COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Post-mortem ecosystem engineering by oysters creates habitat for a rare marsh plant

Hongyu Guo · Steven C. Pennings

Abstract Oysters are ecosystem engineers in marine ecosystems, but the functions of oyster shell deposits in intertidal salt marshes are not well understood. The annual plant *Suaeda linearis* is associated with oyster shell deposits in Georgia salt marshes. We hypothesized that oyster shell deposits promoted the distribution of *Suaeda linearis* by engineering soil conditions unfavorable to dominant salt marsh plants of the region (the shrub *Borrichia frutescens*, the rush *Juncus roemerianus*, and the grass *Spartina alterniflora*). We tested this hypothesis using common garden pot experiments and field transplant experiments. *Suaeda linearis* thrived in *Borrichia frutescens* stands in the absence of neighbors, but was suppressed by *Borrichia frutescens* in the with-neighbor treatment, suggesting that *Suaeda linearis* was excluded from *Borrichia frutescens* stands by interspecific competition. *Suaeda linearis* plants all died in *Juncus roemerianus* and *Spartina alterniflora* stands, regardless of neighbor treatments, indicating that *Suaeda linearis* is excluded from these habitats by physical stress (likely water-logging). In contrast, *Borrichia frutescens*, *Juncus roemerianus*, and *Spartina alterniflora* all performed poorly in *Suaeda linearis* stands regardless of neighbor treatments, probably due to physical stresses such as low soil water content and low organic matter content. Thus, oyster shell deposits play an important ecosystem engineering role in influencing salt marsh plant communities by providing a unique niche for *Suaeda linearis*, which otherwise would be rare or absent in salt marshes in the southeastern US. Since the success of *Suaeda linearis* is linked to the success of oysters, efforts to protect and restore oyster reefs may also benefit salt marsh plant communities.

Keywords Oyster shell · *Suaeda linearis* · Microhabitat · Competition · Salt marsh

Introduction

Ecosystem engineers are organisms that directly or indirectly modify environmental conditions, and thereby affect other species without direct trophic interactions (Jones et al. 1994, 1997, 2010). These modifications may occur while the engineers are living, or be mediated by their remains (e.g., effects of a fallen tree trunk on stream or soil processes; Jones et al. 1994, 1997). Ecosystem engineers play important roles in mediating biodiversity and ecological functioning in many ecosystems (Gutiérrez and Iribarne 1999; Bruno 2000; Crooks 2002; Cuddington and Hastings 2004; Wright and Jones 2006; Hastings et al. 2007).

Oysters are well-known ecosystem engineers (Grabowski and Peterson 2007) that create essential habitats for fish and invertebrates (Gutiérrez et al. 2003; Coen and Grizzle 2007). By providing three-dimensional biogenic structure with multiple microhabitats, oyster reefs promote species diversity and abundance (Larsen 1985; Coen et al. 1999; Lenihan 1999; Harding and Mann 2001; Lehnert and Allen 2002). Oyster reefs not only provide sources of food (Meyer 1994; Szedlmayer and Howe 1997), but also function as nursery areas and refuges for many species, thereby enhancing recruitment and survival of these species (McDonald 1982; Auster et al. 1991; Dittel et al. 1996). In addition, oyster reefs may reduce wave energy and protect estuarine marshes from erosion (Meyer et al. 1997).

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Although considerable attention has been paid to the services provided by oyster reefs in marine ecosystems and at marsh fringes, ecologists have largely ignored the potential importance of the dead oyster shells that have washed away from reefs and into the intertidal salt marshes, or that are part of relict middens deposited by Native Americans (Saunders 2002; Thompson and Worth 2011).

Salt marsh plant communities are typically comprised of a few halophytic species, most of which are perennial (Chapman 1974; Adam 1990). Annual plants tend to be rare and distributed in patches with low occupancy of perennials (Watkinson and Davy 1985; Ellison 1987; Bertness et al. 1992; Tessier et al. 2000). Populations of many annual plants in salt marshes are maintained by disturbances which create gaps in the stands of dominant perennials (Brewer et al. 1998; Tessier et al. 2000; Varty and Zedler 2008) or by the tolerance of annual plants to microhabitats that are prohibitively stressful for the dominant perennials (Ingold and Havill 1984; Thibodeau et al. 1998).

In Georgia salt marshes, on the South Atlantic Coast of the United States, we observed that the annual plant *Suaeda linearis* is usually found in association with oyster shell deposits. Accumulations of oyster shells occur as patches in the intertidal zones of many estuaries on the southeastern coast of the United States, particularly along waterways impacted by wind and waves (Anderson et al. 1979; Bahr and Lanier 1981; Coen and Grizzle 2007). These patches occur at the marsh edge where shells wash up from oyster reefs, but can extend a considerable distance into the marsh platform depending on wave action (Coen and Grizzle 2007; Guo and Pennings, personal observations). Patches of oyster shell also occur in the high marsh where the marsh contacts middens deposited by Native Americans. Oyster shell deposits support low densities of dominant salt marsh plants, but are the locations where we commonly find *Suaeda linearis*, which is otherwise rare in the salt marshes. We hypothesized that oyster shell deposits promoted the distribution of *Suaeda linearis* by engineering soil conditions that were unfavorable to the dominant salt marsh plants. We tested this hypothesis using a combination of common garden pot experiment and field transplant experiment comparing the performance of *Suaeda linearis* and three dominant salt marsh perennials, with and without competition, on soils typical for stands of each species.

Materials and methods

Study sites and field survey

Fieldwork was conducted at salt marshes near Sapelo Island, Georgia, USA (31°27′N, 81°16′W). In these salt marshes, *Borrichia frutescens* and *Juncus roemerianus*

occur in monospecific or mixed stands at higher marsh elevations, and *Spartina alterniflora* at lower marsh elevations (Wiegert and Freeman 1990; Pennings and Moore 2001). *Suaeda linearis* occurs in discrete stands at high marsh elevations adjacent to *Borrichia frutescens* or *Juncus roemerianus*, and at low marsh elevations adjacent to *Spartina alterniflora* along large tidal creeks and channels (all plants will be referred to generically hereafter). To document the association between *Suaeda* and oyster shell deposits, we took soil samples from stands of *Suaeda* at 20 separate locations. For comparison, we also took soil samples respectively from stands of *Borrichia* ($n = 10$ locations), *Juncus* ($n = 10$ locations) and *Spartina* ($n = 10$ locations) that were adjacent to *Suaeda* stands. Discrete stands of *Suaeda* were identified from a distance of ~50 m (at this distance, we could not see whether soils had a high shell content or not). At each location, we collected soil samples (0–10 cm depth) at 3–5 spots from within a stand, and combined them into a mixed soil sample of ~4 L in volume. We measured the wet weight of a subsample (50 ml volume) of each soil sample, and dried the subsamples for 3 days at 60 °C, then weighed them again to determine water volume, assuming 1 g/ml as the water density. We calculated the volumetric soil water content using the formula: volumetric soil water content = water volume (ml)/total soil volume (ml). We separated the rest of each soil sample into oyster shell versus sand and clay using a sieve (mesh size 5.6 mm). The very few gravel and rock pieces found were included with the sand/clay fraction. We calculated oyster shell content in the soil using the formula: oyster shell content = oyster shell dry mass (g)/soil total dry mass (g).

Common garden pot experiments

In order to determine the importance of abiotic stress associated with oyster shell deposits and biotic interactions on the performance of *Suaeda*, *Borrichia*, *Juncus*, and *Spartina*, we conducted two common garden pot experiments. In experiment I, which was carried out in 2008, we grew *Suaeda*, *Borrichia*, and *Juncus* alone (without-neighbor treatments, 1 plant per pot) and in the combinations of *Suaeda* + *Borrichia* and *Suaeda* + *Juncus* (with-neighbor treatments, 1 plant of each species per pot) in 20-L (~29 cm wide, ~35 cm high) pots. Pots were filled with three media treatments: (1) high marsh soil collected from a single high marsh, (2) oyster shell collected from a single tidal channel bank, and (3) a mixture of 50 % (volume) soil (from the high marsh) and 50 % (volume) shell ($n = 10$ replicates per species combination per media treatment). For each species, healthy individual plants (seedlings for *Suaeda*, because it is an annual species) within a narrow range of size were collected from a single site in June 2008.

The roots of each plant were separated from the soil and rinsed before potting. Pots assigned to without-neighbor treatments were placed apart from each other by ~0.5 m to ensure minimal shading from plants in adjacent pots, whereas pots with same combination of plants in with-neighbor treatments were placed close to each other to simulate an extensive mixed stand as best as possible given a pot experiment.

Common garden pot experiment II was conducted in 2009 with a similar design as described above. In this experiment, we grew *Suaeda* and *Spartina* alone (without-neighbor treatments) and together (with-neighbor treatment) with three media treatments: (1) low marsh soil, (2) shell, and (3) a mixture of 50 % (volume) soil (from the low marsh) and 50 % (volume) shell ($n = 10$ replicates per species combination per media treatment).

Both experiments ran from June to October. Plants were maintained outside (exposed to rain) and watered evenly with fresh water (1 L per pot) on non-rainy days. The pots received full sun during the middle of the day and partial shade from trees and a building in the early morning and late afternoon. At the end of growing season (October), aboveground biomass of all plants was harvested and dried for 3 days at 60 °C and weighed. We measured the volumetric water content of media at the end of growing season by drying soils (~8 h after watering) as described above.

Field transplant experiments

To further test the hypothesis that oyster shell deposits promote the distribution of *Suaeda linearis* by engineering soil conditions unfavorable to the dominant salt marsh plants, we conducted field transplant experiments. We located three representative sites where *Suaeda* occurred associated with oyster shell deposits adjacent to stands of *Borrichia*, *Juncus*, and *Spartina*. Henceforth, we refer to these sites as the *Borrichia–Suaeda* site, *Juncus–Suaeda* site, and *Spartina–Suaeda* site. The *Borrichia–Suaeda* site was at the terrestrial border of a high marsh and only experienced occasional tidal flooding during spring tides that was relatively short in duration; the *Juncus–Suaeda* site was in the high marsh, and experienced irregular tidal flooding that was most prolonged during spring-tides; the *Spartina–Suaeda* site was in the low marsh, and experienced daily tidal flooding.

In each vegetation zone (the monospecific stands of vegetation into which we transplanted experimental plants) of each site, we established eight removal plots (1.5×1.5 m) with background vegetation removed (without-neighbor treatment), and eight control plots with background vegetation left intact (with-neighbor treatment) that were interspersed with the removal plots, for a total of 32 plots per site (2 vegetation zones × 2 neighbor treatments × 8 replicates). The removal plots were created by clipping background vegetation at the soil surface in March 2009, and maintained by monthly weeding. At each site, healthy *Suaeda* seedlings and individuals of the paired species (*Borrichia*, *Juncus*, or *Spartina*), with associated soil blocks ($10 \times 10 \times 10$ cm), were collected and transplanted into each plot in each vegetation zone. Because some soil was transplanted along with the perennial plants, this experiment was conservative with respect to the effect of habitat on the performance of the perennials. For each species, individuals collected were within a narrow size range. The two individuals (of *Suaeda* and the other paired species) in each plot were placed ~1 m apart from each other within the plot to minimize any interactions between them (their canopies never overlapped). We monitored the performance of the transplants and maintained the plots monthly during the course of the experiment. At the end of the growing season (October 2009), all aboveground live plant material was harvested, dried for 3 days at 60 °C, and weighed. For each experimental plot, soil water content (volumetric), porewater salinity, and pH were measured monthly throughout the course of the experiment. Soil porewater salinity was measured by rehydrating dried soils in a known volume of distilled water, measuring the salinity of the supernatant, and back-calculating to the original porewater volume (Pennings and Richards 1998). Soil pH was measured by rehydrating dried soils (another set of samples) with distilled water in a 1:1 soil:water mixture, and measuring the pH of the supernatant (USDA 2004). Soil organic content was determined in July 2009 by combustion (USDA 2004).

Data analysis

All data analyses were performed with R statistical software (R Development Core Team 2010). Biomass data of *Suaeda* from common garden pot experiment II and all biomass data from field transplant experiments were analyzed using Nonparametric Multiple Comparisons (Behrens–Fisher procedure, 'npmc' package in R, with significance level of 0.05), because many plants died by the end of these experiments in some treatments, resulting in heterogeneous variance and non-normality of the data. Biomass data from common garden pot experiment I and biomass data of *Borrichia* and *Juncus* from common garden pot experiment II were log_{10}-transformed to improve normality and analyzed using two-way ANOVAs; post hoc multiple comparisons were performed using Tukey HSD tests with significance level of 0.05. Dead plants were included in these analyses with biomass set at zero.

To quantitatively evaluate biotic interactions in the field transplant experiments, we calculated relative

neighbor interaction intensity (RII) using the formula $RII = (B_{+N} - B_{-N})/(B_{+N} + B_{-N})$, where B_{+N} and B_{-N} are plant biomass in the presence (+) and absence (−) of neighbors, respectively (Armas et al. 2004). Negative RII values indicate competition; positive RII values indicate facilitation. To calculate RII, adjacent control and removal plots were paired within each site. For each plant species at each site, RII values between vegetation zones were compared using t tests, with significance level of 0.05.

Results

Field survey

The distribution of *Suaeda* in the field was strongly associated with oyster shell deposits. Soil from stands of *Suaeda* had a high content of oyster shell. Soil from adjacent stands of *Borrichia* had much lower levels of oyster shell, and soil from adjacent stands of *Juncus* or *Spartina* had almost no oyster shell (Fig. 1a). Volumetric soil water content was generally higher when oyster shell content was lower. Soil water content was highest in *Spartina* stands, intermediate in *Juncus* and *Borrichia* stands, and lowest in stands of *Suaeda* (Fig. 1b).

Common garden pot experiments

Water content varied significantly across media in both of the common garden pot experiments, with water content being the highest in soil, intermediate in the soil:shell mixture and lowest in shell (∼53, ∼38 and ∼21 %, respectively in experiment I, and ∼74, ∼40 and ∼23 %, respectively in experiment II).

In common garden pot experiment I, *Borrichia* performed best in the soil media, and its performance was progressively worse in the soil:shell mixture and the shell media. The presence of *Suaeda* neighbors had no significant effect on *Borrichia* growth (Fig. 2a; Table 1). *Juncus* also achieved the highest biomass in the soil media, and was unaffected by the presence of *Suaeda* (Fig. 2b; Table 1). *Suaeda* performed best in the soil media when grown without neighbors; however, the growth of *Suaeda* was strongly suppressed when grown with *Borrichia* or *Juncus* neighbors (Fig. 2c). Competitive effects on *Suaeda* were greatest in soil or the soil:shell mixture, leading to a significant media × neighbor interaction (Fig. 2c; Table 1).

In common garden pot experiment II, *Spartina*, like *Borrichia* and *Juncus*, performed best in the soil media, and was not significantly affected by the presence of *Suaeda* neighbors (Fig. 3a; Table 1). All *Suaeda* plants died in the low marsh soil media within several weeks, whereas they survived in the soil:shell mixture and in the shell media (Fig. 3b).
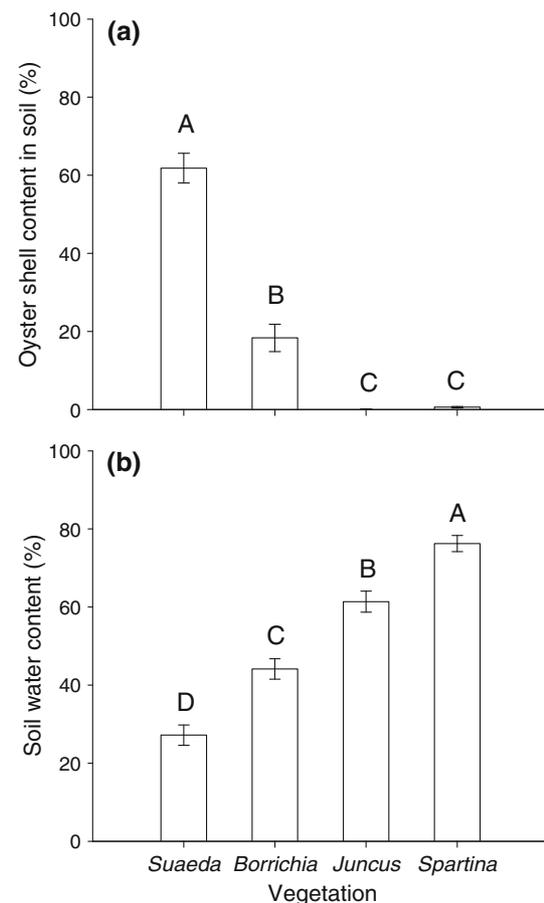

Fig. 1 Composition of soil collected from stands of the four plant species: **a** oyster shell content (% of soil total dry mass) and **b** volumetric water content (% of soil total volume). Data are means ± SE; $n_{Suaeda} = 20$, $n_{Borrichia} = 10$, $n_{Juncus} = 10$, $n_{Spartina} = 10$ (**a** and **b**). *Bars with shared letter* are not significantly different (Tukey HSD tests, $P = 0.05$)

Field transplant experiments

At the *Borrichia*–*Suaeda* site, soil water content and organic matter content were significantly higher in the stands of *Borrichia* versus in the stands of *Suaeda*, whereas soil pH and salinity did not differ among vegetation zones (Fig. 4a). Transplanted *Suaeda* plants grew well in either microhabitat without neighbors, but experienced strong competition from both *Borrichia* and *Suaeda*. Competitive effects of neighbors were stronger (RII more negative) for *Suaeda* plants transplanted into the stands of *Borrichia* than for plants transplanted into the stands of *Suaeda* (Fig. 5a, d). *Borrichia* performed poorly in the stands of *Suaeda* regardless of neighbor treatments (Fig. 5a).

At the *Juncus*–*Suaeda* site, soil from *Juncus* stands had higher water content, lower pH, and lower salinity than soil from *Suaeda* stands, whereas soil organic content did not differ between vegetation zones (Fig. 4b). All *Suaeda* plants
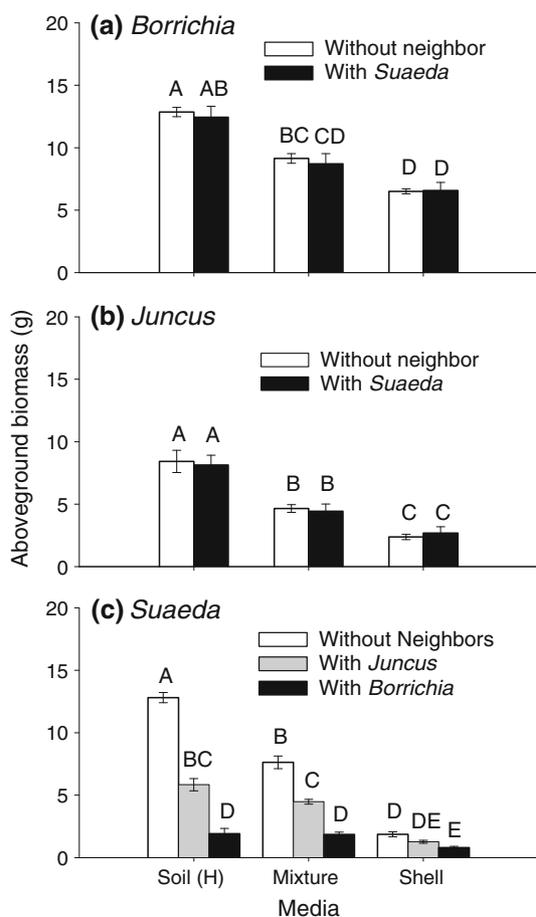
Fig. 2 Aboveground biomass of target species in common garden pot experiment I: grown in different media and neighbor treatments; **a** *Borrichia*, **b** *Juncus*, **c** *Suaeda*. Soil (H) is soil from high marsh. Data are means ± SE; *n* = 10 per treatment per media. Within each species, *bars with shared letters* are not significantly different (Tukey HSD tests, *P* = 0.05)

Table 1 Summary of ANOVA results for the effects of media, neighbor treatments and the interaction between media and neighbor treatments on the aboveground biomass (log$_{10}$-transformed) of plants in the common garden pot experiments

Species and source of variance	df	F	P
Common garden pot experiment I			
Borrichia			
Media	2, 54	44.29	**<0.01**
Neighbor	1, 54	0.96	0.33
Media × neighbor	2, 54	0.04	0.96
Juncus			
Media	2, 54	47.08	**<0.01**
Neighbor	1, 54	0.23	0.63
Media × neighbor	2, 54	0.14	0.87
Suaeda			
Media	2, 81	158.18	**<0.01**
Neighbor	2, 81	141.54	**<0.01**
Media × neighbor	4, 81	8.82	**<0.01**
Common garden pot experiment II			
Spartina			
Media	2, 54	94.31	**<0.01**
Neighbor	1, 54	0.04	0.84
Media × neighbor	2, 54	0.27	0.76

Biomass data of *Suaeda* in common garden pot experiment II were analyzed separately using Nonparametric Multiple Comparisons (see "Materials and methods"), and therefore are not included

Significant *P* values (*P* < 0.05) are in bold

transplanted into *Juncus* stands died by the end of the experiment (Fig. 5b). *Juncus* performed poorly in *Suaeda* stands regardless of neighbor treatments (Fig. 5b).

At the *Spartina–Suaeda* site, soil from *Spartina* stands had higher water content and organic matter content, but lower pH than soil from *Suaeda* stands (Fig. 4c). Soil salinity did not differ significantly between habitats (Fig. 4c). All *Suaeda* plants transplanted into *Spartina* stands died within several weeks (Fig. 5c). *Spartina* also performed poorly in *Suaeda* stands, regardless of neighbor treatments (Fig. 5c).

Discussion

The results of this study demonstrated that oyster shell deposits play an important role in influencing salt marsh plant community structure by providing a unique niche for an annual plant *Suaeda linearis* in salt marshes in the south-

eastern US. Although individual oysters live for only a limited number of years, their shells can continue to play an ecosystem engineering role in marsh habitats long after the oysters die.

Exactly how oyster shells mediate interactions among marsh plants appears to differ between microhabitats. At the *Borrichia–Suaeda* site, which was close to the terrestrial border of the marsh, *Suaeda* thrived in the *Borrichia* stands in the absence of neighbors. When grown with neighbors, *Suaeda* was suppressed by neighboring vegetation both in *Borrichia* and *Suaeda* stands, but *Suaeda* experienced stronger competition from *Borrichia* than from conspecifics, suggesting that *Suaeda* was excluded from the *Borrichia* stands by interspecific competition rather than physical stress. In contrast, *Borrichia* grew poorly in the *Suaeda* stands in both with- and without-neighbor treatments, indicating that the physical condition of oyster shell deposits in the *Suaeda* stands was stressful to *Borrichia* and precluded *Borrichia* from occupying this habitat. In the common garden pot experiments, oyster shell media had a low volumetric soil water content, probably due to better drainage, and thus it is possible that *Borrichia* was drought-stressed when grown in the oyster shell and the soil:shell
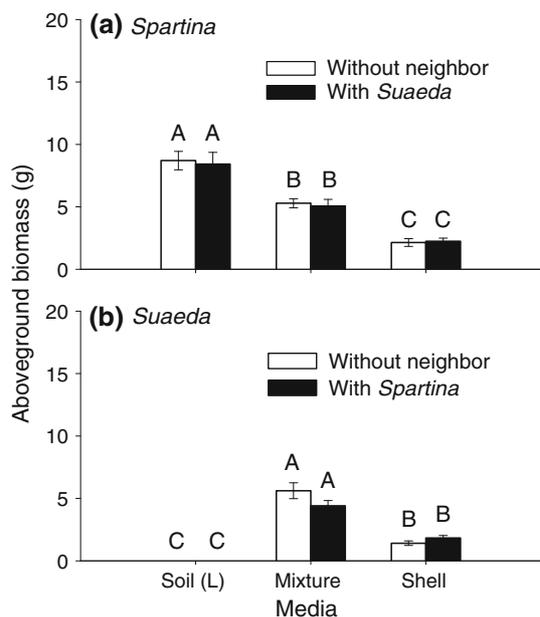
Fig. 3 Aboveground biomass of target species in common garden pot experiment II: grown in different media and neighbor treatments; **a** *Spartina*, **b** *Suaeda*. *Soil (L)* is soil from the low marsh. Data are means ± SE; *n* = 10 per treatment per media. Within each species, *bars with shared letters* are not significantly different (Tukey HSD tests for **a** *Spartina*; and Non-parametric Multiple Comparisons for **b** *Suaeda*; *P* = 0.05)

Fig. 4 Edaphic factors in the field transplant experiments; **a** *Borrichia–Suaeda* site, **b** *Juncus–Suaeda* site, **c** *Spartina–Suaeda* site. Data are means ± SE, *n* = 24 per vegetation zone for volumetric soil water content (*WC*), soil porewater salinity (*SAL*) and *pH* respectively, *n* = 8 per vegetation zone for soil organic matter content (*OMC*). *Asterisks* indicate means that are significantly different (*t* tests, *P* < 0.05)

mixture media. In the field, soil from *Suaeda* stands had lower water content and organic matter content than soil from *Borrichia* stands (Figs. 1b, 4a), which might contribute to the poor performance of *Borrichia* on oyster shell deposits. Thus, oyster shell deposits appear to function as a barrier limiting the distribution of *Borrichia*, likely by presenting physical stresses such as low soil water content and nutrient availability, thereby creating open space where *Suaeda*, which is competitively subordinate but can tolerate the physical stresses present on oyster shell deposits, can survive. In New England salt marshes, it has been found that hypersaline bare patches resulting from disturbance functioned as refugia for plants that have high salt tolerance but subordinate competitive ability (Bertness et al. 1992). Several other studies have also identified an association between the development of annual plants and small gaps in the matrix of dominant perennials in tidal marshes, revealing the importance of creating open space in maintaining annual plant populations (Watkinson and Davy 1985; Brewer and Grace 1990; Bakker and de Vries 1992; Tessier et al. 2000; van de Koppel et al. 2006; Varty and Zedler 2008).

The mechanisms affecting the performance of *Juncus* and *Spartina* were similar to those affecting the performance of *Borrichia*. *Juncus* and *Spartina* grew poorly in *Suaeda* stands in the field regardless of neighbor treatments, indicating that oyster shell habitat was also stressful
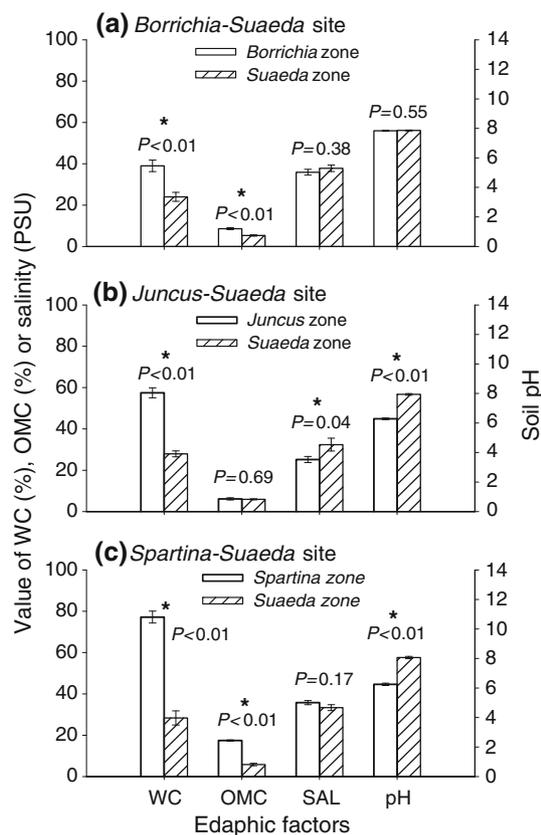
to these two salt marsh dominant plant species. Similarly, both *Juncus* and *Spartina* performed poorly in the common garden pot experiments when grown in the oyster shell and the mixture media (high marsh soil:shell for *Juncus*, low marsh soil:shell for *Spartina*, respectively), both of which had relatively low water content compared with marsh soils. In the field, soil from *Suaeda* stands had lower water content than soil from *Juncus* or *Spartina* stands, and it is likely that *Juncus* and *Spartina* are excluded from shell deposits by drought stress (Drake 1989; Hessini et al. 2008). Also, the higher soil salinity in the *Suaeda* stands might further stunt the growth of *Juncus*, which is not tolerant of high salinities, in this microhabitat (Wiegert and Freeman 1990; Pennings et al. 2005). Finally, the lower soil organic matter content in the *Suaeda* stands might also constrain the growth of *Spartina* in this microhabitat (Linthurst and Seneca 1981; Drake 1989).

Although *Suaeda* performed well in *Borrichia* stands in the absence of competition, it performed poorly in *Juncus* and *Spartina* stands, regardless of the presence of neigh-
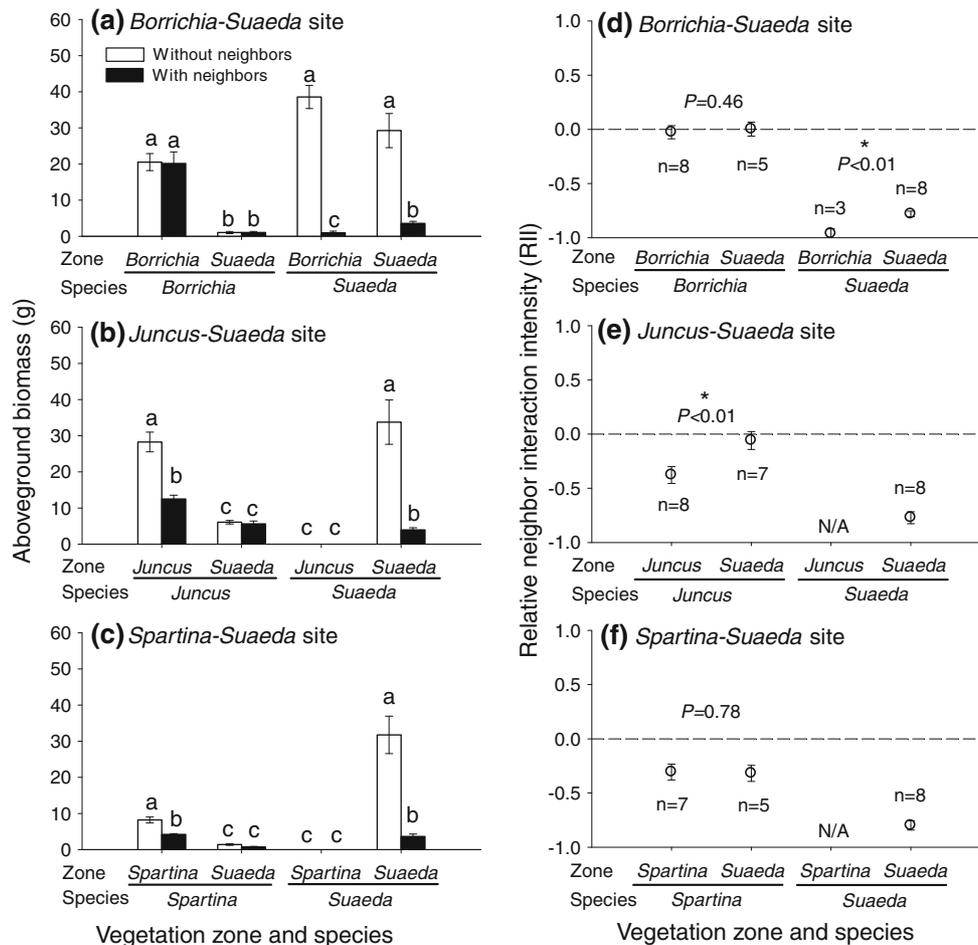
Fig. 5 Aboveground biomass of target species **a–c** and relative neighbor interaction intensity (**d–f**) in the field transplant experiments; **a**, **d** *Borrichia–Suaeda* site; **b**, **e** *Juncus–Suaeda* site; **c**, **f** *Spartina–Suaeda* site. For plant aboveground biomass, data are means ± SE, *n* = 8 per neighbor treatment in each vegetation zone; for relative neighbor interaction intensity (RII), data are means with 95 % CI, sample sizes

(*n*) are shown. Within each species, *bars with shared letters* (in **a–c**) are not significantly different (non-parametric multiple comparisons, *P* = 0.05). *Asterisks* indicate that means are significantly different (*t* tests, *P* < 0.05). *Species* is the target plant species studied in these experiments, *zone* is the background vegetation stands into which the experimental plants were transplanted

bors. *Suaeda* plants all died in the *Juncus* and *Spartina* stands, regardless of neighbor treatment, indicating that the physical conditions in the *Juncus* and *Spartina* stands were extremely stressful to *Suaeda*. One possible physical stressor limiting the distribution of *Suaeda* in the *Juncus* and *Spartina* stands might be tidal flooding, which causes frequent water-logging in the low marsh and occasionally prolonged water-logging in the high marsh. Water-logging of salt marsh soils leads to anoxia and the production of toxic sulfides (Adam 1990; Pezeshki 1997; Pennings and Bertness 2001). Studies with other species of *Suaeda* have found that frequent tidal flooding resulted in high mortality of *Suaeda,* probably due to soil anoxia or up-rooting of seedlings (Tessier et al. 2000; He et al. 2009). In common garden pot experiment II, *Suaeda* survived in the oyster shell and low marsh soil:shell mixture media, but experienced 100 % mortality in the low marsh soil media

(Fig. 3b). Moreover, soil pH was significantly lower in *Juncus* and *Spartina* stands versus *Suaeda* stands, which raises the possibility that variation in soil chemistry driven by pH might also play a role in eliminating *Suaeda* from *Juncus* and *Spartina* stands. Oyster shell deposits may reduce water-logging by improving drainage and physically increasing surface elevation. Also, the larger grain size of oyster shell versus marsh soil results in higher porosity and aeration, which can decrease anoxia. In addition, oyster shell can buffer low soil pH (Whitaker et al. 2004; Carlsson et al. 2008; Lee et al. 2008), and may thereby alter chemical conditions in the soil. The exact nature of these alterations was not investigated in this study; however, calcium-rich soils occur in several regions of the world and host unique floras (Etherington 1981; Walker et al. 2001; Bigelow and Canham 2002; de Souza et al. 2007). In these cases, since the physical structure such as the one provided

by oyster shells is lacking, differences in vegetation composition between calcium-rich and normal soils are thought to be driven primarily by soil chemistry.

In New England, *Suaeda* (*S. linearis*) is a major component of the plant community growing on cobble beaches behind beds of *Spartina alterniflora* which reduces water velocity and thus stabilizes the cobble substrate (Bruno 2000, 2002). In these communities, *Suaeda* is competitively excluded from the *Spartina alterniflora* zone (van de Koppel et al. 2006). Another species, *Spartina patens*, which is strong competitor in salt marshes, cannot tolerate the stress on cobble beaches, regardless of whether *Spartina alterniflora* buffers water movement in the low zone (van Wesenbeeck et al. 2007). Thus, *Suaeda* and other less-competitive cobble beach plants enjoy a refuge from competition on cobble beaches in microhabitats where hydrodynamic stress is sufficiently buffered by *Spartina alterniflora* beds. Cobble beaches do not occur in the sediment-rich estuaries of the South Atlantic Bight, which are formed by sediments that are eroded and transported to the coast by major river systems (Milliman et al. 1972; Meade 1982); however, oyster shell deposits are common in the intertidal zone of many southern estuaries (Bahr and Lanier 1981; Coen and Grizzle 2007). We argue that, in the case of *Suaeda*, oyster shell deposits in the Southeast function similarly to cobble beaches in New England, providing an essential habitat that allows the persistence of *Suaeda*, which otherwise would be extremely rare or even absent in southeastern US marshes.

The occurrence of oyster shell deposits in salt marshes also promotes environmental heterogeneity, which in general is critical in influencing community structure and diversity (MacArthur and MacArthur 1961; Connell 1978; Tilman 1982; Huston 1994). In wetland communities, studies have shown that microtopographic variability produces high diversity of plant community structure (Vivian-Smith 1997; Tessier et al. 2002). Similarly, ice and wrack-burial disturbances in salt marshes increase plant community structure diversity by creating a dynamic mosaic of patches which allow the emergence of competitively subordinate plants (Bertness and Ellison 1987; Adam 1990; Brewer et al. 1998; Pennings and Bertness 2001). Finally, disturbances caused by consumer foraging can also result in more diverse marsh plant communities (Hik et al. 1992; Pennings and Callaway 1996; Gough and Grace 1998). In a similar way, oyster shell deposits create microhabitat allowing *Suaeda* to grow in multiple vegetation contexts, and thus enhance plant community diversity in salt marshes by increasing habitat heterogeneity.

Although oyster shell deposits play an important role in promoting the distribution of *Suaeda* and plant community diversity in southeastern US salt marshes, the sustainability of oyster shell is facing serious challenges (Powell and

Klinck 2007). Oysters have been heavily harvested for food (Hargis and Haven 1999; Banks et al. 2007), and oyster populations have also declined due to disease (Andrews and Frierman 1974; Krantz and Jordan 1996; Cook et al. 1998). The decline of oyster populations and consequent loss of oyster shell resources has been observed in many estuaries in the southeastern US (Rothschild et al. 1994; NCDENR 2001; Woods et al. 2005; Coen and Grizzle 2007; Powell et al. 2008). The dependence of *Suaeda* distribution upon oyster shell habitat suggests that the declines over the past decades in oyster populations due to overfishing and disease may have negative impacts on *Suaeda* populations as existing stocks of shells are slowly buried and lost. This adds another reason for making more efforts to protect and restore oyster reefs, which play important ecosystem engineering roles not only when they live, but also after they die (Gutiérrez et al. 2003).

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