

## Maintenance of salt barrens inhibited landward invasion of *Spartina* species in salt marshes

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**Abstract.** *Spartina* spp. (cordgrasses) often dominates intertidal mudflats and/or low marshes. The landward invasion of these species was typically thought to be restrained by low tidal inundation frequencies and interspecific competition. We noticed that the reported soil salinity levels in some salt marshes were much higher than those at the mean higher high water level, which might inhibit the landward invasion of cordgrass. To test this possibility, we transplanted *Spartina alterniflora* across an elevational gradient in an invaded salt marsh in the Yellow River Delta National Nature Reserve, where a salt accumulation zone (i.e., salt barren) was previously observed. We found that *S. alterniflora* was significantly inhibited by the salt barren in high marsh regions, although it performed better at upland and low marsh regions. A common garden experiment further elucidated that *S. alterniflora* performed best at low salinity levels and that this species is less sensitive to inundation frequency. Our results indicated that the salt barren inhibited the landward invasion of *S. alterniflora* in salt marshes and provided a natural barrier to protect the upland from invasion. Though field observations suggest that *S. alterniflora* could propagate along tidal channels, which provide low-salinity corridors for the dispersal of propagules, natural salt barrens can inhibit the landward invasion of *Spartina* in salt marshes. However, artificial disturbances that break the salt barren band in salt marshes (e.g., artificial ditches) might accelerate the invasion of *Spartina* spp. This new finding should alert salt marsh managers to pay attention to artificial ditches and/or other human activities when attempting to control *Spartina* invasion.

**Key words:** elevational gradient; invasion control; salinity gradient; salt marsh; stress tolerance; tidal flooding; wetland conservation.

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### INTRODUCTION

Over recent decades, populations of non-native *Spartina* species have been introduced (both deliberately and accidentally) to estuaries in Europe, the United States of America, Australia, New Zealand, and Asia. Because of their high growth potential and ecological breadth, these non-native species are highly aggressive in new environments, and they frequently become the dominant plant species in tidal mud flats (Callaway and Josselyn 1992, Vasquez et al. 2006, Byers and

Chmura 2007, Wang et al. 2010, Medeiros et al. 2013).

Tidal inundation and salinity are key factors that affect the colonization of *Spartina* and their competition with native species (Yuan et al. 2013). Although all *Spartina* species are inundation tolerant, no *Spartina* species has been found to persist in areas subjected to consistent wave action (Moberley 1956). Furthermore, researchers found that long periods of continuous tidal inundation significantly reduced the biomass and density of *Spartina alterniflora* (Long et al. 2013, Smith and

Lee 2015). On the other hand, continuous tidal action is certainly not a prerequisite for growth, as evidenced by vigorous growth in greenhouses. However, surveys of *Spartina* spp. found that the invasive species of the genus were conspicuously absent (even within their native ranges) from all sites that experienced seasonal absence of tidal action or those with very little tidal activity (Adams 1963, Christiansen and Møller 1983, Silvestri et al. 2005, Xiao et al. 2011). Similarly, native *S. alterniflora* found along the Atlantic coast of North America was found to grow to heights of >1.0 m near tidal creeks, whereas those found at locations relatively distant from tidal creeks were dwarfed in size (Morris 1980).

Diverse chemical and physical gradients might contribute to different growth forms at local scale. Among these, salinity, nutrients, soluble sulfide, and metabolic toxins have received the most attention. An obvious gradient of increased salinity with distance from creek banks was observed in the salt marshes of Georgia (Christian et al. 1974) and in southeastern salt marshes in America, with concentrations ranging from less than that of seawater around creek banks to approximately 50 ppt in inner marshes (Pomeroy and Wiegert 1981). Moreover, a hypersaline zone was observed in high marshes (Adams 1963, Haines and Dunn 1976, Pennings and Callaway 1992, Morris 1995, Silvestri et al. 2005). Haines and Dunn (1976) demonstrated that *S. alterniflora* growth was inhibited by high salinity, and Nestler (1977) also observed an inverse correlation between *Spartina* growth and intertidal salinity in salt marshes. An experimental study indicated that increased salinity reduced the efficiency of nitrogen uptake and caused nitrogen deficiency in *Spartina* (Morris 1980, Bradley and Morris 1991, Tyler et al. 2007). In other salt marsh regions of Georgia and the gulf coast marshes of Louisiana, where the salinity gradient is not high enough to restrict plant growth, higher sulfide concentrations in more elevated regions limited *Spartina* height and productivity (King et al. 1982, Delaune et al. 1983, Bradley and Dunn 1989, Bradley and Morris 1991).

Salinity has long been considered the primary determinant of species composition in salt marshes (Adams 1963, Pennings and Callaway 1992). Previous field studies (Morris 1995, Bertness and Pennings 2000, Silvestri et al. 2005) found that a soil salinity maximum band exists in

the vicinity of high marsh zones, where soil salinity is too high for plant survival. This zone is also known as a salt barren/flat. Wang et al. (2007) provided a mechanistic explanation of salt barren formation in the Atlantic and gulf coastal regions. They suggested that the soil salinity of low and middle marsh zones tends to reflect that of the incoming tide (around 20 ppt) because of frequent tidal inundation; soil salinity then increases to a maximum (peaking at  $90 \pm 44$  ppt) at an elevation of several centimeters above the mean higher high water (MHHW) level, because the decreased duration of tidal inundation allows evapotranspiration (ET) to concentrate pore water salt and minimize salt output caused by drainage; soil salinity is then reduced to a lower level and quickly graded into the freshwater level at the upland border. In addition, the simulation of Wang et al. (2007) indicated that MHHW determined salt barren locations in a coastal salt marsh, incoming tidal salinity largely controlled the extent of salt accumulation in marshes, and tidal irregularity primarily controlled salt barren width, together with ET, temperature, and hydraulic conductivity.

Because most salt barrens were observed in low-latitude salt marshes, including the Carolina and Carpinteria salt marshes in the United States and Venice lagoon in Italy (Adams 1963, Pennings and Callaway 1992, Morris 1995, Silvestri et al. 2005), Bertness and Pennings (2000) stated that a salinity accumulation band would not exist in high-latitude salt marshes, such as those in New England. However, the simulation study of Wang et al. (2007) indicated that a less pronounced salinity maximum band should occur, even in the New England salt marshes.

The landward invasion of the *Spartina* species was extensively studied, especially their competitive relationship with native species and how the competitive dominance varied with environmental factors like salinity, waterlogging, and sediment type (Dethier and Hacker 2005, Wang et al. 2006, 2010, Tang et al. 2016). These studies showed that *Spartina* spp. had a higher tolerance to salinity and waterlogging than native species, and it gained competitive dominance at conditions of high salinity and full immersion. However, the importance of a hypersaline zone in inhibiting landward invasion of *Spartina* has not been recognized. Thus, this study aimed at

answering two questions of (1) whether the hypersaline zone is a natural barrier for landward invasion of the salt-tolerant *Spartina* and (2) how *Spartina* perform if they surpass the hypersaline zone and reach inland areas that are characterized by low-salinity substrate and less inundation frequency. To answer these questions, we transplanted one of the most invasive species of the genus *Spartina*, *S. alterniflora*, across the elevational gradient in an invaded salt marsh of the Yellow River Delta National Nature Reserve (YRDNNR), and we measured its tolerance to salinity and inundation using common garden experiments. Finally, we assessed the landward invasion risk of *S. alterniflora* by incorporating the spatial characteristics of elevation and salinity.

## MATERIALS AND METHODS

### Study area

The YRDNNR (37°35'–38°12' N, 118°33'–119°20' E) is located near the Yellow River

Estuary, a continental estuary with a weak tide, in Dongying City, Shandong Province, China (Fig. 1). This region is characterized by a warm temperate continental monsoon climate, with distinct seasons and a hot rainy summer. The YRDNNR consists of vast floodplains and unique wetlands, shaped in part by high sediment loads from the Yellow River (Cui et al. 2009). Large salt marsh expanses occur along the shoreline. The tide in the intertidal zone of the Yellow River Estuary is an irregular semidiurnal tide (twice a day), and the mean tidal range is 0.73–1.77 m (Li et al. 1991).

The flora of the estuary is relatively simple, and plant zonation in the marshes is affected by both biological interactions and physical stressors, including soil salinity and tidal flooding, across elevation gradients (Cui et al. 2008, 2010, 2011, He et al. 2009, 2011, 2012). Soil-pore-water salinity levels in the summer can vary substantially, reaching a peak in the high marshes. This range is represented by approximately 4 PSU in

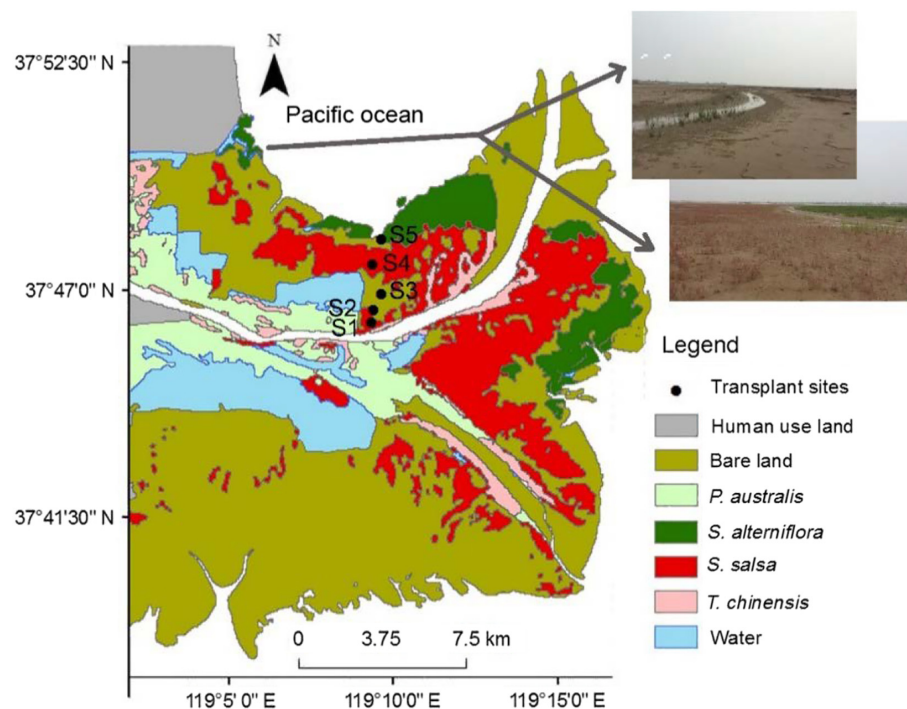


Fig. 1. Location of the Yellow River Delta National Nature Reserve (YRDNNR) and field transplanting sites (S1–S5) in upland, terrestrial border, high marsh, low marsh, and mudflats, respectively. Land cover information was produced using supervised maximum-likelihood classification from Landsat 8 remote sensing image of 2014. Photographs on the right, taken in July 2015, showed the invasion of *Spartina alterniflora* (green ramets) along tidal creeks into *Suaeda salsa*'s habitats (red shoots); higher resolution photographs can be found in Appendix S1: Fig. S1.

uplands, 17 PSU in mudflats, 30 PSU in low marsh areas, 55 PSU at terrestrial borders, and 120 PSU in the high marshes (Cui et al. 2011). Flooding frequency varies from 0% in uplands, 1% in terrestrial borders to 12.5% in high marsh areas, 55% in low marshes, and 95% in mudflats (Cui et al. 2011, He et al. 2011). At higher elevations (i.e., uplands, terrestrial borders, and high marsh), salinity and competitive relationships play a major role in mediating community structure. At lower elevations (i.e., mudflats and low marsh), flooding becomes important in determining the patterns of vegetation (He et al. 2009).

The dominant vascular plant species include *Phragmites australis* (dominating the upland area near the river course), *Tamarix chinensis* (dominating terrestrial borders of the salt marshes), and *Suaeda salsa* (dominating high and low marshes). Together, these species account for more than 60% of the total vegetative biomass across the salinity gradients in the YRDNNR (Cui et al. 2011). Other plant species, including *Salicornia europaea*, *Scirpus* spp., and *Juncus* spp., only occur sparsely in small patches in the marsh habitats. In the uplands, plant species are much more diverse, and species include *Calamagrostis pseudophragmites*, *Triarrhena sacchariflora*, and *Imperata cylindrica*. *Spartina alterniflora* has become a dominant species in the mudflats, and it is expanding rapidly. In some regions, we observed the spread of *S. alterniflora* upward through tidal creeks, and it reached the low marshes occupied by *S. salsa* (photographs in Fig. 1).

#### Field transplantation experiments

To determine the effect of physical filters on the performance of *S. alterniflora* along the elevation gradient, we transplanted this species into mudflat, low marsh, high marsh, terrestrial border, and upland zones (as shown in Fig. 1) in mid-May 2014. At each transplant site, we selected a quadrat of 2 × 2 m that was covered by native plants, and cleared the natural vegetation within it to exclude the competition from other species. Then, we selected four sub-quadrats (with a size of 0.5 × 0.5 m, and 0.5 m away from each other) within the 2 × 2 m quadrat to transplant *S. alterniflora*. We excavated substrate blocks (10 cm length × 10 cm width × 20 cm deep) that only contained healthy *S. alterniflora* ramets from mudflats near the transplant site S5, and evenly

planted 25 substrate blocks within each sub-quadrat. The transplants were watered with freshwater every day for one week to reduce transplant shock. In late June, late July, and late September, we collected soil cores of the topsoil (5.05 cm diameter × 5 cm deep) at the center and four corners of each sub-quadrat and made a composite soil sample for each sub-quadrat. Soil samples were brought to the laboratory to monitor soil-pore-water salinity. In mid-October 2014, we counted the survival rate of transplants and measured the maximum ramet height of each 10 × 10 cm transplant with a metric ruler. Successively, the aboveground biomass of each transplant was harvested, dried, and weighed. Finally, we tested the differences in performance of *S. alterniflora* at each transplant site with Tukey HSD multiple comparisons if the data meet the assumptions of ANOVA.

Soil cores of the top soil (5 cm deep) were weighed and dried at 60°C for 48 h in an oven and were then reweighed to determine the moisture content. Dried soil was mixed with deionized water (5:1 aqueous suspension; vibration for 30 min). The salinity of the supernatant was measured after 24 h using an NaCl meter (HANNA HI98188, Nusfalau, Romania), and the original soil-pore-water salinity was then calculated based on the initial moisture content of the core (Pennings et al. 2005).

#### Common garden experiments

We quantified the stress tolerance of *S. alterniflora* to soil salinity and inundation frequency by means of common garden experiments. To conduct these tests, *S. alterniflora* ramets were collected from mudflats near transplant site S5 (Fig. 1). Specifically, we randomly excavated 120 substrate blocks (10 × 10 × 20 cm) containing emerging *S. alterniflora* tillers with a height of 20 cm at site S5 (Fig. 1). These substrate blocks were then transplanted into pots in the greenhouse and were reared for two weeks with freshwater to allow acclimation to greenhouse conditions before exposure to salinity and inundation treatments. Plants that exhibited transplant-related stress were discarded and replaced by those that handled the process well.

The samples were reared in the greenhouse over a wide range of salinity and inundation treatments. The experiment began in late April 2014. The salinity and inundation treatments were



in progress by 7 May and were maintained for four months. Our experimental setup included five inundation levels (every day, every other day, every five days, every ten days, and no inundation) and seven salinity levels, that is, 35 treatments in total, and there were three replicates of each treatment. Soil salinity gradients were achieved by watering salt solutions at seven salinity levels (0.5, 2.0, 5.0, 10.0, 15.0, 30.0, and 60.0 PSU). Each time, inundation/flooding lasted for 24 h by adding water with the corresponding saline solution to pots until the water level was 5 cm higher than the soil surface. Thus, above five inundation levels represented five flooding frequencies, that is, 100%, 50%, 20%, 10%, and 0%.

The soil salinity of the topsoil (5 cm deep) was measured every month. The soil salinity of each replicate achieved stability by July, and we took the averaged salinity of August and September as the soil salinity level of a given treatment. The experiment was terminated in September 2014, and the aboveground biomass and belowground biomass of all replicates were harvested, dried, and weighed. We fit the *S. alterniflora* performance response (standardized biomass calculated by  $(x_i - \min(x_i)) / (\max(x_i) - \min(x_i))$ ) to soil

salinity and flooding frequencies with Gaussian surfaces via *sftool* in MATLAB (The MathWorks, Inc., Natick, Massachusetts, US).

### Spatial characteristics of elevation and salinity in the YRDNNR

To characterize the elevation and salinity of YRDNNR, 55 evenly distributed sampling sites were selected to measure elevation in July 2016. The Global Position System (GPS) positions meet precision 0.02 m on the XY plane and 0.04 m on the Z direction under national GPS D and E level. The GPS positions were surveyed by Real Time Kinematic supported by national GPS network. The GPS positions are in 118°30' under Xi'an 1980 coordinate system.

Geostatistical methods of local polynomial interpolation were then performed to explore the spatial distribution of elevation. Spatial analysis methods, including extraction and reclassification, were used to draw the elevation map. The geostatistics and spatial analyses were conducted with ArcGIS version 9.3 (ESRI, Redlands, California, US).

Soil salinity distribution data referred to field survey results obtained by Yu et al. (2014) in June 2010, where 82 soil samples (0–10 cm depth) were

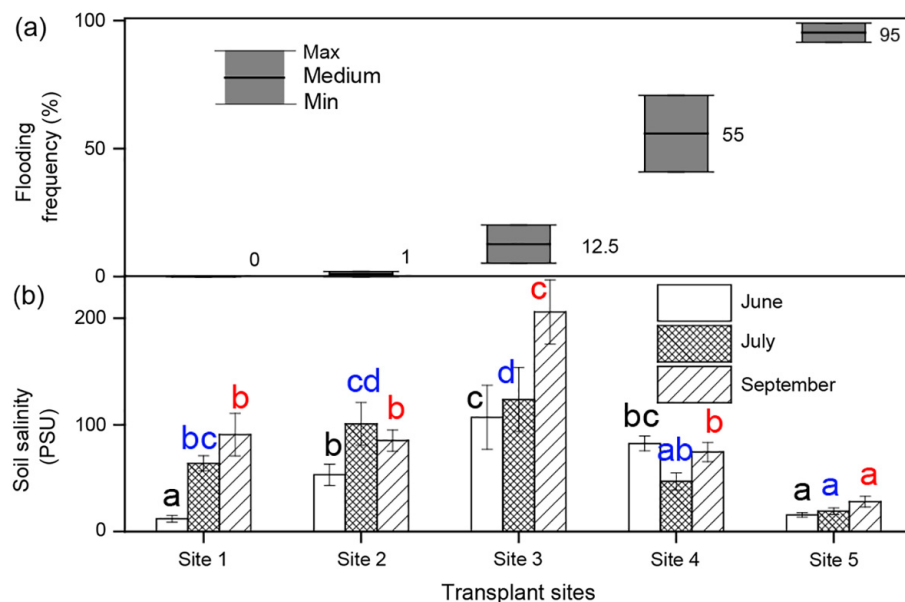


Fig. 2. Seasonal variations in abiotic factors from June, July, and September 2014. (a) flooding frequency (estimated maximal, minimum, and medium values); (b) soil salinity (means  $\pm$  SE) ( $n = 4$ ): Black, blue and red letters above bars represent soil salinity difference among transplant sites in June, July, and September, respectively, and bars sharing a letter are not significantly different from one another ( $P > 0.05$ ).

collected from the YRDNNR and measured in laboratories. Geostatistics and spatial analyses were used to draw the salinity map (Yu et al. 2014).

## RESULTS

### Physical stress and vegetation

Soil salinity and flooding frequency measurements from the transplant sites (Fig. 2) indicated the existence of a salt barren in the area, specifically in places where the soil salinity was >100 PSU. The performance of transplanted *Spartina alterniflora* (Fig. 3) was closely related to soil salinity. Transplanted *S. alterniflora* performed

best in mudflat zones (its source area, Site 5) where the soil salinity was the lowest, and actually, these areas had already been invaded by *S. alterniflora*. As for other habitats (sites 1–4), there was no significant difference in the survival rate of transplanted ramets; however, their biomass and stem height at upland (Site 1) were significantly higher than in hypersaline regions like high marsh and low marsh, which indicated that *S. alterniflora* growth was significantly inhibited in low marsh and high marsh regions with increased salinity, whereas it was less inhibited in the upland, characterized by lower soil salinity than in the salt barren areas.

### Stress tolerance

The greenhouse results revealed that the maximum biomass production of *S. alterniflora* over four months occurred at physical conditions of a 69% inundation frequency and a soil salinity of 7 PSU (Fig. 4). Furthermore, *S. alterniflora* was generally more sensitive to soil salinity than it was to the inundation frequency. When soil salinity was higher than 60 PSU, performance was approximately 20% of its maximum value. *Spartina alterniflora* is more sensitive to decreased inundation frequency when soil salinity is low.

### Spatial characteristics of elevation and salinity

The soil salinity level of hypersaline in YRDNNR can be as high as approximately 100 PSU. Its location is highly related to elevation characteristics (situated at 0.5–1.0 m; Fig. 5).

After comparing the elevation characteristics (Fig. 5a) to the spatial distribution of *S. alterniflora* (Fig. 1), we found that *S. alterniflora* mainly invaded mudflat regions at elevations <0.5 m. The landward *S. alterniflora* invasion was inhibited by the aforementioned salt barren zone. However, the inland regions have low salinity levels and open water zones (Figs. 1, 5b), which provide suitable habitats for *S. alterniflora*.

## DISCUSSION

The results of our common garden experiments revealed that *Spartina alterniflora* performed best in frequently flooded and less salty regions, which is consistent with recent field observations and greenhouse experiments (Daehler and Strong 1996, Xiao et al. 2011, Snedden et al. 2015). The

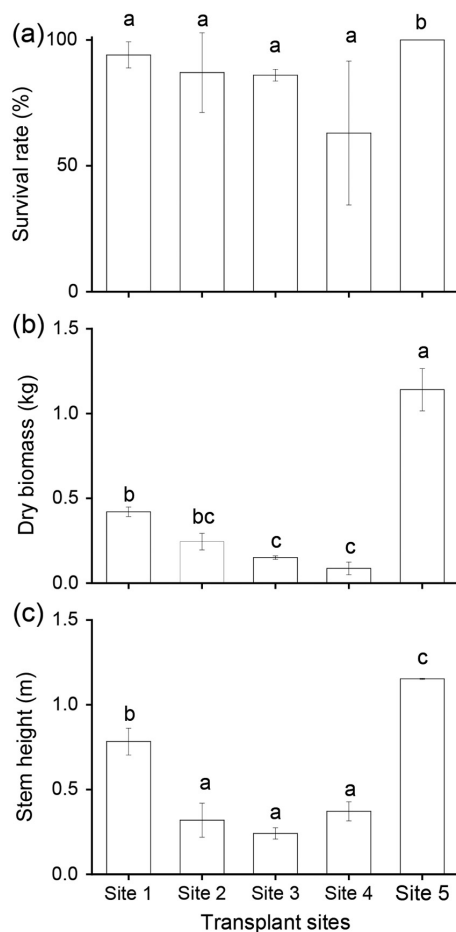


Fig. 3. Summary of the transplanting experiments of *Spartina alterniflora* across the elevational gradient in 2009. Data are shown as means  $\pm$  SE ( $n = 4$ ). Bars sharing a letter are not significantly different from one another ( $P > 0.05$ ).

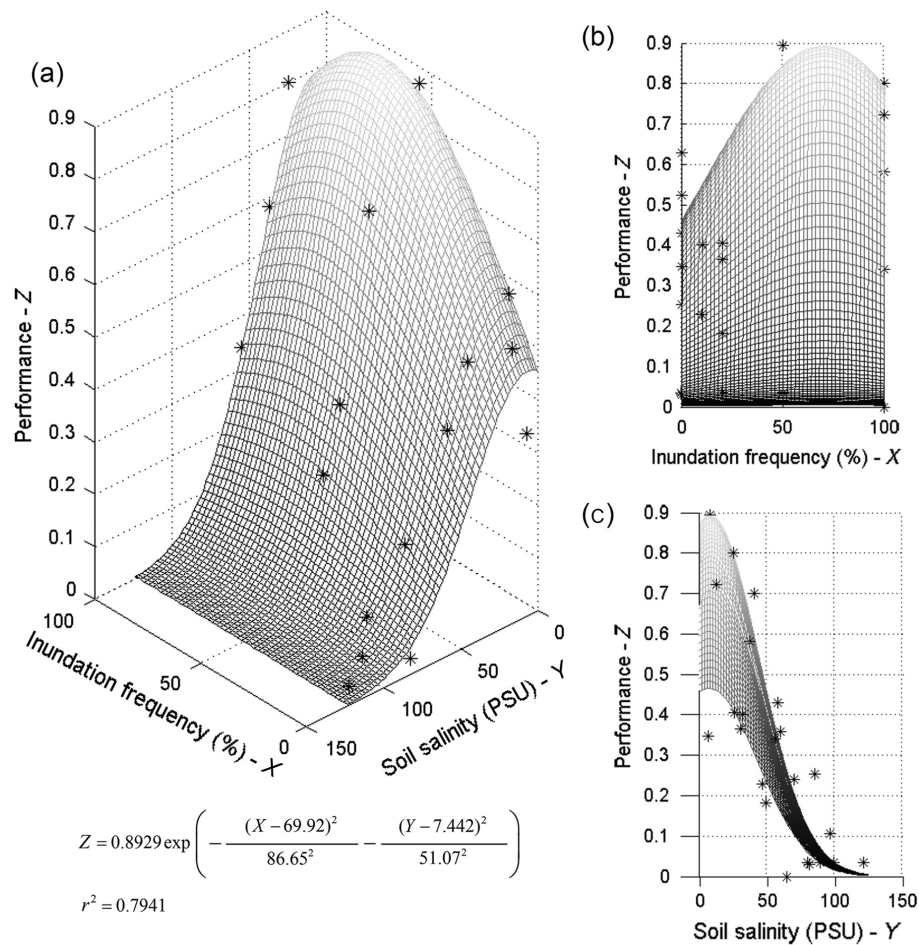


Fig. 4. Salt and inundation tolerance of *Spartina alterniflora* in common garden experiments. (a) shows the regression surface. (b and c) regression surfaces from XZ view and YZ view, respectively.

performance of transplanted *S. alterniflora* in high marshes was primarily limited by the hypersaline substrate, indicated by poor performance at salinity levels higher than 100 PSU (Fig. 4). This indicates that maintenance of the salt barren band might be an effective method of preventing the upward invasion of the species.

Although *S. alterniflora* is less restrained by salinity stress in upland areas, a significant difference in performance between transplanted *S. alterniflora* in upland areas and mudflats was detected. This might be caused by two factors. Firstly, greater seasonal variance in soil salinity occurs in uplands, with higher soil salinity in the late growing season (July–September), which might restrain the growth of *S. alterniflora*. Secondly, infrequent inundation might also be

stressful, because as we observed in the common garden experiments at lowest salinity level, the performance of *S. alterniflora* without inundation was only half its maximum performance.

A limitation of our experiments is that we recorded the performance of field transplanted *S. alterniflora* for one year only, which overlooks its potential transgenerational plasticity if any, since we did find historical evidence of its transgenerational effects. According to our observation in the following year (2015), we found that new ramets were produced from previously transplanted *S. alterniflora* in the upland areas (Site 1), although these were not as vigorous as those in the mudflats (Site 5). However, no new ramets were observed at the other transplant sites. This demonstrated that *S. alterniflora* could

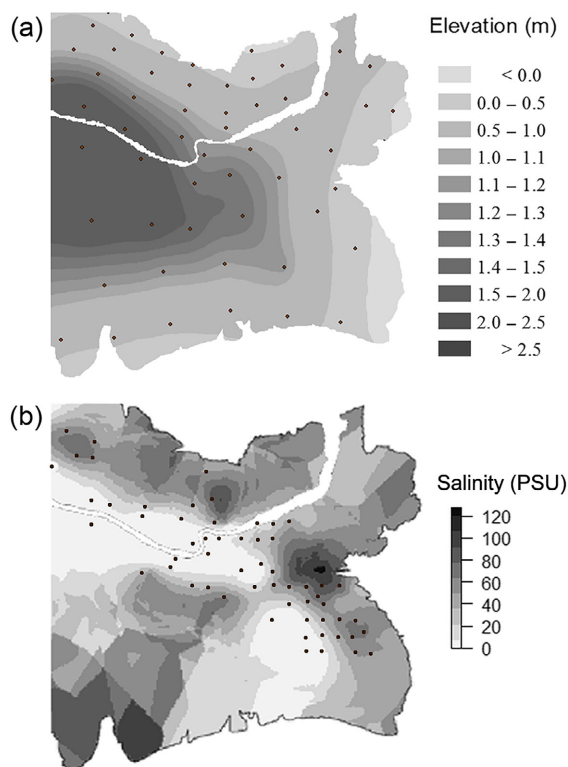


Fig. 5. Elevation and salinity characteristics in the Yellow River Delta National Nature Reserve. (a) Elevation characteristics interpolated and reclassified based on in situ elevation information of 55 evenly distributed sampling sites (dark points) and (b) soil salinity from interpolation results of a field soil salinity survey in 2010 (Yu et al. 2014), and dark points are soil salinity sampling sites.

regenerate successfully in the upland areas, and it is potentially a great threat for upland communities if it reaches those areas by whatever means. Intuitively, the colonization of *S. alterniflora* in the upland sites was determined by factors such as interspecific competition, herbivory, or water level, in addition to substrate salinity level. Unfortunately, contemporary research focuses more on the competition between *Spartina* and other low marsh species, whose habitat is directly occupied by *S. alterniflora* (Tang et al. 2009, Medeiros et al. 2013, Yuan et al. 2013), whereas the competition between upland plant species and low marsh *Spartina* is rarely studied. The Yellow River Delta, upland region is characterized by seasonally inundated

wetland and dry land occupied by *Phragmites australis* or *Tamarix chinensis*. For dry land where there is low salinity level and non-immersion, previous research indicated the native *P. australis* would gain competitive dominance (Wang et al. 2006), because *S. alterniflora* is less susceptible to low inundation frequency (Fig. 4). However, for seasonally inundated wetlands, *S. alterniflora* has a higher inundation tolerance ability than *P. australis* (Wang et al. 2010), and these two species were observed co-existing in the Yangtze River Estuary (Tang et al. 2016). To date, we have found no other studies that have investigated the competition between *S. alterniflora* and other upland species, although we can infer that uplands would be under threat once *S. alterniflora* surpasses the hypersaline band.

We found that *S. alterniflora* mainly invaded mudflat regions, where the elevation is <0.5 m. In the southeast part of the Yellow River Estuary, there is a region with an elevation lower than 0.5 m that could be a suitable habitat for *S. alterniflora*, but has not yet been colonized. According to historic remote sensing data (Landsat 7), *S. alterniflora* first invaded the northernmost region in YRDNNR, followed by a gradual southward invasion (*unpublished*). Therefore, this species might take some time to propagate and colonize the southeast part of YRDNNR. Thus, the southeast region might be under threat of invasion.

The salt barren band on the southern side of the YRDNNR is not as distinct as that in the other regions (Fig. 5). This might result from increased error in spatial interpolation in this region, owing to the small sample size for soil salinity there. Notably, the spatial interpolation result of Yu et al. (2014) is only partially reliable (Fig. 5), and areas with more sampling sites have higher soil salinity than those with fewer sampling sites, which implies that soil salinity of the less sampled regions within the salt barren area might be underestimated.

Historic surveys reveal that hypersaline zones in salt marshes are observed worldwide (Adams 1963, Pennings and Callaway 1992, Morris 1995, Silvestri et al. 2005), although the extent of salt accumulation was different for different salt marshes. However, in some salt marsh regions, salt barren areas were not observed (Yuan et al. 2013). This might be caused by anthropogenic activities, such as dam construction, that have



changed tidal action, and probably groundwater salinity (Yuan et al. 2013). As demonstrated by Silliman and Bertness (2004), shoreline development decreased soil salinity and was the driving force behind a *P. australis* invasion in the New England Salt Marshes. Similarly, a precise prediction of salinity alteration caused by artificial construction would be very important for *Spartina* containment.

In the field, we observed that *S. alterniflora* had invaded some tidal creeks in the YRDNNR (photographs in Fig. 1 and Appendix S1: Fig. S1), which is consistent with reports of the native habitats of *S. alterniflora*, where this species grows better near tidal creeks (Adams 1963, Christiansen and Møller 1983, Silvestri et al. 2005, Xiao et al. 2011). The *Spartina* species might benefit more from frequent inundation and low-salinity conditions in tidal creeks. Our analysis of the development of salt barren suggests that there should be a hypersaline band surrounding tidal creeks that inhibits their spread to other regions.

Although natural salt marshes with salt barrens can inhibit the invasion of *Spartina*, construction in salt marshes can increase the threat of landward invasion by *Spartina*. Apart from the abovementioned artificial structures that alter the hypersaline band, artificial ditches in salt marshes that connect the mudflats or tidal creeks with upland regions might pose greater risks, because they might break the salt barren band and provide a pathway for *Spartina* species to bypass the natural salinity limitation and propagate upward along these ditches.

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## SUPPORTING INFORMATION

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