MANAGEMENT AND POTENTIAL IMPACT OF *SPARTINA ALTERNIFLORA* INVASION ON TIDAL MARSH CARBON STOCKS IN SOUTHERN HANGZHOU BAY

WANG, T.[1*] – ZHAO, L. X.[1,2] – YAO, W. M.[1] – JI, H. H.[1] – YANG, Y.[1] – YAN, P. F.[1] – JIA, J. H.[1]

[1]*Key Laboratory of Marine Ecological Monitoring and Restoration Technologies, East China Sea Ecology Center, MNR, Shanghai 201206, China*

[2]*Key Laboratory of Ocean Space Resource Management Technology, MNR, Hangzhou, Zhejiang 310012, China*

[*]*Corresponding author*
e-mail: wt2782377@126.com; phone: +86-139-1664-3965; fax: +86-021-6090-1505

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Abstract. To mitigate the adverse effects of *Spartina alterniflora* invasion on coastal wetlands, extensive control measures have been implemented along the Chinese coastline. This study investigates the carbon sequestration capabilities of *S. alterniflora*, *Phragmites australis*, and *Scirpus mariqueter* along the southern Hangzhou Bay. The findings reveal that the replacement of *P. australis* by *S. alterniflora* does not enhance the existing tidal marsh carbon stock. However, the invasion by *S. alterniflora* in areas dominated by *S. mariqueter* results in an increase in the vegetation carbon pool without significantly affecting the sediment carbon pool. The management of *S. alterniflora* would lead to a reduction in the vegetation carbon pool of tidal marshes. Nonetheless, as most of the removed plants are buried in the sediment, their decomposition would indirectly contribute to an increase in the sediment carbon pool. Therefore, in the short term, the management of *S. alterniflora* will not significantly impact the tidal marsh carbon pools in this area. To maintain the stability of the tidal marsh carbon pools on the southern coast of Hangzhou Bay following the management of *S. alterniflora* and to effectively prevent its future re-invasion, we recommend the prompt restoration of *P. australis* in the managed areas. The insights from this study provide valuable guidance for the development of restoration plans post-management of *S. alterniflora* and for enhancing the ecological service functions of China's coastal wetlands.
Keywords: *organic carbon, vegetation, sediment, carbon sequestration capability, restoration*

Introduction

Tidal marshes are ecosystems situated in the transitional zones between marine and terrestrial areas, regularly or irregularly flooded by tides, and characterized by the presence of herbaceous or shrub plants (He et al., 2010). As an important ecological barrier in coastal zones, tidal marshes provide diverse ecosystem services including storm surge protection, pollutant purification, sand stabilization, sediment accumulation, and habitat provision, among other essential functions (Shepard et al., 2011; Adams et al., 2021; zu Ermgassen et al., 2021). Additionally, tidal marshes, along with mangroves and seagrass beds, constitute coastal blue carbon ecosystems (BCEs), which are among the most effective carbon sinks on Earth (Tang et al., 2018). Globally, BCEs are estimated to store over 3.0×10^4 Tg C across approximately 1.85×10^6 km^2, with their preservation potentially avoiding emissions of 304 (141–466) Tg carbon dioxide equivalent (CO_2e) annually (Macreadie et al., 2021).

China is a significant global region for tidal marshes. By 2019, the area of tidal marshes in China had reached 1274.77 km^2 (Hu et al., 2021). Research indicates that these marshes have a carbon burial rate of 1.19 Tg C·a^{-1}, identifying them as the most efficient

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blue carbon ecosystems for carbon sequestration (Wang et al., 2021). The total stored carbon in China's tidal marshes is estimated at 25 Tg, which is 17.8 times that of mangroves and 3.6 times that of seagrass beds (Wang et al., 2023). However, the area of these tidal marshes has been diminishing due to human activities such as coastal development. A national-scale study revealed that over 7500 km^2 of China's coastal wetlands were lost to reclamation between 1985 and 2010, and that the permanent water area has been in long-term decline at most coastal Ramsar sites, which raises ecological and environmental concerns (Tian et al., 2016; Fan et al., 2023). Additionally, the degradation of tidal marshes is causing previously anaerobic soils to be exposed to the atmosphere. This exposure is speeding up the decomposition of organic carbon (OC) in the soil and the release of CO_2, resulting in the loss of already sequestered OC (Zhou et al., 2016; Senger et al., 2021).

In 2018, the State Council issued the "Notice on Strengthening the Protection of Coastal Wetlands and Strictly Controlling Reclamation", which aimed to enhance the protection of coastal wetlands, strictly regulate reclamation activities, and halt the approval of new reclamation projects, except for those deemed major national strategic projects (Zhu et al., 2024). This action has reversed the trend of continuous reduction in China’s coastal wetlands. However, the restoration of native species in these tidal marshes remains slow, primarily due to the invasive species *Spartina alterniflora*, which has progressively displaced native vegetation. Since its introduction to China in 1979, *S. alterniflora* has rapidly proliferated along the coastal regions (Liu et al., 2018). By 2019, it covered an area of 615.7 km^2, representing approximately 48.3% of China's total tidal marsh area, and its spread continues (Hu et al., 2021). The invasion of *S. alterniflora* has resulted in a decrease in native tidal marsh vegetation and has had profound negative impacts on biodiversity, affecting benthic organisms and bird species (Li et al., 2009; Lyu et al., 2023; Zheng et al., 2023). For instance, the invasion of *S. alterniflora* into the *Scirpus mariqueter* tidal marsh in the Yangtze River estuary has significantly reduced the abundance and diversity of waterbird species (Ma et al., 2009; Zou et al., 2016). Furthermore, the invasion has led to a reduction in mudflat areas, consequently hindering the development of mudflat aquaculture industry in China (Wan et al., 2009). To effectively manage the spread of *S. alterniflora* and improve the quality and stability of coastal wetland ecosystems, the Chinese government has launched a three-year action plan starting in 2023. The goal of this plan is to eradicate 90% of *S. alterniflora* across the nation.

During the engineering implementation process, coastal provinces and cities primarily used physical plowing and herbicide spraying methods to eradicate *S. alterniflora* effectively. Rigorous environmental impact assessments were conducted at each stage of the project, specifically focusing on the impact of *S. alterniflora* management on hydrodynamics, biological communities, and the aquatic environment. *S. alterniflora* is known for its high photosynthetic rate, primary productivity, and biomass, which leads to a significant contribution of organic matter into sediments. This results in a higher carbon sequestration capacity compared to some native tidal marsh vegetation (Jin et al., 2017; Zheng et al., 2023; Zhou et al., 2023). The removal of *S. alterniflora* will unavoidably affect the structure and size of the BCE carbon pool in the short term; however, there is currently no definitive research conclusion on this aspect. This study focuses on the southern coast of Hangzhou Bay, a typical tidal marsh region in China that has been severely impacted by *S. alterniflora* invasion (Cai et al., 2023). In 2023, a restoration project was initiated on the southern coast of Hangzhou Bay to manage

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S. alterniflora. By comparing the carbon sequestration capacities of different plant species in this area and analyzing the primary influencing factors, we explored the potential impacts of *S. alterniflora* invasion and management on the tidal marsh carbon pool. Furthermore, this paper offers recommendations for vegetation restoration following *S. alterniflora* removal, serving as a reference to ensure the efficacy of invasive species management along China's coasts and the enhancement of BCE carbon pools.

Materials and methods

Study site

The southern shore of Hangzhou Bay is a typical coastal wetland in China and is situated in the northeastern part of Zhejiang Province (*Fig. 1a*). Due to the influence of the delta at the mouth of the sea, the area is rich in beach resources with large tide siltation, small tide scouring (Jing et al., 2023). As elevation increases from sea to land, there is a sequential development of mudflats, *S. mariqueter*, *S. alterniflora*, and *Phragmites australis*. *S. alterniflora* began invading this region around 1997 and has since become the dominant tidal marsh vegetation (Li et al., 2005).

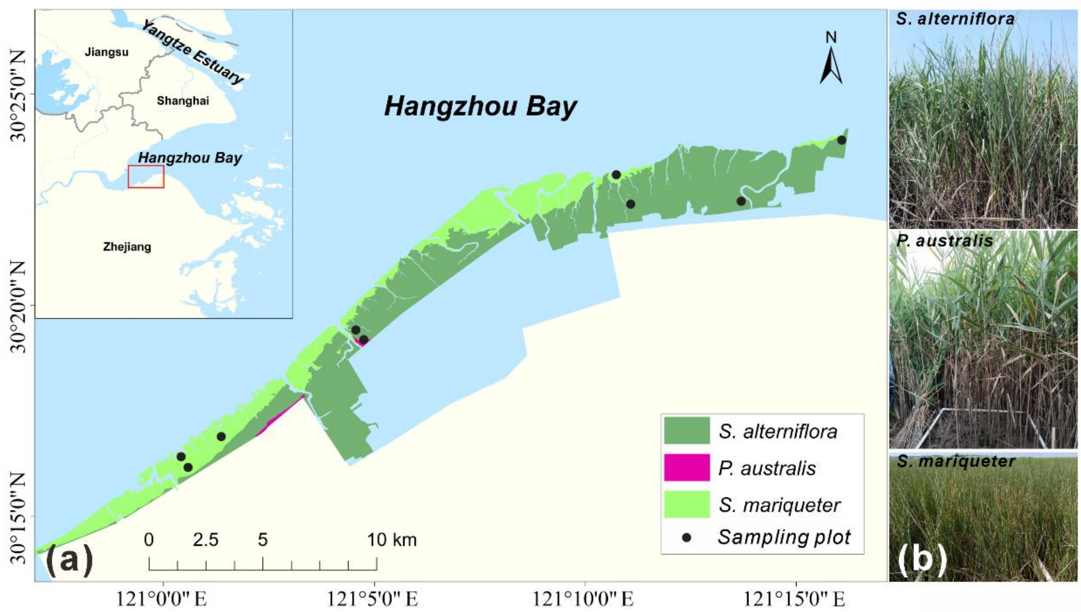

Figure 1. *Location of the study area, including the distribution of different tidal marsh ecosystems and the location of the sampling plot (a), as well as photos of three tidal marsh plants (b)*

Tidal marsh map

This research utilized remote sensing imagery with a 2-meter resolution from ZY1-02E and GF-1 to examine the distribution of tidal marsh before the management of *S. alterniflora*. Based on the distinct differences in color, texture, and structure exhibited by various vegetation types in remote sensing images, remote sensing interpretation markers are established. By utilizing an interactive human-machine identification method and referring to these established markers, we interpret different vegetation types to

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generate a vegetation distribution map. We then verify selected interpreted vegetation patches on-site through field inspections to confirm boundary, type, and other relevant information, resulting in an overall classification accuracy that exceeds 85%. According to the field verification results, the vegetation patches of salt marshes are revised, the vegetation distribution map is finalized, and area statistics are compiled.

The results revealed that the areas covered by *S. alterniflora*, *P. australis*, and *S. mariqueter* were 44.12 km^2, 0.35 km^2, and 19.84 km^2, respectively, representing 68.6%, 0.5%, and 30.9% of the total tidal marsh area. *S. alterniflora* predominantly occupies the high and middle tidal flats, while *S. mariqueter* is located on the outer edges. *P. australis* is sparsely distributed in some parts of the high tidal flats and occasionally intermixed with *S. alterniflora* (*Fig. 1a*).

Plot and quadrant

In August 2023, field sampling was carried out in the tidal marsh on the southern Hangzhou Bay. During this period, management efforts to control *S. alterniflora* were in progress. The primary control strategy for *S. alterniflora* in this area involved physical interventions: cutting the aboveground parts and subsequently using excavators to plow the underground roots, ensuring the complete removal of the vegetation. To ensure the feasibility and representativeness of the sampling, four plots, each 10 m by 10 m, were established in the areas where *S. alterniflora* and *S. mariqueter* were distributed (*Fig. 1a*). Due to the limited area occupied by *P. australis*, one plot was established within its distribution area (*Fig. 1a*). Each plot is randomly distributed to encompass a diverse range of vegetation types. A buffer zone of at least 10 m surrounds each plot, and the vegetation within the buffer zone is consistent with that inside the plot. Three quadrants were set up in each plot for the collection of vegetation and sediment samples, with distances between plots exceeding 5 m.

Sample collection

The sample area for *S. alterniflora* and *P. australis*, taller plants, was set to 1 m^2 above ground. For *S. mariqueter*, which has shorter and more evenly distributed plants, the sample area was set to 0.25 m^2. During sampling, all aboveground living parts within the quadrants were cut, the soil was removed, and the samples were placed in plastic bags. In each plot within the distribution areas of *S. alterniflora* and *P. australis*, a certain amount of litter was present. The litter species were homogeneous, and the litter in each plot was collected and placed into sample bags during the sampling process.

For the collection of underground root and sediment samples, a PVC pipe with an inner diameter of 10.4 cm was employed. One core sample was obtained from the central area of each plot. Following the Blue Carbon Manual (Howard et al., 2014), a standard sampling depth of 1 m is recommended for assessing sediment organic carbon (SOC) stocks in coastal ecosystems, and this study adhered to that depth. A sharp stainless steel drill bit was affixed to the lower end of the PVC pipe to minimize sediment disruption during sampling. After extracting the PVC pipe, bulk density samples were obtained from the sediment profile at 10 cm intervals, each with a volume of 30 cm^3. Except for the bulk density samples, which were kept at room temperature and shielded from light, all other collected samples are stored at -20°C until processing.

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Sample processing

The collected aboveground live vegetation and litter samples were dried at 60°C and subsequently weighed to determine their dry mass. Samples extracted from the PVC pipe were segmented into 10 cm sections, and live roots from each segment were gathered, cleaned, dried at 60°C, and then weighed to ascertain their dry mass. The biomass for each component is calculated by dividing the dry weight by the sampling area. Subsequently, an appropriate quantity of the dried vegetation samples was ground using a micro grinder and then sieved. The sieved plant material was weighed, and the OC content was analyzed using an elemental analyzer (Model: varioISOTOPE2400499, Manufacturer: Elementar).

After extracting the roots from each stratified sample, the remaining sediment was thoroughly mixed and subsequently used to determine the SOC content and conduct grain size analysis. The SOC was determined by the potassium dichromate volumetric method, while grain size was determined with a laser particle size analyzer (Model: LS13320, Manufacturer: Beckman Coulter). For bulk density determination, the samples were dried at 60°C and subsequently weighed. The dry weight was then divided by the sample volume to calculate the bulk density.

Data analysis

The vegetation OC density (VOCD, Mg C/ha) for different components was determined using the following formula:

$$VOCD_i = VB_i \times VOC_i \times 10^{-2} \quad \text{(Eq.1)}$$

where $VOCD_i$ represents the OC density of various vegetation parts, including the living aboveground biomass, litter, and belowground biomass. VB_i denotes the biomass (g/m^2) of these components, and VOC_i is the respective OC content (%) of each part.

The SOC density (SOCD, Mg C/ha) in the top 1 m profile was calculated using the following formula:

$$SOCD = \sum_{i=1}^{n} SOC_i \times BD_i \times H_i \times 10^2 \quad \text{(Eq.2)}$$

where SOC_i is the OC (%) of the i-th depth (i=1, 2, 3, …, 10), BD_i is the bulk density (g/cm^3) of the i-th depth, and H_i is the sediment thickness (cm) of the i-th depth.

The total OC density of a sample quadrant was calculated by summing the VOCD and SOCD values. The total OC density was then multiplied by the area of the vegetation to estimate the OC stock within the tidal marshes.

Prior to conducting comparative and correlation analyses, each dataset was subjected to the Shapiro-Wilk normality test and Levene's test for homogeneity of variances. If the data from each group followed a normal distribution and exhibited homogeneity of variances, a one-way ANOVA followed by an LSD post-hoc test was conducted at a significance level of 0.05. If the data did not follow a normal distribution, a transformation was applied. If the transformed data still did not conform to a normal distribution, the rank-sum test was used for comparative analysis. The correlation between SOC content and indicators such as grain size and water content was evaluated using the Spearman correlation coefficient, with $p < 0.05$ considered statistically significant.

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Results

Vegetation carbon sequestration capacity

Vegetation biomass

In the study area, there is a disparity in biomass among the vegetation types. The living aboveground biomass of *S. alterniflora*, *P. australis*, and *S. mariqueter* is 1938.8 ± 779.1 g/m², 1652.4 ± 212.8 g/m², and 352.8 ± 98.4 g/m², respectively. Correspondingly, their belowground biomass amounts to 1528.6 ± 1200.9 g/m², 2924.4 ± 937.5 g/m², and 738.1 ± 140.1 g/m². The variation in biomass of *S. alterniflora* and *P. australis* is greater than that of *S. mariqueter*, primarily due to the less consistent distribution of the former two species. Specifically, the densities of *S. alterniflora* and *P. australis* are 61 ± 16 plants/m² and 102 ± 28 plants/m², with coefficients of variation of 26.2% and 27.5%, respectively, whereas the density of *S. mariqueter* is 1932 ± 409 plants/m², with a coefficient of variation of 21.2%. The total live biomass of *S. alterniflora*, *P. australis*, and *S. mariqueter*, calculated by summing their aboveground and belowground biomass, is 3467.4 ± 857.1 g/m², 4576.8 ± 864.7 g/m², and 1090.9 ± 137.7 g/m², respectively (*Fig. 2a*). *S. alterniflora* and *P. australis* have higher biomass compared to *S. mariqueter*, which has lower biomass due to its shorter stature. A comparative analysis shows that there is no significant difference in biomass between *S. alterniflora* and *P. australis* ($p > 0.05$), but both are significantly higher than *S. mariqueter* ($p < 0.05$) in terms of biomass. This indicates that the encroachment of *S. alterniflora* into *P. australis* tidal marshes does not increase the existing total vegetation biomass. Conversely, the invasion into *S. mariqueter* tidal marshes would increase the total vegetation biomass to some extent.

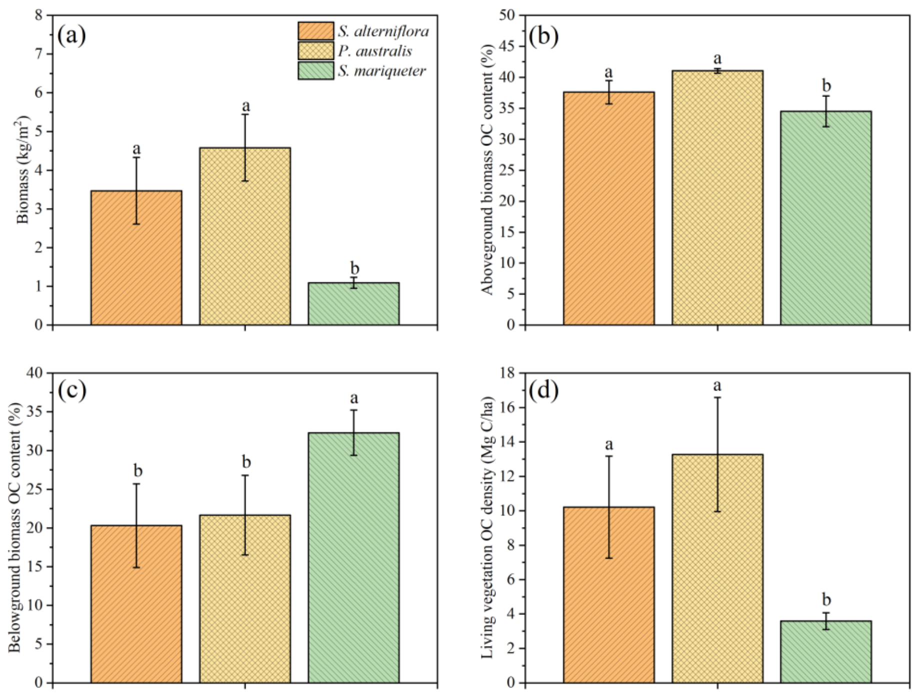

Figure 2. *The biomass (a), aboveground and belowground biomass OC content (b and c), and living vegetation OC density (d) of S. alterniflora, P. australis, and S. mariqueter in the study area. Different lowercase letters signify the significant differences in the same indicators among different plants (p < 0.05, rank-sum test)*

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Litter samples were collected exclusively from quadrats containing *S. alterniflora* and *P. australis* vegetation. The recorded litter biomass for *S. alterniflora* was 297.9 ± 122.6 g/m², compared to 63.1 ± 16.0 g/m² for *P. australis*. The litter biomass of *S. alterniflora* in the study area is greater than that of *P. australis*, but statistical analysis revealed no significant difference between the two plants ($p > 0.05$). Conversely, the litter biomass of both plant species was significantly lower than their respective living aboveground biomass ($p < 0.05$), representing only 15.4% and 3.8% of the living aboveground biomass, respectively (*Fig. 3a*).

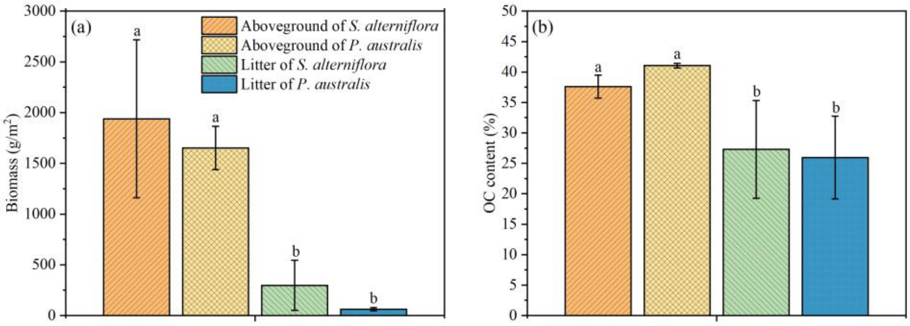

Figure 3. *The biomass (a) and OC content (b) of living aboveground parts and litter of S. alterniflora and P. australis in the study area. Different lowercase letters signify the significant differences in the same indicators among different plants (p < 0.05, rank-sum test)*

Vegetation organic carbon

The results indicate that the OC content in the aboveground living vegetation of *S. alterniflora*, *P. australis*, and *S. mariqueter* is 37.59 ± 1.88%, 41.05 ± 0.38%, and 34.51 ± 2.48%, respectively (*Fig. 2b*). Statistical analysis reveals that the OC content in the aboveground living vegetation of both *S. alterniflora* and *P. australis* is significantly higher than that of *S. mariqueter* ($p < 0.05$), while no significant difference is observed between *S. alterniflora* and *P. australis* ($p > 0.05$). The root OC content is 20.30 ± 5.41%, 21.66 ± 5.12%, and 32.29 ± 2.92% for *S. alterniflora*, *P. australis*, and *S. mariqueter*, respectively (*Fig. 2c*). The roots of *S. mariqueter* exhibit a significantly higher OC content compared to those of *S. alterniflora* and *P. australis* ($p < 0.05$), with no significant difference between *S. alterniflora* and *P. australis* ($p > 0.05$). Additionally, the OC content in the aboveground living parts of *S. alterniflora* and *P. australis* is significantly greater than that in their roots ($p < 0.05$), suggesting a higher efficiency of carbon storage in the aboveground living parts. Furthermore, the OC content in the litter of *P. australis* (25.96 ± 6.80%) is slightly lower than that in *S. alterniflora* (27.28 ± 8.02%). As shown in *Figure 3b*, the OC content in the litter is significantly lower than that in the living aboveground parts ($p < 0.05$), indicating some degree of degradation of stored OC after plant death.

Vegetation carbon density

The OC density of the vegetation was evaluated based on biomass and OC content. In the study area, the OC densities for the aboveground living parts of *S. alterniflora*, *P. australis*, and *S. mariqueter* were 7.26 ± 2.89 Mg C/ha, 6.78 ± 0.86 Mg C/ha, and 1.23 ± 0.39 Mg C/ha, respectively. For the roots, the densities were 2.95 ± 2.28 Mg C/ha,

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6.49 ± 3.09 Mg C/ha, and 2.36 ± 0.38 Mg C/ha, respectively. Significant variations were observed in the OC densities between different parts of the vegetation types. The OC densities of aboveground and belowground parts of *P. australis* were nearly equal. In contrast, the aboveground biomass of *S. alterniflora* was 2.5 times higher than that of the belowground biomass. On the other hand, *S. mariqueter* stored more OC in its roots. When combining aboveground and belowground parts, the total living vegetation OC densities were 10.21 ± 2.96 Mg C/ha for *S. alterniflora*, 13.27 ± 3.32 Mg C/ha for *P. australis*, and 3.59 ± 0.49 Mg C/ha for *S. mariqueter* (*Fig. 2d*). The living vegetation OC density in *S. alterniflora* and *P. australis* was significantly higher than in *S. mariqueter* ($p < 0.05$), which can be attributed to the taller plant structures and greater biomass of the former two species. No significant difference was found between *S. alterniflora* and *P. australis* ($p > 0.05$). Furthermore, OC was found in the litter of both *S. alterniflora* and *P. australis*, with densities of 0.78 ± 0.28 Mg C/ha and 0.16 ± 0.06 Mg C/ha, respectively.

Sediment carbon sequestration capacity

Sediment grain size

To determine the mean median grain size of sediments within each quadrant, the median grain size values of sediment layers at various depths were calculated as an average. In this study, the average sediment median grain sizes in *S. alterniflora*, *P. australis*, and *S. mariqueter* were 5.80±0.18 Φ, 6.21±0.29 Φ, and 5.53±0.13 Φ, respectively (*Fig. 4a*). The sediment particles of *P. australis* are the finest, followed by *S. alterniflora*, with *S. mariqueter* has the coarsest particles. Significant variations were observed among the three species ($p < 0.05$). Additionally, sediment particles in salt marshes typically show a coarsening trend from the surface downward (*Figs. 5a-c*). Statistical analysis reveals no significant difference in sediment grain size across the various layers of the *P. australis* salt marsh. However, a significant difference in particle coarseness is observed between the upper and lower layers of the *S. alterniflora* and *S. mariqueter* salt marsh sediments ($p < 0.05$).

Sediment bulk density

The findings reveal that the bulk density of sediments across the study area ranges from 1.20 to 1.55 g/cm³, with an overall average of 1.35 ± 0.09 g/cm³. Specifically, the average bulk densities for sediments in *S. alterniflora*, *P. australis*, and *S. mariqueter* were 1.38 ± 0.11 g/cm³, 1.30 ± 0.09 g/cm³, and 1.33 ± 0.05 g/cm³, respectively (*Fig. 4b*). Despite the relatively higher bulk density observed in *S. alterniflora* sediments, no significant differences were noted among the three species ($p > 0.05$). An increase in depth corresponded with a general rise in the bulk density of tidal marsh sediments (*Figs. 5d-f*). Specifically, the average bulk density of surface sediments (0–10 cm) in each quadrant was 1.15 ± 0.20 g/cm³, while the deepest layer (90–100 cm) exhibited a significantly higher value of 1.43 ± 0.15 g/cm³ ($p < 0.05$).

Sediment organic carbon

The OC content of sediments from various quadrants within the study area ranged from 0.43% to 0.74%, with an average of 0.53 ± 0.06%. Specifically, the mean OC content of sediments dominated by *S. alterniflora*, *P. australis*, and *S. mariqueter* was 0.53 ± 0.08%, 0.55 ± 0.03%, and 0.52 ± 0.05%, respectively (*Fig. 4c*). Although

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P. australis exhibited a slightly higher value than both *S. alterniflora* and *S. mariqueter*, the differences among the three species were not statistically significant ($p > 0.05$). In contrast, the OC content of sediments across different vegetation types displayed a general decreasing trend from the surface to deeper layers, unlike the variation in bulk density (*Figs. 5g-i*). The average OC content in the 0–10 cm layer was 0.59±0.15%, while it decreased significantly to 0.47 ± 0.12% in the 90–100 cm layer compared to the surface layer ($p < 0.05$). This indicates that the upper layer sediments may serve as the primary sites for OC absorption and transformation in the tidal marshes of this region.

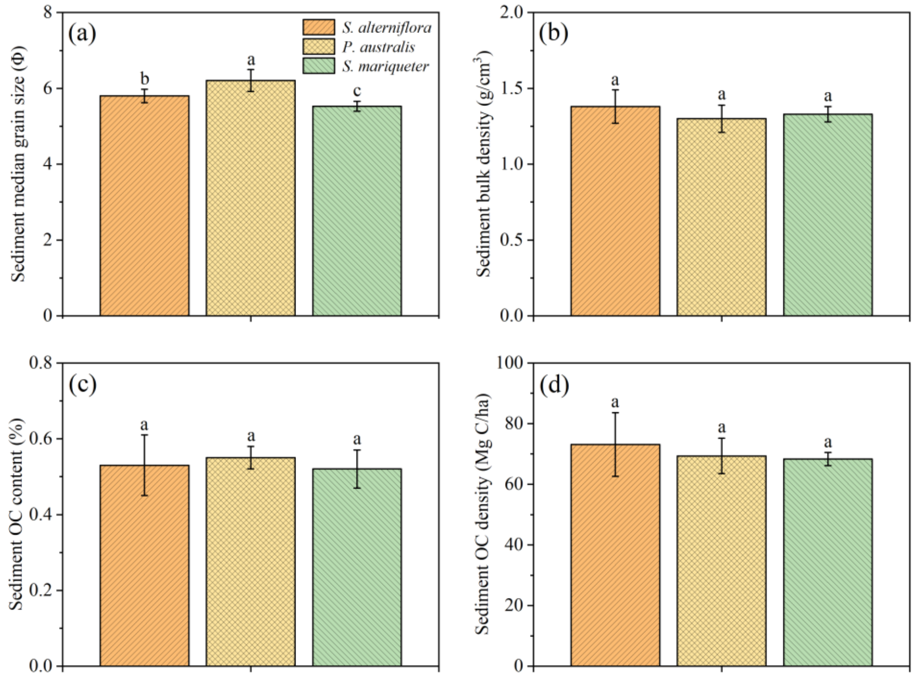

Figure 4. *The sediment median grain size (a), bulk density (b), OC content (c), and OC density (d) of S. alterniflora, P. australis, and S. mariqueter in the study area. Different lowercase letters signify the significant differences in the same indicators among different plants (p < 0.05, ANOVA, LSD post-hoc test)*

Sediment carbon density

Based on sediment bulk density and OC measurements, the SOCD within the study area was determined. The results showed that the average SOCD of *S. alterniflora* marsh was 73.08 ± 10.48 Mg/ha, slightly higher than that of *P. australis* (69.33 ± 5.84 Mg/ha) and *S. mariqueter* (68.31 ± 2.14 Mg/ha) (*Fig. 4d*). However, no statistically significant differences were observed among the three species ($p > 0.05$). Compared to vegetation biomass, the sediments in this region exhibit a greater carbon sequestration potential. Specifically, the average SOCD for *S. alterniflora*, *P. australis*, and *S. mariqueter* is 6.8, 5.5, and 19.0 times that of the living vegetation, respectively. Furthermore, the SOCD varied across different layers of the three types of tidal marshes, with the middle layer exhibiting relatively higher SOCD (*Figs. 5j-l*). Statistical analysis revealed significant differences in SOCD between the individual layers of *S. alterniflora* and *S. mariqueter*, whereas no significant differences were observed between the layers of *P. australis*.

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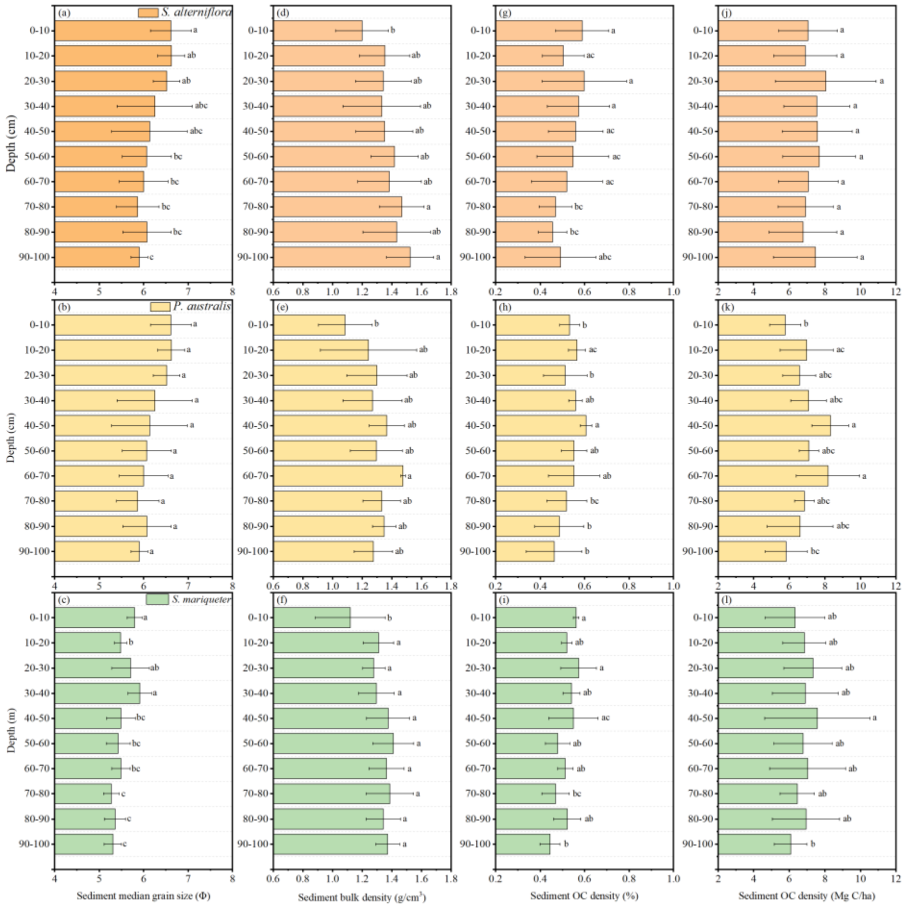

Figure 5. *The vertical variation of sediment median grain size (a-c), bulk density (d-f), OC content (g-i), and OC density (j-l) of S. alterniflora, P. australis, and S. mariqueter in the study area. Different lowercase letters signify the significant differences in the same indicators among different plants (p < 0.05, ANOVA, LSD post-hoc test)*

Assessment of carbon stock in tidal marshes

Utilizing OC density data from live vegetation, litter, and sediments, we evaluated the total OC density of various tidal marsh vegetations along the southern coast of Hangzhou Bay. The study revealed that during the sampling period, the average total OC densities for *S. alterniflora*, *P. australis*, and *S. mariqueter* tidal marshes were 84.07 ± 9.14 Mg/ha, 82.76 ± 4.75 Mg/ha, and 71.9 ± 5.96 Mg/ha, respectively (*Fig. 6a*). The live vegetation and litter of *S. alterniflora* and *P. australis* exhibited significantly higher OC density compared to *S. mariqueter*, leading to higher total OC densities for the former two species ($p < 0.05$). Nevertheless, no significant difference was observed between *S. alterniflora* and *P. australis* ($p > 0.05$).

In recent years, the persistent sedimentation of tidal flats has promoted the seaward expansion of *S. alterniflora*, indirectly enhancing the long-term carbon capture capacity of tidal marshes in southern Hangzhou Bay. Prior to the management of *S. alterniflora*, the total OC stock in these tidal marshes had already reached approximately $51.65\times10^4 \pm 4.20\times10^4$ Mg C. The largest contributor to this was the sediment, which held $46.05\times10^4 \pm 4.64\times10^4$ Mg C, accounting for 89.1% of the total. This was followed by live vegetation, storing $5.26\times10^4 \pm 1.31\times10^4$ Mg C, representing 10.2%, and litter, which had

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the lowest stock at $0.34{\times}10^4 \pm 0.12{\times}10^4$ Mg C, making up 0.7% of the total. Additionally, there were significant differences in carbon stock among various vegetation types. The OC stock for *S. alterniflora*, *P. australis*, and *S. mariqueter* tidal marshes were $37.09{\times}10^4 \pm 4.03{\times}10^4$ Mg C, $0.29{\times}10^4 \pm 0.02{\times}10^4$ Mg C, and $14.27{\times}10^4 \pm 1.18{\times}10^4$ Mg C, respectively, representing 71.8%, 0.6%, and 27.6% of the total (*Fig. 6b*). The OC stock of *S. alterniflora* was significantly higher than that of other vegetation types, and its management is expected to impact the carbon pool of the tidal marshes in this area, mainly by directly altering the vegetation carbon pool through the removal of aboveground live plants and roots.

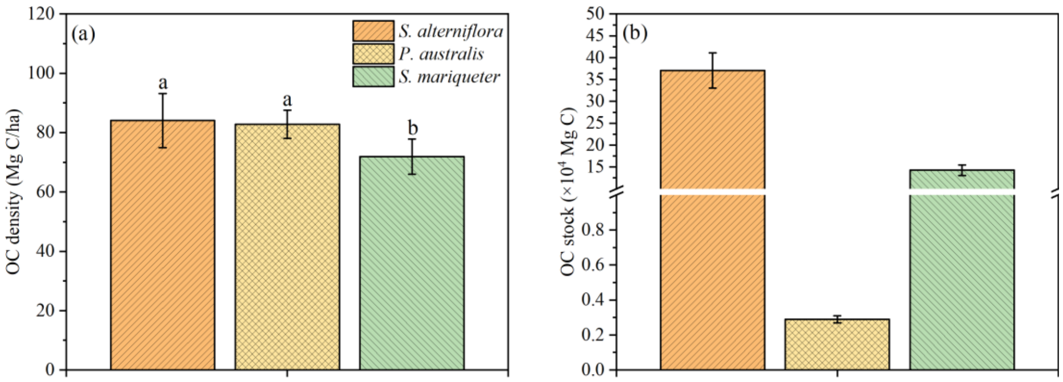

***Figure 6.** The total OC density (a) and OC stock (b) of S. alterniflora, P. australis, and S. mariqueter in the study area. Different lowercase letters signify the significant differences in the same indicators among different plants ($p < 0.05$, rank-sum test)*

Discussion

Factors influencing carbon stocks in tidal marshes

Tidal marsh carbon pools can be categorized into vegetation carbon pools (including live vegetation and litter) and sediment carbon pools, depending on the medium of OC storage (Chen and Chen, 2023; Li et al., 2024). Variations in biomass and sediment characteristics among different tidal marsh vegetations result in distinct carbon sequestration capacities (Van de Broek et al., 2018; Cai et al., 2023). The carbon storage capacity in vegetation is primarily determined by biomass and OC content. In the study area, the biomass of live *S. alterniflora* and *P. australis* is approximately 3.2 and 4.2 times greater than that of *S. mariqueter*, respectively. Moreover, the aboveground OC content in live vegetation is significantly higher in *S. alterniflora* and *P. australis* compared to *S. mariqueter*. Additionally, more litter was observed in *S. alterniflora* and *P. australis* quadrants, whereas no litter was found in *S. mariqueter* areas. As a result of these factors, carbon sequestration per unit area is significantly higher in *P. australis* and *S. alterniflora* compared to *S. mariqueter* in the study area.

Additionally, it is important to note that carbon sequestration in tidal marsh vegetation exhibits seasonal variations. Vegetation biomass steadily increases post-germination in the spring, with most plants reaching their maximum biomass in late summer and early autumn. Conversely, the OC content within the vegetation fluctuates across different developmental stages. For example, the OC content in the stems of *S. alterniflora* initially declines and then increases throughout the growth period in Jiaozhou Bay and the Yangtze River estuary (Liu et al., 2013; Fan et al., 2019). Nonetheless, the overall

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fluctuation in OC content throughout developmental stages is less pronounced compared to biomass. Additionally, our research indicates that the OC content in the aboveground parts of various vegetation types on the southern shore of Hangzhou Bay is higher than in the underground roots. This discrepancy is mainly attributed to the greater metabolic and productive activity in aboveground plants, which absorb and store more carbon. The roots primarily serve to supply nutrients to the aboveground parts, resulting in a relatively lower OC content (Pan et al., 2012).

Compared to vegetation carbon pools, sediment carbon pools have a more significant impact on the carbon storage capacity of blue carbon ecosystems (Tang et al., 2018; Senger et al., 2021). This study found that sediment carbon stock in various vegetated tidal marshes accounted for 83.8% to 95.0% of the total carbon stock, and in some regions, it even exceeded 98% (Duarte et al., 2013). OC in tidal marsh sediments originates partly from the decomposition of dead vegetation and partly from terrestrial and marine origin, with notable regional differences in these proportions (Van de Broek et al., 2018; Chen and Chen, 2023). The carbon-nitrogen ratio results for tidal marsh sediments along the southern coast of Hangzhou Bay indicate that the sediment carbon pool in this region is primarily influenced by marine organic matter input (Xia et al., 2019). In this study, sediment particles in tidal marshes exhibit a general trend of coarsening from land to sea. This trend suggests that hydrodynamic intensity decreases from *P. australis* and *S. alterniflora* marshes to *S. mariqueter* marshes. Weaker hydrodynamic intensity promotes the deposition of materials from the open sea, leading to higher OC content in the sediments of *P. australis* and *S. alterniflora* compared to *S. mariqueter*.

Regarding the properties of the sediment itself, finer particles exhibit a larger specific surface area, which facilitates organic matter adsorption and results in higher OC content in fine-grained sediments (Burdige, 2007). This study identified a positive correlation ($p < 0.05$) between OC content and median grain size in sediments from various depths across different sampling sites, indicating that sediment grain size is a crucial factor influencing OC content (*Fig. 7a*). This correlation has been confirmed in locations such as Yancheng and the Yangtze River Estuary (Yuan et al., 2020; Peng et al., 2023). Additionally, a significant positive correlation ($p < 0.05$) was observed between sediment water content and OC content in this region (*Fig. 7b*). Water content primarily affects internal aeration and the distribution of dissolved oxygen within sediments (Luo et al., 2019). In sediments with higher water content, oxygen availability decreases, leading to greater anaerobic mineralization, reduced microbial activity, slowed decomposition of organic matter, and easier accumulation of soil organic carbon (Chapman et al., 2019; Erb et al., 2024). Conversely, when water content decreases, oxygen diffuses into deeper sediment layers, stimulating aerobic respiration and increasing the decomposition rate of organic carbon in the sediments (Han et al., 2015). However, the variation in OC density among sediments from different vegetation types in the study area is less pronounced compared to the differences in plant biomass. This is due to the significantly smaller differences in bulk density and OC content of the sediments among the three vegetation types.

Impact of S. alterniflora invasion and management

The invasion of *S. alterniflora* not only modifies vegetation composition but also alters sediment grain size, pore structure, mineralization rate, redox potential, and microbial diversity, which collectively impact the OC storage capacity of tidal marshes (Sardans et al., 2017; Zhang et al., 2018). Given the substantial variation in carbon sequestration

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potential across different regions and vegetation types, the influence of *S. alterniflora* invasion on OC stocks is inconsistent. Typically, when *S. alterniflora* invades mudflats or native vegetation communities with low OC content, it tends to enhance the carbon stock of the affected area to some degree. For instance, Zhang et al. (2018) observed that in the Yellow River Delta, the OC density of native vegetation tidal marsh sediments in the upper 100 cm ranged from 2.32–2.73 kg/m², and following *S. alterniflora* invasion, this density increased to 3.04–3.45 kg/m². In the Hangzhou Bay region, the sediment OC burial rates for *S. alterniflora*, *S. mariqueter*, and mudflat regions were 1.59 Mg C/ha·a, 1.39 Mg C/ha·a, and 0.63 Mg C /ha·a, respectively, indicating that the invasion of *S. alterniflora* enhanced the carbon sequestration capacity of coastal wetlands in that area (Cai et al., 2023). Conversely, in regions such as mangroves where OC stocks are higher, *S. alterniflora* invasion can result in a decrease in the original carbon stock (Xu et al., 2022). This study found no significant difference in the OC density of plants and sediments between *S. alterniflora* and *P. australis* tidal marshes along the southern coast of Hangzhou Bay ($p > 0.05$). This suggests that *S. alterniflora* invasion in *P. australis* tidal marshes does not significantly modify the original tidal marsh OC stock. On the other hand, when *S. alterniflora* invades *S. mariqueter* tidal marshes, it partially increases the OC stock of the original tidal marsh vegetation due to its significantly higher plant OC density compared to *S. mariqueter* ($p < 0.05$). However, this invasion does not have a significant impact on the sediment OC density ($p > 0.05$).

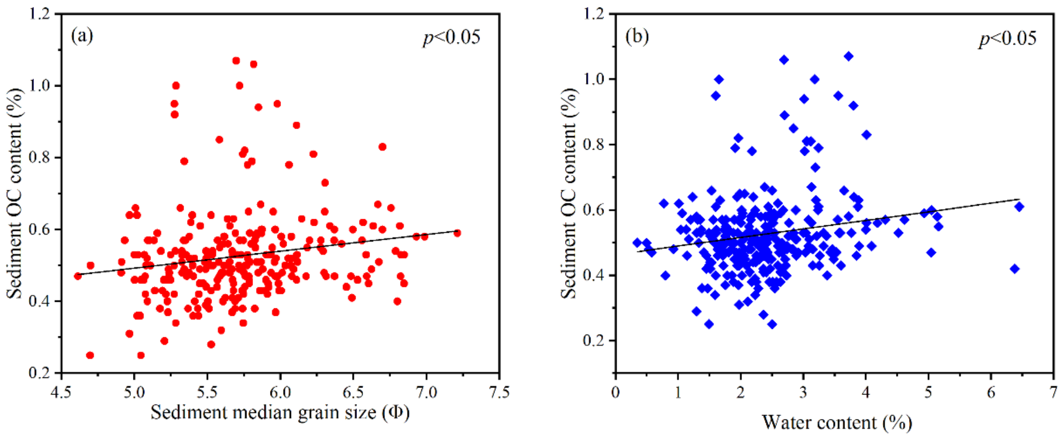

Figure 7. *Comparison of OC content and median grain size in sediments of P. australis, S. alterniflora, and S. mariqueter, and their variations from land to sea (a). Relationships between OC concent with median grain size (b) and water content (c) were analyzed in all sediment samples*

If *S. alterniflora* is eradicated from the southern shore of Hangzhou Bay, the tidal marsh vegetation carbon pool in this area is projected to decrease by $4.50 \times 10^4 \pm 1.31 \times 10^4$ Mg C, approximately 8.7% of the total tidal marsh carbon stock prior to management. Typically, the aboveground biomass and belowground roots of the removed plants would eventually be buried in the sediment. Influenced by the microbial carbon pump, the OC stored in these plants would integrate into the sediment carbon pool (Liang et al., 2017; Erb et al., 2024). And the carbon sequestered in the tidal marshes of this region predominantly originates from allochthonous OC, with a comparatively smaller portion derived from autochthonous OC from the macrophytes (Xia et al., 2019).

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Consequently, the short-term effect of *S. alterniflora* management on tidal marsh carbon stock in this area is expected to be negligible. In particular, the practice of harvesting plant biomass and burying it in soil has proven to be an effective strategy for carbon sequestration (Zeng et al., 2013; Keiblinger et al., 2023). According to the management strategy for *S. alterniflora* in southern Hangzhou Bay, the removed plant biomass will be buried at depths greater than 1 meter. This method not only effectively prevents the re-establishment of the invasive species but also positively influences OC accumulation and long-term sequestration.

Furthermore, compared to C_3 plants such as *P. australis*, the C_4 plant *S. alterniflora* has demonstrated a higher capacity for greenhouse gas emissions (Wails et al., 2021). Fuchs et al. (2025) analyzed CH_4 and N_2O emissions data before and after the invasion of *S. alterniflora* and *P. australis* in multiple regions, finding that total emissions flux increased from 37.1 CO_2e ha^{-1} $year^{-1}$ to 57.1 CO_2e ha^{-1} $year^{-1}$ in the *S. alterniflora* invasion zone, whereas in the *P. australis* invasion zone, it decreased from 34.1 CO_2e ha^{-1} $year^{-1}$ to 29.1 CO_2e ha^{-1} $year^{-1}$. Several studies have similarly demonstrated that CH_4 emissions from *S. alterniflora* marshes in China's coastal zone are significantly higher than those from native vegetation marshes (Zhang et al., 2011; Liu et al., 2019). The removal of *S. alterniflora* a in this region is expected to reduce greenhouse gas emissions, thereby indirectly enhancing the carbon sequestration capacity of tidal marshes. However, this hypothesis requires further validation with additional data.

Based on the restoration guidelines outlined in the special action plan for controlling *S. alterniflora*, managed regions may transition to mudflats or *P. australis* tidal marshes. The local climate is not conducive to mangrove growth, and the elevation and sediment characteristics of the original *S. alterniflora* habitat impede the survival of *S. mariqueter*. Nevertheless, *P. australis* has already been coexisting with *S. alterniflora*, indicating that planting *P. australis* in the managed area is feasible. Given that the carbon sequestration capacity of mudflats is significantly lower than that of *S. alterniflora* tidal marshes (Cai et al., 2023), it is recommended to promptly initiate *P. australis* vegetation restoration after the removal of *S. alterniflora*. This approach would also positively impact the stability of the tidal flats and enhance biodiversity in the area. However, it is crucial to understand that the increase in biodiversity within tidal marshes after the removal of *S. alterniflora* is not immediately observable. Compared to waterbirds, the recovery of benthic organisms is generally slower and may take over a year (Lyu et al., 2023). The removal of *S. alterniflora* represents only the initial phase of restoration. Developing subsequent scientifically informed strategies is imperative to bolster the ecological functions of coastal salt marshes. Additionally, it is essential to intensify the monitoring of restoration outcomes to prevent adverse effects on the habitat due to changes in vegetation type (Choi et al., 2022).

Given the diverse restoration measures implemented across various regions post-control of *S. alterniflora*, coupled with the considerable differences in the carbon sequestration capacity of blue carbon ecosystems along the Chinese coastline (Wang et al., 2023), we refrained from predicting the impact of large-scale *S. alterniflora* control on the structure and extent of tidal marsh carbon pools. Additionally, the nationwide eradication of *S. alterniflora* is incomplete, necessitating long-term monitoring studies to precisely evaluate the prolonged effects of *S. alterniflora* control on tidal marsh carbon pools in China. Despite the challenges in quantifying the large-scale, long-term impacts on carbon pools following the removal of *S. alterniflora*, the species' notable carbon sequestration function introduces new challenges in the protection and management of

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China's coastal wetlands. Specifically, it raises the need for an effective and scientific approach to combining invasive species control with the enhancement of carbon sequestration capacity.

Based on research by Yan et al. (2018) and Xu et al. (2022), as well as the findings of this study, it is recommended that northern and southern coastal provinces and cities prioritize *P. australis* and native mangroves for restoration in areas where *S. alterniflora* has been controlled. This should be based on a thorough assessment of habitat suitability. These restoration strategies will help prevent the reduction of carbon stock in coastal wetlands and mitigate the recurrence of *S. alterniflora*, reducing the likelihood of reinvasion (Wang et al., 2008; Chen et al., 2014). In conclusion, the adoption of reasonable and scientifically sound restoration methods, alongside the control of *S. alterniflora* and the restoration of native vegetation, will significantly enhance the ecological service functions of China's coastal wetlands.

Conclusion

Based on field data collected from the southern coast of Hangzhou Bay during the control of *S. alterniflora*, this study evaluated the potential effects of *S. alterniflora* invasion and its management on tidal marsh carbon stocks. The findings reveal that *S. alterniflora* stores more carbon per unit area than *S. mariqueter*. When *S. alterniflora* invades *S. mariqueter* tidal marshes, carbon storage is likely to increase, whereas no significant enhancement is observed in *P. australis* tidal marshes. Prior to management intervention, the tidal marsh OC stock in this region was approximately $51.65 \times 10^4 \pm 4.20 \times 10^4$ Mg C, while the post-management loss of live vegetation OC stock is estimated to be around $4.50 \times 10^4 \pm 1.31 \times 10^4$ Mg C. The overall tidal marsh OC stock is not anticipated to be significantly affected in the short term by the management of *S. alterniflora*, as a portion of the lost vegetation carbon stock is expected to convert to sediment carbon stock.

The carbon sequestration capacity of *P. australis* is comparable to that of *S. alterniflora* in this region. Given the habitat suitability and the need to maintain the ecological functions of coastal wetlands, we recommend the timely restoration of *P. australis* vegetation in areas where *S. alterniflora* has been managed. Additionally, we suggest prioritizing *P. australis* and native mangroves as alternative species in suitable habitats along the Chinese coast following the removal of *S. alterniflora*. This comprehensive approach aims to ensure the effectiveness of *S. alterniflora* management and enhance coastal wetland carbon sinks. It is important to note that this study only assessed the short-term potential impact of *S. alterniflora* management on the structure and scale of tidal marsh carbon stocks along the southern coast of Hangzhou Bay. Future research should incorporate data from more regions and over longer time scales to gain a deeper and more accurate understanding of the impact of *S. alterniflora* management on tidal marsh carbon sequestration in China. This will facilitate the development of more targeted restoration recommendations and better support the continuous improvement of the ecological functions of coastal wetlands nationwide.

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