



Tidal channel-mediated gradients facilitate *Spartina alterniflora* invasion in coastal ecosystems: implications for invasive species management

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ABSTRACT: Understanding how geomorphic landscape features affect physical habitat conditions is essential for predicting if such geomorphic landscape features may act as conduits facilitating invasive species expansion in coastal ecosystems. Although the effects of various abiotic and biotic factors on plant invasion in salt marshes have been well studied, little is known about the impact of tidal channels on plant invasion. Here, we examined the effects of bottom-up determinants on the lateral expansion of *Spartina alterniflora* in tidal channel margins of different elevational marsh zones: the low, middle and high marsh, in the Yellow River Delta, China. Field observations and experiments showed that the microhabitats of tidal channel margins are characterized by relatively low soil salinity and high inundation, which significantly facilitated the establishment, growth, colonization and sexual reproduction of *S. alterniflora*. Moreover, the facilitating effect of tidal channel margins on plant landward invasion appeared more sensitive in middle and high marshes compared with the low marshes. High propagule pressure combined with suitable physical conditions of the structural microhabitats formed within tidal channels potentially promoted the rapid expansion of *S. alterniflora* along the tidal channel margins. Based on these results, a conceptual model was built illustrating the lateral expansion mechanisms of the invasive plant mediated by tidal channels. These results highlight the importance of tidal channel-mediated gradients in bottom-up abiotic and biotic-dispersal factors in facilitating the expansion of coastal invasive plants. For wetlands management, our results imply that geomorphic landscape features should be incorporated into ecological management and risk assessment of invasive plants.

KEY WORDS: Geomorphic landscape feature · Plant invasion · Abiotic factor · Biotic-dispersal factor · Propagule pressure · Salt marsh

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1. INTRODUCTION

Coastal salt marshes are extremely unique and valuable ecosystems that occur worldwide (Costanza et al. 1997, Barbier et al. 2011). They play an impor-

tant role in providing a variety of ecosystem services to local and global livelihoods, such as carbon sequestration, shoreline protection, fisheries production, nutrient removal and biodiversity maintenance (Temmerman et al. 2013, Möller et al. 2014). How-

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ever, despite their significant importance, salt marshes worldwide have been threatened by multiple stresses induced by global changes, especially biological invasion during the past century, leading to approximately 25–50% losses of the world's salt marshes in terms of area (Mcowen et al. 2017). Most of the invasive species are usually capable of ecosystem engineering with powerful effects on both plant and animal communities in their non-native ranges, through altering the physical, chemical and biological environments/processes of salt marshes (Crooks 2002, Gedan et al. 2009, Strong & Ayres 2013). In addition to areal loss, shifts in species composition caused by biological invasion may also affect the functionality and biogeomorphology of salt marshes (Bouma et al. 2013, Schwarz et al. 2018).

Spartina alterniflora Loisel. (Loiseleur-Deslongchamps, Fl. Gall. 719. 1807) invasion is a major threat to the native vegetation characterizing salt marshes around the world (Molnar et al. 2008, Strong & Ayres 2009, 2013). In recent decades, exotic plants of the genus *Spartina* have been deliberately and accidentally spread over many salt marshes on the shorelines of the US west coast, Australia, New Zealand, southern Africa, Europe and East Asia (Ning et al. 2019). Exotic *Spartina* sp. has successfully invaded almost all coastlines in China (Liu et al. 2018). Physical stresses such as low inundation and hypersalinity (He et al. 2012, Qi et al. 2017), interacting with plant competition (Emery et al. 2001, Pennings et al. 2005, Wang et al. 2006), can inhibit the distribution and landward expansion of *S. alterniflora* from low marshes to high marshes, even without considering the effect of tidal channels. Nevertheless, *S. alterniflora* is rapidly expanding its range landward along the tidal channel margins in coastal salt marshes (Schwarz et al. 2016, Ning et al. 2020, Sun et al. 2020), resulting in several negative ecological consequences, such as alterations of drainage density, sediment composition and habitat configuration (Lathrop et al. 2003, Schwarz et al. 2016).

The invasive mechanism of *S. alterniflora* is complex and driven by multiple interactions of physical factors and biotic resistance (Alpert et al. 2000, Zhang et al. 2018). The suitable physical environments of habitats and the reduced biotic resistance of native communities, such as lack of natural enemies and lower competitiveness of native plants, provide a niche opportunity or invasion windows for the establishment and spread of *S. alterniflora* populations in new ranges (Crain et al. 2004, Dethier & Hacker 2005, Ma et al. 2020). For physical environments, inundation regimes and salinity are 2 critical

bottom-up abiotic factors affecting the establishment and colonization of *S. alterniflora*, and its competitiveness against native species in salt marshes (Tang et al. 2016). On the one hand, both prolonged tidal inundation and continuous wave action drastically reduce the seedling density, biomass, and physiological and biochemical responses of invasive *S. alterniflora*, thus limiting its range expansion (Smith & Lee 2015, Shao et al. 2019). On the other hand, field surveys and greenhouse experiments have indicated that it is difficult for *S. alterniflora* to invade habitats that experience periodic or continual absence of tidal activity (Xiao et al. 2011, He et al. 2012). Salinity has long been considered a primary determinant of exotic species invasion in salt marshes (He et al. 2012, Ning et al. 2019). Indeed, the growth, colonization and sexual reproduction of *S. alterniflora* is negatively correlated with soil salinity, resulting in the landward restriction of *S. alterniflora* invasion by hypersaline zones, such as salt barrens in high marshes (He et al. 2012). Overall, the combined effect of soil salinity with tidal inundation influences *S. alterniflora* invasiveness, in line with greenhouse experiments revealing that the maximum biomass is produced under conditions of low soil salinity and high inundation (Qi et al. 2017). In the field, the distributions or regimes of such bottom-up abiotic factors are generally mediated by the tidal channels of salt marshes (Fagherazzi et al. 2013, Ning et al. 2020). Remarkably little is known about the extent to which tidal channels may generate bottom-up abiotic gradients in soil salinity and inundation conditions, and thereby affect *S. alterniflora* invasiveness.

In addition to the above-mentioned bottom-up abiotic factors, propagule pressure may also act as a key bottom-up biotic factor contributing to the successful establishment and spread of exotic species (Lockwood et al. 2005, Simberloff 2009). Increased propagule quantity can diminish the impacts of environmental stochasticity, and thereby drive higher invasion success (Simberloff 2009). Hence, in the field, propagule availability combined with suitable environmental conditions together facilitate plant invasions. For example, human-introduced ditches in high salt marshes may cause more *S. alterniflora* seeds to end up in the high marsh, thereby potentially increasing the opportunity for successful establishment of *S. alterniflora* (Ning et al. 2019). Although the effects of various bottom-up factors on *S. alterniflora* landward invasion have been broadly investigated (Schwarz et al. 2011, Qi et al. 2017), surprisingly little is known about the extent to which

tidal channel-mediated gradients via bottom-up biotic-dispersal factors may regulate the *S. alterniflora* invasion range.

Tidal channels play an important role in the functioning of salt marshes (Fagherazzi et al. 2013). They are fundamental geomorphic structures that determine the composition, distribution and diversity of salt marsh vegetation to a large extent, and may potentially be susceptible to exotic plant invasions (Sanderson et al. 2000, Ning et al. 2020). Some native (Sanderson et al. 2001, Mason & Scott 2004) and even invasive plants (e.g. *S. alterniflora*, *Phragmites australis* (Cav.) Trin. ex Steud., *Tamarix chinensis* Lour., etc.) grow aggregated in zones closer to the edges of tidal channels (Lathrop et al. 2003, Schwarz et al. 2016). Observations along the tidal channel margins in China's coastal salt marshes (Fig. 1B, Sites a–d; Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m659p059_supp.pdf), as well as in many other tidal channel salt marshes globally (Fig. 1A, Sites e–i), suggest that these tidal channels may facilitate the invasion pattern of plants of the *Spartina* genus. Whereas the effect of various bottom-up factors on the invasibility of habitats to exotic plant species has been well studied (Alpert et al. 2000, Tyler et al. 2007), the role of the tidal channel margins remains unclear.

To be able to predict the future landward invasion of *S. alterniflora* in salt marshes, the present study aims to answer how *S. alterniflora* expansion in tidal channel margins of different elevational marsh zones (i.e. low, middle and high marsh) is affected by (1) bottom-up abiotic factors (e.g. salinity, inundation), as measured from *S. alterniflora* growth performance (i.e. number of stems, inflorescences, maximum stem height and total biomass), and (2) a bottom-up biotic factor (i.e. propagule pressure). We hypothesized that tidal channels could act as conduits facilitating the range expansion of *S. alterniflora* by mediating the bottom-up abiotic and biotic-dispersal factors. Field surveys and transplant experiments were conducted to examine the combined effects of these bottom-up factors on the expansion of *S. alterniflora* along with the tidal channel margins in salt marshes. Based on the results, a conceptual model is presented that illustrates the lateral expansion mechanisms of invasive *S. alterniflora* in tidal channel margins under the effects of these bottom-up factors. We also discuss the implications for the conservation and restoration of salt marshes, when facing potential landward invasion of *S. alterniflora* along the tidal channels.

2. MATERIALS AND METHODS

2.1. Study site and study species description

The study was conducted in a natural tidal channel margin located in the Yellow River Delta (37° 77'–38° 12' N, 118° 68'–119° 34' E), North China (Fig. 1B, Site a). *Spartina alterniflora* was purposely introduced to China in the 1970s but has since been listed as one of the top 16 most serious invasive plants by the Chinese government (Zuo et al. 2012). More details about the study site and species are given in Text S1 in the Supplement. The field experiment was conducted on the tidal channel margins in 3 elevational marsh zones (i.e. low marsh, middle marsh and high marsh). The elevational marsh zones were determined by the tidal range and the vegetation types in previous studies (Adam 1993, Wang et al. 2018, Xie et al. 2019). The low marsh is located between the lowest average tide and the mean high water neap (MHWN), which is dominated by *S. alterniflora*. The middle marsh is located between the MHWN and the mean high water spring tide (MHWS), which is dominated by *Suaeda salsa*. The high marsh is located between the MHWS and the highest average tide, which is dominated by *Suaeda salsa* and *Tamarix chinensis*. In every marsh zone, 3 microhabitats with a lateral increased distance gradient from the tidal channel were also distinguished (Fig. S1): (1) near distance to the tidal channel edge (0 m, at the border of *S. alterniflora* expansion belt, hereinafter 'N'), (2) middle distance to the tidal channel edge (50 m from the border of the *S. alterniflora* expansion belt, hereinafter 'M') and (3) far distance to the tidal channel edge (200 m from the border of the *S. alterniflora* expansion belt, hereinafter 'F').

2.2. Transect survey: *S. alterniflora* and abiotic stressor distribution along tidal channels

To quantify the differences of the *S. alterniflora* expansion in relation to the distance from the tidal channel margins for the 3 elevational marsh zones (i.e. low, middle and high marsh), a set of aerial images (Fig. S3 in the Supplement) were taken by an unmanned aerial vehicle in August 2017. The lateral expansion border of *S. alterniflora* in the tidal channel margins was visible in these images, and 10 of the aerial images that were taken vertically at the same height in each elevational marsh zone were selected to measure the lateral expansion distance.

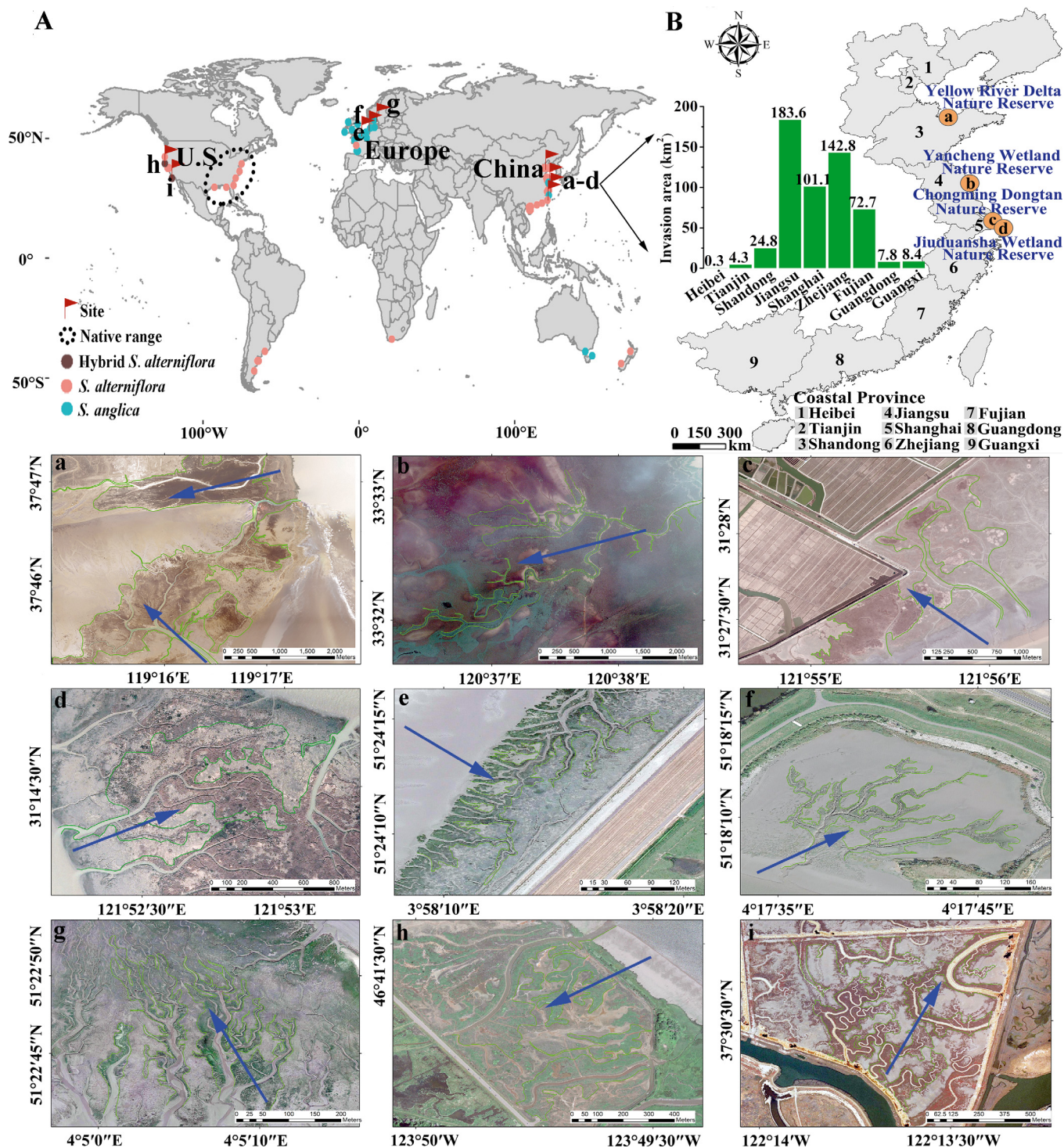


Fig. 1. (A) Distribution of invasive *Spartina* spp. (e.g. *S. alterniflora*, *S. anglica* and hybrid *S. alterniflora*) along the world's coasts (may not include the complete distribution). Typical sites showing the invasion pattern of *Spartina* species spreading along tidal channels of coastal salt marshes in (a) Yellow River estuary, (b) Yancheng Wetlands, (c) Chongming Dongtan wetlands and (d) Jiuduansha Wetlands in Yangtze River estuary, China; (e–g) Scheldt estuary on the Atlantic coast of Europe; (h) Willapa Bay and (i) San Francisco Bay on the US Pacific coast. Images mapped based on Google Earth images in 2016, using ArcGIS 10.3 software. Green lines: the spatial pattern of *Spartina* species expanding its range along the tidal channel margins; blue arrows: the landward direction. (B) Total invasion areas of *Spartina* in the coastal provinces of mainland China until 2015 (data obtained from Liu et al. 2018)

Then, the width of the *S. alterniflora* expansion belt in each elevational marsh zone was identified by calculating the mean value of the 10 lateral expansion distances. All aerial images were processed in ImageJ software (US National Institutes of Health). In order to calibrate the image processing results, field measurements were also conducted in August 2017. Ten lateral expansion distances of *S. alterniflora* were randomly measured using a leather measuring tape in the margins of tidal channels of each elevational marsh zone, and the mean values of the expansion distance in each elevational marsh zone were also calculated.

To quantify the lateral distribution of soil abiotic stresses (i.e. soil moisture and soil salinity), a sampling line of 300 m in length was set perpendicular to the tidal channel across the tidal channel margins of each elevational marsh zone (i.e. low, middle and high marsh). Along each sampling line, we laid 16 to 19 parallel transects of 40 m in length (i.e. $n = 16$ transects in low marsh, $n = 19$ transects in middle marsh and $n = 18$ transects in high marsh; Fig. S4 in the Supplement shows the transect distribution in each zone). We set a 1×1 m quadrat every 10 m along each transect (4 replicate quadrats for each transect), and a soil core (5.05 cm diameter \times 5.00 cm depth) was collected at the center of each quadrat to determine soil salinity and moisture content in April 2017. As previous studies performed in this region have documented seasonal variation in such abiotic factors (He et al. 2009, Cui et al. 2011), we simply quantified relative differences among the different transects, and did not sample multiple months. Soil cores were oven-dried for 48 h at 60°C and weighed to determine the soil moisture. We used the soil rehydration method to measure the soil salinity (Pennings et al. 2005) through a salinometer (Jenco 3010M).

2.3. Field measurements: quantification of soil salinity, soil moisture and inundation conditions

To be able to relate soil salinity and soil moisture to other parameters such as elevation, flooding frequency and inundation time, the fine-scaled transects (see Fig. S4 in the Supplement) were expanded by detailed point measurements in 3 contrasting zones (N, M and F). To compare the differences in soil salinity and soil moisture among the 3 microhabitats (i.e. N, M and F) which have a lateral distance gradient in each elevational marsh zone (i.e. low, middle and high marsh), eight 1×1 m quadrats were set (8 replicates set > 5 m away

from each other), marked by 4 PVC pipes installed at each corner for preparation for the following transplant experiments. We collected a soil core of topsoil (5.05 cm diameter \times 5.00 cm depth) at the center of each quadrat to determine soil salinity and soil moisture. In each microhabitat of 3 elevational marsh zones, a water-level recorder (Odyssey water-level loggers, Dataflow Systems) was settled in the field to precisely auto-record the inundation information for the entire year of 2017. Flooding frequency was determined by dividing the total number of the days the microhabitat had been flooded by 365 d, and inundation time was the average time length of the flooding days in a year. Furthermore, to compare the differences in elevation among the 3 microhabitats in each marsh zone, the absolute elevation of each quadrat was measured, based on the Chinese national height datum 1985, using a real-time kinematic technique (RTK-i70, CHC Navigation Company).

2.4. Field measurements: *S. alterniflora* seed dispersal and soil seed retention

To quantify the spatial dispersal patterns of *S. alterniflora* seed along tidal channel margins, 3 manufactured seed traps were installed in each microhabitat (i.e. N, M and F) of the 3 marsh zones in early November 2017, during the seed dispersal period (3 replicates, 27 seed traps in total). Each seed trap contained 8 tapered nylon net bags (1 mm mesh size, 50 cm in diameter) which were divided into 2 rows. In order to simultaneously capture the seeds carried by the tide during high tide and low tide, each net bag was placed in the opposite direction from the adjacent one in every row (Fig. S5 in the Supplement). All seed traps were placed perpendicular to the tidal currents. Three weeks later, after seed dispersal in late November 2017, seeds of *S. alterniflora* trapped in the net bags were collected and counted in the laboratory.

To compare the differences in soil seed retention of the margins of tidal channels among the microhabitats in the 3 elevational marsh zones, we surveyed the *S. alterniflora* seeds persistent in the topsoil in November 2017. Forty-eight soil samples (8 replicates per microhabitat) were collected from the topsoil by an excavator sized 25 cm length \times 25 cm width \times 5 cm height. All soil samples were brought to the laboratory and washed using a 1 mm fine sieve. Then, we counted the number of *S. alterniflora* seeds after removing all fine soil particles.

2.5. Manipulative field experiments: *S. alterniflora* tiller and seedling transplant experiment

To determine the invasibility of the tidal channel margins to *S. alterniflora* in different elevational marsh zones (i.e. low, middle and high marsh), we transplanted *S. alterniflora* replicates into the microhabitats of tidal channel margins with a lateral distance gradient (i.e. N, M and F) in each elevational marsh zone in May 2017 and 2018. As *S. alterniflora* can grow from both vegetative tiller and sexual seedling, the experimental design was conducted with a tiller transplant experiment in May 2017 and a seedling transplant experiment in May 2018. We excavated a number of substrate blocks (20 cm diameter × 15 cm depth) containing emerging *S. alterniflora* tillers from nearby tidal channel margins in May 2017, using a transplanter. Analogously, numerous substrate blocks containing 10 to 20 *S. alterniflora* seedlings were excavated in May 2018. These substrate blocks were instantly transplanted to the eight 1 m × 1 m quadrats (8 replicates per microhabitat, >5 m away from each other) marked by PVC pipes. We watered these transplants with fresh water every 2 d for a week to alleviate transplant shock. Tillers and seedlings from each quadrat were thinned to 10 individuals for standardization. After a growing season, we measured the number of stems and inflorescences, and maximum stem height of each transplant in September 2017 and 2018. Then, both above-ground and below-ground biomass were harvested, oven-dried for 48 h at 60°C, and weighed.

2.6. Statistical analysis

One-way ANOVA with Tukey's post hoc multiple tests were conducted to compare the differences in soil abiotic stresses among the 3 microhabitats (i.e. N, M and F) in each elevational marsh zone (i.e. low, middle and high marsh), after testing the normality and homogeneity of variance for the relevant data series. Differences in elevation among the microhabitats of each marsh zone were tested by nonparametric Kruskal-Wallis test, because the data did not satisfy the assumptions of ANOVA. Differences in inundation time, seed capture by seed traps and soil seed density among microhabitats and zones were analyzed using generalized linear models (GLMs) with post hoc tests, as these data could not be transformed to meet the assumptions of ANOVA. We used Gaussian distribution for inundation time, and Poisson distribution for seed capture and soil seed den-

sity data. We also analyzed the effects of microhabitat and marsh zone on the performances of *S. alterniflora* (i.e. number of stems, inflorescences, maximum stem height and total biomass) using GLMs followed by post hoc tests with Gaussian distribution. Moreover, the relationships among soil abiotic stresses, elevation, inundation conditions (i.e. flooding frequency and inundation time) and total biomass of *S. alterniflora* were examined by 1-variable linear regression models. Statistical analyses in this study were conducted in R 3.5.3 (R Core Team 2019).

3. RESULTS

3.1. Lateral distribution of soil abiotic stresses and *S. alterniflora* zone width along tidal channel margins

In the longitudinal elevation gradient, from low marsh to high marsh, the soil salinity of the tidal channel margins presented an upward trend, while soil moisture exhibited a downward trend (Fig. S4, Table S1 in the Supplement). In the lateral distance gradient of the tidal channel margins, an obvious gradient of increased soil salinity with distance from the tidal channel edge was observed in all 3 elevational marsh zones, while a sharp decreasing trend occurred in soil moisture (Fig. S4). The width of the *S. alterniflora* expansion belt in tidal channel margins varied by elevational marsh zone: 149.4 ± 2.9 m in low marsh, 61.6 ± 1.6 m in middle marsh and 13.4 ± 1.1 m in high marsh (mean ± SE; Table S1). Although the expansion range of *S. alterniflora* in the tidal channel margins of low marsh was much higher than that in middle and high marsh (Table S1), the soil in the *S. alterniflora* expansion belt of the tidal channel margins in all marsh zones was characterized by low salinity and high moisture (Fig. S4).

3.2. Lateral distribution of *S. alterniflora* seed along tidal channel margins: seed capture and buried seeds

The quantity of the seeds captured by the manufactured seed traps was significantly affected by the interaction between microhabitat and marsh zone ($p < 0.001$; Fig. 2a; Table S2 in the Supplement). Although several thousand *S. alterniflora* seeds were captured per seed trap in all 3 marsh zones, each marsh zone revealed different spatial dispersal patterns of *S. alterniflora* seed along the lateral distance gradient of the tidal channel margins. In the tidal channel margins of low marsh, no significant differ-

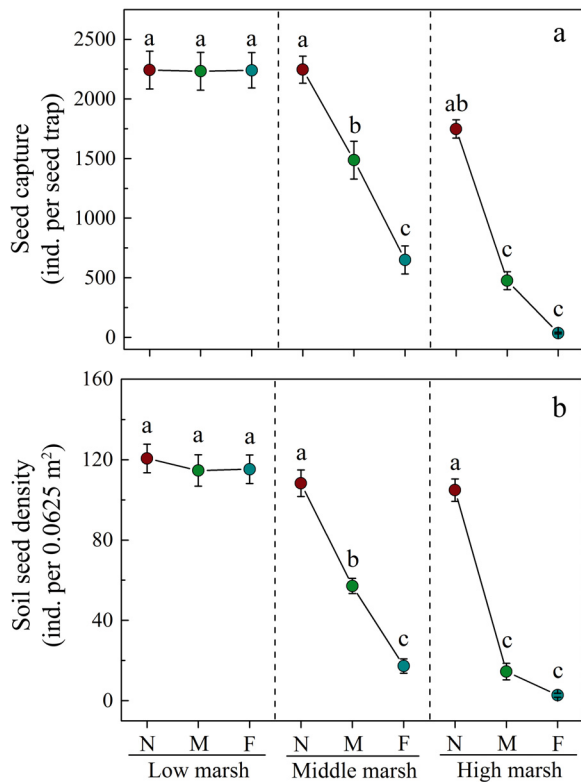


Fig. 2. Differences in (a) *Spartina alterniflora* seed capture by seed traps and (b) soil seed density of *Spartina* among the 3 microhabitats that have a lateral increased distance gradient from the tidal channel (i.e. N: near creek zone, dark red; M: middle zone, green; F: far from creek zone, blue) in the low, middle and high marsh. Data are mean \pm SE; $n = 3$ replicates in (a) and $n = 8$ replicates in (b). Significant differences (tested by GLM) are shown by different lowercase letters above the error bars ($p < 0.05$)

ences ($p > 0.05$, Fig. 2a) were found among the 3 microhabitats. In contrast, in both in the tidal channel margins of middle marsh and high marsh, the amount of seed captured significantly decreased with increased distance to the tidal channels ($p < 0.05$, Fig. 2a). Similar patterns were observed for the number of *S. alterniflora* seeds that existed in the surficial soil for both the microhabitat and the elevational marsh zone ($p < 0.001$, Fig. 2b, Table S2).

3.3. Lateral distance gradients of soil abiotic stresses, elevation, and inundation conditions along tidal channel margins

In the lateral distance gradient along tidal channel margins, lower soil moisture and higher soil salinity were observed in the F microhabitat compared to N

and M microhabitats. Meanwhile, soil salinity and soil moisture among the 3 microhabitats in each elevational marsh zone were significantly different from each other, except for the low marsh, where there were also 2 significant comparisons (M vs. N, F vs. N) for soil moisture ($p < 0.05$, Fig. 3a,b).

Generally, elevation of tidal channel margins increased at the lateral distance gradient in all 3 elevational marsh zones (Fig. 3c). Although the difference in elevation in the low marsh was inconspicuous, there were significant differences among the 3 microhabitats (i.e. N, M and F) both in middle marsh and high marsh ($p < 0.05$, Fig. 3c). In addition, microhabitats in low marsh were flooded every day, and decreases in flooding frequency were seen with an increase in lateral distance to the tidal channels, both in middle marsh and high marsh (middle marsh: $100.0 \pm 0.0\%$ in N and M, $48.5 \pm 1.4\%$ in F; high marsh: $100.0 \pm 0.0\%$ in N, $52.6 \pm 3.1\%$ in M and $19.3 \pm 0.5\%$ in F; mean \pm SE; Fig. 3d). In the tidal channel margins of low marsh, there were no significant differences in inundation time among the 3 microhabitats ($p > 0.05$; Fig. 3e). In contrast, the inundation time of M and F microhabitats were significantly lower than that in N microhabitat, both in middle marsh and high marsh ($p < 0.05$; Fig. 3e). All above-mentioned results showed that elevated bottom-up abiotic stresses occurred with increasing lateral distance to the tidal channels in the margins.

3.4. Effects of soil abiotic stresses and inundation conditions on *S. alterniflora* performance: tillers vs. seedlings

Performances of *S. alterniflora* growing from both tiller and seedling were significantly affected by the interaction of marsh zone and microhabitat ($p < 0.001$, Fig. 4; Table S3 in the Supplement). All transplants (both tiller and seedling) grew well in low marsh, but their growth decreased considerably with increasing elevation in the longitudinal gradient ($p < 0.001$). In the lateral distance gradient of the tidal channel margins, the number of stems, inflorescences, maximum stem height and total biomass of all *S. alterniflora* transplants were highest in the N microhabitat in each marsh zone (Fig. 4). In low marsh, none of the fitness parameters differed significantly among the 3 microhabitats. There were significant decreases in *S. alterniflora* performance (both tiller and seedling) in middle marsh and high marsh with increasing lateral distance ($p < 0.05$; Fig. 4).

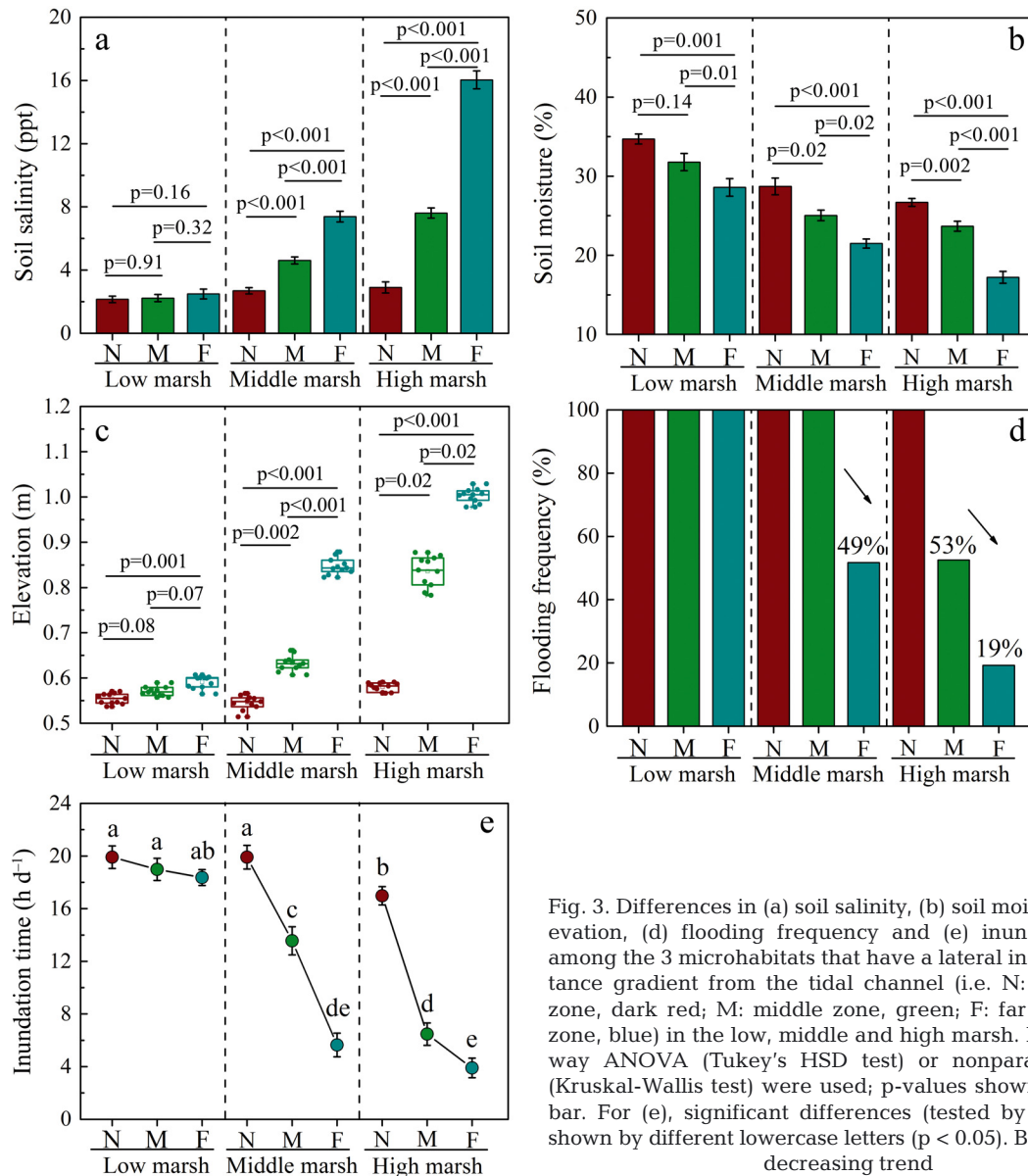


Fig. 3. Differences in (a) soil salinity, (b) soil moisture, (c) elevation, (d) flooding frequency and (e) inundation time among the 3 microhabitats that have a lateral increased distance gradient from the tidal channel (i.e. N: near creek zone, dark red; M: middle zone, green; F: far from creek zone, blue) in the low, middle and high marsh. For (a–c), 1-way ANOVA (Tukey's HSD test) or nonparametric test (Kruskal-Wallis test) were used; p-values shown above the bar. For (e), significant differences (tested by GLMs) are shown by different lowercase letters ($p < 0.05$). Black arrows: decreasing trend

3.5. Relationships between bottom-up abiotic stresses and *S. alterniflora* growth performance

In overall marshes (Fig. 5), the total biomass of *S. alterniflora* was significantly negatively correlated with both soil salinity and elevation of tidal channel margins, with $R^2 = 0.70$ ($p < 0.001$, Fig. 5a) and $R^2 = 0.80$ ($p < 0.001$, Fig. 5c), respectively. However, significant positive relationships were observed between the total biomass of *S. alterniflora* and soil moisture, flooding frequency and inundation time, with $R^2 = 0.59$ ($p < 0.001$, Fig. 5b), $R^2 = 0.71$ ($p < 0.001$, Fig. 5d) and $R^2 = 0.73$ ($p < 0.001$, Fig. 5e), respectively. Similarly, the number of *S.*

alterniflora stems were negatively correlated with both soil salinity and elevation of tidal channel margins in all zones of marshes, with $R^2 = 0.70$ ($p < 0.001$, Fig. 5f) and $R^2 = 0.83$ ($p < 0.001$, Fig. 5h), respectively. In contrast, the number of *S. alterniflora* stems was positively correlated with soil moisture, flooding frequency and inundation time, with $R^2 = 0.55$ ($p < 0.001$, Fig. 5g), $R^2 = 0.77$ ($p < 0.001$, Fig. 5i) and $R^2 = 0.76$ ($p < 0.001$, Fig. 5j), respectively. Moreover, all bottom-up abiotic parameters of tidal channel margins in middle marsh and high marsh were available for predicting the total biomass and number of *S. alterniflora*, but not in low marsh (Tables S4 & S5 in the Supplement).

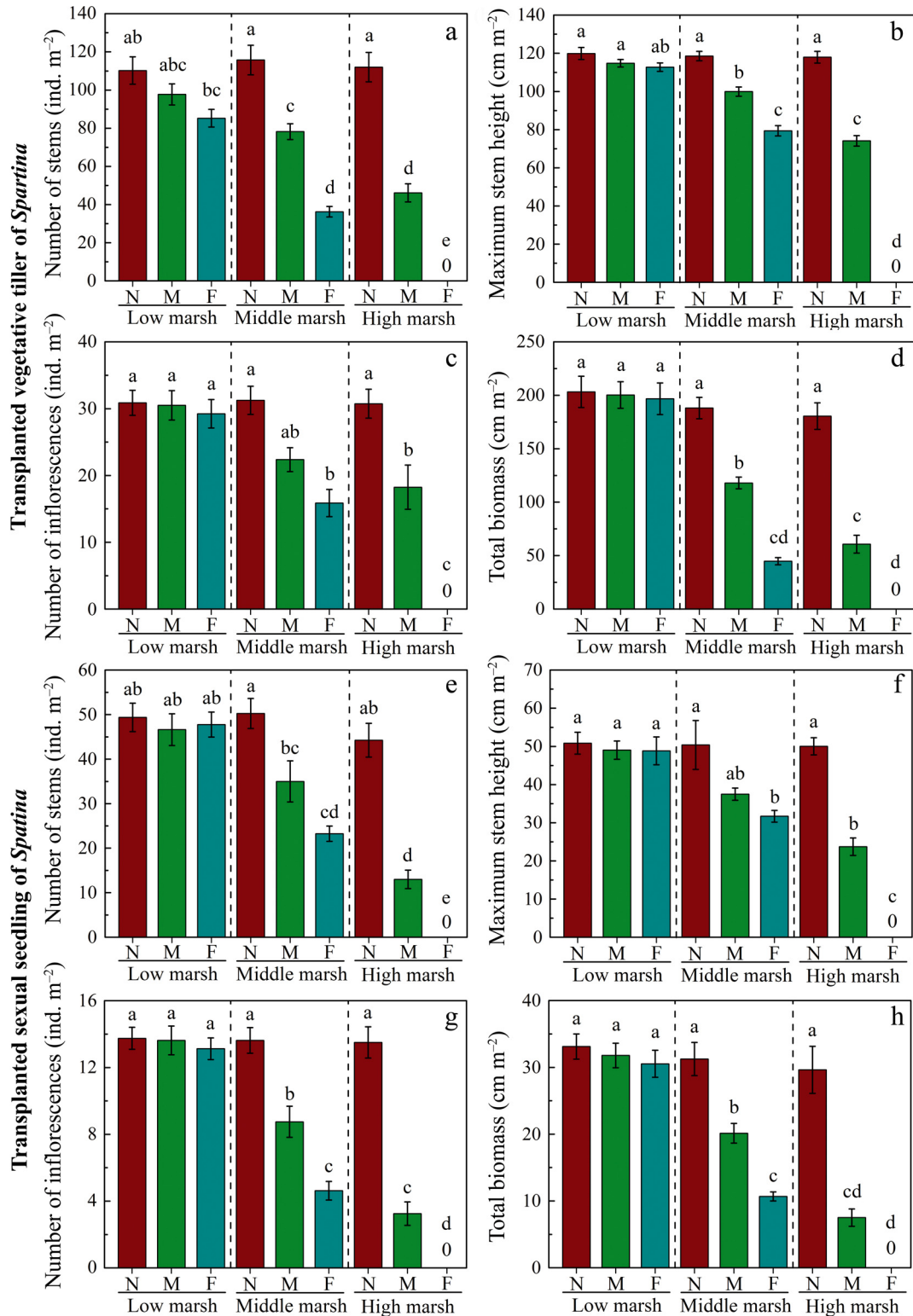


Fig. 4. Performances of *Spartina alterniflora* (a,e: number of stems; b,f: maximum stem height; c,g: number of inflorescences; d,h: total biomass) growing from (a–d) transplanted vegetative tillers and (e–h) transplanted sexual seedlings, among the 3 microhabitats of the tidal channel margins (i.e. N: near creek zone, dark red; M: middle zone, green; F: far from creek zone, blue) in each elevational marsh zone (i.e. low, middle and high marsh). Data are mean ± SE (n = 8 replicates). Significant differences (tested using GLMs) are indicated by different lowercase letters (p < 0.05)

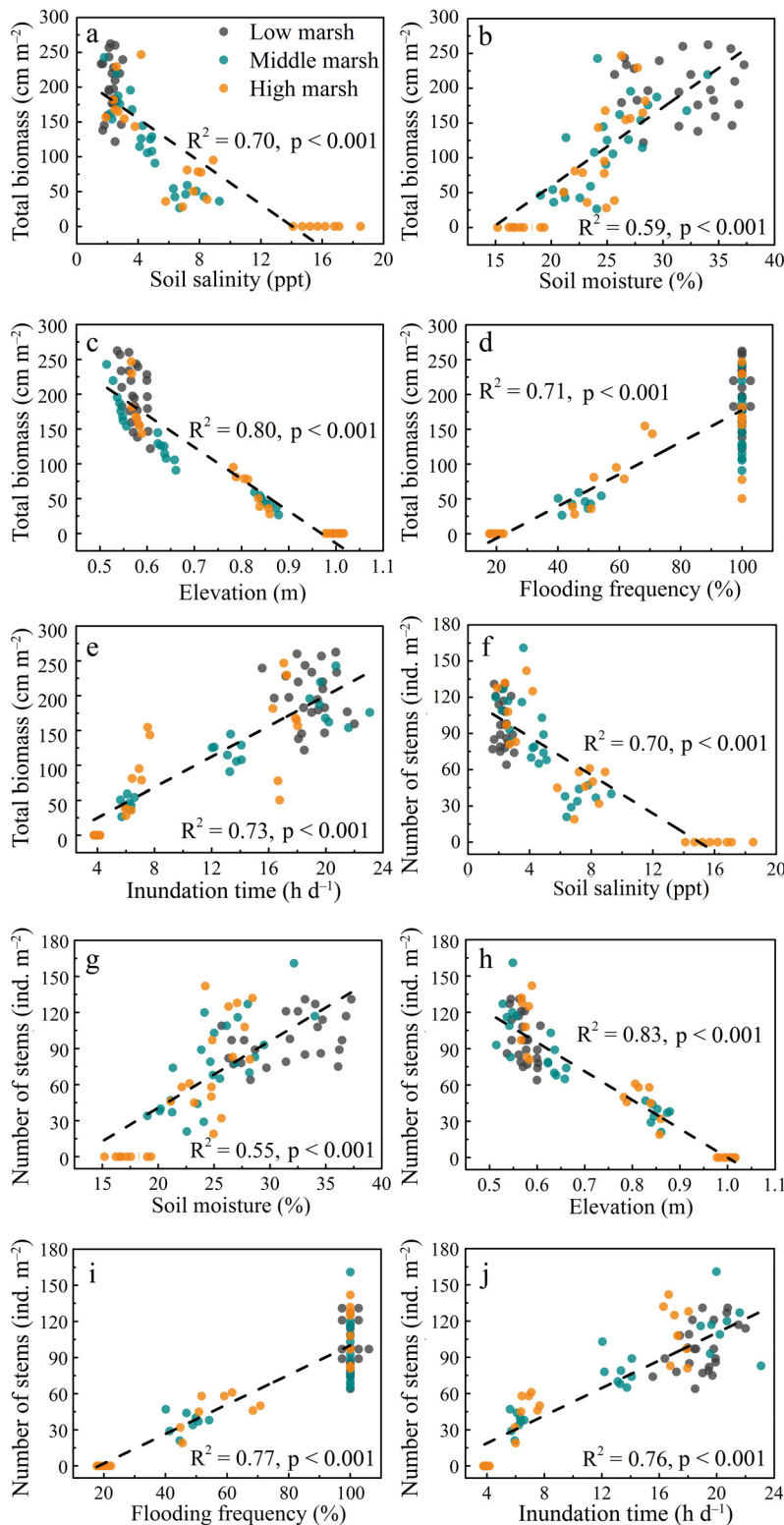


Fig. 5. Relationships between bottom-up abiotic factors (a,f: soil salinity; b,g: soil moisture; c,h: elevation; d,i: flooding frequency; e,j: inundation time) and (a–e) total biomass of *Spartina alterniflora*, and (f–j) number of *S. alterniflora* stems growing from transplanted vegetative tillers. Dashed lines: linear fitting lines. Results of linear regression models accompanied by R² and p-values

4. DISCUSSION

Concerns about the global spread of invasive *Spartina* species raises interest in studying its expansion mechanisms (Liu et al. 2020). We studied the role of a dominant geomorphic salt marsh feature, tidal channels, in regulating *S. alterniflora* invasion via bottom-up abiotic gradients (soil salinity and inundation conditions) and bottom-up biotic factors (propagule pressure). This study revealed the vital mechanisms by which tidal channel margins facilitate the expansion of invasive *S. alterniflora*: a higher propagule pressure, combined with suitable physical conditions of the microhabitats that tidal channels formed, facilitated the establishment, growth, colonization and sexual reproduction of *S. alterniflora*. As such, tidal channel margins contribute substantially to the rapid expansion of *S. alterniflora*. The present study results indicate that geomorphic landscape features such as marsh channels can profoundly influence plant invasion in coastal ecosystems via changes in abiotic and biotic-dispersal factors.

4.1. Spatial heterogeneity of bottom-up abiotic stresses and *S. alterniflora* invasion intensity along tidal channel margins

Topographic gradients of bottom-up abiotic stresses are typical characteristics in salt marshes (Cui et al. 2011). Our results showed that soil salinity and elevation were increased with increasing distance from tidal channels, whereas soil moisture, inundation frequency and inundation time were decreased. The same spatial patterns for these bottom-up abiotic factors have also been observed in salt marshes in Georgia, San Francisco Bay and Florida (Schile et al. 2011, Pomeroy & Wiegert 2012). Furthermore, the differences in the soil abiotic stresses and inundation conditions among the 3 microhabitats (i.e. N, M and F) of low marsh were relatively in-

significant in comparison with middle marsh and high marsh (see Fig. 3). This might be caused by the interaction of elevation and tide activity. In low marshes, there was no significant difference in elevation variation of tidal channel margins, with increasing distance from tidal channels, and thus high homogeneity of the tidal action existed in this marsh zone. Other studies have also found no significant spatial heterogeneity of abiotic factors (e.g. salinity and moisture) within low marshes, which is frequently influenced by tides (Pennings et al. 2005, Cui et al. 2011).

The results from field surveys revealed that in spite of *S. alterniflora* aggregating in zones closer to the tidal channel margins, the invasion intensity of *S. alterniflora* decreased along tidal channel margins from low marsh to high marsh. *S. alterniflora* performs better in frequently flooded and lower-salinity regions (Xiao et al. 2011, Qi et al. 2017). In tidal channel margins of all 3 elevational marsh zones, the N microhabitats were generally characterized by frequent flooding and low salinity, which was suitable for the growth of *S. alterniflora*. However, a broader optimized region for *S. alterniflora* expansion existed in tidal channel margins of the low marsh, thus resulting in a higher invasion intensity. Other than the above-mentioned suitable physical factors, lower competition of native plants could be another important factor that caused the higher invasion intensity in the lower marsh zones (Emery et al. 2001, Pennings et al. 2005). This is also consistent with other studies showing that *S. alterniflora* mostly occupies salt marshes with low elevations both within its native and invasion ranges (Li et al. 2009, Ning et al. 2019).

4.2. Effects of bottom-up abiotic stresses on *S. alterniflora* invasion to tidal channel margins

Variations in *S. alterniflora* performance were shown in different margins of tidal channels under the combined effects of bottom-up abiotic stresses. Although the tolerance of salinity and flooding stress in *S. alterniflora* have been well documented (Smith & Lee 2015, Xue et al. 2018), we found that microhabitats with high soil salinity and low inundation conditions, in particular with a hypersaline zone at upper elevations (e.g. the F microhabitat in high marsh), inhibited the performance of *S. alterniflora* transplants. The result is consistent with previous studies that concluded that salinity and inundation are critical physical stresses that have prevented *S. anglica* and *S. densiflora* invasions (Castillo et al. 2000, Dethier & Hacker 2005). The performance of

S. alterniflora is generally believed to increase with decreased soil salinity and increased inundation conditions (Xue et al. 2018). Similarly, the results from our transplant experiments also suggest that the biomass of *S. alterniflora* was negatively correlated with soil salinity and elevation, while the relationships with soil moisture and inundation activity were just the opposite. This may be because infrequent inundation and higher elevation could elevate salt stress for *S. alterniflora* by soil heating and pore water evaporation (He et al. 2012).

Although we did not perform common garden experiments to quantify the thresholds of *S. alterniflora* performance under the interactive effects of salinity and inundation conditions, a greenhouse experiment conducted at the Yellow River Delta revealed that *S. alterniflora* performed best under conditions of low salinity and frequent flooding, and the maximum biomass occurred in conditions of soil salinity of 7 PSU and 69% inundation frequency (Qi et al. 2017). A field experiment conducted in San Francisco Estuary, California, has also shown that invasive *S. densiflora* and its hybrid with *S. foliosa* were fast-growing in low-salinity and inundation stress conditions, and tolerated moderate interactive stresses (Gallego-Tévar et al. 2020). Therefore, tidal channel margins with low salinity and high inundation conditions (i.e. N, M and F microhabitats in low marsh, N microhabitat in middle and high marshes) facilitate *S. alterniflora* invasion. Favorable physical habitat conditions could also provide spatial windows for invasive species establishment (Dethier & Hacker 2005, Ning et al. 2020). Thus, the suitability of the above-mentioned microhabitats provided such spatial invasion windows for *S. alterniflora* to expand rapidly.

4.3. Effects of propagule pressure on *S. alterniflora* invasion to tidal channel margins

Increasing empirical and statistical evidences have revealed that propagule pressure, such as propagule number and spatial patterns of propagule arrival, is the most important among the biotic factors that contribute substantially to the successful establishment and spread of invasive species (Lockwood et al. 2005, Simberloff 2009, Ning et al. 2019). In the present study, we found that seeds of *S. alterniflora* arrived or deposited in the N microhabitat of each elevational marsh zone were maintained in the highest quantities compared with M and F microhabitats, apparently enhancing the propagule pressure for successful invasion of *S. alterniflora*. Previous field surveys have

shown that seed arrival decreased with increased distance from the seed-source area (Chang et al. 2008, Zhu et al. 2014). Furthermore, greenhouse and field experiments have shown that high-moisture and low-salinity conditions are of benefit to *S. alterniflora* seed germination (Wijte & Gallagher 1996, Xiao et al. 2009). Therefore, the high magnitude of preserved viable seeds integrated with suitable abiotic conditions facilitated the successful invasion of *S. alterniflora* in tidal channel margins. Additionally, although no significant differences in seed arrival and deposition were observed among the microhabitats in low marsh, it maintained overwhelming quantities of seeds compared with middle and high marshes. Thus, the propagule pressure in tidal channel margins in the low marsh was higher than in the middle and high marshes, which potentially caused a higher invasion intensity of *S. alterniflora* in the low marsh. In addition, seed viability is an important factor in influencing *Spartina* seed germination and seedling establishment (Xiao et al. 2009, Infante-Izquierdo et al. 2020). Although we did not test the viability of sampled *S. alterniflora* seeds, seeds of *Spartina* species are able to remain dormant in high-salinity and inundation environments without damaging the quality of the embryo, and have the capacity to germinate later when stress is reduced (Elsey-Quirk et al. 2009, Infante-Izquierdo et al. 2019). Therefore, the low-stress environments of the tidal channel margins could

have equipped the trapped *S. alterniflora* seeds with high viability, providing multiple opportunities for their establishment.

4.4. Conceptual framework for the role of tidal channels in *S. alterniflora* invasion

In summary, we present a conceptual model showing the lateral expansion processes and mechanisms of invasive *S. alterniflora* in the margins of tidal channels under the effects of bottom-up abiotic and biotic-dispersal factors (Fig. 6). This conceptual model visualizes that higher propagule pressure integrated with the suitable physical conditions of the microhabitats that tidal channels structurally formed lays a firm foundation benefiting the establishment, growth, colonization and sexual reproduction of *S. alterniflora*, which substantially contributes to the rapid expansion of *S. alterniflora* along the tidal channel margins. In a broad sense, once a geomorphic landscape feature creates spatial invasion windows (e.g. microhabitats with suitable abiotic and biotic conditions) that allow the initial invasive populations to be established successfully, the communities structure and ecosystem functioning can inevitably be damaged by the invasive plant gradually, and even completely destroyed when the invasion reaches a certain threshold.

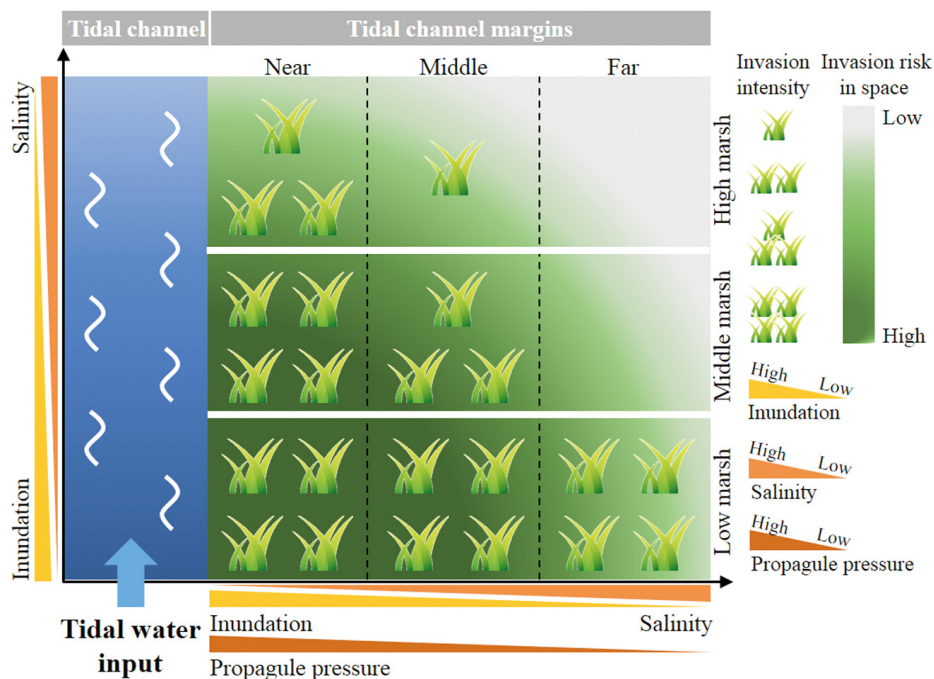


Fig. 6. Conceptual framework showing the lateral expansion mechanism of invasive *Spartina alterniflora* under conditions of bottom-up factors mediated by tidal channels

4.5. Implications for *S. alterniflora* invasion control and coastal wetland management

The invasion pattern of plants of the genus *Spartina* rapidly spreading along with the margins of tidal channels is a widely seen ecological consequence in many salt marshes globally, based on investigating high-resolution satellite images of worldwide coastlines (Fig. 1). This pattern not only existed in our experimental sites in the Yellow River estuary (Fig. 1, Site a), but also in many other important salt marshes in China (e.g. Yancheng salt marshes and Yangtze River estuary; Fig. 1, Sites b–d), on the Atlantic coast in Europe (e.g. Scheldt estuary; Fig. 1, Sites e–g) and the Pacific coast in America (e.g. Willapa Bay and San Francisco Bay; Fig. 1, Sites h,i).

Our results revealed that this landward invasion of *S. alterniflora* benefits from the combination of high propagule pressure and spatial invasion windows in tidal channel margins (i.e. microhabitats with low salinity and high inundation). This invasive mechanism mediated by tidal channels has potential implications for the control of invasive species and ecosystems management in global tidal channel-salt marshes, which have similar invasion patterns. Firstly, more attention should be paid to tidal channel margins, which potentially provide invasion windows for facilitating *S. alterniflora* landward invasion. Invasive *Spartina* and *Phragmites* species expand their invasion ranges rapidly through tidal channels margins (Lathrop et al. 2003, Schwarz et al. 2016, Ning et al. 2020). Secondly, some feasible artificial measures (e.g. propagule removal, tidal flow regulation, geomorphic modification) can be applied to minimize invasion windows for *S. alterniflora* seedling establishment on spatial and temporal scales. Moreover, human activities (e.g. dam construction, channel ditching) and induced climate changes (e.g. increasing wave disturbance, precipitation regime change) inevitably accelerate the variability of environmental conditions in coastal ecosystems (Diez et al. 2012, Balke et al. 2014). This may break the natural barriers that prevent invasions and even potentially increase spatial invasion windows for the initial establishment of invasive species. For example, drastic anthropogenic ditching may damage or destroy the salt barren band in high salt marshes, providing suitable salinity–moisture conditions for *S. alterniflora* invasion as a result of the enhanced propagule pressure (Qi et al. 2017, Ning et al. 2019). Therefore, much stricter management measures need to be implemented to control these above-mentioned human disturbances in order to decrease the potential inva-

sion risk of *S. alterniflora*. Importantly, biodiversity and functioning of coastal ecosystems can be restored through reconstructing tidal channel systems which provide favorable conditions for native species. Taking the interactions explicitly among bottom-up abiotic and biotic factors into account, understanding the relationship between the geomorphic characteristics of tidal channels and invasive species will be of benefit for developing a theoretical supported framework to control tidal channel-mediated plant invasions.

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