies that incorporate carbon inputs, natural feedback mechanisms, and dissolved inorganic C export are needed.

**Acknowledgments** This material was developed in collaboration with the Florida Coastal Everglades Long-Term Ecological Research program under National Science Foundation Grant No. DBI-0620409 and was made possible with support from the South Florida Water Management District and Everglades National Park, who offered site and facility access, equipment, and sampling assistance. This research was also supported through a graduate fellowship from the Everglades Foundation.

## References

- Alongi, D. M., 2008. Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. *Estuarine Coastal and Shelf Science* 76: 1–13.
- Alongi, D. M., G. Wattayakorn, J. Pfitzner, F. Tirendi, I. Zatorskis, G. J. Brunskill, A. Davidson & B. F. Clough, 2001. Organic carbon accumulation and metabolic pathways in sediments of mangrove forests in southern Thailand. *Marine Geology* 179: 85–103.
- Aziz, I. & M. A. Khan, 2001. Effect of seawater on the growth, ion content and water potential of *Rhizophora mucronata* Lam. *Journal of Plant Research* 114: 369–373.
- Baldwin, D. S., G. N. Rees, A. M. Mitchell, G. Watson & J. Williams, 2006. The short-term effects of salinization on anaerobic nutrient cycling and microbial community structure in sediment from a freshwater wetland. *Wetlands* 26: 455–464.
- Boelter, D. H., 1965. Hydraulic conductivity of peats. *Soil Science* 100: 227–231.
- Bouillon, S., J. J. Middelburg, F. Dehairs, A. V. Borges, G. Abril, M. R. Flindt, S. Ulomi & E. Kristensen, 2007.

- Importance of intertidal sediment processes and porewater exchange on the water column biogeochemistry in a pristine mangrove creek (Ras Dege, Tanzania). *Biogeosciences* 4: 311–322.
- Bouillon, S., A. V. Borges, E. Castaneda-Moya, K. Diele, T. Dittmar, N. C. Duke, E. Kristensen, S. Y. Lee, C. Marchand, J. J. Middelburg, V. H. Rivera-Monroy, T. J. Smith & R. R. Twilley, 2008. Mangrove production and carbon sinks: a revision of global budget estimates. *Global Biogeochemical Cycles* 22: 12.
- Cao, Y. P., P. G. Green & P. A. Holden, 2008. Microbial community composition and denitrifying enzyme activities in salt marsh sediments. *Applied and Environmental Microbiology* 74: 7585–7595.
- Capone, D. G. & R. P. Kiene, 1988. Comparison of microbial dynamics in marine and fresh-water sediments: contrasts in anaerobic carbon catabolism. *Limnology and Oceanography* 33: 725–749.
- Castaneda-Moya, E., R. R. Twilley, V. H. Rivera-Monroy, K. Q. Zhang, S. E. Davis & M. Ross, 2010. Sediment and nutrient deposition associated with hurricane Wilma in mangroves of the Florida Coastal Everglades. *Estuaries and Coasts* 33: 45–58.
- Chambers, L. G., K. R. Reddy & T. Z. Osborne, 2011. Short-term response of carbon cycling to salinity pulses in a freshwater wetland. *Soil Science Society of America Journal* 75: 2000–2007.
- Chambers, L. G., T. Z. Osborne, & K. R. Reddy, 2013. Effect of salinity pulsing events on soil organic carbon loss across an intertidal wetland gradient: a laboratory experiment. *Biogeochemistry* 115: 363–383.
- Chen, R. H. & R. R. Twilley, 1999. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River estuary, Florida. *Estuaries* 22: 955–970.
- Craft, C., S. Broome & C. Campbell, 2002. Fifteen years of vegetation and soil development after brackish-water marsh creation. *Restoration Ecology* 10: 248–258.
- Davis, S. M., D. L. Childers, J. J. Lorenz, H. R. Wanless & T. E. Hopkins, 2005. A conceptual model of ecological interactions in the mangrove estuaries of the Florida Everglades. *Wetlands* 25: 832–842.
- DeBusk, W. F. & K. R. Reddy, 1998. Turnover of detrital organic carbon in a nutrient-impacted Everglades marsh. *Soil Science Society of America Journal* 62: 1460–1468.
- Delaune, R. D., C. J. Smith & W. H. Patrick, 1983. Methane release from Gulf-coast wetlands. *Tellus Series B-Chemical and Physical Meteorology* 35: 8–15.
- Donato, D. C., J. B. Kauffman, D. Murdiyarto, S. Kurnianto, M. Stidham & M. Kanninen, 2011. Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience* 4: 293–297.
- Edmonds, J. W., N. B. Weston, S. B. Joye, X. Z. Mou & M. A. Moran, 2009. Microbial community response to sea-water amendment in low-salinity tidal sediments. *Microbial Ecology* 58: 558–568.
- Fagherazzi, S., M. L. Kirwan, S. M. Mudd, G. R. Guntenspergen, S. Temmerman, A. D'Alpaos, J. van de Koppel, J. M. Rybczyk, E. Reyes, C. Craft & J. Clough, 2012. Numerical models of salt marsh evolution: ecological, geomorphic, and climate factors. *Reviews of Geophysics* 50: 28.
- FitzGerald, D. M., M. S. Fenster, B. A. Argow & I. V. Buynevich, 2008. Coastal impacts due to sea-level rise. *Annual Review of Earth and Planetary Sciences* 36: 601–647.
- Gaiser, E. E., A. Zafiris, P. L. Ruiz, F. A. C. Tobias & M. S. Ross, 2006. Tracking rates of ecotone migration due to salt-water encroachment using fossil mollusks in coastal South Florida. *Hydrobiologia* 569: 237–257.
- Hale, R. L. & P. M. Groffman, 2006. Chloride effects on nitrogen dynamics in forested and suburban stream debris dams. *Journal of Environmental Quality* 35: 2425–2432.
- Harvey, J. W. & P. V. McCormick, 2009. Groundwater's significance to changing hydrology, water chemistry, and biological communities of a floodplain ecosystem, Everglades, South Florida, USA. *Hydrogeology Journal* 17: 185–201.
- Howarth, R. W., 1984. The ecological significance of sulfur in the energy dynamics of salt-marsh and coastal marine-sediments. *Biogeochemistry* 1: 5–27.
- Ikenaga, M., R. Guevara, A. L. Dean, C. Pisani & J. N. Boyer, 2010. Changes in community structure of sediment bacteria along the Florida Coastal Everglades marsh–mangrove–seagrass salinity gradient. *Microbial Ecology* 59: 284–295.
- IPCC, 2007. *Climate Change 2007: A Synthesis Report*. In: XXVII IP (ed.). Valencia, Spain: p 22.
- Jakobsen, P., W. H. Patrick & B. G. Williams, 1981. Sulfide and methane formation in soils and sediments. *Soil Science* 132: 279–287.
- Joye, S. B. & J. T. Hollibaugh, 1995. Influence of sulfide inhibition of nitrification on nitrogen regeneration in sediments. *Science* 270: 623–627.
- Jun, M., A. E. Altor & C. B. Craft, 2012. Effects of increased salinity and inundation on inorganic nitrogen exchange and phosphorus sorption by tidal freshwater floodplain forest soils, Georgia (USA). *Estuaries and Coasts*. doi:[10.1007/s12237-012-9499-6](https://doi.org/10.1007/s12237-012-9499-6).
- Kelble, C. R., E. M. Johns, W. K. Nuttle, T. N. Lee, R. H. Smith & P. B. Ortner, 2007. Salinity patterns of Florida Bay. *Estuarine Coastal and Shelf Science* 71: 318–334.
- King, G. M. & W. J. Wiebe, 1980. Regulation of sulfate concentrations and methanogenesis in salt-marsh soils. *Estuarine and Coastal Marine Science* 10: 215–223.
- King, G. M., M. J. Klug, R. G. Wiegert & A. G. Chalmers, 1982. Relation of soil–water movement and sulfide concentration to *Spartina-alterniflora* production in a Georgia salt marsh. *Science* 218: 61–63.
- Kirwan, M. L. & L. K. Blum, 2011. Enhanced decomposition offsets enhanced productivity and soil carbon accumulation in coastal wetlands responding to climate change. *Biogeosciences* 8: 987–993.
- Kirwan, M. L., G. R. Guntenspergen, A. D'Alpaos, J. T. Morris, S. M. Mudd & S. Temmerman, 2010. Limits on the adaptability of coastal marshes to rising sea level. *Geophysical Research Letters* 37: 5.
- Koch, M. S., I. A. Mendelssohn & K. L. McKee, 1990. Mechanism for the hydrogen sulfide-induced growth limitation in wetland macrophytes. *Limnology and Oceanography* 35: 399–408.

- Kool, D. M., P. Buurman & D. H. Hoekman, 2006. Oxidation and compaction of a collapsed peat dome in Central Kalimantan. *Geoderma* 137: 217–225.
- Kostka, J. E., A. Roychoudhury & P. Van Cappellen, 2002. Rates and controls of anaerobic microbial respiration across spatial and temporal gradients in saltmarsh sediments. *Biogeochemistry* 60: 49–76.
- Krauss, K. W. & J. L. Whitbeck, 2012. Soil greenhouse gas fluxes during wetland forest retreat along the Lower Savannah River, Georgia (USA). *Wetlands* 32: 73–81.
- Krauss, K. W., J. L. Whitbeck & R. J. Howard, 2012. On the relative roles of hydrology, salinity, temperature, and root productivity in controlling soil respiration from coastal swamps (freshwater). *Plant and Soil* 358: 265–274.
- Kristensen, E., S. I. Ahmed & A. H. Devol, 1995. Aerobic and anaerobic decomposition of organic matter in marine sediment: which is fastest? *Limnology and Oceanography* 40: 1430–1437.
- Kristensen, E., S. Bouillon, T. Dittmar & C. Marchand, 2008. Organic carbon dynamics in mangrove ecosystems: a review. *Aquatic Botany* 89: 201–219.
- Laanbroek, H. J., 2010. Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes. A mini-review. *Annals of Botany* 105: 141–153.
- Lugo, A., S. Brown & M. Brinson, 1989. Concepts in wetland ecology. In Lugo, A., S. Brown & M. Brinson (eds), *Ecosystems of the World* 15. Elsevier, Amsterdam: 53–85.
- Marshall, N., 1994. Mangrove conservation in relation to overall environmental considerations. *Hydrobiologia* 285: 303–309.
- McKee, K. L., 2011. Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuarine Coastal and Shelf Science* 91: 475–483.
- McKee, K. L., D. R. Cahoon & I. C. Feller, 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* 16: 545–556.
- Moorhead, K. K. & M. M. Brinson, 1995. Response of wetlands to rising sea-level in the lower coastal-plain of North Carolina. *Ecological Applications* 5: 261–271.
- Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve & D. R. Cahoon, 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83: 2869–2877.
- Naidoo, G., 1985. Effects of waterlogging and salinity on plant water relations and on the accumulation of solute in 3 mangrove species. *Aquatic Botany* 22: 133–143.
- Neubauer, S. C., 2011. Ecosystem responses of a tidal freshwater marsh experiencing saltwater intrusion and altered hydrology. *Estuaries and Coasts*. doi:10.1007/s12237-011-9455-x.
- Neubauer, S. C., W. D. Miller & I. C. Anderson, 2000. Carbon cycling in a tidal freshwater marsh ecosystem: a carbon gas flux study. *Marine Ecology-Progress Series* 199: 13–30.
- Nicholls, R. J., F. M. J. Hoozemans & M. Marchand, 1999. Increasing flood risk and wetland losses due to global sea-level rise: regional and global analyses. *Global Environmental Change-Human and Policy Dimensions* 9: S69–S87.
- Patrick, W. H. & R. D. DeLaune, 1977. Chemical and biological redox systems affecting nutrient availability in the coastal wetlands. *Geoscience and Man*. 18: 131–137.
- Portnoy, J. W. & A. E. Giblin, 1997. Biogeochemical effects of seawater restoration to diked salt marshes. *Ecological Applications* 7: 1054–1063.
- Rietz, D. N. & R. J. Haynes, 2003. Effects of irrigation-induced salinity and sodicity on soil microbial activity. *Soil Biology & Biochemistry* 35: 845–854.
- Rivera-Monroy, V. H. & R. R. Twilley, 1996. The relative role of denitrification and immobilization in the fate of inorganic nitrogen in mangrove sediments (Terminos Lagoon, Mexico). *Limnology and Oceanography* 41: 284–296.
- Rivera-Monroy, V. H., K. de Mutsert, R. R. Twilley, E. Castaneda-Moya, M. M. Romigh & S. E. Davis, 2007. Patterns of nutrient exchange in a riverine mangrove forest in the Shark River Estuary, Florida, USA. *Hydrobiologia* 17: 169–178.
- Romigh, M. M., S. E. Davis, V. T. Rivera-Monroy & R. R. Twilley, 2006. Flux of organic carbon in a riverine mangrove wetland in the Florida Coastal Everglades. *Hydrobiologia* 569: 505–516.
- Rysgaard, S., P. Thastum, T. Dalsgaard, P. B. Christensen & N. P. Sloth, 1999. Effects of salinity on  $\text{NH}_4^+$  adsorption capacity, nitrification, and denitrification in Danish estuarine sediments. *Estuaries* 22: 21–30.
- Saha, A. K., S. Saha, J. Sadle, J. Jiang, M. S. Ross, R. M. Price, L. Sternberg & K. S. Wendelberger, 2011. Sea level rise and South Florida coastal forests. *Climatic Change* 107: 81–108.
- Sangiorgio, F., A. Basset, M. Pinna, L. Sabetta, M. Abbiati, M. Ponti, M. Minocci, S. Orfanidis, A. Nicolaidou, S. Moncheva, A. Trayanova, L. Georgescu, S. Dragan, S. Beqiraj, D. Koutsoubas, A. Evagelopoulou & S. Reizopoulou, 2008. Environmental factors affecting *Phragmites australis* litter decomposition in Mediterranean and Black Sea transitional waters. *Aquatic Conservation-Marine and Freshwater Ecosystems* 18: S16–S26.
- Seo, D. C., K. Yu & R. D. Delaune, 2008. Influence of salinity level on sediment denitrification in a Louisiana estuary receiving diverted Mississippi River water. *Archives of Agronomy and Soil Science* 54: 249–257.
- Sherman, R. E., T. J. Fahey & P. Martinez, 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. *Ecosystems* 6: 384–398.
- Smith, C. J., R. D. Delaune & W. H. Patrick, 1983. Carbon-dioxide emissions and carbon accumulation in coastal wetlands. *Estuarine Coastal and Shelf Science* 17: 21–29.
- Smoak, J. M., J. L. Breithaupt, T. J. I. Smith & C. J. Sanders, 2012. Sediment accretion and organic carbon burial relative to sea-level rise and storm events in two mangrove forests in Everglades National Park. *Catena*.
- Spalding, M., M. Kainuma & L. Collins, 2010. *World Atlas of Mangroves*. Earthscan, London.
- Stagg, C. L. & I. A. Mendelssohn, 2010. Restoring ecological function to a submerged salt marsh. *Restoration Ecology* 18: 10–17.
- Twilley, R. R., R. H. Chen & T. Hargis, 1992. Carbon sinks in mangrove and their implications to carbon budget of tropical coastal ecosystems. *Water Air and Soil Pollution* 64: 265–288.
- Valiela, I., J. L. Bowen & J. K. York, 2001. Mangrove forests: one of the world's threatened major tropical environments. *Bioscience* 51: 807–815.

- Wanless, H., R. Parkinson & L. Tedesco, 1994. Sea level control on stability of Everglades wetlands. In Davis, S. & J. Ogden (eds), *Everglades: The Ecosystem and its Restoration*. St. Lucie, Boca Raton: 198–224.
- Weston, N. B., R. E. Dixon & S. B. Joye, 2006. Ramifications of increased salinity in tidal freshwater sediments: geochemistry and microbial pathways of organic matter mineralization. *Journal of Geophysical Research-Biogeosciences* 111: 14.
- Weston, N. B., M. A. Vile, S. C. Neubauer & D. J. Velinsky, 2011. Accelerated microbial organic matter mineralization following salt-water intrusion into tidal freshwater marsh soils. *Biogeochemistry* 102: 135–151.
- Wichern, J., F. Wichern & R. G. Joergensen, 2006. Impact of salinity on soil microbial communities and the decomposition of maize in acidic soils. *Geoderma* 137: 100–108.
- Wright, A. L. & K. R. Reddy, 2001. Heterotrophic microbial activity in northern Everglades wetland soils. *Soil Science Society of America Journal* 65: 1856–1864.