COMMUNITY ECOLOGY - ORIGINAL PAPER

Determinants of annual–perennial plant zonation across a salt–fresh marsh interface: a multistage assessment

Baoshan Cui · Qiang He · Kejiang Zhang · Xin Chen

Abstract Vegetation zonation patterns in coastal marshes are hypothesized to be the result of both physical stress and competitive interactions. How these patterns may be driven by these factors at different life history stages remains poorly understood. We investigated the relative importance of species tolerance (response to physical stress) and competitive ability in determining the distributions of two dominant marsh species across a salt–fresh marsh interface in the Yellow River Estuary, China. There is a steep gradient in salinity across this interface and *Suaeda salsa*, an annual, dominates the saline side of the interface, while *Phragmites australis*, a perennial species, dominates the freshwater side. Using a series of field transplants, we examined the roles of physical stress and competition in mediating this zonation at different life history stages. *Suaeda salsa* performed well in its home zone, but seedling emergence, seedling survival, adult survival and adult growth were significantly suppressed by competition in the freshwater *P. australis* zone. Emergence, survival and growth of *P. australis* were inhibited in the saline *S. salsa* zone, regardless of neighbor treatments, but it performed well in its home zone. The magnitude of the competitive effect on the performance of *S. salsa* differed among the life history stages. Competition from *P. australis* had a much stronger effect on *S. salsa* seedling emergence and adult growth than on seedling survival and adult survival. Our results reveal that both physical stress and competition contributed to the observed zonation patterns in this marsh system. However, for *S. salsa*, the effect of competition varied with life-history stage. Insight into these ecological processes is critical to understanding how the zonation pattern in the marsh system is formed and maintained.

Keywords Competition · Life history stage · Plant zonation · Salinity · Salt marsh

Communicated by John Silander.

B. Cui (✉) · Q. He
State Key Laboratory of Water Environmental Simulation, School of Environment, Beijing Normal University, Beijing 100875, China
e-mail: cuibs@bnu.edu.cn

K. Zhang
The Centre of Environmental Engineering Research and Education (CEERE), University of Calgary, Alberta T2N 1N4, Canada

X. Chen
Department of Biology and Environmental Science, Concordia University College of Alberta, Edmonton, AB T5B 4E4, Canada

Introduction

Coastal marshes characterized by distinct vegetation zones across steep environmental gradients have been widely used as a model system to elucidate mechanisms of species distribution patterns in natural communities (Pennings and Bertness 2001; Crain et al. 2004). Although early studies (see Pennings and Bertness 2001 for a review) appear to draw a general paradigm that marsh plant zonation is the product of competitively superior plants dominating physically benign habitats and displacing competitively subordinate plants to physically more severe habitats, the spatial and temporal generality of this paradigm needs to be examined more fully. Several recent studies testing the

spatial generality of this paradigm have prompted a debate over whether the roles of physical stress and plant competition vary geographically (e.g., Costa et al. 2003; Pennings et al. 2005; Fariña et al. 2009; He et al. 2009a). However, whether and how these factors may vary temporally and spatially, and among different plant life-history stages for example, need to be investigated further.

Salt marsh ecologists often use the final yield of transplanted species to assess the roles of physical stress and plant competition in mediating plant zonation. However, final yield is only one of the many components of fitness across multiple life history stages, and it represents only the cumulative effect over the growing season. Besides final yield, other components of fitness, such as seedling emergence and survival, may also significantly influence the abundances and distributions of many plant species in tidal marshes (Ungar 1987; Bertness et al. 1992; Shumway and Bertness 1992; Brewer et al. 1998; Rand 2000). Simply assessing the roles of physical stress and/or biotic interactions by final yield may not reveal how these factors substantively influence the organizations of plant communities (Howard and Goldberg 2001; Giménez-Benavides et al. 2008). This is because harsh physical stress and/or biotic interactions acting at just one life history stage could control a species' presence or absence at a particular site (Giménez-Benavides et al. 2008); there may be one or more critical life-cycle transitions responsible for the observed community patterns.

Although critical life-cycle transitions mediated by various abiotic and biotic factors are well known in population biology and life history ecology (e.g., Silvertown et al. 1993; Weppler et al. 2006), they have been largely overlooked in community ecology. A few recent studies (e.g., Howard and Goldberg 2001; Gulias et al. 2004; Giménez-Benavides et al. 2008) point to the need to assess multiple, sequential life history stages, as these are affected by abiotic and/or biotic factors. The distribution of a plant species in Mediterranean high mountains (Giménez-Benavides et al. 2008), for example, has been found to be determined by the processes controlling seedling emergence and survival. In marine-influenced systems, however, multistage studies of the roles of physical stress and biotic interactions in mediating organizations of plant communities remain few (but see the cobble beach study in Bruno 2000 and the discussion in Goldenheim et al. 2008), despite a large number of marsh plant zonation studies (e.g., Bertness 1991; Pennings et al. 2005; Fariña et al. 2009).

It is possible that the roles of physical stress and plant competition vary with life-history stage in mediating marsh zonation. For example, stress tolerance of marsh plants (Adam 1990; Houle et al. 2001), biotic interactions experienced by marsh plants (Callaway and Walker 1997; Alberti et al. 2008) and salinity and tidal regimes (the most

common physical stressors in tidal marshes; see Ungar 1987; Olff et al. 1988; Odum 1988; Adam 1990) have all been found to vary significantly with plant life history stage. Several authors have also mentioned that marsh plant zonation may be determined by different responses to physical stress and/or competition just during the seed germination or seedling development stages (Wijte and Gallagher 1996; Zedler et al. 1999; Rand 2000). However, detailed experimental studies at multiple stages are still scarce, probably because the field experiments required are so labor intensive. In the study reported here, using a series of field transplants, we tested whether and how the role of plant competition may vary with life-history stage in mediating marsh plant zonation in the estuarine marshes of the Yellow River, China.

We focused on a striking annual–perennial plant zonation pattern across the salt–fresh marsh interface of the Yellow River Estuary (see Fig. S1 of the Electronic supplementary material, ESM). Between the inland river bank and the shore edge of the estuary, the annual plant *Suaeda salsa* (*Suaeda* hereafter) dominates the hypersaline terrestrial borders of salt marshes that are seldom flooded except occasionally during storm tides, while the perennial plant *Phragmites australis* (*Phragmites* hereafter) occupies freshwater (or brackish) riparian marshes at upper elevations near the river bank (see Fig. S1c of the ESM). This salt (terrestrial border)–fresh (riparian marsh) marsh interface, with its distinct plant zonation pattern, and a steep gradient in salinity, offers an ideal system to investigate the roles of physical stress and competition in mediating plant zonation.

In this article, we first document *Suaeda* and *Phragmites* species distributions and salinity patterns across the salt–fresh marsh interface, and then investigate the roles of physical stress and competition in mediating the zonation patterns experimentally using a series of field transplants. We address the following questions: (1) what are the roles of physical stress and competition in mediating this plant zonation, and (2) does the role of competition in mediating the zonation vary among different plant life-history stages?

Materials and methods

Study area

Field work was conducted at a site (37°46′N, 119°09′E) in the Yellow River Estuary located in the core zone of the Yellow River Delta National Nature Reserve, northeastern China (Fig. S1a of the ESM). The climate of the field site is temperate monsoonal, with hot, rainy summers and cool, dry winters.

Patterns of plant zonation in the estuary are generally striking (Fig. S1c of the ESM). *Suaeda* plants spread from frequently flooded low marshes to infrequently flooded, hypersaline, high marshes, but are replaced by other plant species in brackish to fresh riparian marshes, including *Phragmites* at upper elevations and *Calamagrostis pseudophragmites* and *Typha* spp. at lower elevations. In high marshes, *Suaeda* co-dominates at some sites with the shrub *Tamarix chinensis*, and its distribution may also be interrupted by unvegetated salt pans where soil salinity is extremely high, or by small *Phragmites* patches where wrack cover reduces salt accumulation and significantly decreases soil salinity (He et al. 2009b). *Phragmites* in the upper riparian marshes is accompanied by small patches of *C. pseudophragmites*, *Triarrhena sacchariflora* and *Imperata cylindrical*. Nevertheless, the zonation of *Suaeda* and *Phragmites* we focused on in this study is one of the most common vegetation patterns across the estuarine system.

Zonation patterns

To quantify the zonation patterns of *Suaeda* and *Phragmites*, ten transects (50 m in length, >20 m between transects) were set perpendicular to the zonal border in August 2008 (Fig. S1b and c of the ESM). Quadrats (0.5 m long × 2 m wide) were placed at 2-m intervals with their long edges parallel to the zonal border. The first quadrats in the *Suaeda* zone and the *Phragmites* zone were centered at 1 m on each side of the zonal border. Percentage cover of *Suaeda* and *Phragmites* was estimated by subdividing the quadrat into 100 (10 × 10 cm) sampling units and recording the total number of shoot presences for each species in all the sampling units (Crain et al. 2004; Ewanchuk and Bertness 2004).

Salinity patterns

In each of the quadrats along four of the ten transects described above, we collected a soil core (5.05 cm diameter × 5 cm deep) in August 2008 to quantify the salinity levels from the *Suaeda* zone to the *Phragmites* zone. To document seasonal variations in salinity, we collected 20 soil cores in each zone in March, May and July 2008. Soil pore water salinity was determined based on the initial water content and the salinity of the water extract from the soil core (see details in Pennings et al. 2005; He et al. 2009a). Repeated-measures ANOVA was used to examine differences in salinity among different zones and sampling dates. Salinity data were $\log_{10}(x + 1)$ transformed to increase homogeneity of variance and normality.

Transplant experiments

General considerations

The field transplant study ran from November 2007 through August 2008 (Fig. 1). Ideally transplants should be repeated for more than one growing season, but as the overall weather condition during this period was typical of the average climate at the field site (Du 2009), we

Fig. 1 Diagrammatic representation of experimental design: **a** *Suaeda* and **b** *Phragmites* transplant treatments. Each *square* represents a treatment group of 16 soil blocks. Groups enclosed in *dashed rectangles* were treated in the same way (transplanted into its home zone or the other species' zone, with neighbors removed or unmanipulated). *NE* neighbor effect; *Transplant 1, 2 and 3* indicate the transplant experiments at different life-history stages of *Suaeda* and *Phragmites* (see details in "Materials and methods")
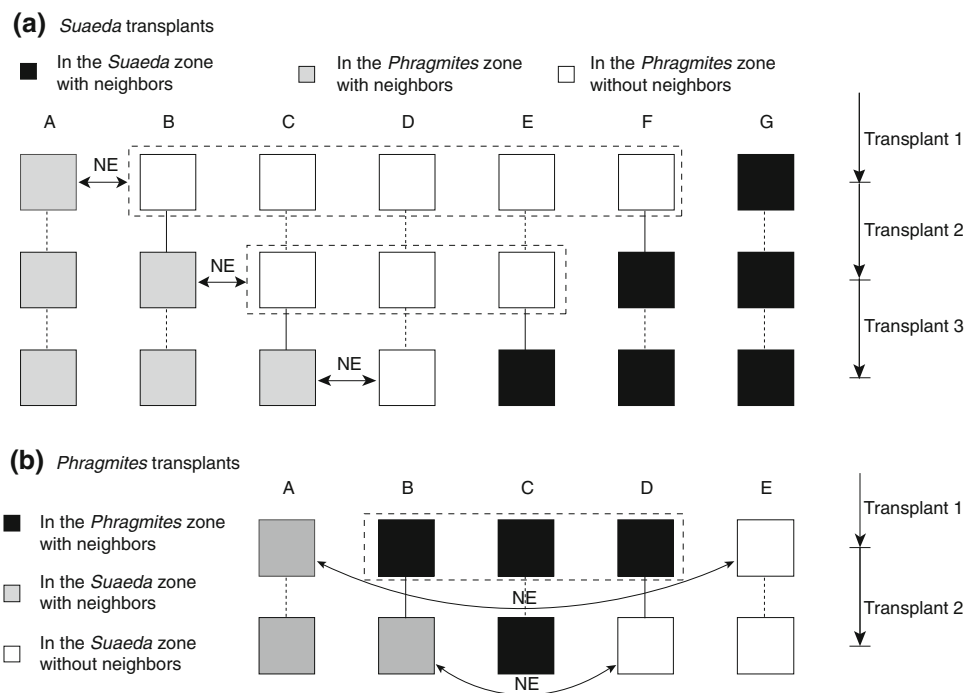
believe that it is reasonable to consider the results as representative.

We focused on several developmental stages of the life cycles for both *Suaeda* and *Phragmites*. This was done using a series of reciprocally transplanted blocks of soil containing adults or seeds of each species, and by following their performance over time. For the annual *Suaeda*, four life-history stages were examined: seedling emergence, seedling survival, adult survival, and adult growth. In the perennial *Phragmites* which mainly spreads via rhizomes, three life-history stages were examined: emergence, survival, and growth of new ramets. Sexual reproduction could also be a critical life history stage, but was not examined in this study due to logistical considerations, and *Phragmites* seedlings are rarely observed at this site (see also in "Discussion"). We did not investigate how clonal growth of non-transplanted, in situ *Phragmites* plants would respond to physical stress and competition, as previous marsh zonation studies (e.g., Pennings and Moore 2001; Pennings et al. 2005) indicated that results from transplant and non-transplant experiments would be similar. Also, the majority of previous studies (e.g., Bertness 1991; Ewanchuk and Bertness 2004; Fariña et al. 2009) have employed transplant experiments to examine the mechanisms of salt marsh plant zonation.

To minimize the potential effects of residual edaphic factors carried along with the transplanted soil, relatively small soil blocks (15 × 15 × 4 cm for seedlings and 15 × 15 × 10 cm for adults) were used for the *Suaeda* transplants. However, in soil blocks of such a size, only a few *Phragmites* ramets would emerge, and transplanting may thus affect the vigor of plants that emerged from rhizomes (Pennings and Callaway 1992; Emery et al. 2001). Therefore, we used large soil blocks (30 × 30 × 30 cm) for *Phragmites* transplants. Given the large blocks of low-salinity soil and the relatively short duration of the experiment in the *Suaeda* zone, the effect of physical stress on the performance of *Phragmites* was expected to be conservative in our study. This was in contrast to the *Suaeda* transplants, where the soil blocks of *Suaeda* were much smaller. As we mainly focused on the factors that excluded one species from the other species' zone, the effect of neighbors was examined only in the other species' zone. We removed aboveground competition and did not consider belowground competition, because it was very difficult to reduce belowground competition in the field and to completely excavate the belowground portions of highly clonal *Phragmites* plants (see Pennings et al. 2005). Neighbors surrounding all the soil blocks transplanted back into their home zones were left unmanipulated (similar to Pennings and Moore 2001; Pennings et al. 2005).

For both *Suaeda* and *Phragmites*, we compared the performance of transplants in the presence and absence of

neighbors to determine the effect of neighbors at each life history stage. This statistical approach followed many previous studies on salt marsh plant zonation (e.g., Bertness 1991; Ewanchuk and Bertness 2004; Pennings et al. 2005). There are also a number of other multistage studies that have used the same statistical approach (e.g., Bruno 2000; Goldenheim et al. 2008). As some of our data did not meet the assumptions of ANOVA, we used nonparametric Kruskall–Wallis tests with SAS (version 9.1, SAS Institute, Cary, NC, USA) to examine the effect of neighbors throughout this article. Nonparametric multiple comparisons (Steel's test) were used to test differences between each pair of treatments at each life-history stage. Nonparametric multiple comparisons were performed using R (version 2.7, R Development Core Team 2008).

Suaeda transplants

Transplant experiment 1

In November 2007, we excavated 112 soil blocks (15 × 15 × 4 cm) with surface soil as seed banks within a 4 × 1.5 m site in the *Suaeda* zone. These soil blocks were randomly assigned to 7 groups of different treatments denoted A to G (16 blocks per group; Fig. 1a). We transplanted all of the soil blocks, except those of group G, to identically sized holes distributed in the *Phragmites* zone (>2 m between individual transplants, >30 m beyond the zonal border). To establish the no-competition treatments (treatment groups B, C, D, E, and F), we removed all existing plants within 20 cm from the soil blocks by clipping at the soil surface biweekly. We left plants surrounding the soil blocks of group A unmanipulated. The soil blocks of group G were transplanted back into their home zone. All soil blocks were censused to determine *Suaeda* seedling emergence in mid-April 2008, coinciding with the peak of natural seedling emergence. As *Suaeda* emerged at a low rate until early June and the censuses were done only once, seedling emergence could have been underestimated. To examine the effect of neighbors on *Suaeda* seedling emergence, we compared the number of *Suaeda* seedlings per soil block of group A to that of a random subset (*n* = 16) of the soil blocks of group B, C, D, E, and F (Fig. 1a).

Transplant experiment 2

After seedling emergence was documented, the soil blocks were re-transplanted to specifically test the effect of neighbors on seedling survival. We transplanted the soil blocks of group B and F into the *Phragmites* zone and the *Suaeda* zone, respectively. All other transplants were re-transplanted into randomly selected locations but

maintained the same status of neighbors and physical stress as in transplant experiment 1 in order to reduce possible influences of transplanting. We watered the transplants every other day in the first week to reduce transplant shock. Since the groups we used (i.e., groups B to F) had similar numbers of *Suaeda* seedlings (see "Results"), we did not weed them to a consistent number. About one and a half months later, all soil blocks were censused to determine *Suaeda* seedling survival in late May 2008. To examine the effect of neighbors on *Suaeda* seedling survival, we compared the number of *Suaeda* survivors per soil block of group B to that of a random subset ($n = 16$) of the soil blocks of group C, D and E (Fig. 1a).

Transplant experiment 3

After seedling survival was documented, the soil blocks were re-transplanted to specifically test the effect of neighbors on *Suaeda* adult survival and growth. We transplanted the soil blocks of group C and E into the *Phragmites* zone and the *Suaeda* zone, respectively. All other transplants were re-transplanted. When transplanting, soil blocks in both zones were expanded to the size of $15 \times 15 \times 10$ cm in order to reduce possible damage to *Suaeda* roots. We watered the transplants in the first week. Aboveground biomass of *Suaeda* plants in each soil block was harvested in mid-August 2008, then counted for adult survival, oven-dried for 48 h at 70°C, and weighed to the nearest 0.01 g. To examine the effect of neighbors on *Suaeda* adult survival (growth), we compared the number (biomass) of *Suaeda* survivors per soil block of group C to that of the soil blocks of group D (Fig. 1a).

Phragmites transplants

Transplant experiment 1

In November 2007, we excavated 80 soil blocks of substrate ($30 \times 30 \times 30$ cm) containing dense *Phragmites* rhizomes in the *Phragmites* zone. These soil blocks were assigned to five treatment groups, i.e., A, B, C, D and E (16 blocks per group; Fig. 1b). We transplanted the soil blocks of group A and E into identically sized holes in the *Suaeda* zone. Then we removed all plants surrounding the soil blocks of group E by clipping a 50-cm radius border around the transplants biweekly, and we left plants surrounding the soil blocks of group A unmanipulated. We transplanted the remaining soil blocks of group B, C and D back into the *Phragmites* zone. All transplants into the *Suaeda* zone and the *Phragmites* zone were distributed with > 2 m distances between individual transplants and with > 30 m distances beyond the zonal border. All the transplants were censused to determine the total number of *Phragmites* ramets in mid-April 2008. To

determine the effect of neighbors on *Phragmites* emergence, we compared the number of *Phragmites* ramets per soil block of group A with that of the soil blocks of group E (Fig. 1b).

Transplant experiment 2

After *Phragmites* ramet emergence was documented, the soil blocks were re-transplanted to specifically test the effect of neighbors on *Phragmites* survival and growth. We transplanted the soil blocks of group B and D into the *Suaeda* zone. All plants surrounding the soil blocks of group D were clipped bi-weekly. We left plants surrounding the soil blocks of group B unmanipulated. All other transplants were re-transplanted. We watered the transplants in the first week. In mid-August 2008, aboveground biomass was harvested, then counted for survival, oven-dried and weighed. In order to determine the effect of neighbors on *Phragmites* survival (growth), we compared the number (biomass) of *Phragmites* survivors per soil block of group B with that of group D (Fig. 1b).

Results

Zonation patterns

Across the salt–fresh marsh interface, *Phragmites* dominated the riparian marsh and was displaced abruptly by *Suaeda* in the terrestrial border of the salt marsh (Fig. 2a). *Phragmites* occurred only a couple of meters beyond the zonal border and then dropped to zero or close to it, while *Suaeda* continued to occur in the *Phragmites* zone but at very low cover values. There was an exponential decline in the abundance of both species across the zonal border, despite the more dramatic decline for *Phragmites* than *Suaeda*.

Salinity patterns

Across the salt–fresh marsh interface, soil salinity increased steeply from the *Phragmites* zone to the *Suaeda* zone (Fig. 2a). Soil salinity was much higher in the *Suaeda* zone than in the *Phragmites* zone, and significantly varied through the growing season (zone effect, $F_{1,38} = 541.41$, $P < 0.001$; time effect, $F_{2,37} = 20.04$, $P < 0.001$; zone × time effect, $F_{2,37} = 15.53$, $P < 0.001$; repeated-measures ANOVA). Soil salinity peaked in May for both zones (Fig. 2b).

Transplant experiments

Suaeda transplants

Suaeda transplants performed well in their home zone with competition from conspecifics (Fig. 3). In the *Phragmites*
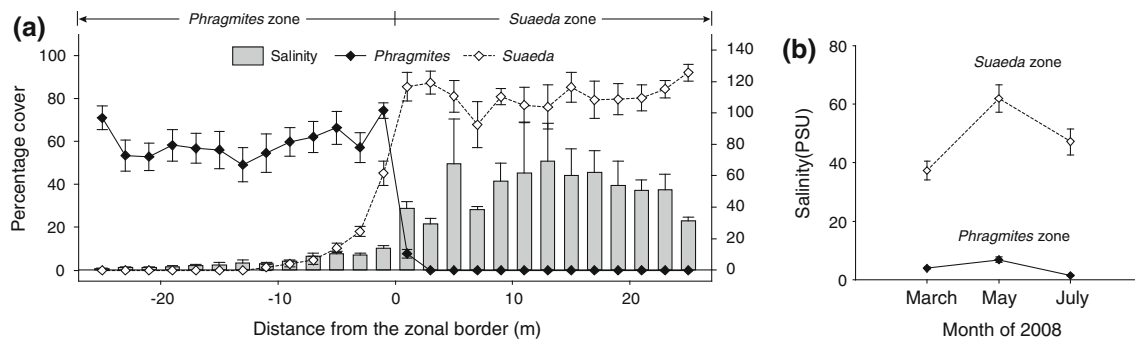
Fig. 2 a Changes in percentage cover of *Suaeda* and *Phragmites* and salinity in relation to distance from the zonal border. Species cover was determined from 1-m² quadrats along 10 parallel transects. Each value is the mean ± SE. Salinity data are means (+SEs) of the four transects sampled. **b** Seasonal variations in salinity (mean of 20 samples ± SE) in the *Phragmites* and the *Suaeda* zones in 2008

zone, *Suaeda* transplants performed well with neighbors removed but were significantly inhibited with neighbors present (Table 1). The magnitude of neighbors' effect differed among life history stages (Fig. 3, Fig. S2a of the ESM). Neighbors had the strongest effect on *Suaeda* seedling emergence and adult growth in the *Phragmites* zone, but they had a much weaker effect on *Suaeda* seedling survival and adult survival (Fig. 3, Fig. S2a of the ESM). There was a clear cumulative effect of competition across the various life-history stages. *Suaeda* transplants that had experienced competition with *Phragmites* from seedling emergence on were at the greatest disadvantage, those experiencing competition from seedling survival on were the next most disadvantaged, etc. (Fig. 3).

Phragmites transplants

Phragmites transplants performed well in their home zone but performed poorly in the *Suaeda* zone, regardless of neighbor treatments and life-history stage (Fig. 4, Table 1). In the *Suaeda* zone, there was no *Phragmites* ramet emergence in most transplanted soil blocks; only a few of the transplanted *Phragmites* plants survived and the survivors reached only a small final size (Fig. 4). However, neighbors in the *Suaeda* zone appeared to have a somewhat negative effect on *Phragmites* emergence but a positive effect on *Phragmites* survival and growth (Fig. S2b of the ESM). No apparent cumulative effect of competition from *Suaeda* was observed across these life-history stages (Fig. 4).

Discussion

Our results show that the zonation of an annual and a perennial plant species is maintained by a trade-off between competitive ability and stress tolerance. This
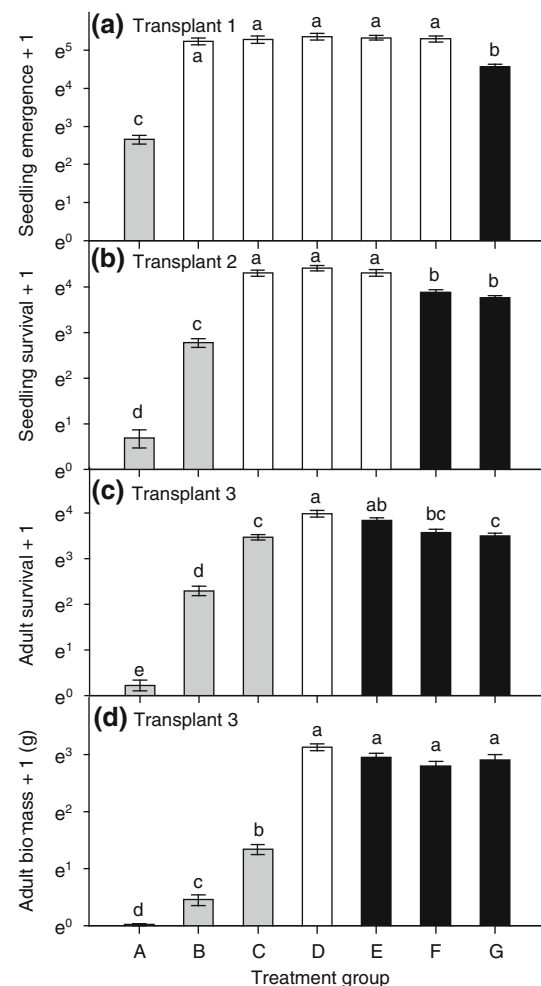

Fig. 3 Treatment effects on the performance of *Suaeda* transplants at different life history stages: **a** seedling emergence; **b** seedling survival; **c** adult survival; and **d** adult growth. *Bars* are mean ± SE (n = 16). *Open bars* indicate *Suaeda* transplants in the *Phragmites* zone without neighbors, *gray bars* in the *Phragmites* zone with neighbors, and *black bars* in the *Suaeda* zone with neighbors. *Bars with the same letters* are not significantly different. Treatment groups are defined in "Materials and methods"

Table 1 Summary of the effect of neighbors on the performance of *Suaeda* and *Phragmites* at each life-history stage in the transplant experiments

Life-history stage	H_1	P
Suaeda		
Seedling emergence	23.29	<0.0001
Seedling survival	23.30	<0.0001
Adult survival	12.17	0.0005
Adult growth	23.27	<0.0001
Phragmites		
Emergence	0.29	0.59
Survival	2.12	0.15
Growth	2.93	0.087

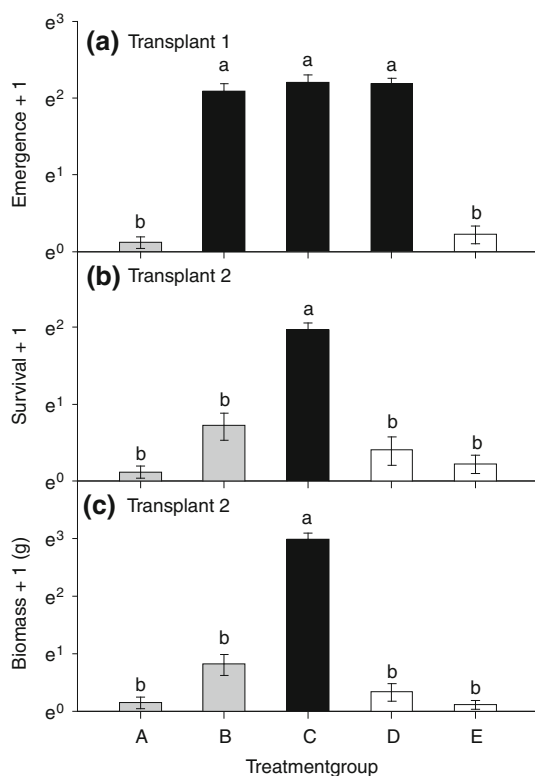Results from Kruskall–Wallis tests are reported by H_1 and P values

Fig. 4 Treatment effects on performance of *Phragmites* transplants at different life-history stages: **a** emergence; **b** survival; and **c** growth. *Bars are mean* ± SE ($n = 16$). *Black bars* indicate *Phragmites* transplants in the *Phragmites* zone with neighbors, *gray bars* in the *Suaeda* zone with neighbors, and *open bars* in the *Suaeda* zone without neighbors. *Bars with the same letters are not significantly different.* Treatment groups are defined in "Materials and methods"

finding can be observed at multiple life-history stages and is generally consistent with previous studies that focused on the zonation of perennial plants on both sides of the zonal border (e.g., Bertness 1991; Pennings and Callaway 1992; Pennings et al. 2005). Our results also suggest that

the magnitude of the competitive effect differs among different life-history stages of the plants and among species, and hence there may be some critical stages that control the formation of the marsh zonation patterns.

Zonation of annuals and perennials

Our results show that the annual *Suaeda* has a wide tolerance of salt stress but a weak competitive ability (see also in Zhao et al. 2003; He et al. 2009a), excluding it from the low-salinity *Phragmites* zone and restricting it to more saline marshes. *Suaeda* plants can grow well in the *Phragmites* zone if neighbors are absent. This finding can be observed at multiple life-history stages of *Suaeda* plants. In the *Phragmites* zone, *Suaeda* germination from soil seed banks in the shade of neighbors may be delayed and seeds may persist in the seed banks (Orrock and Christopher 2010 and references therein), but we did not explicitly test this in the present paper. *Suaeda* seeds can remain viable in soil seed banks for at least 1 year (Yang et al. 1995), and seed dormancy may help the species persist; lower seedling survival in the presence of neighbors may also reflect a failure to break seed dormancy in the presence of neighbors. In addition, neighbors reduced *Suaeda* adult survival and growth in the *Phragmites* zone. Lower final biomass may result in lower seed production in *Suaeda* plants (Yang and Zhang 1992), which could also play a role in excluding *Suaeda* from the *Phragmites* zone.

In contrast to *Suaeda*, the perennial *Phragmites* is not significantly affected by neighbors in the *Suaeda* zone at any life-history stage we examined, indicating that *Phragmites* is most likely excluded from the *Suaeda* zone by physical stress. In the *Suaeda* zone, salinity is probably the primary physical stressor that limits *Phragmites*, although we did not examine other possible factors. The *Suaeda* zone is hypersaline, with salinities that are 4–6 times higher than those observed in the *Phragmites* zone (Fig. 2). Such hypersaline environments may be fairly stressful to *Phragmites*, which has limited salt tolerance (Adams and Bate 1999; Colmer and Flowers 2008). In contrast to salinity, flooding is unlikely to be a significant stressor, since both zones are seldom flooded throughout the year (Qiang He, personal observation), and both *Suaeda* (He et al. 2009a) and *Phragmites* (see Colmer and Flowers 2008 for a review) are tolerant of flooding and anoxic stress. Although previous studies (e.g., Bertness et al. 1992; Ewanchuk and Bertness 2004) suggest that salt marsh annuals often dominate disturbance-generated bare patches where long-lived perennials are inhibited, disturbance is unlikely to be a controlling factor that mediates the absence of *Phragmites* from the *Suaeda* zone. Our field observation suggests that: (1) intensive human disturbances (e.g., burning and mowing) have occurred neither in the *Suaeda*

zone nor in the *Phragmites* zone, and; (2) natural disturbances, such as windstorms and floods, are similar between the two zones (Qiang He, personal observation). Despite these observations, more subtle disturbances, including the activities of herbivores, decomposing organisms and pathogens (as defined by Grime 2002), should be investigated further. Wrack disturbance does have an important effect on the presence of *Phragmites* in the *Suaeda* zone, but the areas disturbed by wrack overall are few across the marshes dominated by *Suaeda* (He et al. 2009b; Qiang He, personal observation). In contrast to the perennial-dominated salt marshes that have been extensively studied in North America, salt marshes on the coast of northeastern China tend to be dominated in general by annuals (Editorial Committee of Wetland Vegetation in China 1999). Annuals have also been found to dominate salt marshes in California and Europe, probably reflecting similar floristic compositions and climatic conditions in these regions (see a review in Adam 1990).

Understanding plant zonation at multiple stages

Our study demonstrates that the role of competition in mediating the zonation of *Suaeda* varies with life-history stage, suggesting that there may be some stages that are critical to the formation of the zonation patterns. Even though competition from *Phragmites* significantly reduces the performance of *Suaeda* at all stages of its life cycle, the magnitude of the competitive effect nonetheless varies with life-history stage.

Of the life-history stages we examined, competitive inhibition of *Suaeda* seedling emergence in the *Phragmites* zone appears to be one of the critical stages responsible for the absence of *Suaeda* from the *Phragmites* zone. Because the inhibition was nearly complete at this stage, *Suaeda* was precluded from successful recruitment and subsequent establishment. In contrast to seedling emergence, a considerable number of *Suaeda* plants can survive competition in the *Phragmites* zone (Fig. 3). Seedling emergence is one of the critical stages in the life cycles of plants. Processes operating at this stage are generally considered to be particularly important in determining plant distribution (Harper 1977; Grime 2002). In marsh habitats, competitive suppression of seedling emergence has also been suggested to play a role in mediating distribution limits of plants (Wijte and Gallagher 1996), especially for forbs that spread via sexual reproduction (Rand 2000). Bruno (2000) has also found that seedling emergence (rather than other stages) is the proximate life-history stage limiting adult distribution of several cobble beach forbs. In addition to seedling emergence, *Suaeda* adult growth is also, and just as severely, inhibited by competition in the *Phragmites* zone. This may thus be another critical stage in the life

cycle of *Suaeda* plants that controls their distribution in this marsh system. As described above, lower final biomass may result in lower seed production in *Suaeda* plants (Yang and Zhang 1992), which may in turn tend to exclude *Suaeda* from the *Phragmites* zone.

The role that physical stress may play in preventing *Phragmites* from occurring in the *Suaeda* zone needs to be examined further, especially as this may vary with life-history stage. But in any case, our study does demonstrate life-stage variations in the role of competition in generating marsh plant zonation patterns, and indicates the critical role that these stages may play in the formation of zonation patterns. This process has been proposed previously, but has not been directly tested in prior studies on marsh plant zonation (Wijte and Gallagher 1996; Rand 2000; He et al. 2009a).

In conclusion, the zonation of annuals and perennials in our marsh system appears to be regulated by a trade-off between competitive ability and stress tolerance; however, the precise role of competition in mediating plant zonation varies with life-history stage. Plant competition at critical stages of plant development is of primary importance in the formation of plant zonation patterns in the marsh system. As the critical life-history stages may be important to understanding how the marsh system is formed and maintained (Bruno 2000), insight into the ecological processes operating at these stages will benefit marsh restoration and management.

References

Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge

Adams JB, Bate GC (1999) Growth and photosynthetic performance of *Phragmites australis* in estuarine waters: a field and experimental evaluation. Aquat Bot 64:359–367

Alberti J, Escapa M, Iribarne O, Silliman B, Bertness M (2008) Crab herbivory regulates plant facilitative and competitive processes in Argentinean marshes. Ecology 89:155–164

Bertness MD (1991) Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology 72:138–148

Bertness MD, Gaugh L, Shumway SW (1992) Salt tolerances and the distribution of plants across a New England salt marsh. Ecology 72:1842–1851

Brewer SJ, Levine JM, Bertness MD (1998) Interactive effects of elevation and burial with wrack on plant community structure in some Rhode Island salt marshes. J Ecol 86:125–136

Bruno JF (2000) Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. Ecology 81:1179–1192

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965

Colmer TD, Flowers TJ (2008) Flooding tolerance in halophytes. New Phytol 179:964–974

Costa CSB, Marangoni JC, Azevedo AG (2003) Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. J Ecol 91:951–965

Crain CM, Silliman BR, Bertness SL, Bertness MD (2004) Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85:2539–2549

Du JH (2009) Dongying yearbook. Zhonghua Book Company, Beijing

Editorial Committee of Wetland Vegetation in China (1999) Wetland vegetation in China. Science Press, Beijing

Emery NC, Ewanchuk PJ, Bertness MD (2001) Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. Ecology 82:2471–2485

Ewanchuk PJ, Bertness MD (2004) Structure and organization of a northern New England salt marsh plant community. J Ecol 92:72–85

Fariña JM, Silliman BR, Bertness MD (2009) Can conservation biologists rely on established community structure rules to manage novel systems? Not in salt marshes. Ecol Appl 19:413–422

Giménez-Benavides L, Escudero A, Iriondo JM (2008) What shapes the altitudinal range of a high mountain Mediterranean plant? Recruitment probabilities from ovule to seedling stage. Ecography 31:731–740

Goldberg DE, Turkington R, Olsvig–Whittaker L, Dyer AR (2001) Density dependence in an annual plant community: variation among life history stages. Ecol Monogr 71:423–446

Goldenheim WM, Irving AD, Bertness MD (2008) Switching from negative to positive density-dependence among populations of a cobble beach plant. Oecologia 158:473–483

Grime JP (2002) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. Wiley, Chichester

Gulias J, Traveset A, Riera N, Mus M (2004) Critical stages in the recruitment process of *Rhamnus alaternus* L. Ann Bot 93:723–731

Harper JL (1977) Population biology of plants. Academic, New York

He Q, Cui B, Cai Y, Deng J, Sun T, Yang Z (2009a) What confines an annual plant to two separate zones along coastal topographic gradients? Hydrobiologia 630:327–340

He Q, Cui BS, Lv JZ, Cai YZ, Deng JF (2009b) Facilitation of *Phragmites australis* growth by wrack disturbance in high salt marsh in the Yellow River Estuary, China. Wetland Sci 7:335–341

Houle G, Morel L, Reynolds CE, Siégel J (2001) The effect of salinity on different developmental stages of an endemic annual plant, *Aster laurentianus* (Asteraceae). Am J Bot 88:62–67

Howard TG, Goldberg DE (2001) Competitive response hierarchies for germination, growth, and survival and their influence on abundance. Ecology 82:979–990

Odum WE (1988) Comparative ecology of tidal freshwater and salt marshes. Annu Rev Ecol Syst 19:147–176

Olff H, Bakker JP, Fresco LEM (1988) The effect of fluctuations in tidal inundation frequency on a salt-marsh vegetation. Vegetatio 78:13–19

Orrock JL, Christopher CC (2010) Density of intraspecific competitors determines the occurrence and benefits of accelerated germination. Am J Bot 97:694–699

Pennings SC, Bertness MD (2001) Salt marsh communities. In: Bertness MD, Gaines SD, Hay M (eds) Marine community ecology. Sinauer Associates, Sunderland, pp 289–316

Pennings SC, Callaway RM (1992) Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73:681–690

Pennings SC, Moore DJ (2001) Zonation of shrubs in western Atlantic salt marshes. Oecologia 126:587–594

Pennings SC, Grant MB, Bertness MD (2005) Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. J Ecol 93:159–167

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rand TA (2000) Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. J Ecol 88:608–621

Shumway SW, Bertness MD (1992) Salt stress limitation of seedling recruitment in a salt marsh plant community. Oecologia 92:490–497

Silvertown J, Franco M, Pisanty I, Mendoza A (1993) Comparative plant demography: relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J Ecol 81:465–476

Ungar IA (1987) Population ecology of halophyte seeds. Bot Rev 53:301–334

Weppler T, Stoll P, Stöcklin J (2006) The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant *Geum reptans*. J Ecol 94:869–879

Wijte AHBM, Gallagher JL (1996) Effect of oxygen availability and salinity on early life history stages of salt marsh plants. II. Early seedling development advantage of *Spartina alterniflora* over *Phragmites australis* (Poaceae). Am J Bot 83:1343–1350

Yang Y, Zhang B (1992) The models on density dependence to natural *Suaeda heteroptera* population of alkalization meadow in the Songnen Plain of China. Acta Phytoecol Geobot Sin 16:363–371

Yang Y, Zhu L, Zhang H (1995) Analysis on the flux of soil seed bank and the seedling morality in the communities of two species of *Suaeda* in the Songnen Plain in China. Acta Ecol Sin 15:66–71

Zedler JB, Callaway JC, Desmond JS, Vivian-Smith G, Williams GD, Sullivan G, Brewster AE, Bradshaw BK (1999) Californian salt-marsh vegetation: an improved model of spatial pattern. Ecosystems 2:19–35

Zhao K, Fan H, Zhou S, Song J (2003) Study on the salt and drought tolerance of *Suaeda salsa* and *Kalanchoe claigremontiana* under iso-osmotic salt and water stress. Plant Sci 165:837–844