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Sediment Type Affects Competition between a Native and an Exotic Species in Coastal China

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Different types of sediments in salt marsh have different physical and chemical characters. Thus sediment type plays a role in plant competition and growth in salt marsh ecosystems. *Spartina anglica* populations have been increasingly confined to upper elevation gradients of clay, and the niche sediment has changed. Because the niches of *S. anglica* and the native species *Scirpus triqueter* overlap, we conducted a greenhouse experiment to test the hypothesis that plant competition has changed under different types of sediments. Biomass and asexual reproduction were analyzed, and inter- and intraspecific competition was measured by log response ratio for the two species in both monoculture and combination under three sediment types (sand, clay and mixture of sand and clay). For *S. anglica*, biomass, ramet number and rhizome length in combination declined significantly compared with those in monoculture, and the intensity of interspecific competition was significantly higher than that of intraspecific competition under all sediments. For *S. triqueter*, the intensities of intra- and interspecific competition were not significantly different. This indicates that *S. triqueter* exerts an asymmetric competitive advantage over *S. anglica* across all sediments, but especially clay. Thus the sediment type changes competition between *S. anglica* and *S. triqueter*.

Zonal distribution of plant communities is an obvious characteristic of salt marsh ecosystems[1–4]. The plant zonation pattern is typically correlated with a combination of multiple factors, such as the saturated or unsaturated flow in the soil[2] and sediment accretion[5,6]. In fact, plant community spatial distribution and abundance of species are both an indication of the relative physiological tolerance of an individual species to abiotic conditions and competition among species[1,4,7–9].

Plant competition can be affected not only by resource availability[10], but also by environmental factors within a salt marsh[4,11–13], such as sediment[9,14,15], sea level[4,5] and salinity[7,16]. It has been shown that competition between species, especially between exotic and native species, often depend on nutrient supply[9,17,18], flooding[19], elevation[4] and other factors[20]. Elevation, which varies with plant zonation, is highly correlated with the redox potential in salt marsh sediment[21]. Also, interspecific competition has also identified as always disproportionate, resulting in the replacement of one species by another[16]. However, there is typically little information available about competition between exotic and native species in different sediments types.

Salt marsh sediments are mainly influenced by plant activity, elevation and tidal flooding[14,22–25]. Because much of the organic matter in tidal flooding originates from external sources or from benthic microalgae, sediments are usually rich in organic matter and phosphorus[26–28]. Also, sediments of salt marshes are characterized with high concentrations of sulfides and ammonium originating from the high rates of anaerobic reduction[5,23], which can affect plant root respiration[29]. Research has shown that poor water drainage of marsh sediments can be a critical factor limiting plant root growth and causing decay[23]. In addition, moderate levels of sediment slurry enrichment can have beneficial effects on the soil by increasing elevation and soil bulk density[30], which could assist with the restoration of the macro-invertebrate community and its related habitat[31]. Thus supplementary sediments from tides ameliorate environmental factors for plant growth for some species[27], including *Spartina anglica*[32,33].

Spartina anglica C. E. Hubbard (hereafter called *Spartina*) is an exotic species originating in England that was first introduced in China in 1963[34,35]. It developed populations successfully for 30 years on Chinese salt marsh[36] and provided significant economic benefits, including protection for dams and feed for livestock. Yet, in recent years, *Spartina* populations have been in decline on the Chinese coast, and the cover has decreased to less than 50 ha[34,36]. *Spartina* has been pushed to a higher elevation gradient due to the recovery of the salt marsh and the expansion of *Spartina alterniflora*, which is another exotic and invasive species[36]. Also there are differences in physical and chemical characters between sediments at low and high tide zones.

Scirpus triqueter L. (hereafter called *Scirpus*) is species native to China[37]. It grows on low-lying moist sites, where an overlapping niche exists with *Spartina*, and it likely results in competition between the two plant species. Although research has been conducted regarding the ecological interaction between the two plant species with different nitrogen levels[38], little is known of competition between the two plant species under different types of sediment.

In this experiment we used three kinds of sediment, i.e. clay, sand and a mixture of those two sediments, to test competition outcomes between the native species, *Scirpus*, and the exotic species, *Spartina*. As sediment structure is known to vary within saltmarshes, we investigated how such variation might influence competitive outcomes between *Spartina* and *Scirpus*. Here, we quantified competition using various growth measurements when plants were grown with and without their competitor present.

Results

Competition intensity. The more negative the values of the log response ratio (LogRR) were, the greater was competition intensity. Sediment type significantly affected competition intensity, as measured by LogRR, in both species (Table 1). For *Spartina*, both inter- and intraspecific competitions were greater when it grew in clay than when it grew in sand or in the sand-clay mixture (Figure 1A). For *Scirpus*, competition in sand and clay did not differ significantly, but it was greater than that in the sand-clay mixture (Figure 1B).

The competition type significantly affected LogRR of *Spartina*, but not that of *Scirpus* (Table 1B). For *Spartina*, interspecific competition was significantly greater than intraspecific competition (Figure 1A). For *Scirpus*, intraspecific competition did not differ significantly from interspecific competition (Figure 1B).

Growth measures. Sediment type and competition between species affected significantly ($P < 0.05$) or tended to affect ($P < 0.1$) all growth measures of both *Spartina* and *Scirpus* (Table 2). The interaction between sediment type and competition type was statistically significant for all measures of growth for *Spartina* (except rhizome length), however the interaction term was never statistically significant for *Scirpus* (Table 2).

For *Spartina*, all growth measures were significantly larger when the sediment was clay than when it was sand or the mixture of sand and clay; they did not differ significantly between the sand and sand-clay mixture treatments (Table 2A, Figure 2, SNK tests). Overall, growth measures of *Spartina* were the largest in SA2, smallest in SA2 + ST2 and intermediate in SA4 (Table 2A, Figure 2). Such effects were larger when the sediment was clay than when it was sand or the sand-clay mixture (Table 2A, Figure 2).

For *Scirpus*, all growth measures except number of ramets were significantly larger when the sediment was clay than when it was sand or the sand-clay mixture (Table 2B, Figure 3, SNK tests). The number of ramets of *Scirpus* in clay was significantly higher than that in the sand-clay mixture, but did not differ from that in sand (Figure 3B). All growth measures except number of ramets were significantly larger in ST2 than in SA2 + ST2 and ST4, but they did not differ between SA2 + ST2 and ST4 (Table 2B, Figure 3).

Table 1 | Effects of sediment type and competition type (inter- *vs.* intraspecific competition) on interaction intensity (LogRR) of the two species

Variable	Sediment type (S)		Competition type (C)		S × C	
	$F_{2, 29}$	*P*	$F_{1, 29}$	*P*	$F_{2, 29}$	*P*
(A) *Spartina anglica*						
LogRR	8.26	0.001	9.73	0.004	0.67	0.521
(B) *Scirpus triqueter*						
LogRR	5.25	0.011	1.99	0.169	1.12	0.339

Discussion

Our results suggest that sediment type has significant effects on the growth of *Spartina*. Although *Spartina* could adapt to different sediments[1,24,29], it still performs better in more nutrient-rich sediments such as clay[39], likely because the ability of clay to preserve moisture and nutrients is greater than sand. *Scirpus* had good growth performance in all sediments, perhaps because of its low nutrient needs[38].

The sediment type in salt marsh depends on factors such as plant species[27], sea level[40], tide[32], tidal creeks[15] and elevation[21]. Tidal flooding gives salt marsh increased vigor because of the sediment component of the substrate, which increases the soil mineral matter and decreases nutrient deficiency[30,32]. Tidal creeks shape sequential geomorphic features, which receive different types of sediment (coarse or fine) from tides and channels[15]. The clay is a fine-type sediment driven by hydro-geomorphic processes with low bulk density, which yields poor drainage conditions and limits plant root growth and causing decay[15,23]. The clay can also change the redox conditions and sulphide concentrations, which can affect plant growth[39]. For instance, the health of plants shows a sharp decline when the redox potential falls below −50 mv[21], and the sulphide concentration can reach about 320 mg kg^{-1} in the sediment water interface of *Spartina alterniflora*[39]. Simply, abiotic factors including the sediment electric conductivity, sediment oxygenation and salinity affect seed germination and subsequent plant growth[41]. These physical and chemical sediment traits may greatly influence the growth and adaption of plant species[30,41,42], such as *Spartina* and *Scirpus*, thus changing their competition.

The intensities of interspecific and intraspecific competition for both species were significantly different with sediment types. For *Spartina*, interspecific competition from *Scirpus* was larger than intraspecific competition, and competition intensity was greatest in clay (Figure 1A). On the other hand, for *Scirpus*, overall there was no significant difference between interspecific and intraspecific competition, and intraspecific competition tended to be higher than interspecific competition in clay (Figure 1B). These results suggest that, when the two species grow together, *Scirpus* had a stronger competitive effect on *Spartina* in clay.

Competition between plant species can be changed by environmental factors[4,8,11,17,43,44], and our previous study has also shown that nitrogen level could change competition between *Spartina* and *Scirpus*[38]. In this study, we found that competition between *Spartina* and *Scirpus* became stronger when the sediment was clay than when they were sand or a clay-sand mixture. Similarly, sediment type has been found to significantly alter competition between *Puccinellia maritima* and *Spartina*[1] and between *S. alterniflora* and *P. australis*[43]. Changes in competition between *Spartina* and *Scirpus* under different sediment type suggest that in the upper zone salt marsh where *Spartina* is currently distributed and where *Scirpus* is abundant replacement of *Spartina* by *Scirpus* may happen. Therefore, we predict that further declines in *Spartina* are likely to take place in the upper zone salt marsh. Because *S. alterniflora* invasion drives up[45,46], there are some differences in sediment types among low and high zone salt marsh[47–50]. However, for a more accurate prediction, effects of other environmental factors such as tide action and salinity on competition between two species should be taken into consideration. Our findings might facilitate the development of schemes to control the *Spartina* invasion that is occurring in some countries in the world.

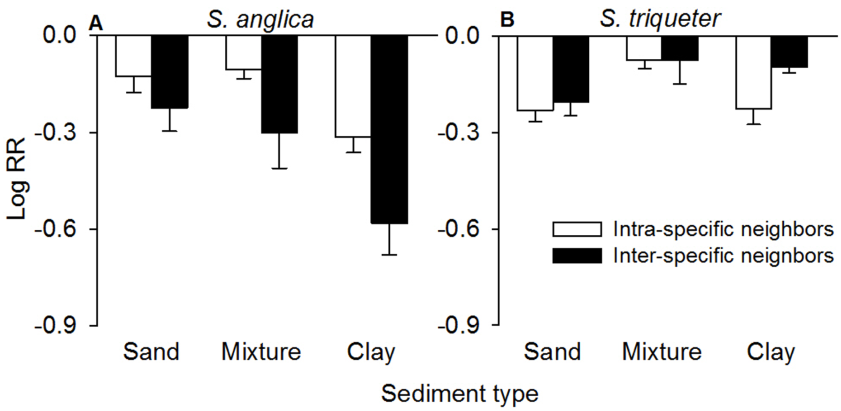

Figure 1 | Interspecific and intraspecific log response ratio (LogRR) of *Spartina anglica* (A) and *Scirpus triqueter* (B). Means ± SE are presented.

Methods

The species. *Spartina* is a rhizomatous perennial grass that is highly invasive in German, Australian, Irish estuarine mudflats, sand flats and salt marshes[35,51,52]. The plant may reach a height of 50–100 cm, and its leaf blades are flat or in-rolled and 5–12 mm wide. *Spartina* is mainly wind pollinated, and produces abundant flowers and viable seeds in Europe[36]. However, on the coastal areas of China, *Spartina* rarely produces viable seeds due to its poor pollen quality and abnormal pollen tube; it spreads mainly by clonal growth[36,53]. The growth form of *Spartina* varies in different habitats[35].

Scirpus is a rhizomatous perennial sedge native to China[37]. The plant may reach a height of about 20–100 cm. Its stem is trigonous, with leaves 1.5–5.5 cm in length and 1.5–2.5 mm in width. *Scirpus* flowers and produces seeds from June to September. It occurs in different habitats in tidal wetlands, ranging from brackish to freshwater along the coast[37].

Experimental design. Plants of both *Spartina* and *Scirpus* were collected from the mash zone of Xinyang Harbor in Yancheng Wetland National Nature Reserve in Jiangsu Province, China. The plant collection was authorized by the management of Yancheng Wetland National Nature Reserve because the field studies did not involve endangered or protected species. Similar-sized plants (ramets), each consisting of a single tiller with attached roots, were selected and used for this experiment. All the ramets of both species were collected within about 500 m, which should reduce the chance of different genotypes. All selected ramets were about 6 cm tall and were cultivated in pots (28 cm in diameter and 20 cm in height) containing a 1 : 1 (v : v) mixture of sand and clay. For the experiment, we used similar-sized ramets with a height of 12.6 ± 0.5 cm (mean ± SE) for *Spartina* and 15.2 ± 0.5 cm for *Scirpus*. The ramets were selected at random from the cultivated stock population to reduce the possible influence of clonal variation and plant history.

The experiment had three types of sediment and five species combinations in a factorial design, resulting in 15 treatments. The three sediment types were (1) sand, (2) clay and (3) a mixture of sand and clay at a volume ratio of 1 : 1. The amounts of available nitrogen and phosphorus were measured before the experiment. The amount of available nitrogen was 43.65 ± 2.49 (mean ± SE, n = 3) mg kg^{-1} in sand, 76.34 ± 1.23 mg kg^{-1} in clay and 52.5 ± 3.59 mg kg^{-1} in the sand-clay mixture. The amount of available phosphorus was 1.42 ± 0.25 mg kg^{-1} in sand, 8.31 ± 0.76 mg kg^{-1} in clay and 5.09 ± 0.18 mg kg^{-1} in the sand-clay mixture. There were five species combination treatments, i.e. each pot was planted with (1) two ramets of *Spartina* (coded as SA2), (2) two ramets of *Scirpus* (ST2), (3) four ramets of *Spartina* (SA4), (4) four ramets of *Scirpus* (ST4), and (5) two ramets of *Spartina* and two ramets of *Scirpus* (SA2 + ST2).

We sampled the salt water in the natural habit of *Spartina* and *Scirpus* to measure the salinity, which was about 1.48 ± 0.02% (mean ± SE, n = 3). To simulate the marsh conditions that these two species commonly experienced, salt water containing 1.5% NaCl was added to the pots, and water was maintained 2 cm above the soil surface level. The salt water was produced by dissolving crude salt into tap water. The crude salt had been directly extracted from seawater in Jiangsu Province. The salinity content in the water in the pots was monitored weekly and adjusted to the initial conditions (1.5% NaCl) when it was below 1.4% or above 1.6%. The experiments lasted 26 weeks (from 20 May to 4 December) and were carried out in a greenhouse at the Pukou campus of Nanjing University. There were six replicates for each treatment.

Table 2 | Effects of sediment type and species competition on the growth of the two species

Variable	Sediment type (S)		Competition (C)		S × C	
	F	P	F	P	F	P
(A) *Spartina anglica*						
Biomass	26.13	<0.001	17.79	<0.001	6.73	<0.001
No. of ramets	8.45	0.001	5.73	0.006	2.83	0.036
Rhizome length	12.61	<0.001	9.75	<0.001	2.07	0.101
(B) *Scirpus triqueter*						
Biomass	49.04	<0.001	11.55	<0.001	2.07	0.100
No. of ramets	4.53	0.016	3.00	0.060	0.43	0.784
Rhizome length	8.93	0.001	6.48	0.003	0.89	0.478

Degrees of freedom for sediment type, species competition and the interaction were (2, 44), (2, 44) and (4, 44) for *Spartina* and (2, 44), (2, 44) and (4, 44) for *Scirpus*.

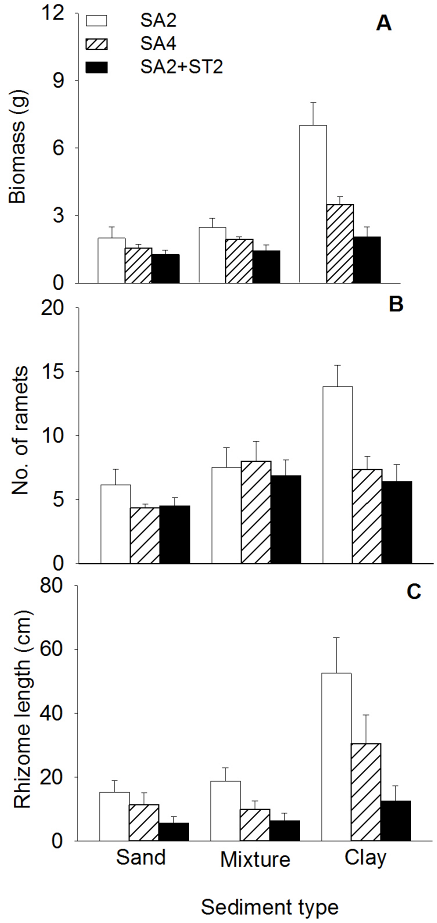

Figure 2 | Biomass and asexual characteristics of *Spartina anglica* in different sediment types and species competition experiments. Means ± SE are presented.

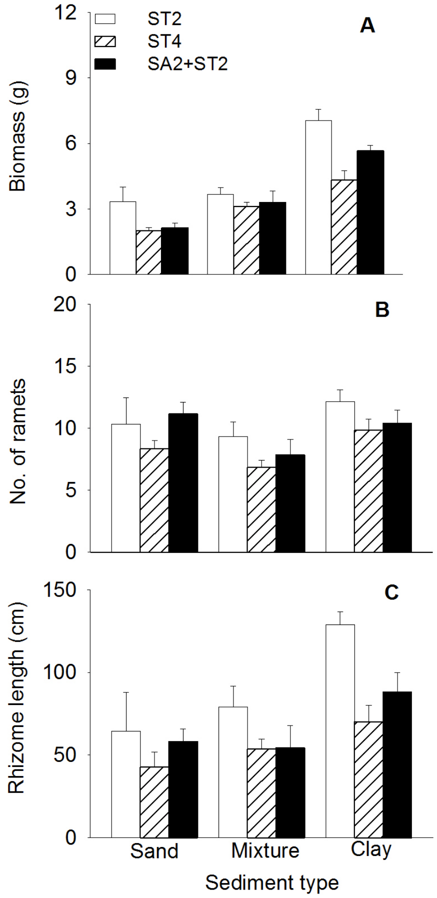

Figure 3 | Biomass and asexual characteristics of *Scirpus triqueter* in different sediment types and species competition experiments. Means ± SE are presented.

Data collection. At harvest, we measured total biomass, the number of ramets and rhizome length of each plant for the two plant species. Biomass is a typical measure of plant growth, the number of ramets a measure of asexual (clonal) reproduction, and rhizome length a measure of clonal expansion (the distance of lateral clonal spreading). We counted the number of ramets and measured the rhizome length of *Spartina* and *Scirpus* separately. Plants of *Spartina* and *Scirpus* were dried at 80°C for 72 h, and weighed.

No plants produced flowers or set seeds during the experiment. One plant of *Spartina* in SA2 + ST2 grown in the sand-clay mixture died during the experiment and this replicate was excluded from harvest and subsequent analysis for the two species.

Data analysis. Before analysis, we normalized the data from each plant. For each replicate, we calculated biomass, number of ramets and rhizome length per initial ramet. For instance, for SA2 the final biomass was divided by two and for SA4 it was divided by four. Thus all these measures were standardized to per initial plant level. The subsequent analyses were based these derived data.

We used two-way ANOVA to test the effects of sediment type and species competition on all growth measures of each species. Sediment type and species competition were treated as two fixed factors. Sediment type had three levels (sand, sand-clay mixture and clay) and species competition had also three levels (no competition, with intraspecific competition and with interspecific competition). For species competition of *Sparina*, SA2, SA4 and SA2 + ST2 were used, treating SA2 as no competition, SA4 as with intraspecific competition and SA2 + ST2 as with interspecific competition. Similarly, for competition of *Scirpus*, ST2, ST4 and SA2 + ST2 were used, treating ST2 as no competition, ST4 as with intraspecific competition and SA2 + ST2 as with interspecific competition. We used the Student-Newman-Keuls (SNK) test to compare the overall means among the three sediment treatments and among the three competition treatments.

To measure the intensity of interspecific competition, we calculated the log response ratio (LogRR) as LogRR = log (B+/B0), where B+ is biomass of plants in the presence of the interspecific neighbors, and B0 is the mean biomass of plants in the absence of neighbors across the six replicates[55,56]. Similarly, we also measured the intensity of intraspecific competition by calculating LogRR, where B+ is biomass of plants in the presence of the intraspecific neighbors, and B0 is the mean biomass of plants in the absence of neighbors across the six replicates[54,55]. A positive value of LogRR indicates facilitation and a negative value indicates competition[54–56].

In this study, the absence of neighbors (i.e. no competition) meant the treatments in which one pot was planted with two ramets (either *Spartina* or *Scirpus*), the presence of intraspecific neighbors (with intraspecific competition) referred to the treatments in which one pot was planted with four ramets of the same species, and the presence of interspecific neighbors (with interspecific competition) referred to the mixture treatment in which each pot was planted with two ramets of both *Spartina* and *Scirpus*. In other words, intraspecific competition encompassed competition mainly from the same species, while interspecific competition encompassed competition mainly from other species. We used two-way ANOVA to test the effects of sediment type (three levels: sand *vs.* sand-clay mixture *vs.* clay) and interaction type (two levels: intraspecific competition *vs.* interspecific competition) on LogRR.

Statistical analyses were conducted with SPSS 18.0 for Windows (SPSS Inc., USA). The effects were considered significant if $P < 0.05$. Measures of biomass were log transformed to improve homogeneity of variance prior to ANOVA.

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Author contributions

H.L.L. and S.Q.A. designed the experiment, H.L.L. and Y.B.Z. executed the experiment. H.L.L. and Y.Y.W. contributed to analyzing the data, and making the figures. H.L.L., G.C.L. and M.X.Z. contributed to writing and editing the manuscript.

Additional information

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