Biogeochemistry (2018) 140:217–232
https://doi.org/10.1007/s10533-018-0486-2

Salinity effects on greenhouse gas emissions from wetland soils are contingent upon hydrologic setting: a microcosm experiment

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Received: 29 April 2018 / Accepted: 13 August 2018 / Published online: 21 August 2018

Abstract Coastal forested wetlands provide important ecosystem services such as carbon sequestration, nutrient retention, and flood protection, but they are also important sources of greenhouse gas emissions. Human appropriation of surface water and extensive ditching and draining of coastal plain landscapes are interacting with rising sea levels to increase the frequency and magnitude of saltwater incursion into formerly freshwater coastal wetlands. Both hydrologic change and saltwater incursion are expected to alter carbon and nutrient cycling in coastal forested wetlands. We performed a full factorial experiment in which we exposed intact soil cores from a coastal forested wetland to experimental marine salt treatments and two hydrologic treatments. We measured the resulting treatment effects on the emissions of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) over 112 days. Salinity effects were compared across four treatments to isolate the effects of increases in ionic strength from the impact of adding a terminal electron acceptor (SO_4^{2-}). We compared control treatments (DI addition), to artificial saltwater (ASW, target salinity of 5 parts per thousand) and to two treatments that added sulfate alone (SO_4^{2-}, at the concentration found in 5 ppt saltwater) and saltwater with the sulfate removed (ASW-SO_4^{2-}, with the 5 ppt target salinity maintained by adding additional NaCl). We found that all salt treatments suppressed CO_2 production, in both drought and flooded treatments. Contrary to our expectations, CH_4 fluxes from our flooded cores increased between 300 and 1200% relative to controls in the ASW and ASW-SO_4^{2-} treatments respectively. In the drought treatments, we saw virtually no CH_4 release from any core, while artificial seawater with sulfate increased N_2O fluxes by 160% above DI control. In contrast, salt and sulfate decreased N_2O fluxes by 72% in our flooded treatments. Our results indicate that salinization of forested wetlands of the coastal plain may have important climate feedbacks resulting from enhanced greenhouse gas emissions and that the magnitude and direction of these emissions are contingent upon wetland hydrology.

Keywords Greenhouse gases · Saltwater intrusion · Drought · Sea level rise

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Responsible Editor: Egbert Matzner.

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Introduction

Coastal forested wetlands provide important ecosystem services such as carbon sequestration, flood abatement, habitat for obligate wetland species, and retention of nutrients and other water pollutants (Doyle et al. 2007). Accumulation of soil carbon in coastal wetlands has the potential to offset greenhouse gas emissions and mitigate climate change (Mcleod et al. 2011). Coastal wetlands, however, also have the potential to provide positive feedbacks to climate change through the emission of greenhouse gases, such as carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4, Reddy and DeLaune 2008). The balance between carbon sequestration and greenhouse gas emissions in coastal wetlands is being altered by changes in precipitation and increased frequency of salinization due to sea level rise (Moorhead and Brinson 1995; Herbert et al. 2015).

Sea level rise (SLR) has already caused marine salt increases to coastal wetlands in many regions of the world (Herbert et al. 2015). This trend is expected to become more widespread as rates of SLR will increase from current rates of 2.2–3.6 mm year^{-1} up to 15.6 mm year^{-1} by 2100 (Church et al. 2013). However, the contribution of SLR to coastal wetland salinization is hard to forecast due to the spatial variation in geology, geomorphology, water salinity, and surface winds (Church et al. 2013; Herbert et al. 2015). Before coastal wetlands are inundated with high salinity water due to rising seas, increased salinization of wetlands is likely to become more common due to human water withdrawals, ditching and dredging, and more frequent and longer droughts (Anderson and Lockaby 2012). In order to forecast the ability of coastal forested wetlands to serve as carbon sinks and nutrient filters, it is important to understand the individual and combined effects of drought and salinity on soil nutrient pools and greenhouse gas emissions from wetland soils.

Increased salinization of low lying coastal forested wetlands could increase emissions of CO_2 and reduce CH_4 emissions from anoxic wetland sediments (Herbert et al. 2015). Elevated salinity increases the availability of terminal electron acceptors (such as Fe(III), Mn(IV), and SO_4^{2-}), which can shift microbial metabolism towards more energetically favorable processes (iron and sulfate reduction; Chambers et al. 2011; Meiggs and Taillefert 2011; Weston et al. 2011; Neubauer 2013). The responses of soil CO_2 emissions to experimental salt additions or salinity gradients have thus far been mixed. Several experimental studies have documented increased CO_2 fluxes in response to saltwater addition (Neubauer et al. 2013; Chambers et al. 2013). Other studies have found no effect of salinization on CO_2 emissions (Setia et al. 2010; Marton et al. 2012). Still others have documented declines in CO_2 fluxes with increased salinity (Brouns et al. 2014) or along salinity gradients (Ikenaga et al. 2010). Given that CO_2 is often the dominant greenhouse gas emitted from coastal wetlands, it is important to understand how increased salinity will affects its emissions.

One of the most consistent results of the effects of increased salinity on freshwater wetlands has been the suppression of CH_4 production (Weston et al. 2006; Chambers et al. 2013). A meta-analyses of CH_4 fluxes from marshes along natural salinity gradients showed that CH_4 release decreased with increasing salinity (Poffenbarger et al. 2011). However, at least one study has shown increased CH_4 fluxes from freshwater marshes in response to increased salinity (Weston et al. 2011), highlighting our incomplete understanding of the complexities of how increased salinity alters CH_4 production and consumption (Herbert et al. 2015).

Compared to CH_4 fluxes, far less is known about the effects of increased salinity on N_2O emissions. Marine salts have been shown to affect both nitrification and denitrification, two of the main pathways responsible for N_2O production and consumption in wetland soils. Increased salinity in former freshwater wetlands has been shown to decrease rates of nitrification (Pathak and Rao 1998; Ardón et al. 2013), due to sulfide inhibition of nitrifying bacteria (Joye and Hollibaugh 1995). Experimental tests of denitrification response to salinity have had more mixed results, with studies documenting increases, decreases, or no changes in denitrification in response to salinity (Fear et al. 2005; Aelion and Warttinger 2009). Increased concentrations of sulfide, a product of sulfate reduction, can inhibit the reductase enzymes of the final steps of denitrification, leading to incomplete denitrification, which can lead to N_2O release (Brunet and Garcia-Gil 1996). This effect is likely to be more apparent in soils enriched in NO_3, as was seen in a field study that documented a tenfold increase in N_2O emissions from flooded soils at the interface of both saltwater incursion and agricultural runoff (Helton et al. 2014). Given the high global warming potential of N_2O (250–270 times global warming potential of CO_2 on a 100 year time scale; Neubauer and Megonigal 2015), it is important to understand how increased salinity will alter its emissions from coastal wetlands.

The consequences of increased salinity on greenhouse gas emissions from coastal wetlands are expected to be contingent upon the hydrologic setting. While wetlands are characterized by their shallow water table depths, there is considerable spatial and temporal variability in this attribute within any wetland. When saltwater enrichment is accompanied by increased flooding, the subsequent decline in oxygen could offset the impact of increased availability of terminal electron acceptors from salinization, leading to an overall decline in carbon losses (Herbert et al. 2015). In contrast, cycles of drying and rewetting soils have been shown to increase overall carbon mineralization and emission rates (Fierer and Schimel 2002), and pulses of salinity to a hydrologically dynamic wetland soil might exacerbate this trend by adding terminal electron acceptors that extend the degree of reduction under flooded conditions (Chambers et al. 2011). It is important to understand the combined and individual effects of changes in hydrology and salinity on greenhouse gas emissions from coastal wetland soils.

We previously reported that drought-induced salinization increased dissolved inorganic nitrogen export and decreased dissolved organic carbon export from mature and restored coastal forested wetlands (Ardón et al. 2013, 2016, 2017). Increased salinity and sulfate from agricultural fields also led to decreased CH_4 fluxes and increased N_2O fluxes from flooded areas of a large restored wetland (Helton et al. 2014). In this study, we examined the extent to which the effects of salinity on greenhouse gas emissions are contingent upon the hydrologic status of the receiving wetland soil. We designed our experiment to isolate the effects of sulfate from other salt ions, given that sulfate can be used as a terminal electron acceptor. We predicted that: (1) salinity and sulfate additions will increase CO_2 emissions due to increased sulfate availability, and the magnitude of CO_2 stimulation will be higher in flooded cores due to increased sulfate reduction in anoxic conditions; (2) increased salinity and sulfate will increase N_2O emissions in flooded cores due to limitation of the last step of denitrification; and (3) salinity and sulfate additions in flooded cores will decrease CH_4 fluxes due to increased sulfate reduction as observed in other studies.

Methods

Field site and microcosm set up

On July 26, 2010, we collected 50 soil cores from the Timberlake Observatory for Wetland Restoration (TOWeR; Ardón et al. 2010) from an area that has not experienced saltwater incursion in at least the last 20 years due to drainage for agriculture and subsequent restoration. This area was planted with Atlantic white cedar (*Chamaecyparis thyoides*) as part of the wetland restoration (Ardón et al. 2010). We collected organic soils, which are mapped as Terric Haplosaprists, corresponding to Eutric Histosols (Arnold et al. 2009; Natural Resources Conservation Service 2009). We used intact soil cores (30 cm deep, 5 cm diameter) to build microcosms based on a design modified from Clark et al. (2006). Each microcosm consisted of the main soil core connected to a PVC reservoir. The reservoir allowed us to manipulate both the chemistry of soil solution and the water level within the soil core. We installed microlysimeters (5 cm, glass fiber, Rhizon MOM, Rhizosphere Research Products, The Netherlands) at 3 depths (5, 15 and 25 cm) within each core to sample soil solution. For more details on core design and an image of the set up see Ardón et al. (2013).

Of the 50 cores we collected, we destructively harvested ten soil cores at the outset of the experiment to determine initial soil nutrient and physical characteristics. We assigned the remaining 40 cores to one of four water chemistry treatments by modifying an artificial saltwater recipe from Kester et al. (1967) (Appendix Table 5): control (deionized water), SO_4^{2-} only (SO_4^{2-}, target > 100 mg L^{-1}), artificial saltwater (ASW, target 5 parts per thousand, $Cl^- > 1000$ mg L^{-1} and $SO_4^{2-} > 100$ mg L^{-1}), and artificial saltwater without sulfate (ASW-SO_4^{2-}, Cl > 1000 mg L^{-1}). The 5 ppt salinity was chosen because we have documented large increases in nitrogen and decreases in DOC during drought induced increases in salinity to that level (Ardón et al. 2013, 2016). Half of the cores assigned to each water chemistry treatment were randomly assigned to one of two hydrologic treatments. Cores were either continuously flooded with water at or just above the soil surface (flooded treatment) or drained to maintain a water table depth 20 cm below the soil surface (drought treatment). We set up the cores on August 9th, 2010 by flooding each core with deionized water and allowing them to equilibrate for 2 weeks before applying treatments. We maintained the water treatments for the duration of the experiment by monitoring water levels in the reservoirs every 2 days and refilling with the appropriate solution when necessary. The cores were incubated in an environmental chamber maintained at 30 °C and 20% humidity in the dark for the duration of the experiment.

After 2 weeks of equilibration, we sampled soil solution and greenhouse gas emissions (CO_2, CH_4, N_2O) from all cores and then initiated our chemical treatments the following day. We sampled soil solution and greenhouse gases from each core on days 7, 14, 21, 28, 42, 56, 70, 82, 100, and 112. Soil solution sampling consisted of connecting a 5 mL syringe to each of the microlysimeters, adding a vacuum and leaving the syringes to collect soil solution overnight. We collected the sample the next day into a clean HDPE scintillation vial. Samples were either analyzed immediately or frozen until analyses.

Soil solution water chemistry analyses

We analyzed soil solution dissolved organic carbon (DOC, measured as non-purgeable organic carbon) and total dissolved nitrogen (TDN) concentrations on a Shimadzu TOC-V total carbon analyzer with a TNM-1 nitrogen module (Shimadzu Scientific Instruments, Columbia, Maryland, USA). We measured soil solution Cl^-, SO_4^{2-}, NO_3–N concentrations on a Dionex ICS-2000 ion chromatograph (Dionex Corporation, Sunnyvale, California, USA). We measured NH_4–N with the phenate method on a Lachat QuickChem 8000 automated system (Hach, Colorado, USA). To examine the effects of salinity on the aromaticity of the dissolved organic matter, we measured $SUVA_{254}$, which is commonly used as a measure of aromaticity and humics in water (Jaffe et al. 2008). On one soil solution sampling date (day 80), we measured water absorbance at 254 nm to estimate specific UV corrected for DOC ($SUVA_{254}$ (Weishaar et al. 2003) using a 1 cm path length quartz cuvette on a Perkin Elmer 559 UV/visible spectrophotometer.

Greenhouse gases measurements

We measured greenhouse gas fluxes by closing each core with a gas tight lid with a Swagelok brass sampling port with a rubber septum (0.6 cm). Headspace gas samples were collected immediately (time = 0) and after 1 h into evacuated 8 ml gas vials. We ran trials before the start of the experiment, which showed that 1 h was long enough for measurable gas accumulation. Given the number of cores and frequency of sampling, we were unable to collect more than two timepoints each time we measured gas fluxes. Accumulation of each of the gases over 1 h and the ideal gas law were used to estimate gas fluxes (Morse et al. 2012). We determined concentrations of CO_2, N_2O, and CH_4 from gas samples on a Shimadzu 17A gas chromatograph with electron capture detector (ECD) and flame ionization detector (FID, Shimadzu Scientific Instruments, Columbia, MD, USA), with a methanizer to allow all three gases to be measured from the same sample (Morse et al. 2012).

Soil parameter measurements

We measured soil characteristics on subsamples obtained after destructively sampling each core, either before or after the conclusion of the experiment. We separated soil cores into top and bottom 5 cm, and middle 20 cm. After separation, we homogenized and sieved soil core segments through a 2-mm mesh. We used standards methods to measure soil characteristics (pH, %C, and %N) on top and bottom 5 cm. We present results from the top 5 cm because they showed the biggest difference among treatments. We extracted inorganic N from duplicate 2.5 g soil samples with 25 mL of 2 M KCl, and analyzed the extracts for NH_4–N (phenate method) and NO_3–N (using the hydrazine reduction method) on a Lachat QuickChem 8000 automated system. To estimate active microbial biomass, we used substrate induced respiration (SIR) with methods from (Bradford et al. 2008). We added autolyzed yeast as a substrate to 4 g of soil and measured CO_2 accumulation over 4 h. CO_2 was measured as described above.

Statistical analyses

We compared soil nutrient pools, soil solution nutrients, and greenhouse gas emissions using analysis of variance (ANOVA, alpha = 0.05) and post hoc Tukey tests. For the GHG emissions we ran ANOVAs on the total (sum) of the emissions across all sampling points at the end of the experiment. ANOVA factors were hydrology (drought or flooded), salinity (present or absent), and sulfate (present or absent) and the interaction terms. Soil solution and greenhouse gas emissions data were log-transformed to meet assumptions of normality. All analyses were conducted on JMP statistical software (SAS, Cary, North Carolina).

Results

Experimental treatment

We were successful in maintaining distinct salinity treatments throughout the experiment (Fig. 1). Chloride concentrations were > 1000 mg Cl^{-} L^{-1} in the saltwater (ASW) and saltwater without sulfate treatments (ASW-SO_4), compared to < 10 mg Cl^{-} L^{-1} in the control and sulfate (SO_4) only treatment (Fig. 1A-D). Similarly, we maintained sulfate concentrations > 80 mg $SO_4{}^{2-}$ L^{-1} in the sulfate and saltwater with sulfate treatments, compared to < 12 mg $SO_4{}^{2-}$ L^{-1} in the DI and artificial saltwater without sulfate treatments (Fig. 1f–h).

Soil solution responses

The addition of saltwater (with or without sulfate) increased TDN concentrations by 3-5 fold under both hydrologic settings (Fig. 1i–k, significant salt effect in Table 1), while sulfate added alone did not lead to significant changes in TDN (Fig. 1i, j). We found that soil solution NO_3 concentration responses were contingent upon both hydrologic, salt, and sulfate treatments and their interaction (hydrology, hydrology by salt, and three way interaction significant terms, Table 1). In our drought cores, sulfate enrichment (with or without salt, mean = 20.0 mg L^{-1} NO_3–N) caused an 11-fold increase in NO_3-N concentrations compared to treatments without sulfate (mean = 1.79 mg L^{-1} NO_3–N, Fig. 1m and n, p = 0.04). In flooded cores NO_3–N was lower overall, but it was 33-fold higher in the ASW with SO_4 treatment (mean = 5.28 mg L^{-1} NO_3–N) compared to the other water chemistry treatments (mean = 0.16 mg L^{-1} NO_3–N, Fig. 1e and h). Salinity additions led to 5–10 fold higher NH_4–N concentrations, but these treatment effects also depended on hydrology and sulfate concentrations (Fig. 1, salt, hydrology, hydrology by salt, and salt by sulfate significant interactions, Table 1).

Soil parameters

There were no differences in %C or %N at the end of the experiment across the treatments (Table 2). Despite the addition of marine cations and their associated alkalinity, we did not see any significant increase in soil pH with our salinity treatments, though soil pH was ~ 0.5–1 unit higher under flooded conditions (Table 2). Extractable NH_4–N and NO_3–N concentrations increased above the initial conditions in all cores over the course of the experiment in all treatments (initial NH_4–N = 8.8 ± 0.73 mg N kg^{-1} soil, initial NO_3–N = 3.88 ± 0.29, Fig. 2). In the flooded cores, soil NH_4–N concentrations were 4-fold higher in the salt treatments compared to the other treatments (Fig. 2a). There were no significant differences in soil NH_4–N concentrations across the drought treatments (Fig. 2a). Extractable soil NO_3–N concentrations were not affected by salinity treatment, but were more than 10X higher in dry cores than in their flooded counterparts (Fig. 2b). Microbial biomass, measured as substrate induced respiration (SIR), was twice as high in the DI and sulfate flooded treatments, compared to the salt treatments (Fig. 2c).

Greenhouse gas emissions

Carbon dioxide fluxes declined over time in all treatments with added salinity during the experiment (Fig. 3c–d); controls and treatments with added sulfate alone did not change significantly with time (Fig. 3a–b). In both hydrologic settings, the negative effects of salinity treatment on CO_2 fluxes became more extreme over time (Fig. 3c and d). The most extreme treatment effect was observed for the ASW without sulfate to flooded cores, with total CO_2 fluxes from these cores ~ 52% lower than in flooded control cores (Fig. 4a). Although CO_2 fluxes did not significantly change over time when sulfate was added alone, total CO_2 fluxes were lower relative to controls in both hydrologic treatments, leading to a 22% reduction in drought and a 48% reduction in flooded cores by the end of the experiment (Fig. 4a). Salt,

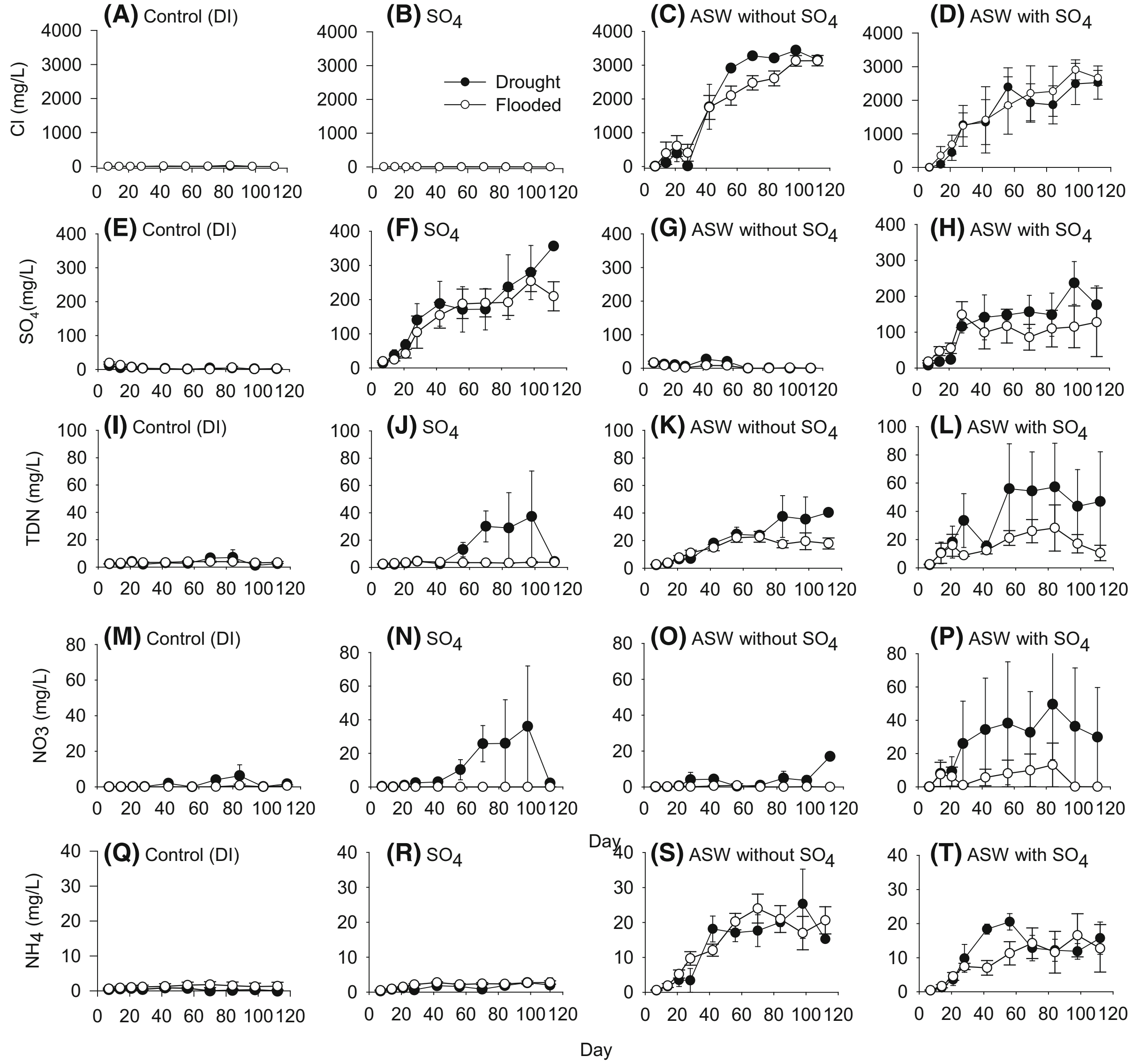

Fig. 1 Time series of soil solution (mean concentrations ± standard error) of Cl (**a**, **b**, **c**, **d**), SO_4^{2-} (**e**, **f**, **g**, **h**), TDN (**i**, **j**, **k**, and **l**), NO_3–N (**m**, **n**, **o**, **p**) and NH_4–N (**q**, **r**, **s**, **t**) in 15 cm piezometers for the duration of the experiment. Water chemistry treatments are in different panels, hydrology is indicated by symbol (black symbols are drought, white symbols are flooded treatments)

sulfate, and their interaction each led to significant declines in total CO_2 fluxes (Table 3).

Methane fluxes were higher in the flooded treatments (mean = 17.5 ± 2.6 mg CH_4 m^{-2} h^{-1}) compared to the drought treatments, where they were often below detection and were unresponsive to salt or sulfate additions (mean = 0.06 ± 0.02 mg CH_4 m^{-2} h^{-1}, Fig. 3e–h). In our flooded cores, the addition of ASW without SO_4^{2-} led to an 1100% increase in CH_4 flux (Fig. 3g). When added alone, SO_4^{2-} decreased total CH_4 fluxes by 88% relative to DI control (Fig. 4b). Addition of ASW with SO_4^{2-} led to 300% increase in total CH_4 flux (Fig. 4b). Drought and SO_4^{2-} led to declines in total CH_4 fluxes, while salt increased CH_4 fluxes in flooded cores (Fig. 4, Table 3). We found that CH_4 fluxes measured on day 80 increased as $SUVA_{254}$ (a measure of aromaticity and humics in solution) in soil solution declined

Table 1 Summary of ANOVA results on log-transformed soil solution data from 15 cm piezometers in microcosm experiment

Parameter	F ratio	p
TDN		
Hydrology	2.60	0.11
Salt	**124.22**	**< .0001**
Hydrology*salt	0.00	0.96
SO_4	1.00	0.32
Hydrology*SO_4	2.11	0.15
Salt*SO_4	0.08	0.77
Hydrology*salt*SO_4	0.00	0.96
NO_3–N		
Hydrology	**55.82**	**< .0001**
Salt	**5.73**	**0.02**
Hydrology*salt	**0.92**	**0.01**
SO_4	**4.48**	**0.04**
Hydrology*SO_4	0.38	0.54
Salt*SO_4	2.12	0.15
Hydrology*salt*SO_4	**4.64**	**0.03**
NH_4–N		
Hydrology	**27.40**	**< .0001**
Salt	**104.57**	**< .0001**
Hydrology*salt	**6.53**	**0.01**
SO_4	1.08	0.30
Hydrology*SO_4	0.82	0.36
Salt*SO_4	**9.51**	**0.01**
Hydrology*salt*SO_4	0.26	0.61

Bold values denote significant differences $p < 0.05$

Table 2 Mean (and standard error) soil carbon (%C), nitrogen (%N) and pH at the end of the experiment. Different letters denote significant differences among treatments determined from ANOVA and post hoc Tukey ($p < 0.05$)

	%C	%N	pH
Drought			
DI	15.90 ± 1.4	0.66 ± 0.06	3.65 ± 0.03^{b}
SO_4	15.20 ± 0.92	0.62 ± 0.04	3.72 ± 0.11^{b}
ASW-SO_4	15.50 ± 1.20	0.66 ± 0.05	3.64 ± 0.06^{b}
ASW	16.10 ± 0.99	0.65 ± 0.04	3.86 ± 0.12^{b}
Flooded			
DI	15.20 ± 0.69	0.60 ± 0.03	4.08 ± 0.03^{ab}
SO_4	16.20 ± 0.51	0.65 ± 0.03	4.19 ± 0.03^{ab}
ASW-SO_4	13.90 ± 0.64	0.55 ± 0.02	4.44 ± 0.10^{a}
ASW	14.40 ± 0.83	0.58 ± 0.03	4.44 ± 0.24^{a}

(Fig. 5a). A regression on log transformed CH_4 data versus $SUVA_{254}$ explained 33% of the variation (Fig. 5a). We also found that CH_4 fluxes were positively correlated to NH_4 concentrations ($r^2 = 0.54$, $p < 0.001$; Fig. 5b).

Both the magnitude and the direction of salinity addition on N_2O fluxes were contingent upon hydrologic treatment (Fig. 3, Table 3). Adding ASW with SO_4^{2-} caused a 160% increase in total N_2O emissions in the drought cores compared to the DI, even though the difference was not significant (Fig. 4c). While under flooded conditions, adding ASW with SO_4^{2-} caused a 72% decrease in N_2O production compared to the DI treatment, even though the difference was also not significant (Fig. 4c). The highest total N_2O flux (6.85 mg m^{-2}) we measured was in our drought and ASW treatment, while the lowest N_2O flux (0.95 mg m^{-2}) was in the flooded SO_4^{2-} treatment (Fig. 4c).

Discussion

We did not find support for our initial predictions. Our first prediction was that salinity and SO_4^{2-} would increase CO_2 emissions due to increased SO_4^{2-} availability, and the magnitude of stimulation would be higher under flooded conditions. Contrary to our prediction, we found that increased salinity and SO_4^{2-} caused substantial declines in CO_2 fluxes under both hydrologic treatments. Our second prediction was that salinity would increase N_2O fluxes in flooded cores, due to limitation of the last step of denitrification. We found that salinity did increase N_2O fluxes, but only under drought conditions. N_2O decreased with increased sulfate under flooded conditions. Our third prediction was that increased salt and sulfate in the flooded cores would decrease CH_4 fluxes. We were surprised to find the opposite, with salinity causing substantial increases in CH_4 fluxes in the flooded treatments (Fig. 3). These results are inconsistent with the majority of salt enrichment experiments conducted to date (Table 4). Below we examine possible mechanisms to explain the unexpected direction of the CO_2 and CH_4 fluxes, and the unexpected increase in N_2O under the drought treatment. Overall, we found that

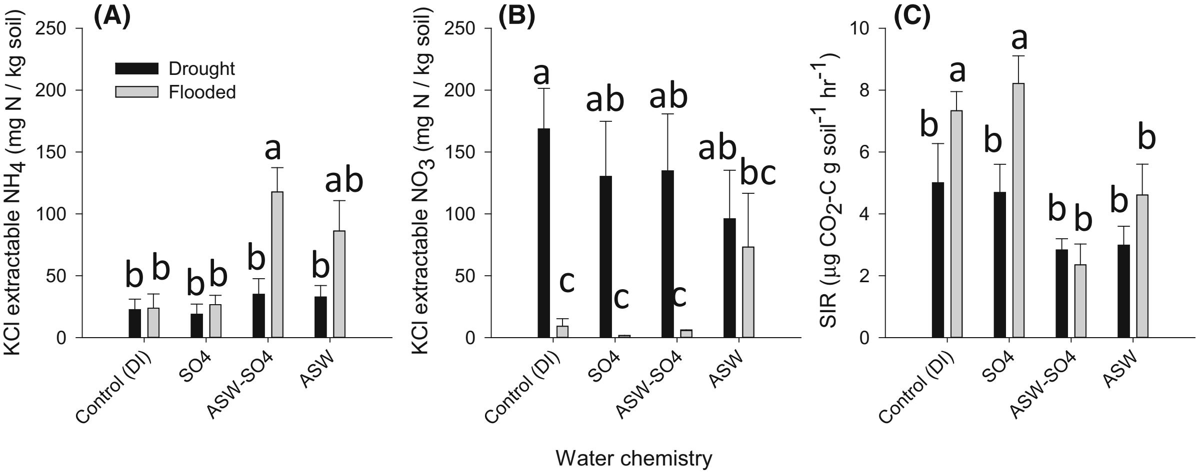

Fig. 2 Concentrations (mean concentrations ± standard error) of soil KCl-extractable NH_4–N (**a**), NO_3–N (**b**), and substrate induced respiration (SIR, µg CO_2–C g soil^{-1} h^{-1}) from the top 5 cm of soil cores at the end of the experiment. Letters denote significant differences based on ANOVA and post hoc Tukey test

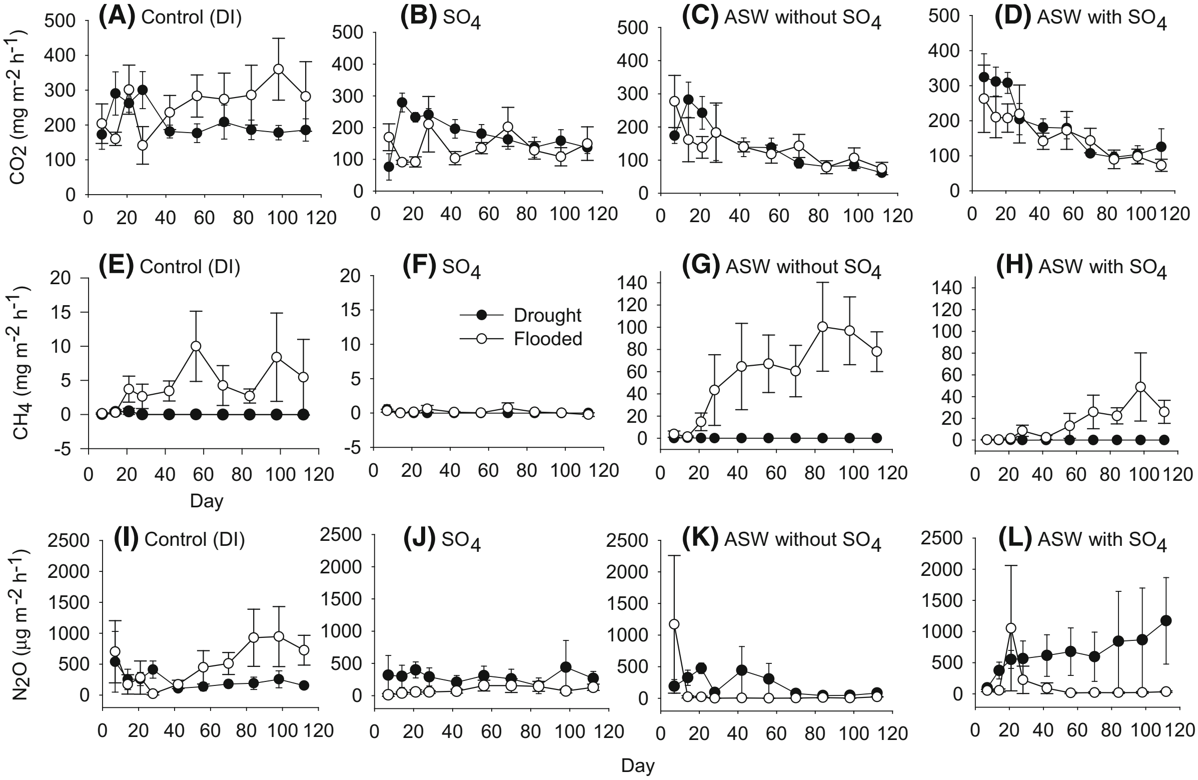

Fig. 3 Time series of greenhouse gas emissions (mean fluxes ± standard error) of CO_2 (**a**, **b**, **c**, **d**), CH_4 (**e**, **f**, **g**, **h**), and N_2O (**i**, **j**, **k**, **l**) for the duration of the experiment. Water chemistry treatments are in different panels, hydrology is indicated by the symbols (black symbols are drought, white symbols are flooded treatments). Note different scale on the y-axes in panels **e** and **f** versus **g** and **h**

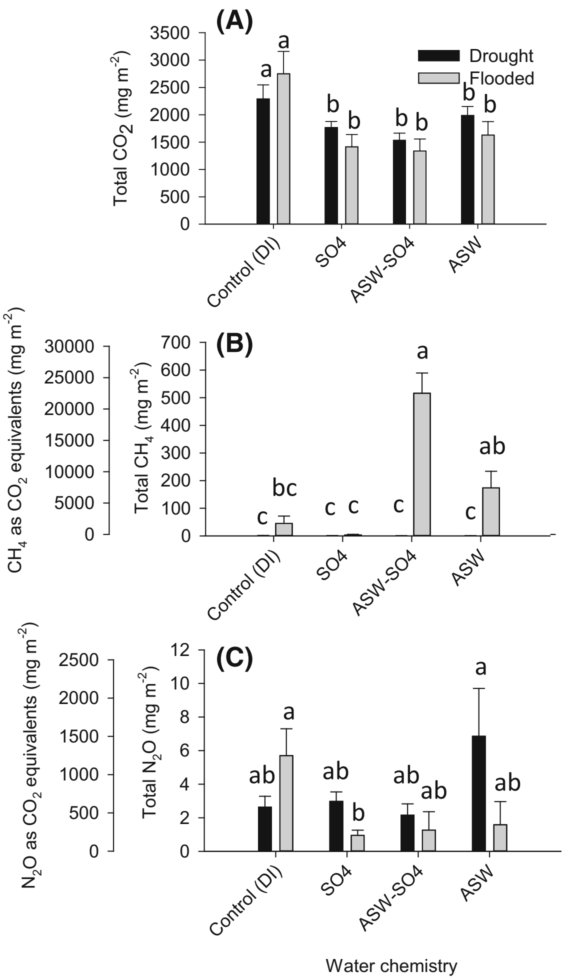

Fig. 4 Total CO_2 (**a**), CH_4 (**b**), and N_2O (**c**) fluxes in drought (black bars) and flooded (gray bars) treatments. Second y-axes in B and C denote total fluxes in CO_2 equivalents. Letters denote significant differences based on ANOVA and post hoc Tukey test

Table 3 ANOVA results of total fluxes of greenhouse gases at the end of the experiment

Parameter	F ratio	Prob > F
CO_2		
Hydrology	0.73	0.39
Salt	**18.41**	**> 0.001**
Hydrology*salt	1.71	0.19
SO_4	**11.77**	**0.001**
Hydrology* SO_4	2.51	0.12
Salt*SO_4	**13.68**	**> 0.001**
Hydrology*salt*SO_4	0.98	0.32
CH_4		
Hydrology	**11.59**	**0.001**
Salt	**9.12**	**0.005**
Hydrology*salt	**9.35**	**0.005**
SO_4	**4.93**	**0.03**
Hydrology*SO_4	4.13	0.06
Salt*SO_4	0.06	0.80
Hydrology*salt*SO_4	0.01	0.91
N_2O		
Hydrology	0.65	0.42
Salt	**7.27**	**0.01**
Hydrology*salt	**6.29**	**0.01**
SO_4	1.72	0.19
Hydrology*SO_4	3.27	0.07
Salt*SO_4	3.49	0.07
Hydrology*salt*SO_4	1.34	0.25

Bold values indicate significant differences at $p < 0.05$

both drought and increased salinity can lead to positive feedbacks to climate change through increased greenhouse gas emissions from wetland soils.

Soil nutrients

Our previous work showed increased NH_4–N in surface water and soil solution with higher salinity (Ardón et al. 2013). The results here show that soil NH_4–N also increases in response to salinization (Fig. 2a). This agrees with previous laboratory (Baldwin et al. 2006; Weston et al. 2006) and field studies (Weston et al. 2010), which support the hypothesis that cations in marine salts displace NH_4^+ ions from cation exchange sites and allow dissolved NH_4^+ to accumulate. The highest NH_4–N concentrations occurred in the flooded treatment, as we would expect given that nitrification in the more oxic soils in the drought treatments led to the transformation of NH_4^+ to NO_3^-. Soil NO_3–N concentrations were highest in the drought treatment, again as we would expect, given that denitrification would be inhibited in the oxic soils in the drought treatments. Among the flooded treatments, the ASW with sulfate led to the highest soil NO_3–N concentrations, suggesting that salinity might have inhibited denitrification. Despite changes in the KCl extractable nutrients, there was no difference in %C and %N among treatments (Table 2), suggesting that mineralization of organic N did not vary among

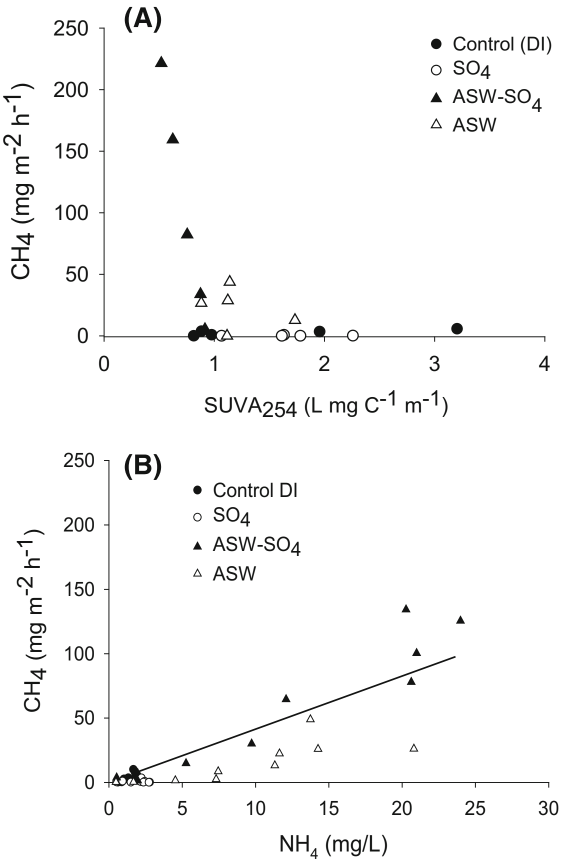

Fig. 5 Specific UV absorbance at 254 nm ($SUVA_{254}$, L mg C^{-1} m^{-1}) in soil solution versus CH_4 fluxes (mg m^{-2} h^{-1}) for flooded cores during one sampling date (day 80; **a**). NH_4–N (mg/L) concentrations in soil solution versus CH_4 fluxes (mg m^{-2} h^{-1}; **b**). Regression of log transformed $SUVA_{254}$ and CH_4 fluxes explained 33% of the variation ($p < 0.05$), regression of NH_4–N versus CH_4 fluxes explained 54% of the variation ($p < 0.05$). Symbols indicate different water chemistry treatments

treatments. Other studies have measured declines in soil carbon content as a result of salinity addition (Weston et al. 2011; Chambers et al. 2014), but those studies also measured increases in C respiration from the soils, which we did not find. Our results suggest that for these forested wetland soils, increased salinity and drought can increase soil nutrients, without increasing soil C loss.

Carbon dioxide fluxes

The CO_2 fluxes measured in these soil cores were similar to rates measured in the field (20–1000 mg CO_2 m^{-2} h^{-1}) from the same site (Morse et al. 2012). The lack of a decrease in CO_2 fluxes over time in the controls and sulfate only treatments suggests that, even in the absence of plants to replenish carbon in the soils, carbon limitation was not severe in the absence of salt. Our results showed that salt led to both declining CO_2 fluxes over time and lower total fluxes at the end of the experiment, which is in contrast to what most studies similar to this one have found (Table 4). Below we examine potential mechanisms to explain the decline in CO_2 fluxes.

One potential mechanism to explain the decreased CO_2 fluxes is reduced microbial respiration due to salt stress. Several previous studies have reported decreases in microbial respiration due to increased salinity (Brouns et al. 2014), while others have reported no change (Baldwin et al. 2006, Table 4). Yet the majority of experimental studies similar to our study design have observed the opposite response, with microbial respiration increasing in response to salinity addition (Table 4). This increase is most frequently attributed to an increase in sulfate or iron reduction after the introduction of terminal electron acceptors (particularly SO_4^{2-}) that are abundant in seawater (Weston et al. 2006). Most studies have been conducted in freshwater marshes that occasionally experience episodes of saltwater exposure during high tides or storms. Perhaps these occasional saltwater exposures allow microbes that are more salt tolerant to persist and to take advantage of the addition of terminal electron acceptors (Morrissey et al. 2014). The soils used in this study had been protected from saltwater exposure for at least 20 years (due to field drainage and active dewatering by high capacity pumps). It is thus possible that the microbial community in our experimental cores may have been particularly vulnerable to increases in salinity (Rath and Rousk 2015). The decline in SIR observed in the salt treatments (Fig. 2) supports the hypothesis that osmotic stress caused a decrease in microbial biomass and respiration despite the enhanced terminal electron acceptor supply.

A reduction in DOC caused by salt addition is a complementary explanation for the observed decrease in CO_2 fluxes. We previously reported 50% declines in DOC concentrations in response to seasonal or experimental saltwater addition in both the field and laboratory experiments (Ardón et al. 2016). In this microcosm experiment the combination of salt and drought led to a 49% decline in DOC concentrations

Table 4 Summary of microcosm studies on the effects of salinity on greenhouse gas emissions from wetland soils. Positive values denote salinity led to an increase, negative values denote a decrease

Paper	Wetland type	CO_2 (% change)	CH_4 (% change)	N_2O (% change)
This study	Freshwater forested	− 76	300 to 1180	− 72 to 160
Liu et al. (2017)	Freshwater forested	10	− 17	− 95
Brouns et al. (2014)	Peatlands	− 40 to − 60	No change	
Chambers et al. (2011)	Freshwater marsh	32	− 79 to − 94	
Chambers et al. (2013)	Intertidal marshes	112	− 98	
Chambers et al. (2014)	Mangroves	50	− 74	
Weston et al. (2006)	Tidal freshwater marshes	25	− 77	
Weston et al. (2011)	Tidal freshwater marshes	45	1200	
Marton et al. (2012)	Tidal freshwater forests	150	− 89	900
Neubauer et al. (2013)	Tidal freshwater marshes	39	− 35 to − 46	
Baldwin et al. (2006)	Freshwater floodplain	0	− 44	

(34.8 ± 3.14 mg/L DOC in salt treatments compared to 69.3 ± 2.2 mg/L in control and SO_4^{-2} only treatments; Ardón et al. 2016). Declines in DOC at the ecosystem scale may result from both decreased plant production and the flocculation of dissolved organic matter in salt water rich in divalent cations (Ca^{2+} and Mg^{2+}, Ardón et al. 2016). In this experiment, we hypothesize that saltwater enrichment induced DOC flocculation and decreased C availability to microbes. Other studies have reported increases in DOC due to salt addition (Chambers et al. 2014), or no changes (Weston et al. 2011). Differences in soil characteristics and dominant forms of organic matter across different wetland ecosystems might explain the divergent responses across studies.

Methane

One of the most consistent results in salt addition experiments has been the decline in CH_4 fluxes, with most studies reporting a 35–90% suppression of CH_4 (Table 4). Our results and those of Weston et al. (2011) are the only published studies to date that report a stimulation of CH_4 fluxes during experimental saltwater enrichment (Table 4). Both studies measured remarkably large positive impacts on CH_4 flux ($\sim$ 1200%, Table 4) despite being conducted on different wetland habitats (forested wetland soils vs tidal freshwater marsh sediments). The large increase in CH_4 production we observed in response to saltwater was contrary to theoretical expectations, given that the addition of sulfate has typically been shown to allow sulfate reducing bacteria to outcompete methanogens for available organic carbon (Vile et al. 2003; Weston et al. 2006; Gauci et al. 2010). Several previous experimental studies have measured the expected reduction of CH_4 release and increase in sulfate reduction in response to salt additions (Weston et al. 2006; Neubauer 2013). However, a review of CH_4 fluxes from wetlands along salinity gradients found that oligohaline marshes (salinities 0.5–5 ppt) had the highest and most variable CH_4 fluxes (Poffenbarger et al. 2011). The field sites from which our soils and Weston et al.'s (2011) sediments were collected both fall under that salinity range. But it is still unclear under what conditions increased salt could lead to increased CH_4 fluxes in the field.

One potential mechanism to explain the large increase in CH_4 fluxes we observed is that increased salinity could have led to a decrease in humic substances through salt-induced flocculation of dissolved organic matter. Humic substances have been shown to decrease the production of CH_4 by serving as thermodynamically favorable organic electron acceptors (Keller and Bridgham 2007). In peatlands, the large percentage of anaerobic carbon mineralization that cannot be explained by commonly measured processes (iron reduction, sulfate reduction, methanogenesis) results from the use of humic acids as alternative electron acceptors (Keller et al. 2009).

Humic substances have been shown to decrease CH_4 fluxes when added to peatland soils (Minderlein and Blodau 2010), and there is growing evidence that humics might have direct toxic effects on microbial processes (Cervantes et al. 2000). A recent study found that the metabolic reduction of humics dominated anaerobic carbon mineralization and competitively suppressed CH_4 production in peatland soils (Keller and Takagi 2013). Humic substances are known to precipitate with the presence of multivalent cations (Mulholland 1981; Tipping and Woof 1991; Yamashita et al. 2008). Our soil cores came from an area dominated by Atlantic white cedar, which is known to have recalcitrant leaf litter and roots (Crawford et al. 2007), which could increase humics in the soils. We hypothesize that salt addition led to loss of humics and thus release of methanogens from the inhibitory effects of humics. The higher CH_4 flux we observed with lower $SUVA_{254}$ values is consistent with this hypothesis (Fig. 5), though it was only for one sampling date so it merits further research. The only study we are aware of that looked at changes in humics in response to salt addition in soils from forested wetlands, did not find any significant changes in humic-like components of soil solution (Liu et al. 2017). However, that study used NaCl to experimentally increase salinity, which does not include multivalent cations that are known to precipitate humics (Mulholland 1981). We hypothesize that under our experimental conditions, the reduction in humic acid suppression, through enhanced precipitation due to saltwater cations, had a greater impact on methanogens than the stimulation of sulfate reducers due to increased ${SO_4}^{2-}$. When added alone, ${SO_4}^{2-}$ did reduce CH_4 fluxes as anticipated, adding support to our hypothesis that cations in seawater can release methanogens from humic acid suppression.

Another line of evidence that can support the role of humics in anaerobic C mineralization in this system comes from examining the ratio of CO_2 and CH_4. The CO_2:CH_4 ratio is expected to be around one under methanogenic conditions (Reddy and DeLaune 2008). In our study CO_2:CH_4 ratios ranged between 0.9 and 10 in both salt treatments, while the ratio was > 1000 in the DI water and ${SO_4}^{2-}$ only treatments. Previous field estimates from the site documented low CH_4 fluxes, with a typical CO_2:CH_4 ratio of $\sim$ 125 (Morse et al. 2012). A study in a nearby pocosin wetland also found low CH_4 fluxes, and attributed relatively low CO_2 fluxes to high concentrations of phenolics in soil solution produced by the vegetation (Wang et al. 2015). In other work, we have seen increases in CH_4 fluxes when we add salt to field plots (Helton et al. in review), but as mentioned before most studies have found the opposite result (Table 4). Further research into how salinity might affect concentrations of humic substances could be very important, as salt induced loss of humics could lead to large increases in CH_4 fluxes, as observed in this study.

Another potential mechanism that could explain enhanced CH_4 fluxes following saltwater enrichment could be a positive response of methanogens to large increases in available N. Nitrogen enrichment has been found to increase CH_4 emissions by an average of 95%, and to decrease methanotrophy by 38% across a variety of different ecosystems (Liu and Greaver 2009). In the literature review there was no difference on CH_4 emissions among the different forms on N (NO_3, NH_4, or urea; Liu and Greaver 2009). In our experiment CH_4 fluxes were positively correlated to NH_4 (Fig. 5b), but not to NO_3 (data not shown). Future studies should examine if this the case in other systems. The mechanistic explanation for N stimulation of CH_4 remains an open question, but because methane oxidizing bacteria, ammonia oxidizers, and Archaea all depend on similar enzymes for their metabolism (Bodelier and Steenbergh 2014), there are a variety of ways in which N cycling microbes interact with both methanogens and methanotrophs.

Most attempts to understand the effect of saltwater exposures on microbial C cycling have focused on the effects on methanogens. But, because so much of the CH_4 produced in any ecosystem is consumed by methanotrophs, more attention should be paid to the effects of salinity on rates of methane consumption. Increased salinity has been found to reduce both aerobic and anaerobic methanotrophy (Dalal et al. 2008). Aerobic methanotrophy is more sensitive to increased salinity (Dalal et al. 2008), and perhaps the increased CH_4 flux was caused by salt stress for aerobic methanotrophs (Weston et al. 2011). We need a better understanding of how salinity effects on methanotrophs might alter methane fluxes from wetlands undergoing salinization.

Nitrous oxide

It is difficult to predict how any experimental treatment will alter the fluxes of N_2O, emitted by both chemoautotrophic nitrifiers who are obligate aerobes and by heterotrophic denitrifiers that are facultative anaerobes. Previous field studies at the TOWeR site documented much higher N_2O fluxes from drier soils (Morse et al. 2012) and used an isotope tracer experiment to determine that nitrification was the dominant source of N_2O from soil cores (Morse and Bernhardt 2013). We expected that salinization would indirectly stimulate N_2O emissions from nitrification in well drained soils because divalent cations in marine salts should displace NH_4^+ ions from cation exchange sites and allow NH_4^+ to accumulate in soil solution. We found that this prediction only held for the ASW with SO_4^{2-} treatment. We found strong support for the cation displacement part of this hypothesis, as both ASW treatments generated large increases in soil solution NH_4–N, however the increase in NH_4–N did not translate to an increase in nitrification rates in both saltwater treatments (Ardón et al. 2013) or increased N_2O fluxes (Fig. 4). Soil solution NO_3–N only increased when SO_4^{2-} was added (Fig. 1) and not in the ASW without SO_4^{2-} treatment. Fluxes of N_2O were stimulated only in the drought and ASW with SO_4^{2-} treatment. These results are challenging to interpret, but suggest that the multiple components of saltwater enrichment (base cation loading, sulfate loading, and increases in ionic strength) are having non-additive effects.

For our flooded cores, where nitrification is inhibited by anoxic conditions, we expected that SO_4^{2-} enrichment might lead to higher N_2O fluxes because we have previously observed a positive correlation between water SO_4^{2-} and N_2O efflux across our field site (Helton et al. 2014), and because we hypothesized that increases in SO_4^{2-} could enhance sulfur driven denitrification. Instead we found that the addition of either ASW with SO_4^{2-} or SO_4^{2-} alone led to reductions of N_2O flux (Fig. 4).

Our results add two disparate data points to the two published studies that previously measured the effects of saltwater exposure on N_2O fluxes (Table 4). Marton et al. (2012) documented a 900% increase in N_2O emissions from tidal freshwater wetland sediments treated with salt, while Liu et al. (2017) documented a 95% decline in N_2O fluxes from soil slurries in response to saltwater enrichment (Liu et al. 2017). All three experiments added salt in similar concentrations ($>$ 5 ppt), and the soils were all from forested wetlands, so it is interesting our results differ. In Marton et al.'s and our work, we added salt as a complex mixture, which included divalent cations. Liu et al. used NaCl (as mentioned previously) which lacks divalent cations, so the differences in results could be due in part to the different salt additions used for the experiment. The only emerging 'consensus' from this limited synthesis is that the effects of saltwater enhancement on N_2O production are highly variable in both direction and magnitude. Given that the N_2O is an intermediate product of multiple N transformation pathways, it may prove more useful to examine component process rates rather than the aggregate N_2O fluxes arising from multiple microbial functional groups under disparate environmental controls.

Conclusion

Results from our experiment add to a growing body of literature documenting the effects of saltwater enrichment on freshwater wetland ecosystems. While there is no question that sea level rise and increasing drought frequency and duration are likely to expand the spatial and temporal reach of marine salts into coastal plains, there is considerable uncertainty about the resulting effects on ecosystem nutrient and carbon cycles. Our results show that saltwater exposure leads to clear and substantial impacts on both cycles that are (a) highly contingent upon the hydrologic setting and (b) not consistent with predictions that are based on the supply of sulfate as a terminal electron acceptor. We found that salinity decreased CO_2 fluxes, while salinity and drought interacted to alter the magnitude of N_2O fluxes. Based on the results of our experiment we proposed three different mechanisms to explain the unexpected increase in CH_4 we observed (loss of humics, increased nitrogen availability, and salinity stress on methanotrophs), and these mechanisms are not mutually exclusive and could be working simultaneously. Our results illustrate the importance of examining the consequences of the different components of salt (sulfate versus divalent cations) on ecosystem processes. Our results show that drought and salinity can lead to increased release of greenhouse gases and nitrogen from soils, which may result in positive feedbacks to global change and exacerbate local and regional N pollution.

Acknowledgements We thank Dr. Ben Colman, Medora Burke-Scoll, and Anna Fedders for help with the microcosm experiments. We thank the staff at the Phytotron at Duke University for their help with this experiment. We thank Dr. E. Matzner and three anonymous reviewers for their helpful comments and suggestions which helped improve the manuscript. This work was supported NSF DBI-0805576, DEB-1713592, and EF-1713435 to M. Ardón.

Appendix

See Table 5.

Table 5 Recipe for saltwater treatments modified from Kester et al. (1967)

Salt	Unit	SO_4	ASW-SO_4	ASW
Gravimetric salts				
NaCl	g	0	25.970	23.944
K_2SO_4	g	4.009	0.000	4.011
KCl	g	0	2.670	0.679
$NaHCO_3$	g	0	0.192	0.198
KBr	g	0	0.098	0.010
H_3BO_3	g	0	0.028	0.028
NaF	g	0	0.004	0.003
Volumetric salts				
$MgCl_2–6H_2O$ (1.0 M)	mL	0	57.053	57.053
$CaCl_2–2H_2O$ (1.0 M)	mL	0	11.208	11.208
$SrCl_2–6H_2O$ (0.1 M)	mL	0	0.912	0.912

This recipe is for 1 L of full strength seawater (35 ppt), so we diluted it to the target salinity of 5 ppt before adding it to the treatments. Reagent grade of the gravimetric salts were dried and added. Volumetric salts ($MgCl_2$, $CaCl_2$, and $SrCl_2$) contain water, which makes weighing problematic (Kester et al. 1967), so we made concentrated solutions and added the salts volumetrically (molarity is given in parenthesis)

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