1 Introduction

Carbon dioxide (CO₂), the most important greenhouse gas in atmosphere has been increased from 280 ppm in the 1750s to 391 ppm in 2013 [1]. Carbon (C) sequestration in terrestrial ecosystems has been identified by the Intergovernmental Panel on Climate Change as one of the options for moderating the current rise in atmospheric CO₂ concentration [1]. As a result, CO₂ flux between terrestrial ecosystem and atmosphere has received renewed attention in recent decades due to the concerns over its potential feedback to future climate change [2–5].

Whether an ecosystem is a carbon source or a sink largely depends on net ecosystem exchange (NEE). NEE is a difference between terrestrial ecosystem and atmosphere has received renewed attention in recent decades due to the concerns over its potential feedback to future climate change [2–5].

We investigated carbon (C) fluxes from Spartina alterniflora community comparing with native C₃-plant (Suaeda salsa and Phragmites australis) communities as well as mudflat in a coastal marsh in eastern China by determining the net ecosystem exchange (NEE), ecosystem respiration (Rₑco) and soil respiration (Rₕₒiland) monthly with static chambers over one year. Plant biological traits and soil organic carbon (SOC) were measured at the end of the growing season. Gross primary production (GPP) was calculated as the sum of Rₑco and NEE, while the respiration of aboveground plant (Rₐₕₒiland) was assessed by the difference between Rₑco and Rₕₒiland. The invasion of S. alterniflora significantly increased Rₑco, GPP, and Rₐₕₒiland in salt marsh. The NEE in the S. alterniflora community was significantly lower than in mudflat and S. salsa community (p < 0.05), but was comparable to that in P. australis community (p > 0.05). Rₕₒiland among sites with different communities did not show significant variations (p > 0.05). Surface water inhibited Rₕₒiland and made it insensitive to changes in environmental factors across communities. Relative to other communities, the lower shoot–root ratio of S. alterniflora community together with its higher Rₑco and Rₐₕₒiland determined a higher proportion of C allocated in belowground, which ultimately resulted in increment of SOC as well as increased GPP.

The invasion of S. alterniflora potentially induces a negative feedback to the global climate change by regulating the C sequestration in salt marsh ecosystems.

Keywords: Ecosystem respiration; Gross primary production; Invasive plants; Net ecosystem exchange; Soil respiration

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Abbreviations: GPP, gross primary production; NEE, net ecosystem exchange; PAR, photosynthetic active radiation; Rₐₕₒiland, respiration of aboveground plant; Rₑco, ecosystem respiration; Rₕₒiland, soil respiration; SOC, soil organic carbon; TC, total carbon; TN, total nitrogen

increased soil C and nitrogen (N) in eastern coast of China [15, 19, 20]. The output of SOC, however, largely depends on the soil respiration \( (R_{\text{SOIL}}) \). \( R_{\text{SOIL}} \) is a biotic process (including root and microbial respirations) regulated by environmental factors such as temperature and moisture [2, 21, 22]. In particular, soil surface water in wetland could potentially inhibit \( R_{\text{SOIL}} \) due to water acting as a diffusion barrier [23, 24].

\( \text{Spartina alterniflora} \), a smooth cordgrass species from North America, has been introduced into China since the 1970s for coastal protection [25]. This exotic plant has great advantages in competing for distribution area with native species: \( \text{Phragmites australis}, \text{Suaeda salsa}, \text{Cyperus malaccensis}, \) and \( \text{Scirpus maritimus} \) [26–28]. As a successful example of colonization in eastern coast of China, \( \text{S. alterniflora} \) has been considered as a serious problem to the structure and function of native ecosystems [29–34]. For example, Cheng et al. [19] indicated that \( \text{S. alterniflora} \) significantly increases soil C following 7 years of colonization in an estuarine wetland. Liu et al. [20] also showed the similar conclusion that the colonization of \( \text{S. alterniflora} \) enhanced the C sink capacity of the intertidal ecosystem, which probably alleviates the global warming effect. Besides the change in the soil C content caused by invasion of \( \text{S. alterniflora} \), the alteration of \( C \) flux pattern also attracted attentions during the past few years [26, 27, 35–39]. However, to our knowledge, there is little study to integrate the \( C \) fluxes.

In this study, we selected the Yancheng National Nature Reserve where \( \text{S. alterniflora} \) was introduced in the 1970s as our field experiment site to evaluate the effects of invasion of \( \text{S. alterniflora} \) on CO\(_2\) fluxes and try to interpret the change of SOC with CO\(_2\) fluxes. Specifically, our objectives are to (1) evaluate the effects of invasion of \( \text{S. alterniflora} \) on CO\(_2\) fluxes (NEE, \( R_{\text{ECO}} \) and \( R_{\text{SOIL}} \)) in salt marsh ecosystems; (2) explain the change in SOC with CO\(_2\) fluxes; and (3) investigate the relationships between CO\(_2\) fluxes and environmental factors in salt marsh.

### 2 Materials and methods

#### 2.1 Study site

This study was conducted in Yancheng National Nature Reserve (119°29′ to 121°16′E, 32°20′ to 34°37′N), which is one of the largest and important coastal salt marsh in China [40]. The Reserve is a typical coastal salt marsh ecosystem where have a standard semi-diurnal tide with a tidal range of 2.5–4.0 m on average. The annual solar radiation in this district is about 502.42 kJ cm\(^{-2}\) per year, average temperature and rainfall are about 18.7°C and 1000–1080 mm, respectively [40–42]. For the purposes of ecological engineering, \( \text{S. alterniflora} \) was introduced into the Yancheng National Nature Reserve in 1979 and successively colonized [43]. After that, \( \text{S. alterniflora} \) rapidly expanded its distribution and became one of three dominate species distributing exclusively in this area. They are native species \( \text{P. australis} \) and \( \text{S. salsa} \), and the exotic species \( \text{S. alterniflora} \).

#### 2.2 Field sample collection

In March 2011, three transects (5000 m × 20 m) including mudflat, \( \text{S. salsa}, \text{S. alterniflora} \), and \( \text{P. australis} \) communities were planted. Within each transect, four sites were randomly selected in mudflat, \( \text{S. salsa}, \text{S. alterniflora} \), and \( \text{P. australis} \) communities. Nine static chamber bases were randomly inserted into the selected sites permanently except for mudflat where only three chamber bases were used. To minimize disturbance to soil surface during insertion special attention was paid, especially for the chamber inside. Areas of 50 cm × 50 cm (various heights depending on the plants) were covered by static chambers. Three transparent Plexiglas chambers were used to measure CO\(_2\) fluxes of the plants for NEE evaluation; another three transparent chambers were used to measure CO\(_2\) fluxes with clipping treatment for \( R_{\text{SOIL}} \) results. The clipping treatment was performed at the very beginning of the experiment, and the new materials in each base were cut down weekly and removed from the bases. Three opaque PVC chambers were used to measure CO\(_2\) fluxes of plants for \( R_{\text{ECO}} \) interpretation. During the sampling process, the chambers were placed on notch collars and the airtight was ensured by water-filled sealing [35]. The air inside the chambers was mixed by battery driven fans during the sampling period. Generally, four samples were pulled into 100 mL syringes at 0, 15, 30, and 45 min after enclosure. Samples were injected into pre-evacuated gas bags for laboratory analysis.

The air temperature inside the chambers was recorded simultaneously for each measurement. The sampling started from April 2011 to March 2012 (eleven times in total) except for \( R_{\text{SOIL}} \) in the \( \text{S. salsa} \) community, where the sampling started from July 2011 to March 2012 (eight times in total). Besides, we also measured the air temperature with a digital thermometer, soil temperature with a mercurial thermometer, water depth on soil surface with a stainless steel ruler and PAR with an illuminometer \((n = 3)\) in each sampling site, respectively. We collected soil samples with a 28-mm soil sampler in each site from 0 to 5 cm \((n = 3)\) for soil moisture using the oven drying method. We also randomly collected three soil samples at each site from 0 to 15 cm on May 5, August 25, December 23, and March 28, respectively, for total carbon (TC), total nitrogen (TN) and SOC measurements. The aboveground plants were collected at the end of growing season in 2012, and the stem density and average plant height were recorded simultaneously.

#### 2.3 Laboratory analysis

Soil samples were stored in a freezer and sent to the Nanjing Soil Research Institute of Chinese Academy of Sciences for analysis of TN and TC with a Vario MAX elemental analyzer and of SOC by titration. Aboveground plants were dried at 85°C to constant weight for aboveground biomass. The CO\(_2\) concentrations were analyzed at the Key Laboratory of Ecosystem Network Observation and Modeling, Chinese Academy of Sciences, Beijing, using GC (7890A, Agilent, USA). Gas fluxes were calculated by liner model regression analysis of the change of gas concentration in the chambers with time over a 45 min period \((n = 4)\) with an average chamber temperature [34].

\[
F = \frac{M}{V} \frac{dC_{273H}}{dt} + T
\]

where \( F \) is the gas flux (mg m\(^{-2}\) h\(^{-1}\)), \( M \) the gas molecular weight, \( V \) the volume of gas in standard condition, \( dc/dt \) the ratio of gas concentration, \( H \) the effective height of chamber and \( T \) the air temperature inside chambers. The regression coefficients from liner regression were rejected when \( r^2 < 0.9 \).
We considered the CO₂ flux in the transparent chambers with plants as NEE [44], the CO₂ flux in the opaque chambers with plants as RSCO and the CO₂ flux with clipping treatment as RSOL. Consequently, GPP was calculated as the sum of RSCO and NEE, respiration of aboveground plant (RAG) was calculated as the difference between RSCO and RSOL.

### 2.4 Statistical analyses

The data analysis was performed using PASW statistics 18.0 (SPSS, USA). Soil properties (TN, TC, and SOC) and biological traits (aboveground biomass, density, and height) reported here are the means of measurements from each community. Monthly CO₂ fluxes from each plot were calculated by averaging the replicates, and annual mean CO₂ fluxes from each community were calculated by averaging all measured values of the sampling periods. One-way ANOVA was performed to examine the differences in soil properties, plant biological traits and environmental factors. Significance of effects of community, time, and their interactions on CO₂ fluxes were tested by factorial ANOVA. As the variance is irregular, we used non-parametric test to examine the effects of community on the annual mean CO₂ fluxes. The Pearson coefficients of CO₂ fluxes to environmental factors were tested by simple linear regression mode.

### 3 Results

#### 3.1 Soil properties, plant biological traits, and environmental factors

SOC in S. alterniflora community was significantly higher than others (p < 0.01), while the differences in soil TN and TC were all insignificant across communities (p > 0.05; Table 1). Plant density was the highest in S. salsa community, followed by S. alterniflora and P. australis communities, but the plant height and aboveground biomass showed opposite trends with the order: P. australis > S. alterniflora > S. salsa community (p < 0.05; Table 1).

The annual soil temperature behaved similar to the air temperature, with the highest temperature in July and the lowest in December (Fig. 1a; p > 0.05). Water depth varied significantly across communities (Fig. 1b; p < 0.05), but showed a similar seasonal pattern with higher water depth from July to December compared to other season. Soil moisture in S. alterniflora community was significantly higher than others (Fig. 1c; p < 0.05). Variations of PAR showed a similar seasonal trend as the temperature (Fig. 1d; p > 0.05) (Table 2).

#### 3.2 CO₂ fluxes

NEE in all communities was negative during growing season with more negative values in S. alterniflora and P. australis communities than mudflat and S. salsa community (Fig. 2a). Annual mean NEE in S. alterniflora and P. australis communities were significantly lower than that from mudflat and S. salsa community (Fig. 2b; p < 0.05). RSCO was generally higher in S. alterniflora community, following the seasonal pattern of environmental factors (Figs. 1a,c and 2c), accordingly, the annual mean RSCO was the highest in the S. alterniflora community (Fig. 2d; p < 0.05). RSOL was generally lower from July to December when the water depth was relative high in each community (Figs. 1b and 2e). There was no significant difference in the annual mean RSOL across communities (Fig. 2f; p > 0.05). GPP in S. alterniflora community was positive through experimental period, and the annual mean GPP in S. alterniflora community was significantly higher than others (Fig. 3a,b; p < 0.05). Generally, the respiration of RAG and the annual mean GPP in the S. alterniflora community were significantly higher than in S. salsa and P. australis communities (Fig. 3c,d; p < 0.05).

#### 3.3 Effects of environmental factors

NEE was negatively correlated with air temperature, soil moisture and water depth (Table 3; p < 0.05), while RSCO was positively correlated with air temperature, soil moisture and PAR (Table 3; p < 0.05). GPP displayed a positive correlation with air temperature and soil moisture (Table 3; p < 0.05). Across communities, environmental factors can explain 30.1, 64.8, and 57.8% of variation for NEE, RSCO, and GPP, respectively (Table 4), but exhibited no significant correlations with RSOL (Table 3).

### 4 Discussion

In this study, the invasion of S. alterniflora significantly increased the SOC content (Table 1), being consistent with previous studies [15, 19, 20, 33, 45]. Increased SOC induced by S. alterniflora invasion was generally attributed to its high biomass and low decomposition rate in soil [15, 33, 45]. Our results showed that the increment of SOC induced by invasion of S. alterniflora was probably due to the...

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**Table 1.** Soil properties and plant biological traits from mudflat, S. salsa, S. alterniflora and P. australis communities in Yancheng National Nature Reserve, Jiangsu Province, China

<table>
<thead>
<tr>
<th></th>
<th>MD</th>
<th>SS</th>
<th>SA</th>
<th>PA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total nitrogen (%)</td>
<td>0.034 ± 0.02a</td>
<td>0.026 ± 0.01a</td>
<td>0.063 ± 0.02a</td>
<td>0.032 ± 0.00a</td>
</tr>
<tr>
<td>Total carbon (%)</td>
<td>1.293 ± 0.21a</td>
<td>1.321 ± 0.11a</td>
<td>1.768 ± 0.21a</td>
<td>1.447 ± 0.02a</td>
</tr>
<tr>
<td>Soil organic carbon (%)</td>
<td>0.173 ± 0.04a</td>
<td>0.427 ± 0.06b</td>
<td>1.234 ± 0.14a</td>
<td>0.421 ± 0.05a</td>
</tr>
<tr>
<td>Density (individuals/m²)</td>
<td>n.d.</td>
<td>816.0 ± 143.5a</td>
<td>160.7 ± 11.9b</td>
<td>70.7 ± 7.1c</td>
</tr>
<tr>
<td>Height (cm)</td>
<td>n.d.</td>
<td>48.9 ± 2.0c</td>
<td>149.9 ± 2.8b</td>
<td>199.24 ± 3.2a</td>
</tr>
<tr>
<td>Aboveground biomass (g m⁻²)</td>
<td>n.d.</td>
<td>508.5 ± 40.4a</td>
<td>1177.1 ± 103.7b</td>
<td>1533.9 ± 110.5a</td>
</tr>
<tr>
<td>Shoot-root ratio</td>
<td>n.d.</td>
<td>11.9</td>
<td>0.3</td>
<td>1.1</td>
</tr>
</tbody>
</table>

Values are mean with standard error.
Different suffixes (a–c) indicate statistical significance between the communities (p < 0.05).
MD, mudflat; SS, S. salsa; SA, S. alterniflora; PA, P. australis.
preference in belowground C allocation, increased GPP, and inhibited R\textsubscript{SOIL} by surface water (Table 1 and Fig. 3).

The invasion of \textit{S. alterniflora} significantly decreased the NEE compared to that in mudflat and \textit{S. salsa} community (Fig. 2a and b), which was probably due to high photosynthetic potential (Fig. 3a and b). In addition, the higher water depth in August caused massive death in \textit{S. salsa} community, making the CO\textsubscript{2} flux change from negative to positive (Figs. 1b and 2a), which was also responsible for the significant difference in NEE between communities of \textit{S. salsa} and \textit{S. alterniflora}.

NEE in communities of \textit{S. alterniflora} and \textit{P. australis} showed no significant difference, while both of them were significantly lower

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**Table 2. Significance of the effects of community, time and their interactions on CO\textsubscript{2} fluxes based on factorial ANOVA analysis**

<table>
<thead>
<tr>
<th>CO\textsubscript{2} fluxes</th>
<th>Source of variation</th>
<th>Community</th>
<th>Time</th>
<th>Community × time</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEE</td>
<td></td>
<td><strong>**</strong></td>
<td><strong>*</strong></td>
<td><strong>***</strong></td>
</tr>
<tr>
<td>R\textsubscript{ECO}</td>
<td></td>
<td><strong>**</strong></td>
<td><strong>*</strong></td>
<td><strong>***</strong></td>
</tr>
<tr>
<td>R\textsubscript{SOIL}</td>
<td></td>
<td><strong>**</strong></td>
<td><strong>*</strong></td>
<td><strong>***</strong></td>
</tr>
<tr>
<td>GPP</td>
<td></td>
<td><strong>**</strong></td>
<td><strong>*</strong></td>
<td><strong>***</strong></td>
</tr>
<tr>
<td>R\textsubscript{AG}</td>
<td></td>
<td><strong>**</strong></td>
<td><strong>*</strong></td>
<td><strong>***</strong></td>
</tr>
</tbody>
</table>

\*\*p < 0.05.  
**p < 0.01.

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**Figure 1.** Monthly patterns of temperature, water depth, soil moisture, and PAR. Error bars represent the ±1 standard error of the means. See Table 1 for abbreviations.

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**Figure 2.** Monthly patterns and the annual mean CO\textsubscript{2} fluxes across communities. Error bars represent the ±1 standard error of the means. Different suffixes indicate statistical significance between the communities (p < 0.05). See Table 1 for abbreviations.
Altered Carbon Exchange by *S. alterniflora*

Figure 3. Monthly patterns and the annual mean GPP, *R* \(_{AG}\) across communities. Error bars represent the ±1 standard error of the means. Different suffixes indicate statistical significance between the communities (*p* < 0.05). See Table 1 for abbreviations.

| Table 3. Pearson coefficients (r) of fluxes (NEE, *R* \(_{ECO}\), *R* \(_{SOIL}\), and GPP) on environmental factors (AT, ST, SM, WD, and PAR) across communities. |
|----------------|----------------|----------------|----------------|----------------|
|                | AT             | ST             | SM             | WD             | PAR            |
| NEE            | −0.318*        | −0.265         | −0.362*        | −0.517**       | 0.232          |
| *R* \(_{ECO}\) | 0.519**        | 0.38*          | 0.789**        | −0.095         | 0.465**        |
| *R* \(_{SOIL}\)| 0.2            | 0.099          | 0.045          | −0.354         | −0.149         |
| GPP            | 0.564**        | 0.441**        | 0.767**        | 0.227          | 0.117          |

AT, air temperature; ST, soil temperature; SM, soil moisture; WD, water depth

*P* < 0.05.

*P* < 0.01.

than those in mudflat and *S. salsa* community (Fig. 2a and b). The lower NEE in communities of *S. alterniflora* and *P. australis* may result in an increment of C accumulation in aboveground and/or belowground biomass. However, the aboveground biomass in *P. australis* community was significantly higher than that in *S. alterniflora* community, which was potentially derived from the significantly lower respiration of *R* \(_{AG}\) in *P. australis* community and more accumulation of photosynthetic product (Fig. 3d). Compared with native species, *S. alterniflora* allocated more photosynthetic production into belowground with a significantly lower shoot–root ratio (Table 1) [45–47]. A previous study conducted in *S. alterniflora*’s original habitat also revealed the same pattern of biomass distribution [48, 49] suggested that this preference in biomass distribution in belowground is one of the mechanisms for its successive colonization in Chinese costal wetland, because a better developed root system make it be more competitive in absorbing nutrition such as nitrogen. The pattern of biomass distribution in *S. alterniflora* favors SOC accumulation because the belowground biomass is a more direct and continuous organic carbon source than aboveground biomass. On the other side, the aboveground biomass may not remain as standing dead materials instead of falling into soil directly after growing season [50]. As a part of litters from aboveground, they were washed away by water movement [51]. The importance of belowground biomass in controlling SOC has been reported by previous studies as well. For example, Cheng et al. [19] have distinguished the contributions of SOC from *S. alterniflora* and native species, separately by using the δ\(^{13}\)C technique, and the result suggested that percentage SOC from *S. alterniflora* have significant correlation with allocation of belowground biomass.

Our results showed that the invasion of *S. alterniflora* significantly increased *R* \(_{ECO}\) (Fig. 2c and d), which was mainly constituted by the *R* \(_{AG}\) and *R* \(_{SOIL}\). Since there was no significant difference in *R* \(_{SOIL}\) across communities and it kept relatively low, the difference in *R* \(_{ECO}\) was thus mainly contributed by *R* \(_{AG}\). The *R* \(_{AG}\) not only significantly correlated with *R* \(_{ECO}\) (*p* < 0.01), but also accounted for 60–74% of the *R* \(_{ECO}\) differences between communities of *S. alterniflora* and *P. australis*. However, the percentage of *R* \(_{AG}\)’s contribution for *R* \(_{ECO}\) in *S. salsa* community was smaller (around 35%) probably because of the low aboveground biomass in stand (Table 1) and the massive death caused by inundation in August (Figs. 1b and 2a). The small contribution of *R* \(_{SOIL}\) to *R* \(_{ECO}\) is important because it indicated a relatively stable organic carbon pool in soil which is helpful in accumulating SOC.

The stability of SOC probably resulted from the inhibition effect of surface water on organic carbon decomposition. According to previous studies, *R* \(_{SOIL}\) in *S. alterniflora* was higher than that in other communities because community of *S. alterniflora* has a considerable higher autotrophic and heterotrophic respiration rate in soil [52, 53]. In our study, however, the invasion of *S. alterniflora* did not significantly alter the *R* \(_{SOIL}\) rate in salt marsh (Fig. 2e and f), and *R* \(_{SOIL}\) was close to zero from July to December across communities when water depth was relative high (Figs. 1b and 2e). It suggested that the inundation inhibited *R* \(_{SOIL}\) because surface water can limit O\(_2\) exchange which was largely depended by *R* \(_{SOIL}\) and decomposition process [23, 24, 54–57].

GPP calculated by *R* \(_{ECO}\) and NEE showed a higher photosynthetic production in *S. alterniflora* community (Fig. 3a and b). It is probably because the *S. alterniflora*, as a C\(_4\)-plant, has a higher photosynthetic efficiency than C\(_3\)plants [25, 58]. Specifically, its longer growing season (Fig. 3a), higher leaf index and net photosynthetic rate compared with natives [15] were important characteristics responsible for its distinctive primary production. The highest GPP in *S. alterniflora* community suggested that *S. alterniflora* can fix more carbon and potentially allocate more C to belowground as biomass and root residue input (Fig. 3a and b) [19], which contributes to the SOC accumulation. Furthermore, we also believed the root exudates

| Table 4. Regression analysis of fluxes (NEE, *R* \(_{ECO}\), and GPP) against significantly related environmental factors across communities. |
|----------------|----------------|----------------|
| Regression equation | Adj. R\(^2\) | P |
| NEE             | *F* = −1.20AT - 8.26SM - 2.491WD + 263.12 | 0.301 | 0.001 |
| *R* \(_{ECO}\)  | *F* = −5.863AT + 7.008ST + 29.81SM + 0.027PAR - 614.414 | 0.648 | 0.000 |
| GPP             | *F* = −4.744AT + 16.93ST + 39.32SM - 899.656 | 0.578 | 0.000 |

See Table 1 for abbreviations.
in S. alterniflora also played an important role in SOC accumulation due to the high photosynthetic production potential and well-developed belowground biomass, but we cannot quantify the contribution of root exudate because of the lack of approach for measurement [59, 60].

Temperature and soil moisture are important factors in regulating C flux processes [18, 61, 62]. In this study, the R_ECO increased with increasing temperature (Table 3), which is consistent with previous studies [9, 63, 64]. Increasing temperature can not only stimulate the microbial respiration [9], but also enhance the enzymatic processes of plant respiration, and further promote plant respiration [65]. In the present study, the correlation between R_ECO and temperature was mainly contributed by plant respiration, because the R_SOIL was insensitive to environmental factors (Table 3). Although the R_ECO increased with increasing temperature and soil moisture, the NEE was negatively correlated with the two environmental factors (Tables 3 and 4), probably because increasing rate in GPP with environmental factors was higher than any enhancement in R_ECO. Generally, temperature and soil moisture greatly affects the R_SOIL process [18, 66–68]. However, R_SOIL in our study was not significantly related to any one of the environmental factors (Table 3), probably because the inhibition effect of surface water made the R_SOIL insensitive to variations of environmental factors [57, 69]. Considering the significant role of water, other factors such as the tidal cycle, pattern of rain fall supposed to be brought into the further study.

5 Conclusions
In this study, we found that the invasion of S. alterniflora significantly increased the SOC content in eastern salt marsh of China, and there are three mechanisms together determined the increment of SOC. First, the S. alterniflora prefers allocated more proportion of photosynthetic productions into belowground, which may favor SOC accumulation in salt marsh. Second, O2 exchange inhibited by surface water depressed decomposition of organic matter [represented by a decreased R_SOIL] in salt marsh and made the salt marsh a more stable C pool. Third, sites with invasion of S. alterniflora displayed an increased GPP, potentially suggesting that S. alterniflora allocated more C to belowground as biomass and exudates. The invasion of S. alterniflora potentially induced a negative feedback to current global climate change by regulation of C sequestration in salt marsh ecosystems.

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The authors have declared no conflict of interest.

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