Effects of Salinity and Inundation on Carbon Storage of Tidal Salt Marsh Vegetation in the Yangtze River Estuary: Postprint

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Abstract

Halophytes serve as "temporary pools" for organic carbon storage in salt marshes and constitute a primary source of soil organic carbon accumulation; the magnitude of their carbon storage is crucial for the "carbon sink" function of salt marsh ecosystems. Using the native species Phragmites australis and Scirpus mariqueter, along with the invasive species Spartina alterniflora in the Yangtze River estuary tidal flats as study subjects, single-factor pot experiments were conducted to simulate and analyze the effects of varying inundation salinity (0, 5, 10, 15, 25, and 35), inundation depth (0, 10, 20, 40, 60 cm, and 80 cm), and inundation frequency (daily, every 3 days, every 7 days, every 10 days, and every 15 days) on aboveground, belowground, and total carbon storage of each halophyte. The results demonstrated that with increasing inundation salinity, aboveground and total carbon storage in Phragmites australis, Spartina alterniflora, and Scirpus mariqueter all decreased significantly. Soil salinity could explain 47.2%, 66.5%, and 72.7% of the variation in aboveground carbon storage, and 34.7%, 45.0%, and 62.0% of the variation in total carbon storage, respectively. With increasing inundation depth, aboveground carbon storage in Phragmites australis, total carbon storage in Phragmites australis, and aboveground carbon storage in Scirpus mariqueter all decreased significantly, with 68.6%, 28.5%, and 71.1% of their variation attributable to changes in inundation depth (10–80 cm). Spartina alterniflora maintained relatively high aboveground and total carbon storage even at 80 cm inundation depth. The responses of carbon storage to inundation frequency variations did not differ significantly among the three halophytes, and differences in belowground carbon storage across all treatments also failed to reach significant levels. Overall, Spartina alterniflora exhibited greater tolerance to water-salt stress than the native species Phragmites australis and Scirpus mariqueter. Although Spartina alterniflora and Phragmites australis possessed relatively high carbon storage, the significant inhibitory effects of water-salt stress on their carbon storage cannot be overlooked. The carbon storage of Scirpus mariqueter was inherently low, with limited organic carbon input to the soil; adverse stressors such as sea-level rise and saltwater intrusion would further diminish its contribution to the salt marsh "carbon sink."

Full Text

Preamble

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Effects of Salinity and Inundation on Carbon Storage of Halophytes in the Tidal Salt Marsh of the Yangtze River Estuary, China

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Abstract

Halophytes are the key component of estuarine ecosystems and possess tremendous capacity to capture atmospheric carbon dioxide (CO) through photosynthesis, storing organic compounds in plant tissues to form a temporary pool of fixed carbon. Soil carbon primarily originates from decayed aboveground and belowground plant tissues, constituting a long-term carbon pool that holds considerable potential for climate change mitigation and adaptation. Estuarine salt marshes have been identified as important natural carbon sinks that are highly susceptible to human- and climate-driven threats. Understanding how halophytes respond to environmental stresses becomes increasingly important under anticipated sea-level rise and aggravated saltwater intrusion. This study focused specifically on carbon storage of halophytes and highlighted the importance of salinity and inundation regimes as crucial abiotic drivers influencing the ability of halophytes to alter carbon input into the soil.

Controlled outdoor pot experiments were conducted to quantify the independent impacts of flooding salinity (0, 5, 10, 15, 25, and 35), flooding depth (0, 10, 20, 40, 60, and 80 cm), and flooding frequency (every day, every 3 days, every 7 days, every 10 days, and every 15 days) on three dominant halophytes in the Yangtze River Estuary: the native species *Phragmites australis* and *Scirpus mariqueter*, and the invasive species *Spartina alterniflora*.

With increasing flooding salinity, both aboveground and total carbon storage of *S. alterniflora* and *S. mariqueter* decreased significantly ($P < 0.05$). Soil salinity could explain approximately 47.2%, 66.5%, and 72.7% of the variation in aboveground carbon storage, and 34.7%, 45.0%, and 62.0% of the variation in total carbon storage for *P. australis*, *S. alterniflora*, and *S. mariqueter*, respectively. Elevated flooding depth exerted significant effects on aboveground and total carbon storage of *P. australis* and *S. mariqueter*, with approximately 68.6%, 28.5%, and 71.1% of their variations caused by gradient changes in flooding depth (10-80 cm). In contrast, *S. alterniflora* still maintained high aboveground and total carbon storage at a flooding depth of 80 cm, with less severe impact than on the two native species. No significant differences were observed in the flooding frequency treatments or in belowground carbon storage of each species among all treatments. Elevated flooding salinity and depth caused by rising sea levels and saltwater intrusion might lead to significant decreases in carbon storage of these three halophytes, which could directly affect soil carbon pools through limited input of plant carbon into the soil. For *S. mariqueter*, these stressful environmental conditions would potentially further weaken its low carbon storage capacity, thus making a "negligible" contribution to carbon sinks of estuarine salt marshes. Although carbon storage was higher in *S. alterniflora* and *P. australis* than in *S. mariqueter*, the negative responses to elevated salinity and inundation regimes should not be ignored.

Keywords: halophyte; salinity; flooding; carbon storage; sea-level rise; Yangtze River Estuary

1. Introduction

Estuarine and coastal salt marshes have become hotspots in ecological research due to their significant carbon sequestration functions and rapid responses to global change [1-3]. As an essential component of salt marsh ecosystems, halophytes can fix atmospheric CO through photosynthesis and convert synthesized organic matter into their own biomass, which enters the ecosystem [4-5]. After plant senescence and death, residues deposit and become buried in soil, representing the primary pathway for organic carbon input into salt marsh ecosystems [5-6]. The unique geographical location at the intersection of land and sea facilitates the reception of large amounts of organic matter and nutrients transported by runoff and tides [2], which can supplement nutrients required for growth and development to some extent. Plants can also directly capture carbon-bearing sediment suspensions through their branches and leaves, and reduce turbulence energy through the buffering effect of plant communities, thereby influencing sedimentation rates of suspended particles in tidal water and helping maintain relatively high primary productivity [1,7]. These two mechanisms of capture jointly promote vertical accretion of salt marsh surfaces and are critical for realizing carbon sequestration functions.

With decreasing distance from the sea across salt marsh surfaces, terrain gradually lowers, and the degree of disturbance from tides and storm surges increases significantly, making abiotic stress more severe. For most plants, this represents an extremely stressful habitat environment [9-10]. The ability of halophytes to colonize these environments reflects their strong adaptability to tidal flat physical and chemical conditions [10-11]. Soil salinity gradients and inundation gradients that co-vary with elevation within the tidal range are recognized as key stress factors affecting halophyte growth, reproduction, and spatial distribution [9-10]. However, against the backdrop of global climate change, accompanied by intense human activity interference, increased frequency and intensity of storm surges seriously affect the stability of salt marsh ecosystem structure and function [12-13], further leading to changes in the water-salt environment of tidal flats by raising the base water level of tidal action, causing increased inundation depth and frequency, and aggravating saltwater intrusion.

The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) indicated a global sea-level rise rate of approximately 3.2 mm/a. According to monitoring data from the U.S. National Oceanic and Atmospheric Administration (NOAA), the sea-level rise rate at Lüsi Station in the Yangtze Estuary (Qidong, Jiangsu) reached 4.97 mm/a (1961-2011), and 3.7 mm/a (1993-2015), higher than the global average. High sea levels can cause coastal erosion and saltwater intrusion. In February 1993, saltwater intrusion at the Yangtze Estuary lasted over 20 days, with the maximum chloride concentration at the Qingcaosha Reservoir intake reaching 5000 mg/L. Excessive inundation or high-salinity environments can directly limit halophyte primary productivity and reduce plant carbon storage, and can also decrease the efficiency of plant branches and leaves in capturing suspended sediment particles, thereby altering organic carbon accumulation and cycling processes in salt marsh ecosystems.

Although the Yangtze Estuary salt marsh plant community composition is simple, with gradual zonation from sea to land and obvious abiotic stress gradients—providing an ideal experimental site for analyzing the effects of water-salt environmental changes on carbon storage capacity—it must be acknowledged that the current scale and spatial distribution pattern of salt marsh carbon storage result from the combined effects of multiple factors. It is difficult to exclude interference from other biotic or abiotic factors, quantify the actual contribution of different environmental factors to variation in carbon storage of different halophytes, or accurately simulate the impacts of extreme environmental changes such as sea-level rise and saltwater intrusion. This study employed pot cultivation control experiments to divide water-salt changes brought by tidal action into three factors: flooding salinity, flooding depth, and flooding frequency, to explore the response of halophyte carbon storage to changes in single environmental factors. This is of great significance for enriching research on carbon cycling in coastal wetland ecosystems, coping with sea-level rise, and developing strategies for enhancing salt marsh ecosystem functions. It also provides a beneficial and necessary supplement to field sampling and observation experiments.

2. Study Area

Chongming Dongtan (31°25 -31°38 N, 121°50 -122°05 E) is located in the eastern part of Chongming Island and represents the largest and most developed estuarine tidal flat wetland in the Yangtze River Estuary, playing important roles in climate regulation, siltation, and storm surge resistance [17-18]. The area was listed as an internationally important wetland in 2002 and promoted to a national nature reserve in 2005. Situated in the marine monsoon climate zone of eastern Eurasia and northern Asia, the region has an average annual temperature of 15.3°C, average annual sunshine hours of 2138 h, a frost-free period of 229 days, and average annual rainfall of 1022 mm. Summer tropical cyclones and accompanying heavy rains and storm surges occasionally occur [19-20].

Chongming Dongtan experiences irregular semidiurnal tides with two flood and ebb processes daily, and two spring tides monthly. The maximum and average tidal ranges are 4.62-5.95 m and 1.96-3.08 m, respectively, with pronounced diurnal inequality. Due to needs for siltation and coastline stabilization, *Spartina alterniflora* was introduced. Salt marsh vegetation is dominated by *Phragmites australis* communities, *Scirpus mariqueter* communities, and *S. alterniflora* communities [17,20]. Due to its strong adaptability and dispersal ability, *S. alterniflora* rapidly developed into one of the dominant species in the region, forming a typical vegetation zonation pattern of *S. mariqueter* zone, *S. alterniflora* zone, and *P. australis* zone [22]. Recent ecological control of *S. alterniflora* and restoration of *S. mariqueter* populations have significantly affected the spatial pattern of salt marsh vegetation in Chongming Dongtan, particularly with the distribution range of *S. alterniflora* being markedly reduced.

3. Experimental Design

This study selected three typical halophytes from the Yangtze River Estuary tidal flats: the native species *Phragmites australis* and *Scirpus mariqueter*, and the invasive species *Spartina alterniflora*. Single-factor pot experiments were established to quantify the effects of flooding salinity (0, 5, 10, 15, 25, and 35), flooding depth (0, 10, 20, 40, 60, and 80 cm), and flooding frequency (every day, every 3 days, every 7 days, every 10 days, and every 15 days) on aboveground, belowground, and total carbon storage of halophytes. To highlight the effects of single environmental factor gradients, the other two factors were uniformly set to common environmental conditions in Chongming Dongtan salt marshes. In the flooding salinity experiment, flooding depth and frequency were set at 20 cm and once daily, respectively, to simulate diurnal tides. In the flooding depth experiment, flooding salinity and frequency were set at 5 and once daily, respectively. In the flooding frequency experiment, flooding salinity and depth were set at 5 and 20 cm, respectively. Since Chongming Dongtan experiences rapid tidal flooding with each vegetation zone submerged for about 4-5 hours, and the time difference from bare flat to each vegetation zone experiencing tide is small, short-term simulated tidal control experiments cannot accurately reflect differences caused by small inundation time variations. Therefore, flooding frequency was not included as a treatment factor, and single inundation time was set at 4-5 hours (5-9 am and 5-9 pm), simplifying the diurnal inequality pattern of tides.

In early March, target plant clones of uniform height, healthy growth, and undisturbed status were excavated from intertidal zones of Chongming Dongtan, ensuring intact root systems with native soil. After trimming aboveground parts to 20-30 cm, plants were transplanted into pots (32 cm diameter, 26 cm height) at field density once new shoots emerged (2-5 cm for *S. mariqueter*). *P. australis* and *S. alterniflora* were transplanted directly, while *S. mariqueter* received a buffer period due to its shallow root system and small seedling size. The experiment included a pre-cultivation period (7-10 days) and a treatment period; stress treatments were not applied immediately after transplanting to minimize effects of transplant shock on results. *S. mariqueter* was treated earlier due to its phenological characteristics. No rooting powder or slow-release fertilizer was applied during the experiment. Potted plants showed no disease or pest damage, and weeds were removed weekly to avoid interspecific competition effects.

Plant densities in experimental pots were 306±32 (n=51) for *P. australis*, 48±9 (n=51) for *S. alterniflora*, and 12±2 (n=51) for *S. mariqueter*, with no significant differences in background soil salinity among pot types. Each tidal simulation device consisted of two water tanks (97 cm and 70 cm height) connected by pipes and faucets at the bottom. One tank held target plants, the other held saline water of set concentration. For flooding depth treatments, larger buckets (100 cm and 135 cm height) were used. Simulations were achieved using water pumps, with pump operation time not counted as inundation time. Artificial seawater salt and filtered ditch water were used; freshwater (0 salinity) used tap water or rainwater that flowed through the device once and was discarded, while other saline solutions were recycled. Portable salinometers (Master-S/Mill , ATAGO) were used to measure and adjust salinity before each treatment by adding salt or water to meet requirements.

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4. Analysis Methods

After the control experiment, aboveground parts of *P. australis* and *S. alterniflora* were harvested, while *S. mariqueter* was harvested completely. All plants were cut at ground level, separated into stems, leaves, fruits, and standing dead material, placed in paper bags, oven-dried at 105°C, and weighed. After aboveground biomass harvest, a PVC tube (4.5 cm diameter) was inserted to the bottom of each pot to collect a soil column (0-30 cm), which was washed to remove impurities. After drying, rhizomes and fibrous roots were obtained as belowground biomass. Aboveground and belowground biomass together constituted total biomass, all converted to dry weight per unit area (g/m^2). Dried plant component samples were ground to measure organic carbon content using an elemental analyzer (Vario Macro, Elementar Analysensysteme GmbH). Carbon storage of each component was calculated by multiplying biomass by organic carbon content, then summed to obtain aboveground, belowground, and total carbon storage for each plant. Soil salinity was monitored monthly using digital conductivity meters and converted to total salt content (g/kg).

Data analysis was performed using SPSS 22.0 and Origin 9.0. One-way ANOVA was used to test significance of differences in plant carbon storage across environmental gradients, with Least Significant Difference (LSD) tests for pairwise comparisons ($P < 0.05$). Data were transformed before analysis to meet normality and homogeneity of variance assumptions. Stepwise regression analysis quantified the relative contribution of environmental variation.

5. Results

5.1 Effects of Flooding Salinity on Plant Carbon Storage

With increasing flooding salinity, aboveground carbon storage of *S. alterniflora* and *S. mariqueter* decreased significantly ($P < 0.05$) [Figure 1a: see original paper]. Total carbon storage of all three species also decreased significantly with increasing salinity ($P < 0.05$), while belowground carbon storage differences were not significant ($P > 0.05$) [Figure 1b: see original paper]. Under seawater treatment (35), total carbon storage of *P. australis*, *S. alterniflora*, and *S. mariqueter* was only 51.0%, 57.2%, and 76.0% of that under freshwater treatment (0), and 57.4%, 76.4%, and 42.2% of that under brackish water treatment (15), respectively ($P < 0.05$).

Both aboveground and total carbon storage of *S. alterniflora* and *S. mariqueter* showed significant linear relationships with soil salinity ($P < 0.05$) [FIGURE:2a, 2b, 2e, 2f]. As soil salinity increased, aboveground and total carbon storage of all three halophytes decreased significantly ($P < 0.05$). Soil salinity explained 47.2%, 66.5%, and 72.7% of aboveground carbon storage variation, and 34.7%, 45.0%, and 62.0% of total carbon storage variation for *P. australis*, *S. alterniflora*, and *S. mariqueter*, respectively.

5.2 Effects of Flooding Depth on Plant Carbon Storage

With increasing flooding depth, aboveground carbon storage of *P. australis* and *S. mariqueter* decreased significantly ($P < 0.05$), while belowground carbon storage differences were not significant ($P > 0.05$) [Figure 1c: see original paper]. Total carbon storage of *P. australis* and *S. mariqueter* showed significant decreasing trends ($P < 0.05$). When flooding depth increased to 80 cm, *S. alterniflora* showed the opposite pattern, with increased aboveground and total carbon storage ($P < 0.05$) [Figure 1d: see original paper], but showed no clear response trend to increasing flooding depth. Flooding depth treatments (10-80 cm) were more favorable for aboveground and total carbon storage of *S. alterniflora*.

Monthly soil salinity monitoring revealed no significant differences in soil salinity among flooding depth treatments for the same plant type (10-80 cm, $P > 0.05$), but all were significantly higher than the 0 cm treatment ($P < 0.05$). Thus, differences in *S. alterniflora* and *S. mariqueter* carbon storage responses to flooding depth were unrelated to soil salinity. Regression equations were constructed between flooding depth (10-80 cm) and aboveground/total carbon storage of halophytes. Aboveground and total carbon storage of *P. australis* decreased significantly with increasing flooding depth ($P < 0.05$), with flooding depth explaining 68.6% and 28.5% of their variation, respectively [FIGURE:2c, 2d]. No significant linear relationships existed between aboveground, belowground, or total carbon storage of *S. alterniflora* and flooding depth ($P > 0.05$) [FIGURE:2g, 2h, 2i]. Aboveground carbon storage of *S. mariqueter* decreased significantly with increasing flooding depth ($P < 0.05$), with flooding depth explaining 71.1% of its variation [Figure 2k: see original paper], but total carbon storage showed no significant regression relationship with flooding depth ($P > 0.05$) [Figure 2l: see original paper].

5.3 Effects of Flooding Frequency on Plant Carbon Storage

No significant differences were observed in aboveground, belowground, or total carbon storage of the three halophytes among different flooding frequency treatments ($P > 0.05$). Monthly soil salinity monitoring showed that soil salinity under daily flooding treatment was significantly higher than under other frequencies ($P < 0.05$), but differences narrowed with extended treatment duration. Although flooding frequency affected carbon storage in relation to soil salinity, carbon storage did not show significant decreasing trends with increasing soil salinity.

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6. Discussion

6.1 Responses of Halophyte Carbon Storage to Water-Salt Changes

Water-salt changes represent the most typical environmental characteristics distinguishing estuarine and coastal salt marshes from other ecosystems. Soil salt content primarily threatens plant growth and development through osmotic stress (causing physiological drought) and ion stress [23]. Flooding often leads to low-oxygen or even anoxic soil conditions, affecting plants' ability to maintain normal metabolic processes [24]. All three halophytes showed sensitivity to water-salt stress. Plants mainly adopt two strategies to adapt: genetic differentiation at the gene level and phenotypic plasticity at the individual level, where individuals of the same species can differ in size, organ allocation, and reproductive strategies to increase environmental fitness [25]. Plant primary productivity and carbon storage serve as intuitive, comprehensive indicators after offsetting stress impacts, effectively reflecting tolerance to adverse conditions.

When flooding salinity increased from freshwater (0) to seawater (35), aboveground and total carbon storage of *S. alterniflora* decreased by 70.3% and 49.0%, respectively. Increasing flooding depth significantly reduced aboveground carbon storage of *P. australis* (49.5%) and *S. mariqueter* (77.8%), and total carbon storage of *P. australis* (42.6%) and *S. mariqueter* (57.8%). However, *S. alterniflora* maintained relatively high aboveground and total carbon storage even at 80 cm flooding depth, demonstrating stronger tolerance to water-salt stress than native *P. australis* and *S. mariqueter*, consistent with previous research [26-27]. Under current continuous sea-level rise and saltwater intrusion, these differences in tolerance among the three halophytes will to some extent promote the dominance and spatial expansion of *S. alterniflora* in community composition under stressful conditions, thereby affecting organic carbon accumulation dynamics in estuarine and coastal salt marsh ecosystems.

Plants and soil serve as the two major reservoirs of organic carbon storage in salt marsh ecosystems [1,28]. Plants act as precursors of soil organic matter [5], but due to growth cycle limitations, aboveground and belowground debris decomposes and transforms under soil microbial action after plant senescence and death, eventually stabilizing as soil organic carbon. In contrast to long-term, stable soil carbon accumulation, plant carbon storage is temporary. Under the water-salt gradients set in this study, carbon storage of all three halophytes was inhibited to varying degrees, significantly reducing plant carbon input to soil. Despite *S. alterniflora* and *P. australis* having relatively high plant carbon storage ((2597±590) g/m² (n=51) and (1533±318) g/m² (n=51), respectively), the inhibitory effects of sea-level rise and saltwater intrusion cannot be ignored. *S. mariqueter* had inherently low carbon storage ((636±168) g/m² (n=51)), and water-salt stress would further weaken its contribution to soil carbon pools.

6.2 Comparison of Carbon Storage Between Pot Experiments and Field Surveys

Comparative analysis of field survey data from different regions is influenced by many factors including climate conditions, nutrient supply, and genetic characteristics. To reduce regional differences, this study only selected field survey data from Chongming Dongtan, Jiuduansha, and Hangzhou Bay for comparison with control experiment results, aiming to examine the degree of limitation imposed by pot cultivation on halophyte carbon storage.

Aboveground carbon storage of *P. australis* in pots was lower than measurements by Mei and Zhang [29] and Shao et al. [30] in Chongming Dongtan and

Hangzhou Bay, but higher than measurements by Liu et al. [31] and Zhang [32] in Jiuduansha and Chongming Dongtan. Aboveground carbon storage of both *S. alterniflora* and *S. mariqueter* in pots was higher than field monitoring data. Due to limited belowground root carbon accumulation in pots, total carbon storage of *P. australis* was slightly lower than field data, while total carbon storage of *S. alterniflora* was similar to field data, and belowground and total carbon storage of *S. mariqueter* were higher than field survey data .

Although pot cultivation inevitably affected plant growth due to space limitations and mechanical damage from transplanting, it did not excessively restrict carbon storage magnitude and did not affect research on carbon storage responses to water-salt changes. The ranking of carbon storage among the three halophytes (*S. alterniflora* > *P. australis* > *S. mariqueter*) was consistent with field survey results from Chongming Dongtan [32], confirming the important contributions of *P. australis* and *S. alterniflora* to organic carbon accumulation in estuarine salt marshes [29-30].

Due to obvious spatiotemporal heterogeneity in organic carbon or nutrient input fluxes carried by freshwater runoff and tides, control experiments cannot accurately simulate natural nutrient conditions, so their effects on halophyte carbon storage were not considered. Water and salinity changes caused by sea-level rise and saltwater intrusion often occur simultaneously, but this study used single-factor control experiments to analyze quantitative relationships between halophytes and individual environmental factors. This approach is an important prerequisite for understanding complex ecological problems and forms the basis for evaluating the combined effects of environmental factors in ecosystems, though it does not consider interactions between factors and thus deviates somewhat from field reality. The next step requires understanding the coupling mechanisms between water and salinity and exploring the impacts of sea-level rise and saltwater intrusion on salt marsh carbon sequestration capacity over longer time scales, which is crucial for maintaining and enhancing the carbon sequestration potential of estuarine and coastal wetlands to cope with global climate change.

7. Conclusion

Spartina alterniflora had the highest aboveground, belowground, and total carbon storage, while *Scirpus mariqueter* had the lowest, indicating that *S. alterniflora* and *Phragmites australis* make important contributions to organic carbon accumulation in the Yangtze River Estuary salt marsh ecosystem. With intensifying water-salt stress, aboveground and total carbon storage of all three halophytes were inhibited to varying degrees, significantly reducing plant carbon input to soil. However, *S. alterniflora* demonstrated stronger tolerance to water-salt stress than native *P. australis* and *S. mariqueter*. The inherently low carbon storage of *S. mariqueter* means that sea-level rise and saltwater intrusion will further weaken its relative contribution to soil carbon pools.

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Note: Figure translations are in progress. See original paper for figures.