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PRIMARY RESEARCH PAPER

What confines an annual plant to two separate zones along coastal topographic gradients?

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Abstract We investigated the roles of flooding, salinity, and plant competition in creating a bimodal zonation pattern of the marsh dominant annual plant, *Suaeda salsa*, along coastal topographic gradients on the Pacific coast of northern China. In two consecutive years, we manipulated salinity and flooding, salinity, and competition for *S. salsa* seedlings that had been transplanted into the mudflat, the high marsh, and the upland, respectively. *S. salsa* plants that had been transplanted into the mudflat were completely eliminated in the non-elevated treatments whereas they performed much better in the 10 cm elevated treatments, regardless of salinity treatments. Although the performance of *S. salsa* transplanted into the high marsh did not differ between the fresh (watered) and the salt (control) treatments, *S. salsa* seedling emergence in the high marsh was nearly completely inhibited in the salt treatments. In contrast, a large number of *S. salsa* seedlings did emerge in the fresh treatments. *S. salsa* transplanted into the upland performed well when neighbors were removed, whereas it appeared to be strongly suppressed when neighbors were present. These data indicated that flooding, salinity, and competition all played a role in determining the zonation pattern of *S. salsa*. Furthermore, the importance of salinity was found to vary with life-history stage. Based on the results from these field manipulative experiments, we suggest that the marsh plant zonation paradigm may hold true for plant distributions along landscape-scale topographic gradients from mudflats to uplands in general. The relative importance of flooding, salinity, and competition, however, may vary at different elevations within a site and between sites.

Keywords Competition · Flooding · Salt marsh · Soil salinity · *Suaeda salsa* · Wetland

Introduction

Shoreline habitats, which often exhibit a distinct pattern of vegetation zonation along steep environmental gradients (Fig. 1A) have been repeatedly used to elucidate the mechanisms of species spatial distributions (Crain et al., 2004). For at least the past three decades, researchers have experimentally investigated the mechanisms of plant distribution patterns in these habitats. These experimental studies all focused on a few heavily studied sites (Snow & Vince, 1984; Bertness & Ellison, 1987; Bertness, 1991a, b; Bertness et al., 1992; see Bertness & Pennings, 2000 for a

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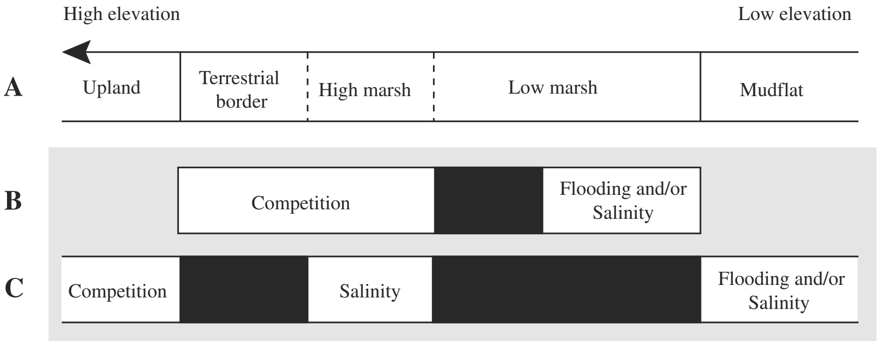

Fig. 1 Mechanisms of vascular plant distribution in shoreline habitats. **A** Different zones along topographic gradients on shorelines. The zones partitioned by *vertical solid lines* represent different zones at the landscape-scale, and those partitioned by *vertical dashed lines* represent different zones within salt marshes. This picture of shoreline habitats is developed based on the zones that have been described in previous study (see Zedler et al., 1999 for a review), in order to reflect the general patterns on shorelines. However, it only partially reflects shorelines that have no mudflats or shorelines where the continuum from marsh to upland has been interrupted by sea walls. In the present study, the seaward border and the terrestrial border of high marsh are named as high marsh and terrestrial border, respectively, following Bertness (1991b). **B** and **C** Distribution of a given species (*filled area*) and its limiting factors (*indicated in open area*) within salt marshes (**B**), and along the coastal topographic gradient from mudflats to uplands in the present study (**C**). The model **B** is based on previous studies while the model **C** is based on the hypotheses of the present study. See *Introduction* for more details

review) and have led to an emerging paradigm which suggests that the stressful boundaries of different marsh plants across stress gradients are determined by their varied tolerances to physical stresses, such as salinity and flooding, and that the benign boundaries of these species across stress gradients are determined by competition with plants in more benign habitats (hereafter “plant zonation paradigm”, shown in Fig. 1B). However, the generality of this paradigm of marsh plant distribution has not been determined (Bertness & Pennings, 2000). It remains to be examined whether this paradigm can be applied generally to multiple sites and to larger spatial scales (Bertness & Pennings, 2000; Pennings et al., 2003).

Although the above paradigm of marsh plant zonation is generally useful in elucidating marsh plant distribution patterns, as Pennings et al. (2005) argued, the relative importance of the different factors involved is likely to vary between sites. The few existing studies from salt marshes that experience irregular flooding in southern Brazil (Costa et al., 2003) and low-latitude salt marshes at Sapelo Islands, US (Pennings et al., 2005) show that competition plays only a minor role in generating plant distribution patterns compared with physical stress, which is indicative of variations in the relative importance of physical stress and competition. These variations are most easily attributed to differences in the physical environment between sites (Pennings et al., 2005), such as patterns of salinity and flooding. Both flooding and salinity decrease in severity from the water’s edge to the marsh–upland border (Pennings & Bertness, 1999, 2001) in New England salt marshes, where most experimental studies on salt marsh plant distribution patterns have been conducted (Pennings et al., 2005 and references therein). However, contrarily and more generally, soil salinity has been found to reach a peak near the high marsh zone (e.g., for North America, Adams, 1963; Pennings & Callaway, 1992; Morris, 1995; Bertness & Pennings, 2000; for Europe, Chapman, 1939; Gillham, 1957a, b; for Australia, Clarke & Hannon, 1969). Thus, further studies are necessary to test the relative importance of different factors in mediating marsh plant organization, especially in salt marshes where soil salinity and flooding are not parallel (Pennings et al., 2005).

To our knowledge, few studies have addressed whether the plant zonation paradigm based on studies within salt marshes can be applied to larger spatial scales. This paradigm has previously been found to hold true for shifts in plant species composition along a horizontal, landscape-scale, and estuarine salinity gradient (Crain et al., 2004). Other studies showed that plant composition markedly shifts along topographical gradients from low marshes to uplands (James & Zedler, 2000; Traut, 2005). Although the mechanisms of plant distribution within salt marshes has been examined often, it remains unclear whether the paradigm holds true for plant distribution along such complete landscape-scale topographic gradients from mudflats to uplands (see Fig. 1A).

Along the topographic gradients in the Yellow River Delta on the Pacific coast of northern China, shoreline habitats exhibit steep, but differential salinity and flooding patterns (see *Results*). Flooding frequency decreases as the elevation increases while soil salinity reaches a peak near the high marsh zone. *Suaeda salsa* (hereafter *Suaeda*), the only marsh dominant vascular plant in most marshes in the Yellow River Delta, occupies two separate zones along the topographic gradients from mudflats to uplands. *Suaeda* dominates both low marshes and terrestrial borders of the high marshes (*sensu* Bertness, 1991b, hereafter terrestrial borders) while the species is absent from mudflats, seaward borders of the high marshes (*sensu* Bertness, 1991b, hereafter high marshes), and uplands. High marshes are overall salt pans where only scattered *Suaeda* plants occur as well as stunted *Tamarix chinensis*, while uplands are occupied by dense patches of *Apocynum venetum*, *Imperata cylindrica*, *Cynanchum chinense*, and *Phragmites australis*. These shoreline habitats with relatively simple but distinct zonal patterns (see Fig. 1C) offer an ideal system to examine the roles of various biotic and abiotic factors and their relative importance in mediating species distribution.

In this article, we focus on the factors affecting *Suaeda* distribution along a topographic gradient from mudflats to uplands in the Yellow River Delta. We hypothesize that: (1) within the salt marshes, the absence of *Suaeda* from high marshes is determined by salinity, (2) at the mudflat–marsh interface, the absence of *Suaeda* from mudflats is determined by both flooding and salinity, and (3) at the marsh–upland interface, the absence of *Suaeda* from uplands is determined by competition (shown in Fig. 1C). We document *Suaeda* distribution and abiotic conditions along the topographic gradient, and experimentally examine these hypotheses. Subsequently, we discuss whether the plant zonation paradigm based on studies within salt marshes can be applied to landscape-scale topographic gradients on shorelines and whether the relative importance of different factors involved in marsh plant organization varies at different elevations within a site and between sites.

Materials and methods

Site description

Field work was conducted at the Yiqian'er Salt Marsh (38°05′ N, 118°42′ E; Fig. 2) located in the core area of the Yellow River Delta National Nature Reserve on the Pacific coast of northern China. The salt marshes are 1–5 km in width, and rise about 0.5–2 m across that distance, extending from the coast to an inland boundary of shrub uplands. The marshes have remained free of intensive anthropogenic impacts, since the reserve was established in 1990; before 1990, fishing had been free in these marshes and some of the uplands had been reclaimed.

The climate is warm-temperate with distinct seasons. An annual mean air temperature is 12.1°C. An annual mean rainfall and evaporation are 551.6 and 1 962 mm, respectively (He et al., 2008). Tidal fluctuation is irregularly semidiurnal, with the range of two successive tides being unequal (Huang & Fan, 2004). Tidewater erosion has created many tidal creeks in the salt marshes (Huang & Fan, 2004). Although the salt marshes have become increasingly eroded, the intensity of this erosion is declining toward a balance of accretion and erosion (Sun et al., 2006).

The flora of the Yiqian'er Salt Marsh is very simple. Large-area mudflats are generally bare without vegetation cover. Low marshes are mainly dominated by thin dwarfish *Suaeda* plants. High marshes around the mean high water level are salt pans with only scattered *Suaeda* plants and stunted *Tamarix chinensis*, a shrubby recretohalophyte. Terrestrial borders are dominated by *Suaeda* plants again, which grow vigorously and form dense canopies there. *Tamarix chinensis* is less suppressed in terrestrial borders. Other species with a relatively broad salt tolerance, such as *Suaeda glauca*, *Scorzonera mongolica*, *Limonium sinense*, and *Phragmites australis* can also be found at low densities along with *Suaeda* in terrestrial borders. Uplands are occupied by dense patches of *Apocynum venetum*, *Imperata cylindrica*, *Cynanchum chinense*, and *Phragmites australis*. *Tamarix chinensis* also thrives in uplands.

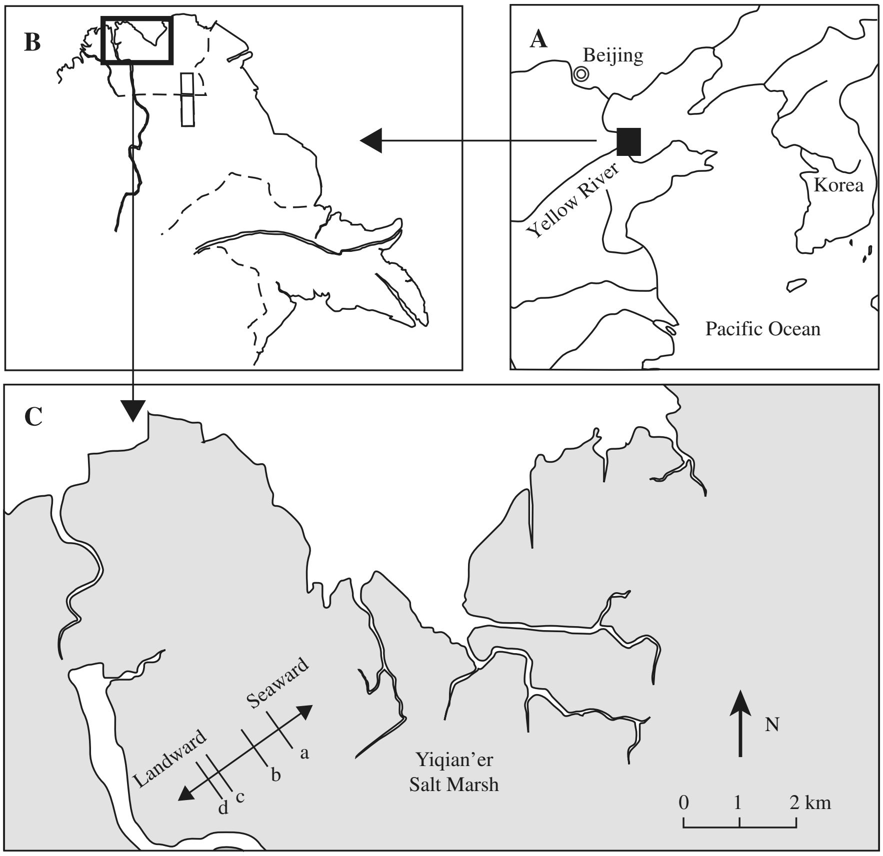

Fig. 2 Map of the study site and field sampling locations. **A** Location of the Yellow River Delta National Nature Reserve on the Pacific coast of northern China. **B** Location of the Yiqian'er Salt Marsh in the Yellow River Delta National Nature Reserve (*dashed lines* show the landward boundaries of the reserve). **C** The Yiqian'er Salt Marsh and field sampling. Sampling transects are perpendicular to the *arrow-headed line* showing seaward and landward. Line a, b, c, and d indicate the divisions between mudflat and low marsh, between low marsh and high marsh, between high marsh and terrestrial border, and between terrestrial border and upland, respectively

Quantification of *Suaeda* distribution

In order to document a typical zonal distribution pattern of *Suaeda* along topographical gradients in the Yiqian'er Salt Marsh, in August 2008, we surveyed 20 m transects parallel to the zonal boundaries of *Suaeda* at 25 m intervals, from mudflats (about 375 m seaward from the lower limits of *Suaeda*) to uplands (Fig. 2C). Every 5 m along each transect, we determined the percentage covers of *Suaeda* by subdividing 1 × 1 m quadrats into 100 (10 × 10 cm) sampling units, recording the total number of *Suaeda* presence in all the sampling units. We sampled in total 450 quadrats along 90 transects.

Quantification of abiotic factors

In order to document salinity patterns along the topographical gradient from mudflats to uplands, a soil core of topsoil (5.05 cm in diameter × 5 cm in depth) was collected in each quadrat as described above in August 2008. In order to quantify seasonal variations in salinity in different zones, 15 soil cores were collected in each zone monthly from May through August 2008. It was infeasible to collect soil pore water due to soil hardness and low water content, especially at higher elevations. Thus, we followed the method suggested by Pennings et al. (2003, 2005) to determine soil salinity. Soil cores were weighed, then oven-dried at 60°C for 48 h and reweighed to determine water content. Dried soil was mixed with a known volume of deionized water (5:1 aqueous suspension, 1 min vibration). The salinity of the supernatant was measured using an electronic meter (HI98188, HANNA, Canada) after 24 h, and the original soil pore water salinity was calculated based on the initial water content of the core.

Flooding was observed for the quadrats at the midpoint of each transect (as described in *Quantification of* Suaeda *distribution*) daily from 1 June through 15 August 2008. Flooding frequency of each of these quadrats was then determined by dividing the total number of the days it had been flooded by 76. Relative elevation of each of these quadrats above the midpoint of the last transects seaward was measured at its center with laser controlled survey equipment.

Field manipulative experiments

Flooding, salinity, and the absence of Suaeda from mudflats

In order to examine the roles of flooding and salinity in determining the absence of *Suaeda* from mudflats, we transplanted *Suaeda* into the mudflat in a full factorial experiment that manipulated flooding and salinity. In early May 2007, we transplanted soil blocks (12 cm in diameter × 5 cm in depth) containing more than 30 *Suaeda* seedlings into 16 cm diameter PVC pipe sections (gaps were infilled with surrounding soils). All seedlings were then thinned with forceps to 30 seedlings of a similar size (2–3 cm in height). In order to manipulate flooding, plants were either elevated 10 cm above ambient (flooding frequency was reduced by around 30%, and the surface of these treatments were generally equivalent in elevation to nearby *Suaeda*-vegetated marshes) or not elevated. For the elevated treatment, the pipe sections were 15 cm long, and were pressed 5 cm into the soil; for the non-elevated treatment, plants were planted in a 5 cm long section of pipe that was fully pressed into the soil surface (similar to Webb et al., 1995; Pennings et al., 2005). In order to manipulate salinity, plants were either unmanipulated (salt treatments) or were watered with freshwater (fresh treatments) without significantly affecting soil water content (similar to Pennings et al., 2005). Watering treatments were repeated 2–6 times a week in accordance to the flooding regime to effectively reduce salinity by 10–20 PSU till late June when all *Suaeda* seedlings were found to have been eliminated in the non-elevated treatments (see *Results*). Then watering treatments were repeated 2–3 times a week only for the elevated treatments from early July through the end of the experiment. Each treatment combination was replicated 12 times. In August 2007, all *Suaeda* plants within each PVC pipe were counted for survival; above-ground biomass was harvested, oven-dried for 48 h at 70°C and weighed to the nearest 0.01 g. The same experiment (8 replicates for each treatment combination) was conducted from May through August 2008. Watering treatments in 2008 slightly differed from those in 2007 due to differences in flooding regimes and survivorship of the transplanted *Suaeda* seedlings, despite that they were generally identical.

Salinity and the absence of Suaeda from high marshes

In order to examine the roles of salinity in determining the absence of *Suaeda* from high marshes, in early May 2007, we transplanted soil blocks (12 cm in diameter × 5 cm in depth) containing more than 30 *Suaeda* seedlings into the high marsh. In order to manipulate salinity, plants remained either without additional treatment (salt treatments) or were watered with freshwater twice a week throughout the entire duration of the experiment (fresh treatments). All seedlings were thinned with forceps to 30 seedlings of a similar size (2–3 cm in height). Each treatment was replicated 12 times. In August 2007, all *Suaeda* plants in each transplant were counted for survival; above-ground biomass was harvested, oven-dried for 48 h at 70°C, and weighed to the nearest 0.01 g. The same experiment (8 replicates for each treatment) was conducted from May through August 2008.

As the absence of *Suaeda* from high marshes (salt pans) may be due to salinity-driven inhibition of seedling emergence rather than subsequent development, in early March 2008, we randomly established 20 (1 × 1 m) bare patches (>10 m between patches) in the high marsh, and half of the patches were flushed with freshwater twice a week (fresh treatments, similar to Bertness et al., 1992 and Shumway & Bertness, 1992). We left other patches unmanipulated as control (salt treatments). The central 50 × 50 cm area in each patch was censused for *Suaeda* seedling emergence in early May 2008.

Competition and the absence of Suaeda from uplands

In order to examine the roles of competition in determining the absence of *Suaeda* from uplands, in May 2008, we transplanted soil blocks (12 cm in diameter × 5 cm in depth) containing more than 30 *Suaeda* seedlings into patches of the 4 most common plant species (i.e. *Apocynum venetum*, *Imperata cylindrica*, *Cynanchum chinense*, and *Phragmites* *australis*) in uplands. For each of these 4 species, we selected 4 patches and transplanted 6 soil blocks (3 were assigned to neighbors-present treatments and 3 to neighbors-removal treatments) containing *Suaeda* seedlings into each patch (>2 m between soil blocks; 24 soil blocks in total for each of the 4 species in uplands). In order to manipulate competition, we removed the surrounding vegetation in half of the blocks by clipping a 0.25 m radius border around the soil blocks at the soil surface. Clipping treatments were repeated biweekly as needed. We left the 12 control blocks unmanipulated. All seedlings were thinned with forceps to 30 seedlings of a similar size (2–3 cm in height). In August 2008, all *Suaeda* plants in each transplant were counted for survival; aboveground biomass was harvested, oven-dried for 48 h at 70°C, and weighed to the nearest 0.01 g.

Statistical analyzes

Salinity data even after usual transformations did not meet the assumptions of ANOVA, and thus non-parametric multiple comparisons (Steel test) were used to compare salinity between different zones. Non-parametric k related samples Friedman's tests were used to compare salinity in each zone between months. Flooding frequency data did not meet the assumptions of non-parametric multiple comparisons (Steel test) and ANOVA, and thus, were analyzed by non-parametric Kruskall–Wallis tests.

One-way ANOVAs were used to compare performances of *Suaeda* between treatments. High mortality of the *Suaeda* seedlings transplanted into the mudflat in non-elevated treatments resulted in heteroscedasticity and non-normality of the data, precluding the complete two-way ANOVA. Thus, one-way ANOVAs were conducted instead. Prior to all ANOVAs, survivorship data were arcsin (x) transformed and biomass data were $\log_{10}(x + 1)$ transformed; data that did not meet the assumptions of ANOVA even after usual transformations were analyzed by non-parametric Kruskall–Wallis tests. One-way ANOVAs followed by pos hoc multiple comparisons (Tukey test) were used to compare performances of *Suaeda* between different neighboring plant species in the upland.

All statistical analyzes were performed using SAS Version 9.1 (SAS Institute, Cary, North Carolina, USA), except that non-parametric multiple comparisons were performed using npmc package in R Version 2.7 (R Development Core Team, 2008).

Results

Zonal distribution of *Suaeda*

Suaeda plants were widely distributed in the Yiqian'er Salt Marsh. Results from the transect survey (Fig. 3a) showed that *Suaeda* occurred primarily in two zones: the low marsh and the terrestrial border. While in the low marsh its coverage was relatively low, *Suaeda* formed dense canopies in the terrestrial border. Except for near creeks, *Suaeda* plants were rare in the high marsh. *Suaeda* plants were nearly completely absent from the upland and the mudflat (Fig. 3a).

Abiotic factors

Results from the transect survey showed that except for near creeks, flooding frequency steeply decreased as the elevation increased from the mudflat to the upland, while soil salinity conspicuously reached a peak in the high marsh (Fig. 3b).

Soil salinity significantly differed among different zones (Table 1). Soil salinity was lowest in the upland and highest in the high marsh. The two *Suaeda*-dominated zones, the terrestrial border, and the low marsh, generally had similar levels of soil salinity. Soil salinity was lower in the mudflat than in the low marsh. Besides, soil salinity showed significantly seasonal variations in each of the zones (Table 1). Except in the high marsh, soil salinity generally decreased over the growing season. Soil salinity in the high marsh slightly increased over the growing season.

Flooding frequency also significantly differed among different zones (Table 1). Flooding was most frequent in the mudflat. The high marsh was flooded with a low frequency. The upland and the terrestrial border were not flooded throughout the duration of the field observation.

Flooding, salinity, and the absence of *Suaeda* from mudflats

Survivorship of *Suaeda* that had been transplanted into the mudflat in both 2007 and 2008 was

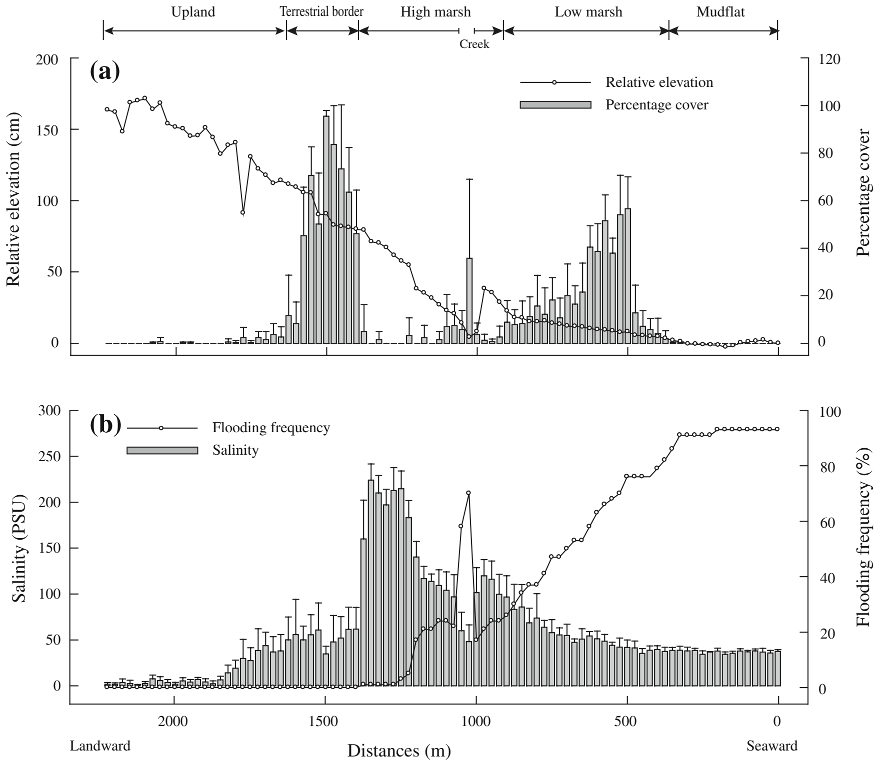

Fig. 3 Zonal distribution of *Suaeda* and abiotic factors along a topographic gradient in the Yiqian'er Salt Marsh in August 2008. Distances are relative to the midpoint of the last transect seaward. Relative elevation is given in cm above the midpoint of the last transect seaward. Percentage cover and salinity data are means of five samples ± SE

Table 1 Patterns of soil salinity in different zones and months, and flooding frequency in different zones

	Upland	Terrestrial border	High marsh	Low marsh	Mudflat
Soil salinity (*PSU*)					
May	11.73 ± 8.86a	85.52 ± 39.23bc	142.98 ± 41.06d	89.32 ± 13.61c	66.02 ± 6.45be
June	8.67 ± 7.12a	60.44 ± 27.88b	175.57 ± 37.76c	91.96 ± 18.74d	65.56 ± 6.91b
July	9.72 ± 9.36a	70.02 ± 40.89bc	155.24 ± 49.65d	65.27 ± 23.37b	49.17 ± 5.42c
August	4.29 ± 3.80a	61.59 ± 29.41bc	157.31 ± 50.92d	53.60 ± 11.65b	38.91 ± 2.13c
On average	8.60 ± 6.69a	69.39 ± 32.23bc	157.77 ± 40.17d	75.04 ± 11.65b	54.91 ± 3.39c
Friedman's test	21.69 (**<0.0001**)	18.36 (**0.0004**)	13.88 (**0.0031**)	33.96 (**<0.0001**)	38.84 (**<0.0001**)
Flooding frequency (%)	0a	0a	12 ± 10b	61 ± 12c	92 ± 2d

Data are mean ± SE. The sample sizes are 15, except flooding frequency in the terrestrial border zone whose sample size is 10. Flooding frequency data in different zones are based on the data from the transect survey excluding the two samples around the creek. For salinity data, within each row, cells sharing a letter are not significantly different from one another (non-parametric multiple comparisons, Steel test, $P < 0.05$)

Cells within the Friedman's test row give results (test statistics and *P*-values in *brackets*, d.f. = 3) from tests for differences among months (non-parametric *k* related samples Friedman's tests); significant *P*-values are given in bold

significantly higher in the elevated treatments than that in the non-elevated treatments (Fig. 4a, Table 2). *Suaeda* plants were nearly completely eliminated in the non-elevated treatments, regardless of the salinity treatments (Fig. 4a). Biomass of *Suaeda* plants was also significantly higher in the elevated treatments than that in the non-elevated treatments (Fig. 4b, Table 2). These data indicated that flooding played an important role in mediating the absence of *Suaeda* from mudflats.

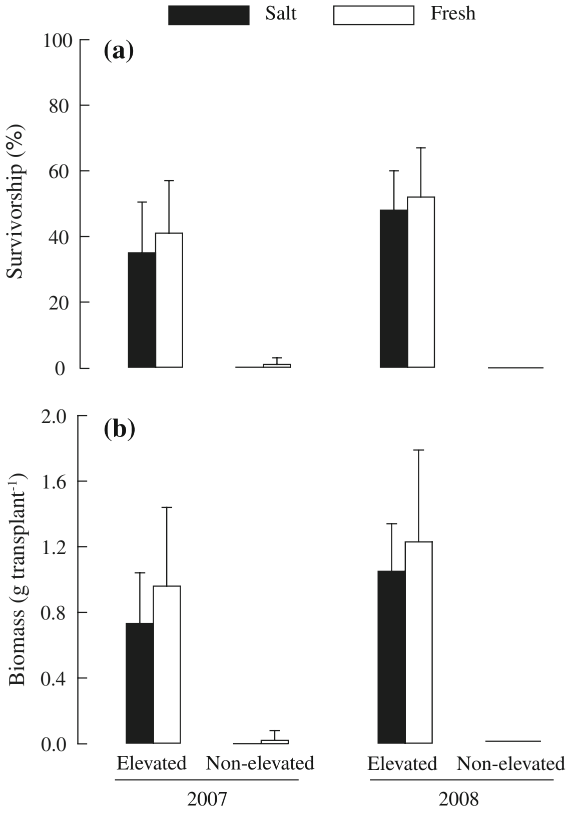

Fig. 4 Survivorship (**a**) and biomass (**b**) of *Suaeda* transplanted into the mudflat in different flooding and salinity treatment combinations. Data are shown as mean ± SE. Sample sizes in 2007 and 2008 are 12 and 8, respectively

Measured by both survivorship and biomass, *Suaeda* plants showed no significant differences between the fresh and the salt treatments, although in the elevated treatment survivorship and biomass were slightly higher if watered than those if not in both 2007 and 2008 (Fig. 4, Table 2). These data indicated that salinity did not control the absence of *Suaeda* from mudflats.

Salinity and the absence of *Suaeda* from high marshes

Survivorship of the *Suaeda* seedlings that had been transplanted into the high marsh was significantly higher in the fresh treatments than that in the salt treatments in 2007, but they did not differ significantly in 2008 (Fig. 5a). There was no difference in biomass between the salt and the fresh treatments in both 2007 and 2008 (Fig. 5b). These data indicated that salinity appeared to have no significant effects on the performance of *Suaeda* in the high marsh.

However, salinity in the high marsh strikingly suppressed *Suaeda* seedling emergence. *Suaeda* emergence in the high marsh was significantly higher if watered than that if not (Fig. 5c). *Suaeda* emergence in the high marsh was nearly completely inhibited in the salt treatments (i.e., control); in contrast, a large number of *Suaeda* seedlings did emerge in the fresh treatments (Fig. 5c).

Competition and the absence of *Suaeda* from uplands

About 60–70% of the *Suaeda* seedlings that had been transplanted into the upland in the neighbors-removal treatments survived at the end of the growing season (Fig. 6a). For all neighboring species, *Suaeda* survivorship in the upland showed a significant decline when neighbors were present (Fig. 6a). However, the effect of competition on *Suaeda* from different neighboring species differed significantly. *Suaeda* survivorship was lowest when the neighboring species was *Apocynum venetum* and highest when the neighboring species was *Phragmites australis* (Fig. 6a).

For all neighboring species, biomass of *Suaeda* plants was significantly higher when neighbors were removed than that when neighbors were present (Fig. 6b). All *Suaeda* plants with neighbors present in the upland only grew to an extremely small size. When neighbors were removed, *Suaeda* plants grew better in patches of *Apocynum venetum* and *Cynanchum chinense* than in patches of *Imperata cylindrica* and *Phragmites australis*. When neighbors were present, *Suaeda* plants grew better in patches of *Imperata cylindrical* and *Phragmites australis* than in patches of *Apocynum venetum* and *Cynanchum chinense* (Fig. 6b).

Discussion

Our study suggests that the absence of *Suaeda* from mudflats was caused by flooding, the absence of *Suaeda* from high marshes by salinity, and the absence of *Suaeda* from uplands by competition. These abiotic and biotic factors acting together confined *Suaeda* to two separate zones along coastal topographic gradients in the Yiqian'er Salt Marsh.

Table 2 Summary of analyzes of variances for experiments examining the roles of flooding and salinity in mediating the absence of *Suaeda* from mudflats

	d.f.	The effects of flooding				The effects of salinity			
		Salt		Fresh		Elevated		Non-elevated	
		F (H_1)	P	F (H_1)	P	F (H_1)	P	F (H_1)	P
2007									
Survival	1, 22	(19.78)	**<0.0001**	(18.65)	**<0.0001**	0.80	0.38	(2.09)	0.15
Biomass	1, 22	(19.73)	**<0.0001**	(18.10)	**<0.0001**	1.61	0.22	(2.09)	0.15
2008									
Survival	1, 14	(12.80)	**0.0003**	(12.91)	**0.0003**	0.52	0.48	(1.00)	0.32
Biomass	1, 14	(12.91)	**0.0003**	(12.89)	**0.0003**	0.40	0.54	(1.00)	0.32

Results from ANOVAs are reported by F, d.f., and P while results from Kruskal–Wallis tests are reported by H_1 (*in brackets*) and P. For “the effects of flooding”, we compare performances of *Suaeda* between elevated and non-elevated treatments in the “salt” or the “fresh” treatments; for “the effects of salinity”, we compare performances of *Suaeda* between fresh and salt treatments in the “elevated” or the “non-elevated” treatments. Significant P-values are given in bold

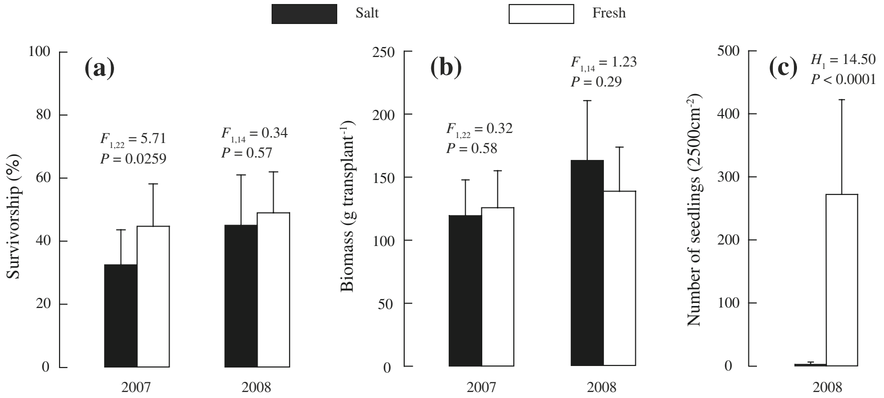

Fig. 5 Survivorship (**a**) and biomass (**b**) of *Suaeda* transplanted into the high marsh, and *Suaeda* emergence (**c**) in the high marsh in the salt and the fresh treatments. Data are shown as mean ± SE. Sample sizes in 2007 and 2008 are 12 and 8, respectively, except that the sample size of seedling emergence in 2008 is 10. Results from ANOVAs for differences between the fresh and the salt treatments are indicated above the groups of bars. Seedling emergence data did not meet the assumptions of an ANOVA, and hence a non-parametric Kruskall–Wallis test was used to test the effects of salinity on seedling emergence

Determinants of *Suaeda* distribution along coastal topographic gradients

Previous studies within salt marshes (Snow & Vince, 1984; Bertness, 1991b; Pennings & Moore, 2001; Caçador et al., 2007) have confirmed that the stressful boundaries of different marsh plants across stress gradients are determined by their varied tolerances to physical stresses, of which salinity and flooding are the most pronounced (Fig. 1B). Generally, our results are consistent with these studies since they indicated that the absence of *Suaeda* plants from mudflats at the mudflat–marsh interface was determined by physical stress. Webb et al. (1995) and Barry et al. (2004) also found similar results at the mudflat-marsh interface. Our study further determined that flooding rather than salinity was the primary physical stress. Although we did not directly examine all factors related specifically to flooding (e.g., depth, frequency, and duration) or associated details (e.g., soil anoxia, sediment

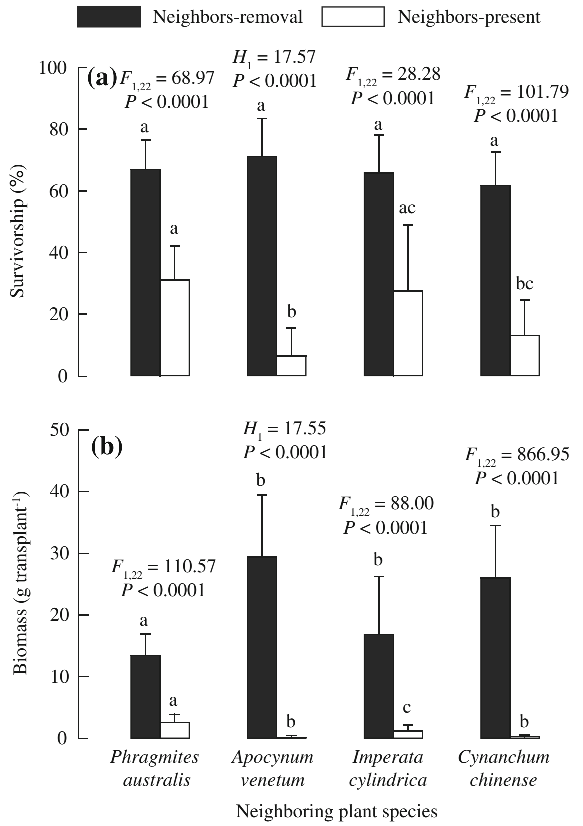

Fig. 6 Survivorship (**a**) and biomass (**b**) of *Suaeda* transplanted into the upland in different competition and neighboring species treatments in 2008. Data are shown as mean ± SE ($n = 12$). Results from ANOVAs are reported by $F_{1,\ 22}$ and P while results from Kruskall–Wallis tests are reported by H_1 and P. Within each competition treatment (neighbors-present or neighbors-removal), bars sharing a letter above them are not significantly different from one another (pos hoc multiple comparisons, Tukey test, $P < 0.05$)

disturbance, and sulfide concentration), flooding frequency is generally believed to be one of the major components showing correlation with other components (Vince & Snow, 1984; Bertness, 1991b; Casanova & Brock, 2000; Silvestri et al., 2005). In the low marsh, where flooding frequency was about 40–80%, *Suaeda* performed well (Fig. 3). Individual biomass, leaf area, plant height, and stem basal area of *Suaeda* plants were significantly higher in the low marsh than in the non-elevated treatments in the mudflat in 2008 (*Suaeda* plants measured in the low marsh were natural rather than transplanted, thus they are not a direct control and comparisons should be interpreted with caution; Cai & He, unpublished data). *Suaeda* in the intertidal zones is usually submerged completely in seawater (Song et al., 2008). However, more frequent flooding in the mudflat completely eliminated *Suaeda* plants. It should be mentioned that although we did not examine whether infauna played a destructive role in *Suaeda* establishment in mudflats as suggested by Hughes and colleagues (Hughes & Paramor, 2004; Paramor & Hughes, 2004, 2005; see Wolters et al., 2005 for a review), inhibition of *Suaeda* survival to the utmost extent indicated the major role of flooding.

Although flooding, rather than salinity, appears to be the major physical stress mediating the absence of *Suaeda* from mudflats, salinity does play an important role in precluding *Suaeda* plants from high marshes. Despite that *Suaeda*'s tolerance of high levels of soil salinity (Zhao et al., 2003; Song et al., 2008), extremely high levels of salinity in the high marsh completely inhibited *Suaeda* emergence, and thus subsequent development was prevented, resulting in salt pans with little vegetation cover in the high marsh. The hypersaline conditions in the high marsh were likely determined by infrequent tidal flooding and high intensity of evaporation in the Yiqian'er Salt Marsh (He et al., 2008). Wang et al. (2007) also suggested that evapotranspiration, temperature, hydraulic conductivity, and incoming tidal salinity significantly affect the salinity maximum in the high marsh, which may leads to the formation of salt pans when reaching a threshold level. This finding supports the hypothesis that salt pans in the high marsh zones, which are one of the most characteristic features of low-latitude southern US marshes, are determined by climate-driven elevated salinities (Bertness & Pennings, 2000).

Although physical stresses determine the absence of *Suaeda* from mudflats and high marshes, plant competition mediates the absence of *Suaeda* from uplands. While *Suaeda* performed well in the upland when neighbors were removed, it was significantly suppressed when neighbors were present. Individual biomass, leaf area, plant height, and stem basal area of *Suaeda* plants were similar or only slightly less in the neighbors-removal treatments in uplands than in the terrestrial border (native zone); in contrast, individual biomass, leaf area, plant height, and stem basal area of *Suaeda* plants were significantly less in the neighbors-present treatments in uplands than in the terrestrial border in 2008 (Again, *Suaeda* plants measured in the terrestrial border were natural rather than transplanted, thus they are not a direct control and comparisons should be interpreted with caution; Cai & He, unpublished data). This indicates a trade-off in *Suaeda* plants between stress tolerance and competitive ability. Inherent trade-offs in plants between stress tolerance and competitive ability (Grime, 1977) have generally been believed to be a key factor in generating vegetation patterns in both salt marshes (Snow & Vince, 1984; Bertness & Ellison, 1987; Bertness, 1991a, b; Bertness et al., 1992; Pennings & Callaway, 1992; Castillo et al., 2008) and freshwater habitats (Grace & Wetzel, 1981; Wilson & Keddy, 1986). Our study suggests that this trade-off in *Suaeda* plants mediates the absence of *Suaeda* from the upland. Cui & He (unpublished data) also found that such trade-offs played an important role in determining the conspicuous zonation of *Suaeda* dominating high marshes and *Phragmites australis* dominating uplands in another site in the Yellow River Delta. Besides, James & Zedler (2000) also suggested that *Iycium californicum* dominating the transition between salt marshes and uplands was restricted from uplands by competition with species at higher elevations. However, sufficient data are not yet available to determine whether our findings are generally applicable. The physical environment in uplands may also be limiting the growth of marsh plants due to low moisture levels (Traut, 2005).

Taken together, the zonal distribution pattern of *Suaeda* in the Yiqian'er Salt Marsh appears to be the product of mediation of both physical and biotic factors. Our findings along a topographic gradient from mudflats to uplands are in broad agreement with those within salt marshes (Snow & Vince, 1984; Bertness & Ellison, 1987; Bertness 1991a, b; Bertness et al., 1992), suggesting that the plant zonation paradigm based on studies within salt marshes may hold true for plant distribution along topographic gradients from mudflats to uplands. Nevertheless, we acknowledge that further studies should be conducted at a wide range of sites to test the generality of our findings.

Relative importance of various factors

Our study further emphasizes the relative importance of salinity and flooding in determining the absence of *Suaeda* from mudflats. Flooding, rather than salinity, determined the lower limits of *Suaeda*. This finding is consistent with studies conducted by Bertness (1991b) and Bertness et al. (1992). However, Snow & Vince (1984) suggested that salinity determined the lower limits of plant distribution in an Alaskan salt marsh, and Pennings et al. (2005) found that both flooding and salinity were important in determining the lower limits of *Juncus roemerianus* in salt marshes around Sapelo Island. Thus, the relative importance of different physical factors involved in marsh plant organization is likely to vary between different sites. In addition, the relative importance of physical stress and competition may also vary between sites (Costa et al., 2003; Pennings et al., 2005). Even within a marsh ecosystem, the relative importance of flooding, salinity, and competition has been found to vary at different elevations (Pennings & Callaway, 1992). Although we did not conduct a full factorial experiment to investigate the relative importance of flooding, salinity, and competition, our study demonstrated that different factors were controlling different distribution boundaries of *Suaeda* in the Yiqian'er Salt Marsh, indicating variations in the relative importance of these factors at different elevations.

Variations in the relative importance of factors involved in marsh plant organization can at least be attributed to differential physical environments between sites. In order to investigate how variations in the physical environment affect marsh plant organization, recent studies have taken advantage of latitudinal variations in climate (Pennings & Moore, 2001; Bertness & Ewanchuk, 2002; Pennings et al., 2003; Ewanchuk & Bertness, 2004; Pennings et al., 2005), which may determine the importance of soil salinity in influencing the distribution and abundance of plants across marsh habitats (Bertness & Pennings, 2000). Salinity generally reaches a peak near the high marsh in warmer lower-latitude salt marshes where evaporation and temperatures are higher, in contrast to cooler higher-latitude salt marshes in the USA (Bertness & Pennings, 2000; Wang et al., 2007). Our study shows that salinity also reaches a marked peak in the high marsh of the Yiqian'er Salt Marsh on the Pacific coast of northern China. These differences in salinity patterns between sites indicate that addressing variations in the physical environment in different sites are crucial to our understanding of the relative importance of different factors in mediating marsh plant organization.

Taken together, the relative importance of different factors involved in the marsh plant organization may vary at different elevations within a site (Pennings & Callaway, 1992) and between geographic sites (Costa et al., 2003; Pennings et al., 2005) due to variations in the physical environment. Our work contributes to this growing body of knowledge.

Salt tolerance of *Suaeda* and life-stage dependence

In order to understand the zonation patterns of *Suaeda*, it is also necessary to understand the salt tolerance of this species. *Suaeda* occurred primarily at the two zones of the low marsh and the terrestrial border, where soil salinity remained fairly high throughout the growing season (Table 1). Although *Suaeda* seedling emergence was strongly inhibited, once established, *Suaeda* could thrive in the high marsh, where soil salinity was extremely high. Previous studies have confirmed that the obligate halophyte *Suaeda* has a high salt tolerance (Zhao et al., 2003; Song et al., 2008). In contrast to other salt marsh plant species, which are generally thought to grow better in benign habitats than in saline habitats (Hellings & Gallagher, 1992; Houle et al., 2001; Crain et al., 2004), *Suaeda* thrives best in habitats with low levels of salinity (Zhao et al., 2003; Song et al., 2008). The reason for the high salt tolerance of *Suaeda* may be due to its ability to absorb substantial amounts of Na and Cl from the soil and compartmentalize them in vacuoles in order to lower the plant water potential, and hence *Suaeda* can absorb water from the soil (Zhao et al., 2003). Song et al. (2008) indicated that an increased production of brown seeds (one type of *Suaeda* seeds) whose embryos were better developed may be an adaptive feature of the species to salt stress in intertidal zones, for brown seeds were more salt resistant.

In addition, we perceived that salt tolerance of *Suaeda* differed between seeds and seedlings. Using the ability to germinate as an estimate of salt tolerance (*sensu* Ungar, 1996), *Suaeda* seedlings appeared to be more salt-tolerant than seeds. This finding is consistent with previous studies (Ungar, 1996; Houle et al., 2001). The seedlings transplanted into the high marsh performed well in both 2007 and 2008, regardless of salinity treatments, while seedling emergence was nearly completely inhibited in the control treatments (Fig. 5). Thus, the salinity-driven inhibition of seedling emergence, rather than subsequent development, appears to be primarily responsible for the absence of *Suaeda* plants from high marshes.

In conclusion, our study demonstrates that the bimodal zonation of *Suaeda* along coastal topographic gradients from mudflats to uplands in the Yiqian'er Salt Marsh is mediated by both physical stresses and plant competition, and that the controlling factors differ at different elevations. The plant zonation paradigm based on studies within salt marshes may hold true in general for plant distribution along coastal topographic gradients from mudflats to uplands on shorelines, however, the relative importance of different abiotic and biotic factors may vary at different elevations within a site and between sites.

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