The importance of facilitation in the zonation of shrubs along a coastal salinity gradient

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Abstract

Question: What are the interactive roles of abiotic stress and plant interactions in mediating the zonation of the shrub *Tamarix chinensis* along a salinity gradient?

Location: Yellow River estuary (37°46′N, 119°09′E), northeast China.

Methods: We surveyed the zonation of *T. chinensis* along a salinity gradient and quantified its salt tolerance using a pot experiment. In two field experiments, we transplanted *T. chinensis* seedlings into salt marsh, transitional zone and upland habitats, manipulated neighbours and quantified survivorship and biomass to examine neighbour effects. We also quantified vegetation effects on abiotic conditions in each zone.

Results: *Tamarix chinensis* dominated the transitional zone, but was absent in upland and salt marsh habitats. In the pot experiment, *T. chinensis* grew well in freshwater treatments, but was inhibited by increasing salinity. Field experiments revealed that competition from neighbours limited *T. chinensis* growth in the uplands, while *T. chinensis* transplants were limited, with or without neighbours, in the salt marsh by high soil salinity. In the transitional zone, however, *T. chinensis* transplants performed better with than without neighbours. Vegetation removal significantly elevated soil salinity in the transitional zone, but not in other zones.

Conclusions: Competition, facilitation and abiotic stress are all important in mediating the zonation of *T. chinensis*. Within its physiological stress tolerance range, or fundamental niche, it is limited by plant competition in low salinity habitats, and facilitated by neighbours in high salt stress habitats, but cannot survive in salt marshes having salinities above its salt stress tolerance limit. Our results have implications for understanding the relationships between facilitation and stress gradients.

Introduction

The role of facilitative interactions in mediating the organization of natural communities has been increasingly recognized (Bruno et al. 2003; Brooker et al. 2008). Benefactor species alleviate abiotic (or biotic) stress that restricts beneficiary species and expands the distribution range and fundamental niche of beneficiary species (Callaway 1995). The stress-gradient hypothesis (SGH; Bertness & Callaway 1994) is one of the best-known and widely tested facilitation hypotheses. In plant communities, the SGH predicts that the importance or intensity (*sensu* Brooker et al. 2008) of competition and facilitation will change inversely along abiotic stress gradients, with facilitation being more important in high abiotic stress relative to more benign abiotic conditions. At lower abiotic stress levels competition and consumer pressure become increasingly important determinants of sessile species distributions. Although a large number of empirical and modelling studies have found consistent support for the SGH (e.g. Bertness 1989; Bertness & Hacker 1994; Callaway et al. 2002; Lortie & Callaway 2006; Maestre et al. 2009), some studies have suggested that the role of facilitation may decrease in extremely severe environments (e.g. Kitzberger et al. 2000; Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Maestre et al. 2005, 2006). While these extremely stressful environments may lie outside of the physiological stress tolerance range or

fundamental niche of a species (Bruno et al. 2003), Holmgren & Scheffer (2010) recently suggested that it may be the rule rather than the exception to find strong facilitative effects in mild conditions, since in extremely harsh environments, facilitative amelioration of conditions could be insufficient to allow growth. Why stress-alleviating facilitation would benefit plants in physically mild habitats is unclear. Empirical field studies testing the SGH across strong physical stress gradients are uncommon in vascular plant communities. This is not the case for studies with sessile invertebrates and seaweeds on rocky intertidal physical stress gradients, which largely support the SGH (see Bruno & Bertness 2001 for review). Most previous studies testing the SGH in vascular plant communities have not examined plant interactions across discrete physical stress gradients, but have taken a less informative 'high versus low stress' approach (*sensu* Brooker et al. 2008). Other studies addressing plant interactions across entire stress gradients are often meta-analyses (e.g. Maestre et al. 2005, 2006) or empirical work (e.g. Kitzberger et al. 2000; Tielbörger & Kadmon 2000; Maestre & Cortina 2004) on arid or semi-arid ecosystems, where the major abiotic stress gradient is driven by water resource limitation. Whether the abiotic stress gradient is driven by a potentially limiting resource or a non-resource stress can complicate stress-gradient models (Maestre et al. 2009). However, field experimental studies that have tested the SGH across strong, entire non-resource stress gradients, such as cold, heat and salinity, are still scarce in plant community studies (but see Hacker & Bertness 1999; Holzapfel & Mahall 1999; Callaway et al. 2002). In this study, we test the hypothesis that the role of facilitation increases with increasing physical stress within the physical tolerance range or fundamental niche of a plant, but not at physical stress levels higher than those tolerated by the plant species in question.

Coastal habitats with steep abiotic stress gradients and relatively simple plant communities are particularly attractive for studying the roles of abiotic and biotic conditions on community structure (Pennings & Bertness 2001). Early studies of coastal plant communities have demonstrated that plant competition mediates salt marsh plant zonation (e.g. Bertness & Ellison 1987; Pennings & Callaway 1992) and that facilitation is important in mediating plant performance and diversity in marshes with high salinity/flooding stress (e.g. Bertness & Hacker 1994; Bertness & Yeh 1994; Hacker & Bertness 1999). More recent studies on facilitative and competitive interactions in salt marshes (e.g. Bertness & Pennings 2000; Bertness & Ewanchuk 2002; Pennings et al. 2003) have focused on latitudinal patterns. The ability of the SGH to predict latitudinal patterns of facilitation, however, is limited by selection-driven differences in intraspecific

and interspecific salt tolerance between low- and high-latitude plants (Pennings et al. 2003).

Like the well-investigated salt marshes of North America, salt marshes along Chinese coasts also exhibit striking vegetation zonation patterns across steep abiotic stress gradients (e.g. Dong et al. 1995; He et al. 2009; Wang et al. 2010), yet the processes that mediate vegetation patterns in these marshes remain largely poorly investigated. Recent studies (He et al. 2009; Cui et al. 2011a, b) on Chinese salt marshes found that their zonation patterns were similarly mediated by trade-offs between plant stress tolerance and competitive ability.

In this study, we examine the roles of facilitation and competition in determining zonation of the woody shrub *Tamarix chinensis* (hereafter, *Tamarix*) in the Yellow River estuary, northeast China. Salinity, the most limiting abiotic stress in this estuary, sharply increases with decreasing elevation from uplands to salt marshes in the high marsh, i.e. the portion of the marsh that is not flooded on a daily basis. *Tamarix* and the annual succulent *Suaeda salsa* dominate the transitional zone between upland and salt marsh, but *Tamarix* disappears in salt marshes monopolized by *S. salsa* and is replaced in uplands by *Phragmites australis*. We hypothesized that the zonation of *Tamarix* is a result of three factors: (1) abiotic stress excludes *Tamarix* from salt marshes due to salinity stress; (2) plant competition excludes *Tamarix* from heavily-vegetated uplands; and (3) facilitation enables *Tamarix* to survive in the transitional zone by ameliorating high soil salinities. We first document the typical zonation pattern of *Tamarix* in this coastal system, and then experimentally test these hypotheses with two field experiments and a pot experiment. Our results underscore the importance of facilitation in mediating vegetation zonation patterns in coastal systems and have implications for understanding the relationships between facilitation and stress gradients.

Methods

Study site and species

Fieldwork was conducted at high marsh elevations of the Yellow River estuary (37°46′N, 119°09′E) in the Yellow River Delta National Nature Reserve, China (see Cui et al. 2011a for a map of the study site). The study site has a temperate monsoonal climate. Tidal flooding is irregularly semi-diurnal. Salt marshes in the estuary are extensive and are rapidly developing at low elevations due to high sediment deposition.

Vegetation zonation is obvious along elevation gradients in the estuary (Cui et al. 2011a, b). The annual *S. salsa* extends from salt marshes at lower elevations to the terrestrial salt marsh border at upper elevations. The shrub *Tamarix* dominates the terrestrial borders, while

P. australis and several other plant species, including *Calamagrostis pseudophragmites*, *Triarrhena sacchariflora* and *Salix matsudana*, occupy the uplands. The smooth cord-grass *Spartina alterniflora*, native to North America, has also recently invaded the mudflats at low elevations, and a conspicuous *S. alterniflora* zone is developing in many parts of the estuary.

Tamarix is a shrubby recretohalophyte, tolerant of salt and flooding stress. It is abundant in saline inlands and coastal habitats in Asia, and has recently invaded riparian wetlands in the western United States (Natale et al. 2010). *S. salsa* is an annual euhalophyte more tolerant of salt and flooding stress than *Tamarix* (He et al. 2008, 2009). *P. australis* is a tall perennial species that is less tolerant of salt stress than *S. salsa* and *Tamarix*, but it is more flood tolerant (He et al. 2008).

Quantification of *Tamarix* zonation

To document the zonation of *Tamarix* along the salinity gradient, we positioned a transect (480 m in length) from the *P. australis*-dominated upland through the salt marsh dominated by *S. salsa* in August 2008. Four 10×10 m parallel plots were set every 20 m along the transect. The number of *Tamarix* plants in each of these plots was counted.

Field experiments

To investigate the effect of neighbours in mediating the zonation of *Tamarix* plants, we conducted two field experiments. In May 2009, we established 20 1×1 m plots (> 20 m distance between plots) in each zone of the upland, the transitional zone and the salt marsh. We transplanted one *Tamarix* seedling (25–30 cm in height, collected from the transitional zone) with associated soil ($16 \times 16 \times 20$ cm) into each of these plots. We used *Tamarix* seedlings rather than adult plants for our experiments as, (1) we aimed to determine factors affecting the early establishment of *Tamarix*, not propagule dispersal or adult growth, across salinity zones; and (2) *Tamarix* spreads mainly by sexual reproduction (Brotherson & Field 1987; Glenn & Nagler 2005; Natale et al. 2010). Although the stress tolerance and competitive ability of *Tamarix* can vary with life-history stage, its distribution patterns are set by seedling success (Glenn & Nagler 2005).

We watered *Tamarix* transplants every other day with fresh water for the first 2 weeks (approximately the same amount for all transplants) to reduce transplant shock. We discarded the transplants that exhibited any transplanting stress and assigned half of the remaining transplants in each zone to neighbour removal and control treatments, respectively. Neighbour removal was done

bi-weekly throughout the growing season of 2009 and 2010 by standing outside the plot area and clipping the above-ground vegetation to the soil surface with scissors. We did not manipulate below-ground competition, as it would be difficult to reduce below-ground competition and keep disturbance negligible. Most previous studies on salt marsh plant zonation have not considered below-ground competition for similar reasons (see Pennings et al. 2005). In September 2010, the number of *Tamarix* survivors in each zone was counted, and above-ground biomass of *Tamarix* in each plot was harvested, oven-dried at 60 °C for 48 h and weighed. To document the effects of neighbour removal on abiotic factors, we collected a soil core (5 cm diameter $\times$ 5 cm deep) in each plot of all three zones in September 2010. Soil water content, pH and pore water salinity were then determined (see Cui et al. 2011a for methods).

We conducted a second transplant experiment in May 2010. The experimental procedure was generally the same as the transplant experiment initiated in May 2009, except that we did more transplants into each zone ($n = 24$) and that the *Tamarix* seedlings were transplanted just before heavy rain and so did not need watering after transplanting. We determined the number of *Tamarix* survivors and their biomass, soil water content, pore water salinity and pH in each plot in each of the three zones using the same methods as described above.

For data analysis, because (1) we were interested primarily in how the effect of neighbours varied by zone and (2) the experimental duration for the above two transplant experiments differed (two growing seasons for the 2009 transplants, one for the 2010 transplants), we did not conduct analyses that pooled data of the two experiments, but focused on examining the effect of neighbours in a given zone for each transplant experiment. Differences in *Tamarix* survivorship between neighbour removal and control treatments were tested using Chi-square tests. *Tamarix* biomass (biomass of dead plants was included as equal to zero) and abiotic factor data were analysed using one-way ANOVAs if the data (original or log- or square root-transformed) met the assumptions of ANOVA. Data that did not meet the assumptions of ANOVA after the usual transformations were analysed using nonparametric two-sample Kolmogorov-Smirnov Z-tests. All the statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA).

Pot experiment

To specifically examine the effect of salt stress on *Tamarix* plants, we conducted a common garden pot experiment at our field station in the Yellow River estuary. In early May 2010, we collected 60 soil blocks each containing one

Tamarix seedling (25–30 cm in height), and transplanted seedlings into plastic pots. We watered these transplants with fresh water every other day in the first 2 weeks to reduce transplant shock. Then we discarded *Tamarix* seedlings that exhibited any transplant stress and randomly assigned 40 of the remaining *Tamarix* seedlings to five different salinity treatments: 0, 20, 40, 60 and 80 g kg^{-1} (eight replicates per salinity treatment; sea salt was used for these treatments). Pots were submerged in standing water of different salinities. We adjusted the salinity treatments by adding fresh water or salt. We chose this approach (submerging pots in water and adjusting water salinity) to control salinity, to make our manipulation of salinity levels more precise and since *Tamarix* plants are tolerant of flooding stress (Glenn & Nagler 2005). Water salinity of 40, 60 and 80 g kg^{-1} treatments was increased gradually to avoid shock (following Crain et al. 2004). Eight weeks after all salinity treatments were initiated, *Tamarix* height in each pot was measured and live above-ground biomass was harvested, oven-dried at 60 °C for 48 h and weighed.

Results

Tamarix zonation pattern

The zonation pattern of *Tamarix* in the Yellow River estuary was striking. *Tamarix* plants were most abundant (50–200 plants/100 m^2) in the transitional zone, but became rare in the upland and salt marsh (Fig. 1). *Tamarix* plants gradually decreased to 10–30 individuals/100 m^2 at the interface, and were completely absent from the lower elevations of the salt marsh. The decline in abundance of *Tamarix*, however, was very sharp at the interface to the

Fig. 1. Zonation pattern of *Tamarix* plants at the upper elevations of the Yellow River estuary. Data are shown as means ± SE (*n* = 4). Distances are relative to the plots with the highest mean density of *Tamarix* along the sampling transect.

upland. There were often fewer than 10 *Tamarix* plants/100 m^2 in the upland.

Field experiments

For the transplant experiment initiated in 2009, all the *Tamarix* transplants with neighbours removed in the upland survived after two growing seasons, but only about 60% of the transplants with neighbours present survived (Fig. 2a). The biomass of *Tamarix* transplants was also much higher with neighbours removed than with neighbours present in the upland (Fig. 2b). However, in the transitional zone, *Tamarix* transplants with neighbours removed cannot grow at all; in contrast, a large portion of the transplants survived if neighbours were present, although the biomass of *Tamarix* transplants was still limited (Fig. 2a and b). None of the *Tamarix* transplants in the salt marsh survived, regardless of neighbour treatments (Fig. 2a). In the second transplant experiment in 2010, neighbours significantly restricted the biomass of *Tamarix* transplants in the upland, but in the salt marsh neighbours had no effect on the biomass of *Tamarix* transplants (Fig. 2c and d). Although there was no statistically significant effect of neighbours on the survival and biomass of *Tamarix* transplants in the transitional zone (Fig. 2d), *Tamarix* survivorship tended to be higher with neighbours present than with neighbours removed (Fig. 2c).

For both transplant experiments, soil salinity was significantly elevated if neighbours were removed in the transitional zone, but neighbour removal treatments did not affect soil salinity in the upland and the salt marsh (Fig. 3a and b). Neighbour removal did not affect soil water content or pH, except in the upland, where neighbour removal significantly decreased soil water content (Fig. 3).

Pot experiment

The pot experiment revealed that *Tamarix* grew better under lower salinity treatments and that growth was inhibited by increasing salinity (Fig. 4). Although all the *Tamarix* were able to cope with 40 g kg^{-1} salinity, only three of the eight *Tamarix* in 60 g kg^{-1} salinity and none of the *Tamarix* in 80 g kg^{-1} salinity survived 8 weeks after all salinity treatments were implemented.

Discussion

Our results demonstrate that *Tamarix* zonation in the Yellow River estuary is mediated by plant interactions and abiotic stress. Competition from neighbours excludes *Tamarix* from the upland, but neighbours have no effect on *Tamarix* performance in the salt marsh, suggesting that abiotic stress is likely responsible for excluding *Tamarix*
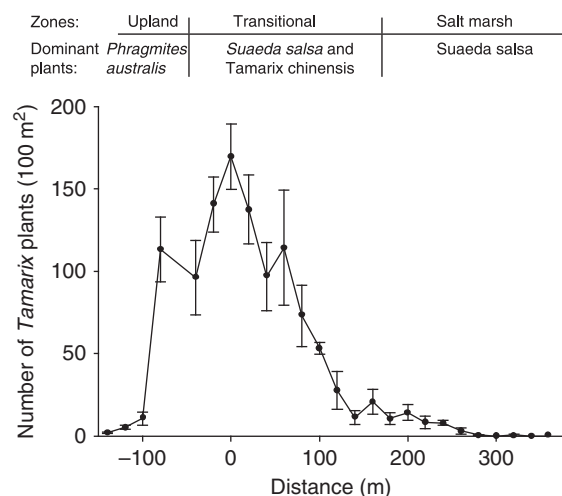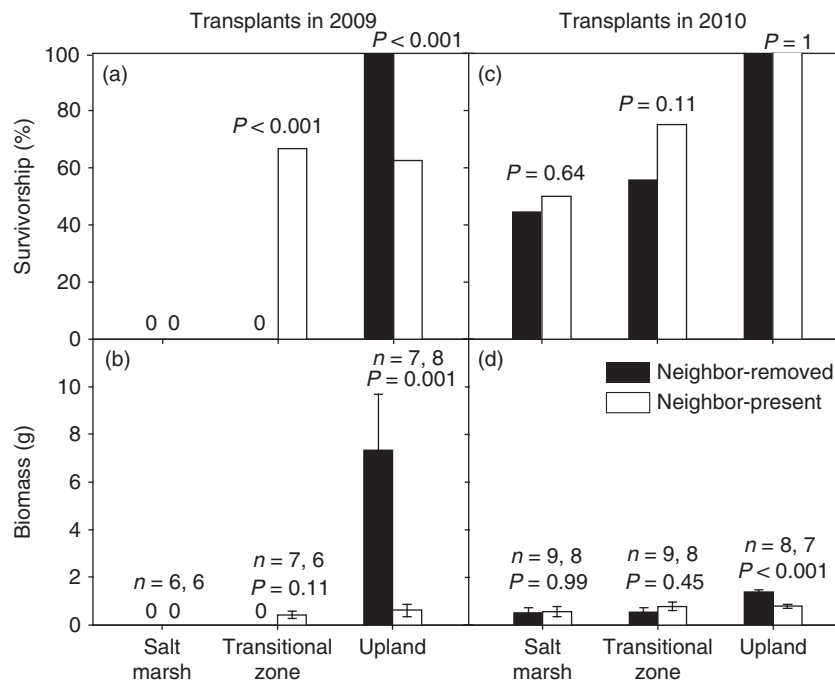
Fig. 2. Survivorship (**a**, **b**) and above-ground biomass (**c**, **d**) of *Tamarix* transplants with neighbours present and with neighbours removed in the different zones in September 2010. For **b** and **d**, data are shown as means ± SE. Number of replicates for each treatment is indicated above each bar.

from the salt marsh. These results are strikingly similar to previous studies of salt marsh plant zonation (e.g. Bertness & Hacker 1994; Pennings & Moore 2001; Pennings et al. 2005). In New England salt marshes, the woody shrub *Iva fructescens* is limited from establishing in the physically benign terrestrial border of the marsh through interspecific competition (Bertness & Yeh 1994; Bertness et al. 2002); short stature *I. fructescens* can establish in high marsh elevations when facilitated by neighbour salt stress amelioration (Bertness & Hacker 1994), but *I. fructescens* is unable to survive at lower marsh elevations due to salt and flooding stress (Hacker & Bertness 1999).

Mechanisms explaining *Tamarix* zonation

Our results suggest that the upper border of *Tamarix* is set by competition in the upland dominated by *P. australis*. *Tamarix* appears to have weaker competitive ability than the highly clonal and taller *P. australis*, excluding it from the relatively benign, low salinity upland dominated by *P. australis*. This result from our study is consistent with several previous studies that also suggest *P. australis* should be competitively superior to the woody shrub *I. fructescens* in New England salt marshes (Bertness et al. 2002; Silliman & Bertness 2004; but see Pennings & Moore 2001). In spite of lower competitive ability, *Tamarix* has wider stress tolerance than *P. australis*, since *P. australis* cannot survive with or without neighbours in

the transitional zone (Cui et al. 2011b), while *Tamarix* can survive here in the presence of neighbours. In the Yellow River Delta and many other coastal regions in China, *Tamarix* always dominates saline marsh zones where *P. australis* is not found (Editorial Committee of Wetland Vegetation in China 1999), and *Tamarix* is generally considered as a species capable of coping with salt stress (Glenn & Nagler 2005; Merritt & Poff 2010). This implies trade-offs between competitive ability and stress tolerance (Grime 1977) in *Tamarix*.

Although *Tamarix* has relatively wide stress tolerance, it cannot tolerate the extreme hypersaline conditions in the salt marsh. In both of our transplant experiments, neighbours had no effects on *Tamarix* transplants in the salt marsh, suggesting that the lower distribution of *Tamarix* is set by abiotic stress. Soil salinities in the Yellow River estuary often peak at upper elevations of the salt marsh where the transplant experiments were conducted, and limit the distributions of most plant species (He et al. 2009; Cui et al. 2011a). Although we did not explicitly test the precise abiotic stress limiting *Tamarix* growth in the salt marsh, our pot experiment suggests that salinity is the limiting factor. None of the *Tamarix* in our pot experiment exposed to the $80\,g\,kg^{-1}$ salinity survived, and soil salinities of $80\,g\,kg^{-1}$ are common in the salt marsh at our study site, suggesting that high soil salinities limit *Tamarix* in the salt marsh. Flooding, another abiotic stressor in salt marshes, should be unimportant in limiting *Tamarix*
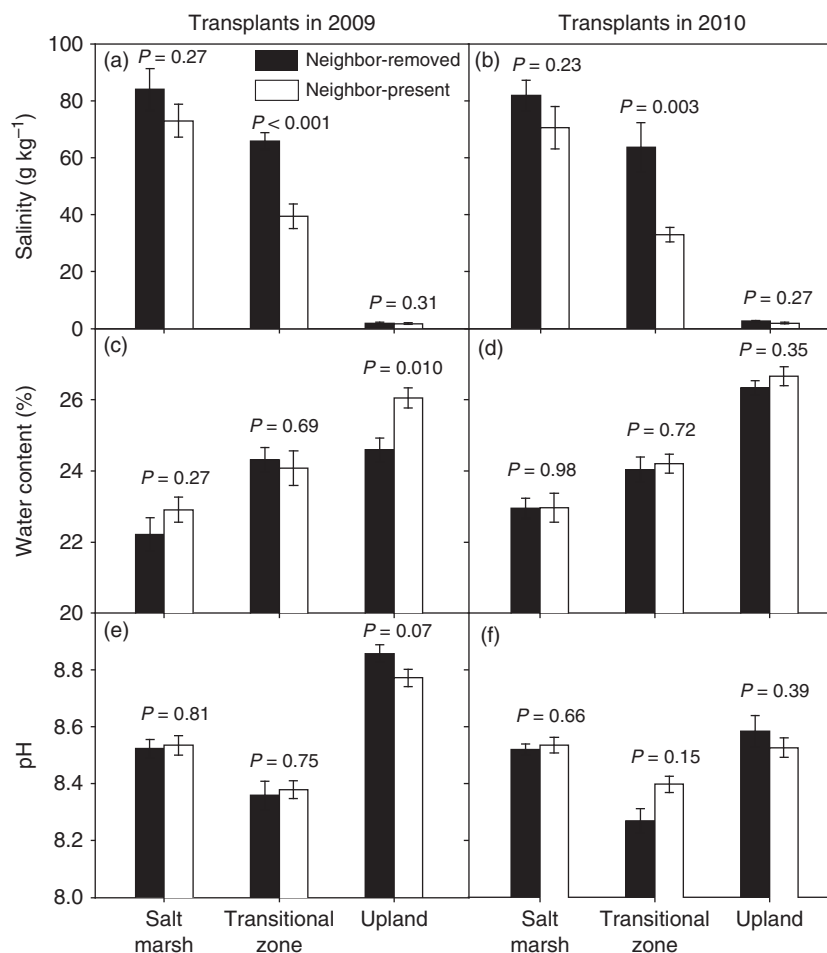
Fig. 3. Effects of neighbour removal on soil salinity (**a**, **b**), water content (**c**, **d**) and pH (**e**, **f**) in the transplant experiments initiated in 2009 (**a**, **c**, **e**) and 2010 (**b**, **d**, **f**). Data are shown as means ± SE. Number of replicates for each treatment is the same as indicated in Fig. 2.
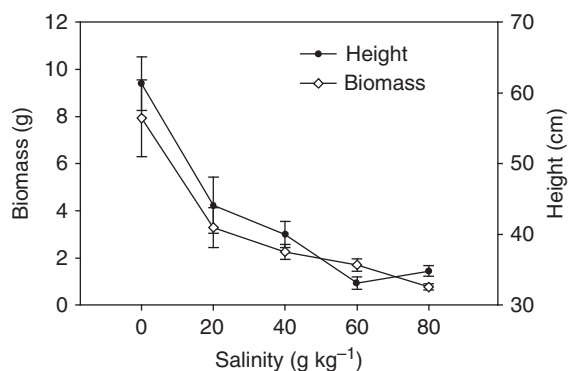

Fig. 4. *Tamarix* height and biomass under different salinity treatments in the pot experiment. Data are shown as means ± SE ($n = 8$).

performance at our study site since (1) salt marsh upper elevations are infrequently flooded (Qiang He, pers. obs.), and (2) *Tamarix* is known to be tolerant to flooding stress (Lesica & Miles 2004; Natale et al. 2010 and references therein).

In the transitional zone between upland and salt marsh, *Tamarix* transplanted in 2009 performed better with neighbours present than without neighbours in September 2010 after two growing seasons, although those transplanted in 2010 did not (Fig. 2). This may result from the short duration (one growing season) of the 2010 transplant experiment. Nevertheless, our results reveal that neighbours can play a positive role in mediating the performance of *Tamarix* plants in the transitional zone, probably due to a reduction of salt stress (Fig. 3) through shading of the *S. salsa* canopy. *S. salsa* grows vigorously, forms dense canopies and strongly reduces soil salinity through shading in the transitional zone. Vegetation feedback through shading is a key mechanism generating positive interactions among salt marsh plants (e.g. Bertness & Yeh 1994; Hacker & Bertness 1999; Pennings et al. 2003), as vegetation shading can significantly reduce evaporation and salt accumulation in salt marshes, particularly at upper elevations where flooding is infrequent and solar radiation and soil heating can lead

to high evaporation of pore water and elevated salinities (Bertness & Pennings 2000). Our results suggest that in addition to physical stress and plant competition, facilitation can also be important in mediating vegetation zonation in salt marshes. This is consistent with previous studies on vegetation zonation patterns in New England salt marshes (e.g. Bertness & Hacker 1994; Hacker & Bertness 1995, 1999) and cobble beaches (e.g. Bruno 2000; Bruno & Kennedy 2000; van de Koppel et al. 2006).

It is necessary to consider that the life history stages may affect the outcomes of plant–plant interactions (Tewksbury & Lloyd 2001; Sthultz et al. 2007). In this study, we focused on the roles of abiotic and biotic factors on *Tamarix* seedling performance, how these factors may affect the performance of mature *Tamarix* plants with large canopies needs further investigation.

Strong facilitation at intermediate stress levels?

Our study has demonstrated that the effect of neighbours on *Tamarix* transplants varied among zones, thus having implications for the SGH. Neighbours have negative, competitive effects on *Tamarix* plants in the upland where soils have low salinity, had positive, facilitative effects in the transitional zone with intermediate salinities, and had no effect in the salt marsh with extremely high salinities where *Tamarix* died with or without the presence of neighbours. These results indicate stronger facilitative effects can occur in intermediate salt stress environments, rather than in extremely stressful environments, but the results from our pot experiment and quantification of soil salinity conditions in the field revealed that soil salinities in the salt marsh are higher than the salt stress tolerance range of *Tamarix*. This suggests that physical conditions in the salt marsh lie outside of the fundamental niche of *Tamarix*. Furthermore, the presence of plant neighbours ameliorated high soil salinities in the transition zone within the salinity tolerance range of *Tamarix*, but in the salt marsh neighbours had a small but insignificant habitat amelioration effect on soil salinity, but did not reduce soil salinity to levels within the soil salinity tolerance level of *Tamarix*.

Our results are consistent with earlier studies (see Bertness & Hacker 1994; Hacker & Bertness 1995, 1999) that demonstrated that the effect of neighbour facilitation on the shrub *I. fructesens* in New England salt marshes was most important at intermediate elevations. At higher, physically benign elevations, *I. fructesens* was competitively eliminated by interspecific plant competition (Silliman & Bertness 2004), while at lower elevations *I. fructesens* died with or without neighbours present because flooding and salinity stresses were above the stress tolerance range of *I. fructesens* (Hacker & Bertness 1995,

1999). It is unclear whether several previous studies on arid and semi-arid grassland communities (e.g. Kitzberger et al. 2000; Tielbörger & Kadmon 2000; Maestre & Cortina 2004), which suggest that facilitation may also be most important in environments of intermediate water resource stress, are also examples of the inability of plants to live outside of their physical tolerance limit or fundamental niche. In addition to these relatively uncommon vascular plant community studies, facilitative interactions among sessile rocky intertidal invertebrates and seaweeds can also be unimportant in the extreme high intertidal zone since it lies outside of the stress tolerance levels of these aquatic organisms (see a review in Bruno & Bertness 2001). In rocky intertidal systems, which have a very strong temperature and desiccation physical stress gradient, the high intertidal border of stress-sensitive sessile invertebrates and seaweeds is very abrupt, and dependent on high neighbour densities which ameliorate physical stresses and allow sessile invertebrates and seaweeds to live at higher elevations on the shore than they could without neighbours (Bertness & Leonard 1997; Bertness et al. 1999; Stachowicz 2001).

Since 'stress' is species-specific and relative, when testing the SGH, the high end of a stress gradient should be defined as the harshest environments that a given organism can tolerate or the physical limit of its fundamental niche over a specific study area/habitat type (Bruno et al. 2003; Maestre et al. 2009). The SGH predicts that neighbour facilitation expands the fundamental niche of species and allows them to colonize and persist in habitats that would otherwise be outside of their stress tolerance limit (Bertness & Callaway 1994; Bruno et al. 2003). There is no robust mechanistic basis for predicting whether habitat-ameliorating facilitations will be most common at intermediate or mild stress levels.

Conclusions

We conclude that competition, facilitation and abiotic stress are all important in mediating the zonation of *Tamarix*, and that the importance of facilitation for plant and sessile organisms increases with increasing physical stress within the abiotic range limits or the physical fundamental niche of a given species. Our results have implications for understanding the relationships between facilitation and stress gradients, suggesting that the predictions of the original SGH are correct when it is applied within the physiological stress range or fundamental niche of a species. We suggest that recent proposals that stress ameliorating facilitations should be more common in physically mild than physically stressful habitats have no robust mechanistic basis, occur when the physical stress gradient considered is outside of the

physiological stress tolerance range or fundamental niche of the organism under consideration, or involve multiple stress gradients affecting species interactions. A refined understanding of facilitation along stress gradients would help inform successful restoration and management of vegetation.

Acknowledgements

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