

Salinity and disturbance mediate direct and indirect plant–plant interactions in an assembled marsh community

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Abstract Direct and indirect plant–plant interactions play important roles in structuring plant communities, but the relative importance of physical stress and biological disturbance in mediating competitive outcomes remains debated. We conducted two common garden experiments to examine the influence of salinity and disturbance (sediment accretion and clipping) on competitive interactions among three native sedges (*Scirpus mariqueter*, *Scirpus triqueter*, and *Carex scabrifolia*) in the Yangtze estuary. In both experiments, the relative competitive abilities of these plants shifted among different treatments. Competition importance rather than intensity significantly decreased with increasing stress. At the community level, competition importance showed reduced variation along the stress gradient in the disturbance experiment. Notably, the performance of these sedges in three-species mixtures could not be predicted by their competitive relationships in two-species mixtures, which was an indication of indirect interactions. Salinity, disturbance and indirect interactions all affected the competitive dynamics of these sedges, which could explain their different performances and natural distributions in the Yangtze estuary. Our findings of the complex effects of physical factors and multi-species interactions, as well as the different patterns of competition

importance along stress gradients at the species level and the community level can improve our understanding of plant community organization in salt marshes and other ecosystems with sharp environmental gradients.

Keywords Competition · Facilitation · Indirect interaction · Salt marsh · Sedge

Introduction

Competition along environmental gradients has long been considered a major force in structuring plant communities (Austin and Austin 1980; Bartelheimer et al. 2010; Connell 1983), but the role of this process in community organization remains controversial. One theory predicts that competition is reduced in unproductive environments (Grime 1979), whereas Tilman (1982, 1988) proposes that competition plays a similar role along the productivity gradient, but the underlying mechanisms change. With the recent emphasis on facilitation, this historic debate has been included in a new conceptual model of stress-gradient hypothesis (SGH) that predicts a shift of plant–plant interactions from competitive to facilitative with increasing physical stress (Bertness and Callaway 1994; Brooker et al. 2005).

Over the past two decades, numerous empirical studies have been conducted to address the validity of SGH but fail to agree on its generality and applicability of the findings that facilitative effects may increase, remain constant, or even decrease along stress gradients (Brooker et al. 2008; Michalet et al. 2006). These discrepancies may be attributed to different research approaches (e.g., experimental vs. observational) (Maestre et al. 2005), performance measures (Brooker et al. 2008; Lortie and Callaway

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2006), plant traits considered (Gross et al. 2010; Maestre et al. 2009a), stress-gradient types (Maestre et al. 2009a; Smit et al. 2009) and its length (Lortie and Callaway 2006), and ontogenetic effects (le Roux et al. 2013; Schiffers and Tielborger 2006) among different studies. In addition, most previous studies have simplified the complexity of natural communities by examining the interactions between only a single or a few pairs of species (Brooker et al. 2008; Maestre et al. 2005). This design evaluates the variation of magnitude and direction of pairwise interactions rather than shifts of competition and facilitation frequencies along stress gradients as opposed by the original SGH, and frequency does not necessarily correlate to the intensity or importance of interactions (Maestre et al. 2009a). Many attempts have been made to resolve this long-standing debate by adding complexity to the general conceptual framework of SGH, including consideration of biotic stress (Smit et al. 2009), species life history strategies (Bowker et al. 2010), and non-linear relationships between interaction and stress (le Roux and McGeoch 2010). Malkinson and Tielborger (2010) argued that the net outcome of facilitation and competition should be reflected in the fitness of individual plants as a product rather than the addition of these two processes, which may lead to more realistic non-linear stress–interaction relationships (SIR).

Another frequently ignored issue is the difference between “importance” and “intensity” of interactions (Brooker et al. 2005; Gaucherand et al. 2006), which are not always well-correlated (Brooker and Kikvidze 2008). Because the relative contribution of competition to plant performances compared to other factors (i.e., competition importance) may decrease with increasing stress, while competition intensity remains constant, the studies using different indices may draw contradictory conclusions (Brooker 2006). Hence, the actual response norm of plant–plant interactions may not be as simple as previously assumed.

In natural communities with multiple species, indirect interactions, including facilitation, can also influence community structure (Callaway and Pennings 2000; Tielborger and Kadmon 2000), especially when competition mechanisms vary between species pairs (Brooker et al. 2008). This can result from direct competitive interactions, such as “a competitor’s enemy is a friend” (Miller 1994), or from diffuse effects when target species are influenced by multiple competitors (Wilson and Keddy 1986). Few studies have examined the generality and importance of these indirect interactions in structuring plant communities (but see Levine 1999).

No plant germinates as a competitive dominant. Competitive hierarchies shift under different physical conditions (Wang et al. 2006), which contributes to the maintenance of diversity in heterogeneous environments (Reynolds 1997; Tilman 1994). In coastal salt marshes, competitive

dominants have been found to displace other species to more stressful areas uninhabitable to the dominants (Bertness 1991; Pennings and Callaway 1992; Pennings et al. 2005). In such ecosystems, salinity and soil anoxia are the most important factors affecting the competitive outcome of co-existing species (Bertness 1991; Wang et al. 2006). However, disturbances, such as accretion and grazing by mammals, can also modify plant communities through direct effects on physiological processes and the mediation of competitive interactions (Geho et al. 2007). In the Yangtze estuary, sedge communities dominate the seaward edge of the marsh with varying composition in different areas, but how competitive outcomes and their roles shift along environmental gradients remains unclear. Exploration of these issues can improve our understanding of community organization, and help predict community dynamics under different scenarios of global change.

Because salt marshes have steep physical gradients and contain relatively few plant species, they are ideal for studying the determinants of biotic interactions. We here studied interspecific interactions among three sedges in Chongming Dongtan wetland in the Yangtze estuary, with two controlled experiments to precisely examine the change of competition intensity (or importance) and competitive outcomes of sedge species along salinity and disturbance (accretion and clipping) gradients. Specifically, we addressed the following questions: (1) How do salinity and disturbance affect the competitive outcomes among dominant sedges (*Scirpus mariqueter*, *Scirpus triqueter*, and *Carex scabrifolia*) in species-poor salt marshes? (2) How do the nature and magnitude of plant–plant interactions vary along the stress gradients? (3) Are there any indirect interactions among competing species that may affect plant community structure and functioning?

Materials and methods

Study area

Dongtan Wetland of International Importance is on Chongming Island in the Yangtze estuary (31°25′–31°38′N, 121°50′–122°05′E), and occupies 230 km². In this ecosystem, salinity ranges from 1 to 20 g NaCl L⁻¹ in different areas, which affect the performance and distribution of halophytic plants (Wang et al. 2009). The sedimentation rate exceeds 10 cm year⁻¹ in seaward areas in this rapidly developing marsh (personal observation), which may have both positive (nutrient input) and negative effects (burial) on pioneer plants (Mendelsshon and Kuhn 2003; Werner and Zedler 2002). In addition, cattle are pastured in the south part of the marsh in sedge-dominated areas, which greatly affects the distribution and structure of plant

Table 1 Description of habitat characteristics of three sedge communities in Chongming Dongtan salt marsh

Community	Habitat characteristics					
	Coverage (%)	Elevation (m)	Salinity (ppt)	Sedimentation rate (cm a ⁻¹)	Grazing intensity	Distribution area
<i>Scirpus mariqueter</i>	10–80	3–3.6	2–15	5–25	Low–mid	Northeast, middle, southeast
<i>Scirpus triqueter</i>	30–90	3.2–3.5	2–10	0–10	Mid–high	Southeast
<i>Carex scabrifolia</i>	50–90	>3.4	5–20	0–5	Low	Middle, southeast

Grazing intensity was assessed according to the performance of these sedge species and the number of cattle pastured in unit area. Low grazing intensity: plant height >30 cm, cattle density <1 ha⁻¹. Mid grazing intensity: plant height 10–30 cm, cattle density 1–10 ha⁻¹. High grazing intensity: plant height <10 cm, cattle density >10 ha⁻¹.

communities in Chongming Dongtan wetland. Native herbivores (crabs and insects) are found throughout the marsh, but have less effect on the target species in our study.

We worked with three native sedge plants (*S. mariqueter*, *S. triqueter*, and *C. scabrifolia*), because they are important pioneer species in this marsh with similar growth forms. *S. mariqueter* and *S. triqueter* are perennial rhizomatous, corm-forming sedges that reproduce both sexually and vegetatively. *S. mariqueter* is endemic to China, and distributed in salt marshes from the Yangtze estuary to the Hangzhou Bay. *S. mariqueter*-dominated salt marshes are the most important habitats for migratory birds in the area (Sun et al. 2001). *S. triqueter* is a widely distributed sedge on brackish mudflats in estuaries, ditches, lakes, ponds, rivers, and rice fields (Deegan et al. 2005). *C. scabrifolia* is a perennial rhizomatous sedge found on beaches, coastal wetlands, and brackish riversides (Li 1998). In the Yangtze estuary and Hangzhou Bay, *C. scabrifolia* is a pioneer species found in the early-to-middle stage of salt marsh succession (Wu et al. 2008).

At Chongming Dongtan, sedge and invasive *Spartina alterniflora* (smooth cord grass) meadows dominate the seaward areas, whereas *Phragmites australis* (common reed) and *S. alterniflora* dominate higher marsh elevations (Wang et al. 2009). In the seaward area, *S. mariqueter* monocultures occupy the marsh edge at lower elevations and the middle intertidal zone with high salinity and sedimentation rates, and in mixtures with *S. triqueter* at the same elevation with less saline water and higher grazing pressure. *C. scabrifolia* is a subordinate species occasionally found in disturbance-generated saline bare patches at the seaward edge of the high marsh and at the landward edges of sedge meadows (Table 1). These three species are often found in mixtures and as monocultures in the field.

Experimental design

We collected ramets of *S. mariqueter*, *S. triqueter*, and *C. scabrifolia* in late April 2008 from their pure stands in the intertidal zone of Chongming Dongtan salt marsh in

the Yangtze estuary. Ramets of similar size were selected as the material for common garden experiments at the Coastal Ecosystems Research Station of the Yangtze estuary on Chongming Island. We performed two experiments with a shared control (at a salinity of 8 ppt, unmanipulated). The first was a two-factor (salinity × species combination) controlled experiment with three salinity treatments: 0 g NaCl L⁻¹ (0 ppt), 8 g NaCl L⁻¹ (8 ppt), and 16 g NaCl L⁻¹ (16 ppt) to quantify the effect of environmental factors on sedge interactions. The other was a two-factor (disturbance × species combination) experiment with four disturbance treatments (unmanipulated control, accretion, clipping, and accretion + clipping) at a constant salinity of 8 ppt which was approximately the average salinity at the site of ramet collection. Ramets were planted in all possible combinations of these three species (seven species combinations in total: *S. mariqueter*, *S. triqueter*, *C. scabrifolia*, *S. mariqueter* + *S. triqueter*, *S. mariqueter* + *C. scabrifolia*, *S. triqueter* + *C. scabrifolia*, and *S. mariqueter* + *S. triqueter* + *C. scabrifolia*). All treatments were replicated four times for a total of 168 pots (6 treatments × 7 species combinations × 4 replicates). The total plant density was set to six ramets per pot following a replacement design (i.e., six ramets in monoculture, three ramets of each species in two-species mixture, and two ramets of each species in three-species mixture). Under this design, the competition intensity actually represented the interspecific interaction relative to the intraspecific interaction. However, the replacement design was acceptable for our study, as the intraspecific competition of these three sedge species was minor at a wide range of the initial planting density (from 1 to 16 ramets per pot), probably due to the clonal regulation by genets (Wang, unpublished data). Besides, we focused on the competition hierarchy of these three sedge species and the variation of interspecific interactions along stress gradients rather than the absolute value of competition intensity (or importance) in certain conditions.

Pots were 20 cm (diameter) × 25 cm (height), with drainage holes at the bottom. Sediments were washed sand

with 4 g Osmocote slow-release fertilizer (N/P/K 14:14:14, the Scotts Company, Marysville, OH, USA) added to each pot. We used 24 concrete pools (6 treatments \times 4 replicates) of 1.2 \times 1.2 \times 0.8 m, each containing 7 pots of all the species combinations randomly assigned to certain salinity or disturbance treatment. The water level was maintained at the sediment surface.

In late April, all the ramets were planted and those that died within 2 weeks were replaced. The pots were placed in fresh water until the treatments were performed in late May. Water level and salinity were adjusted weekly or after rain and accretion treatments. Every month, all the water in the pools was replaced, and the pots were rotated randomly between pools to avoid position effects. Accretion and clipping treatments were applied every 3 weeks from late May to mid-August (five times in total). In the accretion treatment, washed sand was added until the sediment surface increased by 1 cm each time. The accretion rate (\sim 5 cm/growing season) was similar to that in the area, where the ramets were collected (Wang 2010). The sediment surface of accretion pots was 5 cm lower initially, so the sand volume in each pot was equal at the end of the experiment. The accretion treatment was designed to mimic the burial effect but not the nutrient input effect of natural sedimentation process. However, pioneer sedge plants are usually not nutrient limited in Chongming Dongtan (Wang 2010), so the difference should have minor effect on plant performance. In the clipping treatment, all the plants were clipped to a height of 10 cm above the sediment surface to simulate cattle grazing, which was common in the south part of the marsh (Xu and Zhao 2005). In mid-October, approximately 2 months after the last accretion and clipping treatment, all plants were harvested and separated by species into fruits, shoots, and roots. Then, fruit number and total ramet number of each species were counted, and the height of the six tallest ramets of each species was measured. All harvested plant materials were oven dried at 80 °C to a constant mass and then weighed.

We used a full pairwise design rather than the phytometer approach to obtain sufficient information on interspecific interactions. By the end of the experiment, the sedges under benign physical conditions (i.e., low salinity and disturbance) had grown to fully occupy their pots both above- and belowground, suggesting that the experiment had run long enough to examine plant–plant interactions.

Data analysis

Performances (total biomass, root:shoot ratio, density, height, and flowering ratio) of *S. maritima*, *S. triquetra*, and *C. scabrifolia* were analyzed by one-way ANOVA (post hoc Tukey's HSD test) testing the effects of salinity or disturbance treatments. Competition intensity was

quantified by the relative neighbour effect (RNE) of each competing species in the mixture following Markham and Chanway (1996):

$$\text{RNE} = (P_{-N} - P_{+N}) / \max(P_{-N}, P_{+N})$$

in which P_{-N} is the performance of a species (indicated by biomass) in a monoculture, and P_{+N} is the performance of a species (indicated by biomass) in a mixture. The RNE value varies between -1 (maximum facilitation) and 1 (maximum competition). When calculating RNE, we used biomass per pot rather than biomass per ramet, because all three species were clonal and could reach maximum biomass within a growing season at a wide range (1–16 ramets per pot) of the initial transplant density (Wang, unpublished data). These sedge species mainly competed for space if provided with sufficient nutrients. Therefore, competition would result in a decline of ramet number and total biomass rather than a decline of biomass per ramet of each competing species (which is often observed in solitary plants). RNE values from different species' combinations were analyzed by nested design ANOVA (post hoc Tukey's HSD test) to test treatment and species (nested in treatment) effects on competition intensity. We assessed relative competitive ability based on the RNE values of competing species in the mixture (plants with lower RNE values were less affected by their neighbour and considered the competitive dominant).

Stress intensity was assessed as percentage performance reduction of each species in the monoculture under each treatment compared with the maximum monoculture performance of each species among all treatments to avoid the confusion of stress gradients and environmental gradients (see He and Bertness 2014). Competition importance was quantified as the impact of competition relative to total magnitude of environmental and biotic factors, modified from Seifan et al. (2010):

$$C_{\text{imp}} = (P_{-N} - P_{+N}) / (|P_{\text{max}-N} - P_{-N}| + |P_{-N} - P_{+N}|)$$

in which P_{-N} is the performance of a species (indicated by total biomass) in a monoculture under certain treatment, P_{+N} is the performance of a species (indicated by total biomass) in a mixture under certain treatment, and $P_{\text{max}-N}$ is the maximum P_{-N} among all treatments. The numerator ($P_{-N} - P_{+N}$) represents the impact of competition on plant performance, and the denominator is composed of two parts: environmental effects ($|P_{\text{max}-N} - P_{-N}|$) and competition effects ($|P_{-N} - P_{+N}|$). We defined environmental effects as the difference between the maximum plant performance without neighbours and its performance in monoculture at the certain point along the stress gradient ($|P_{\text{max}-N} - P_{-N}|$) rather than the definition of Seifan et al. (2010) ($|P_{\text{max}\pm N} - P_{-N}|$). As demonstrated in Mingo (2014), the importance index of Seifan et al. (2010) can

never exceed the value of 0.5 in facilitation, probably because they include the biotic interaction impact in the environmental effect term in the case of facilitation. However, our C_{imp} index has a definite range between -1 and 1 , with a positive value indicating competitive interaction and a negative value indicating facilitative interaction. When only competitive interactions occur ($P_{-N} > P_{+N}$), the equation can be simplified as follows, which is equal to the initial importance index proposed by Brooker et al. (2005):

$$C_{\text{imp}} = (P_{-N} - P_{+N}) / (P_{\text{max}-N} - P_{+N}).$$

Because of the difficulty in testing the SGH at an entire community scale along true stress gradients (Bowker et al. 2010), we attempted to assess stress intensity, competition intensity, and competition importance at the community level on a biomass basis, assuming all the competing plants in a pot were a single species. Community P_{-N} was calculated as the expected mixture biomass of co-existing species with no interspecific interactions (i.e., average monoculture biomass of each species in a certain species combination) in a certain treatment, community P_{+N} was the actual mixture biomass of a certain species combination in a certain treatment, and $P_{\text{max}-N}$ was the maximum P_{-N} among all treatments. The relationships between competition intensity or importance and stress intensity were analyzed using linear regression.

To evaluate indirect interactions among the sedges, we tested the effects of the presence of two competing species and the interaction term on the biomass of the target species using two-way ANOVA (post hoc Tukey's HSD test). Data were log transformed if necessary to improve the homogeneity of variance for analysis.

Results

Species responses to salinity and disturbance

Both high salinity and disturbance had negative effects on all species, but the response patterns were not consistent among different parameters and species. Total biomass of all these sedges significantly decreased with increasing salinity (Fig. 1a). The most sensitive species, *S. triquetra*, had a biomass reduction of nearly 66 % at 16 ppt compared with that at 0 ppt, whereas the biomass of *S. maritima* and *C. scabrifolia* was suppressed by 42 and 52 %, respectively (Fig. 1a). Root:shoot ratio increased along the salinity gradient but not significantly (Fig. 1b). Ramet density did not change much in *S. maritima* but decreased with increasing salinity in *S. triquetra* and *C. scabrifolia* (Fig. 1c). Ramet height slightly increased at 8 ppt and was

significantly reduced at 16 ppt in all three species (Fig. 1d). *C. scabrifolia* did not flower during the growing season, and the other two species showed a similar decline of flowering ratio with increasing salinity (Fig. 1e).

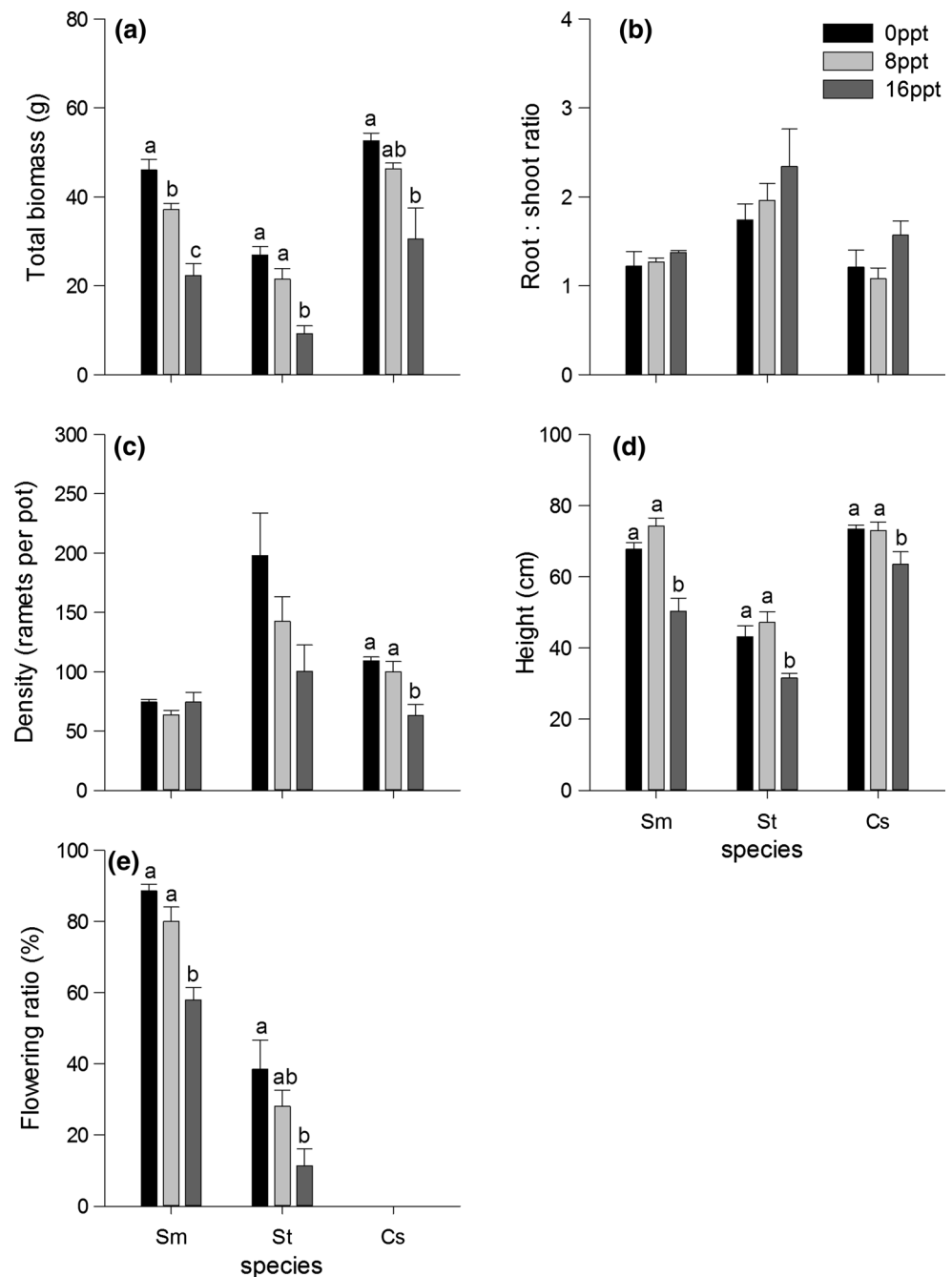
In the disturbance experiment, the clipping treatment had more significant effects on plant performance than the accretion treatment. For all three species, total biomass was significantly reduced in clipping and accretion + clipping treatments (Fig. 2a). *S. triquetra* was the most tolerant to disturbance (especially clipping), which only had a biomass reduction of 54 % in monoculture under the most severe disturbance treatment (accretion + clipping) compared with *S. maritima* (82 % biomass reduction) and *C. scabrifolia* (87 % biomass reduction) (Fig. 2a). Root:shoot ratio increased with increasing disturbance, but the difference was only marginally significant for *S. triquetra* (ANOVA, $P = 0.07$) (Fig. 2b). Responses of ramet density and height were similar to those of biomass except that *S. triquetra* had the highest density in accretion treatment (Fig. 2c, d). Flowering ratio of *S. maritima* was significantly reduced in clipping and accretion + clipping treatments, whereas that of *S. triquetra* did not vary significantly among disturbance treatments at a relatively low level (Fig. 2e).

Competitive hierarchy among sedge species

In the salinity experiment, although the relative competitive ability of the three sedge species differed, competition intensity across all competing species did not vary among salinity treatments except in *S. triquetra*–*C. scabrifolia* mixtures (Table 2; Fig. 3). The competitive dominant *S. maritima* was always less affected by neighbours, especially at high salinities (Fig. 3a, c), and the competitive hierarchy between *S. triquetra* and *C. scabrifolia* reversed from low to high salinity (Fig. 3e). In the three-species mixture, *S. triquetra* was less affected by neighbours (i.e., more competitive) than *S. maritima* at 0 ppt (Fig. 3g), which differed from the competitive outcomes of pairwise competition (Fig. 3a).

Similar to the results of the salinity experiment, disturbance did not alter the average competition intensity of all competing species on the whole but did affect the relative competitive abilities of these sedges (Table 2; Fig. 3). In two-species mixtures, *C. scabrifolia* was the competitive inferior in all treatments (Fig. 3d, f), but the dominance of *S. maritima* over *S. triquetra* disappeared in the accretion + clipping treatment (Fig. 3b). In the three-species mixture, the competitive hierarchy of *S. maritima* > *S. triquetra* > *C. scabrifolia* was maintained except in the clipping treatment (Fig. 3h).

Fig. 1 Growth and reproduction performances (mean \pm SE, $n = 4$) of *Scirpus mariqueter* (Sm), *Scirpus triqueter* (St), and *Carex scabrifolia* (Cs) in monoculture in relation to salinity. **a** Total biomass, **b** root:shoot ratio, **c** density, **d** height, **e** flowering ratio. Different lower cases denote significant differences (Tukey's HSD test) of each species among different salinity treatments



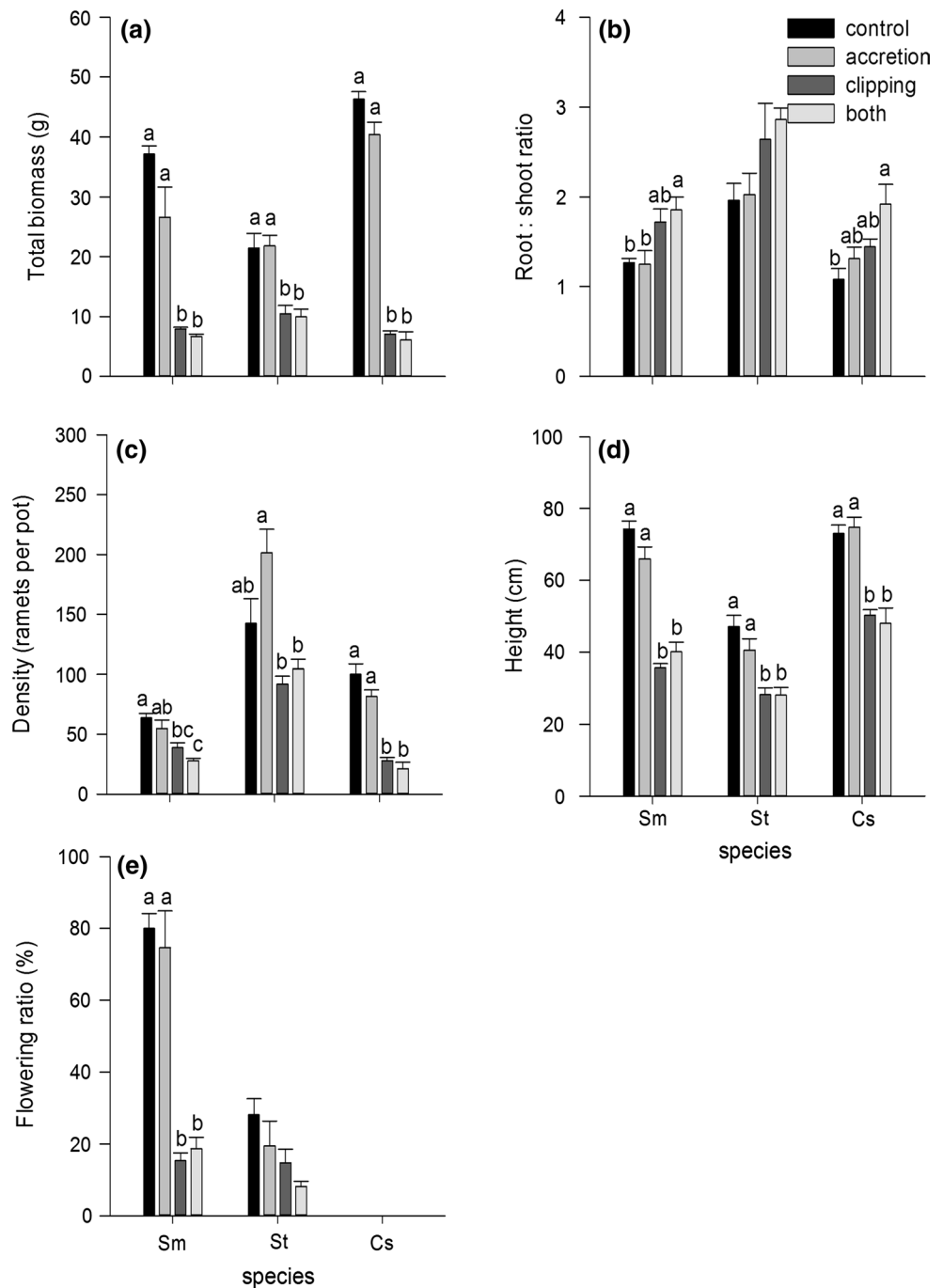
Variation of plant–plant interactions along the stress gradient

The stress–interaction relationship (SIR) was affected by competition indices used, plant traits and species considered, but did not vary between stress types (Fig. 4). In both salinity and disturbance experiments, competition intensity was relatively constant along the stress gradient (Fig. 4a, c). Competition importance, however, significantly decreased with increasing stress (Fig. 4b, d).

Although these three sedge species have similar morphology, their response norms were not consistent. In the salinity experiment, the competition intensity of *S. triqueter* was the lowest at intermediate stress (around 0.2–0.3), whereas that of the other two species slightly decreased with increasing stress (Fig. 4a). In the disturbance experiment, these sedges responded similarly as in the salinity disturbance, but only *S. triqueter* occupied the entire stress gradient (Fig. 4c).

At the community level, however, negative relationships between competition importance and stress disappeared

Fig. 2 Growth and reproduction performances (mean ± SE, $n = 4$) of *Scirpus mariqueter* (Sm), *Scirpus triqueter* (St), and *Carex scabrifolia* (Cs) in monoculture in relation to disturbance. **a** Total biomass, **b** root:shoot ratio, **c** density, **d** height, **e** flowering ratio. Different lower cases denote significant differences (Tukey’s HSD test) of each species among different disturbance treatments



(Fig. 5). Notably, the whole communities were either highly suppressed or facilitated in low stress conditions, but the interactions became neutral at the harshest end of the stress gradient (i.e., competition importance variation decreased along the stress gradient) (Fig. 5).

Indirect interactions

Indirect interactions were detected for all three species in different treatments in both experiments. In the salinity

experiment, there were significant interactions between two competitors (i.e., indirect interactions) on *S. mariqueter* at low salinity, on *S. triqueter* at high salinity, and on *C. scabrifolia* in all treatments (Table 3).

Similarly, indirect interactions were not consistent among disturbance treatments. *S. mariqueter* was significantly affected by the interaction between two competitors in the control only, *S. triqueter* was significantly influenced in the clipping treatment only, and *C. scabrifolia* was significantly affected in the control, accretion, and clipping treatments (Table 3).

Table 2 Results of nested design ANOVA testing the effects of treatment and species (nested in treatment) on the competition intensity (indicated by relative neighbour effect values of competing plants) in different species combinations

	Source of variation	Species combination			
		Sm + St	Sm + Cs	St + Cs	Sm + St + Cs
Salinity experiment	Treatment	NS	NS	*	NS
	Species (treatment)	*	NS	**	***
Disturbance experiment	Treatment	NS	NS	NS	NS
	Species (treatment)	*	***	*	*

Relative neighbour effect (RNE) quantifies the proportion of biomass reduction of each species due to neighbour existence. See “Materials and methods” for more details

Sm, *Scirpus mariqueter*; St, *Scirpus triqueter*; Cs, *Carex scabrifolia*;

NS, not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Discussion

Our results showed that the relative competitive abilities of salt marsh sedges in the Yangtze estuary shifted under different physical conditions. At the species level, competition intensity remained relatively consistent along the stress gradient, but competition importance decreased with increasing stress. However, competition importance tended to be neutral and less variable with increasing stress at the community level. Sedge responses to interspecific competition, salinity, sediment burial (accretion), and simulated herbivory (clipping) appeared to explain their distribution in the Yangtze estuary. Indirect interactions among competitors in three-species mixtures, however, were common, reducing the negative effects of dominant species and promoting coexistence.

Competitive hierarchy along environmental gradients

Although the role of competition in generating plant zonation along physical gradients has long attracted the attention of ecologists (Whittaker 1975), the relative importance of competition in generating community structure is not predictable even in well-studied plant communities (Farina et al. 2009; Lamb and Cahill 2008). Our results suggested that environmental factors (e.g., salinity) or disturbances (sedimentation and grazing) altered the performances and competitive abilities of the sedge species, which might in turn affect their distributions in estuarine salt marshes.

Salinity is the most important physical factor in the Chongming Dongtan wetland, explaining most of the habitat partitioning among the dominant plants (Wang et al. 2009; Wang 2007). In addition, this marsh is exposed to various types of natural and anthropogenic disturbances. Sedimentation can potentially promote plant growth by reducing inundation and increasing nutrient inputs (Mendelsshon and Kuhn 2003) but can negatively affect plants through burial (Werner and Zedler 2002). Grazing by herbivores can strongly influence the distribution and abundance of plants in salt marsh systems as well (Geho et al. 2007;

Holdredge et al. 2009). We recognize that the clipping treatment assumed equal palatability and herbivore preference among different species, which is not true in the field. However, because these three sedge species have similar morphology and nutrient composition, selective herbivory by cattle is minor in the area, where the materials were collected (personal observation). Of the sedges we studied, *S. triqueter* was more salt sensitive but less affected by clipping (simulated grazing) than the other two competitors, whereas *S. mariqueter* was less affected by high salinity (Figs. 1, 2). Consequently, the competitive hierarchy of the three sedges shifted along the salinity and disturbance gradients. *S. triqueter* was competitively dominant in freshwater and clipping treatments but became competitively inferior under saline conditions (Fig. 3g, h). The field distribution of these sedges at Chongming Dongtan with spatially heterogeneous salinity and disturbance gradients is consistent with these findings (Xu and Zhao 2005), suggesting that salinity and grazing mediate competitive outcomes and dictates community organization in this system.

Co-occurrence of different environmental factors has also been shown to affect the outcome of plant–plant interactions in non-intuitive ways (Baumeister and Callaway 2006; Riginos et al. 2005; Smit et al. 2009). Hence, disturbance may interact with salinity (e.g., Gilbert and Fraser 2013) and affect natural plant communities differently than demonstrated by our common garden experiment. However, we did not examine these effects because of the unacceptable workload with a full factorial design considering salinity and disturbance types simultaneously in our study.

Notably, the complex nature of plant–plant interactions could not be simply interpreted by either the “competitive release” or “competitive change” hypothesis. Most previous studies used a phytometer approach to examine the competitive abilities of various species rather than a full pairwise design because of space and time constraints in most cases (Fraser and Miletti 2008). However, the competition hierarchy may be non-transitive in some cases (Buss and Jackson 1979), and complex interactions among competitors may limit the validity of results from such

Fig. 3 Relative neighbour effect (RNE) (mean \pm SE, $n = 4$) of competing species in different species combinations in **a, c, e, g** salinity and **b, d, f, h** disturbance experiments, indicating the proportion of biomass reduction of each species in the presence of neighbours. **a, b** Sm + St mixture, **c, d** Sm + Cs mixture, **e, f** St + Cs mixture, **g, h** Sm + St + Cs mixture. *Dashed lines* indicate the average RNE level of species composing the mixture assuming no interspecific interactions. *Abbreviations* are identical to those in Fig. 1. *Different upper cases* denote significant differences (Tukey's HSD test) among different treatments, and *different lower cases* denote significant differences among different species in each treatment

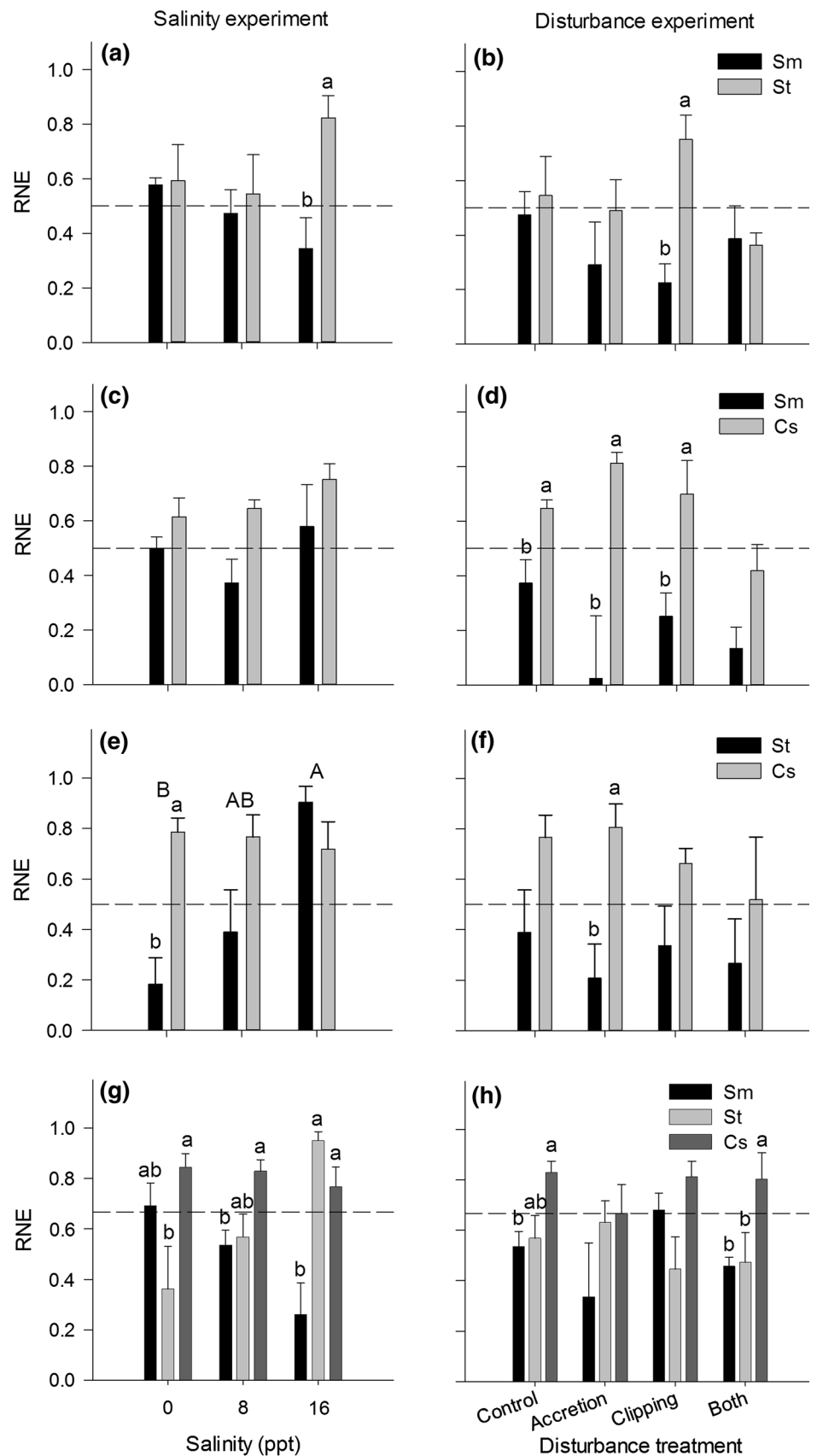
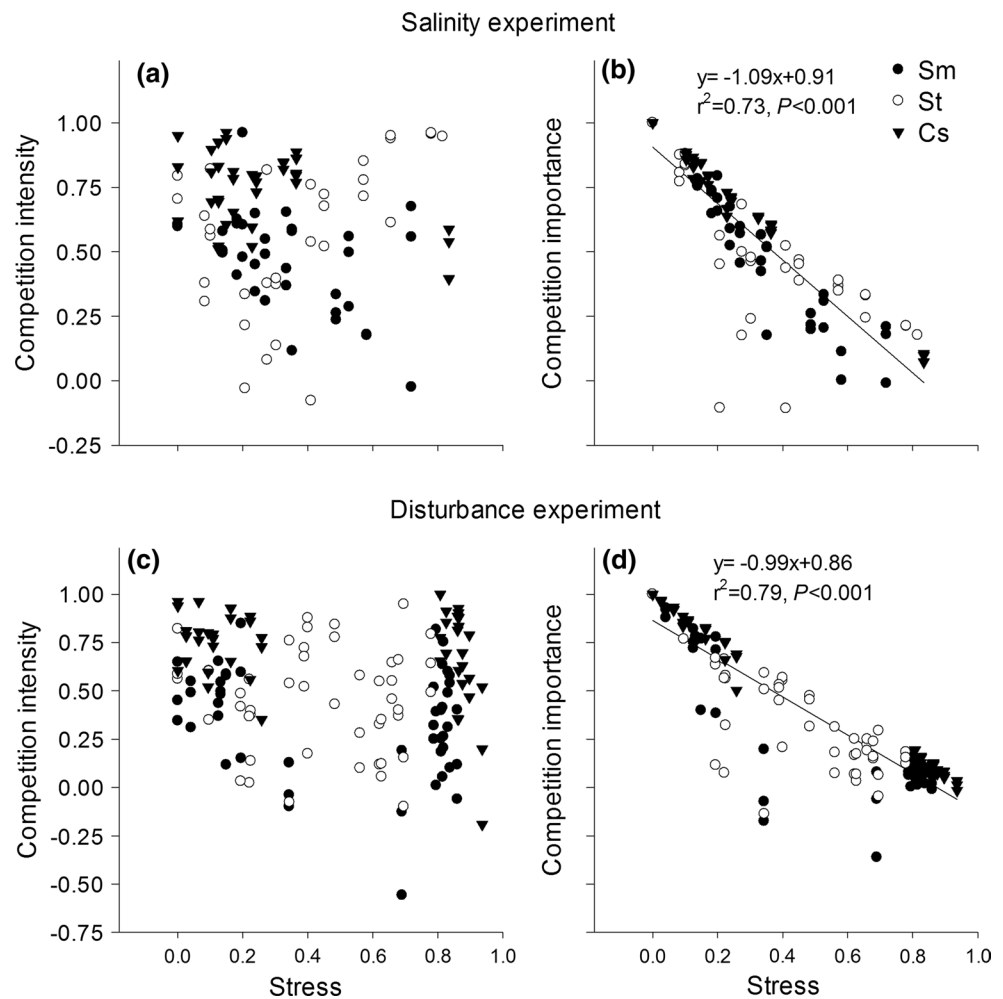


Fig. 4 Variation in **a, c** competition intensity, calculated as the proportion of biomass reduction in the presence of neighbour, and **b, d** competition importance, calculated as the proportion of biomass reduction due to competing neighbours to total biomass reduction due to salinity and disturbance stress and competition. Stress is calculated as the proportion of biomass reduction due to the salinity or disturbance of each species in monoculture. See “Materials and methods” for more details of calculating stress, competition intensity, and competition importance



experiments. In addition, the two aspects of competitive ability, “competitive effect” and “competitive response” (Goldberg and Landa 1991), are not always correlated. Recent studies have revealed that the hierarchy of competitive effect ability of perennial North American prairie species is consistent along environmental gradients, whereas that of competitive response abilities varies among the treatments (Fraser and Miletti 2008; Wang et al. 2010). Indeed, some consistent competition hierarchy might be an artefact of the measured competitive ability traits. Shift of competitive hierarchies along environmental gradients is common (Wang et al. 2006) and can be the main driving force in structuring community composition. This, together with competitive intransitivity (Laird and Schamp 2008), can contribute to the maintenance of diversity in heterogeneous environments (Reynolds 1997; Tilman 1994).

Surprisingly, the competitive abilities of these sedges in mixtures could not be directly predicted by their individual physiological responses to the disturbances. *S. mariqueter* was competitively dominant over *S. triqueter* in the clipping treatment (Fig. 3b), but it was less tolerant of clipping

in monocultures (Fig. 2a). *S. mariqueter* was also more competitive than *C. scabrifolia* in accretion treatments (Fig. 3d), but *C. scabrifolia* was more tolerant of accretion than *S. mariqueter* in monocultures (Fig. 2a). Gross et al. (2010) found similar results that “dominant species were not always the least strained,” highlighting the importance of explicitly distinguishing between responses to physical stresses and competition abilities.

Test of stress-gradient hypothesis

The stress-gradient hypothesis (SGH) predicts that competition is more frequent in benign environments, whereas facilitation plays more important roles with increasing stress. Although He et al. (2013) argued in a recent meta-analysis that competition was consistently reduced with increasing stress across stress types, plant traits, ecosystems, and methodologies, they might have overlooked the complex nature of stress-interaction relationships (SIR), because the authors used a competition intensity index and data at only two extremes along the stress gradient.

Fig. 5 Variation in **a, c** competition intensity and **b, d** competition importance based on total biomass at the community level along stress gradients in salinity and disturbance experiments. See “Materials and methods” for more details of calculating stress, competition intensity, and competition importance at the community level

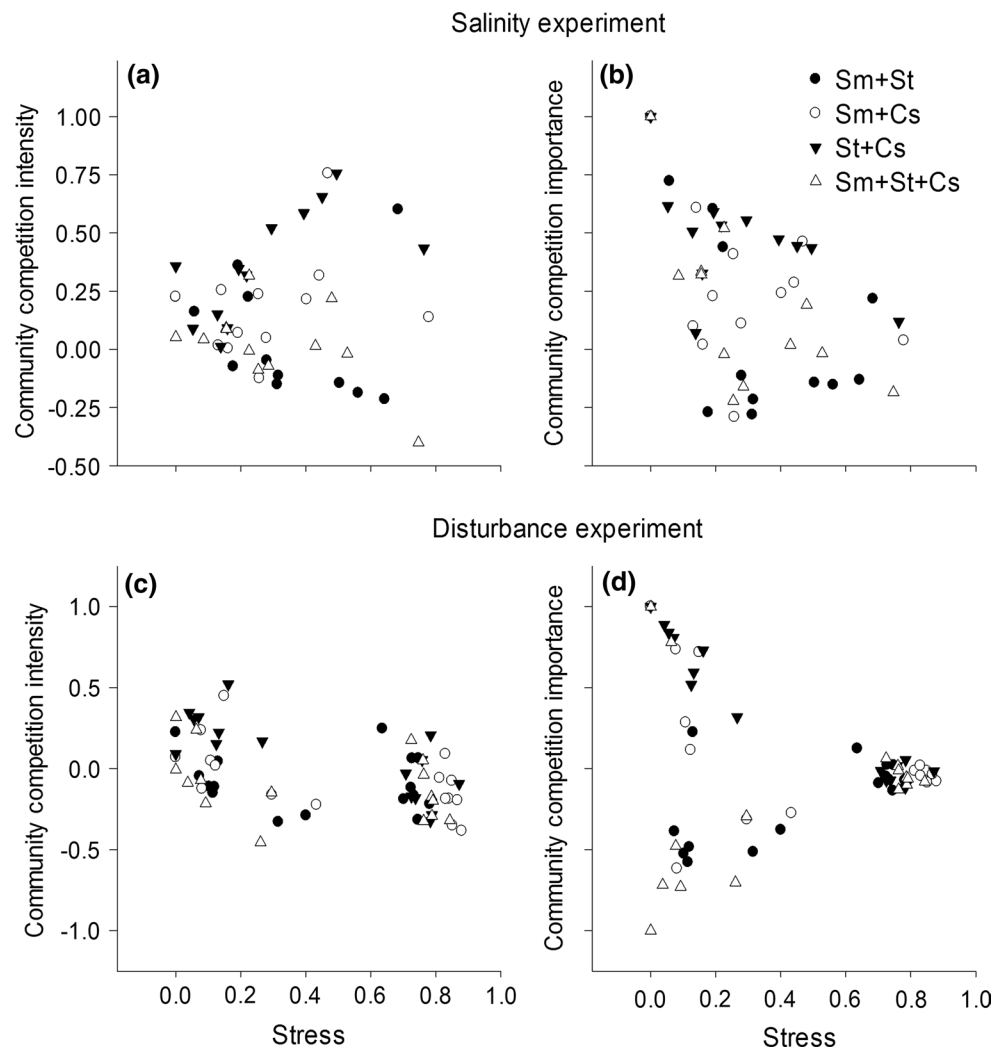


Table 3 Results of two-way ANOVA testing the main and interactive effects of competing species *A* and competing species *B* on the total biomass of three target species in different salinity (0, 8 or 16 ppt) or

disturbance [control, accretion (Acc), clipping (Clip) or both accretion and clipping (Both)] treatments

Source of variation	<i>Scirpus mariqueter</i>			<i>Scirpus triqueter</i>			<i>Carex scabrifolia</i>		
	0 ppt	8 ppt	16 ppt	0 ppt	8 ppt	16 ppt	0 ppt	8 ppt	16 ppt
Salinity experiment									
Species <i>A</i>	***	***	NS	**	*	*	***	***	**
Species <i>B</i>	***	**	NS	NS	NS	*	***	***	**
<i>A</i> × <i>B</i>	**	*	NS	NS	NS	*	***	***	**
Disturbance experiment									
Species <i>A</i>	Acc	Clip	Both	Acc	Clip	Both	Acc	Clip	Both
Species <i>A</i>	*	***	***	**	**	NS	***	***	*
Species <i>B</i>	NS	***	NS	NS	NS	NS	***	***	**
<i>A</i> × <i>B</i>	NS	NS	NS	NS	*	NS	***	**	NS

Eight ppt (unmanipulated) is the shared control treatment for both the salinity and disturbance experiments. Species *A* and species *B* denote *Scirpus triqueter* and *Carex scabrifolia* for *Scirpus mariqueter*, *Scirpus mariqueter* and *Carex scabrifolia* for *Scirpus triqueter*, and *Scirpus mariqueter* and *Scirpus triqueter* for *Carex scabrifolia*, respectively

NS, not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

We found that the role of competition in proportion to abiotic factors (i.e., competition importance) decreased with increasing stress with relatively constant competition intensity, but the results were dependent on the quantification of stress. Because the outcome of biotic interactions depends on the relative positions of target species from their niche optima (Liancourt et al. 2005), in most species combinations, no significant differences of competition intensity among different treatments can be detected because of their different stress tolerance (Table 2; Fig. 3). In the salinity experiment, the most salt sensitive sedge, *S. triqueter*, suffered more from competition in the most stressful environment (Fig. 4a), but the other two species had a slight decline of competition intensity with increasing stress. This result indicates that the response norm is species-specific and depends on tolerance to certain stress type (Maestre and Cortina 2004; Michalet et al. 2006).

The SIR became more explicit when we quantified species-level stress for each species in each pot separately: competition intensity remained relatively constant along the stress gradient, but competition importance decreased proportionally with increasing stress in both salinity and disturbance experiments (Fig. 4). However, these commonly found negative relationships might be partially caused by the definition and calculation of the competition importance index. Indeed, competition importance is always 1 in an optimum environment (when all biomass reduction is caused by competition) and 0 in the harshest environment (when no plants survive, and all biomass reduction is caused by stress), which cannot exceed the diagonal line with a slope of -1 . This can easily lead to the negative relationship.

Most studies have examined the stress-gradient hypothesis at the species level, but this may not necessarily reflect the trend of average interactions within a community (Brooker et al. 2008). When assessing SGH at the community level using spatial co-occurrence patterns of soil lichen communities, Maestre et al. (2009b) found that the variation of relative frequency of positive and negative interactions depended on the type of abiotic stress (water or nutrient) and spatial scales considered. Instead of this approach, we evaluated the commonly used competition intensity and importance indices integrated across all species in the sedge community to produce results more comparable to those of the previous studies. The negative relationship between competition importance and stress disappeared at the community level. Instead, competition importance became less predictable in benign conditions in both the salinity and disturbance experiments (Fig. 5). The reason may be that “because stress can act as a filter, a greater number of species interactions are possible under low stress conditions” (Bowker et al. 2010). The previous research also suggested that even when competition

intensity decreased with increasing stress at the species level, the relative importance of competition did not necessarily change with environmental stress at the community level (La Peyre et al. 2001), indicating that the response of the entire plant community to a changing environment may differ from that of the component species.

Indirect interspecific interactions

The inconsistency of competitive outcomes in three-species and two-species mixtures reveals that indirect interactions are common among these sedges. These complex interactions play important roles in species coexistence (Brooker et al. 2008). In general, competitive effects do not increase proportionally with the addition of an extra competitor, which allows many species to survive in mixed communities.

As demonstrated in a previous study, competitively inferior species may be released from a dominant species by another strong competitor (Levine 1999). In our study, *C. scabrifolia* was inferior to *S. mariqueter* and *S. triqueter* under most conditions, and hence experienced strong indirect facilitation in accretion treatments (75 and 72 % biomass increase in 3-species mixture, respectively), because the two *Scirpus* species competed heavily with one another. However, the occurrence of indirect facilitation could not be predicted by the competitive abilities of target species and the distances from their environmental optima in our study. Although *C. scabrifolia* was less competitive than *S. triqueter*, it facilitated *S. triqueter* in three-species mixtures in clipping treatment (109 % biomass increase in the three-species mixture compared to the results of the *S. mariqueter*–*S. triqueter* mixture) most likely because of its suppression on the dominant *S. mariqueter*. Another reason for this result was that competition with *S. mariqueter* and *C. scabrifolia* reduced the shoot allocation of *S. triqueter*, which might also reduce its loss from aboveground clipping. This result was consistent with those of Gross et al. (2010), who found that even dominant species could be facilitated in some cases.

Because of the limitations of common garden experiments which may underestimate facilitation among interacting species, the results should be treated carefully when extrapolated to field conditions. Besides, the effects of indirect interactions on diversity and how they vary with community productivity and limiting resources need to be tested in further field work.

Conclusions

Our results suggest that salinity, disturbance and interspecific interaction plays important roles in dictating the performance and distribution of sedges in salt marshes in the

Yangtze estuary. In our experiments, the stress-interaction relationship (SIR) depends on the scale and competition indices considered but not the stress types. They also reveal, however, that indirect interactions are common within the sedge assemblage, diffusing competitive dominance and promoting coexistence in this system of closely related plants. These results contribute to our understanding of the mechanisms of segregation and coexistence of similar plant species in heterogeneous habitats.

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