Interactions between mangroves and exotic *Spartina* in an anthropogenically disturbed estuary in southern China

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Abstract. Cordgrass (*Spartina alterniflora*) was introduced to China in 1979 from the United States for reducing coastal erosion. It grows vigorously in China and has spread over much of the Chinese coast, from Leizhou Peninsula to Liaoning, a range of more than 19 degrees of latitude. On the southern coast of China, *S. alterniflora* has invaded mangrove-dominated habitats during the last two decades, but little is known about interactions between native mangroves and invasive *S. alterniflora*.

We studied the distribution and competitive interactions between native mangroves and *S. alterniflora* in the Zhangjiang Estuary at four tidal sites along a salinity gradient: oligohaline upstream, mesohaline, polyhaline, and euhaline downstream. *S. alterniflora* occurred at all four sites, and several mangrove species occurred at all but the downstream euhaline site. *S. alterniflora* has invaded the estuary widely and has spread to the lower tidal margins of mangroves. It has not invaded mangrove areas with a closed canopy but has established in the mangrove zone where the canopy was opened by human disturbance.

Ramets of *S. alterniflora* transplanted into the understory of mangrove stands with closed canopies died within 10 weeks, but 37.5% survived and grew well on open mud flats. *S. alterniflora* had virtually no competitive effect on mangrove seedlings planted at the upstream oligohaline site. However, *S. alterniflora* competitively reduced biomass of mangrove seedlings to 33% over a period of 14 weeks at the mesohaline and polyhaline sites where human disturbance has opened the mangrove canopy. In contrast, *S. alterniflora* marginally facilitated growth and survival of experimental seedlings at the downstream euhaline site.

In China, mangroves occur along the coastline south of Whenzhou, but they have been severely disturbed and removed widely, mainly by mariculture activities. Natural vegetation patterns and our experimental results suggest that, without intervention, *S. alterniflora* could gradually replace these mangroves in mid-salinity regions of Chinese estuaries.

Key words: biological invasion; human disturbance; mangrove–salt marsh ecotone; mangroves; positive and negative interactions; salinity gradient; salt marsh; Spartina alterniflora; *Zhangjiang Estuary, Fujian, China; Zhangjiang Estuary Mangrove National Nature Reserve.*

Introduction

Mangroves create a complex and distinctive habitat with great value for biodiversity and human societies (Feller et al. 2010). Mangroves coexist and interact with salt marsh ecosystems in many places in the world, including the temperate regions of Australia, New Zealand, and the southern United States (West 1977, Mitsch and Gosselink 2000, Saintilan et al. 2009). In recent decades, mangroves have replaced salt marshes on the shorelines of Australia and North America, possibly because climatic changes have enhanced the competitive advantage of mangroves (Saintilan and Williams 1999, McKee et al. 2004, Rogers et al. 2005, Stevens et al. 2006).

The salt marsh grass *Spartina alterniflora*, native to the southern and east coasts of North America, was introduced to China from the United States in 1979 (Xu and Zhuo 1985). It has spread over more than 19 degrees in latitude since, from Leizhou Peninsula in the south to north of Liaoning (An et al. 2007*a*, *b*; Y. H. Zhang, *personal observation*). It has aggressively invaded stands of native mangroves along the southern coasts of China during the last two decades (An et al. 2007*a*, Chen et al. 2009). In order to predict the future state of low-latitude wetlands subjected to climate change and biological invasion, we need a better understanding of how salt marsh plants and mangroves interact.

Despite the enormous literature on mangroves and salt marshes as separate habitats, there have been surprisingly few studies on biological interactions in the mangrove–salt marsh ecotone, especially in the context of human disturbance. Most of the existing studies focus on documenting the spatial and temporal

changes of the mangrove–salt marsh transition zone (Burns and Ogden 1985, Everitt et al. 1996, Saintilan and Williams 1999, Roy et al. 2001). Only a few studies have explored the factors mediating mangrove growth and interactions with salt marsh plants (Patterson et al. 1993, Rogers et al. 2005, McKee et al. 2007, McKee and Rooth 2008, Perry and Mendelssohn 2009). Some of this evidence suggests that *S. alterniflora* can play a significant ecological role as a nurse plant in mangrove primary succession by stabilizing sediments, trapping propagules, and ameliorating stressful soil conditions (Lewis 2005, McKee et al. 2007). In contrast, other studies suggest that *S. alterniflora* competitively inhibits growth of a mangrove, *Avicennia germinans* (Patterson et al. 1993, McKee and Rooth 2008). Similarly, dense stands of saltbush (*Tecticornia* spp.) may inhibit mangrove establishment in salt marshes in Western Port Bay, Australia, by either shading seedlings or collecting sediments and building up the marsh surface to exclude mangroves (Rogers et al. 2005).

McKee and Rooth (2008) suggest that the interaction between *A. germinans* and *S. alterniflora* will depend on the interactive effects of disturbance, climate, atmospheric CO_2, and pore-water nitrogen concentrations. To the best of our knowledge, no studies have experimentally examined the mechanisms mediating the horizontal distribution patterns of mangrove salt–marsh communities along estuarine salinity gradients. In particular, few studies have explored the interactions between exotic *S. alterniflora* and native mangroves in China. Mangroves in China are distributed in areas where the human population density is among the highest in the world (Chen et al. 2009), and the population boom and rapid economic development have already reduced mangrove areas by 55% (from 50 000 ha in the 1950s to 23 000 ha in 2001). Furthermore, the high intensity of anthropogenic disturbance, exacerbated by global change, has resulted in the large-scale degradation of the remaining mangrove ecosystems in China, and has decreased their resilience to disturbance (Lin 1999, Wang and Wang 2007, Chen et al. 2009). For example, our study site, Zhangjiang Estuary, Fujian, China, is under strict protection as a national nature reserve and a designated "Wetland of International Importance" under the Ramsar Convention (Ramsar 1971). Nevertheless, local residents routinely disturb and fragment mature mangrove habitats in this estuary, construct shrimp ponds in or adjacent to mangrove wetlands, and clear mangrove and other seedlings (e.g., *S. alterniflora*) every year on the intertidal mudflat for mariculture activities (Lin 1999, 2001, Wang and Wang 2007).

The exotic invasive *S. alterniflora* arrived in the Zhangjiang Estuary in the late 1990s through intentional planting and natural seed dispersal, and is now a very common intertidal species whose spread could greatly affect native mangrove species and related ecosystems. Although the effects of *S. alterniflora* invasion into salt marshes in China (An et al. 2007*a*, Li et al. 2009) and

other regions of the world (Daehler and Strong 1996, Ayres et al. 2004, Grosholz et al. 2009) have been well documented, interactions between mangroves and invasive *S. alterniflora* in low-latitude wetlands have not been well studied, nor is it known whether *S. alterniflora* will have similar effects at all salinity regions of estuaries.

We investigated the distribution and interactions of mangrove species and *S. alterniflora* along a salinity gradient in Zhangjiang Estuary, Fujian Province, China. We asked three specific questions: (1) What are the current distribution patterns of *S. alterniflora* and mangroves along the salinity gradient within the estuary? (2) How does *Spartina* influence the establishment of mangroves over the salinity gradient in this estuary? (3) How does human disturbance of mangroves affect the ability of *S. alterniflora* to invade mangrove habitats? Based on the answers to these questions, we discuss the prognosis for mangrove forests in southern China given the invasion by *S. alterniflora*.

METHODS

Description of study sites along salinity gradient

The study was conducted in the estuary of the Zhangjiang River, which runs into Dongshan Bay, Fujian (23°53′–23°57′ N, 117°23′–117°30′ E), in the monsoonal subtropics of Southeast China (Fig. 1). The river experiences a semidiurnal tide, with an annual mean tidal variation of 2.32 m. The temperature and salinity of surface seawater in Dongshan Bay, which is the site furthest downstream with the highest salinity, ranged between 14.9 and 28.6°C, and 29 and 32 PSU, respectively. Annual average rainfall at the Yunxiao weather station between 2000 and 2009 was 1871.2 mm, most of which occurs from April to September. Annual mean air temperature between 2000 and 2009 was 22.2°C, with the highest monthly mean temperature (29.5°C) in August, and the lowest (13.3°C) in January. Salinity was measured weekly throughout the growing season by squeezing porewater from $2 \times 2 \times 2$ cm blocks of substrate onto a hand-held NaCl refractometer (Master-S/Mill-E; Atago, Tokyo, Japan).

Four sites were chosen along a salinity gradient in the Zhangjiang Estuary and all were under tidal influence (Fig. 1; Appendix: Figures. A1–A4). Using the terminology of Cowardin et al. (1979) and Madden et al. (2009), the sites examined in this study were designated as "oligohaline," "mesohaline," "polyhaline," and "euhaline."

The oligohaline site was located in the upmost tidal reach of the river, 13.3 km upriver from the river mouth. About one-third of the upper intertidal consists of stands of the grass *Alternanthera philoxeroides*, with the remaining area covered by stands of the rush *Cyperus malaccensis*, mangroves, and *Spartina alterniflora*. This site was chosen since it was the upstream range limit of *S. alterniflora* and the mangroves *Kandelia obovata*, and *Aegiceras corniculatum*. At the time of this study these species extended upstream for only about another 100 m
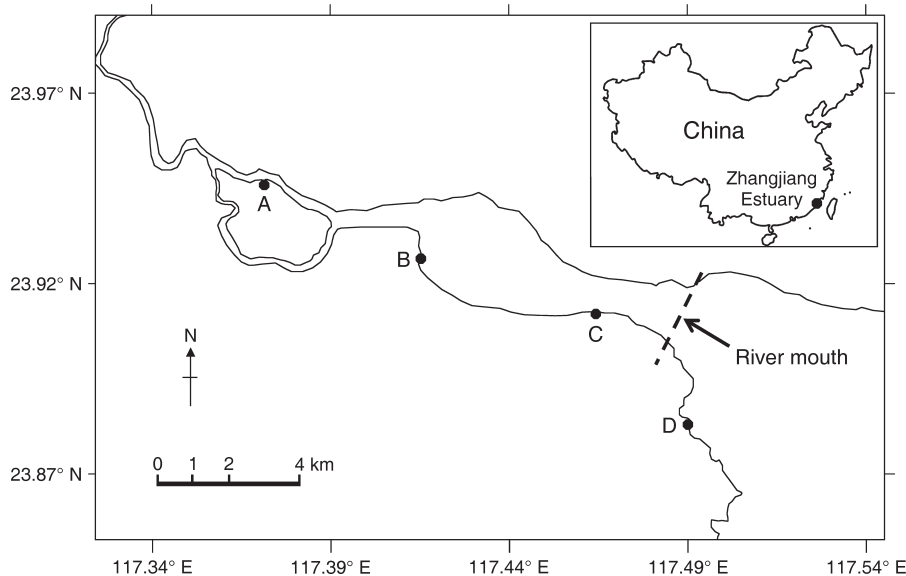
FIG. 1. Study sites in the Zhangjiang Estuary, Fujian, China. (A) Oligohaline upstream; (B) mesohaline; (C) polyhaline; (D) euhaline downstream. All sites have tidal influence.

from this site. Soil porewater salinity at this site varied from 0 to 6 PSU during our study period. The mesohaline site was 8.6 km upriver from the river mouth. Human disturbance (clearing of vegetation for aquaculture) maintains large areas of bare mud at this site. Vegetation at this site was dominated by the exotic grass *S. alterniflora* and the native mangroves *K. obovata*, *A. corniculatum*, and *Avicennia marina*. Soil porewater salinity at this site varied from 13 to 18 PSU. The polyhaline site was 3.2 km upriver from the river mouth, was dominated by *S. alterniflora*, and was close to the downstream limit of *K. obovata*, *A. corniculatum*, and *A. marina*. The elevational gradient at this site was steep, leading to less aquaculture and less bare mud. Soil porewater salinity at this site varied from 21 to 26 PSU. The euhaline site was 2.3 km outside the river mouth in Dongshan Bay. This site was near the lower limit of *S. alterniflora* distribution in the estuary. Aquaculture efforts and human disturbance at this site are moderate, and the shallow slope of the intertidal produces expansive mudflats. Seedlings of *K. obovata* were occasionally present at this site, but all died within 1 or 2 years after establishment. Soil porewater salinity at this site varied from 29 to 32 PSU.

Vegetation patterns

To characterize the vegetation patterns in the estuary, we sampled the intertidal vegetation at each site during the growing season (March to October) of 2007. To sample mangroves, we ran three transect lines perpendicular to the main river channel at 20-m intervals at each site. All of the plots were located in areas containing mangroves (i.e., they describe the mangrove community rather than the wetland community as a whole). Along each 60–80 m transect, three 10×10 m

plots (about 10–20 m apart) in a group were located at three locations about 20 m apart, for a total of 9 plots/ site. Within each plot, we measured the height, basal stem diameter (30 cm above the soil surface), and canopy diameter (the lengths of the major and the minor axes of the canopy) of all mangroves.

To sample *S. alterniflora*, we located four blocks at each site at 20–30 m intervals within the middle intertidal zone. These blocks were located within mangrove woodlands with open canopies at the oligohaline site, on the margins of mangrove forests at the mesohaline and polyhaline sites, and mudflat at the euhaline site (no mangroves nearby). Blocks were located at the edges of *S. alterniflora* patches, each block with the size of $\sim 8 \times 2$ m. All 16 blocks were located within 35 cm vertical elevation of each other and had similar durations of tidal flooding (within 30–35 min per tidal period). The growth of *S. alterniflora* over a year in Zhangjiang Estuary can be conceptualized as occurring in 3 stages: early growth (March to April), middle growth (May to June), and reproductive growth (July to August). On 11–14 March 2007 we established three parallel 1×1 m quadrats at 2-m intervals at the lower edge of each block. During the period between March and August of 2007 we sampled one of the three quadrats during each of the growth stages, with four replicates at each site at each growth stage. We counted all the stems in the quadrat, and harvested 10 random shoots in the quadrat to measure shoot height, stem diameter, leaf number, leaf area, and dry mass of each shoot. Aboveground biomass (g/m^2) was estimated by multiplying shoot density ($shoot/m^2$) by individual dry mass ($g/shoot$).

Mangrove transplant experiment

To examine the role of physical stress and interspecific competition in generating the observed distribution of mangroves along the estuarine salinity gradient, we conducted a transplant experiment with propagules of *K. obovata*, the most common mangrove species in this estuary (Zhang et al. 2006). On 27 March 2008, 320 mature propagules of *K. obovata* were collected from trees at the mesohaline site, weighed (fresh mass, 12.1 ± 1.3 g [mean ± SE]), and measured (length, 20.1 ± 1.2 cm [mean ± SE]). On the following day the propagules were planted into 1 × 1 m plots within the four blocks of *S. alterniflora* at each of the four sites (transplant plots were 2–3 m away from the *Spartina* sampling quadrats within each block). Propagules were planted at equivalent tidal elevations in two conditions: (1) with neighboring *S. alterniflora* vegetation (at the fringe of the *S. alterniflora* patch) and (2) without neighboring *S. alterniflora* (in bare mudflat 2–3 m away), for a total of 320 propagules ($n = 10$ propagules × 2 treatments × 4 blocks × 4 sites). This approach relied on natural variation in *S. alterniflora* density rather than a manipulation of *S. alterniflora* density; however, *S. alterniflora* is rapidly expanding at this site, and we believe that whether or not a given location was occupied by *S. alterniflora* at the time of this experiment was largely due to chance colonization events. We counted the number of surviving *K. obovata* seedlings in each quadrat at two-week intervals for the first six weeks, and then at four-week intervals until 6 July 2008. This survey period (>3 months) was long enough to evaluate whether mangrove seedlings could establish successfully in new habitats (Tomlinson 1986, Lin 1999, Wang and Wang 2007). We then harvested, dried, and weighed the aboveground biomass of surviving *K. obovata* seedlings, and weighed the shoot and leaf, discarding the viviparous hypocotyls. To compare interactions between *S. alterniflora* and *K. obovata* seedlings among the four sites, we calculated the relative interaction intensity index, RII (Armas et al. 2004) for each block as follows (where "nbrs" stands for "neighbors"):

$$RII = \frac{(Biomass_{nbrs} - Biomass_{no\ nbrs})}{(Biomass_{nbrs} + Biomass_{no\ nbrs})}.$$

Spartina transplant experiment

To determine whether *S. alterniflora* can invade intact mangrove forest, we conducted a transplant experiment with *S. alterniflora* at the mesohaline site. We focused on this site because it was where mangroves grew the best and human disturbance (marine aquaculture, mangrove cutting of trees to clear areas for ponds, and so forth) was most common. The other three sites had less space available for conducting experiments and less human disturbance. On 13 March 2008, 300 young ramets of *S. alterniflora* were collected at the mesohaline site. After a recovery period of 2 weeks in a greenhouse, 150 healthy ramets were selected (height, 28.7 ± 4.1 cm [mean ± SE])

and planted into 1 × 1 m plots (27 March 2008) under three growing conditions: (1) continuous stands of mangrove, (2) the edge of mangrove stands, and (3) the unvegetated mudflat ($n = 10$ ramets × 5 plots × 3 treatments). Plots for the three treatments were located within a narrow range of elevation (14.0 cm); however, on average the plots represent a gradient of decreasing relative elevation (mangrove, 11.9 ± 2.3 cm; edge, 5.3 ± 1.2 cm; unvegetated, 0.7 ± 0.8 cm, with the elevation of the lowest plot set to 0) as well as decreasing mangrove cover. In the absence of human disturbance, however, all of these plots would historically have been occupied by mangroves. We did not have permission to do a mangrove-removal experiment within the reserve, and so we relied on this pre-existing, human-generated gradient in mangrove density within the natural elevational range of mangroves. *S. alterniflora* currently occurs at this site well above and well below the elevation of these plots, and so we do not think that the modest difference in elevation between plots had much of an effect on the outcome of the experiments. We counted the number of surviving *S. alterniflora* ramets in each quadrat at two-week intervals for the first six weeks, and then at four-week intervals. For each ramet, we measured the height of the original shoot, the number of leaves on the original shoot, the total area of all leaves on the original shoot, and the number of daughter ramets that had grown from each original shoot. After 10 weeks we harvested all plants in the plots, and measured the dry aboveground biomass of the plants that had grown from the planted ramets (no *S. alterniflora* resprouted from the rhizomes left in the soil). At this time, we observed that all *S. alterniflora* ramets transplanted into continuous stands of mangroves had died.

Statistical analysis

Biomass data from the field survey and transplant experiments were $\log_{10}(x + 1)$-transformed when necessary to increase homogeneity of variance and normality before testing with ANOVA. Data were analyzed with R statistical software (R Development Core Team 2010). Growth of adult mangrove trees, natural *S. alterniflora* in three growing stages, and the relative interaction intensity (RII) of mangrove seedlings and *Spartina* neighbors were compared among four sites (salinity zones), using one-way ANOVA and Tukey's HSD comparisons. Survival rates and aboveground biomass of transplanted *K. obovata* were analyzed using two-way ANOVA, with sites and neighbors as fixed factors. To evaluate the effect of neighbors at each site, with and without-neighbor treatments were compared using *t* tests. Survival rates of transplanted *S. alterniflora* were compared across time using repeated-measures ANOVA. Growth of transplanted *S. alterniflora* ramets at the end of the experiment was compared among three growing conditions (mangrove understory, forest edge, and unvegetated mudflat) using one-way ANOVA and Tukey's HSD comparisons. For all analyses of biomass

in transplant experiments, transplanted plants that died were included with biomass set to 0.

RESULTS

Vegetation patterns

The oligohaline site was dominated at lower elevations by the rush *Cyperus malaccensis*, with a low density of *Kandelia obovata* and *Aegiceras corniculatum* at intermediate elevations (Appendix B). Dense patches of *Spartina alterniflora* occupied the mudflats lower on the tidal gradient, occurred within mangrove woodlands in areas with open canopies, and interrupted otherwise monospecific stands of *C. malaccensis*. At the end of the growing season (August 2007), the *S. alterniflora* canopy at this site was taller (Appendix C) than the canopy of *C. malaccensis* (1.2~1.5 m), *A. corniculatum* adult shrubs (Appendix B), and a large proportion of the *K. obovata* adult trees (Appendix B).

At the mesohaline site, the mangrove species occurred as dense monospecific stands (Appendix B), with a mostly closed canopy (79–90% closed). Humans practicing mariculture activities clear *S. alterniflora* from most of the broad mudflats in this area. As a result, monotypic stands of *S. alterniflora* occurred only close to the margins of the mangrove forests. Patches of *S. alterniflora* also occurred within the mangrove forest where the canopy was relatively open. Occasional *K. obovata* and *A. corniculatum* saplings occurred within the *S. alterniflora* patches. Furthermore, small patches of *C. malaccensis* also occurred on the margins of, or in gaps within, the mangrove communities.

At the polyhaline site, *Avicennia marina* was the dominant mangrove, although *K. obovata* and *A. corniculatum* were present at low densities (Appendix B). Monospecific stands of *S. alterniflora* covered nearly all of the low-elevation and most of the mid-elevation area.

At the euhaline site, mangroves were absent (Appendix B) but *S. alterniflora* was present at low density (Appendix C). Seedlings of *K. obovata* were occasionally present at this site, but always died within 1 or 2 years after establishment.

The morphology of the dominant mangrove species varied along the estuarine salinity gradient (Appendix B). *K. obovata* and *A. corniculatum* were the tallest at the mesohaline site, but their basal stem diameter and canopy diameter were the greatest at the oligohaline site. *A. marina* was taller at the polyhaline site, but individual plants (growing at low densities) had larger canopies at the mesohaline site than at the polyhaline site.

The aboveground parts of *S. alterniflora* grew from spring to early winter and senesced during late winter. During the growing season, the height, leaf number, and aboveground biomass of individual shoots increased, but the stem diameter and leaf area decreased at the reproductive stage relative to the vegetative growth stage at the three downstream sites (Appendix C). The clonal populations at all four sites expanded rapidly from the early growth stage to middle stage, and then slowed down from the vegetation stage to reproductive stage. From the upstream to downstream sites, the total distance that clones expanded were 2.0, 2.7, 2.6, and 1.0 m over the growing season of 2008, respectively. Although stem density decreased with time due to self-thinning of shoots, aboveground biomass was the greatest at the reproductive stage.

The growth of individual shoots (height, stem diameter, leaf area, and aboveground biomass) of *S. alterniflora* generally decreased across sites with increasing salinity (Appendix C). Stem density and quadrat-level biomass, however, were higher at the mesohaline and polyhaline sites than the other two sites at the end of the growing season. The euhaline site had very high stem densities of *S. alterniflora* in the early growth stage, but ended the season with the poorest individual and population growth.
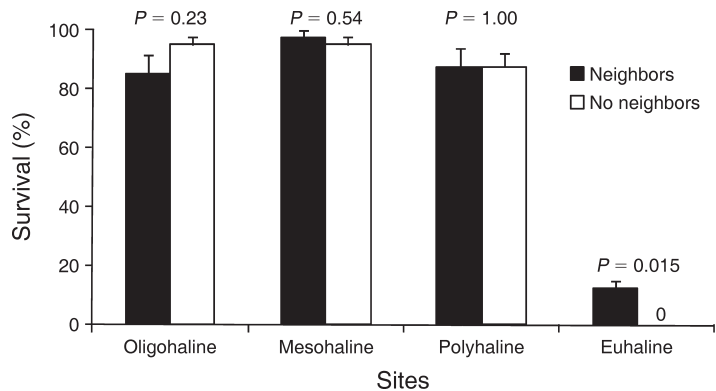
Mangrove-transplant experiment

After 14 weeks the transplanted *K. obovata* propagules survived well (85.0% to 97.5%) at the oligohaline, mesohaline, and polyhaline sites, irrespective of whether neighboring *S. alterniflora* vegetation was present or not. In contrast, survival was low at the euhaline site, where only 12.5% of the transplants survived in the plots with neighbors, and 0.0% of the transplants survived in the plots without neighbors (Fig. 2). The ANOVA site × neighbor interaction term for *K. obovata* transplant survival was marginally significant ($F_{7,24} = 2.56$, $P = 0.078$) (Appendix D: Table D1) for the euhaline site, but a direct comparison of the with- and without-neighbor treatments with a t test indicated that transplants survived significantly better with neighbors present ($t = 5.00$, $P = 0.015$). Similar t tests for the other three sites did not find any differences in survival between plots with and without neighbors (Fig. 2).

Transplanted *K. obovata* seedlings grew best at the mesohaline site when neighbors were absent (Fig. 3A). The effect of neighbors on plant growth varied with salinity (significant ANOVA site × neighbor interaction term for biomass; $F_{7,24} = 71.69$, $P < 0.001$) (Appendix D: Table D2). Transplanted mangrove seedlings were strongly suppressed by neighboring *S. alterniflora* at the mesohaline and polyhaline sites (Fig. 3A) but were not strongly affected by *S. alterniflora* at the oligohaline site. As a result, the RII of *Spartina* on *Kandelia* was positive at the euhaline site, negative at the mesohaline and polyhaline sites, and close to 0 at the oligohaline site (Fig. 3B).

Spartina-transplant experiment

Survival of transplanted *S. alterniflora* shoots decreased with time within each treatment. A significant time-by-habitat interaction (repeated-measures ANOVA, $F_{3,56} = 6.79$, $P = 0.002$) indicated that survival rates varied among habitats (Fig. 4). After two weeks 15.0% of the *S. alterniflora* transplants died in the unvegetated mudflat, while only 2.2% and 4.0% of the transplants died in the mangrove understory and forest edge, respectively. From

FIG. 2. Survival after 14 weeks (July 2008) of *Kandelia obovata* seedlings transplanted along the estuary salinity gradient with and without neighboring *Spartina alterniflora* vegetation. Data are means + SE; $n = 4$ replicates per treatment. To evaluate the effect of neighbors at each site, treatments with and without neighbors were compared using t tests.

week 4 to week 10 the highest mortality occurred in the understory, with all the transplanted ramets in this habitat dying by the end of the experiment. In contrast, only 76.0% and 62.5% of the transplants died in the forest edge and unvegetated mudflat habitats, respectively.

In addition to surviving best in the unvegetated mudflat, surviving transplanted *S. alterniflora* ramets also grew better in this habitat than in the forest-edge habitat, with higher leaf number, leaf area, aboveground biomass, and newborn daughter ramet number (Appendix E). Shoot height did not differ between the forest edge and unvegetated mudflat habitats.

DISCUSSION

Our results demonstrate that environmental variability and human disturbance influences the distribution patterns and competitive interactions between mangroves and introduced *Spartina alterniflora*. In Zhangjiang Estuary (Fujian, China) colonizing *S. alterniflora* established on mudflats and riverbanks where soils were bare, and where it could grow intermingled with individual mangroves, yet it performed poorly when planted in the mangrove understory. In turn, mangrove propagules were unaffected by *S. alterniflora* at the oligohaline site, competitively suppressed in growth at the mesohaline and polyhaline sites, and were facilitated at the euhaline site.

Mangrove distribution and the encroachment of S. alterniflora *along the estuary*

Our field surveys showed that mangroves and *S. alterniflora* broadly co-occurred along the salinity gradient in Zhangjiang Estuary. From the oligohaline site upstream to the mesohaline and polyhaline sites in the middle of the estuary, *S. alterniflora* occurred on the margins of mangrove forests, within mangrove woodlands
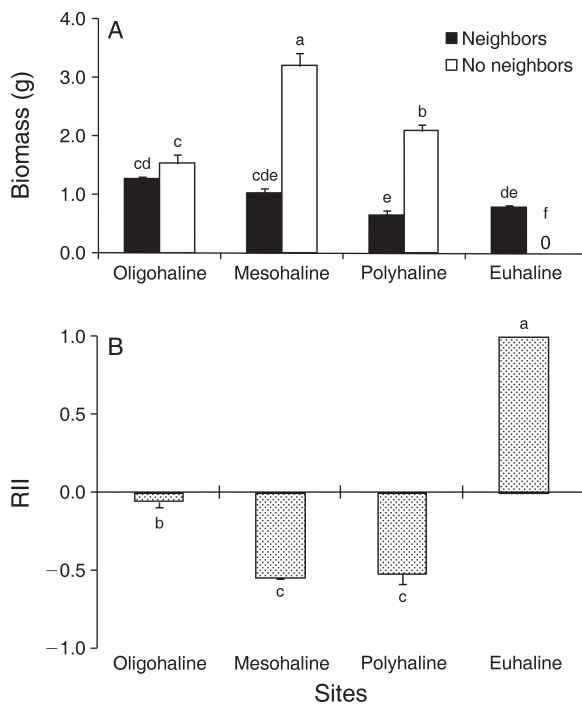

FIG. 3. (A) Aboveground biomass of transplanted *Kandelia obovata* seedlings along the estuary salinity gradient with and without neighboring *Spartina alterniflora* vegetation. Data are means + SE. Identical lowercase letters above the bars indicate means that do not differ from each other at $P < 0.001$ (Tukey's HSD). (B) Relative interaction intensity (RII) of neighboring *Spartina alterniflora* vegetation on *Kandelia obovata* seedlings transplanted along the estuary salinity gradient. Data are means + SE for four replicates per treatment. Identical lowercase letters above the bars indicate means that do not differ from each other at $P < 0.001$ (Tukey's HSD).
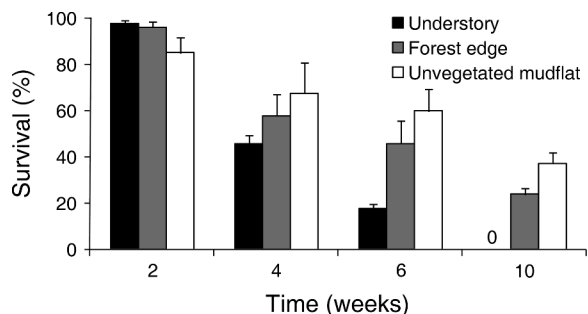

FIG. 4. Survival of *Spartina alterniflora* ramets, from March to June 2008, transplanted into the mangrove understory, forest edge, and unvegetated mudflat habitats at the mesohaline site. Data are means + SE for five replicates per treatment.

with more open canopies, and in disturbed areas. Similar distribution patterns can be found in coexisting mangrove and salt marsh communities in Mexico, Central America, and Florida (West 1977). Both mangroves and *S. alterniflora* were most productive at the mesohaline site in Zhangjiang Estuary, perhaps because of the combination of relatively low stress and higher nutrients provided by the turbidity maximum in brackish waters (Loomis and Craft 2010, Wieski et al. 2010).

The exotic *S. alterniflora* had a wider distribution range along the estuarine salinity gradient than did the native mangroves. *S. alterniflora* occurred in the saline coastal areas outside the river mouth, but mangroves could not survive in this habitat. Similar distribution patterns of salt marsh and mangrove vegetation occur in Australia (Roy et al. 2001) and New Zealand (Burns and Ogden 1985). The downstream distribution of estuarine vegetation is limited by tolerance to physiological stressors, with salinity as the major influence (Tomlinson 1986, Adam 1990). *S. alterniflora* is known to be quite tolerant of salt stress, both in its original habitat of North America (Hester et al. 2001, Vasquez et al. 2006) and in the introduced habitat of China (An et al. 2007a, Li et al. 2009). In contrast, *Kandelia obovata* does not tolerate high salinities (Tomlinson 1986, Wang and Wang 2007). Moreover, wave disturbance is a factor at the more exposed euhaline site. In the control plots at the euhaline site, transplanted *K. obovata* propagules always washed away and presumably died within 4 weeks (Y. H. Zhang, *unpublished data*). Although the presence of *S. alterniflora* facilitated propagule survival in this habitat after 14 weeks, presumably by buffering wave action (Bruno 2000), growth of the propagules was nevertheless suppressed by the high salinity, and naturally occurring propagules always died within one or two years after establishment.

S. alterniflora has invaded a wide range of coastal wetlands in China (An et al. 2007a, Li et al. 2009) and other regions of the world (Daehler and Strong 1996, Ayres et al. 2004, Grosholz et al. 2009). Our study indicates that *S. alterniflora* is highly invasive in Zhangjiang Estuary (23°53′ N), even though the site is near the low-latitude end of the range of introduced *S. alterniflora* in China (20°53′ N). *S. alterniflora* has invaded a large fraction of the unvegetated mudflats, from the oligohaline upstream to the polyhaline reaches of Zhangjiang Estuary. It continues to spread by seed dispersal and rapid clonal enlargement (Y. H. Zhang, *personal observation*; Appendix C). In the oligohaline habitats, *S. alterniflora* has occupied most microhabitats originally suitable for the mangrove *K. obovata*, which performs poorly and does not develop a continuous canopy under oligohaline conditions (Wang and Wang 2007). Although *S. alterniflora* has to date been excluded by compact mangrove stands in mesohaline and polyhaline habitats, consistent with the view that mangrove forests are difficult ecosystems to invade (Lugo 1998), patches of *S. alterniflora* have encroached

into the mangrove forest where the canopy was opened by human activities (e.g., cutting trees to clear areas for mariculture). Our results suggest that *S. alterniflora* will limit mangrove recolonization of these areas within the forest by strongly suppressing growth of mangrove seedlings. There appears to be no reason that *S. alterniflora* will not continue to spread and encroach upon mangroves, aided by human disturbance of mangrove stands, with resulting negative impacts on native marsh and mangrove vegetation.

Physical and biotic influences on mangrove recruitment

Adult *K. obovata* mangroves were largest at the mesohaline site. Similarly, the transplanted *K. obovata* seedlings grew best at the mesohaline site in the absence of competition from *S. alterniflora*. While *S. alterniflora* facilitated survival and growth of mangrove propagules over 14 weeks in 2007 in the euhaline area, by stabilizing them and so improving early establishment, this invasive grass strongly suppressed mangrove seedlings in the mesohaline and polyhaline habitats. *S. alterniflora* had a similar effect on mangroves in the oligohaline habitat as in other sites (Fig. 3A), yet mangroves without neighbors had lower biomass than at the meso- and polyhaline sites (Fig. 3A), suggesting another limitation to mangrove growth at this site. These results illustrate that, in addition to physical factors, the success of mangrove seedlings also depends on the biotic interaction with exotic *S. alterniflora* species, and that the outcome of such mangrove–*Spartina* interaction varies dramatically along the estuarine salinity gradient.

In general, it is theorized that the relative importance of positive and negative interactions between plant species will change along environmental gradients (Callaway and Pennings 2000, Callaway et al. 2002, Callaway 2007). In particular, as was found in this study, positive interactions are suggested to prevail in high-stress conditions, and negative interactions in low-stress conditions (Bertness and Leonard 1997, Ungar 1998, Crain et al. 2004, Krauss et al. 2008). However, the negative interactions at the oligohaline site, where abiotic stress would presumably be the lowest, were not as obvious as those at the mesohaline and polyhaline sites. This may have been because the *S. alterniflora* densities were not as high at this site as at the other sites, and so the negative effect of *S. alterniflora* may have been less. Alternatively, as mentioned above, the low salinities at the oligohaline site represent suboptimal environmental condition for growth of *K. obvata*, and it may be that the surviving seedlings were simply unable to take advantage of the lack of competition because they were stressed by abiotic conditions.

Previous studies have suggested that salt marsh and mangrove plants may interact by competing for nutrients, light, and space. Dense stands of saltbush (*Tecticornia* spp.) have been suggested to inhibit mangrove establishment in salt marshes in Western Port Bay, Australia by either shading seedlings or collecting

sediments and building up the marsh surface to exclude mangroves (Rogers et al. 2005). Mangroves and *S. alterniflora* have also been reported to compete in marshes in Louisiana (Patterson et al. 1993, McKee and Rooth 2008). Our results are consistent with previous studies suggesting that marsh plants such as *S. alterniflora* can facilitate mangrove succession by stabilizing sediments and trapping propagules (Lewis 2005), but also provide evidence that human disturbance favors *S. alterniflora* at the sites where mangroves are most productive in the absence of this invading grass. McKee et al. (2007) found that in some extreme environments, establishment, survival, and growth of mangrove seedlings were facilitated by herbaceous species, *Sesuvium portulacastrum* and *Distichlis spicata*. Both species promoted mangrove success by trapping propagules and ameliorating soil conditions. Taken together, these results suggest that the effect of marsh plants on mangroves is likely to change from facilitation to competition as mangroves mature from seedlings to small shrubs, and from competition to facilitation with increasing abiotic stress. However, our study illustrates that disturbance can reverse the advantage held by mangroves even at the most productive intertidal sites. More generally, the fact that interactions between salt marsh plants and mangroves are context-dependent weakens generalizations based upon any single factor.

Disturbance increases susceptibility of mangrove forests to invasion by S. alterniflora

Our vegetation survey found few *S. alterniflora* plants inside intact mangrove forests. Our transplant experiment confirmed that *S. alterniflora* did poorly when planted in intact mangrove forest. In general, mangrove forests often contain no understory plants (Janzen 1985, Corlett 1986, Lugo 1986, 1998), suggesting that they can exclude marsh vegetation under normal conditions. Our results provide experimental evidence that intact mangrove forests in Zhangjiang Estuary can exclude highly invasive grasses such as *S. alterniflora*. In contrast, mangrove woodlands with more open canopies, or in disturbed areas, showed less resistance to encroachment by *S. alterniflora*.

An emergent property of mangrove systems is stability, which was defined as the persistence of this distinctive and important group of plants relatively unchanged through time (Feller et al. 2010). Any disturbance that alters the interaction of physical, chemical, and biological components chronically or on a large scale can cause the system to change. For example, mangroves have invaded and converted salt marshes on shorelines of Australia and North America (Saintilan and Williams 1999, Stevens et al. 2006). Kangas and Lugo (1990) suggested that the boundary between tropical mangroves and temperate salt marshes can be attributed to a combination of frost stress on mangroves and, in the absence of stress, a competitive advantage by mangrove vegetation over salt marsh grasses. In sharp contrast, human activity has accelerated

the spread of exotic *S. alterniflora* in southern China, and humans still chronically disturb and fragment mangrove habitats on a large scale. As a result, human activity increases the vulnerability of mangrove communities to biological invasion, promotes the colonization of *S. alterniflora*, and consequently reduces the success of mangrove seedlings and the regeneration of mangrove forests. At the same time, villagers conducting aquaculture activity also cut stands of *Spartina* that threaten their operations; however, villagers only cut the *Spartina* in certain areas, and usually not in areas adjacent to mangrove stands. As a result, *Spartina* continues to spread in the estuary, and especially spreads rapidly when in patches intermingled with mangrove stands. The likely outcome will be a slow transition from mangroves to *S. alterniflora* salt marsh as existing mangrove trees die and are not replaced by new recruits due to competitive exclusion by the invasive.

Our study comes with three caveats. First, the experiments were short in duration and conducted in only one year. It is possible that longer experiments would give different results, or that experiments conducted in different years would have different outcomes. However, we believe that the vegetation dynamics in this system are largely determined during initial establishment of vegetation, and that the duration of the experiments was sufficient to document these dynamics. Moreover, the year in which we conducted the experiment was not unusual in terms of climate or river discharge, and so we believe that we would get similar results during most "normal" years, although different results might obtain during years with extreme climate conditions. Second, the mangrove-transplant experiment potentially confounded *S. alterniflora* density with unknown abiotic conditions; however, as we explain in the *Methods*, we think that this concern is unfounded. Third, the *Spartina*-transplant experiment plot confounded mangrove density with plot elevation; however, as we explain in the *Methods*, we believe that the effect of elevation was modest and did not affect the outcome of the experiment.

Conclusions and implications

Our study in Zhangjiang Estuary suggests that mangrove habitats are vulnerable to being replaced by *S. alterniflora* marsh, especially in the areas where human disturbance creates gaps in the mangrove canopy. We suggest that studies on mangrove disturbance regimes and their impact on seedling regeneration are key to understanding the long-term future of native mangrove forests in China, where mangrove forests experience intense anthropogenic disturbance.

In China more than 2000 ha of mangrove forests have been restored (Chen et al. 2009), but the invasion of *S. alterniflora* into coastal areas where mangrove ecosystems occur may threatens the long-term success of these restoration efforts. In addition, future mangrove restoration efforts may have to be designed to achieve rapid

canopy closure in order to exclude *S. alterniflora* and improve the long-term success of the projects. Even when mangrove forests have been established, it may be necessary to actively reduce human-disturbance regimes in order to ensure sufficient regeneration of mangroves to maintain a healthy forest and exclude *S. alterniflora* invasion.

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SUPPLEMENTAL MATERIAL

Appendix A

Four figures documenting vegetation cover at each of the study sites in the Zhangjiang Estuary (*Ecological Archives* E093-052-A1).

Appendix B

A table presenting density and vegetation structure of three dominant mangrove species along a salinity gradient in Zhangjiang Estuary in 2007 (*Ecological Archives* E093-052-A2).

Appendix C

A table presenting density and vegetative growth, and lateral expansion of *Spartina alterniflora* stands along a salinity gradient in Zhangjiang Estuary in 2008 (*Ecological Archives* E093-052-A3).

Appendix D

ANOVA tables for survival and aboveground biomass of *Kandelia obovata* seedlings transplanted along the estuary salinity gradient with and without neighboring *Spartina alterniflora* vegetation (*Ecological Archives* E093-052-A4).

Appendix E

A table summarizing growth of *Spartina alterniflora* ramets 10 weeks after being transplanted into mangrove understory, forest edge, and unvegetated mudflat habitats in 2008 (*Ecological Archives* E093-052-A5).