Wetlands
DOI 10.1007/s13157-017-0890-8

ORIGINAL RESEARCH

Identifying the Salinity Thresholds that Impact Greenhouse Gas Production in Subtropical Tidal Freshwater Marsh Soils

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Received: 4 March 2016 / Accepted: 15 February 2017

Abstract Increasing salinity due to sea level rise is an important factor influencing biogeochemical processes in estuarine wetlands, with the potential to impact greenhouse gas (GHG) emissions. However, there is little consensus regarding what salinity thresholds will significantly alter the production of GHGs or the physiochemical properties of wetland soils. This study used a fine-scale salinity gradient to determine the impact of seawater concentration on the potential production of CH_4, CO_2 and N_2O and associated soil properties using bottle incubations of tidal freshwater marsh soils from the Min River estuary, SE China. Potential CH_4 production was unaffected by salinities from 0 to 7.5‰, but declined significantly at 10‰ and above. Potential CO_2 production was stimulated at intermediate salinities (5 to 7.5‰), but inhibited by salinities ≥15‰, while potential N_2O production was unaffected by salinity. In contrast, soil dissolved organic carbon and NH_4^+-N generally increased with salinity. Overall, this research indicates salinities of ~10–15‰ represent an important tipping point for biogeochemical processes in wetlands. Above this threshold, carbon mineralization is reduced and may promote vertical soil accretion in brackish and salinity wetlands. Meanwhile, low-level saltwater intrusion may leave wetlands vulnerable to submergence due to accelerated soil organic carbon loss.

Keywords Sea level rise · Seawater intrusion · Salinity · Methanogenesis · Soil carbon · Tidal freshwater marsh

Introduction

Atmospheric greenhouse gas (GHG) concentrations have been rising since pre-industrial times, with CO_2, CH_4, and N_2O increasing by 40, 150, and 20%, respectively, between 1750 and 2011 (IPCC, 2013)). Wetlands occupy only ~4–6% of the land's surface, yet can serve as a significant source of GHGs to the atmosphere due to the combined effects of high productivity and anaerobic conditions (Anselman and Crutzen 1989; Mitra et al. 2005). The rate of GHG emissions from wetlands is known to vary widely in space and time, with temperature and water level often cited as important factors (Smith et al. 2003). However, salinity (saltwater intrusion) can also play a key role in determining the rates and ratios of GHGs emitted from coastal/estuarine wetlands due to, 1) osmotic stress altering the activity and composition of the soil microbial community (Hart et al. 1991; Van Ryckegem and Verbeken 2005; Chambers et al. 2016), 2) the abundance of SO_4^{2-} in seawater favoring sulfate reduction over other metabolic pathways (Weston et al. 2006; Edmonds et al. 2009; Chambers et al. 2011), and 3) changes in the availability of

Electronic supplementary material The online version of this article (doi:10.1007/s13157-017-0890-8) contains supplementary material, which is available to authorized users.

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nutrients due to cation exchange and/or changes in water sources (Blood et al. 1991; Portnoy and Giblin 1997).

Estuarine wetlands are considered one of the most productive ecosystems in the world, often functioning as a significant carbon (C) sink (Chmura et al. 2003; McLeod et al. 2011), while also being highly vulnerable to sea level rise (Nicholls et al. 1999). Unless estuarine wetlands are able to accrete vertically at a rate that meets or exceeds that of relative sea level rise, saltwater intrusion is predicted to convert many freshwater wetlands into oligohaline or brackish wetlands (Neubauer et al. 2013; Ramsar 2013). Several studies indicate increased salinity in freshwater wetland soils can rapidly accelerate CO_2 production through sulfate reduction, while decreasing CH_4 production as the sulfate reducers outcompete methanogens due to their higher thermodynamic energy yield (Jakobsen et al. 1981; Weston et al. 2006; Chambers et al. 2011). However, the salinity concentration, or threshold, at which this shift in metabolic pathways occurs is the subject of debate. For example, Marton et al. (2012) found that CH_4 production in bottle incubations was inhibited in freshwater forest soils by 77% and 89% when exposed to 2 and 5 ppt saltwater, respectively, while CO_2 production generally increase with salinity (between 0 and 5 ppt). Chambers et al. (2011) found the tipping point for near-complete CH_4 suppression to be somewhere between 3.5 and 14 ppt, and a review of field data by Poffenbarger et al. (2011) determined that marshes with salinities >18 ppt has significantly lower CH_4 emissions than less saline marshes.

The relationship between salinity and N_2O production is even less clear. Many wetland studies have correlated N_2O production to NO_3^- availability and water level, as incomplete nitrification and denitrification are the primary sources of N_2O production in wetlands (Freeman et al. 1993; Davidson et al. 2000; Yu et al. 2006; Yu et al. 2008). This has led some to suggest saltwater intrusion could increase N_2O flux because sea salts have been shown to increase the availability of NH_4^+ through cation exchange, which is a precursor to nitrification and denitrification (Michener et al. 1997). While several studies have confirmed a positive correlation between NH_4^+ availability and salinity in freshwater and oligohaline soils (Weston et al. 2006; Edmonds et al. 2009; Giblin et al. 2010; Chambers et al. 2013), there is also evidence that salinity can directly suppress nitrifiers and denitrifiers through osmotic stress, Cl^-, or HS^- toxicity (Joye and Hollibaugh 1995; Seo et al. 2008; Wu et al. 2008; Craft et al. 2009; Marks et al. 2016). In field studies along coastal wetland salinity gradients, N_2O flux has been found to decrease as salinity increases (Chen et al. 2012), or show no correlation with salinity (Krauss and Whitbeck 2012).

This study sought to provide a better understanding of how salinity concentration influences the production of CH_4, CO_2, and N_2O in freshwater wetland soils by using a fine-scale salinity gradient of 0, 0.5, 2.5, 5, 7.5, 10, 15, 20, 25 and 30 ‰. Additionally, two estuarine tidal freshwater marshes soils were used to assess the consistency of the GHG responses across different sites, and the soil physiochemical properties were measured before and after the incubation experiment to identify salinity impacts on soil pH, conductivity, DOC, SO_4^{2-}, Cl^-, NH_4^+ and NO_2^-. We hypothesized that soils incubated at low salinities ($< \sim 10$ ppt) would have the highest soil carbon mineralization rates due to combined $CO_2 + CH_4$ emissions, and mineralization would decrease with salinity beyond the threshold of methanogen suppression. We further predicted N_2O emissions would be negatively correlated with salinity due to the inhibition of nitrifiers and denitrifiers.

Materials and Methods

Site Description

Tidal freshwater marshes soils were collected from two sites in the Min River estuary of the southeast of China: Tajiaozhou wetland (TW) and Daoqingzhou wetland (DW) (Fig. 1). The climate of this subtropical region is warm and wet, with a mean annual temperature of 19.6 °C and annual precipitation of 1200–1740 mm, which falls primarily during the wet season, March through September (Zheng et al., 2006). The Min River estuary receives semi-diurnal tides (Tong et al., 2010). *Cyperus malaccensis* var. brevifolius Boecklr is the dominant species at both sites and the typical soil conductivity is <0.5 mS cm^{-1}.

Experimental Design

A representative stand of *C. malaccensis* was randomly selected in each of the two wetlands and sampled during a neap tide on October 14, 2013. At each site, four quadrats (1 m × 1 m) were established at intervals of 5 m along a line parallel with the river. Four soil cores (5 cm diameter × 15 cm deep) were collected in each quadrant using a steel soil corer. Four cores collected within a quadrant were homogenized in the field to form one representative sample. This resulted in a total of eight soil samples (four each from TW and DW). All soil samples were transported on ice to the laboratory within 6 h of collection. Once at the laboratory, soils were sieved through a #10 mesh and each of the eight samples were sub-divided into 10 replicate 50-g (wet weight) samples and placed into 300 mL glass serum bottles. Bottles were capped with butyl stoppers and flushed with O_2-free N_2 gas for 1–2 min to create anaerobic conditions (Marton et al. 2012).

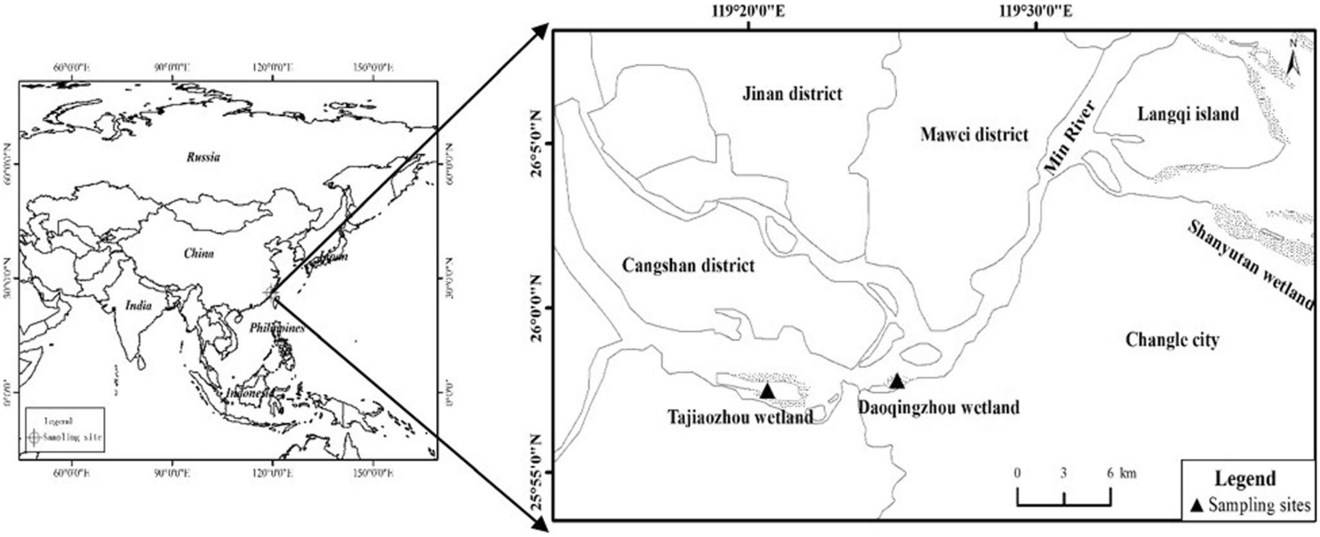

Fig. 1 Location of two sampling sites in the middle section of the Min River estuary, Tajiaozhou wetland (TW), Daqingzhou wetland (DW)

One of nine salinity treatments (0.5, 2.5, 5, 7.5, 10, 15, 20, 25, 30 ‰) or the deionized (DI) water (0 ‰) control treatment were randomly assigned to each bottle. Salinity treatments were created using an artificial seawater salt mix (Tropic Seawater Reef Salt, Cnsic Marine Biotechnology Co., Ltd., China) diluted with DI water. The salinity of the resulting mixtures were confirmed using a salinity meter (Eutech Salt 6+, ThermoFisher Scientific, USA). Slurries were created by adding 50 mL of the assigned treatment solution to each bottle. All incubations were purged with O_2-free N_2 gas, stored in the dark at 25 C, and continuously shaken. Approximately 20 mL headspace gas was extracted and measured on a gas chromatograph (GC-2014, Shimadzu Scientific Instruments, Japan) equipped with an electron capture detector (ECD), flame ionized detector (FID), and methanizer, to determine the concentrations of N_2O, CH_4, and CO_2, respectively. Headspace samples were collected on days 1, 2, 3 and 5 to create a daily production rate. After the day 5 sample was extracted, all bottles were then purged with O_2-free N_2 gas for 1–2 min to prevent the GHGs accumulation in the headspace (Chambers et al. 2011; Marton et al. 2012), and the sampling cycle was repeated again. The sampling and purging sequence was repeated for three cycles (i.e., for three weeks). The rates of GHGs production were determined by comparing peak areas to a standard curve, then applying the ideal gas law to calculate moles of gas in the headspace. The amount of dissolved CH_4 and CO_2 in the liquid phase were accounted for using Henry's Law, after Bridgham and Ye (2013), including a term for liquid dissolved inorganic C for total CO_2. To calculate N_2O production, the Bunsen absorption coefficient (a = 0.544) was used to account for N_2O in the aqueous phase, after Tiedje (1982) (see supplementary materials for formulas).

Soil Properties

Soil temperature, pH, and electrical conductivity (mS cm^{-1}) were measured in-situ at the time of field sampling at a depth of 10 cm using a temperature/pH meter (IQ Scientific Instruments, USA) and a 2265FS electrical conductivity meter (Spectrum Technologies Inc., USA), respectively. Soil water content was determined gravimetrically by oven-drying a subset of soil at 70 °C until constant weight. Four soil subsamples of each of the 8 field samples were extracted using DI water and analyzed for: 1) dissolved organic carbon (DOC) content using a TOC-VCPH analyzer (Shimadzu Scientific Instruments, Japan), 2) soil SO_4^{2-} and Cl^- content using an ICS-2100 Ion chromatograph (American Dionex Production, USA), and 3) soil NH_4^+-N and NO_2^--N content using a sequence flow analyzer (San++ SKALAR Production, Netherlands). NO_3^--N content could not be quantified due to an instrument malfunction. Initial SO_4^{2-} and Cl^- concentrations were calculated based on the field properties of the soil and the amounts added to each bottle in the salt mix at the start of the incubation experiment. All soil properties (pH, electrical conductivity, DOC, SO_4^{2-}, Cl^-, NH_4^+-N and NO_2^--N) were quantified at the end of the three week incubation experiment following the same methods outlined above.

Statistical Analysis

All data sets were first tested to determine if the assumptions of normality and homogeneity were met using the Shapiro-Wilk test and Levene's test, respectively. If these assumptions were not met, the data was log transformed and statistical analyses were conducted on the transformed data. An independent t-test was used to determine significant difference in initial soil properties between the two field sites. A two-way ANOVA model was used to identify significant differences between post-incubation soil properties and the independent variables of salinity treatment and site. The interactions of salinity treatment, site, and time on the GHG production were examined using a general linear model and were applied to the average rates for all three weeks, and as well as each week individually. A one-way ANOVA model was used to identify significant differences in total soil carbon mineralization and CO_2:CH_4 ratio between salinity treatments for each site. All significant differences were further examined using the least square means post-hoc test. Pearson's product correlation analysis was used to examine the relationship between GHGs production and measured soil properties. In all tests, differences were considered significant at $p < 0.05$. Results are presented as mean values for site replicates ($n = 4$ for each site) and standard error, unless otherwise indicated.

Results

Soil Properties

Characterization of field soil properties revealed DW had lower soil water content, SO_4^{2-}, DOC, and NH_4^+-N than TW, but higher conductivity and Cl^- content (Table 1). At the start of the incubation experiment, SO_4^{2-} and Cl^- concentrations increased linearly based on the salinity treatment assigned to each soil, but varied slightly by site based on the field properties of the soil used (Fig. 2). Following the three week incubation experiment, both SO_4^{2-} and Cl^- exhibited an interaction between salinity and site (both $p < 0.001$; Table 2) with SO_4^{2-} concentration being largely consumed at both sites when salinity was between 0 and 15‰ (averaging 14.0 ± 2.0 mg kg^{-1}). At salinities of 20, 25, and 30‰, some SO_4^{2-} remained available in solution, but to differing degrees according to site (Fig. 2b). Cl^- continued to generally increase with each salinity treatment at the end of the study, with TW soil Cl^- concentration higher than DW at salinities >7.5‰ (Fig. 2a). Soil pH varied significantly according to salinity treatment and site ($p < 0.001$; Table 2). In general, pH had a non-linear inverse relationship with salinity and was higher in DW soils than TW soils at high salinities (≥15‰) only (Fig. 3a). Final soil conductivity differed among salinity treatments ($p < 0.001$), increasing linearly with concentration (Table 2; Fig. 3b). Finally, both DOC and NH_4^+-N exhibited a salinity*site interaction (both $p < 0.001$; Table 2), with generally increasing concentrations as salinity increased and higher values in TW soils compared to DW soils at the conclusion of the incubations (Fig. 3e and f).

Table 1 Field soil physiochemical properties of the two freshwater marsh sampling sites located in the upper section of the Min River estuary, TW = Tajiaozhou wetland and DW = Daoqingzhou wetland

	TW	DW
pH	5.50 ± 0.12^a	5.73 ± 0.05^a
Water content (%)	118.29 ± 0.08^a	82.34 ± 0.02^b
Conductivity (mS cm^{-1})	0.23 ± 0.01^a	0.40 ± 0.03^b
SO_4^{2-} (mg kg^{-1})	7.80 ± 0.43^a	5.19 ± 0.58^b
Cl^- (mg kg^{-1})	3.23 ± 0.11^a	23.33 ± 5.64^b
DOC (mg kg^{-1})	25.87 ± 2.29^a	16.39 ± 1.16^b
NH_4^+ (mg kg^{-1})	18.54 ± 1.96^a	11.78 ± 1.01^b
NO_2^- (mg kg^{-1})	0.04 ± 0.01^a	0.05 ± 0.01^a

Means ± standard deviations for the data in the table ($n = 4$), different letters within the same column represent significant differences at $p < 0.05$ based on an independent sample T test

Potential Methanogenesis

Average methane production rate over the 3 week study did not differ significantly between salinity treatments that ranged from 0 and 7.5‰ for both sites, averaging 17.80 ± 0.43 μg g^{-1} d^{-1} (Table 3; Fig. 4). At salinities of 10‰ and greater, average CH_4 production rate declined linearly with increasing salinity by 21 to 41% compared with that at low salinities (0–7.5‰). Potential CH_4 production rate was significantly greater during week 1 than weeks 2 and 3, and time had a significant interaction with salinity treatment ($p < 0.001$). However, the significant main effect of salinity on CH_4 production persisted in week 1 ($p < 0.001$), week 2 ($p = 0.002$) and week 3 ($p = 0.002$), with the post-hoc analysis continuing to show a significant decrease in CH_4 production rate between the 7.5‰ and 15‰ treatments (Fig. 4, data not shown). The rates of potential CH_4 production in soils from both sites were negatively correlated with soil conductivity, SO_4^{2-}, Cl^-, DOC and NH_4^+-N concentration (all $p < 0.01$), and positively correlated with soil pH ($p < 0.05$ in TW; $p < 0.01$ in DW; Table 4).

Potential Microbial Respiration

The average rate of potential CO_2 production was highest at the intermediate salinities of 5 to 7.5‰, averaging 12.20 ± 0.62 mg g^{-1} d^{-1} among the two sites, and lowest at salinities ≥15‰, averaging 5.79 ± 0.19 mg g^{-1} d^{-1} among the two sites (Table 3; Fig. 4). All rates decreased with time, and time exhibited a significant interaction with salinity ($p < 0.001$). In particular, the main effect of salinity was significant in weeks 1 and 2 of the study ($p < 0.001$ in week 1 and 2), but was not significant in week 3 (Fig. 4; data not shown). At both sites, potential CO_2 production was negatively correlated with soil conductivity, SO_4^{2-}, Cl^-, DOC and NH_4^+-N concentration (all $p < 0.01$, except DOC at DW, $p < 0.05$), and positively correlated with soil pH in TW soils only ($p < 0.01$; Table 4).

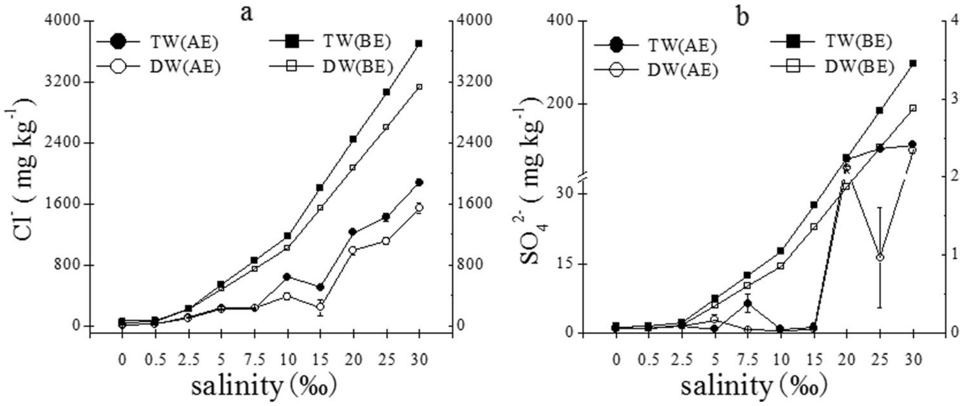

Fig. 2 Chloride (Cl^-) and sulfate (SO_4^{2-}) concentrations according to salinity treatment at the beginning (BE) of the bottle incubations, and after (AE) the completion of the 3 week study according to site (Tajiaozhou wetland (TW); Daoqingzhou wetland (DW))

Nitrous Oxide Production

Salinity treatment had no effect on N_2O production, but rates were significant higher in TW soils, as compared to DW soils, and decreased with time ($p < 0.001$) (Table 3; Fig. 4). The interactions of site*time and salinity*time were significant for N_2O production rate ($p < 0.01$). N_2O production was negatively correlated with SO_4^{2-} in TW soils (Table 4).

Total Soil Carbon Mineralization

Total carbon mineralization was significantly reduced by salinities of 15‰ and above among the two sites (Fig. 5). This tipping point equates to an average reduction in mineralization rate of 35% in TW soils and 46% in DW soils. CO_2 production comprised over 99% of the total C mineralization at all salinities in both soils. The ratio of C as CO_2:CH_4 varied slightly among salinity treatments, but showed no clear pattern (Fig. 6).

Discussion

Salinity is a critical environmental stressor in freshwater tidal wetlands, with the potential to alter the pathways and rates of soil carbon mineralization and GHG production (Weston et al. 2006; Chambers et al. 2011; Neubauer et al. 2013). This study sought to provide a more precise quantification of the impacts of salinity on GHG production and associate physiochemical changes in wetland soils through a controlled laboratory study that used a fine-scale salinity gradient.

Salinity 'Tipping Points' for Carbon Mineralization

The competitive advantage of sulfate reducers over methanogens in anaerobic soils has long been established (Jakobsen et al. 1981), but an understanding of the specific salinity thresholds (i.e., sulfate concentration) at which CH_4 production is significantly suppressed has been the subject of significant debate (see Table 5). In this study, average

Table 2 Results of a two-way ANOVA model analyzing the effect of site, salinity, site x salinity, on soil physiochemical properties after the completion of the three week incubation experiment

	Site	Salinity	Site * salinity
pH	**F(1,60) = 49.7**	**F(9,60) = 69.1**	**F(9,60) = 7.9**
	***p* < 0.001**	***p* < 0.001**	***p* < 0.001**
Conductivity	F(1,60) = 1.8	**F(9,60) = 199.8**	F(9,60) = 1.1
	p = 0.19	***p* < 0.001**	*p* = 0.36
SO_4^{2-}	**F(1,60) = 37.0**	**F(9,60) = 136.3**	**F(9,60) = 16.4**
	***p* < 0.001**	***p* < 0.001**	***p* < 0.001**
Cl^-	**F(1,60) = 72.5**	**F(9,60) = 495.9**	**F(9,60) = 7.9**
	***p* < 0.001**	***p* < 0.001**	***p* < 0.001**
DOC	**F(1,60) = 157.6**	**F(9,60) = 26.5**	**F(9,60) = 4.5**
	***p* < 0.001**	***p* < 0.001**	***p* < 0.002**
NH_4^+-N	**F(1,60) = 157.4**	**F(9,60) = 82.5**	**F(9,60) = 4.4**
	***p* < 0.001**	***p* < 0.001**	***p* < 0.001**

Significant differences are in bold. F (numerator degrees of freedom, denominator degrees of freedom) = F value, p = *p* value

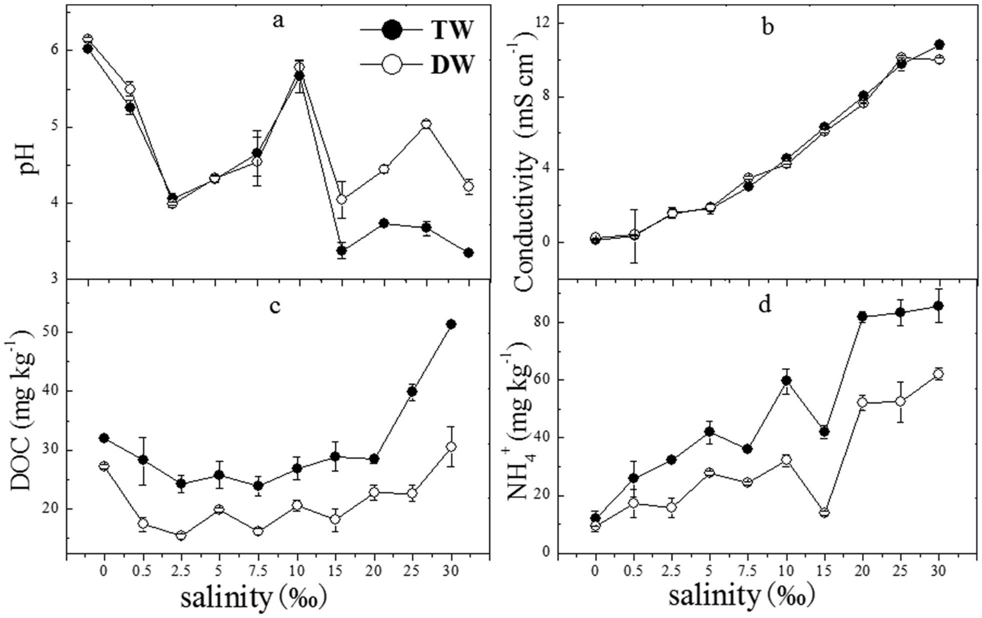

Fig. 3 Variation of soil properties under different salinity treatments after the completion of the 3 week incubation experiment. Tajiaozhou wetland (TW) and the Daoqingzhou wetland (DW) refer to the site where the soils were collected in the Min River estuary

potential CH_4 production rate was unchanged when exposed to salinity concentrations of 0 to 7.5‰ (Table 3), a pattern that persisted over all 3 weeks of the study. At these low salinities (<10‰), the added SO_4^{2-} was depleted to near zero by the conclusion of the 3 week study (Fig. 2), indicating that sulfate reduction was co-occurring, but did not negatively impact the activity of methanogens. Methanogens may have been utilizing non-competitive substrates (e.g., dimethyl sulfide, dimethylamine, methanol, etc.) that allowed for co-existence with sulfate reducers, at least in the short-term (Capone and Kiene 1988). Salinities of 10‰ and greater significantly suppressed the average potential CH_4 production rate among the two tidal freshwater marsh soils analyzed (Fig. 4, Table 3), which corresponded with the treatments that sustained a pool of available sulfate until the conclusion of the study (Fig. 2b) and suggests that at high salinities, sulfate-inhibition of methanogenesis is driving the decline in CH_4 flux rates. This salinity 'tipping point' around 10‰ resulted in a 24% reduction in average potential CH_4 production rate, which continued to decline incrementally with salinities up to 30‰ (the maximum salinity treatment in this study). Other research has also indicated that a salinity of 10‰ is an important tipping point for biogeochemical processes in wetlands. Rysgaard et al. (1999) determined that NH_4^+ adsorption capacity was complete at a salinity of 10‰; no additional NH_4^+ could be extracted from soils as salinities increased beyond this threshold. Weston et al. (2006) found that sulfate reduction replaced methanogenesis as the dominated pathway (>50%) of organic matter mineralization in freshwater sediments within 2 weeks at a salinity of 10‰, and accounted for >95% of total organic matter mineralization after 4 weeks. Furthermore, Chambers et al. (2011) found that potential CH_4 production in freshwater soils was not affected by a salinity of 3.5‰, but was significantly suppressed at 14 and 35‰. A few researchers have found the salinity threshold for potential CH_4 production suppression to be slightly lower (between 0 and 2‰) in freshwater tidal forest soils (Marton et al. 2012); this variability among soils may be influenced by the abundance and type of electron donors, which is likely also related to vegetation type.

Under field conditions, CH_4 emissions to the atmosphere are a net result of CH_4 production, oxidation, and transport. These factors are independently controlled by temperature, precipitation, soil carbon input quantity and quality, soil texture, etc., in addition to salinity (Conant et al. 2011; Schipper et al. 2014), thereby resulting in a complex response of CH_4 emission to salinity. Numerous field studies have reported the same negative relationship between CH_4 emission and salinity in wetland soils that are seen in lab studies (Table 5), with two notable exceptions in which an oligohaline environments released more CH_4 than their freshwater counterparts (Abril and Iversen 2002; Weston et al. 2014).

Salinity also had a significant effect on the rate of anaerobic microbial respiration (Fig. 4, Table 3). Salinities ranging from 0 to 10‰ had higher rates of average CO_2 production than those ≥15‰, with 5 and 7.5‰ exhibiting the highest rates average rates- possibly due to a slight priming effect from the saltwater (and SO_4^{2-}) addition. This is consistent with numerous studies indicating that increased SO_4^{2-} availability can accelerate CO_2 production in environments where electron acceptors limit microbial respiration (Weston et al. 2006; Chambers et al. 2011; Marton et al. 2012; Neubauer et al. 2013; Chambers et al. 2013). Additionally, improved soil nutrient status due to cation exchange with salts (e.g., NH_4^+, Fe^{2+} and Al^{3+} displaced by seawater cations, such as Na^+, Mg^{2+}, Ca^{2+} and K^+) may promote microbial respiration at low

Table 3 Greenhouse gas production rates and full statistical results for the general linear model of average rates over the 3 week incubation, as affected by sites, salinity, time, and their interactions. The model was also run with data for each individual week (1, 2, and 3) and key findings are presented in the text

		CH_4 $\mu g\ g^{-1}\ d^{-1}$	CO_2 $mg\ g^{-1}\ d^{-1}$	N_2O $\mu g\ g^{-1}\ d^{-1}$
Site	TW	15.25 ± 0.80	9.36 ± 0.58	1.25 ± 0.05
	DW	13.95 ± 0.67	8.24 ± 0.56	1.07 ± 0.03
	F,P	F(1,60) = 0.001	F(1,60) = 3.978	**F(1,60) = 20.378**
		p = 0.980	*P* = 0.051	***P* < 0.001**
Salinity	0	16.86 ± 1.01a	9.61 ± 1.01b	1.15 ± 0.07ab
	0.5	17.50 ± 0.82a	10.77 ± 0.82b	1.18 ± 0.09ab
	2.5	19.01 ± 0.70a	10.08 ± 0.89b	1.11 ± 0.03ab
	5	18.13 ± 1.10a	11.95 ± 0.91ab	1.17 ± 0.06ab
	7.5	17.52 ± 1.22a	12.45 ± 0.93a	1.28 ± 0.07a
	10	13.39 ± 1.28b	9.99 ± 1.09b	1.29 ± 0.06a
	15	12.90 ± 0.89bc	5.69 ± 0.27c	1.17 ± 0.18ab
	20	10.31 ± 0.89c	6.19 ± 0.25c	1.07 ± 0.11bc
	25	10.50 ± 0.79c	5.32 ± 0.27c	0.95 ± 0.04c
	30	9.88 ± 0.57c	5.96 ± 0.63c	1.19 ± 0.08ab
	F,P	**F(9,60) = 13.715**	**F(9,60) = 19.196**	F(9,60) = 1.950
		***p* < 0.001**	***P* < 0.001**	*p* = 0.062
Time	week 1	32.57 ± 1.19	21.16 ± 0.94	1.44 ± 0.04
	week 2	3.16 ± 0.17	4.38 ± 0.17	1.08 ± 0.04
	week 3	6.82 ± 0.25	0.61 ± 0.05	0.92 ± 0.05
	F,P	**F(2,120) = 1103.489**	**F(2,120) = 1418.770**	**F(2,120) = 70.028**
		***p* < 0.001**	***p* < 0.001**	***p* < 0.001**
Site * salinity	F,P	F(9,60) = 0.860	F(9,60) = 1.982	F(9,60) = 0.903
		p = 0.565	*p* = 0.057	*p* = 0.532
Site * time	F,P	F(2, 120) = 0.898	**F(2,120) = 3.272**	**F(2,120) = 10.714**
		p = 0.410	***p* = 0.041**	***p* < 0.001**
Salinity * time	F,P	**F(18,120) = 8.285**	**F(18,120) = 19.966**	**F(18,120) = 3.088**
		***P* < 0.001**	***p* < 0.001**	***p* < 0.001**
Site* salinity * time	F,P	F(18,120) = 0.928	F(18,120) = 1.585	F(18,120) = 1.311
		p = 0.547	*p* = 0.074	*p* = 0.193

Significant differences are in bold. F (numerator degrees of freedom, denominator degrees of freedom) = F value, p = *p* value. Data are means ± standard deviations; different letters within the same column represent significant differences at $p < 0.05$

salinities (Weston et al. 2006; Marton et al. 2012). Generally, sulfate reduction is considered the dominant source of CO_2 emissions in brackish and saline wetlands (Howarth 1984; Weston et al. 2006), but the percent of CO_2 production attributed to sulfate reduction can vary spatially (Gribsholt and Kristensen 2003). In addition to direct sulfate reduction pathways, high concentrations of SO_4^{2-} may also produce CO_2 through CH_4 oxidation (Beal et al., 2009), all of which likely contributed to high potential CO_2 production rates at low and intermediate salinities.

The suppression of CO_2 production at salinities of 15‰ and greater may be attributed to several factors, including: 1) the accumulation of deleterious byproducts of sulfate reduction reducing microbial activity (Larsen et al. 2010; Marton et al. 2012); 2) a general reduction in microbial metabolism as more energy is devoted to osmoregulation and adjustment to the high salt environment (Nie et al., 2011; Chambers et al. 2013); 3) a reduction in the size of the microbial community due to an inability to adjust to high salt concentrations (Nie et al., 2011); 4) a decrease in soil enzyme activity with increased salinity (Thottathil et al. 2008; Chambers et al. 2016); and/or 5) excessive Cl^- content interfering with denitrification and subsequently reducing overall CO_2 production (Hale and Groffman 2006; Seo et al. 2008). Moreover, studies in anaerobic reduction reaction systems indicate an excessive supply of exogenous electron acceptors can inhibit anaerobic metabolism (Sun et al. 2012). In this study, the concentration of remaining sulfate in treatments with salinities >15‰ increased sharply relative to the other treatments (Fig. 2b) and the potential impact of excessive electron acceptor availability on respiration in wetland soils warrants additional study. Interestingly, the effect of salinity on CO_2 production was

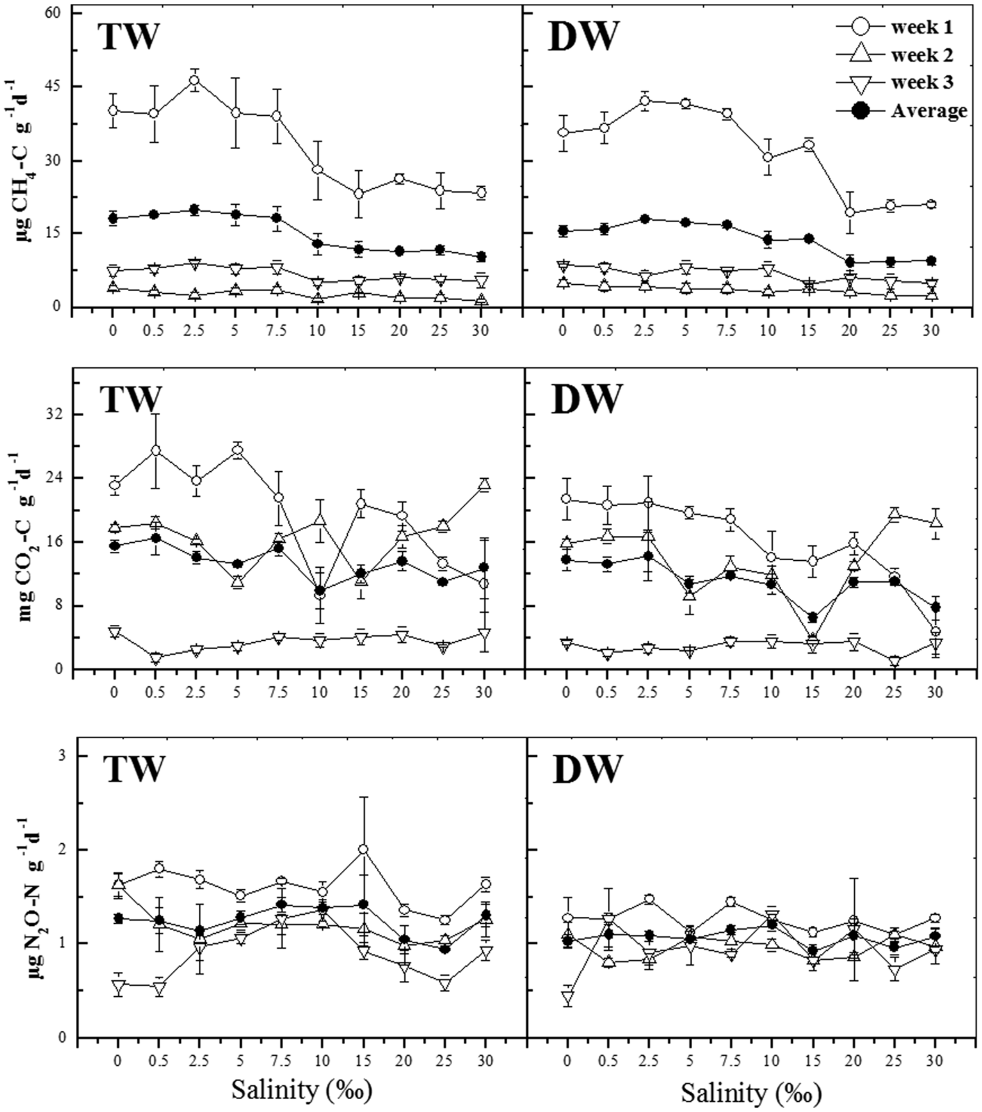

Fig. 4 Greenhouse gas production rates by week, and the 3 week average, according to salinity treatment. Tajiaozhou wetland (TW) and the Daoqingzhou wetland (DW) refer to the site where the soils were collected in the Min River estuary

only significant in weeks 1, 2, and the average rate (not week 3), demonstrating microbial communities have a capacity to acclimate and adapt to salinity, as suggested by previous researchers (Zahran 1997; Oren 2008; Edmonds et al. 2009).

The combined effects of reduced CO_2 and CH_4 production at salinities of 15‰ and above translated into significant declines (35–46%; Fig. 5) in soil carbon mineralization rates. Field studies in China have found similar patterns of decreasing carbon emissions as one travels seaward (increasing salinity) along an estuarine wetland salinity gradient (Chen et al. 2010; Nie et al. 2011). The salinity effects on respiration has the greatest impact on overall carbon mineralization because CO_2 production accounted for >99% of gaseous C loss in all treatments. The dominance of CO_2 flux as the major pathway

Table 4 Pearson's correlation coefficients for greenhouse gas production rates and soil properties ($n = 40$) for the two sampling sites, Tajiaozhou wetland (TW) and Daoqingzhou wetland (DW) in the Min River estuary, China

Site	Gas	pH	Conductivity	SO_4^{2-}	Cl^-	DOC	NH_4^+	NO_2^-
TW	CH_4	0.502*	-0.795**	-0.627**	-0.774**	-0.539**	-0.724**	-0.058
	CO_2	0.613**	-0.661**	-0.645**	-0.639**	-0.495**	-0.517**	-0.294
	N_2O	0.244	-0.219	-0.413**	-0.268	-0.039	-0.268	-0.168
DW	CH_4	0.441**	-0.824**	-0.807**	-0.862**	-0.636**	-0.816**	-0.237
	CO_2	0.118	-0.748**	-0.506**	-0.645**	-0.402*	-0.540**	0.175
	N_2O	0.283	-0.116	-0.032	-0.075	-0.155	-0.055	-0.236

*indicates significance at $p < 0.05$; **indicates significance at $p < 0.01$

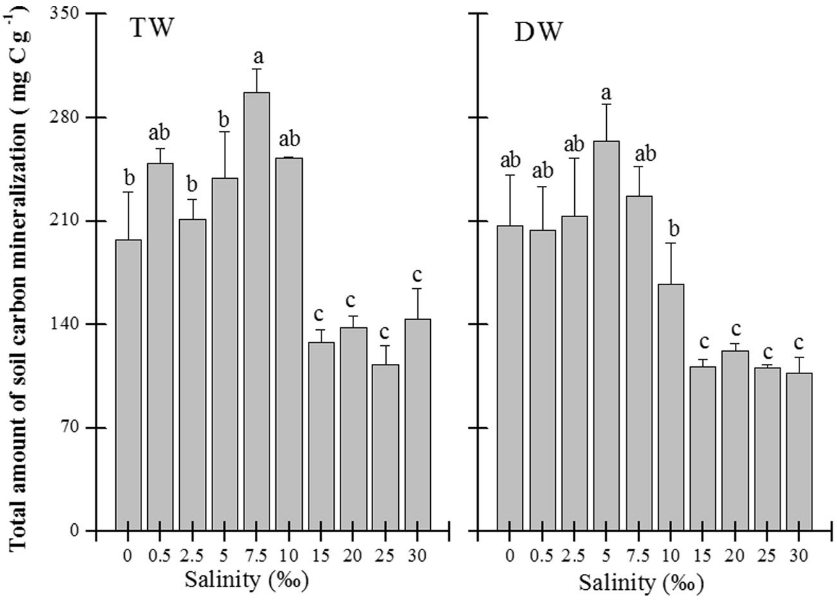

Fig. 5 Soil total carbon mineralization ($CO_2 + CH_4$) according to salinity treatment in the Tajiaozhou wetland (TW) and the Daoqingzhou wetland (DW) soils from the Min River estuary. Different letters indicate significant differences among salinity treatments according a one-way ANOVA

for soil organic C loss in estuarine wetlands has been found in previous lab studies (Chambers et al. 2013), but did not result in a significant change in the ratio of C as CO_2:CH_4 (Fig. 6).

Salinity Effects on Nitrous Oxide Production

The present study found no relationship between potential N_2O production and salinity, which may be a result of the complex effects of salinity on a variety of transformations within the nitrogen cycle. First, salinity can enhance the efflux of NH_4^+-N in sediments by both physical and chemical mechanisms, thereby increasing the concentration of a critical precursor to nitrification, and thus N_2O production (Rysgaard et al. 1999; Baldwin et al. 2006; Weston et al. 2006; Edmonds et al. 2009; Giblin et al. 2010). However, salinity (particularly Cl^-) has also been shown to inhibit nitrification (Roseberg et al. 1986) and denitrification (Hale and Groffman 2006; Seo et al. 2008). Studies investigating the relationship between salinity and nitrogen cycling have produced widely variable results, from those that find higher rates of denitrification in freshwater systems (Wu et al. 2008; Craft et al. 2009), peaks in nitrification at intermediate salinities (Magalhaes et al. 2005), or no relationship between salinity and denitrification (Nielsen et al. 2003; Krauss and Whitbeck 2012). Other work has suggested salinity can promote dissimilatory nitrate reduction to ammonia (DNRA) (Giblin et al. 2010) or that the H_2S produced by sulfate reduction can interfere with nitrogen

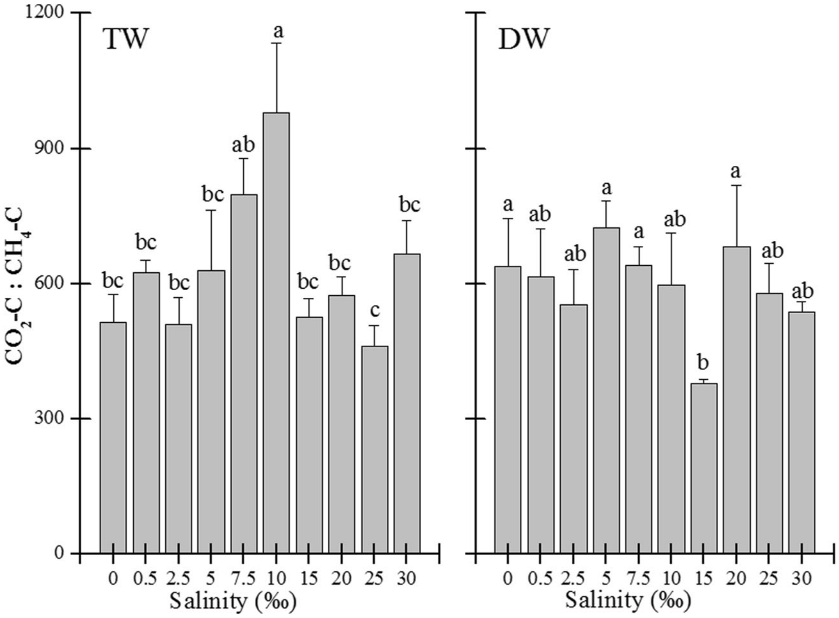

Fig. 6 Soil CO_2-C: CH_4-C ratio in different salinity in the Tajiaozhou wetland (TW) and the Daoqingzhou wetland (DW) in the Min River estuary. Different letters indicate significant differences among salinity treatments according a one-way ANOVA

Table 5 Summary of the relationship between salinity and soil methanogenesis/ methane emission from literature published for wetlands

Study site	Method	Salinity treatments[a] (‰)	CH_4 production/ emission rate by salinity treatment[b] (‰)	Reference
Methane Production				
FW tidal forests, various rivers (GA, USA)	Anaerobic soil slurries	0, 2, and 5	0 > 2 = 5	Marton et al. 2012
FW marsh, St John River (FL, USA)	Anaerobic soil slurries	0, 3.5, 14, and 35	0 = 3.5 > 14 > 35	Chambers et al. 2011
Oligohaline marsh (LA, USA)	Anaerobic soil slurries	1.5 and 20	1.5 > 20	Kiehn et al. 2013
FW marsh, Min River (China)	Anaerobic soil slurries	0, 0.5, 2.5, 5, 7.5, 10, 15, 20, 25, and 30	[0 = 0.5 = 2.5 = 5 = 7.5] > [(10 = 15) > (20 = 25 = 30)]	This study
Methane emissions				
Estuarine salinity gradient (Randers Fjord, Denmark)	Intact sediment core flux	0, 3–7, and 17–23	0 < 3–7 > 17–23	Abril and Iversen 2002
Queen's Creek (VA, USA)	Field dark chamber	5.1–16.6	Log $YCH_4 = -0.079$ x salinity +2.123	Bartlett et al. 1987
Oligohaline marshes, Min River (China)	Field light chamber	2.5–5.0 ($mS\ cm^{-1}$)	$YCH_4 = 2537$ x e-1.8117 x salinity	Tong et al. 2010
Estuarine salinity gradient, Delaware River (DE, USA)	Field light chamber	freshwater, oligohaline, mesohaline	oligohaline > freshwater > mesohaline	Weston et al. 2014
Mangrove-dominated estuary (Sundarbans, India)	extraction from estuarine water	18–27	$YCH_4 = -0.5626$ x salinity +23.94	Dutta et al. 2015

FW = freshwater

[a] Salinity in references of Marton et al. 2012, Chambers et al. 2011, Kiehn et al. 2013 and this study were from the added treatment solution, salinity for references of Abril and Iversen 2002 was from river and estuarine water, salinity for reference of Bartlett et al., 1987 was from porewater, salinity for reference Tong et al. 2010 was from sediment, salinity for reference Dutta et al. 2015 was from surface and bottom estuarine water

[b] Functions for references of Bartlett et al., 1987, Tong et al. 2010 and Dutta et al. 2015 indicated that a negative relationships between CH4 emission and salinity

cycling by decoupling nitrification-denitrification and producing toxic effects on microbial communities (Larsen et al. 2010). Clearly, there are still many unanswered questions regarding the mechanistic response of microorganisms involved nitrogen cycling to salinity, as well as what other environmental factors may be contributing to the variation in findings.

Relationship between Soil Properties and GHGs Production

Soil pH is an important variable that could govern the ionization of organic molecules, as well as the activity and function of soil microorganism (Min et al., 2014). The optimum pH range for methanogens is 6.8 to 7.2 (Wang et al., 2003). In our study, field soil pH was below this range, and decreased during the incubation (Fig. 3). This may have contributed to low CH_4 production potential, as support by the positive correlation between the GHGs production and soil pH (Table 4). These post-study pH values may also be artificial lower than what was actually occurring during the bottle incubation because soils may have oxidized during the process of quantifying pH in the laboratory. The negative correlation between the GHGs production and soil DOC or NH_4^+-N concentration (Table 4) is likely driven by the positive relationship between these two variable and salinity (Fig. 3c and d), but the higher concentrations in TW soils than DW soils may have contributed to the greater rates of GHG production observed at TW.

Experimental Design Considerations

It is important to note that the design of this study (i.e., closed bottle incubations) resulted in a rapid decline of all microbial activity in weeks 2 and 3, and the overall response of average GHG production to the salinity treatments was most influenced by the production rates observed during week 1 of the study. High microbial activity in week 1 may have resulted from the onset of ideal conditions, such as the removal of diffusion gradients in shaken slurries, or could be an artifact of soil collection, which can sever roots and release labile C and nutrients. Moreover, cation exchange between soil nutrients and added salt can may provide a short-lived nutrient supply for soil microbes (Weston et al. 2006). Since no additional C or nutrient source was added to the bottles over time, all microbial activity likely became limited by these factors over time, resulting in lower production rates. Additionally, microbial communities are known to be able to adapt to shifts in the ionic strength of their environment, which can lead to differential responses of GHG production in short-term vs. long-term studies, as well as in laboratory vs. field studies (Chambers et al. 2011; Neubauer et al. 2013),

Conclusions

Evidence of saltwater intrusion in estuarine wetlands due to sea level rise has been documented world-wide, with shifts in vegetation communities often being the most visible indication of increasing salinity (Ross et al. 2000; Hussein 2009; Sutter et al. 2015; Stofberg et al. 2015). However, as this study demonstrates, microbial activity and biogeochemical processes in wetland soils can respond to increasing salinity within days, resulting in significant changes in GHG production and soil physiochemical properties long before plant communities shift. Our results suggest the existence of a salinity threshold around 10–15‰ in the freshwater marsh soils of the Min River estuary, at which potential CH_4 and CO_2 production rates decline significantly, resulting in an overall decrease in soil carbon mineralization. The observed reduction in carbon mineralization above ~15‰ may indicate a beneficial negative feedback loop, in which increasing salinity slows carbon loss via microbial metabolism. If carbon inputs remain unchanged (or increase), this could translate into additional soil carbon storage and vertical accretion in estuarine wetlands, enhancing the ability of these systems to keep pace with rising sea levels (Morris et al. 2002; Mudd et al. 2009; Fagherazzi et al. 2012). However, our findings also indicate that salinities below this tipping point, particularly around 5–7.5‰, exhibit enhanced potential respiration rates, which may make freshwater soils exposed to low-levels of saltwater intrusion the most vulnerable to submergence to due accelerated soil organic C loss (Chambers et al. 2013). Furthermore, we found no relationship between salinity and potential N_2O production, despite increasing NH_4^+-N availability with higher salinities, indicating a complex response of nitrogen cycling to salinity. Future work should test the robustness of these findings under field conditions and attempt to discriminate between short-term and long-term responses of soil biogeochemical processes to saltwater intrusion.

Acknowledgements This work was financially supported by the National Science Foundation of China (Grant No: 41371127), the Key Sciences and Technology Project of Fujian Province (2014R1034-1), and the Program for Innovative Research Team at Fujian Normal University (IRTL1205). We thank Weiqi Wang, Jiafang Huang, Xuming Wang, Hongchang Ren, Qinyang Ji, Jingyu Zhang, Shaoyan Zheng, Weining Du for their assistance.

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