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Declines in Plant Productivity Drive Carbon Loss from Brackish Coastal Wetland Mesocosms Exposed to Saltwater Intrusion

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Abstract

Coastal wetlands, among the most productive ecosystems, are important global reservoirs of carbon (C). Accelerated sea level rise (SLR) and saltwater intrusion in coastal wetlands increase salinity and inundation depth, causing uncertain effects on plant and soil processes that drive C storage. We exposed peat-soil monoliths with sawgrass (*Cladium jamaicense*) plants from a brackish marsh to continuous treatments of salinity (elevated (~20 ppt) vs. ambient (~10 ppt)) and inundation levels (submerged (water above soil surface) vs. exposed (water level 4 cm below soil surface)) for 18 months. We quantified changes in soil biogeochemistry, plant productivity, and whole-ecosystem C flux (gross ecosystem productivity, GEP; ecosystem respiration, ER). Elevated salinity had no effect on soil CO_2 and CH_4 efflux, but it reduced ER and GEP by 42 and 72%, respectively. Control monoliths exposed to ambient salinity had greater net ecosystem productivity (NEP), storing up to nine times more C than plants and soils exposed to elevated salinity. Submersion suppressed soil CO_2 efflux but had no effect on NEP. Decreased plant productivity and soil organic C inputs with saltwater intrusion are likely mechanisms of net declines in soil C storage, which may affect the ability of coastal peat marshes to adapt to rising seas.

Keywords *Cladium jamaicense* · Florida Everglades · Biogeochemistry · Salinity · Marsh · Peat collapse

Introduction

Coastal wetland ecosystems are important global carbon (C) sinks that are directly threatened by climate change (Kirwan and Megonigal 2013). With average global sea level rising ~3 mm year^{-1} (Ryan and Law 2005) and recent increases up to 9 mm year^{-1} in some coastal areas (Wdowinski et al. 2016), saltwater intrusion in low-lying freshwater and brackish water coastal wetlands will increase, potentially altering ecosystem

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C dynamics through effects on plants and soils (Valentine 2002; Whalen 2005). Reduced freshwater delivery to some coastal wetlands and increased soil erosion through reduced sediment delivery in others can further exacerbate the impacts of sea level rise (SLR) and saltwater intrusion on coastal wetlands (Herbert et al. 2015; White and Kaplan 2017). Because C storage is linked to the health of many ecosystem services, including CO_2 sequestration, recreational and commercial fisheries, water quality, wildlife habitat, and storm surge protection (Engle 2011; McLeod et al. 2011), understanding how saltwater intrusion alters C storage in coastal ecosystems is crucial for predicting how these vital services will be affected.

Carbon storage in coastal wetlands is controlled by complex interactions among allochthonous water and material supplies, water residence time and depth, physical soil processes, and the metabolic balance of plant production and organic matter mineralization by soil microbes (Morris et al. 2002; Weston et al. 2006; Neubauer 2013). In wetland soils, increased salinity and water depth associated with SLR can change geochemical and biological processes, resulting in altered C storage capacity (Herbert et al. 2015). Elevated salinity and duration of salinity exposure can create osmotic stress to microbial communities by suppressing cellular respiration

or even lysing cells (Wichern et al. 2006; Chambers et al. 2011). Conversely, exposure to some ionic constituents of saltwater, particularly sulfate (SO_4^{2-}), can increase overall CO_2 efflux from soils through increased sulfate reduction as salinity increases (Chambers et al. 2011; Weston et al. 2011). Unlike sulfate reduction, elevated salinity usually results in decreased rates of methanogenesis as sulfate-reducing bacteria outcompete methanogens, given the higher energy yield of sulfate reduction (Capone and Kiene 1988; Weston et al. 2006; Poffenbarger et al. 2011). Yet low-level saltwater addition has also been shown to stimulate CH_4 production from freshwater marsh soils (Weston et al. 2011), and large CH_4 stocks have been found in saline environments (Wilson et al. 2015). Elevated salinity can produce plant morphological and physiological changes (Larcher 2003; Rejmankova and Macek 2008) that affect photosynthetic efficiencies, growth, maintenance, and nutrient uptake (Pezeshki et al. 1987a; Pezeshki et al. 1987b; Neubauer 2013). Because microbial respiration and plant productivity strongly mediate CO_2 and CH_4 exchange in wetlands, understanding short- and long-term responses to saltwater exposure and increased water depth is critical to understanding soil C storage.

In addition to increasing salinity, SLR can also increase water depth, duration, and residence time. In many coastal wetlands influenced by tidal and riverine sediment inputs, increased water depth causes higher inorganic sedimentation rates and, therefore, higher accretion rates up to a threshold of water depth (Morris et al. 2002). In coastal mangrove and marsh ecosystems that receive little sediment input, however, root production is identified as the primary driver of vertical peat accretion and soil C accumulation (Nyman et al. 2006; McKee 2011; Baustian et al. 2012). Higher water levels create a greater diffusive barrier that prevents oxygen and other gases from entering the soil, affecting plant productivity (Jackson and Colmer 2005) and suppressing aerobic respiration and overall organic C mineralization, which leads to a reduction in overall soil CO_2 efflux to the atmosphere (Neubauer et al. 2000). Longer water residence time leads to a predominance of anaerobic respiratory pathways, typically allowing methanogens to thrive where sulfate concentrations are low (i.e., low salinity (Poffenbarger et al. 2011)), leading to increases in CH_4 efflux (Morse et al. 2012). Increased flooding depth has been shown to decrease plant productivity (Wichern et al. 2006) and gross ecosystem productivity (GEP; Whalen 2005), usually as a result of decreased leaf area available for gas exchange (Schedlbauer et al. 2010), oxygen stress of roots, and increased production of phytotoxins (Rejmankova and Macek 2008). However, a resulting decrease in ecosystem respiration (ER) with inundation can be greater than the effect on GEP, resulting in increased net ecosystem productivity (NEP; Whalen 2005).

Coastal freshwater peat marshes are susceptible to saltwater intrusion and changes in water depth (Herbert et al. 2015; Whittle and Gallego-Sala 2016), but little is known about how

exposure to salinity affects organic matter accumulation and peat stability. In areas with low inorganic sediment input, peatland soils can be highly organic (> 85%) and more vulnerable to external drivers, such as freshwater diversion and effects of climate change (Nyman et al. 1990; Delaune et al. 1994; McVoy et al. 2011). The Everglades is the largest coastal peatland in the USA (> 6000 km^2; Richardson et al. 2008) and one of the most vulnerable to SLR, as 60% of Everglades National Park (ENP) is at or below 0.9 m in elevation (Pearlstine et al. 2010). Freshwater flow through the Everglades has been greatly reduced by compartmentalization (creation of water storage areas) and overall reduction in water delivery, resulting in less freshwater flow into the Everglades, leaving the ecosystem highly vulnerable to saltwater intrusion (Light and Dineen 1994; Saha et al. 2011; Dessu et al. 2018).

The term "peat collapse" has been used to describe a relatively rapid shift in soil C balance, leading to a net loss of organic C and loss of soil elevation, culminating in a conversion of vegetated marsh to open water ponds (Delaune et al. 1994). This process has been documented to varying degrees in different coastal wetlands and has been attributed to changes in microbial processes, increased sulfate reduction, sulfide accumulation, eutrophication from excess nitrogen (N) inputs, inadequate plant production, and vegetation damage from tropical storms, contributing to the instability of inland marshes (Delaune et al. 1994; Cahoon et al. 2003; Deegan et al. 2012; Voss et al. 2013). Areas of peat collapse have been observed in the brackish and saline marsh areas of the coastal Everglades (Fig. 1), yet the mechanisms behind this collapse are not understood (Wanless and Vlaswinkel 2005; Chambers et al. 2015). Therefore, understanding how factors associated
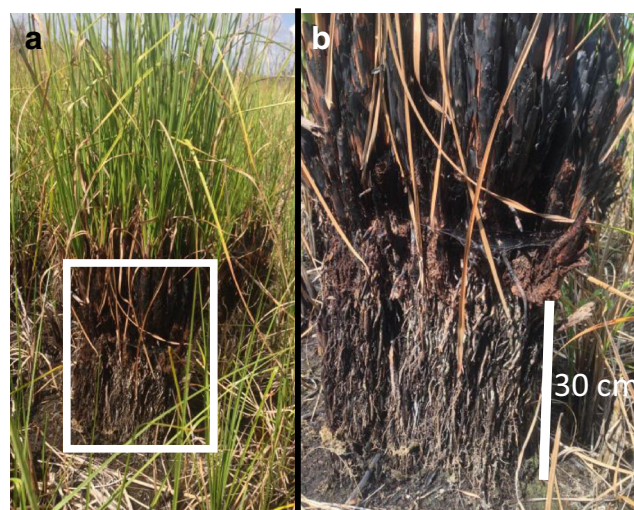

Fig. 1 Photographs taken in March 2015 in the brackish water portion of Everglades National Park showing a group of sawgrass culms forming a "pedestal" (**a**) and a close up of the culms and exposed roots (**b**). The delineation between the bottom of the culms and the exposed roots indicates that the surface of the soil has collapsed about 30 cm (distance from bottom of the culm to current soil surface) over an unknown period of time

with SLR that exacerbate saltwater intrusion in the coastal Everglades and potentially alter C storage and peat stability is critically important for the future of Everglades coastal wetlands.

Past studies have identified C responses to salinity or water depth in soils (Weston et al. 2006; Chambers et al. 2011; Weston et al. 2011; Marton et al. 2012; Chambers et al. 2013), but fewer have investigated interactions between soil and plant processes in vegetated soil systems (Neubauer et al. 2000; Neubauer 2013; Weston et al. 2014). To examine the influence of salt exposure and inundation on soil and plant processes driving coastal peat marsh C cycling, we conducted a mesocosm experiment using Everglades brackish marsh plant-peat monoliths. We hypothesized that elevated salinity would decrease GEP while increasing ER and soil CO_2 efflux, leading to decreased NEP and a change in the marsh from a net C sink to a C source. We also hypothesized that greater water depth would decrease soil CO_2 efflux as a result of more reducing conditions, mitigating some of the effects of elevated salinity and dampening the overall loss of C to the atmosphere.

Methods

Study Site and Experimental Design We collected 24 plant-soil monoliths (25-cm deep × 28-cm diameter) on 7 January 2015 from a brackish marsh in Shark River Slough (25° 13′ 13.52″ N, 80° 50′ 36.70″ W), ENP, a supratidal location about 5-km inland from Florida Bay. The site is typically inundated ~ 8 months out of the year. In 2009, the site had an elevation of 1.6 m above sea level. The site was dominated by dense sawgrass patches (*Cladium jamaicense*), interspersed with buttonwood (*Conocarpus erectus*) and open water ponds with senescing and dead sawgrass plants. Peat was approximately 1-m deep to a ~ 0.5-m mineral layer overlying limestone bedrock. The soil C content within the top 10 cm at this site was $42.6 \pm 0.2\%$ (mean ± 1 standard error from five cores), bulk density was 0.133 ± 0.008 g cm^{-3}, $84.5 \pm 0.5\%$ of the soil was organic matter, and water occupied $88.5 \pm 0.8\%$ of the pore space. At the time of collection, ambient porewater salinity was ~ 9 ppt. Anecdotal evidence suggests that this was a freshwater peat marsh in 1952 (Beard et al. 1952). On site, areas with ~ 3 sawgrass culms per 0.06 m^{-2} were selected for monolith collection. We excavated the peat monoliths intact using shovels and placed them into perforated buckets with mesh screen over the perforations that allowed water exchange while minimizing sediment loss (Chambers et al. 2013). Extracted monoliths were dug out slightly larger than the size of the bucket and were shaved down to a uniform size while being placed into the bucket. Monoliths were transported to an outdoor mesocosm facility at ENP's Florida Bay Interagency Science Center in Key Largo, FL.

We used a randomized split-plot experimental design with repeated measurements. The two manipulated factors were salinity (the whole-plot factor with two nested blocks) and inundation (the sub-plot factor), which were both fixed factors. Once on site, monoliths were carefully immersed in six 250-gal concrete tanks, each equipped with an adjustable inflow spigot, a 30-cm tall standpipe to maintain consistent water level, and an outflow drain; three tanks had elevated salinity (20 ppt), while three had ambient salinity (10 ppt). Within each tank, the water depth for a monolith was controlled by setting it on the bottom of the tank (water level 5 cm above soil surface) or by setting it on a shelf in the tank that elevated it to ~ 4 cm above water surface (exposed). The monoliths were randomly assigned to either an elevated salinity or ambient salinity tank and to either completely submerged or exposed water depth.

Salinity was controlled by mixing water weekly to desired experimental salinity concentrations from four 2000-gal head tanks, two with freshwater and two with saltwater, and the mixture was pumped at a constant flow (36 mL min^{-1}) into each mesocosm tank. Freshwater was collected from a nearby canal and had similar nutrient concentrations to freshwater portions of the Everglades (C-111; 25° 17′ 31.74″ N, 80° 27′ 21.59″ W). Saltwater head tanks were equipped with a pump to draw water from adjacent Florida Bay.

The soil monoliths were allowed to acclimate for 4 weeks under ambient salinity (~ 10 ppt) and completely inundated (water level 5 cm above soil surface) conditions before treatment manipulations and measurements began. The "exposed" designated monoliths were then raised to ~ 4 cm above the water surface. There were two phases in the experiment: a 3-month "ramp up" period (Feb to Apr 2015) in which salinity was incrementally raised from ambient (10 ppt) to treatment (20 ppt) salinity and a 15-month "press" period (until July 2016) in which salinity remained elevated. The four treatments were designated as: (1) Amb.Sub, (2) Amb.Exp, (3) Salt.Sub, and (4) Salt.Exp, where the salinity treatment was defined as either ambient (Amb) or elevated (Salt) and the inundation treatment was defined as either completely submerged (Sub) or top 4 cm of soil exposed above the water surface (Exp).

Surface Water and Porewater Physicochemistry Surface water in each tank was collected monthly using a 60-mL syringe and field filtered through 0.7-µm glass fiber filters (GFF) into new plastic bottles. At the time of collection, temperature (°C), salinity (ppt), and pH were measured on samples of freshwater source, saltwater source, and tank surface water using a YSI Model 600 XL (Xylem, Inc., Yellow Springs, OH, USA). Soluble reactive phosphorus (SRP), total dissolved P (TDP), and dissolved inorganic N (DIN) were analyzed at the South Florida Water Management District Water Quality Laboratory on a four-channel Lachat Flow Injection Analyzer 5000 auto-

analyzer (Lachat Instruments, Loveland, CO, USA). Sulfate (SO_4^{2-}) was analyzed using an ion chromatograph (Metrohm 881, Riverview, FL, USA). Dissolved organic C (DOC) was analyzed using a Shimadzu TOC-L analyzer (Shimadzu Scientific Instruments, Columbia, MD, USA; Eaton et al. 2005).

Porewater sippers (plastic tubing attached to an air stone (4-cm long × 1-cm diameter)) were inserted to 15-cm depth near the middle of each monolith. Porewater was collected monthly using a 60-mL syringe by placing suction on the sipper and evacuating the tubing before collecting a sample. Water was filtered (0.7-μm GFF) into new plastic bottles. Porewater was analyzed for temperature, salinity, and pH immediately after collection. Dissolved constituents (SRP, TDP, DOC, DIN, SO_4^{2-}) were analyzed as described above. Sulfide (HS^-) was measured using standard methods (McKee et al. 1988). Soil redox potential was measured monthly using standard techniques (Faulkner et al. 1989): we inserted three platinum-tipped probes to a depth of 5-cm in each monolith and allowed to equilibrate for 30 min until measurements were taken.

CO_2 and CH_4 Efflux Prior to the experiment, one 10-cm diameter PVC collar was installed 5-cm into the soil in each monolith to allow for soil C efflux to be measured. Soil CO_2 efflux was measured monthly for 120 s using a portable infrared gas analyzer (Li-Cor 8100, Lincoln, NE, USA); the gas analyzer chamber was then moved manually to the next sample collar (Chambers et al. 2013).

Methane was measured on a subset of monoliths using the LI-8100 modified to collect a subset of air for trace gas sampling (Chambers et al. 2013). Four out of the six monoliths for each treatment were randomly chosen at the beginning of the experiment, and measurements occurred monthly on the same monoliths. The chamber was sealed for 15 min, and 25-mL of gas was withdrawn using a 60-mL syringe at both the beginning and end of the 15-min sampling period from a port in-line with the instrument; the gas was sealed in a 20-mL evacuated glass vial and transported back to the lab for analysis. Samples were run on a gas chromatograph (Shimadzu Scientific Instruments GC 8A, Columbia, MD, USA) fitted with a flame ionization detector. During the first year, soil CH_4 was measured monthly, but because of the lack of detectable flux, soil CH_4 efflux measurements were cut to bi-monthly for the last 6 months. Soil CO_2 and CH_4 flux were calculated as the slope of concentration over time. Soil CO_2 and CH_4 efflux were not measured in April 2015 because of equipment failure.

Ecosystem CO_2 Exchange Ecosystem CO_2 exchange (which represents both plants and soils) was measured monthly with a transparent static chamber (53 L × 38 W × 150 H cm) placed over the monoliths and sealed (Neubauer 2013; Weston et al. 2014; Wilson et al. 2015). The chamber was equipped with two fans to circulate air. Carbon flux measurements were made in full light near solar noon and in the dark. After sealing the chamber, the system was allowed to equilibrate for 2 min, and then change in CO_2 concentration was recorded every second for 3 min. During flux measurements, air was pumped from the chamber to a calibrated CO_2/H_2O gas analyzer (LI-COR model LI-840, Lincoln, NE, USA) placed in-line with the chamber. In between light and dark sampling, the chamber top was removed and allowed to equilibrate with atmospheric conditions. NEP was measured in full light, while ER of CO_2 (ER_{CO2}) was measured in the dark immediately after light measurements by covering the chamber with a dark cloth, blocking out all sunlight. GEP was calculated from NEP and ER_{CO2} as:

$$-GEP = -NEP - ER_{CO2} \qquad (1)$$

where NEP is the instantaneous CO_2 flux (μmol m^{-2} s^{-1}) in light, and ER_{CO2} is the CO_2 flux in the dark. Flux was calculated as the linear slope of CO_2 concentration over time.

Aboveground Biomass Aboveground net primary productivity (ANPP) was measured non-destructively at bi-monthly intervals following methods described in Daoust and Childers (1998). Briefly, each sawgrass culm was tagged, and the number of live and dead leaves, shoot height, and culm diameter were measured. Change in ANPP was calculated using previously derived allometric relationships between plant height, culm diameter, and biomass (Childers et al. 2006b).

Data Analyses All statistical analyses were performed using R (R Core Team 2017). Linear mixed effects models (Package *nlme*, Pinheiro et al. 2017) were used to examine the relationship among physicochemistry of surface and porewater, soil oxidation-reduction potential, C flux, and ANPP and the independent variables salinity, inundation, and time (fixed factors). Because of the split-plot, nested nature of our experimental design, each salinity tank was set as a block (random factor), while inundation was nested within each block. Normality and homoscedasticity were tested by visually inspecting plotted residuals, and data were log-transformed in order to increase heteroscedasticity when necessary. Mean differences of porewater physicochemistry, soil oxidation-reduction potential, C flux, and ANPP among treatments were determined from the least-squared means multiple comparison test adjusted to Tukey's HSD (R package *lsmeans*, Lenth 2017). Difference in mean surface and fresh and salt source water physicochemistry was determined using a *t* test. The relationship between soil redox potential and temperature was determined using a Pearson product-moment correlation. Culm density was compared between the beginning and end of the experiment for each treatment individually using a paired *t* test, while culm density among treatments was compared using a *t* test. Linear regressions were used to determine

the relationships between GEP, NEP, ER_{CO2}, and sawgrass biomass. Significance for all analyses was determined by an alpha level of 0.05.

Results

Surface and Porewater Physicochemistry Surface water temperature ranged from 18.5 to 37.2 °C (Table A1). Surface water salinity was maintained at 8 ppt during the 1-month acclimation period. Averaged over the press portion of the experiment, surface water salinity remained near experimental targets in both the ambient and elevated salinity treatments, with some variation because of rainfall and evaporation (Table A1). Averaged over the press portion of the experiment, porewater salinities had less variance than surface water salinities (Table 1; Table A1). The elevated salinity treatment resulted in significantly higher porewater SO_4^{2-} ($F_{(1,4)} = 204.97$, $P < 0.001$) compared to the ambient salinity treatment (Table A2), while there were no other effects of salinity or inundation on any other porewater constituents (Table A2). Soil redox potential at 5-cm depth ranged from $+ 12.3$ mV (Amb.Exp, Mar 2015) to $+ 309.4$ mV (Amb.Exp, May 2016; Fig. A1). Redox potential varied temporally, with the lowest values occurring in summer 2015, and then gradually rising for the duration of the experiment (Fig. A1). Redox was negatively correlated to temperature (Person's r (343) $= -0.198$, $P < 0.001$).

Soil CO_2 and CH_4 Efflux Soil CO_2 efflux varied across the experimental period, with larger efflux during the first half of the experiment and diminished fluxes during the second

half with differences between the treatments (Fig. 2b). Soil CO_2 efflux ranged from $- 0.08$ μmol CO_2 m^{-2} s^{-1} (Amb.Sub, Apr 2016) to 1.86 μmol CO_2 m^{-2} s^{-1} (Salt.Exp, May 2015). Over the entire experiment, inundation led to less soil CO_2 efflux compared to the exposed monoliths ($P = 0.004$), but the effect of salinity was not significant ($P = 0.834$; Tables 2 and 3). Soil CH_4 efflux was very low, ranging from $- 3.6$ nmol CH_4 m^{-2} s^{-1} (Amb.Sub, Sep 14, 2014) to 6.2 nmol CH_4 m^{-2} s^{-1} (Salt.Sub, Sep 14, 2014), with no significant differences with either salinity or inundation (Fig. 2a; Table 2).

Ecosystem Exchange Across the 18-month sampling period, calculated GEP at solar noon ranged from 0.16 (median for Salt.Exp plots, May 2015) to 4.1 μmol CO_2 m^{-2} s^{-1} (median for Amb.Exp plots, Feb 2016, Fig. 3a). Across all treatments, GEP was higher during the second year compared to the first (Fig. 3a), while overall, elevated salinity led to less CO_2 uptake compared to the ambient conditions ($P = 0.003$; Table 3). ER of CO_2 ranged from 0.19 (median rates, Salt.Sub plots, Oct 2015) to 1.3 μmol CO_2 m^{-2} s^{-1} (Amb.Exp, Jun 2016, Fig. 3b). There was a time effect of salinity on ER_{CO2}, with salinity suppressing ER_{CO2}, as duration of saltwater exposure
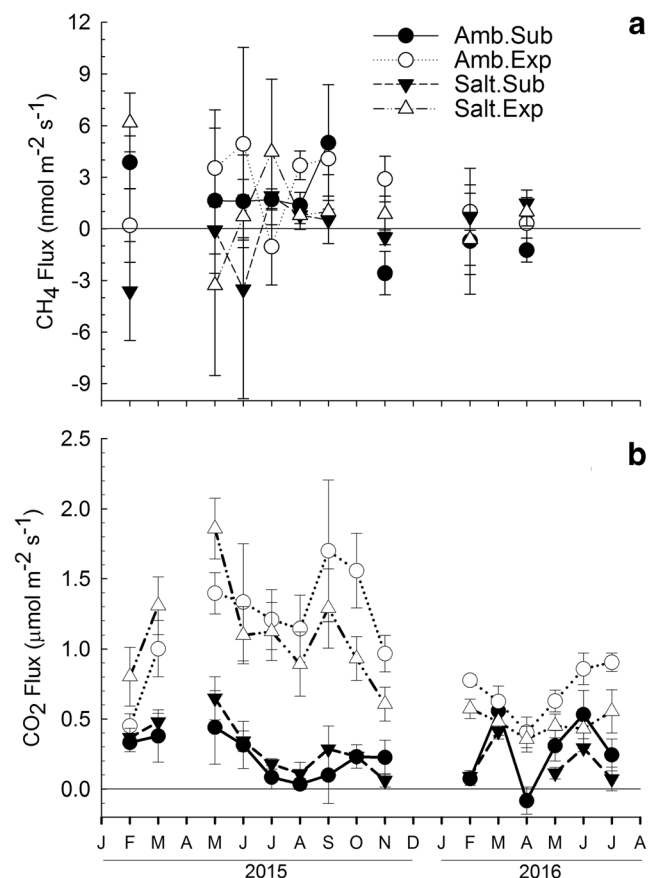
Table 1 Porewater salinity, pH, redox, and dissolved constituents. Data represent mean ± 1 SE ($n = 6$ replicates). Letters represent significant differences among treatments from a multiple comparison test (LSMEANS, Tukey adjusted). DOC, NH_4^+, TDN, and SO_4^{2-} are in mg L^{-1}, HS$^-$ is in mM, TDP and SRP are μM L^{-1}, and redox potential is in mV

	Amb.Sub	Amb.Exp	Salt.Sub	Salt.Exp
Salinity	9.5 ± 0.2[a]	9.8 ± 0.3[a]	18.9 ± 0.5[b]	19 ± 0.6[b]
pH	7.07 ± 0.03	7.07 ± 0.03	7.09 ± 0.03	7.09 ± 0.03
DOC	25.7 ± 1.7[ab]	26.6 ± 1.8[ab]	22.5 ± 1.1[b]	26.4 ± 1.5[a]
NH_4^+	0.56 ± 0.05[ab]	0.39 ± 0.06[ab]	0.55 ± 0.03[b]	0.65 ± 0.04[a]
TDN	1.64 ± 0.09[ab]	1.45 ± 0.1[ab]	1.59 ± 0.08[b]	1.75 ± 0.09[a]
SO_4^{2-}	616 ± 31[a]	641 ± 28[a]	1380 ± 46[b]	1362 ± 52[b]
TDP	1.00 ± 0.09[ab]	0.78 ± 0.08[ab]	0.78 ± 0.04[b]	1.14 ± 0.08[a]
SRP	0.56 ± 0.08[ab]	0.43 ± 0.07[ab]	0.53 ± 0.06[b]	0.71 ± 0.06[a]
Redox	170.0 ± 16.0	162.7 ± 14.5	168.3 ± 18.2	181.9 ± 16.7
HS$^-$	0.41 ± 0.11	0.34 ± 0.1	0.43 ± 0.09	0.48 ± 0.09

Amb = ambient salinity (10 ppt), Salt = elevated salinity (20 ppt), Sub = submerged, Exp = exposed

Fig. 2 Soil CH_4 ($n = 4$) and CO_2 efflux ($n = 6$) over time. Points represent mean ± 1 SE. Amb = ambient salinity (10 ppt), Salt = elevated salinity (20 ppt), Sub = submerged, Exp = exposed

Table 2 Full statistical results for the linear mixed model run with salinity, inundation, and time as independent variables for C flux and aboveground net primary productivity (ANPP). Interpreted results in bold. Data presented as F (numerator degrees of freedom, denominator degrees of freedom) = F value, P = P value

	Salinity	Inundation	Time	Salinity * inundation	Salinity * time	Inundation * time	Salinity * inundation * time
Soil CO_2	$F(1,4) = 0.04$ $P = 0.834$	**$F(1,4) = 35.33$** **$P = 0.004$**	$F(13,268) = 17.00$ $P < 0.001$	$F(1,4) = 0.18$ $P = 0.692$	$F(13,268) = 1.22$ $P = 0.260$	**$F(13,268) = 8.67$** **$P < 0.001$**	$F(13,268) = 0.77$ $P = 0.682$
Soil CH_4	$F(1,4) = 1.10$ $P = 0.352$	$F(1,4) = 0.48$ $P = 0.523$	$F(9,101) = 0.60$ $P = 0.786$	$F(1,4) = 0.24$ $P = 0.643$	$F(9,101) = 1.00$ $P = 0.443$	$F(9,101) = 0.65$ $P = 0.749$	$F(9,101) = 1.35$ $P = 0.221$
GEP	**$F(1,4) = 37.43$** **$P = 0.003$**	$F(1,4) = 3.28$ $P = 0.143$	$F(12,142) = 21.16$ $P < 0.001$	$F(1,4) = 0.42$ $P = 0.550$	**$F(12,142) = 8.06$** **$P < 0.001$**	**$F(12,142) = 8.81$** **$P < 0.001$**	**$F(12,142) = 2.41$** **$P = 0.007$**
ER_{CO2}	**$F(1,4) = 20.97$** **$P = 0.010$**	**$F(1,4) = 23.31$** **$P = 0.008$**	$F(12,142) = 8.36$ $P < 0.001$	$F(1,4) = 0.03$ $P = 0.865$	**$F(12,142) = 9.26$** **$P < 0.001$**	**$F(12,142) = 2.53$** **$P = 0.004$**	$F(12,142) = 1.07$ $P = 0.384$
NEP	**$F(1,4) = 40.29$** **$P = 0.003$**	$F(1,4) = 1.35$ $P = 0.308$	$F(13,155) = 33.73$ $P < 0.001$	$F(1,4) = 0.98$ $P = 0.376$	**$F(13,155) = 7.71$** **$P < 0.001$**	**$F(13,155) = 8.10$** **$P < 0.001$**	**$F(13,155) = 1.92$** **$P = 0.030$**
ANPP	**$F(1,4) = 9.27$** **$P = 0.038$**	$F(1,4) = 2.35$ $P = 0.199$	$F(6,126) = 11.44$ $P < 0.001$	$F(1,4) = 2.23$ $P = 0.209$	**$F(6,126) = 2.32$** **$P = 0.036$**	$F(6,126) = 0.91$ $P = 0.485$	$F(6,126) = 1.66$ $P = 0.134$

GEP, gross ecosystem productivity; ER_{CO2}, ecosystem respiration of CO_2; NEP, net ecosystem productivity

increased (Fig. 3b). Both salinity and inundation had significant effects on ER_{CO2} ($P < 0.05$; Table 2). With both high and low water levels, ER_{CO2} was decreased by 47 and 37% with elevated salinity, respectively (Table 3). With ambient and elevated salinity, ER_{CO2} decreased by 75 and 69% under submerged compared to exposed conditions, respectively (Table 3). ER_{CO2} did not vary much for all treatments for the entire study period (Fig. 3b). NEP ranged from -0.37 (median for Salt.Exp, Mar 2015) to 4.1 μmol CO_2 m^{-2} s^{-1} (Amb.Exp, Dec 2015, Fig. 3c). Overall, elevated salinity led to less CO_2 uptake ($P = 0.003$), while there was no effect of inundation on NEP ($P = 0.308$; Tables 2 and 3).

Aboveground Biomass At ambient salinity, culm density increased from 2.7 ± 0.4 to 5.2 ± 0.9 culms plot^{-1} over the 18-month experiment ($t = 3.61$, $P < 0.01$). At elevated salinity, culm density remained unchanged (2.6 ± 0.5 to 3.2 ± 0.6 culms plot^{-1}; $t = 1.86$, $P = 0.09$) over the same period, so that by the end of the experiment, there was a significant difference in culm density between the ambient salinity and elevated salinity monoliths ($t = 2.72$, $P = 0.01$). There was no change in culm density within the submerged treatment from the beginning to the end of the experiment (2.8 ± 0.3 to $3.8 \pm$

0.7 culms plot^{-1}; $t = 2.00$, $P = 0.07$). Exposed monoliths increased from 2.4 ± 0.2 to 4.8 ± 0.7 culms plot^{-1} over the duration of the experiment ($t = 3.44$, $P < 0.01$). At the end of the experiment, however, there were no significant differences in culm density between the inundated and exposed monoliths ($t = 1.66$, $P = 0.11$). Salinity reduced ANPP ($P = 0.038$), but inundation had no effect on ANPP ($P = 0.199$; Table 2, Fig. 4). GEP was significantly related to biomass in all treatments, whereas GEP was only correlated to ER_{CO2} in the Amb.Exp treatment (Table 4).

Discussion

Our objective was to understand how specific stressors of SLR, and saltwater intrusion (elevated salinity and increased water depth) would affect coastal wetland C and soil biogeochemical dynamics and how these processes influence peat collapse. Soil CO_2 efflux was not affected by salinity, but was influenced by soil exposure to the atmosphere. Elevated salinity, regardless of inundation, significantly reduced marsh C uptake by reducing NEP. The decline in NEP was not caused by an increase in soil respiration or ER but rather by

Table 3 Carbon flux averaged over the experiment. Values represent the mean (μmol CO_2 or CH_4 m^{-2} s^{-1}) ± 1 SE for soil CO_2 ($n = 90$), soil CH_4 ($n = 36$), gross ecosystem productivity (GEP), ecosystem respiration of CO_2 (ER_{CO2}), and net ecosystem productivity (NEP; $n = 52$) compared over the press phase of the experiment for each treatment. Letters represent significant differences among treatments from a multiple comparison test (LSMEANS, Tukey adjusted)

Flux	Amb.Sub	Amb.Exp	Salt.Sub	Salt.Exp
Soil CO_2	0.20 ± 0.04[a]	0.79 ± 0.12[b]	0.24 ± 0.05[a]	0.72 ± 0.14[b]
Soil CH_4	0.0032 ± 0.0021	0.0061 ± 0.0018	-0.0008 ± 0.0018	0.0034 ± 0.0023
GEP	6.13 ± 0.44[a]	7.88 ± 1.09[b]	1.61 ± 0.13[c]	2.34 ± 0.42[c]
ER_{CO2}	2.09 ± 0.15[a]	2.97 ± 0.22[b]	1.11 ± 0.07[c]	1.88 ± 0.10[a]
NEP	4.41 ± 0.52[a]	5.70 ± 1.16[a]	0.64 ± 0.19[b]	0.70 ± 0.49[b]

Amb = ambient salinity (10 ppt), Salt = elevated salinity (20 ppt), Sub = submerged, Exp = exposed
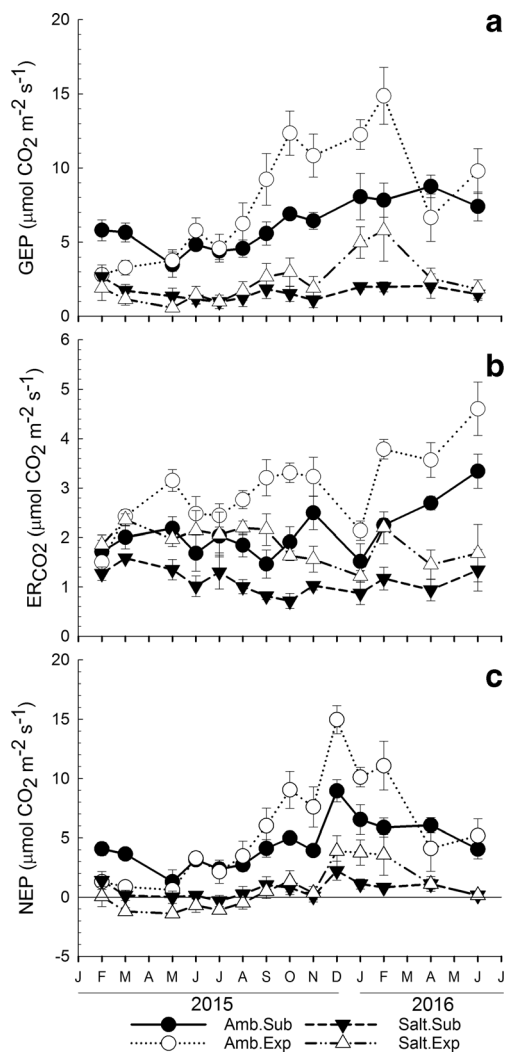
Fig. 3 Monthly instantaneous gross ecosystem productivity (GEP) (**a**), ecosystem respiration of CO_2 (ER_{CO2}) (**b**), and net ecosystem productivity (NEP) (**c**) in micromoles of CO_2 per meter squared per second over the experimental period. A negative value indicates a flux of CO_2 from the marsh to the atmosphere. Points represent means ($n = 4$ replicates) $\pm$ 1 SE. Amb = ambient salinity (10 ppt), Salt = elevated salinity (20 ppt), Sub = submerged, Exp = exposed
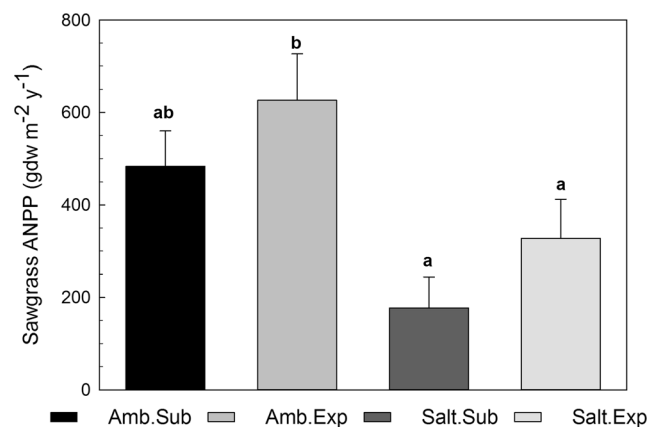

Fig. 4 Mean ($n = 6$ replicates) $\pm$ 1 standard error of *Cladium jamaicense* (sawgrass) aboveground net primary productivity (ANPP) across the four treatments. Letters represent significant differences among treatments from a multiple comparison test (LSMEANS, Tukey adjusted). Amb = ambient salinity (10 ppt), Salt = elevated salinity (20 ppt), Sub = submerged, Exp = exposed

a substantial decrease in plant productivity and GEP. Our results are consistent with an increasing number of studies showing significant changes to ecosystem C cycling in marshes experiencing saltwater intrusion (Neubauer 2013; Herbert et al. 2015; Herbert et al. 2018). Below, we examine how elevated salinity and water depth influence coastal wetland C processing. We then consider the implications C processing may have on coastal wetland survival, given accelerating SLR.

Soil CO_2 and CH_4 Efflux

Salinity has been shown to strongly change soil biogeochemical processes and to lead to both positive and negative feedbacks on soil respiration (Stagg et al. 2017). In our study, there was no effect of elevated salinity or inundation on most porewater physicochemistry. Elevated salinity can increase soil CO_2 efflux because of greater SO_4^{2-} availability (Chambers et al. 2011) or by physical mechanisms that make available an unused pool of labile C (Weston et al. 2011). In our study, salinity had no effect on soil CO_2 efflux (Table 2). In a similar experimental study, Chambers et al. (2013) also found that elevating salinity in mangrove peat soils (16.6 to 32.6 ppt) did not change the rate of soil CO_2 efflux. Because our soils were already brackish in nature, elevating salinity from 10 to 20 ppt likely did not affect microbial processes, especially considering that water for our elevated salinity treatment was sourced from an estuary with high salinity ($\sim$ 38 ppt, Table A1). By using seawater to elevate salinity, we likely changed the microbial structure and function of the soil microbial community to become more salt tolerant (Andronov et al. 2012; Yan et al. 2015), which may explain why soil CO_2 efflux was unchanged.

Hydrology in wetlands strongly drives C remineralization and soil CO_2 efflux. As expected, soil CO_2 efflux was lower in submersed than exposed soils, likely because of lower oxygen availability, which reduces microbial aerobic respiration (Wright and Reddy 2001; Reddy and DeLaune 2008). When soils are exposed, microbes quickly use up labile organic C substrates, which in turn leads to higher CO_2 efflux directly after exposure (Hu et al. 2017). However, over time, that pool of labile C is used up, and C mineralization slows (Yuste et al. 2007). Additionally, water stress can limit microbial respiration (Smith et al. 2003; Malone et al. 2013). This is likely why we saw a significant decline in soil CO_2 efflux between the first and second years in the exposed soil monoliths.

Soil CH_4 efflux in this experiment was also low and not affected by salinity or inundation (Table 3). Methane

Table 4 Coefficient of determination for linear relationships between *Cladium jamaicense* aboveground biomass and ecosystem CO_2 exchange (gross ecosystem productivity (GEP), net ecosystem productivity (NEP), and ecosystem respiration (ER_{CO2}))

	GEP vs. biomass	NEP vs. biomass	ER_{CO2} vs. biomass	GEP vs. ER_{CO2}
Treatment	r^2	r^2	r^2	r^2
Amb.Sub	0.35**	0.22*	0.22*	0.02 ns
Amb.Exp	0.46**	0.47**	0.06 ns	0.27**
Salt.Sub	0.48**	0.27*	0.24*	0.05 ns
Salt.Exp	0.55**	0.50**	0.07 ns	0.04 ns

ns = non-significant ($P > 0.05$), *$P \leq 0.05$, **$P < 0.01$

Amb = ambient salinity (10 ppt), Salt = elevated salinity (20 ppt), Sub = submerged, Exp = exposed

production and efflux typically decrease as salinity increases (Poffenbarger et al. 2011), which is usually the result of sulfate reducers outcompeting methanogens by taking advantage of higher SO_4^{2-} concentrations in seawater (Capone and Kiene 1988). However, given that ambient salinity conditions were already elevated (10 ppt), sulfate reduction was likely already the dominant soil C mineralization process, and an increase to 20 ppt likely did not affect CH_4 production. Low soil CH_4 efflux may also have resulted from our experimental design. Because our soil monolith containers had holes around the sides to allow for water exchange, soil redox potentials were likely higher than what would occur under natural in-situ conditions (Sylvia et al. 2004) (Fig. A1). Higher soil redox potentials indicate higher oxygen availability, which would stimulate aerobic respiration and depress methanogenesis (Reddy and DeLaune 2008). In addition, our measurements only account for soil CH_4 efflux and do not account for any CH_4 loss from plants. In wetlands, a large proportion of soil CH_4 can be lost to the atmosphere via transport through aerenchyma present in the leaf tissue of macrophytes (Whiting and Chanton 1993; Laanbroek 2010). Despite previous work suggesting that sawgrass does not have active gas transport through its aerenchyma (Chabbi et al. 2000), loss of CH_4 through sawgrass stems has been measured in the Everglades and could account for a substantial portion of total CH_4 efflux from the marsh (Steven Oberbauer, Florida International University, pers. comm.). Future work should take CH_4 loss from sawgrass aboveground biomass into account.

Lateral CO_2 Exchange and Aboveground Biomass

Small increases in salinity can significantly impact gas exchange in wetland plants (Pezeshki et al. 1989). Continuously elevated salinity reduced GEP by 74 and 70% compared to the ambient salinity-submerged and -exposed treatments, respectively (Table 5). Our finding is consistent with previous field and laboratory experiments that show significant reduction in plant productivity given elevated salinity (Munns and Tester 2008; Sharpe and Baldwin 2012; Neubauer 2013; Sutter et al. 2014; Herbert et al. 2015). The decline in GEP corresponded to lower culm density, ANPP, and biomass with elevated salinity. Because ANPP was 63 and 47% lower in the Salt.Sub and Salt.Exp compared to the Amb.Sub and Amb.Exp treatments, respectively, some of the decline in GEP with elevated salinity can be attributed to physiological stress (Negrao et al. 2017). Exposure of freshwater plants to elevated salinity can decrease leaf-level CO_2 exchange and reduce aboveground biomass (Pezeshki et al. 1987a; Pezeshki et al. 1987b). Some studies have shown sawgrass to be negatively affected by small increases in salinity with signs of physiological stress at salinities as low as 5 ppt (Macek and Rejmankova 2007; Rejmankova and Macek 2008). Other studies have shown sawgrass to be quite resilient to salinity and grow under oligohaline to mesohaline (5 to 10 ppt) conditions (Troxler et al. 2014; Wilson et al. 2015; Wilson et al. in review). In the Everglades, surface water salinity in some sawgrass marshes can reach 30 ppt,

Table 5 Estimated ecosystem C cycling for net ecosystem productivity (NEP), gross ecosystem productivity (GEP), ecosystem respiration of CO_2 (ER_{CO2}), and soil CO_2 efflux; data show how these variables change with elevated salinity and/or water depth. Values represent mean ($n = 6$) ± 1 SE flux over the experimental timeframe in g C m^{-2} $year^{-1}$. A negative NEP indicates C leaving the marsh to the atmosphere. Letters represent significant differences among treatments from a multiple comparison test (LSMEANS, Tukey adjusted). Annual flux was calculated using established methods and previously derived light response curves for a *C. jamaicense* brackish water marsh (Neubauer 2013; Wilson et al. 2015)

	Amb.Sub	Amb.Exp	Salt.Sub	Salt.Exp
Soil CO_2	95.1 ± 18.1[a]	377 ± 38.3[b]	99.4 ± 17.7[a]	321 ± 41.3[b]
ER_{CO2}	703 ± 20.6[a]	948 ± 52.8[b]	389 ± 9.9[c]	632 ± 36.4[a]
GEP	671 ± 117[a]	825 ± 195[b]	174 ± 41.7[c]	232 ± 74.4[c]
NEP	− 32.2 ± 68.6[a]	− 123 ± 124[ab]	− 215 ± 25.9[ab]	− 401 ± 55.4[b]

Amb = ambient salinity (10 ppt), Salt = elevated salinity (20 ppt), Exp = soil surface exposed 4 cm, Sub = soil surface submerged

though these areas are seasonally flushed with low salinity (< 5 ppt) water (Troxler et al. 2014). In times of high salinity, plants can produce osmolytes, such as proline and glycine (Cavalieri and Huang 1981), to tolerate stress but only up to a certain level (between 10 and 20 ppt). Our study indicates that there may be a level of continuous salinity exposure that negatively affects sawgrass biomass and productivity. Although not a focal point of this study, nutrient availability strongly influences primary productivity in the P-limited Everglades (Childers et al. 2006a). In our study, despite high concentrations of both TDN and TDP in the salt source water (Table A2), GEP decreased with elevated salinity, indicating that salt stress had a much larger impact on the plants than nutrient availability.

Elevated salinity decreased ER_{CO2} by 47 and 37% compared to the ambient salinity-submerged and -exposed conditions, respectively (Table 3), with the salinity effect increasing over time (Fig. 3b). As there was no change in soil CO_2 efflux with elevated salinity, the decrease in ER_{CO2} seen in our experiment can be attributed to decreased leaf respiration. Additionally, ER_{CO2} was relatively stable throughout the entire experiment with very little monthly variation and was not correlated to GEP in most treatments (Fig. 3, Table 4). This runs counter to similar studies that show that GEP and ER_{CO2} are highly correlated and decrease in similar proportions with elevated salinity (Neubauer 2013; Weston et al. 2014; Wilson et al. 2015). Greater inundation decreased ER_{CO2}, which was directly tied to a decrease in soil CO_2 efflux (Table 3). Additionally, under inundated conditions, CO_2 produced in soils can diffuse into the water column and be exported downstream (Butman and Raymond 2011), meaning we may be slightly underestimating the total soil CO_2 efflux. Another important component that we did not account for in this experiment is dissolved inorganic carbon (DIC). In some coastal marshes and mangrove forests, DIC release from soils plays an important role in CO_2 release from the marsh (Bouillon et al. 2008; Sippo et al. 2016), accounting for up to 80% of all total dissolved C flux out of the marsh (Ho et al. 2017). This horizontal flux of C out of the system needs to be taken into account in future studies in order to achieve a full soil C balance estimate.

Overall, elevated salinity decreased NEP by 86 and 88% compared to ambient salinity with inundated and exposed conditions, respectively (Table 3). Although there were a few months in which NEP was negative (Fig. 3c), indicating that the marsh was a net source of CO_2 to the atmosphere, averaged over the entire experimental period, elevated salinity did not lead to a net efflux of CO_2. However, our measurements were taken near solar noon and on sunny days and represent the maximum GEP potential of the vegetation. Therefore, we performed an exercise to integrate our data over a daily, and subsequently, an annual time frame. We took previously derived light response curves for a brackish *C.*

jamaicense marsh (Wilson et al. 2015) and used standard methods to estimate annual flux (Neubauer 2013; Wilson et al. 2015). Briefly, we took our measurement made in full light for each month and scaled it to five different rates and different light levels using the previously derived light response curve for that same month (Wilson et al. 2015). We used temperature and light (PAR) data from a nearby weather tower (MBTS, DBHydro, South Florida Water Management District) to determine the maximum light level for that day. We then used standard equations to estimate daily, monthly, and annual flux (Neubauer 2013; Wilson et al. 2015). After daily integration, we found that all treatments were a net source of CO_2 to the atmosphere, with elevated salinity and soil exposure greatly amplifying CO_2 loss (Table 5). This was mostly driven by a sharp decline in GEP with elevated salinity, with only a disproportionate decline in ER, leading to larger CO_2 loss. The effect of elevated salinity was largest when the soils were exposed. While elevated salinity accelerates CO_2 loss from the marsh, we found the marsh to be a net source of CO_2 to the atmosphere even under ambient salinity conditions. This result was surprising and counter to other studies that conducted similar daily CO_2 flux integrations. Neubauer (2013) found that, although NEP decreased by 55% with elevated salinity in a South Carolina tidal freshwater marsh, the marsh was overall a net CO_2 sink, except during the winter. Weston et al. (2014) found an oligohaline, transitional marsh in Delaware to be a net C source 1 year, and a net C sink the next. In a Georgia freshwater tidal marsh, elevated salinity decreased NEP, but the marsh was still a strong CO_2 sink (Herbert et al. 2018). The brackish marsh where we chose to conduct this study had already experienced visual evidence of peat collapse (Fig. 1), and our finding of the marsh as a net source of CO_2 to the atmosphere under ambient conditions may help explain this collapse.

Global Implications of Saltwater Intrusion on Coastal Wetland Carbon

A number of studies have shown significant changes to ecosystem C cycling in marshes experiencing saltwater intrusion (Neubauer 2013; Herbert et al. 2015; White and Kaplan 2017; Herbert et al. 2018). However, few of these studies focused on coastal peatlands. Our study illustrates how saltwater intrusion alters ecosystem C cycling, resulting in less CO_2 uptake, and how the interaction with greater inundation depth had little influence on aspects of C cycling that we measured. These results indicate that a sustained increase in salinity in brackish coastal marshes, an issue facing coastal wetlands globally, substantially alters C cycling and could disrupt and change ecosystem structure and function. As climate change and increased human alteration of hydrologic cycles continues, instances of wetland salinization will increase (Herbert et al. 2015). Although the specific responses to increased

salinization will vary on a case-by-case basis, depending on frequency and magnitude of exposure, initial soil conditions, hydrologic flow, etc., our results indicated that elevated salinity in coastal wetlands has the potential to dramatically decrease NEP and stimulate CO_2 evasion from the marsh (Table 5). Peat soils and the stabilization of these soils depend on the input of organic material for their existence. Without this input, destabilization of peat soils could occur, potentially leading to collapse and conversion from a marsh to an open pond habitat (Delaune et al. 1994). In fresh- and brackish-water marshes, the potential for peat collapse also is affected by the ability of other, more salt-tolerant, plant species to migrate in and stabilize the soil (Donnelly and Bertness 2001; Smith 2009; Langley et al. 2013). Saltwater intrusion into coastal wetlands is occurring worldwide (Herbert et al. 2015), and the rate will only increase with accelerated SLR. Elevated salinity is usually coupled with other pressures facing coastal wetlands, such as drought (Ardon et al. 2013), altered hydrologic regimes (Green et al. 2017), eutrophication (Deegan et al. 2012), and anthropogenic barriers to migration (Enwright et al. 2016), all potentially interacting to influence the ability of these ecosystems to store organic C. These impacts on storage have global relevance given the importance of these productive peatlands as global C reservoirs.

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