Salinity affects topsoil organic carbon concentrations through regulating vegetation structure and productivity

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Key Points:

- Soil salinity, plant species and soil texture are key factors controlling topsoil organic carbon concentrations

- Soil salinity can affect topsoil organic carbon concentrations through regulating vegetation spatial structure and plant biomass production

- Further invasion of *Spartina alterniflora* will positively affect topsoil organic carbon concentrations in the Chongming Dongtan salt marsh

Abstract

Estuarine salt marshes have been recognized as one of the most efficient carbon sinks in the biosphere, with considerable potential for climate change mitigation. However, there are still uncertainties about the response of soil carbon stocks to enhanced soil salinization caused by accelerated sea-level rises and aggravated saltwater intrusion. We therefore conducted both field investigations in the Chongming Dongtan salt marsh of the Yangtze River Estuary, China, and manipulative experiments on marsh soils occupied respectively by the invasive *Spartina alterniflora*, and the native *Phragmites australis* and *Scirpus mariqueter*, to identify the effects of elevated soil salinity on top soil organic carbon (SOC) concentration. Our field data showed that SOC concentrations were significantly positively associated with soil salinity concentrations, annual net primary productivity and marsh surface elevation, but showed a significant negative relationship with median grain size. Compared with the two native species, *S. alterniflora* preferred more saline conditions and had a higher SOC concentration. Although raised flooding salinities (0–35 ppt) did not strongly affect SOC concentrations, elevated soil salinities significantly corresponded with low SOC concentrations and plant biomass in manipulative experiments. These findings indicated that soil salinity, plant species and soil texture were key factors controlling SOC concentrations in the studied salt marsh. Moreover, soil salinity could affect SOC concentrations through regulating vegetation spatial structure and plant biomass production. The further invasion of the *S. alterniflora* community will exert a positive influence on SOC concentrations in the Chongming Dongtan salt marsh.

Plain Language Summary

Estuarine salt marshes are sedimentary environments that are among the most productive ecosystems on earth, and can continuously sequester carbon through plant production and sedimentary processes. Although sea-level rises and saltwater intrusion may cause widespread soil salinization in estuarine ecosystems, its impact on top soil organic carbon (SOC) concentrations is highly uncertain. We therefore conducted field investigations that revealed the variation in SOC concentrations along a natural salinity gradient, and manipulative experiments that raised flooding salinities from freshwater (0 ppt) to seawater (35 ppt) to identify the independent impacts of soil salinity on SOC concentrations. Our findings indicated that soil salinity was an important factor controlling SOC concentrations through indirectly regulating vegetation spatial structure and plant biomass production.

1 Introduction

Vegetated coastal ecosystems have inspired widespread interest due to their long-term sequestration of organic carbon, which hold considerable potential for climate change mitigation (Kirwan & Mudd, 2012; Mcleod et al., 2011), especially for buffering the increasing atmospheric carbon dioxide (CO_2) concentrations as well as rising sea-levels (Mueller et al., 2016; Reef et al., 2017). Referred to as important "blue carbon" sinks, salt marshes occupy less than 0.2% of the ocean surface, but are globally estimated to bury 4.8–87.3 Tg carbon yr^{-1} in the soil and so rank among the largest carbon reservoirs in the biosphere (Cai, 2011; Duarte et al., 2013). Besides the value in sequestering carbon, their remarkable capacity for coastal protection, land accretion and biodiversity conservation enable salt marshes to be some of the most valuable ecosystems on earth (Luisetti et al., 2014).

Recent research has highlighted that organic matter production generally exceeds decay in anaerobic saline marsh soils, thereby leading to significant accumulation of soil organic carbon (SOC), and contributing to the vertical accretion of marsh surface elevation

over time (Baustian et al., 2012; Kirwan et al., 2016). The SOC inputs via high primary productivity (autochthonous) and effective suspended particles trapping (allochthonous) during tidal inundation greatly enhance carbon burial rates of salt marshes (Morris et al., 2013), whose contributions to the SOC pool are highly variable in space and time (Morris et al., 2016). Strategies for enhancing SOC storage also include decreasing soil respiration, volatilization and leaching of organic compounds, which represent SOC outputs (De Deyn et al., 2008). In addition, highly productive salt marsh plants are likely to export significant amounts of organic detritus as particulate organic carbon and dissolved organic carbon to adjacent tidal creeks, bays and shelf or even the open ocean to greatly influence SOC storage in marsh soils (Barrón & Duarte, 2015).

The persistence of SOC in marsh soils has traditionally been explained as a combination of recalcitrance properties and stabilization processes, which lead to formation of complex chemical compounds (Lorenz et al., 2007; Zhao et al., 2012). However, recent conceptual advances and experimental evidence challenge this view, insisting that SOC persistence is an emergent ecosystem property rather than the result of intrinsic chemical properties (Dungait et al., 2012; Schmidt et al., 2011). For instance, Kleber et al. (2011) found that the old and stable soil organic matter was not necessarily chemically recalcitrant; and Caruso et al. (2018) demonstrated that environmental and ecological factors (e.g., spatially structured microbial activities), rather than molecular recalcitrance, were the predominant controls in determining carbon residence times. As a consequence, long-term viability of salt marshes and their carbon sequestration depend greatly on the balance between organic matter production and decay responses to environmental changes (Kirwan & Mudd, 2012; Stagg et al., 2017).

Soil salinity variation across spatial and temporal scales is generally regarded as a key feature of salt marshes, which is greatly attributed to the combined influence of tidal inundation, freshwater input, precipitation, evapotranspiration and biological action (Ardón et al., 2013; Shen et al., 2015). Rising sea-levels, decreased river discharges and frequent storm surges derived from global climate change and intense anthropogenic activities may result in the increasing frequency, severity and spatial extent of saltwater intrusion, thus causing excessive accumulation of soil salt (Williams & Rosenheim, 2015; Zhou et al., 2017). One of the inevitable outcomes from elevated soil salinity in salt marshes is the significant impact on SOC sequestration by its influence on plant productivity and species composition (Engels et al., 2011; Tang et al., 2014), microbial biomass and community structure (Hu et al., 2014; Rath & Rousk, 2015), extracellular enzyme activity (Morrissey et al., 2014; Saviozzi et al., 2011) and SOC decomposition and mineralization (Craft, 2007; Neubauer et al., 2013).

Although the feedback of SOC concentrations to increased surface/pore water salinity and soil salinity has been studied for decades from different perspectives, there is no consensus regarding the effects of salinity on SOC concentrations. Some studies suggested that elevated salinities can decrease SOC concentrations (Hansen et al., 2017; Więski et al., 2010), some reported increases in SOC concentrations and inhibition of decomposition processes (Hu et al., 2012; Stagg et al., 2017), and others indicated no significant impact on SOC accumulation (Spalding & Hester, 2007). In this context, it is imperative to identify the relationship between soil salinities and SOC concentrations, especially under the accelerated sea-level rises and aggravated saltwater intrusion scenarios. We therefore conducted both field investigations and manipulative experiments to study the variation in SOC concentrations along a salinity gradient. Our objectives were (1) to determine the relationship between SOC concentrations and soil salinity concentrations in the Chongming Dongtan salt marsh of the Yangtze River Estuary, China, (2) to identify the independent impacts of soil

salinity on SOC concentrations in flooding salinity experiments (0–35 ppt) and (3) to assess how future soil salinization may influence SOC concentrations in the studied salt marsh soils.

2 Materials and Methods

2.1 Study sites

The Chongming Dongtan salt marsh (31°25′–31°38′ N, 121°50′–122°05′ E) is located at the eastern part of the Yangtze River Estuary, China (Figure 1), and covers 242 km^2 above 0 m isobaths based on the local Wusong bathymetric benchmark, with elevations less than 2.0 m characterized by bare mudflats, and elevations of 2.0–4.2 m typically dominated by the invasive species *Spartina alterniflora* and two native species *Phragmites australis* and *Scirpus mariqueter* (Ge et al., 2016a). Field investigations were conducted in this salt marsh (Figure 1) and GPS coordinates of the sampling locations are provided in Table S1 in the Supplement. We also transplanted seedlings of *S. alterniflora*, *P. australis* and *S. mariqueter* and transferred topsoil (0–30 cm) from the salt marsh, for use in manipulated pot experiments in the open space near the Chongming Dongtan wetland park (31°31′ N, 121°56′ E) (Figure 1).

The Chongming Dongtan salt marsh has an eastern Asian monsoon climate with an average annual temperature of 15.3°C, average annual precipitation of 1022 mm and average humidity of 82% (Ge et al., 2016b). The salt marsh experiences irregular and semi-diurnal tidal cycles, with maximum and mean tide ranges of 4.62–5.95 and 1.96–3.08 m, respectively (Ge et al., 2016b), and varies in soil pore water salinities from 4 to 18 ppt (Tang et al., 2014). The sea-level in the Yangtze River Estuary, China (610-032 Lüsi Station) rose at a rate of 5.33 mm yr^{-1} during 1961–2016 (NOAA, 2019), which is higher than the mean rate of global sea-level rise of 3.2 mm yr^{-1} (1993–2010) (IPCC, 2013). As a consequence of saltwater intrusion in 2018, there was a much greater increase in the area that suffered from soil salinization in Chongming Island compared with 2017 (Ministry of Natural Resources of the People's Republic of China, 2019).

Invasive *S. alterniflora*, an exotic C4 grass native to North America, was intentionally introduced to China in 1979 for erosion control and dike protection, because this species could act as an "environmental engineer" by accumulating sediments and protecting beaches (Li et al., 2009). Since its initial appearance on the Chongming Dongtan salt marsh during the 1990s, *S. alterniflora* has gradually colonized the bare mudflats and invaded the habitat historically occupied by native *P. australis* and *S. mariqueter* communities (Li et al., 2014; Tang et al., 2014). The *S. alterniflora* was therefore identified as a coastal invasive plant by the State Environmental Protection Administration of China in 2003 (Li et al., 2009; Wang et al., 2018). The distribution area of *S. alterniflora* reached about 1500 ha in the Chongming Dongtan salt marsh, and more than 6000 ha in the Yangtze River Estuary in 2012 (Ge et al., 2015).

2.2 Field sampling and measurements

In early March 2013, before plants sprouted, we randomly selected 16 transects with 70 sites from the northern to southern parts of the Chongming Dongtan salt marsh, to sample undisturbed topsoil cores (0–30 cm), which were mainly distributed at high, middle and low elevations of vegetated salt marsh (Figure 1). At each site, five topsoil cores (0–30 cm) were collected within a 10 m × 10 m plot, and mixed evenly to get a subsample, without discriminating the sediment depth. The soil subsample was then stored in a resealable bag in the field and transported to the laboratory at 4°C. Elevation (m) was determined for the center of each site with the real time kinematic survey (Trimble R8 Receiver and Trimble TSC3

Controller, Trimble Navigation Ltd, Sunnyvale, USA), and expressed in the local Wusong Vertical Datum. Soil bulk density (g cm^{-3}) samples were also collected at the topsoil surface (0–10 cm) for each site using a volume of 100-cm^3 stainless steel cylinder and weighed after oven-drying at 40°C for 72 hours.

Before analysis of soil subsamples (n = 70) in the laboratory, macroscopic root residues were removed manually using tweezers. These soil subsamples were then dried at 40°C for 72 hours to a constant weight and sieved through a 2-mm screen. One set of subsamples was subjected to acid washing with 1 mol L^{-1} HCl and shaken for 24 hours prior to centrifugation, then rinsed with Milli-Q (Gradient, Merck Millipore, Darmstadt, Germany) water and redried several times to remove carbonates. An elemental analyzer (Vario Macro, Elementar Analysensysteme GmbH, Hanau, Germany) was used to measure SOC concentration (g kg^{-1}). SOC stock (kg m^{-2}) in the 0–30 cm soil depth at each site was then estimated using equation (1), according to Yang (2019):

$$SOC\ stock = SOC\ concentration \times BD \times D \times \frac{(1-G)}{100} \tag{1}$$

where BD, D and G represent the soil bulk density (g cm^{-3}), soil depth (cm) and volume percentage of the gravel content (%), respectively. Here G is negligible.

Another set of subsamples, without acid washing, was prepared to measure the median grain size (μm) using a laser diffraction particle size analyzer (LS-100Q, Beckman Coulter Inc, CA, USA) and soil electrical conductivity (μS cm^{-1}) using a digital conductivity meter (DDS-11A, REX Instrument Factory, Shanghai, China). Soil salinity concentrations of dry soil (g kg^{-1}) were calculated as follows:

$$y = \frac{(0.05x + 0.011)}{20} \times 1000 \tag{2}$$

where y and x represent the soil salinity concentration and soil electrical conductivity, respectively. The spatial variability of marsh surface elevation, soil salinity concentration, SOC concentration, SOC stock and median grain size were produced based on the Kriging method in ArcGIS10.2.

Net primary productivity (NPP) in the Chongming Dongtan salt marsh during 2013 was estimated using the Carnegie-Ames-Stanford Approach (CASA) model (Potter et al., 1993), as expressed in equation (3):

$$NPP(x,t) = PAR(x,t) \times FPAR(x,t) \times \varepsilon(x,t) \tag{3}$$

where $NPP(x,t)$ stands for NPP of pixel x in month t, $PAR(x,t)$ is the photosynthetically active radiation (MJ m^{-2} month^{-1}) of pixel x in month t, and expressed as half of the total solar radiation; $FPAR(x,t)$ is the fraction of photosynthetic active radiation absorbed by vegetation (no unit); and $\varepsilon(x,t)$ represents the actual light utilization efficiency (g C MJ^{-1}) of pixel x in month t. We calculated $FPAR(x,t)$ by the following equations (4)–(7):

$$FPAR(x,t) = \frac{FPAR(x,t)_{NDVI} + FPAR(x,t)_{SRVI}}{2} \tag{4}$$

$$FPAR(x,t)_{NDVI} = \frac{[NDVI(x,t) - NDVI_{i,min}] \times (FPAR_{max} - FPAR_{min})}{NDVI_{i,max} - NDVI_{i,min}} + FPAR_{min} \tag{5}$$

$$FPAR(x,t)_{SRVI} = \frac{[SRVI(x,t) - SRVI_{i,min}] \times (FPAR_{max} - FPAR_{min})}{SRVI_{i,max} - SRVI_{i,min}} + FPAR_{min} \tag{6}$$

$$SRVI(x,t) = \frac{1 + NDVI(x,t)}{1 - NDVI(x,t)} \tag{7}$$

where $FPAR_{min}$ (= 0.001) and $FPAR_{max}$ (= 0.95) are independent parameters; $NDVI_{i,max}$ and $NDVI_{i,min}$ are the 95th and 5th percentile of the NDVI values, respectively; and $SRVI_{i,max}$ and $SRVI_{i,min}$ are the 95th and 5th percentile of the SRVI values, respectively. The $\varepsilon(x, t)$ is calculated as the product of maximum light use efficiency and its temperature and moisture stressors, as expressed in equations (8)–(11):

$$\varepsilon(x,t) = T_{\varepsilon1}(x,t) \times T_{\varepsilon2}(x,t) \times W_\varepsilon(x,t) \times \varepsilon_{max}(x,t) \tag{8}$$

$$T_{\varepsilon1}(x,t) = 0.8 + 0.02 \times T_{opt}(x,t) - 0.0005 \times \left[T_{opt}(x,t)\right]^2 \tag{9}$$

$$T_{\varepsilon2}(x,t) = \frac{1.1814}{\{1+exp[0.2(T_{opt}(x,t)-10-T(x,t))]\}} \times \frac{1}{\{1+exp[0.3(-T_{opt}(x,t))-10+T(x,t)]\}} \tag{10}$$

$$W_\varepsilon(x,t) = 0.5 + 0.5 \times EET(x,t)/PET(x,t) \tag{11}$$

where $T_{\varepsilon1}(x, t)$ and $T_{\varepsilon2}(x, t)$ are the temperature stress coefficients indicating the stress of low and high temperature on light use efficiency, respectively (°C); $W_\varepsilon(x, t)$ represents the moisture stress coefficient (no unit); $\varepsilon_{max}(x, t)$ is the maximal light use efficiency of vegetation in ideal conditions (g C MJ^{-1}); $T_{opt}(x, t)$ is defined as the mean temperature (°C) of month t when NDVI reaches its maximum annual amount; $T(x, t)$ is the mean temperature of a certain month t (°C); and $EET(x, t)$ and $PET(x, t)$ are actual and potential evapotranspiration in the region (mm), respectively.

We obtained four cloud-free Landsat-8 images at 30-m spatial resolution (25 May 2013, 29 August 2013, 17 November 2013 and 21 February 2014) from Geospatial Data Cloud (http://www.gscloud.cn/), and interpreted the vegetation types (Figure 1) according to the ground truth investigation. Monthly mean temperature, precipitation, evaporation and solar radiation in 2013 and 2014 were acquired from the Shanghai Statistical Yearbook (http://www.stats-sh.gov.cn/) and the National Meteorological Information Center (http://data.cma.cn/site/). The maximal light utilization efficiencies of the three studied species were cited from Chi et al. (2018), Jiang et al. (2009) and Mei and Zhang (2007), respectively. We then calculated the NPP$_{May}$, NPP$_{August}$, NPP$_{November}$ and NPP$_{February}$ to roughly represent the mean NPP in spring, summer, autumn and winter. The annual NPP (g C m^{-2} yr^{-1}) was finally estimated as the arithmetic mean value of above NPP values in four seasons. The processing of the images were performed in ENVI 5.2 and ArcGIS 10.2.

2.3 Manipulative experiments

We established artificial flooding salinity gradients (0, 5, 10, 15, 25 and 35 ppt) in a series of pot experiments to investigate the effects of flooding salinity on SOC concentrations for three different marsh species (*S. alterniflora*, *P. australis* and *S. mariqueter*) in 2014 (April–October) (Figure 2). The seedlings and topsoil (0–30 cm) for these species were transplanted from the Chongming Dongtan salt marsh (Figure 1) to plastic pots (height = 30 cm, diameter$_{top}$ = 32 cm and diameter$_{bottom}$ = 26 cm) in early April, with the number of plants per pot reaching 44 ± 6 (mean ± SD, n = 18), 11 ± 2 (n = 18) and 301 ± 33 (n = 18), respectively. Seedlings of *S. alterniflora* and *P. australis* (about 20–30 cm) were then cut down to the soil surface to prevent the death of individuals, whereas seedlings of *S. mariqueter* (< 5 cm) were not trimmed. All pots were maintained under common garden conditions and watered every 2 days with prefiltered canal water (2–5 ppt, ~200 mL), allowing plants to acclimate before treatments were initiated.

Flooding salinity treatments were conducted during July–October for *S. alterniflora* and *P. australis*, but treatments for *S. mariqueter* ended 1 month earlier (July–September) owing to the early senescence of this species. Each treatment consisted of two transparent plastic tanks (length = 97 cm, width = 76 cm and height = 70 cm): tank A with three pots of

the same species as three replicates, and tank B with salt water (Figure 2). Tidal regimes, including flooding depth and frequency that were not of interest in this study, were uniformly maintained at 20 cm and every 3 days. The irregular semi-diurnal tide cycle was simplified and conducted regularly twice a day in each treatment during 05:00–09:00 and 17:00–21:00 h. The ebb and flood of tides were accomplished using pumps (caliber 25 mm, 750 W and flow velocity 60 L min^{-1}), and the time spent on such processes was not included in the 4 hours of tidal inundation.

The freshwater (0 ppt) collected from the clean tap water was only passed through the tidal pumping system once. The intended salt water concentrations (5–35 ppt) were obtained respectively by mixing commercially available sea salt (Jinchuangxing Industrial Co. Ltd, Shenzhen, China) with prefiltered canal water (2–5 ppt) in different proportions, and renewed every 2 weeks. Flooding salinities were checked prior to each execution, using an automatic compensation salinity refractometer (Master-S/Millα, Cat. No. 2491, ATAGO, Tokyo, Japan), and corrected to the intended salinities by adding water or sea salt. Before and after the flooding salinity experiments, topsoil samples (0–10 cm) were collected from each pot to measure soil salinity and SOC concentrations. We also harvested the aboveground and belowground parts of plants to estimate the final biomass as g m^{-2}.

2.4 Statistical analyses

Pearson's correlation analysis was used to test linear relationships between different parameters both in field conditions and in manipulative experiments. To test whether soil salinity and SOC concentrations significantly differed among the six flooding salinity gradients for three different species, a one-way analysis of variance was used, after checking for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test) with a level of significance of $p < 0.05$. If the assumptions for statistical analyses were not met, data transformation was then carried out to solve this problem. All statistical analyses were completed in SPSS 22.0 (IBM, Chicago, IL, USA), and figure plots were generated using Origin Pro 9.0 (OriginLab, Northampton, MA, USA).

3 Results

Marsh surface elevation, soil salinity concentrations, and SOC concentrations and stocks were all higher in the northern part than in the southern part of the Chongming Dongtan salt marsh (Figures 3a–3d). In contrast, median grain size was completely opposite (Figure 3e), which was significantly negatively correlated with marsh surface elevation along a low-to-high marsh gradient ($r = -0.625$, $p < 0.001$). The annual NPP exhibited distinct spatial variability that was attributed to dramatic changes in vegetation types, where the *S. alterniflora* community was mainly distributed in the northern part of the Chongming Dongtan salt marsh, and the *P. australis* and *S. mariqueter* communities inhabited the middle and southern part (Figures 1 and 3f).

Interestingly, SOC concentrations and stocks in the Chongming Dongtan salt marsh were significantly positively associated with soil salinity concentrations and annual NPP (Figures 4a–4d, with detailed data provided in Table S1). We also found that SOC concentrations were significantly negatively correlated with median grain size (Figure 4e, Table S1), but SOC stocks showed no significant relationship with median grain size (Figure 4f, Table S1). These findings suggested that soil salinity concentrations, plant primary productivity and median grain size were key factors controlling SOC concentrations in the studied marsh. There was a significant positive relationship between SOC concentrations and marsh surface elevation (Figure 4g, Table S1). However, no obvious relationship was observed between annual NPP and soil salinity concentrations (Figure 4h, Table S1),

indicating that plant species was a more important control on the annual NPP compared to soil salinity concentrations.

As shown in Table 1, marsh surface elevations did not differ among the three species in the Chongming Dongtan salt marsh, which might be attributed to the wider elevation ranges for *S. alterniflora* than for *P. australis* and *S. mariqueter* (coefficients of variation were 12.5%, 2.6% and 7.9%, respectively). The highest soil salinity concentrations, and SOC concentrations and stocks were in the *S. alterniflora* sites, followed by the *P. australis* and *S. mariqueter* sites (Table 1). The *S. mariqueter* had the highest median grain size compared to the other two species (Table 1). The annual NPP for *S. alterniflora* and *P. australis* were significantly higher than for *S. mariqueter* (Table 1). These observations showed the salinity preferences of marsh species and interspecific differences in annual NPP and SOC concentrations and stocks.

Before implementing the flooding salinity treatments, no significant differences were detected either in soil salinity or SOC concentrations for *S. alterniflora*, *P. australis* and *S. mariqueter* pots (Figures 5a and 5b, with detailed data provided in Table S2). Manipulative experiments, which last for 3–4 months, revealed that flooding salinity treatments from freshwater (0 ppt) to seawater (35 ppt) significantly promoted the accumulation of soil salinity for the three species (Figure 5c, Table S2). Raised flooding salinities also significantly lowered SOC concentrations for invasive *S. alterniflora*, but showed gradual and limited decreases in SOC concentrations for native *P. australis* and *S. mariqueter* (Figure 5d, Table S2).

In contrast to the field sampling, which showed a significant positive relationship between SOC concentrations and soil salinity concentrations (Figure 4a), manipulative experiments indicated that elevated soil salinities caused by increasing flooding water salinity significantly corresponded with low SOC concentrations (Figure 6a). Our observations suggested that in both field and pot experiments, higher plant biomass led to higher SOC concentrations (Figures 4c and 6b), revealing that the autochthonous organic carbon input from marsh species was a direct factor controlling the difference in sedimentary organic carbon stocks. There was a significant negative relationship between plant biomass and soil salinity concentrations in manipulative experiments (Figure 6c), whereas plant species played a more important role than soil salinity concentration in regulating the annual NPP in field investigations (Figure 4h).

4 Discussion

4.1 Implementing field investigations and manipulative experiments

Field sampling is a very useful methodology to characterize SOC stocks in estuarine salt marshes and identify the factors influencing SOC concentrations, and was extensively adopted in previous studies (Hansen et al., 2017; Van de Broek et al., 2016). It is important to note that the spatial variability of SOC concentrations in field conditions is likely to be a consequence of numerous abiotic and biotic factors, as well as their interactions, which often integrates all components (e.g., plants, microbes, soil fauna and predators) and cascades through a broad range of ecosystem processes over relatively long-term scales. In contrast, manipulative experiments are typically carried out under comparatively homogeneous conditions to isolate the effect of other variables (e.g., tidal inundation and substrate composition), and provide insight into the responses over relatively short-term scales, or even exclude portions of the ecosystem (e.g., macrobenthos). In the present study, we conducted six flooding salinity treatments for 3–4 months and investigated the independent impacts of

elevated salinity on SOC concentrations, which was an important complement to traditional field investigations.

More specifically, there were several noteworthy differences between the field investigations and manipulative experiments. First, manipulative experiments minimized the influence of other environmental stresses (e.g., tidal inundation), which usually significantly co-varied with salinity in many previous studies (Engels et al., 2011; Kirwan et al., 2013). Second, the effect of interspecific interactions was not addressed in manipulative experiments by allowing only one species to grow in each treatment pot. Third, allochthonous suspended sediment particles did not contribute to SOC concentrations in manipulative experiments because the artificial seawater was prefiltered and equally added. Because some field investigations (Hansen et al., 2017; Van de Broek et al., 2016) have analyzed variations in SOC stocks that derived from both allochthonous and autochthonous inputs along an estuarine salinity gradient, this manipulative experiments attempted to pinpoint the independent impacts of salinity on SOC concentrations for three different species, and neglected the contribution of allochthonous organic carbon inputs, which provided an initial assessment to better explain the complex combined effects of numerous abiotic and biotic factors on SOC sequestration.

4.2 Factors influencing SOC concentrations in salt marshes

4.2.1 Vegetation type

The type of vegetation present in a salt marsh is an important factor contributing to SOC stocks, as it is well-known that SOC mostly originates from decaying aboveground and belowground plant tissues (Cotrufo et al., 2013; De Deyn et al., 2008), and living plants can also regulate decomposition processes by releasing labile organic carbon compounds (e.g., root exudates) to stimulate soil microbial activity (Farrar et al., 2003; Haichar et al., 2014), and by altering soil abiotic conditions (Ward et al., 2015). We found that the annual NPP was significantly positively associated with SOC concentrations in the Chongming Dongtan salt marsh (Figure 4c), which showed a similar pattern to the significant positive relationship between plant biomass and SOC concentration in manipulative experiments (Figure 6b). These results were consistent with prior work by Yang et al. (2013), who observed significant positive relationships between aboveground biomass, root biomass and SOC concentrations in the 0–30 cm soil layer. Thus, an increase in plant biomass probably resulted in more plant-derived organic carbon inputs and, therefore, more SOC accumulation.

In the investigated marsh soils, the annual NPPs for *S. alterniflora* and *P. australis* were nearly 2.5 times greater than for *S. mariqueter*, and their SOC concentrations were also significantly higher than for *S. mariqueter* (Table 1). This tendency was in agreement with studies by Li et al. (2014), who documented that replacement of *S. mariqueter* by *S. alterniflora* and *P. australis* communities might increase SOC sequestration by 4–5 fold in salt marshes of the Yangtze River Estuary, China; and by Yang et al. (2013), who reported that invasion of *S. alterniflora* significantly increased plant biomass and SOC compared to *Suaeda salsa* and *P. australis* communities in the Jiangsu coastal wetland, China. However, Van de Broek et al. (2016) found that variations in SOC stocks both along the salinity gradient of the Scheldt Estuary (Belgium and the Netherlands) and between old and young marshes at a given salinity level could not be explained by variations in plant biomass production. Obviously, the vegetation types in the Scheldt Estuary differ from those in our study, and the specific contribution of vegetation types would be differentiated rather than consistent across regions, because SOC sequestration combines the complex effects of numerous abiotic and biotic factors.

4.2.2 Soil salinity

The Chongming Dongtan salt marsh is characterized by a distinct soil salinity gradient (1.2–15.6 g kg^{-1}) (Figure 3b), and it is likely that salinity is another direct factor controlling the spatial variability of SOC concentrations, because there was a significant positive relationship between soil salinity and SOC concentrations (Figure 4a). Recent studies also revealed that salinity is one of the most important factors determining the spatial variability in abundance of marsh species (Medeiros et al., 2013; Tang et al., 2014), which directly lead to the spatial difference of plant-derived organic carbon inputs. For example, the invasive *S. alterniflora* community preferred the highest soil salt conditions, followed by native *P. australis* and then *S. mariqueter* communities in the Chongming Dongtan salt marsh (Table 1). Because *S. alterniflora* has shown higher salt tolerance (Xue et al., 2018a), stronger competitive ability (Medeiros et al., 2013) and greater plant biomass (Xue et al., 2018b) than *P. australis* and *S. mariqueter*, it has extensively colonized the northern part of the Chongming Dongtan salt marsh (Figure 1), and gradually invaded the habitat historically occupied by the native species (Li et al., 2009), resulting in the relatively high plant productivity and SOC concentrations even in high soil salinity areas (Figures 3b, 3c and 3f).

Raised flooding salinity treatments (0–35 ppt) during 3–4 months had a slight influence on SOC concentrations for *S. alterniflora*, *P. australis* and *S. mariqueter* (Figure 5d). We concluded that SOC sequestration was typically a very slow process, and the short-term simulation of elevated salinity associated with sea-level rises and saltwater intrusion may not be enough to significantly affect SOC concentrations, especially without the active contribution of allochthonous organic carbon inputs controlled by the tidal advection of suspended sediments. However, there was a significant negative relationship between soil salinity concentration and plant biomass in manipulative experiments (Figure 6c), which was in accordance with previous studies (Tang et al., 2014; Xue et al., 2018b) that reported the inhibitory effects of soil salinity on biomass accumulation for *S. alterniflora*, *P. australis* and *S. mariqueter*. Elevated soil salinities (1.4–8.2 g kg^{-1}) caused by increasing flooding salinities also significantly corresponded with low SOC concentrations in manipulative experiments (Figure 6a). Taken together, these observations indicated that salinity was a critical factor in controlling SOC concentrations not only by regulating vegetation spatial structure, but also by altering plant biomass production to indirectly affect plant-derived carbon inputs and SOC concentrations.

4.2.3 Soil texture

Soil texture has been reported to affect SOC stocks in coastal salt marshes (Bai et al., 2016; Yang, 2019), mainly by two ways (Yang et al., 2008): first, increasing clay and silt contents reduces microbial decomposition via stabilizing the SOC and decreasing carbon leaching, thus leading to accumulation of SOC; and second, increasing clay and silt contents stimulates plant production by increasing the water holding capacity, thereby increasing carbon inputs to soil. Our results also highlighted the importance of soil texture in controlling SOC concentrations, as indicated by the significant negative relationship between SOC concentrations and median grain size (Figure 4e), which could at least partly explain the spatial variability of SOC concentrations in the Chongming Dongtan salt marsh. Sediments deposited at higher marsh elevations had a smaller grain size and higher SOC concentrations compared to lower elevations (Figures 3a, 3c and 3e). Consequently, smaller-sized clayey sediments might be beneficial for the carbon sequestration of estuarine salt marshes.

4.3 Implications and future considerations

As global sea-level is predicted to continue to rise during the 21st century (IPCC, 2013), soil salinization in estuarine salt marshes may be expected to be further aggravated by progressive saltwater intrusion (Alizad et al., 2016; Zhou et al., 2017). Previous studies confirmed that elevated salinity will facilitate the spread of invasive *S. alterniflora* in salt marshes of the Yangtze River Estuary (Tang et al., 2014; Xue et al., 2018a). We therefore proposed that further invasion of the *S. alterniflora* community ascribed to aggravated soil salinization might exert a positive influence on SOC concentrations and stocks in the Chongming Dongtan salt marsh, because *S. alterniflora* prefers more saline conditions and has higher SOC concentration and stock than native *P. australis* and *S. mariqueter* communities (Table 1). However, we could not assume that *S. alterniflora* invasion was conducive to increased SOC stock, as another study found that *S. alterniflora* encroachment into mangrove shrubs decreased SOC storage in China's tropical coastal wetlands, owing to the lower aboveground biomass of *S. alterniflora* than native mangrove communities (Wang et al., 2018).

We recognize that the above implication might be site-specific, and we need to explore SOC dynamics and associated environmental changes in coastal ecosystems considering that the large-scale invasion of *S. alterniflora* is ongoing in China. In addition, accumulation of SOC in natural salt marshes requires a positive imbalance between carbon inputs and outputs (De Deyn et al., 2008; Kirwan et al., 2013). It is thus important to identify not only how soil salinity affects the amount of organic matter entering the soil by altering the plant community structure and productivity, but also how it affects carbon decomposition and mineralization, especially when there are different opinions about the responses of CO_2 and CH_4 emissions to elevated salinity gradients (Chambers et al., 2011; Wilson et al., 2015). Our current understanding is still insufficient to quantitatively assess how SOC concentrations in the salt marsh environment may change in future scenarios of sea-level rise and saltwater intrusion. Further research is critically and continuously required to analyze the effects of global climate change on carbon pools, cycles and fluxes in estuarine salt marshes.

5 Conclusions

This study provided insight into the potential consequences of sea-level rises and saltwater intrusion in estuarine salt marshes by investigating the impact of increased soil salinity on SOC concentrations via field investigations and manipulative experiments. Our field sampling revealed that SOC concentrations were significantly positively correlated with soil salinity concentrations, annual NPP and marsh surface elevation, and showed a significant negative relationship with median grain size. The invasive *S. alterniflora* community preferred more saline conditions and had a higher SOC concentration than native *P. australis* and *S. mariqueter* communities. Because raised flooding salinities from 0 to 35 ppt did not strongly affect SOC concentrations, we suggest that the accelerated sea-level rises and aggravated saltwater intrusion would not induce a dramatic change in SOC concentrations over relatively short-time scales (i.e., 3–4 months). However, elevated soil salinities significantly corresponded with low SOC concentrations and plant biomass in manipulative experiments. In sum, these observations indicated that soil salinity, vegetation type and soil texture were all important factors in controlling SOC concentrations. Soil salinity could affect SOC concentrations through regulating vegetation spatial structure and plant biomass production. The further invasion of *S. alterniflora* ascribed to soil salinization would exert a positive influence on SOC concentrations in the Chongming Dongtan salt marsh.

Acknowledgments

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Table 1

Differences in General Characteristics for Three Major Species in the Chongming Dongtan Salt Marsh of the Yangtze River Estuary, China

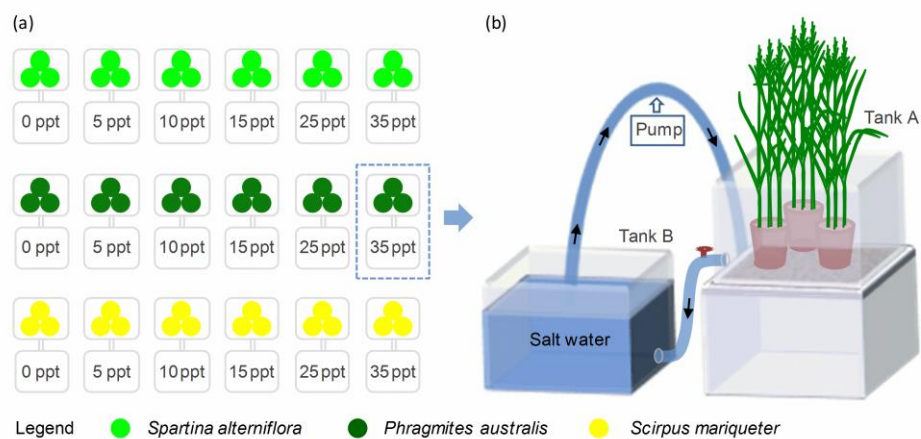| Marsh species	Marsh surface elevation	Soil salinity concentration	SOC concentration	SOC stock	Median grain size	NPP
	(m)	(g kg^{-1})	(g kg^{-1})	(kg m^{-2})	(μm)	(g C m^{-2} yr^{-1})
Spartina alterniflora	4.0 ± 0.5^{ns}	7.5 ± 3.2^{a}	8.8 ± 2.4^{a}	2.5 ± 0.8^{a}	13.5 ± 7.4^{b}	957.9 ± 95.0^{a}
Phragmites australis	3.8 ± 0.1^{ns}	3.5 ± 1.6^{b}	5.7 ± 1.0^{b}	2.0 ± 0.3^{b}	16.2 ± 3.7^{b}	906.1 ± 105.5^{a}
Scirpus mariqueter	3.8 ± 0.3^{ns}	1.7 ± 0.3^{c}	4.7 ± 1.4^{c}	1.8 ± 0.5^{b}	26.7 ± 8.2^{a}	390.9 ± 42.3^{b}

Note. SOC = Soil organic carbon; NPP = Net primary productivity.

Standard deviations are calculated based on 39, 22 and 9 replicates for *Spartina alterniflora*, *Phragmites australis* and *Scirpus mariqueter*, respectively.

Different letters indicate significant differences ($p < 0.05$) among marsh species of the same group according to the Least Significant Difference test; "ns" means there is no significant difference among marsh species.
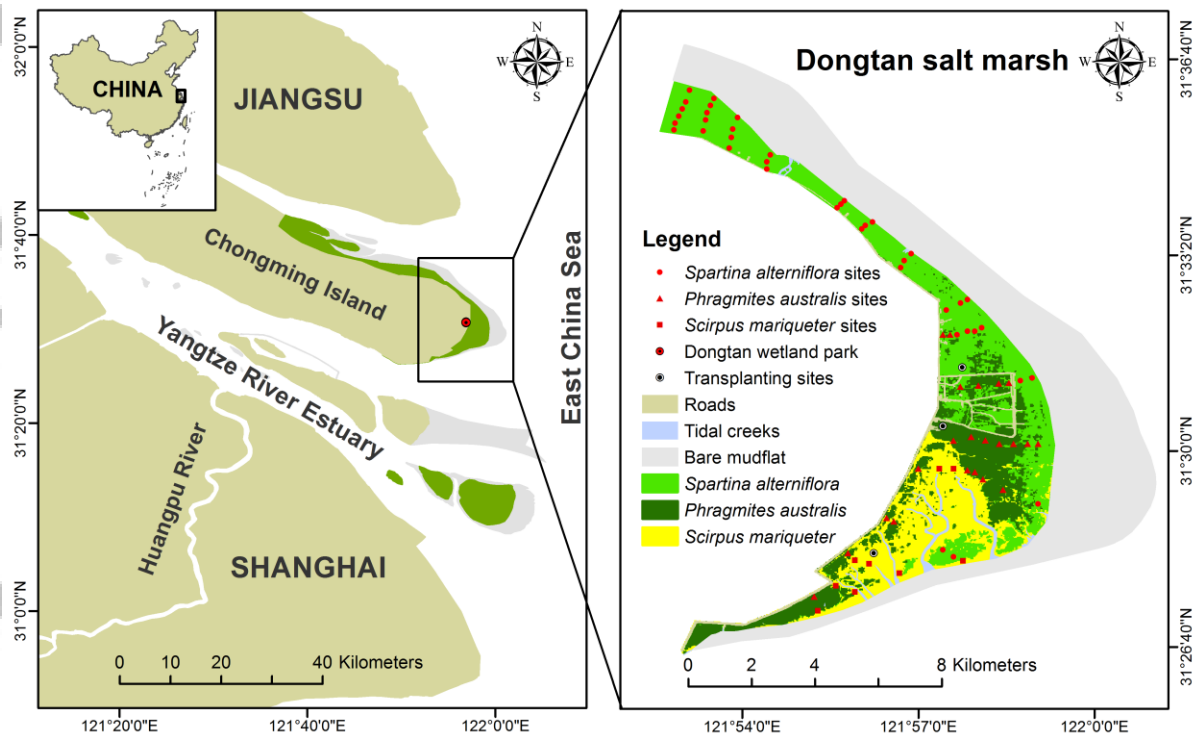
Figure 1. Location of the sampling sites for invasive *Spartina alterniflora* (*n* = 39) and native *Phragmites australis* (*n* = 22) and *Scirpus mariqueter* (*n* = 9) in the Chongming Dongtan salt marsh of the Yangtze River Estuary, China; and location of the transplanting sites where seedlings and topsoil samples were taken for pot experiments.

Figure 2. Schematic representation of the experimental design. Modified from Xue et al. (2018b).
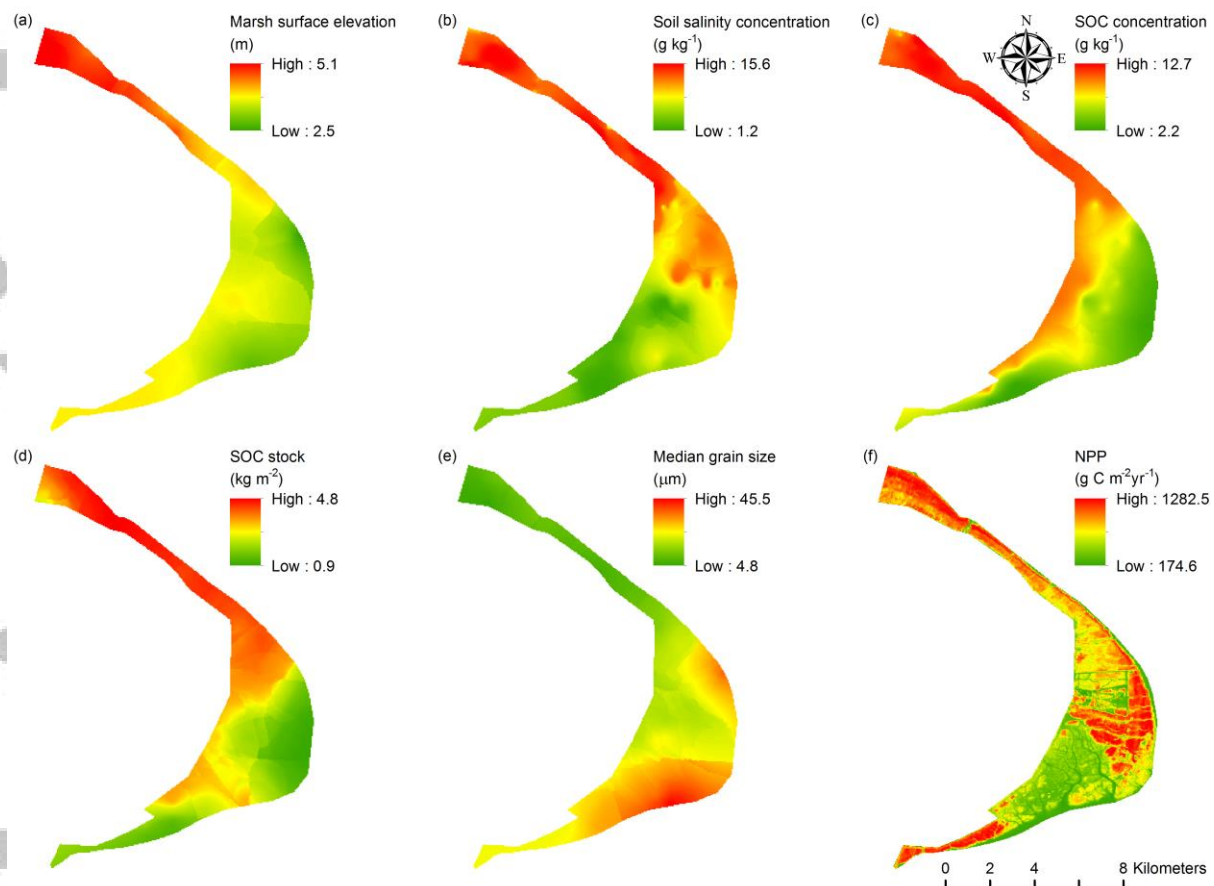
Figure 3. The spatial variability of (a) marsh surface elevation (m), (b) soil salinity concentration (g kg^{-1}), (c) soil organic carbon (SOC) concentration (g kg^{-1}), (d) SOC stock (kg m^{-2}), (e) median grain size (μm) and (f) net primary productivity (NPP, g C m^{-2} yr^{-1}) in the Chongming Dongtan salt marsh of the Yangtze River Estuary, China.
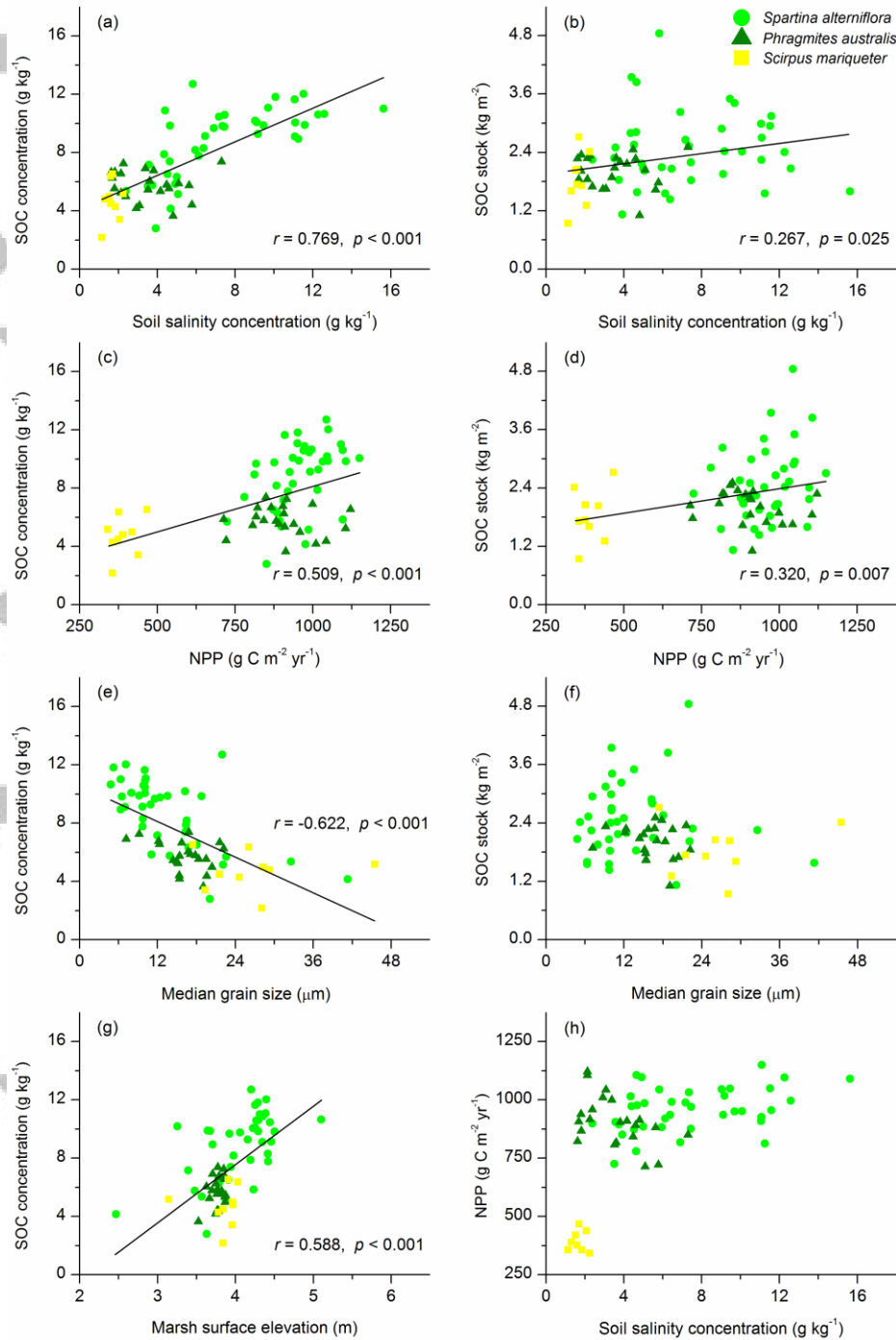
Figure 4. Relationships between (a) soil organic carbon (SOC) concentration (g kg^{-1}) and soil salinity concentration (g kg^{-1}), (b) SOC stock (kg m^{-2}) and soil salinity concentration, (c) SOC concentration and net primary productivity (NPP, g C m^{-2} yr^{-1}), (d) SOC stock and NPP, (e) SOC concentration and median grain size (μm), (f) SOC stock and median grain size, (g) SOC concentration and marsh surface elevation (m) and (h) NPP and soil salinity concentration in the Chongming Dongtan salt marsh of the Yangtze River Estuary, China.
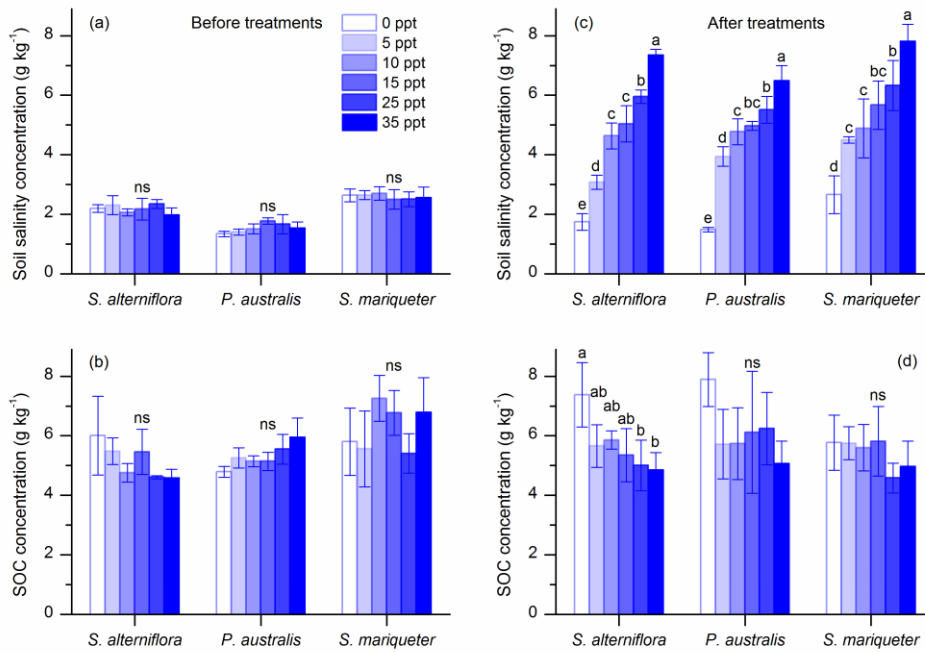
Figure 5. Differences in soil salinity concentration (g kg^{-1}) and soil organic carbon concentration (SOC, g kg^{-1}) before (a and b) and after six flooding salinity treatments (c and d) for three marsh species (invasive *Spartina alterniflora* and native *Phragmites australis* and *Scirpus mariqueter*). Different letters indicate significant differences ($p < 0.05$) among flooding salinity treatments within the same species according to the Least Significant Difference test; "ns" means there is no significant difference among flooding salinity treatments. Standard deviations are calculated based on three replicates.
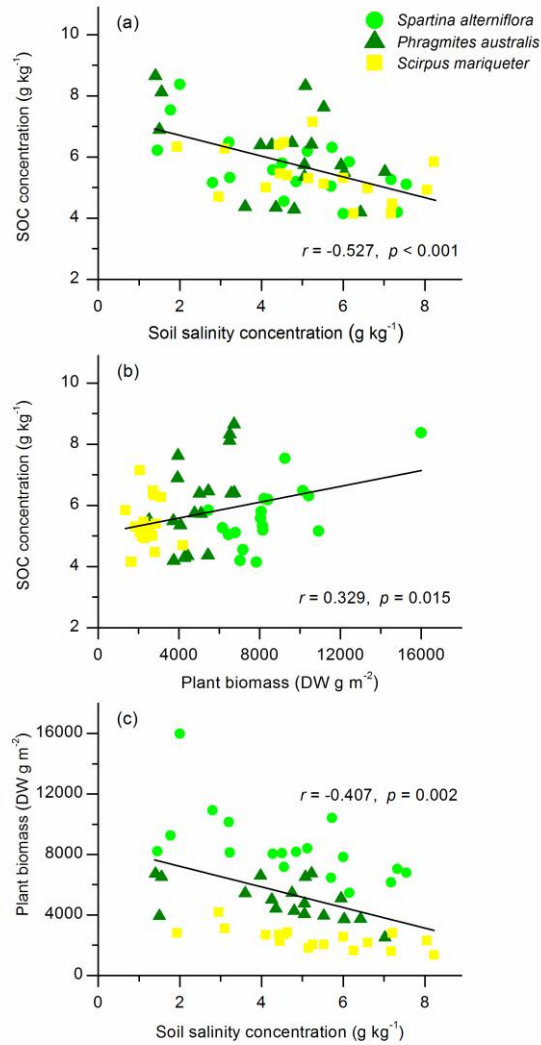
Figure 6. Relationships between (a) soil organic carbon (SOC) concentration (g kg^{-1}) and soil salinity concentration (g kg^{-1}), (b) SOC concentration and plant biomass (DW g m^{-2}) and (c) plant biomass and soil salinity concentration at the end of flooding salinity treatments. "DW" represents dry weight.