Applied Soil Ecology 170 (2022) 104268

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Effects of waterlogging and salinity increase on CO_2 efflux in soil from coastal marshes

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ARTICLE INFO

Keywords:
Salt marsh
Soil CO_2 efflux
Water flooding
Elevated salinity
Soil biochemistry

ABSTRACT

Coastal marshes play a notable role in sequestering carbon in plants and soil; however, coastal ecosystems are vulnerable to global change in terms of sea-level rise and saltwater intrusion. The effects of independent and interactive hydrological treatments of waterlogging and elevated salinity on soil CO_2 effluxes in *Spartina alterniflora* marshes were investigated based on a mesocosm approach. This study highlighted the importance of respective soil respirations during inundation (nondrainage, $R_{s.ND}$) and reaeration (drainage, $R_{s.D}$) in the marshes soils. We found that waterlogging treatments heavily suppressed $R_{s.ND}$ but increased the $R_{s.D}$, regardless of salinity levels. Light salinity enhanced soil respiration, whereas high salinity inhibited soil CO_2 efflux, regardless of the water table level. Waterlogging strengthened the negative effects of salinity on $R_{s.ND}$ and offset the negative effects on $R_{s.D}$. The variations in soil respiration under the hydrological treatments can be mainly attributed to changes in root biomass; indigenous soil microbial biomass; and activities of sucrase, cellulase and dehydrogenase, as well as ionic concentrations and oxidation-reduction potential. The temperature sensitivity (Q_{10} value) of soil respiration (only for $R_{s.D}$) after drainage showed a notable decline under the conditions of waterlogging and high salinity. The effect degree of coupled hydrological treatments on soil respiration and Q_{10} values was similar to a single waterlogging factor before drainage and more strongly than a single factor after drainage. We suggest that the soil CO_2 efflux under water flooding and reaeration, inundation duration, and salinity levels need to be considered to understand the impacts of future hydrological changes on coastal marshes.

1. Introduction

The carbon dioxide (CO_2) efflux of soil respiration (R_{soil}) produced by plant roots, microbes, and soil animals constitutes the second-largest carbon flux between terrestrial ecosystems and the atmosphere (Bond-Lamberty and Thomson, 2010). Variation in R_{soil} might drastically affect the global carbon budget and atmospheric CO_2 concentration (Rustad et al., 2000; Chambers et al., 2013). Vegetated coastal wetlands, which are collectively known as 'blue carbon' ecosystems, have significant potential to sequester carbon in plants and soil (Tan et al., 2020). However, these open ecosystems are highly vulnerable to global change in terms of climatic and hydrological interferences (Lloyd and Taylor, 1994; Rustad et al., 2001; Spivak et al., 2019). Therefore, the effects of global change projections, for instance, climate warming, sea-level rise (SLR) and saltwater intrusion, on soil CO_2 efflux in coastal wetlands need to receive serious attention.

SLR would cause prolonged inundation in coastal wetlands. Some studies have shown that soil respiration is suppressed under inundation mainly due to the blocking of the water barrier to CO_2 gas diffusion (Heinsch et al., 2004; Krauss et al., 2012; Han et al., 2015) and extensive anaerobic respiration with decreased CO_2 production (Megonigal et al., 2004; Neubauer, 2013). Microbial activity is also inhibited, likely due to physiological stress induced by hypoxia (Nyman and DeLaune, 1991; Miller et al., 2001; Wang and Lu, 2006; Chambers et al., 2014). As previously reported in terrestrial grasslands, soil moisture is a major factor that influences the microbial taxonomic composition in soil (e.g., Bell et al., 2009). However, once tidal water drawdown occurs, re-exposed wetland soil emits more CO_2 than when flooding occurs (Happell and Chanton, 1993; Sasaki et al., 2009; Krauss et al., 2012; Chambers et al., 2013; Wang et al., 2019).

In addition, SLR increases the frequency and duration of saltwater intrusion in coastal areas (Ferguson and Gleeson, 2012; Neubauer et al.,

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https://doi.org/10.1016/j.apsoil.2021.104268
Received 2 February 2021; Received in revised form 8 October 2021; Accepted 11 October 2021

2013; Han et al., 2018), and increased water salinity potentially affects carbon processes in plants and soil (Moffett et al., 2010; Neubauer, 2013; Wilson et al., 2018a, 2018b). High salinity will reduce the root growth of wetland plants (Pezeshki and DeLaune, 1993; Krauss et al., 2012) and the activities of indigenous microorganisms (Rath and Rousk, 2015; Ardón et al., 2018; Doroski et al., 2019; Helton et al., 2019), thus resulting in decreased soil respiration. Additionally, elevated salinity can suppress the activities of soil extracellular enzymes involved in carbon mineralization by damaging enzyme molecular stability or limiting the potential source of enzymes (Tripathi et al., 2007; Neubauer et al., 2013). However, some studies have shown neutral or even positive responses of soil respiration to salinity, probably due to an enhanced abundance of sulfate reducers (Weston et al., 2006; Chambers et al., 2011, 2013; Kim et al., 2020), shifts in indigenous microbial composition (Morrissey et al., 2014; Wilson et al., 2018a), or depletion of labile carbon pools (Neubauer et al., 2013).

As expected, interactive hydrological changes might occur simultaneously in coastal ecosystems. Several interactive studies have been conducted to assess the responses of soil respiration to environmental change (Chambers et al., 2013; Wilson et al., 2018a). Prolonged waterlogging can interact with saltwater intrusion to increase the concentrations of Na^+ and Cl^- in plant organs and porewater, thus restricting plant growth or altering the pathways of microbial organic matter mineralization (Barrett-Lennard, 2003; Weston et al., 2006). The temperature sensitivity of soil respiration is characterized in terms of the Q_{10} value, which describes the change in the soil respiration rate with an increase of 10 °C in temperature (Lloyd and Taylor, 1994; Boone et al., 1998). Previous studies have primarily focused on the temperature sensitivity of soil respiration under altered waterlogging conditions (Zhong et al., 2013; Chen et al., 2018), while information on the response of Q_{10} values to changing salinity environments is limited in coastal ecosystems (Li et al., 2018b). Moreover, the existing studies mainly aimed at soil respiration under one kind of hydrological manipulation, and insight into the synchronous effects of SLR projections on soil carbon fluxes simultaneously, including nondrainage and drainage in coastal wetlands, remains lacking.

Spartina alterniflora (cordgrass) is a deciduous perennial flowering plant that is one of the most globally distributed species in coastal wetlands. In this study, we conducted a factorial mesocosm experiment with the plant-soil systems of *S. alterniflora* subjected to waterlogging, elevated salinity, and the combined treatments. In addition to soil respiration and its temperature sensitivity, plant growth, soil properties, and soil microbial biomass and enzyme activities were determined to understand the mechanisms controlling the CO_2 flux changes associated with hydrology. We hypothesized that waterlogging and increased salinity would result in nonlinear responses of the CO_2 flux in soil, depending on the changes in drainage status and soil biochemistry. This simulation experiment might narrow the gap in how the soil carbon efflux in coastal wetlands will respond to multiple global change projections.

2. Materials and methods

2.1. Plant-soil materials and experimental setup

The plant and soil materials were collected in the Chongming Dongtan wetland (121°59′22″ E; 31°30′35″ N) of the Yangtze River estuary. In December (winter) 2015, a monocultural marsh of *S. alterniflora* was selected as the sampling area. The plant growth and soil properties at the sampling site were homogeneous, and the *S. alterniflora* seedlings had the same life forms. A total of 48 intact (unbroken) soil blocks of *S. alterniflora* were excavated, consisting of soil monoliths (L-W-H: 32 cm × 24 cm × 40 cm, matching the size of polyethylene containers) with *S. alterniflora* rhizomes placed in polyethylene containers. The plant densities in the containers were relatively homogenous. A hose with a valve was installed at the bottom of each container to control drainage and water level. Soil material from the same sampling site was collected to fill small gaps in the containers.

Over the periods of March–November 2016 and 2017, the mesocosms were evenly grown in a natural chamber under a transparent shelter to block rain, following ambient temperature conditions (see Fig. 1). As measured over 2017, the daily mean air temperature (T_a) in the shelter and soil temperature (T_s) in the mesocosms were 25.7 ± 4.7 °C and 23.2 ± 5.6 °C, respectively. The shelter and glass restricted part of the infrared radiation and have relatively high (~75%) transparency for visible light.

In the beginning dormancy period (January and February) of 2016, all mesocosms were watered daily using freshwater to homogenize the soil salinity. At the beginning of March 2016 (buds appeared), the mesocosms were fertilized once with revised Hoagland's nutrient solution. Over the periods of March–November 2016 and 2017, two water-level treatments, including a low water table group (LW, the water level was maintained at half of the container height, water table at 15–20 cm below the soil surface) and a waterlogging group (HW, the water level was waterlogged at ~100 mm above the soil surface), were established. Since the surface water salinity ranges from ~0 ppt to ~30 ppt around the freshwater marshes, oligohaline marsh, and mesohaline marshes in the Yangtze Estuary (see Li et al., 2020), we set up four salinity treatments, including a freshwater-treated group (control group) and three saline water (5, 15, and 30 ppt) treatment groups (using a sodium chloride solution). Six replicates were set up for each hydrological treatment. Every two weeks, all 48 mesocosms (two water table groups × four salinity groups × six replicates) were drained for 12 h to renew irrigation (also for soil respiration measurements, see the sections below). Deionized freshwater was used to maintain the water level during the nonirrigation period to avoid excess salt accumulation resulting from water evaporation.

2.2. Measurements of soil respiration

Considering the alternate cycle of tidal inundation and re-exposure in coastal wetlands, the rate of soil respiration under nondrainage conditions ($R_{s.ND}$) and drainage status ($R_{s.D}$) for both LW and HW mesocosms was measured during the 2017 growing season using a soil respiration measurement chamber (LI-6400–09, Li-Cor, Inc., Lincoln, NE, USA) connected to an infrared gas analyzer (Li-Cor, Inc., Lincoln, NE, USA). To minimize disturbances in the soil profile, a PVC soil collar with an inner diameter of 10 cm was permanently mounted (5 cm depth) in the middle of each mesocosm before measurement. The living plants inside the collars were carefully clipped from the soil surface to focus on soil and root contributions below the soil surface.

Soil respiration was measured monthly in April, June, August, and October of 2017. The mesocosms were drained before the $R_{s.D}$ measurements, and drainage manipulation was conducted at 08:00–09:00 for 12 h (20:00–21:00). Each measurement represented the mean from 3 cycles, and each cycle represented a single, short-duration (2–5 min) static flux measurement. The air CO_2 concentration in the chamber was set with 380–450 μmol mol^{-1} as the target concentration for each measurement cycle. Soil temperature was measured simultaneously using a copper/constantan thermocouple penetration probe (LI-6400–09 TC, Li-Cor, Inc., Lincoln, NE, USA) inserted into the soil (10 cm depth) close to the PVC collars. After measurements, the water tables were renewed for both the LW and HW groups.

The van't Hoff equation (van't Hoff, 1898) was used to examine the temperature sensitivity of soil respiration.

$$R_{soil} = a \times exp^{(b \times T_s)} \quad (1)$$

where T_s is the soil temperature, and a and b are fitted parameters. The parameter b was further used to calculate the increase in soil respiration per 10 °C increase in temperature (Q_{10} value), which is widely identified as a key factor that reflects the temperature sensitivity of soil

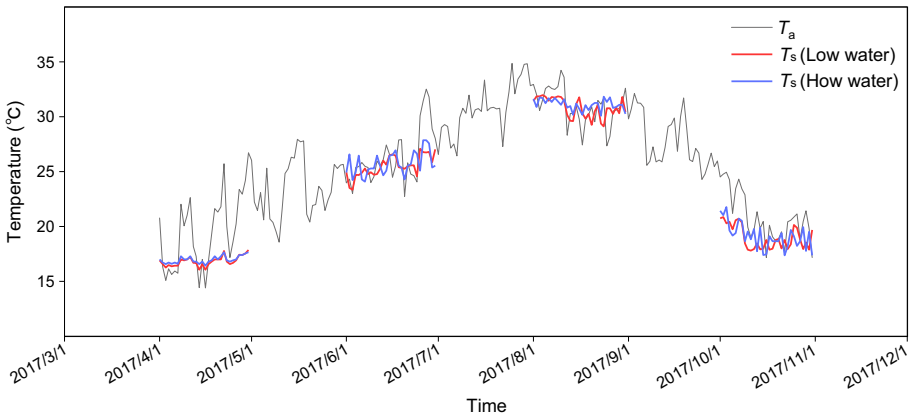

Fig. 1. Seasonal variations in air (T_a) and soil temperature (T_s) of the mesocosms under low (LW) and high water (HW) levels in 2017. Note: black line means the T_a; red and blue lines mean the T_s of mesocosm under LW and HW levels, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

respiration.

$$Q_{10} = exp^{(10\times b)} \quad (2)$$

2.3. Measurement of soil microbial biomass and extracellular enzyme activity

In early October 2017, ten soil cores (2 cm diameter, 15 cm depth) in each container were randomly extracted to determine the soil microbial biomass carbon (MBC) and extracellular enzyme activity. Soil samples around the roots at ~1 cm were mixed and freeze-dried immediately, sieved to 0.6 mm, and stored at 4 °C. The soil MBC was determined based on the chloroform fumigation and direct extraction technique (Vance et al., 1987) using an elemental analyzer (Elementar Vario EL III CHNOS, Elementar Analysensysteme GmbH, Langenselbold, Germany).

The activities of four enzymes (sucrase, cellulase, dehydrogenase, and catalase) involved in soil carbon cycling were selected for measurement. Following Frankeberger and Johanson (1983), sucrase activity was assayed using 3,5-dinitrosalicylic acid colorimetry and expressed as mg glucose hydrolyzed from sucrose sample per 24 h at 37 °C. Cellulase activity was analyzed using 3,5-dinitrosalicylic acid colorimetry and expressed as mg glucose equivalents hydrolyzed from sodium carboxymethyl cellulase g^{-1} dry sample per 72 h at 37 °C (Hayano, 1986). Dehydrogenase activity was analyzed using 2,3,5-triphenyltetrazolium chloride (TTC) colorimetry and was expressed as micrograms of TTC oxidized into triphenylformazan (TPF) per milliliter of solution mixed with 2 g of dry soil in 24 h at 37 °C (Casida et al., 1964). Catalase activity was measured by the titrimetric method using potassium permanganate and expressed as mL 0.002 M (mol L^{-1}) $KMnO_4$ per g dry soil in 20 min (Kappen, 1913). Each enzyme activity measurement was performed in triplicate. All assays included appropriate blanks in each group. The blank reaction was conducted under soil-free conditions to remove possible interference from nonenzymatic reactions, and then all the chemical reagents and experimental procedures were set the same as those for the treatment groups. Standard curves were prepared for enzyme activity based on colorimetric determination.

2.4. Measurement of soil properties

Additionally, in early October 2017 (later growing season), another group of soil cores (40 cm depth) from each container was randomly sampled via a steel corer with an inner diameter of 5 cm. All the roots were eliminated by squeezing the moist soil to pass through a 2 mm sieve. The root-free soil was air-dried, ground into a powder, and then sieved by passing a 1-mm sieve to determine the physiochemical properties. Soil organic carbon (SOC) and total nitrogen (TN) were determined using an elemental analyzer (Elementar Vario EL III CHNOS, Elementar Analysensysteme GmbH) after the samples were acidified with 1 mol L^{-1} hydrochloric acid (HCl) (standard method by Bao, 2000). The C/N ratio could be calculated as the ratio between SOC and TN. Ten grams of soil sample was mixed with 5 volumes of water, and leach liquor was extracted from the mixture to measure the content of major ions, including SO_4^{2-}, CO_3^{2-} and HCO_3^-. The content of SO_4^{2-} was measured using a Dionex ICS-2000 ion chromatograph (Dionex Corporation, Sunnyvale, CA, USA), and CO_3^{2-} and HCO_3^- were determined based on the method of dual indicator-neutralization titration. The soil oxidation-reduction potential (ORP) was measured directly using a portable ORP sensor (SX712, Sanxin Co., Shanghai, China).

2.5. Measurement of root biomass

Also in October 2017, a soil core (4.2 cm diameter, 40 cm length) in the PVC collar was excavated from each mesocosm for the assessment of root biomass. The soil material was washed away using tap water through a 60-mesh screen. The living roots were picked and dried to a constant weight at 60 °C.

2.6. Data analysis

The differences of $R_{s.ND}$, $R_{s.D}$, Q_{10} values, and edaphic variables (including root biomass, MBC, enzyme activities, soil nutrients, and physiochemical factors) under different temperature, water table, and salinity conditions were tested using one-way analysis of variance (ANOVA). The Kolmogorov–Smirnov test showed that all the data groups met the assumptions of normality. The main effects of elevated temperature, high water level and salinity treatments, and their interactive effects on the soil respiration and edaphic variables were tested through the analysis of two-way ANOVA with Tukey's test of multiple comparisons. Pearson's correlation analysis was used to test the relationships between soil respiration and edaphic variables. The level of statistical significance was set to p values (probability) < 0.05. The statistical analyses were performed with SPSS for Windows 23.0 (SPSS, Inc., Chicago, IL, USA).

Redundancy analysis (RDA) was further used to test the multiple effects of climatic factors (warming, water table, and salinity) and their interactions on soil respiration and edaphic factors (Legendre and Legendre, 1998). RDA was performed with CANOCO 4.5 (Microcomputer Power, Ithaca, NY, USA).

3. Results

3.1. Soil biological and physicochemical variables

Despite salinity, HW increased the activities of cellulase and dehydrogenase, SOC, C/N, and SO_4^{2-} ($p < 0.05$) compared to LW (Fig. 2–3). In contrast, HW decreased the MBC, HCO_3^-, and ORP ($p < 0.05$) and slightly decreased the root biomass and activities of sucrase and catalase activity by 0.5–6.5% compared to LW. The effects of waterlogging treatment on the soil factors were significant ($p < 0.05$), except for root biomass, sucrase and catalase activity, and TN (Table 1). Mild salinity (5 ppt) slightly enhanced or did not affect the soil factors, while high salinity (15 and 30 ppt) significantly ($p < 0.05$) decreased all soil factors, except for ionic concentrations, relative to the nonsalinity conditions (Fig. 2–3). Generally, the concentrations of SO_4^{2-} and HCO_3^- consistently increased with increasing salinity. The effects of salinity on the soil factors were notable ($p < 0.05$), except for TN (Table 1). The interactive effects of waterlogging × salinity on the MBC and activities of sucrase and cellulase were significant (Table 1, $p < 0.05$).

3.2. Soil respiration under changed hydrology

When measured under nondrainage conditions, the HW treatments significantly decreased the $R_{s.ND}$ by 74.4% ($p < 0.05$) relative to the LW treatments over the growing season, regardless of salinity treatments. Regardless of water table treatments, the $R_{s.ND}$ at 5 ppt displayed a slight increase by an average of 2.7%, while high salinities of 15 ppt and 30 ppt significantly ($p < 0.05$) decreased $R_{s.ND}$ by on average 17.6% and 28.9%, respectively, compared to the nonsalinity groups throughout the measurement period (Fig. 4). After drainage, HW treatments increased the $R_{s.D}$ by 12.9% relative to LW treatments over the growing season, regardless of salinity treatments. Regardless of the water table treatments, 5 ppt salinity increased $R_{s.D}$ by an average of 10.7%, while high salinities of 15 ppt and 30 ppt significantly ($p < 0.05$) decreased $R_{s.D}$ by an average of 29.0% and 42.4% over the growing season, respectively, compared to the nonsalinity groups (Fig. 4).

The effects of waterlogging and salinity treatments on $R_{s.ND}$ was significant ($p < 0.05$) over the observation period (Table 2), and the interactive impacts of waterlogging × salinity were also notable ($p < 0.05$), except for April. The significant effects of waterlogging treatments on $R_{s.D}$ occurred in April, and significant effects of salinity occurred in June, August, and October ($p < 0.05$). The interactive effects of waterlogging × salinity on $R_{s.D}$ were notable ($p < 0.05$) in October.

3.3. Temperature sensitivity of soil respiration

Both $R_{s.ND}$ and $R_{s.D}$ showed a strong exponential relationship with soil temperature across the experimental treatments (Fig. 5a & 5b), with the estimated Q_{10} values (temperature sensitivity) ranging from 1.16 to 2.68 for $R_{s.ND}$ (mean ± standard error, 1.95 ± 0.45) and ranged from 1.15 to 1.87 for $R_{s.D}$ (1.55 ± 0.21). Regardless of salinity treatments, HW significantly ($p < 0.05$) decreased the Q_{10} values by an average of 28.5 ± 3.2% for $R_{s.ND}$ and 13.4 ± 6.5% for $R_{s.D}$ compared with LW (Fig. 5c & 5d). The salinity levels of 5 ppt and 15 ppt did not significantly change the Q_{10} values for $R_{s.ND}$ and $R_{s.D}$, while 30 ppt salinity significantly ($p < 0.05$) reduced the Q_{10} values for $R_{s.D}$ compared to the nonsalinity groups.

3.4. Effects of edaphic variables on soil respiration

Both $R_{s.ND}$ and $R_{s.D}$ were significantly ($p < 0.05$) positively correlated with root biomass, MBC, enzyme activities, and ORP, except for the relationship between $R_{s.D}$ and the activities of cellulase, dehydrogenase, and catalase under HW treatment (Fig. 6). For the HW treatment, the $R_{s.}$

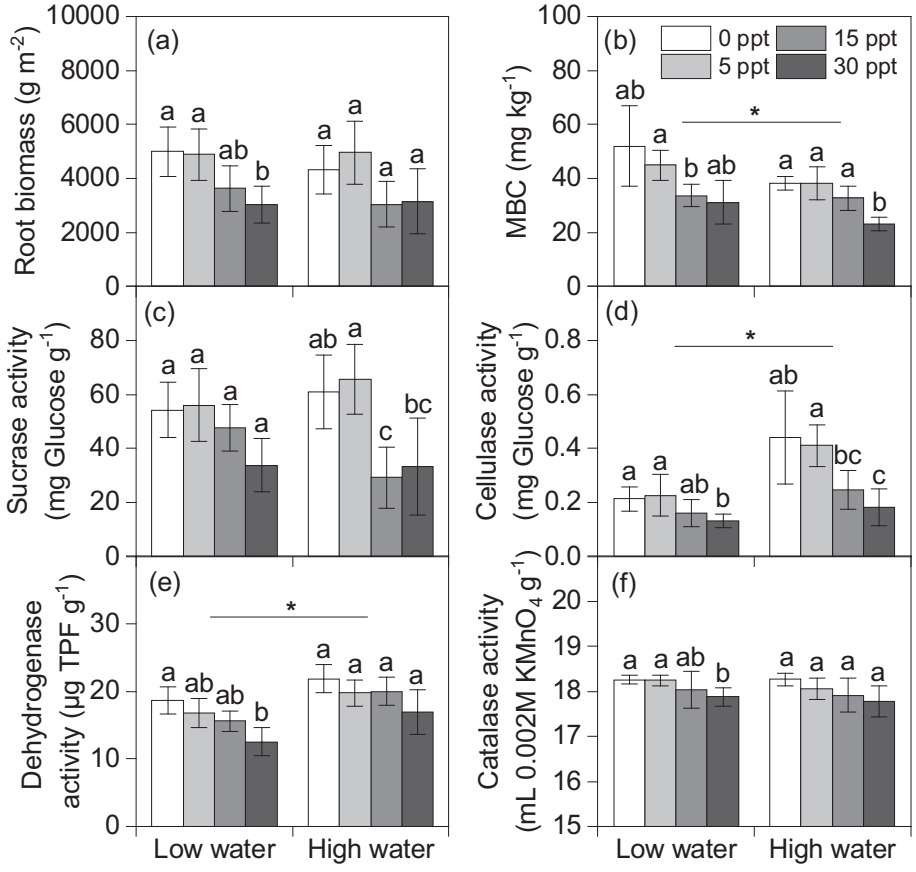

Fig. 2. Soil variables included biological characters of root biomass, microbial and enzyme activities (mean ± standard errors, $n = 6$) under low (LW) and high water (HW) levels and a salinity gradient (0–30 ppt). Different lowercase letters indicate significant differences ($p < 0.05$) in the variables among salinity levels. The asterisks above horizontal lines indicate significant differences ($p < 0.05$) between water table groups (LW vs. HW) (on the average of salinity levels). MBC: microbial biomass carbon.

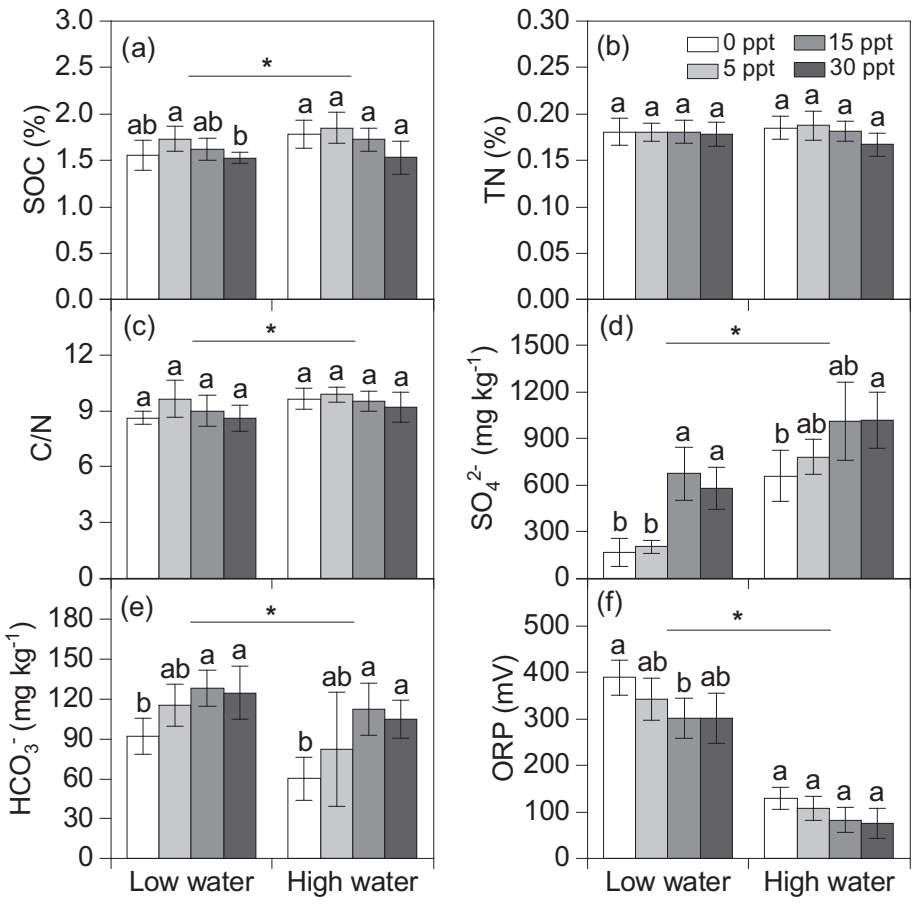

Fig. 3. Soil variables included nutrients and physiochemistry (mean ± standard errors, $n = 6$) under low (LW) and high water (HW) levels and a salinity gradient (0–30 ppt). Different lowercase letters indicate significant differences ($p < 0.05$) in the variables among salinity levels. The asterisks above horizontal lines indicate significant differences ($p < 0.05$) between water table groups (LW vs. HW) (on the average of salinity levels). SOC: soil organic carbon; TN: total nitrogen; C/N: ratio of SOC to TN; SO_4^{2-}: sulfate ion; HCO_3^-: bicarbonate ion; ORP: oxidation-reduction potential.

Table 1
Main and interactive effects (*F*-value) of waterlogging (water) and salinity (salinity) on the edaphic variables.

Factor	Water	Salinity	Water × Salinity
Root biomass	0.953	**11.321****	0.587
MBC	**13.083****	**15.666****	1.649
Sucrase	0.038	**14.111****	**3.011***
Cellulase	**31.409****	**12.085****	**2.953***
Dehydrogenase	**34.895****	**13.093****	0.332
Catalase	1.569	**6.021****	0.273
SOC	**7.851****	**6.804****	1.163
TN	0.008	1.996	1.204
C/N	**8.908****	**3.296***	0.701
SO_4^{2-}	**107.117****	**23.315****	1.286
HCO_3^-	**16.241****	**10.031****	0.482
ORP	**474.457****	**9.388****	0.698

F-values with significance $p < 0.05$ were bolded.
MBC: microbial biomass carbon; SOC: soil organic carbon; TN: total nitrogen; C/N: ratio of SOC to TN; SO_4^{2-}: sulfate ion; HCO_3^-: bicarbonate ion; ORP: oxidation-reduction potential.
* Significance at $p < 0.05$.
** Significance at $p < 0.01$.

$_{ND}$ was significantly ($p < 0.05$) positively correlated with SOC and TN, and $R_{s.D}$ was significantly ($p < 0.05$) positively correlated with SOC. Both $R_{s.ND}$ and $R_{s.D}$ were significantly ($p < 0.05$) negatively related to SO_4^{2-} under the LW treatment.

The ionic concentrations were negatively related to soil biological factors (root biomass, MBC, and enzyme activities) (Fig. 6). The root biomass was significantly ($p < 0.05$) positively related to the MBC and enzyme activities, except for sucrase activity under the LW treatment and the activities of cellulase and dehydrogenase under the HW treatment (Fig. 6). The SOC and TN were significantly ($p < 0.05$) positively related to MBC, sucrase, and cellulase activities under the HW treatment.

Based on the RDA results, the first two principal components explained 68.7% of the total variation in the treatment-induced changes in soil respiration and edaphic variables (Fig. 7). The water level treatments made a stronger contribution (57.2%, $p < 0.01$) to the relative influence on soil respiration than the salinity treatments (13.3%, $p < 0.01$) (Table 3). The combined treatments of waterlogging × salinity contributed 29.4% to the relative influence on soil respiration.

All edaphic factors were negatively associated with salinity and its coupled treatments (waterlogging × salinity), except for ionic concentrations (Fig. 7). Cellulase and dehydrogenase activities were positively related to the waterlogging treatment, whereas catalase activity was negatively affected by the waterlogging treatments. Waterlogging treatments dominated the contribution (44.8%, $p < 0.01$) to the relative influence on the soil variables (Table 3), followed by the interaction of water level and salinity (33.0%, $p < 0.01$) and the single effect of salinity treatments (22.2%, $p < 0.01$).

4. Discussion

4.1. Effects of prolonged waterlogging

Under the waterlogging treatment, keeping inundation heavily inhibited CO_2 efflux ($R_{s.ND}$) of *S. alterniflora* soil. Waterlogging conditions produce a water physical barrier to gas diffusion between the soil and atmosphere, which directly blocks CO_2 respiration by root or soil microorganisms and even completely prevents soil respiration (Krauss et al., 2012; Han et al., 2015). In addition, the water barrier limited O_2 entrance to soil, thus leading to anaerobic wetland soil (low redox

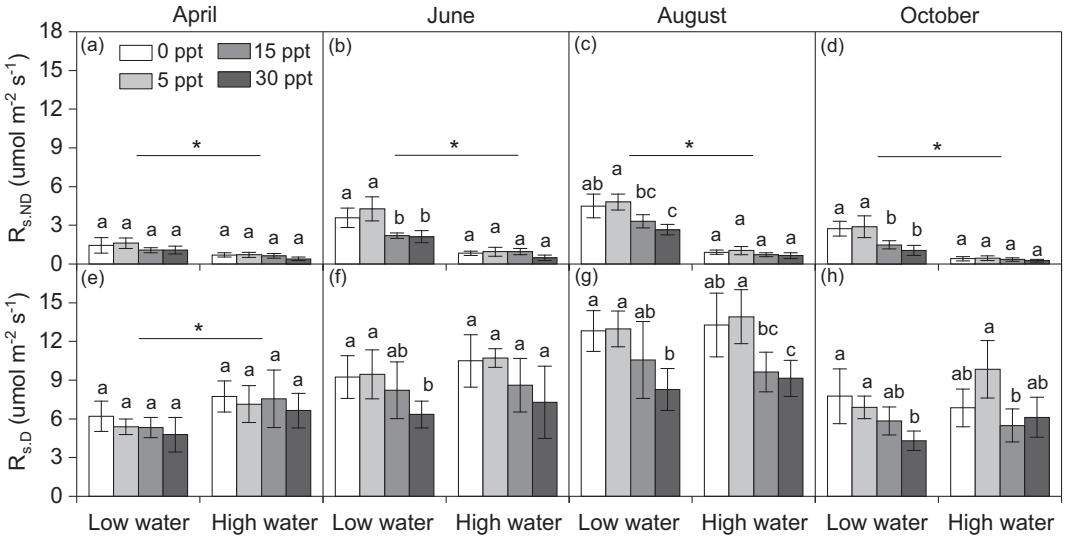

Fig. 4. Soil respiration (mean ± standard errors, $n = 6$) for nondrainage ($R_{s.ND}$) and drainage ($R_{s.D}$) under low (LW) and high water (HW) levels and a salinity gradient (0–30 ppt) in April (*a, e*), June (*b, f*), August (*c, g*), and October (*d, h*). Different lowercase letters indicate significant differences ($p < 0.05$) in the variables among salinity levels. The asterisks above horizontal lines indicate significant differences ($p < 0.05$) between water table groups (LW vs. HW) (on the average of salinity levels).

Table 2
Main and interactive effects (*F* and *p* values) of waterlogging (water) and salinity (salinity) on soil respiration for nondrainage ($R_{s.ND}$) and drainage ($R_{s.D}$) conditions over the growing period.

Treatments	Soil respiration	April	June	August	October
Water	$R_{s.ND}$	**61.142***	**246.255***	**462.144***	**190.823***
Salinity		**4.773***	**17.364***	**18.132***	**16.599***
Water × Salinity		1.069	**11.503***	**9.046***	**11.788***
Water	$R_{s.D}$	**23.029***	3.02	0.347	4.056
Salinity		1.794	**7.635***	**16.472***	**11.384***
Water × Salinity		0.144	0.14	0.596	**4.366***

* Significance at $p < 0.05$, *F*-values with significance $p < 0.05$ are bolded.

potential); thus, the accumulation of toxic compounds would result in a temporary decrease in root respiration (e.g., Krauss et al., 2012).

However, the $R_{s.D}$ measured when reaeration conditions (drainage period) under the HW treatments were ~13% higher than those under the nonwaterlogging treatments. This indicated that the high amounts of anaerobic and saturated soil under HW incubation could stimulate increased CO_2 efflux after drainage. This phenomenon would maintain waterlogging-blocked CO_2 respiration by roots and soil microorganisms due to the existence of a water barrier between the soil surface and atmosphere (e.g., Heinsch et al., 2004; Krauss et al., 2012; Han et al., 2015). When drainage occurs, the previous occurrence of air advection into inundated soil can increase the exposure of organic matter to O_2 and promote aerobic respiration, leading to a dramatic release of CO_2 from root and microbial respiration after acute exposure to air (Sasaki et al., 2009; Krauss et al., 2012; Wang et al., 2019), as observed under the HW treatment. For the LW treatment, the upper soil layer was air-permeable and aerobic, in which soil organic matter was not susceptible to drainage relative to the HW conditions.

Waterlogging treatments did not affect the *S. alterniflora* root mass or the activities of sucrase and catalase in soil, while the activities of cellulase and dehydrogenase were significantly higher under the HW treatment than under the LW treatment. Increased cellulase activity might facilitate the accumulation of secondary products of cellulose in waterlogged soil and stimulate microbial respiration. We also found that the SOC in *S. alterniflora* soil was slightly higher under HW conditions than under LW conditions, which would form a high content of cellulose and carbon substrates, thus promoting cellulase activity (e.g., Shackle et al., 2000; Rietz and Haynes, 2003; Allison et al., 2007). Dehydrogenases can catalyze oxide-reductive reactions and are active under both aerobic and anaerobic conditions, and most dehydrogenases are produced by anaerobic microorganisms (Włodarczyk et al., 2002). Therefore, increased dehydrogenase activity under HW conditions would also positively contribute to microbial respiration compared to that under LW conditions. On the other hand, because most of the assayed enzymes are extracellular, even with high availability of the substrate (cellulose), the secondary products or end-products might be dispersed under HW conditions. Then, it might stimulate high production of extracellular enzymes to overcome this barrier.

Nevertheless, the abundance of sulfate (SO_4^{2-}) was significantly higher under the HW treatment than under the LW treatment and showed a negative correlation with $R_{s.D}$. Abundant sulfate inhibits CO_2 emissions, as well as another greenhouse gas, CH_4, which is quickly oxidized to CO_2 under aerobic conditions (Choi and Wang, 2004). It is speculated that the inhibitory effects of increased SO_4^{2-} might be lower than the stimulatory effects of waterlogging mentioned above. The contribution ratios of the positive and negative effects of biological and edaphic factors on soil CO_2 efflux projected to occur under prolonged flooding conditions deserve more attention in future studies.

The Q_{10} values showed a notable decline under waterlogging treatments. Chen et al. (2018) showed that the Q_{10} values under aerobic conditions were 1.5–2.5 times higher than those under anaerobic incubations for various wetland types, probably due to enhanced microbial and enzyme activity once wetlands become aerobic after drying. However, Inglett et al. (2012) reported an opposite pattern, showing a higher Q_{10} under anaerobic conditions than under aerobic conditions (Table S1). The inconsistency might be ascribed to the fact that their CO_2 production rates were measured during the waterlogging status, while we carried out the measurements under reaeration status.

4.2. Effects of increased salinity

Mild salinity (5 ppt) slightly increased soil respiration, while high salinity (15 ppt and 30 ppt) significantly decreased the effluxes. Two main reasons might contribute to the adaptation of *S. alterniflora* and the responses of soil respiration. First, many halophyte species (such as *S. alterniflora*) can accumulate prolines or glycinebetaine in roots for

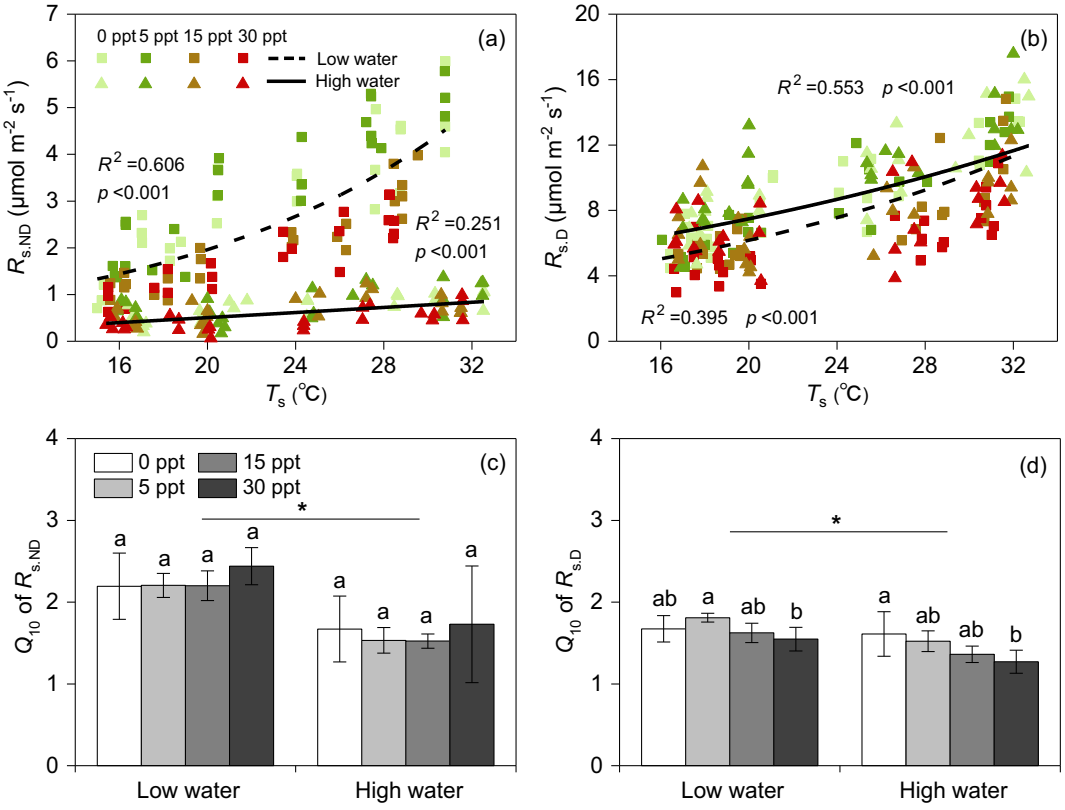

Fig. 5. Soil temperature (T_s) sensitivity of soil respiration (Q_{10} values) in relation to for nondrainage ($R_{s.ND}$, *a, c*) and drainage ($R_{s.D}$, *b, d*) under low (LW) and high water (HW) levels and salinity gradients (0–30 ppt). Different lowercase letters indicate significant differences ($p < 0.05$) in the variables among salinity levels. The asterisks above horizontal lines indicate significant differences ($p < 0.05$) between water table groups (LW vs. HW) (on the average of salinity levels).

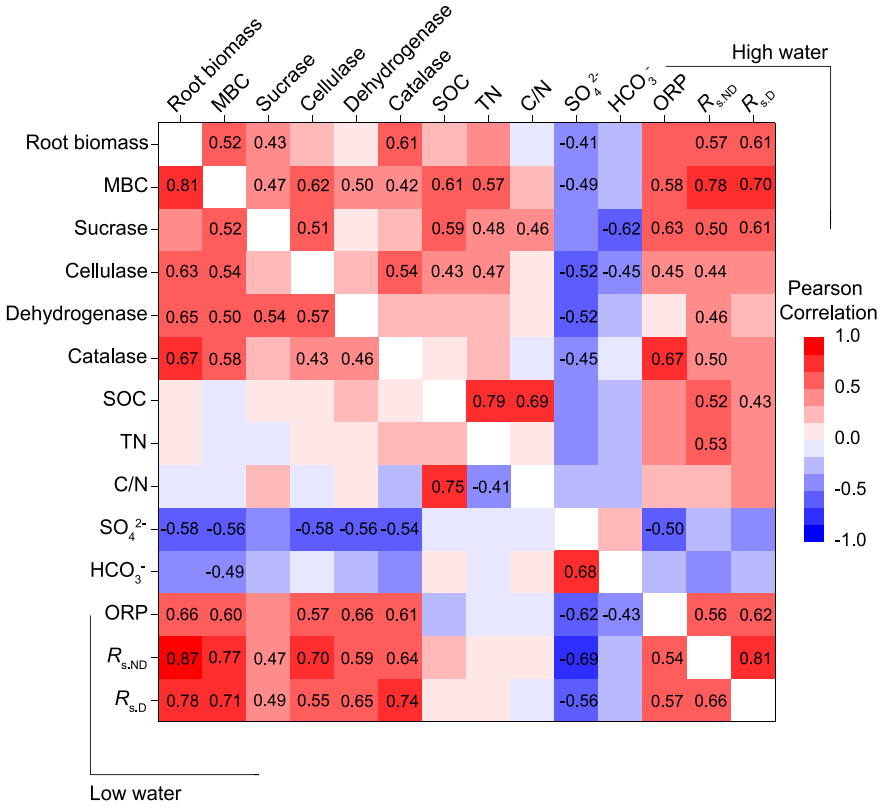

Fig. 6. Heat maps of Pearson's correlation coefficients among soil respiration for nondrainage ($R_{s.ND}$) and drainage ($R_{s.D}$), and soil biological and physicochemical variables (within salinity levels) under low (LW) and high water (HW) levels. Only the coefficients with significant correlations ($p < 0.05$) are shown. MBC: microbial biomass carbon; SOC: soil organic carbon; TN: total nitrogen; C/N: ratio of SOC to TN; SO_4^{2-}: sulfate ion; HCO_3^-: bicarbonate ion; ORP: oxidation-reduction potential.

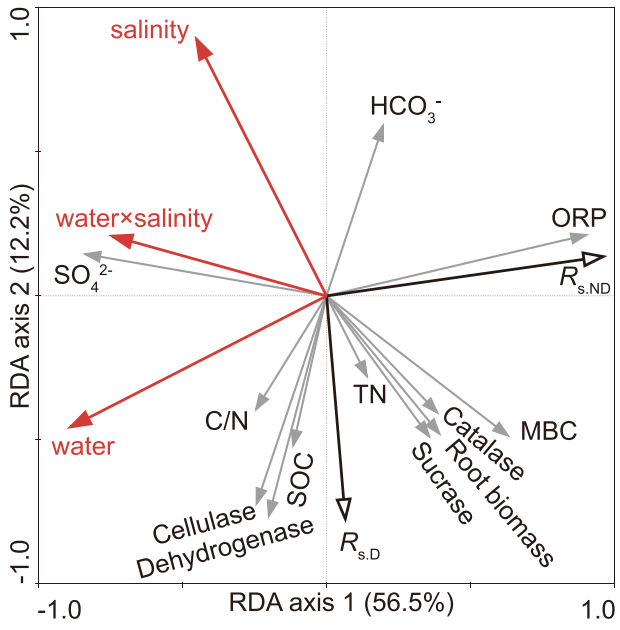

Fig. 7. Ordination diagram based on redundancy analysis (RDA) of the soil respiration (black empty arrows) and edaphic variables (gray arrows) with respect to treatments (red arrows) of waterlogging (water), salinity and their interactions. $R_{s.ND}$: soil respiration for nondrainage condition; $R_{s.D}$: soil respiration for drainage condition; MBC: microbial biomass carbon; SOC: soil organic carbon; TN: total nitrogen; C/N: ratio of SOC to TN; SO_4^{2-}: sulfate ion; HCO_3^-: bicarbonate ion; ORP: oxidation-reduction potential. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Explained variance and relative contributions of the waterlogging (water) and salinity (salinity) treatments to the soil respiration and soil variables, tested with redundancy analysis (RDA).

Explanatory variable	Dependent variable	Explained variance	Relative contribution	*F*-value	*p* -Value
Water	R_{soil}	70.7%	57.2%	110.771	**<0.01**
Salinity		16.5%	13.3%	9.074	**<0.01**
Water × Salinity		36.4%	29.4%	26.283	**<0.01**
Water	Soil factors	43.9%	44.8%	36.036	**<0.01**
Salinity		21.8%	22.2%	12.812	**<0.01**
Water × Salinity		32.3%	33.0%	21.959	**<0.01**

R_{soil}: soil respiration including both nondrainage and drainage conditions.

osmoregulation to defend osmotic pressure from saline environments (Cavalieri and Huang, 1981; Naidoo et al., 1992). *S. alterniflora* can also secrete salt at the shoot surface via salt glands, which help to alleviate the adverse effects of saline stress (Bradley and Morris, 1991). Mild salinity is the most favorable for the growth of *S. alterniflora* (Courtney et al., 2016), as observed by increased shoot biomass (Li et al., 2018a) and root biomass (Fig. 2a), which was positively correlated with soil respiration (Fig. 6). Second, the increased activity of extracellular enzymes involved in carbon cycling (i.e., sucrase) and nutrient supply (SOC, TN) could also partly account for the increased soil microbial activity under mild salinity (Fig. 2c, Fig. 3a and b). Morrissey et al. (2014) even observed that enhanced salinity from freshwater to oligohaline water (<2 ppt) could facilitate bacterial abundance and microbial respiration. Previous studies have already found that some soil microorganism groups and extracellular enzymes are salt-activated under a wide salinity gradient in tidal wetlands (Morrissey et al., 2014; Xie et al., 2020). The adaptation of microbial communities to mild salinity could stimulate the production of adapted enzymes, thus leading to increases in CO_2 production.

However, when salinity continues to increase, high saline conditions physiologically suppress plant growth (Li et al., 2018a). High concentrations of salts in the soil hinder roots from extracting water and induce toxic stress for root growth (Munns and Tester, 2008), thus potentially decreasing soil respiration (Krauss et al., 2012). Burchett et al. (1989) found that the root respiration rates of two coastal species significantly decreased under high salinity due to a limited supply of substrate for the roots to exclude salts. In addition, increased salinity could also suppress microbial respiration by reducing the soil microbial population (Li et al., 2010; Rath and Rousk, 2015; Ardón et al., 2018; Doroski et al., 2019; Helton et al., 2019), which could be reflected by the negative correlation of elevated salinity-driven ionic concentrations vs. MBC and the positive correlation of MBC vs. soil respiration (Fig. 6). Furthermore, we found that the enzyme activities participating in the carbon processes were also suppressed by increased salinity, which coincided with previous results. High salinity could directly suppress extracellular enzyme activities by affecting molecular stability and protein confirmation states, leading to reduced rates of soil CO_2 production (Tripathi et al., 2007; Neubauer et al., 2013).

Elevated salinity did not significantly change the Q_{10} values of $R_{s.ND}$, while high salinity decreased the Q_{10} values of $R_{s.D}$, with a significant effect of 30 ppt. In our experiments, high salinity heavily suppressed the growth of roots and microorganisms. Boone et al. (1998) found that the Q_{10} value of soil respiration decreased with decreasing root system complexity. A reduction in root system complexity could account for the decreased Q_{10} values of $R_{s.D}$; however, this explanation cannot apply to the Q_{10} values of $R_{s.ND}$. Further exploration of the fractions of microbial and root respiration that contribute to temperature sensitivity along salinity gradients is needed.

4.3. Effects of coupling environmental factors

In coastal ecosystems, SLR might synchronously induce prolonged inundation and saltwater intrusion. Distinguishing the interactions of multiple environmental factors on soil CO_2 efflux could improve our understanding of the responses of the coastal wetland carbon cycle. In our simulated mesocosm systems, the interaction of waterlogging and salinity on $R_{s.\ ND}$ was significant throughout the growing season except in April, which might be ascribed to the notable changes in soil enzymatic activities and ionic concentrations (Table 1). The combined stresses of waterlogging and salinity hinder adventitious root formation of coastal vegetation, resulting in restricted O_2 transfer into the soil and inhibiting microbial and enzyme activities (Spalding and Hester, 2007). Combined treatments of waterlogging × salinity could also increase the concentrations of Na^+ and Cl^- in plant organs, thus impairing root function and suppressing root organ respiration (e.g., Barrett-Lennard, 2003). The inhibition of adventitious roots might not disappear with changes to hydrological conditions. Additionally, the combination of flooding and saltwater intrusion could increase sulfide concentrations in natural coastal wetlands because salinity-induced increases in the availability of sulfate could be reduced to sulfide under anaerobic conditions (Webb and Mendelssohn, 1996).

We found that the combined suppression of waterlogging and salinity on soil respiration was less during the drainage period (−5.5% in $R_{s.D}$), relative to the inundation period (−79.3% in $R_{s.ND}$). The reason is that drainage can quickly produce a moderately aerobic environment and alleviate the physiological stress of roots and microbes imposed by inundation and salinity. As summarized based on our study and the previous cases for coastal wetlands (Table S1), the controversial results on the effects of multiple environmental factors on soil CO_2 effluxes were mainly induced by the differences in hydrological manipulation, such as drainage or not, inundation duration, and salinity levels.

The Q_{10} values showed a range from a slight increase by 0.3% under the singular-salinity effect to a decline by −28.6% under the singular-

waterlogging effect (Table S1). In this study, the decreased amplitude of Q_{10} under interactive factors (17.3–27.3%) was similar to that under a singular waterlogging factor (13.4%–28.6%), which suggested that the water level might dominate the effects on the temperature sensitivity of soil CO_2 emissions in tidal marshes. To date, little work has explored the interactive effects of inundation and salinity on the Q_{10} of soil respiration from salt marshes. More studies involving the sensitivity of soil efflux to multiple hydrological factors are necessary for coastal ecosystems.

Regarding our experiment, the mesocosm system is a closed system that did not simulate the entrance of new vegetation and adapted microbial species to the system, as natural succession occurs in the environment. Therefore, it is important to further validate the effects of vegetation growth, microbial adaption, and subsequent enzyme activity on soil CO_2 efflux through a field simulation experiment following realistic tidal hydrology.

5. Conclusions

This mesocosm experiment highlighted the effects of independent and interactive hydrological projections of waterlogging and salinity increase on respective soil CO_2 efflux during inundation (nondrainage) and reaeration (drainage), which corresponds with tidal fluctuations in coastal ecosystems. Our results showed that waterlogging heavily suppressed $R_{s.ND}$, while sharply increasing $R_{s.D}$. Light salinity enhanced both $R_{s.ND}$ and $R_{s.D}$, whereas high salinity inhibited R_{soil}, regardless of drainage manipulation. Waterlogging strengthened the negative effects of salinity on $R_{s.ND}$ and offset the negative effects on $R_{s.D}$. The variations in R_{soil} under the hydrological treatments can be mainly attributed to the changes in root biomass; MBC; and activities of sucrase, cellulase and dehydrogenase, as well as ionic concentrations and oxidation-reduction potential. The Q_{10} values of soil respiration (only for $R_{s.D}$) showed a notable decline under the conditions of waterlogging and high salinity. The effect degree of coupled hydrological treatments on soil CO_2 efflux and its temperature sensitivity was similar to that under a single waterlogging factor before drainage but more strongly than that under a single hydrological factor after drainage. Our results indicated that the variations and response rates of soil CO_2 efflux under alternate water flooding and reaeration statuses, inundation durations, and salinity levels need to be considered to quantify the impacts of future sea level and salinity changes on greenhouse gas emissions from coastal marshes.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.104268.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was funded by the National Natural Science Foundation of China (41871088 and U2040204), the project “Coping with deltas in transition” within the Programme of Strategic Scientific Alliances between China and The Netherlands (2016YFE0133700), the National Key R&D Program of China (2017YFC0506001), and the “ECOLOGY+” initiative foundation of the East China Normal University. We thank two anonymous reviewers for their constructive comments.

References

Allison, S.D., Gartner, T.B., Holland, K., Weintraub, M., Sinsabaugh, R.L., 2007. Soil enzymes, linking proteomics and ecological process. In: Manual of Environmental Microbiology, 3rd edn. American Society of Microbiology Press, Washington, D.C., pp. 704–711

Ardón, M., Helton, A.M., Bernhardt, E.S., 2018. Salinity effects on greenhouse gas emissions from wetland soils are contingent upon hydrologic setting: a microcosm experiment. Biogeochemistry 140, 217–232.

Bao, S.D., 2000. Methods of Soil Agro-chemistry Analysis. Beijing, China (in Chinese).

Barrett-Lennard, E.G., 2003. The interaction between waterlogging and salinity in higher plants: causes, consequences and implications. Plant Soil 253, 35–54.

Bell, C.W., Acosta-Martinez, V., McIntyre, N.E., Cox, S., Tissue, D.T., Zak, J.C., 2009. Linking microbial community structure and function to seasonal differences in soil moisture and temperature in a Chihuahuan desert grassland. Microbial. Ecol. 58, 827–842.

Bond-Lamberty, B., Thomson, A., 2010. Temperature-associated increases in the global soil respiration record. Nature 464, 579–582.

Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.

Bradley, P.M., Morris, J.T., 1991. Relative importance of ion exclusion secretion and accumulation in Spartina alterniflora loisel. J. Exp. Bot. 42, 1525–1532.

Burchett, M.D., Clarke, C.J., Field, C.D., Pulkownik, A., 1989. Growth and respiration in two mangrove species at a range of salinities. Physiol. Plantarum 75, 299–303.

Casida Jr., L.E., Klein, D.A., Santoro, T., 1964. Soil dehydrogenase activity. Soil Sci. 98, 371–376.

Cavalieri, A.J., Huang, A.H., 1981. Accumulation of proline and glycinebetaine in Spartina alterniflora loisel in response to NaCl and nitrogen in the marsh. Oecologia 49, 224–228.

Chambers, L.G., Reddy, K.R., Osborne, T.Z., 2011. Short-term response of carbon cycling to salinity pulses in a freshwater wetland. Soil Sci. Soc. Am. J. 75, 2000–2007.

Chambers, L.G., Osborne, T.Z., Reddy, K.R., 2013. Effect of salinity-altering pulsing events on soil organic carbon loss along an intertidal wetland gradient: a laboratory experiment. Biogeochemistry 115, 363–383.

Chambers, L.G., Davis, S.E., Troxler, T., Boyer, J.N., Downey-Wall, A., Scinto, L.J., 2014. Biogeochemical effects of simulated sea level rise on carbon loss in an Everglades mangrove peat soil. Hydrobiologia 726, 195–211.

Chen, H., Zou, J., Cui, J., Nie, M., Fang, C., 2018. Wetland drying increases the temperature sensitivity of soil respiration. Soil Biol. Biochem. 120, 24–27.

Choi, Y., Wang, Y., 2004. Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. Glob. Biogeochem. Cycles 18, 133–147.

Courtney, A.J., Xu, J., Xu, Y., 2016. Responses of growth, antioxidants and gene expression in smooth cordgrass (Spartina alterniflora) to various levels of salinity. Plant Physiol. Biochem. 99, 162–170.

Doroski, A.A., Helton, A.M., Vadas, T.M., 2019. Greenhouse gas fluxes from coastal wetlands at the intersection of urban pollution and saltwater intrusion: a soil core experiment. Soil Biol. Biochem. 131, 44–53.

Ferguson, G., Gleeson, T., 2012. Vulnerability of coastal aquifers to groundwater use and climate change. Nat. Clim. Chang. 2, 342–345.

Frankeberger, W.T., Johanson, J.B., 1983. Method of measuring invertase activity in soils. Plant Soil 74, 301–311.

Han, G., Chu, X., Xing, Q., Li, D., Yu, J., Luo, Y., Wang, G., Miao, P., Rafique, R., 2015. Effects of episodic flooding on the net ecosystem CO2 exchange of a supratidal wetland in the yellow river delta. J. Geophys. Res-Biogeo. 120, 1506–1520.

Han, G., Sun, B., Chu, X., Xing, Q., Song, W., Xia, J., 2018. Precipitation events reduce soil respiration in a coastal wetland based on four-year continuous field measurements. Agric. For. Meteorol. 256, 292–303.

Happell, J.D., Chanton, J.P., 1993. Carbon remineralization in a North Florida swamp forest: effects of water level on the pathways and rates of soil organic matter decomposition. Global Biogeochem Cycles 7, 475–490.

Hayano, K., 1986. Cellulase complex in a tomato field soil: induction, localization and some properties. Soil Biol. Biochem. 18, 215–219.

Heinsch, F.A., Heilman, J.L., McInnes, K.J., Cobos, D.R., Zuberer, D.A., Roelke, D.L., 2004. Carbon dioxide exchange in a high marsh on the Texas Gulf Coast: effects of freshwater availability. Agric. For. Meteorol. 125, 159–172.

Helton, A.M., Ardón, M., Bernhardt, E.S., 2019. Hydrologic context alters greenhouse gas feedbacks of coastal wetland salinization. Ecosystems 22, 1108–1125.

Inglett, K.S., Inglett, P.W., Reddy, K.R., Osborne, T.Z., 2012. Temperature sensitivity of greenhouse gas production in wetland soils of different vegetation. Biogeochemistry 108, 77–90.

Kappen, H., 1913. The catalytic effect of the soil. Fühlings Landw Ztg 62, 377–392.

Kim, S.Y., Freeman, C., Lukac, M., Lee, S.H., Kim, S.D., Kang, H., 2020. Elevated CO2 and high salinity enhance the abundance of sulfate reducers in a salt marsh ecosystem. Appl. Soil Ecol. 147, 103386.

Krauss, K.W., Whitbeck, J.L., Howard, R.J., 2012. On the relative roles of hydrology, salinity, temperature, and root productivity in controlling soil respiration from coastal swamps (freshwater). Plant Soil 358, 265–274.

Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier Amsterdam, New York.

Li, S.H., Ge, Z.M., Xie, L.N., Chen, W., Yuan, L., Wang, D.Q., Li, X.Z., Zhang, L.Q., 2018a. Ecophysiological response of native and exotic salt marsh vegetation to waterlogging and salinity: implications for the effects of sea-level rise. Sci. Rep. 8, 1–13.

Li, Y., Wang, L., Zhang, W., Zhang, S., Wang, H., Fu, X., Le, Y., 2010. Variability of soil carbon sequestration capability and microbial activity of different types of salt marsh soils at Chongming Dongtan. Ecol. Eng. 36, 1754–1760.

Li, Y., Zhao, M., Li, F., 2018b. Soil respiration in typical plant communities in the wetland surrounding the high-salinity Ebinur Lake. Front. Earth Sci-Prc 12, 611–624.

Li, Y.L., Guo, H.Q., Ge, Z.M., Wang, D.Q., Liu, W.L., Xie, L.N., Li, S.H., Tan, L.S., Zhao, B., Li, X.Z., Tang, J.W., 2020. Sea-level rise will reduce net CO2 uptake in subtropical coastal marshes. Sci. Total Environ. 747, 141214.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8, 315–323.

Megonigal, J.P., Hines, M.E., Visscher, P.T., 2004. Anaerobic metabolism: linkages to trace gases and aerobic processes. In: Schlesinger, W.H. (Ed.), Biogeochemistry, Treatise on Geochemistry. Elsevier, Pergamon, Oxford, pp. 317–424.
Miller, W.D., Neubauer, S.C., Anderson, I.C., 2001. Effects of sea level induced disturbances on high salt marsh metabolism. Estuaries 24, 357–367.
Moffett, K.B., Wolf, A., Berry, J.A., Gorelick, S.M., 2010. Salt marsh–atmosphere exchange of energy, water vapor, and carbon dioxide: effects of tidal flooding and biophysical controls. Water Resour. Res. 46, W10525.
Morrissey, E.M., Gillespie, J.L., Morina, J.C., Franklin, R.B., 2014. Salinity affects microbial activity and soil organic matter content in tidal wetlands. Glob. Chang. Biol. 20, 1351–1362.
Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 59, 651–681.
Naidoo, G., McKee, K.L., Mendelssohn, I.A., 1992. Anatomical and metabolic responses to waterlogging and salinity in Spartina alterniflora and S. patens (Poaceae). Am. J. Bot. 79, 765–770.
Neubauer, S.C., 2013. Ecosystem responses of a tidal freshwater marsh experiencing saltwater intrusion and altered hydrology. Estuar. Coast 36, 491–507.
Neubauer, S.C., Franklin, R.B., Berrier, D.J., 2013. Saltwater intrusion into tidal freshwater marshes alters the biogeochemical processing of organic carbon. Biogeosciences 10, 8171–8183.
Nyman, J.A., DeLaune, R.D., 1991. CO2 emission and soil eh responses to different hydrological conditions in fresh, brackish, and saline marsh soils. Limnol. Oceanogr. 36, 1406–1414.
Pezeshki, S.R., DeLaune, R.D., 1993. Effects of soil hypoxia and salinity on gas exchange and growth of Spartina patens. Mar. Ecol. Prog. Ser. 96, 75–81.
Rath, K.M., Rousk, J., 2015. Salt effects on the soil microbial decomposer community and their role in organic carbon cycling: a review. Soil Biol. Biochem. 81, 108–123.
Rietz, D.N., Haynes, R.J., 2003. Effects of irrigation-induced salinity and sodicity on soil microbial activity. Soil Biol. Biochem. 35, 845–854.
Rustad, L.E., Huntington, T.G., Boone, R.D., 2000. Controls on soil respiration: implications for climate change. Biogeochemistry 48, 1–6.
Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J., GCTE-NEWS, 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.
Sasaki, A., Hagimori, Y., Nakatsubo, T., Hoshika, A., 2009. Tidal effects on the organic carbon mineralization rate under aerobic conditions in sediments of an intertidal estuary. Ecol. Res. 24, 723–729.
Shackle, V.J., Freeman, C., Reynolds, B., 2000. Carbon supply and the regulation of enzyme activity in constructed wetlands. Soil Biol. Biochem. 32, 1935–1940.
Spalding, E.A., Hester, M.W., 2007. Interactive effects of hydrology and salinity on oligohaline plant species productivity: implications of relative sea-level rise. Estuar Coast 30, 214–225.
Spivak, A.C., Sanderman, J., Bowen, J.L., Canuel, E.A., Hopkinson, C.S., 2019. Global-change controls on soil-carbon accumulation and loss in coastal vegetated ecosystems. Nat. Geosci. 12, 685–692.
van't Hoff, J.H., 1898. Lectures on Theoretical and Physical Chemistry. Part 1: Chemical Dynamics. (Translated by Lehfeldt, R. A.). Edward Arnold, London.
Tan, L., Ge, Z., Zhou, X., Li, S., Li, X., Tang, J., 2020. Conversion of coastal wetlands, riparian wetlands, and peatlands increases greenhouse gas emissions: a global meta-analysis. Glob. Chang. Biol. 26, 1638–1653.
Tripathi, S., Chakraborty, A., Chakrabarti, K., Bandyopadhyay, B.K., 2007. Enzyme activities and microbial biomass in coastal soils of India. Soil Biol. Biochem. 39, 2840–2848.
Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707.
Wang, F., Kroeger, K.D., Gonneea, M.E., Pohlman, J.W., Tang, J., 2019. Water salinity and inundation control soil carbon decomposition during salt marsh restoration: an incubation experiment. Ecol. Evol. 9, 1911–1921.
Wang, X., Lu, Q., 2006. Effect of waterlogged and aerobic incubation on enzyme activities in paddy soil. Pedosphere 16, 532–539.
Webb, E.C., Mendelssohn, I.A., 1996. Factors affecting vegetation dieback of an oligohaline marsh in coastal Louisiana: field manipulation of salinity and submergence. Am. J. Bot. 83, 1429–1434.
Weston, N.B., Dixon, R.E., Joye, S.B., 2006. Ramifications of increased salinity in tidal freshwater sediments: geochemistry and microbial pathways of organic matter mineralization. J. Geophys. Res-Biogeosci. 111 (G1).
Wilson, B.J., Servais, S., Charles, S.P., Davis, S.E., Gaiser, E.E., Kominoski, J.S., Jennifer, H.R., Troxler, T.G., 2018a. Declines in plant productivity drive carbon loss from brackish coastal wetland mesocosms exposed to saltwater intrusion. Estuar. Coasts 41, 2147–2158.
Wilson, B.J., Servais, S., Mazzei, V., Kominoski, J.S., Hu, M., Davis, S.E., Gaiser, E., Sklar, F., Bauman, L., Kelly, S., Madden, C., Richards, J., Rudnick, D., Stachelek, J., Troxler, T.G., 2018b. Salinity pulses interact with seasonal dry-down to increase ecosystem carbon loss in marshes of the Florida Everglades. Ecol. Appl. 28, 2092–2108.
Włodarczyk, T., Stępniewski, W., Brzezińska, M., 2002. Dehydrogenase activity, redox potential, and emissions of carbon dioxide and nitrous oxide from cambisols under flooding conditions. Biol. Fertil. Soils 36, 200–206.
Xie, L.N., Ge, Z.M., Li, Y.L., Li, S.H., Tan, L.S., Li, X.Z., 2020. Effects of waterlogging and increased salinity on microbial communities and extracellular enzyme activities in native and exotic marsh vegetation soils. Soil Sci. Soc. Am. J. 84, 82–98.
Zhong, Q., Du, Q., Gong, J., Zhang, C., Wang, K., 2013. Effects of in situ experimental air warming on the soil respiration in a coastal salt marsh reclaimed for agriculture. Plant Soil 371, 487–502.