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The impacts of biotic and abiotic interaction on the spatial pattern of salt marshes in the Yangtze Estuary, China

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ABSTRACT

Over the past 20 years, *S. alterniflora*, as an exotic species, has invaded into large areas covered by the native salt-marsh vegetation in the Yangtze Estuary. The original spatial pattern "mudflat - *S. mariqueter* - *P. australis*" pattern in the Yangtze Estuary was disturbed due to *S. alterniflora* invasion and shifted to three types, i.e. original "mudflat - *S. mariqueter* - *P. australis*" pattern, new "mudflat - *S. alterniflora* - *P. australis*" pattern and transitional "mudflat - *S. mariqueter* - *S. alterniflora* - *P. australis*" pattern. Taking the Chongming Dongtan wetlands in the Yangtze Estuary as a study area, we examined inundation, sedimentary dynamic and hydrodynamic regimes to investigate their impacts on salt-marsh establishment and pattern shifts in coastal wetland ecosystem. The results showed that salt-marsh survival and growth significantly differed under inundation stress on different elevations. The survival thresholds of habitat elevation and inundation duration which determine salt-marsh establishment were identified as 1.9 m and 16 h day^{-1}for *S. mariqueter*, 2.5 m and 11 h day^{-1} for *S. alterniflora,* and 2.9 m and 9 h day^{-1}for *P. australis*. Both accretion/erosion dynamics and wave energy significantly differed among three types of advancing front, which further indicated that establishment and spatial pattern of salt-marsh were also greatly dependent on sedimentation dynamics and hydrodynamic regimes. Our study indicated *S. alterniflora* had sustainable competitive advantages, which might become aggressive and gradually replace *S. mariqueter* and *P. australis* in the future. Therefore, measures protecting native species should be strengthened and the impacts of invasive species on native ecosystem should be evaluated from more objective perspectives.

1. Introduction

All ecosystems are exposed to gradual changes in nature and human activity and respond to these changes in a smooth way (Scheffer et al., 2001). However, the ecosystems with alternative stable states would change abruptly when a major ecological threshold is exceeded due to global climate change and intense human impacts. Once ecosystem tips into a new but quite different dynamic equilibrium, it would influence the stability of ecosystem and present challenges to ecosystem conservation (Scheffer et al., 2001).

Estuarine and coastal wetlands play an important role in protecting coastal regions from storms and providing suitable habitats for several species (Kelleway et al., 2017). The spatial pattern of coastal salt-marsh ecosystems is a result of the long-term interaction between species (e.g. diversity, survival, growth, etc.) and their living environment (e.g. inundation, sedimentary dynamic and hydrodynamic regimes, etc.) (Morris et al., 2002; Early et al., 2016). Inundation regime, as a limiting factor, has important impacts on salt-marsh establishment and growth by inundation duration and submerged depth (Kirwan and Guntenspergen, 2012). Under field conditions, the coastal salt-marsh vegetation is usually inundated by seawater at high tide and exposed to air at low tide (Chen et al., 2005). Each type of salt-marsh vegetation has its own survival threshold to inundation duration (Ge et al., 2013; Voss et al., 2013). If the inundation duration exceeds the threshold of salt-marsh plant survival, the plant will not successfully establish and will be replaced by mudflat or other salt-marsh plants that are more resistant to inundation (Cui et al., 2015), which may change the original spatial pattern of salt-marsh vegetation. Sedimentary dynamic regime, such as accretion or erosion dynamics, also significantly affect salt-marsh establishment and expansion, and further affect the spatial pattern of salt-marsh vegetation (Schwarz et al., 2011; Zhu et al., 2012). In most estuaries, the lateral and vertical accretion or erosion have significant

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impacts on the establishment and expansion of salt marshes (Fagherazzi, 2008; Balke et al., 2013; Cao et al., 2014). For the muddy coasts with a high sediment loading in China, sediment deposition in coastal wetlands increases land elevation and the area of salt marshes, favoring the propagation and expansion of salt marshes (Ge et al., 2015). Moreover, hydrodynamic energy from currents and waves also strongly affects salt-marsh plants survival and establishment in the pioneer zone (Schwarz et al., 2011; Schwarz, 2013).

In the Yangtze Estuary, zonation of coastal wetland is associated with elevation and inundation duration (Ge et al., 2013). The typical spatial pattern is "mudflat - *S. mariqueter* - *P. australis*" along the elevation gradient from the sea to the seawall in the Yangtze Estuary (Zhu et al., 2012). Since 1990s, an exotic species *S. alterniflora* was introduced to the Yangtze Estuary for erosion control and dike protection (Ge et al., 2015). Due to its fast sexual reproduction and asexual propagation, *S. alterniflora* has rapidly colonized large areas of unvegetated mudflats and invaded zone formerly covered by native *P. australis* and *S. mariqueter*, becoming one of the dominant plant species there (Li and Zhang, 2008; Zhu et al., 2012). The area occupied by *S. alterniflora* was >6000 ha in the Yangtze Estuary in 2012 (Ge et al., 2015; Xue et al., 2018). As a result, the original spatial pattern, "mudflat - *S. mariqueter* - *P. australis*" along the elevation gradient from the sea to the seawall, was disturbed and shifted to three kinds of pattern of salt-marsh vegetation in the Yangtze Estuary. They are the original "mudflat - *S. mariqueter* - *P. australis*" pattern, new "mudflat - *S. alterniflora* - *P. australis*" pattern and transitional "mudflat - *S. mariqueter* - *S. alterniflora* - *P. australis*" pattern, respectively. Predicting the potential spread of invasive species is essential because they could threaten native species and change biogeochemical cycling, thus affecting ecosystem structure and functions (Schirmel et al., 2016; Tamura et al., 2017). However, there is still great uncertainty about the exact mechanism of spatial pattern shift of salt-marsh vegetation after *S. alterniflora* invation in the Yangtze Estuary. Therefore, it is essential to understand the expansion mechanism of saltmarshes for conservation of native species.

In this study, we investigated the potential response of salt-marsh vegetation in the Yangtze Estuary to *S. alterniflora* invasion to reveal the mechanism of spatial pattern shift of salt-marsh vegetation. Firstly, based on the constructed mesocosms experiments in the field, we investigated the survival and growth of three typical salt-marsh species under different elevation, and calculated the survival thresholds of salt marshes to elevation and inundation duration. Secondly, we tested the accretion/erosion dynamics and wave energy at three advancing fronts in the field. Thirdly, we investigated the establishment and expansion of exotic and native species at advancing fronts with the different geographical and hydrological features. Finally, we discussed the impact of inundation duration, sedimentary dynamic and hydrodynamic regimes on the spatial pattern shift of salt marshes after *S. alterniflora* invasion. The following questions were addressed: (1) dose exotic species *S. alterniflora* has same or higher thresholds to inundation duration than native species (*S. mariqueter* and *P. australis*)? (2) would the limitation of inundation thresholds to salt-marsh establishment and expansion be modified due to dynamic accretion? (3) would the spatial pattern shift of salt-marsh vegetation be regulated by the interaction of inundation, sedimentary dynamic and hydrodynamic regimes?

2. Materials and methods

2.1. Study area

The field experiment was conducted in the intertidal flat at

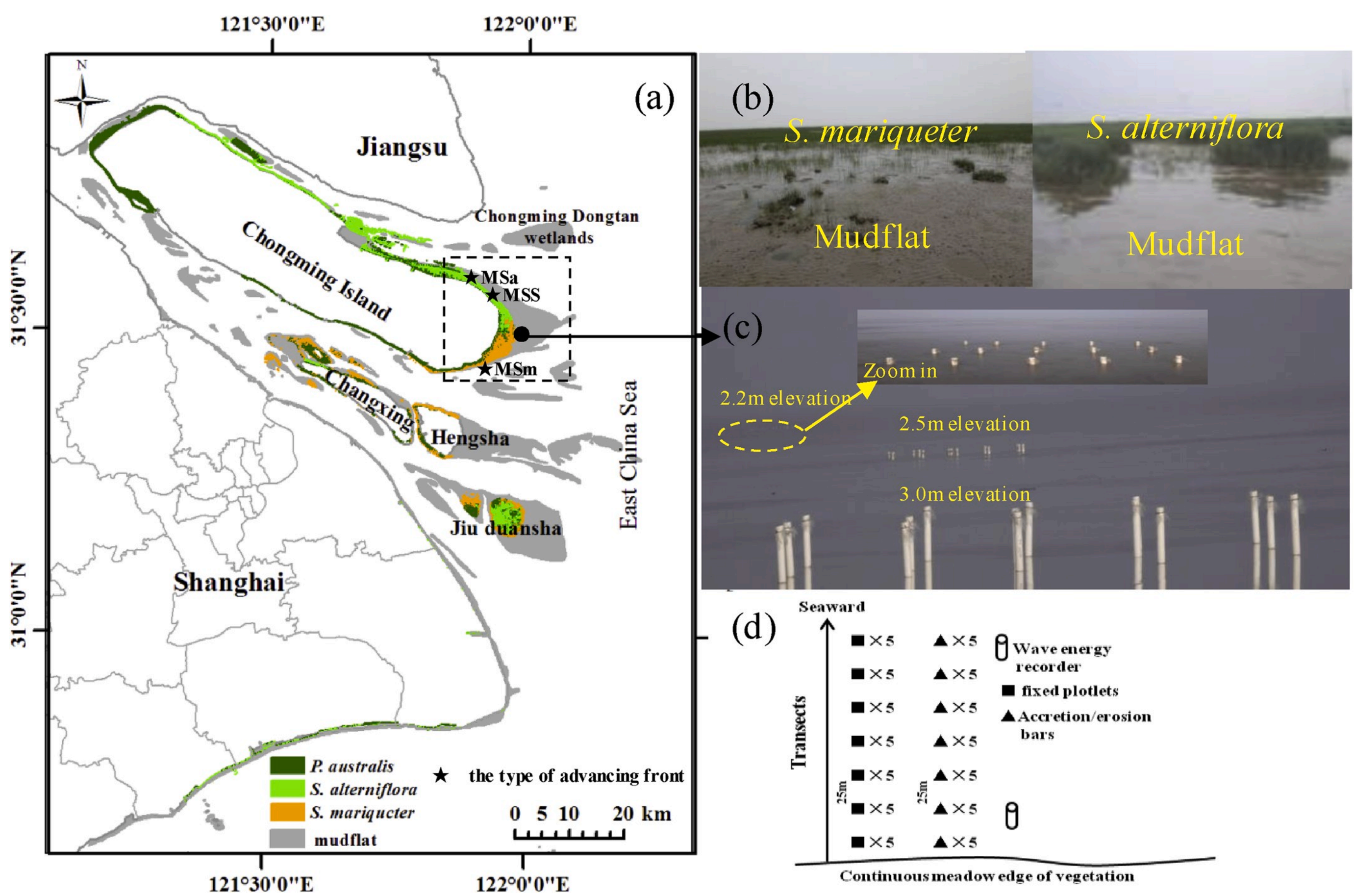

Fig. 1. Overview of the study area and experimental design.

Chongming Dongtan nature reserve in the Yangtze Estuary (31°25′ - 31°38′ N and 121°50′ - 122°05′ E) (Fig. 1a). It was created by the large amount of silt brought down by the Yangtze River (Huang and Zhang, 2007; Ge et al., 2014). The Chongming Dongtan wetland has an eastern Asian monsoon climate with an average humidity of 82% and annual temperature of 15.2–15.8 °C. The average summer and winter temperature is 26 °C and 3 °C, respectively (Wang et al., 2014). Annual precipitation is 1022 mm on average, 60% of which falls in summer months (Gao and Zhang, 2006; Xiao et al., 2009). The maximum and average tidal range is 4.62 m and 2.67 m, respectively (Gao and Zhang, 2006).

The total area of Chongming Dongtan wetlands is 213.2 km^2. The wetland habitats include tidal salt marshes, tidal mudflats and shallow open waters (Cui et al., 2015). *S. mariqueter* salt marshes, as pioneer communities, dominate in middle tidal flat. *P. australis* salt marshes dominate in high tidal flat. The vegetation advancing front was formed originally as "mudflat - *S. mariqueter* (MSm) front" in the north of Chongming Dongtan wetlands (Zhu et al., 2012) (Fig. 1a, b). *S. alterniflora*, one kind of exotic species, was introduced to the north of Chongming Dongtan in 1995. After its introduction, *S. alterniflora* had invaded large areas formerly covered by *P. australis* and *S. mariqueter,* and the area of *S. alterniflora* increased to almost 30.4% of the total intertidal salt-marsh vegetation in Chongming Dongtan (Ge et al., 2015). The typical advancing front (MSm) in Chongming Dongtan shifted to MSm front in the south, "mudflat - *S. alterniflora* (MSa) front" in the north and "mudflat - *S. mariqueter* - *S. alterniflora* (MSS) front" as transition between MSm front and MSa front (Fig. 1a, b).

2.2. Experiment design and survey

2.2.1. Field mesocosms experiment design

To obtain the thresholds of habitat elevation and inundation duration which determine salt-marsh establishment and growth, three platforms containing mesocosms of *S. alterniflora*, *S. mariqueter* and *P. australis* were constructed at different elevations (Fig. 1c) which simulated the response of salt-marsh survival to varying inundation duration and submergence depth. The mesocosms were planted on the open tidal flat during the growing season (April–October).

Each platform contained fifteen mesocosms that were composed of an 11 cm diameter (95 cm^2) PVC pipe for *S. alterniflora*, *S. mariqueter* and *P. australis*, with five replicates of each. The sediments from adjacent mudflat were filled into pipes. The pipes with mesocosms were buried 50–80 cm into the mudflat substrate, and three elevation levels (3.0 m, 2.5 m and 2.2 m, Fig. 1c) of the soil surface in the pipes were obtained. The elevation of the mesocosms was determined using a Real-Time Kinematic Global Position System (Ashtech, USA), and the double-rods method was used to determine the bed-level changes on the Chongming Dongtan wetland following Yang et al. (2005). The rims of the pipes were sawn to allow water leakage, avoiding waterlogging in the pipes. At early April in 2014, seedlings of *S. mariqueter*, *S. alterniflora* and *P. australis* were collected at the same tidal line on the Chongming Dongtan wetland and randomly transplanted to PVC pipes. Each PVC pipes planted five individuals.

2.2.2. Measurements of plants survival and growth under different habitat elevation

To investigate the effect of habitat elevation and inundation duration to salt-marsh plants survival and growth, the survival rates of *S. mariqueter*, *S. alterniflora* and *P. australis* were recorded weekly for every mesocosms between April and May (critical phase of plants survival) and monthly during June–October. The plant height, the number of flowering tillers and tillers in each mesocosms were recorded monthly during the growing season and during the flowering season, respectively. At the same time, three 50 cm × 50 cm quadrates of *S. mariqueter*, *S. alterniflora* and *P. australis* community were randomly selected near our mesocosms platforms as controls. The information of the tidal regimes in Chongming Dongtan (Sheshan tidal gauge station) referred to real-time monitoring and the official annals of the Shanghai Water Authority and the Shanghai Municipal Ocean Bureau.

2.2.3. Calculate thresholds to elevation and inundation duration

To build the relationship between plant survival and inundation duration (reflected by relative elevation), a simple elevation-based logistic function was used to explore the tipping point of the survival rate.

$$f(E) = \frac{1}{1 + \exp\left[\frac{-(E-a)}{k}\right]} \tag{1}$$

Where E is the mudflat elevation, a and k are the fitting parameters, respectively.

In general, the down-regulated curve of the logistic probability law constitutes three meaningful phases: the start of decline, steep decline and irretrievable point. In this study, we searched for the third point to reflect the tolerance threshold (tipping point, P) of plant survival to the inundation duration with a hypothesis (H) of the maximum-entropy.

$$\text{Max} \quad H(P) \;=\; (f^2(E+i) - f^2(E)) - (f(E+i) - f(E)) \tag{2}$$

Where P is identified when the maximum of function was obtained, and i is the regular sample unit of elevation.

2.2.4. Measurement of sedimentary dynamics and hydrodynamics at the advancing front

The accretion/erosion dynamics of tidal flat, as one of key factor of sedimentary dynamics, was measured by marking poles method. Five transects were laid out perpendicular to the fringe of vegetation to the mudflat at MSm, MSS and MSa front in Chongming Dongtan, respectively, in November 2013. Seven wooden poles of 1.5 m long were inserted into mudflats at 25 m intervals along each transect, leaving the top 50 cm of each pole exposed above the mud surface (Fig. 1d). The exposed height of each pole was measured monthly from November 2013 to October 2014. The initial elevations of the tidal flat surface were set to zero as a reference elevation, and the accretion/erosion dynamics were measured as the relative positive or negative change from the initial elevations. Data collected from the five transects were averaged to estimate the accretion/erosion dynamics of MSm, MSS and MSa front, respectively.

The tidal wave energy, the key factor of the hydrological environment, was measured at MSm, MSS and MSa front on 17 April–21 April 2013 using the self-logging wave sensors SBE 26+ (Sea-Bird Electronics Inc., USA; SBE, 2007). At MSm, MSS and MSa front, the wave sensors were mounted 0.15 m above the mudflat surface seaward. The values of the wave energy density were obtained using the manufacturer's software (SBE, 2007). The instruments were programmed to measure the wave energy density by taking 4-Hz pressure measurements over a 128-s period every 10 min respectively.

2.2.5. Survey of seedlings establishment and accretion at vegetation front

Seedlings establishment of *S. mariqueter* and *S. alterniflora* at MSm, MSS and MSa front on Chongming Dongtan wetland were surveyed in May (the key phase of seedling settling) 2014, respectively. In May 2014, a transect with a length of 150 m and a width 50 m, perpendicular to the continuous vegetation edge to the mudflat, was established at MSm, MSS and MSa front. Five 1 m × 1 m fixed plotlets were randomly set up at 25 m interval along the transect (Fig. 1d). The density of *S. mariqueter* and *S. alterniflora* seedlings were recorded in May 2014, respectively. The elevation of vegetation front in 2014 was measured by using a Real-Time Kinematic Global Position System (Ashtech, USA).

2.3. Data analysis

The means of the survival rates under an elevation-gradient were fitted with *S*-curves (Eq. (1)–(2)) to estimate the tipping point of the inundation duration for *S. alterniflora*, *S. mariqueter* and *P. australis*. One-way ANOVA was performed to test the impact of inundation duration on growth index, and Tukey's HSD post hoc test was used to detect differences between experiment sites. The level for statistical significance was set at $p < 0.05$. All the analyses were performed with SPSS 18.0 software (SPSS Inc., Chicago, USA).

3. Results

3.1. Growth and thresholds of salt-marsh plants to inundation duration

The mean survival rates of three salt-marsh plants under different elevations in mesocosms experiment were presented in Figs. 2–3. The results showed that plant survival rates under inundation of 3 m elevation were significantly ($p < 0.05$) higher than those under inundation of 2.5 m and 2.2 m elevation throughout the growing season for three species of saltmarshes. For *S. mariqueter*, under inundation stress of 3.0 m and 2.5 m elevation, the survival rate was 94.4 ± 4.9% and 88.5% ± 4.3% at the early growing season (April–May), and remained 85.0 ± 4.7% and 68.0% ± 6.5% at the end of growing season (Figs. 2 and 3A). Under inundation stress of 2.2 m elevation, the survival rate of *S. mariqueter* rapidly declined from April to May and maintained around 24.2 ± 4.1% after June. The survival rate of *S. alterniflora* also declined during April–May under inundation stress of 3.0 m, 2.5 m and 2.2 m elevation. After June, the survival rate of *S. alterniflora* remained higher survival rate as 86.0 ± 3.2% under inundation stress of 3.0 m but declined to 29.0 ± 5.5% and 0 under inundation stress of 2.5 m and 2.2 m elevation (Figs. 2 and 3B). Similar to other species, the survival rate of *P. australis* also significantly declined during April–June. After June, only under inundation stress of 3.0 m elevation, *P. australis* could survival and kept in survival rate as 58.2% ± 4.3% (Figs. 2 and 3C). Fig. 3 also indicated that under inundation stress of 2.2m and 2.5m elevation, the survival rate of *S. mariqueter* was significantly ($p < 0.05$) higher than that of *S. alterniflora* and *P. australis* over the growing stage.

At early June, seedlings of *S. alterniflora* under the inundation stress of 2.2 m and seedlings of *P. australis* under the inundation stress of 2.2 m and 2.5 m elevation died in mesocosms experiment (Figs. 2–3). The recorded plant height of three salt-marsh species under varying elevation was presented in Fig. 4. It indicated that plant height of three salt-marsh species increased with the rising of elevation over the growing season. There was no significant ($p > 0.05$) difference in plant height of *S. mariqueter*, *S. alterniflora* and *P. australis* between experiment groups (2.2 m, 2.5 m and 3.0 m elevation) and control group (2.7 m elevation) from April to May. After May, the mean plant height of *S. mariqueter* under the inundation stress of 2.2 m elevation and that of *S. alterniflora* under the inundation stress of 2.5 m elevation were significant lower than under other inundation stresses ($p < 0.05$).

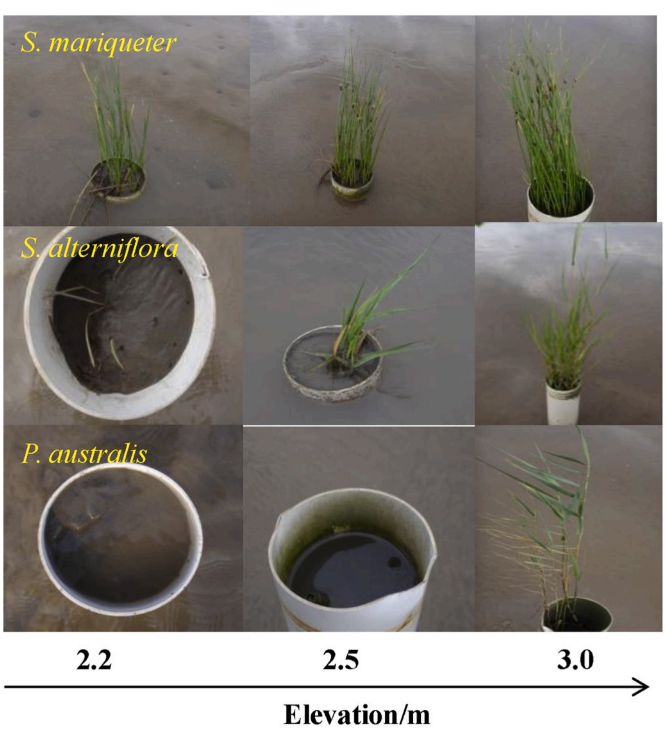

Fig. 2. The growth of *S. mariqueter*, *S. alterniflora* and *P. australis* planted at 2.2 m, 2.5 m and 3.0 m elevation under field condition in April 2014.

Fig. 5 presented that the number of tillers and the percentage of flowering tillers of salt-marsh plant also responded significantly ($p < 0.05$) to varying inundation duration. For three species, the number of tillers and the percentage of flowering tillers at higher elevation were all significantly higher than those at lower elevation, which indicated increasing inundation duration inhibited sexual propagation and asexual reproduction of salt-marsh plants. Fig. 5 also indicated that under the same inundation condition, there were significant differences in the number of tillers and the percentage of flowering tillers between *S. mariqueter* and *S. alterniflora*. Under inundation stress of ≤2.5 m elevation, the number of tillers for *S. alterniflora* was lower than that of *S. mariqueter*. For percentage of flowering tillers, *S. mariqueter* were all higher than those of *S. alterniflora* under different inundation stress.

Based on the mesocosms experiments on the tolerance of plants to varying elevation (i.e. variations of inundation duration), the survival curves (Eq. (1)–(2)) were fitted in relation to elevation for *S. alterniflora*, *S. mariqueter* and *P. australis* (Fig. 6A). With the down-regulated logistic curve, the tipping points of habitat elevation that reflected the threshold (irreversible growth) to habitat elevation were identified to be 1.9 m for *S. mariqueter*, 2.5 m for *S. alterniflora* and 2.9 m for *P. australis*. Across the mean daily tidal range in Chongming Dongtan (Sheshan tidal gauge station), the survival thresholds of the mean daily inundation duration for *S. mariqueter*, *S. alterniflora* and *P. australis* was estimated to be approximately 16, 11 and 9 h day^{-1}, respectively (Fig. 6B).

3.2. Sedimentary dynamic and hydrodynamic regime at the advancing front

There were significant ($p < 0.05$) differences in accretion/erosion dynamic among three types of vegetation front (Fig. 7A). At MSa front, the mudflat showed gradual erosion with a mean erosion of 1.2 ± 1.0 cm during November 2013–April 2014 and a rapid accretion with a mean accretion of 16.6 ± 3.1 cm during May–October 2014, indicating a pattern of autumn/winter erosion and spring/summer accretion. At MSS front, the mudflat remained relatively stable with a small amount of accretion of 0.5 ± 0.9 cm during November 2013–March 2014, and a rapid accretion with a mean accretion of 10.4 ± 1.9 cm during April–October 2014, indicating a pattern of relative autumn/winter stability and spring/summer accretion. At MSm front, the mudflat showed gradual accretion with a mean accretion of 1.1 ± 1.3 cm during November 2013–April 2014 and a rapid erosion with a mean erosion of 3.6 ± 2.1 cm during May–October 2014, indicating a pattern of autumn/winter accretion and spring/summer erosion.

The tidal wave energy at MSa, MSS and MSm front during the critical period of seedlings settlement was presented in Fig. 7B. It indicated that the density of the wave energy at MSm and MSS front was significantly ($p < 0.05$) higher than that at MSa front.

3.3. Establishment and expansion of plants at the advancing front

Salt-marsh establishment and sediment accretion was presented in Fig. 8. The results indicated that both sediment accretion and the seedlings density were highest near the continuous vegetation edge where the elevation was higher and declined from the initial continuous vegetation edge to seaward at MSa, MSS and MSm front. The vertical sediment deposition from initial continuous vegetation edge to seaward

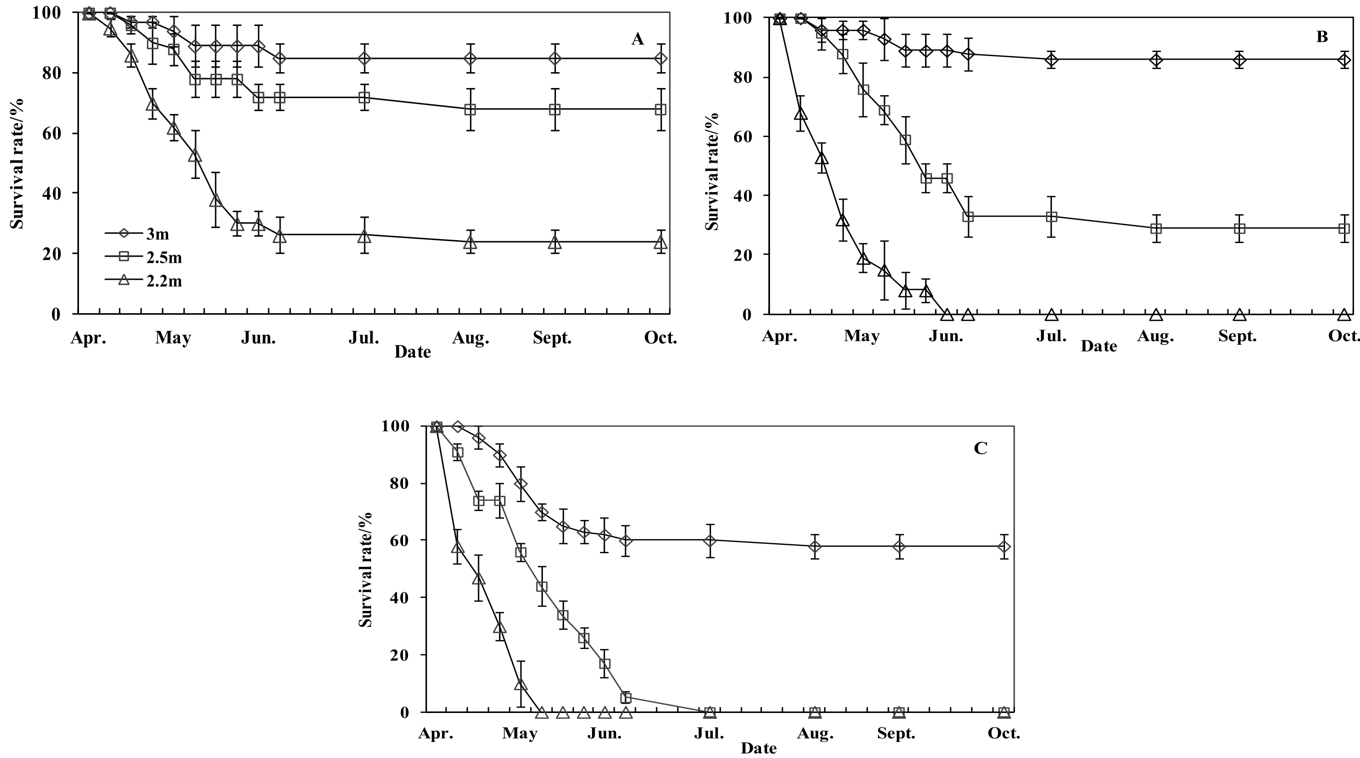

Fig. 3. Means (±S.E.) of survival rate of *S. mariqueter*(A), *S. alterniflora* (B) and *P. australis* (C) planted at 2.2 m, 2.5 m and 3.0 m elevation.

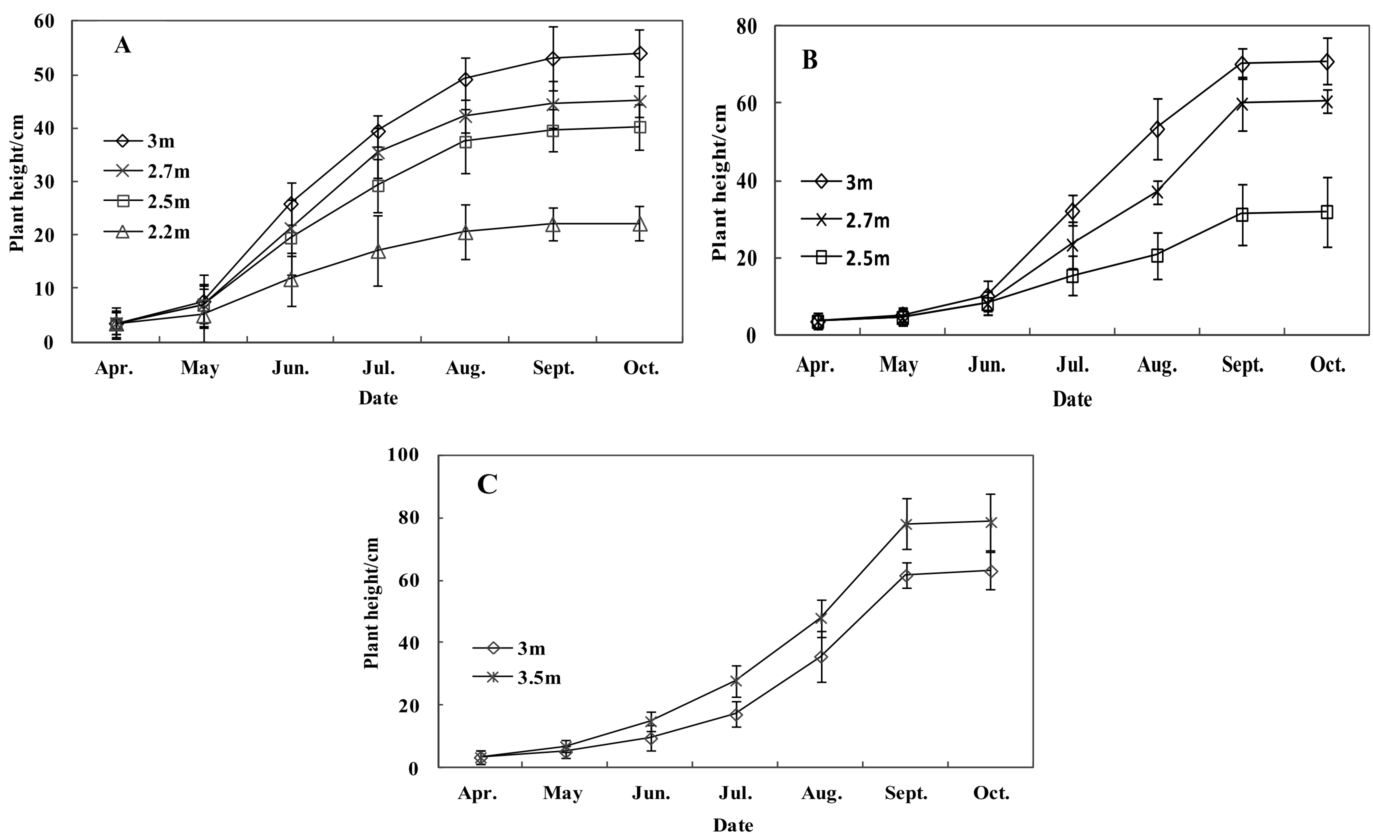

Fig. 4. Comparison of plant height of *S. mariqueter* (A), *S. alterniflora* (B) and *P. australis* (C) at 2.2 m, 2.5 m and 3.0 m elevation with control group.

155 m changed from 27 ± 4.8 cm/a to 10.6 ± 3.5 cm/a at MSa front, from 22.3 ± 4.3 cm/a to 5.0 ± 2.5 cm/a at MSS front, and from −1.5 ± 0.7 cm/a to −7.6 ± 2.1 cm/a at MSm front. MSa and MSS front had a gradual accretion trend and MSm front showed slight erosion trend, which was consistent with the results showed in Fig. 7A.

The vertical sediments deposition at MSS and MSa front decreased

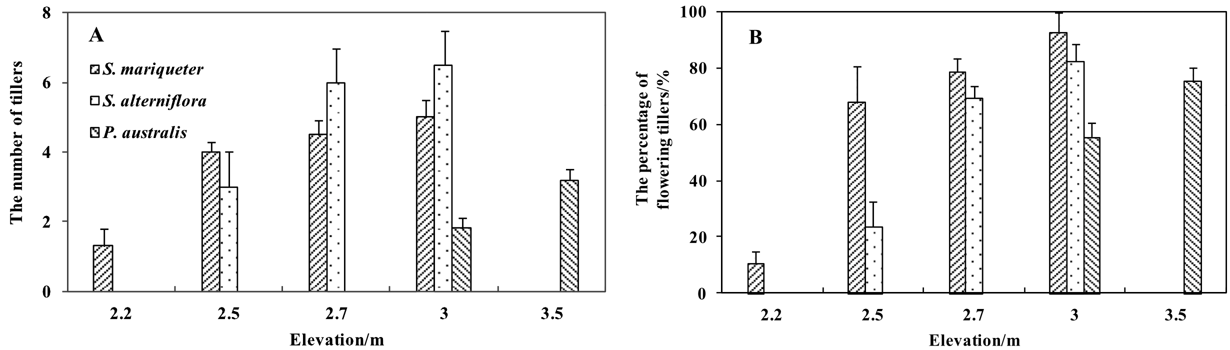

Fig. 5. Comparison of the number of tillers (A) and the percentage of flowering tillers (B) for *S. mariqueter*, *S. alterniflora* and *P. australis* planted at 2.2 m, 2.5 m and 3.0 m elevation with control group.

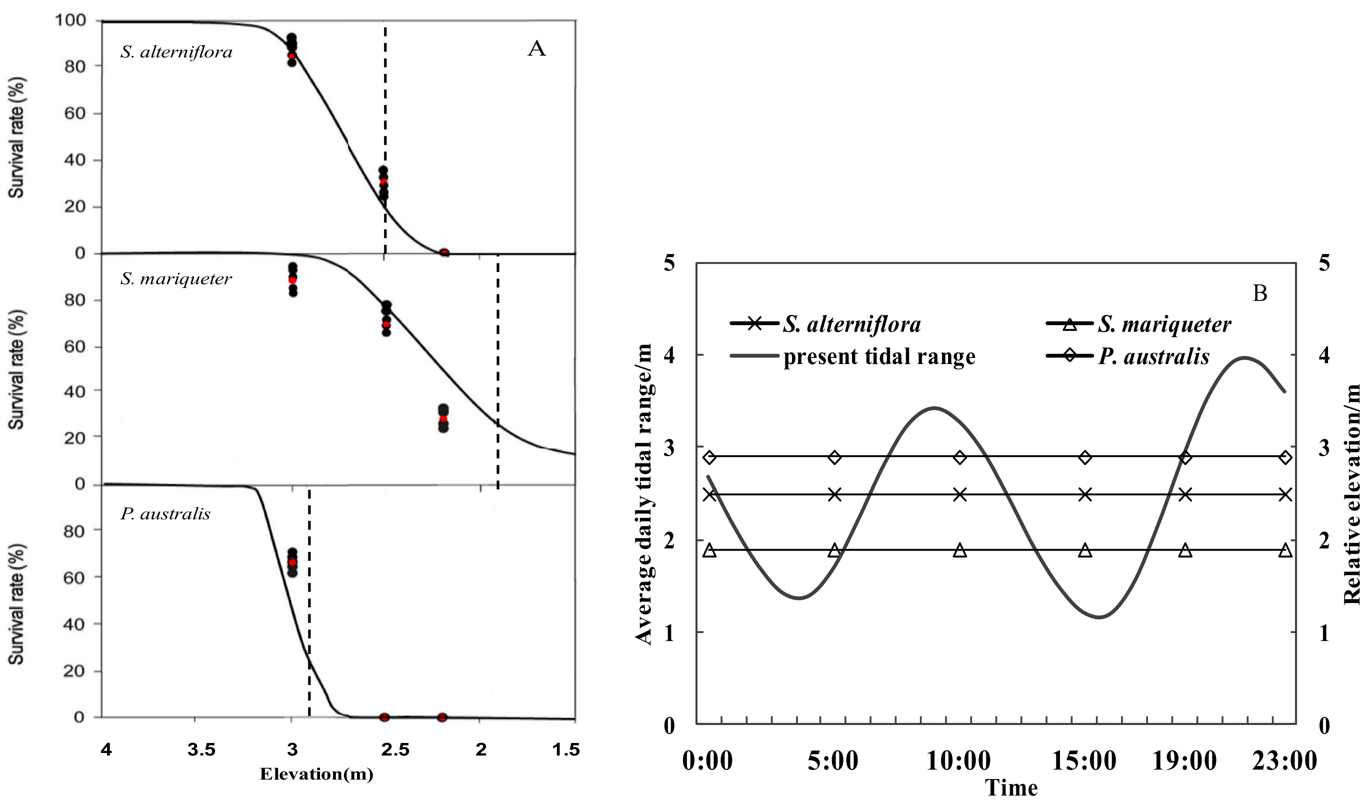

Fig. 6. (A) Fitting curves of plant survival (red points are the means) and threshold (dotted line) under inundation treatments (by variations of elevation); (B) Mean daily tidal range and inundation duration for *S. mariqueter*, *S. alterniflora* and *P. australis*.

inundation duration and promoted the lateral accretion of tidal flat and vegetation expansion. *S. alterniflora* seedlings at MSa and MSS front could establish from continuous vegetation edge to seaward 130 m and 105 m respectively. *S. mariqueter* seedlings at the MSS and MSm front advanced from continuous vegetation edge to seaward 130 m and 105 m, respectively. Although the front location changed, the field monitored elevation of *S. mariqueter* and *S. alterniflora* front were 2.0 m and 2.5 m, respectively, which is approached to our fitting thresholds from mesocosms experiments, i.e. habitat elevation for *S. mariqueter* front was 1.9 m and *S. alterniflora* front was 2.5 m, respectively (Fig. 6).

4. Discussion

4.1. Ecological thresholds of salt-marsh vegetation for inundation duration

Ecological thresholds are ubiquitous in natural ecosystems and closely related to ecosystem stability (May 1977; Scheffer et al., 2012). Many researches on ecological threshold have been carried out in forest, grassland, lake and ocean ecosystems (deMenocal et al., 2000; Steneck et al., 2004; van Nes et al., 2007), but the ecological thresholds of coastal wetlands for inundation duration have received scant attention (Balke et al., 2011; Yang et al., 2013).

The inundation duration was mainly determined by salt-marsh distribution elevation in the tidal zone and tidal regime. It was one of key environment factors related to coastal salt-marsh spatial pattern and stability. Minor elevation difference might affect the survival and

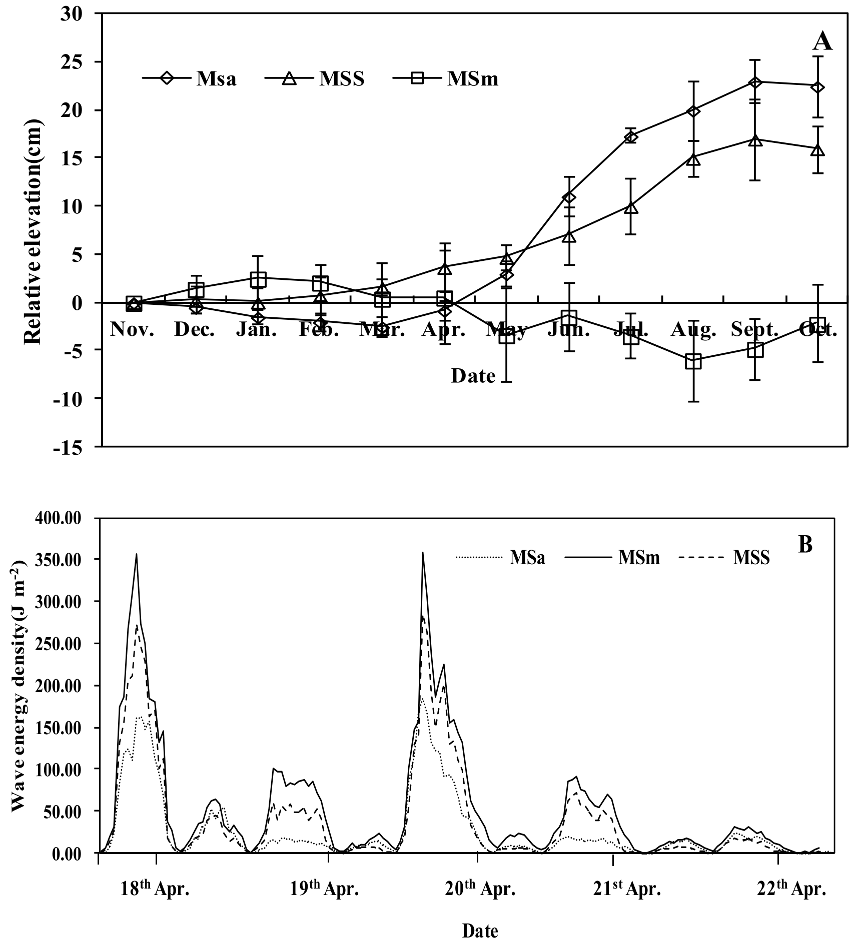

Fig. 7. (A) The accretion/erosion regimes in terms of relative elevation (mean ± S.D.) during November 2013–October 2014 at the vegetation front; (B) the wave energy at the vegetation front.

growth of salt-marsh plants (Komiyama et al., 1996; Morris et al., 2002). If increasing inundation exceeds tolerance range of plant survival, the salt-marsh plant couldn't survive (Voss et al., 2013). In this study, mesocosms experiment in the field was constructed at different elevations (Fig. 1c) to simulate the response of salt-marsh survival to varying inundation duration. The survival rate, plant height, percentage of flowering tillers and the number of tillers all significantly declined with increasing inundation (Figs. 2–5), which indicated that increasing inundation inhibited salt-marsh survival, growth, sexual propagation and asexual reproduction (Chen et al., 2011). Under inundation stress of 2.2 m and 2.5 m elevation, the survival rate, the percentage of flowering tillers and the number of tillers of *S. mariqueter* were significantly higher than that of *S. alterniflora* (Figs. 3 and 5), i.e. the competition capacity of *S. mariqueter* is stronger compared to *S. alterniflora* under longer inundation duration. Under inundation stress of 2.7 m and 3.0 m elevation, the competition capacity of *S. alterniflora* is stronger than *S. mariqueter*. These results indicated that the ecological thresholds of inundation duration were not complete coincide among different salt-marsh species in Yangtze Estuary.

For Yangtze Estuary with high sediment loading, sediment deposition results in increase in land elevation and decrease in inundation duration. The limitation of inundation thresholds to salt-marsh establishment and expansion could be made up due to dynamic accretion. Therefore, inundation duration at certain location and spatial location corresponding to inundation thresholds were not always constant in the estuary, but dynamic regulated by the interactive conditions of absolute elevation of habitat, local tidal range and accretion or erosion dynamics.

4.2. *The impacts of biotic and abiotic interaction on salt-marsh spatial pattern shift*

China's coastline extends for approximately 18,000 km, in which coastal wetlands, with a total area of ~5.8×10^4 km^2, provide enormous ecosystem services. Since the late 1980s, the introduction of *S. alterniflora* to Chinese coastal zones, this exotic grass has been expanding rapidly in 11 coastal provinces and induced the spatial pattern shifts of coastal wetland, damaging the stability of coastal wetland. Previous studies indicated that the rapid invasion of *S. alterniflora* could largely be attributed to the wider ecological niche and stronger competitive capacity with greater distance of seedling dispersal, larger seed bank and higher survival rate of its propagules relative to the dominant native species (Xiao et al., 2009, 2010; Ge et al., 2013, 2015). However, the results of this study showed that *S. mariqueter* has the higher inundation thresholds than *S. alterniflora*. This indicated that *S. mariqueter* would likely form the vegetation front and then success to *S. alterniflora* and *P. australis* along the elevation gradient from the mudflat to the seawall. Then, why three types of spatial pattern at advancing front (MSm front, MSS and MSa front) could be found in Yangtze Estuary?

In estuary, establishment and spatial pattern of saltmarshes are determined by complex biotic and abiotic interaction, rather than the absolute magnitude of one or several environmental factors. Based on our results, the reasons caused spatial pattern shift of salt-marsh vegetation in Yangtze Estuary could be partly explained as follows. Firstly, the sedimentary dynamic results showed a fast accretion trend in the north of Chongming Dongtan and a slow erosion trend in the south of

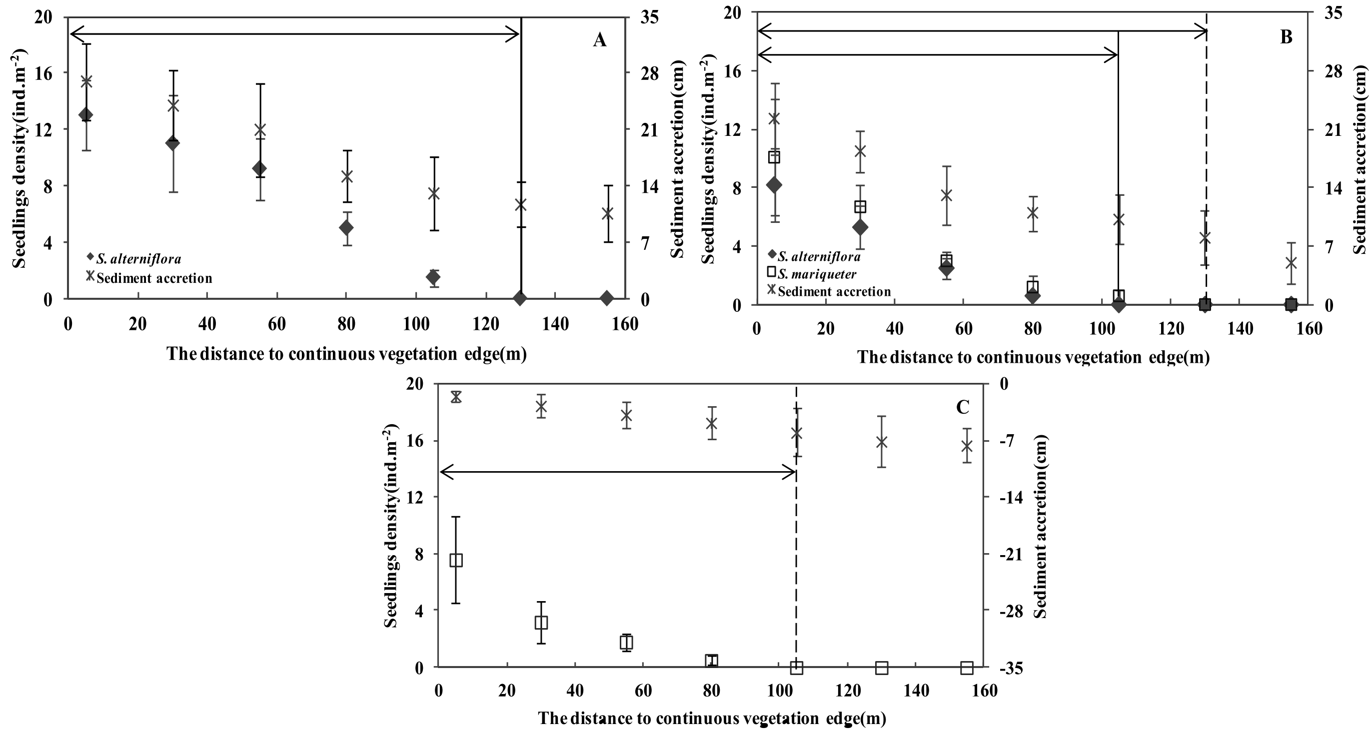

Fig. 8. The salt-marsh density and sediment accretion at MSa (A), MSS(B) and MSm (C) front in 2014 (0 of the horizontal axis was the border of initial continuous vegetation edge. Dashed line and straight line were the advancing front of *S. mariqueter* and *S. alterniflora* in 2014 respectively).

Chongming Dongtan. The fast accretion would raise the habitat elevation, decrease inundation duration and create suitable habitat for *S. alterniflora*. As a result, higher dominance of *S. alterniflora* occurred at the MSa front with higher elevation (>2.5 m) and the absence of *S. alterniflora* at the MSm front with lower elevation (<2.5 m). Secondly, seasonally changes of sedimentary dynamic also greatly affected salt-marsh establishment and expansion pattern. The MSa front in the north of Chongming Dongtan showed a pattern of rapid spring/summer accretion with higher accretion rate (Fig. 7A), which promoted *S. alterniflora* seedlings successfully establish and rapidly grow there. When the sedimentary dynamics at the MSa front shifted to erosion in autumn/winter (Fig. 7A), due to higher resilience to erosion of *S. alterniflora* in muddy sediment (Schwarz, 2013), *S. alterniflora* was more suitable than *S. mariqueter* to grow at the MSa front. The MSm front in the south of Chongming Dongtan showed a relative stable pattern during autumn/winter period (Fig. 7A), which was helpful for *S. mariqueter* to maintain its cover. When dynamics shifted to spring/-summer erosion (Fig. 7A), *S. mariqueter* seedlings were easier to survive than *S. alterniflora* because of higher resilience against sediment erosion in sandy sediment (Schwarz, 2013). Thirdly, hydrodynamic regimes also influenced salt-marsh expansion pattern (Schwarz et al., 2011; Zhu et al., 2012). The wave energy was lower at the MSa front (Fig. 7B) which was more favorable for *S. alterniflora* to establish and grow (Bouma et al., 2005; Mullarney and Henderson, 2010; Schwarz, 2013) but higher at the MSm front. The stiff plant parts of *S. alterniflora* were exposed to substantial drag in strong waves, which was a disadvantage compared to the lower drag experienced by more flexible species like *S. mariqueter* (Bouma et al., 2005; Mullarney and Henderson, 2010; Schwarz, 2013). Therefore, higher wave energy at the MSm front prevented the establishment and growth of *S. alterniflora* at the MSm front. As a result, *S. alterniflora* couldn't invade the tidal zone in the southern of Chongming Dongtan but easily invaded to the north of Chongming Dongtan, thus MSm and MSa fronts formed at south and north in the Chongming Dongtan, respectively. The abiotic factors of MSS front were between that of MSm front and MSa front, thus the spatial pattern of MSS front became a transition part with both *S. mariqueter* and *S. alterniflora* along the elevation gradient. The spatial pattern shift of salt-marsh ecosystem is a very complicated process. It is strongly dependent on the interaction of biotic-abiotic factors. Based on this study, obtaining salt-marsh survival thresholds and understanding the effect of inundation, sedimentary dynamic and hydrodynamic regimes on salt-marsh stability are especially crucial for successful restoration of coastal salt marshes (Thorsten et al., 2011).

4.3. Uncertainty analysis

This study focused on the impacts of inundation, sedimentary dynamic and hydrodynamic regimes on the spatial pattern shift of salt-marsh vegetation in the Yangtze Estuary. However, there are several uncertainties in the mechanism of the pattern shift of salt-marsh vegetation. Compared to most estuarine ecosystems around the world, the coastal wetland of the Yangtze Estuary is a dynamic habitat with a high sediment load and rapid accretion rates (Ge et al., 2013). Additionally, the sea level in the Yangtze Estuary rose at a rate of 4.97 mm yr^{-1} during 1961–2011 (NOAA, 2017). Moreover, in recent years, human activities have an important impact on land subsidence in coastal zone due to development and construction. Therefore, how the change in elevation and the area of wetland interact with salt marshes development is still unclear. Further work is needed to determine the relative importance of biotic and abiotic processes regulating the impacts of invasion species on native ecosystems.

5. Conclusions

In this study, we found that invasive *S. alterniflora* was more tolerant to increased inundation stresses than the two native species *S. mariqueter* and *P. australis*. Both accretion/erosion dynamics and wave energy significantly differed among three types of advancing front, which further indicated that establishment and spatial pattern of salt marshes were also greatly dependent on sedimentation dynamics and hydrodynamic regimes. *S. alterniflora* had sustainable competitive advantages compared to *S. mariqueter* and *P. australis* in the Yangtze River Estuary, which might further promote its expansion and gradually replace the native species in the future. Therefore, measures protecting native species should be strengthened and the impacts of invasive species on native ecosystem should be evaluated from more objective perspectives.

Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.106717.

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