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Phenotypic responses of *Spartina anglica* to duration of tidal immersion

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Abstract Although *Spartina anglica* C.E. Hubbard continues to be invasive in many countries, this species has experienced a drastic decline in coastal China over the last decade. We hypothesize that changes in the duration of tidal immersion were responsible for this decline because the elevation of the *S. anglica*-dominated area in coastal China has increased greatly over the last decade. We examined the effects of the duration of simulated tidal immersion and plant material provenance on growth, asexual reproduction, biomass accumulation, and allocation (percent of above-ground biomass to total biomass) of *S. anglica* in a greenhouse experiment. The provenance of *S. anglica* did not significantly affect any traits measured except for height, stalk diameter, and leaf area. However, all traits were affected by the duration of immersion. Plants grown under 6 h of immersion were taller and had more leaves, more roots, and larger leaf area than those under 2, 4, 8, and 10 h of immersion. Asexual traits and biomass of the plants grown under 6 h of immersion were significantly larger than those under other immersion durations. The results suggested that *S. anglica* benefits from tidal immersion

and decreasing duration of tidal immersion may have resulted in the decline of the *S. anglica* populations in coastal China. Thus, controlling the duration of tidal immersion may be an effective way of controlling invasiveness of this species elsewhere in the world.

Keywords Growth response · *Spartina anglica* · Tidal immersion duration · Simulated tide

Introduction

Environmental factors, especially those related to hydrology and salinity, play a major role in controlling the distribution and abundance of coastal salt marsh plants (Brewer and Grace 1990; Silvestri et al. 2005). Coastal salt marshes are regularly flooded with salt water (Touchette 2006) and the duration of tidal immersion (waterlogging) can markedly influence the survival and growth of the salt marsh plants. As a result, salt marsh vegetation is usually divisible into distinct zones or communities, corresponding to different levels of the marsh surface (Hacker and Bertness 1999; Reynolds et al. 2000; Touchette 2006).

Waterlogging affects plant growth and distribution because it can drastically affect gas exchange in both plants and soil. Waterlogged soils become anoxic and deleterious to plants (Drew and Lynch 1980; Drew 1983) because oxygen deficiency in roots induces anaerobic respiration (Jackson and Armstrong 1999). Only flood-tolerant species can avoid oxygen deficiency and thus grow frequently in waterlogged soils (Laan et al. 1990; Jackson and Armstrong 1999; Voesenek et al. 2006).

Wetland plants usually possess some mechanisms to adapt to waterlogging condition (Visser et al. 2000; Voesenek et al. 2006; Colmer et al. 2009; Wang et al. 2009). When submerged, for instance, *Tecticornia pergranulata* markedly reduced shoot growth to conserve carbohydrates and its tissue sugars declined with time (Colmer et al. 2009). When grown in waterlogged soils, some species reduced biomass allocation to shoots (Visser et al. 2000), and some formed larger, thinner leaves

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(Van Hinsberg and Van Tienderen 1997; Voesenek et al. 2006). For the amphibious plant *Alternanthera philoxeroides*, submerged plant parts could increase their growth by obtaining support from the interconnected plant parts growing in non-waterlogged soils (Wang et al. 2009) through physiological integration (Yu et al. 2009).

Spartina anglica C. E. Hubbard is a hybrid grass between the North American species *S. alterniflora* Loisel and the European species *S. maritima* (Curtis) Fernald (Thompson 1991). This grass inhabits the intertidal area and can flourish under saline and anoxic estuarine conditions that are often uninhabitable by other plants (Thompson 1991; Hacker et al. 2001). Because of its vigorous clonal growth, *S. anglica* was used for cattle fodder, habitat reclamation, dike stabilization, and sea wall protection (Chung 1985; Gray et al. 1991; Chung 1993; Chung et al. 2004). However, it invaded many estuarine habitats and altered the topography by sediment accretion, thereby causing deleterious ecological and economic problems in many countries including England, New Zealand, Australia, the Netherlands, and the USA (Daehler and Strong 1996; Bridgewater and Cresswell 1999; Sanchez et al. 2001; Ayres et al. 2004).

S. anglica was first introduced in the coastal area of Yancheng in Jiangsu Province, China in 1963 (Chung 1985); its population expanded quickly and covered 36,000 ha by 1985 (Chung 1993; An et al. 2007). In the last decade, however, the population of this species in coastal China declined dramatically and the coverage decreased to < 50 ha. Also, the vigor of the remaining populations decreased greatly as shown by, for instance, the shortened culms and reduced seed production. Now *S. anglica* in China is only distributed in the coastal area of Jiangsu and Zhejiang Province (An et al. 2007; Zhi et al. 2007). So far the mechanisms underlying the decline of the species in China remain unclear and elucidating such mechanisms may provide useful information on controlling and managing its invasion in other countries (Roberts and Pullin 2007).

Studies have been conducted to examine the mechanisms for the decline and dieback of marsh vegetation. Webb et al. (1995) suggested that vegetation dieback in a Louisiana salt marsh dominated by *S. alterniflora* was possibly caused by excessive submergence, while McKee et al. (2004) argued that drought stress could also be responsible, as it might be correlated with lower levels of bacterial acetylene reduction activity (de Souza and Yoch 1997). Another force, a combination of drought and increased salinity, was also found to adversely affect *S. alterniflora* in a controlled experiment (Brown et al. 2006). Chemical spills, soil fermentative products (i.e., sulfide) and herbivory were recently ruled out as potential causes of the dieback (Erneberg 1999). Furthermore, Cornick et al. (2005) found that fungal pathogens did not differ between stable and declining beds of *S. anglica*. In general, these studies indicate that environmental factors may be implicated in dieback.

We sampled *S. anglica* plants from two geographic locales in China (i.e., southern and northern distribu-

tional zones) and grew them under five conditions differing in the duration of simulated tidal immersion. We hypothesized that waterlogging duration and the plant material provenance (from the south vs. from north) would affect the growth of *S. anglica* and therefore be responsible for its decline in coastal China.

Materials and methods

Plant materials

S. anglica is a stout, rhizomatous, perennial grass that spreads mainly by clonal growth (Thompson 1991). The plant can be 50–100 cm tall, and leaf blades are flat. However, the growth form of *S. anglica* varies with habitat conditions (Gray et al. 1991; Thompson 1991). In recent years, the maximum height of the plant has decreased to not more than 30 cm in coastal China (An et al. 2007). The flowers occur in numerous, erect, contracted panicles consisting of closely overlapped spikelets (Partridge 1987). The flowers produce viable seeds through both self- and cross-pollination (Partridge 1987). However, seed production can vary greatly over time (Chung 1993). In the Chinese population, little viable seed has occurred since the mid 1990s (An et al. 2007), which is probably due to poor pollen quality and abnormal pollen tube development (Li et al. 2008).

In April 2006, *S. anglica* plants with the similar vigor were collected from sites of the south (120°36.3'E, 33°36.3'N, 2.2 m a.s.l.) and the north marsh zones (120°34.6'E, 33°37.8'N, 1.8 m a.s.l.) of Xinyang Harbor in Jiangsu Province, China. Light quantity reached 1,850 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in August, 2006. The plants were transplanted to big pots (80 cm in length, 76 cm in width, and 50 cm in height) in the greenhouse to prevent desiccation. Individual ramets, each consisting of a single tiller with attached roots, were separated. Similar-sized ramets (6.0 ± 0.5 cm high, $n = 3$) were then selected and planted in pots (26 cm in diameter and 21 cm in height), containing 15-cm-deep sand-loam mixture at a volume ratio of 1:1. Six days before transplanting, the plants in the big pots were transferred outside the greenhouse to allow acclimatization.

Experimental design

The experiment was conducted in the greenhouse at Nanjing University. The light intensity in the greenhouse was 34.1% that of outdoor ($n = 3$) at 10:00 am on September 6, 2006. A set of artificial-tidal trays simulating the tide dynamics were constructed. A 5×2 factorial experiment was established, with five levels of waterlogging duration (2, 4, 6, 8, and 10 h per day) and two plant sources (south and north marsh zone). There were five tidal trays for each waterlogging treatment,

and four pots in each tray, two containing plants from the south and two containing plants from the north.

The trays were set on a bench, and tidal inundation was simulated by submersible pumps operated by auto-electronic time clocks. The auto-electronic time clocks were set based on the tide table for Xinyang Harbor in Jiangsu Province. For example, from June 14 to July 1, the times of tides were, respectively, AM 4:55, 5:46, 6:33, 00:30, 00:50, 00:53, 00:55, 1:09; 1:36; 2:14; 2:59, 3:58, 4:45, and 5:57. Water flowed into the trays, and thus the simulated tides could rise to approximately 30 mm above the tips of the plants. At the end of each tidal submersion, the valves were switched off automatically by the auto-electronic time clocks, and the water flowed back to the holding tank through the return pipes. The tidal regimes were adjustable using the time clocks (Adams and Bate 1995; Boorman et al. 2001).

The holding tanks were filled with artificial sea water produced by dissolving crude salt into fresh water. The salinity content was 1.58%, similar to that of sea water. The salinity was checked regularly and maintained by regularly adding fresh water to compensate for evaporation. During the experiment, any algal content in the water was regularly checked and any excess was removed to ensure easy water flow.

Data collection and analysis

The experiment began on June 14, 2006, and ended on December 15, 2006. Of the two plants (pots) from the same provenance in each tray, we randomly selected one for measurements and harvest on December 16, 2006. It could be statistically analyzed. For growth, we measured height (cm), stalk diameter (mm), number of leaves, leaf area (cm^2), leaf thickness (mm) and number of roots of each plant. Number of ramets, buds, rhizomes and rhizome nodes, total rhizome length, and rhizome biomass (g) were used as measures of asexual reproduction. Plant height and stalk diameter were those of the highest ramet. For each plant we measured thickness of six leaves using a digital caliper and leaf area using a Li-3000 Laser Area Meter with an electronic conveyor. After measuring characteristics of the intact plants, each plant was divided into leaves, culms, rhizomes and roots and their dry mass was measured after drying to constant weight at 80°C. Biomass allocation was measured by percent of above-ground, below-ground, rhizomes, and roots biomass to total biomass, respectively.

Statistical analyses were conducted with SPSS 13.0 for Windows (SPSS Inc., USA). We examined the effects of plant provenance and waterlogging duration on all plant traits using two-way ANOVA, where both provenance and waterlogging duration were treated as fixed factors. When needed, data were log-transformed to increase normality and homogeneity of variance.

Results

Effects of plant provenance and waterlogging duration on growth

Both plant provenance and waterlogging duration significantly affected height, stalk diameter, and leaf area of *S. anglica* ($p < 0.05$, Table 1). Leaf thickness was significantly influenced by waterlogging duration but not plant source. However, number of leaves and roots were significantly affected by waterlogging duration and the interaction of the two factors (Table 1).

Stalk diameter, leaf area, and number of roots of *S. anglica* grown under 6 h of waterlogging were significantly greater than those grown under the other four waterlogging durations (Fig. 1b, d, e) and these traits did not differ significantly among the other four waterlogging duration treatments (i.e., 2, 4, 8, and 10 h of waterlogging) when the plants were from the north site. In contrast, when the plants were from the south site, the number of roots was smaller when the plants were grown under 8 h of waterlogging than when grown under 2, 4, or 10 h of waterlogging (Fig. 1e).

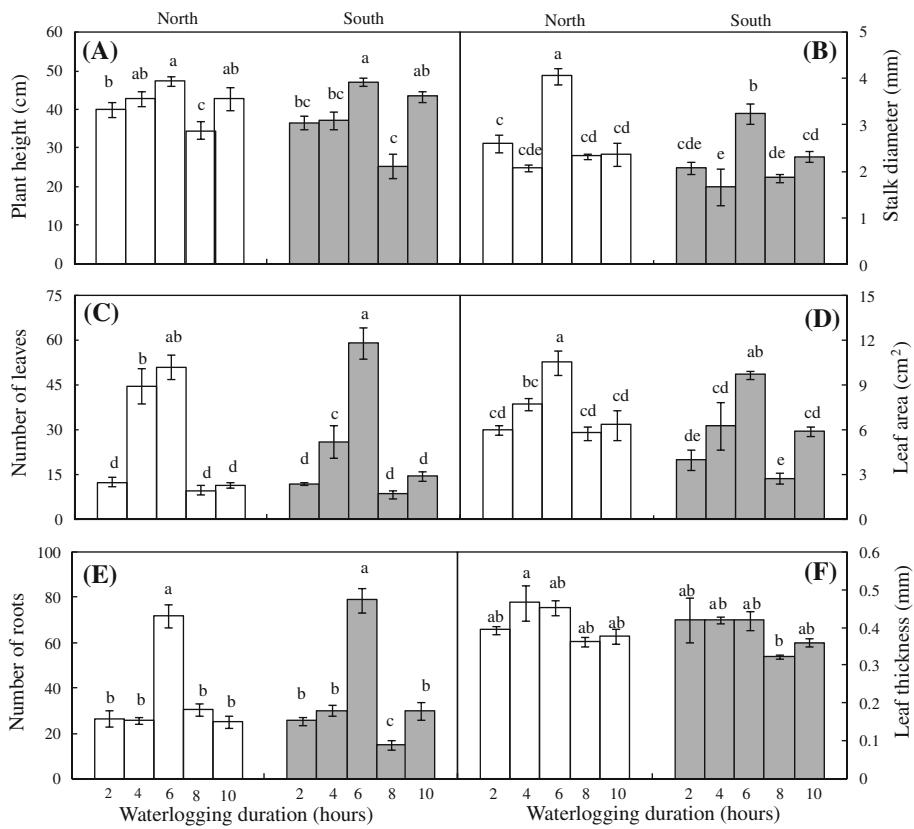
Height of the plants from the northern site did not differ significantly grown under 4-, 6-, or 10-h waterlogging treatments, but the 8-h treatment had significantly lower plant heights than all other treatments. Similar trends for plant height were found for the plants from the southern site (Fig. 1a). When the plants were from the northern site, the number of leaves at 2-, 8-, and 10-h

Table 1 Effects of plant provenance, waterlogging duration, and their interaction on the measured traits of *Spartina anglica*

	Plant provenance (<i>P</i>)	Waterlogging duration (<i>W</i>)	<i>P</i> × <i>W</i>
Height (cm)	7.1*	18.0**	1.8
Stalk diameter (mm)	14.1**	25.9**	0.9
Number of leaves	0.8	61.4**	8.7**
Leaf area (cm^2)	10.7*	18.9**	0.9
Leaf thickness (mm)	1.5	4.858**	0.5
Number of roots	0.0	84.9**	3.8*
Number of ramets	0.4	9.5**	5.4**
Number of buds	0.1	40.5**	2.1
Number of rhizomes	2.3	41.5**	2.2
Number of rhizome nodes	1.3	31.8**	1.9
Total length of rhizome (cm)	0.1	23.8**	1.6
Rhizome biomass (g)	0.9	43.5**	0.6
Above-ground biomass (g)	0.7	80.2**	3.4
Below-ground biomass (g)	0.5	46.9**	0.9
Roots biomass (g)	0.2	39.4**	0.9
Total biomass (g)	0.6	65.4**	1.8
Above-ground biomass allocation	1.3	2.9**	2.1
Roots biomass allocation	1.6	5.9**	0.7
Rhizomes biomass allocation	0.0	7.3**	2.0
Below-ground biomass allocation	1.3	2.9*	2.1
<i>df</i>	1,40	4,40	4,40

F values, significance levels (*0.05 > *p* > 0.01; ***p* < 0.01) and degree of freedom (*df*) of two-way ANOVA are given

Fig. 1 Growth measures of the *Spartina anglica* plants from the two provenances under the five waterlogging duration treatments. Bars sharing the same letters are not different at $p = 0.05$ (by Duncan tests)



waterlogging treatments was significantly fewer than that at 4- and 6-h waterlogging treatments. When the plants came from the south, the number of leaves in the 6-h waterlogging treatment was significantly greater than that at any of the other four waterlogging treatments (Fig. 1c).

Effects of plant provenance and waterlogging duration on asexual performance

Both waterlogging duration and the interaction of the two factors significantly affected number of ramets ($p < 0.05$, Table 1). Number of rhizomes, number of rhizome nodes, number of buds, total rhizome length, and rhizome biomass were all significantly affected by waterlogging duration, but not by plant provenance (Table 1).

The number of rhizome nodes, total rhizome length, and rhizome biomass for plants from the northern provenance were significantly greater in the 6-h treatment than those in the 4-h waterlogging treatment, which were significantly greater than those at the other treatments (Fig. 2d-f). The number of ramets and rhizomes subjected to 6-h waterlogging were significantly greater than those of the other treatments, with the exception of the 4-h treatment (Fig. 2a, c). The number of buds in the 6-h waterlogging treatment was greater than that under any of the other treatments (Fig. 2b). For the plants from the southern provenance, number of ramets, buds, rhizomes, nodes, total length of rhizomes, and rhizome biomass of plants grown under 6-h water-

logging treatment were all significantly greater than those of the other treatments (Fig. 2).

Effects of plant provenance and waterlogging duration on biomass accumulation

Above-ground, below-ground, root, and total biomass were all significantly affected by waterlogging duration, but not by plant provenance or the interaction of the two factors (Table 1).

Above-ground, below-ground, root, and total biomass of the *S. anglica* plants were the greatest grown under 6 h of waterlogging for both provenances. When the plants were from the north, the biomass parameters were significantly higher in the 4-h treatment than in the 2-, 8-, and 10-h treatments, but biomass parameters for plants from the southern provenance were not significantly different among all treatments except the 6-h treatment (Fig. 3).

Effects of plant provenance and waterlogging duration on biomass allocation

Above-ground, below-ground, root, and total biomass allocation were significantly affected by duration of waterlogging, but not plant by provenance or the interaction between the two factors (Table 1).

With northern provenance plant material, biomass allocation to roots was significantly lower at 4- and 6-h

Fig. 2 Asexual characteristics of the *Spartina anglica* plants from the two provenances under the five waterlogging duration treatments. Bars sharing the same letters are not different at $p = 0.05$ (by Duncan tests)

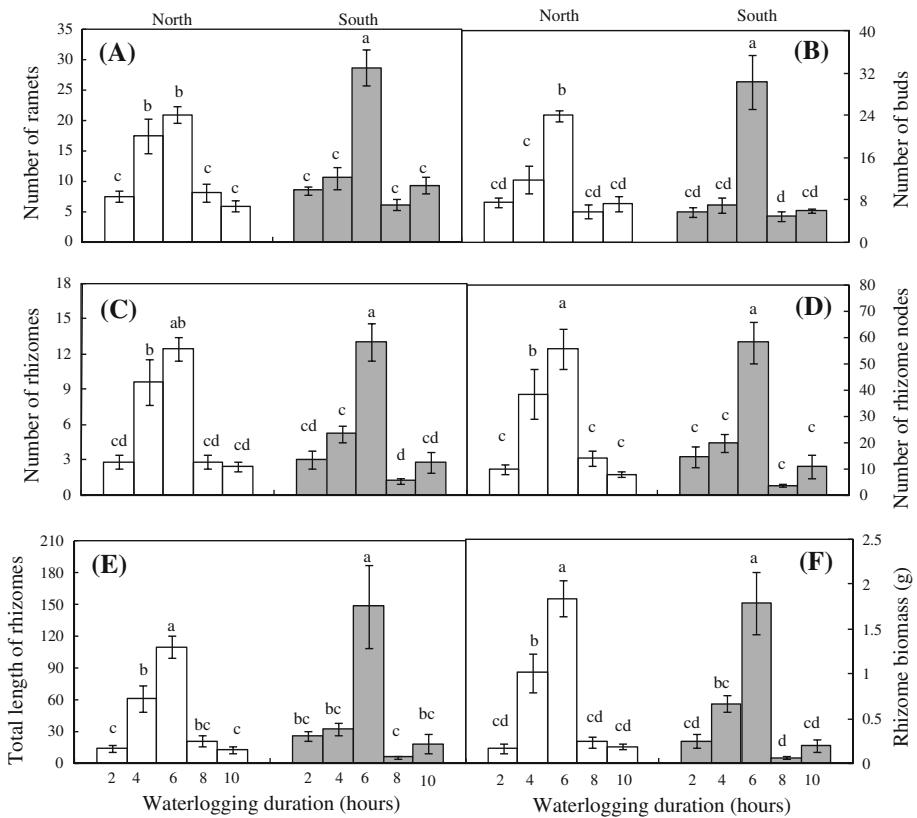
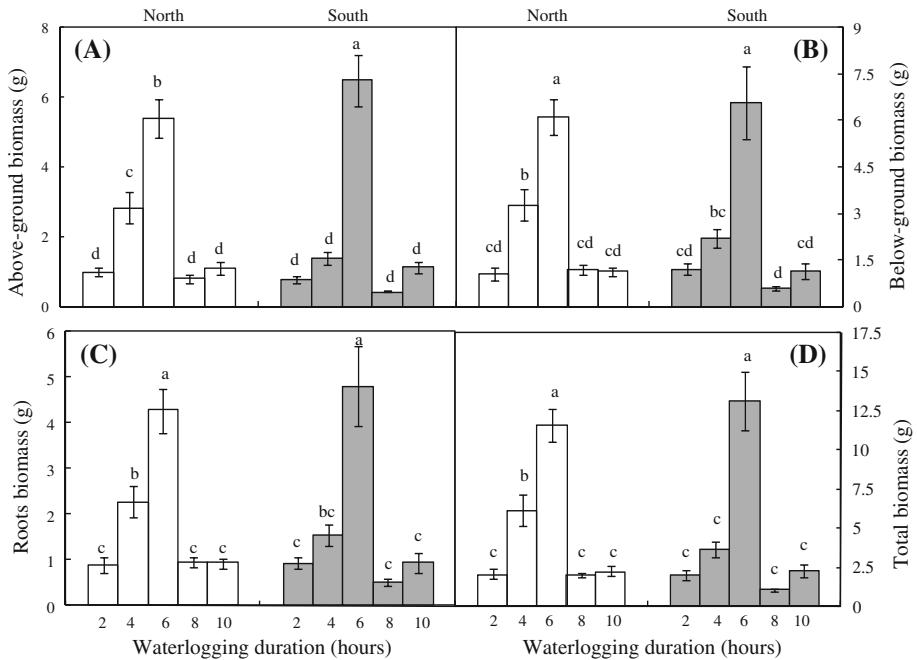


Fig. 3 Biomass parameters of the *Spartina anglica* plants from the two provenances under the five waterlogging duration treatments. Bars sharing the same letters are not different at $p = 0.05$ (by Duncan tests)

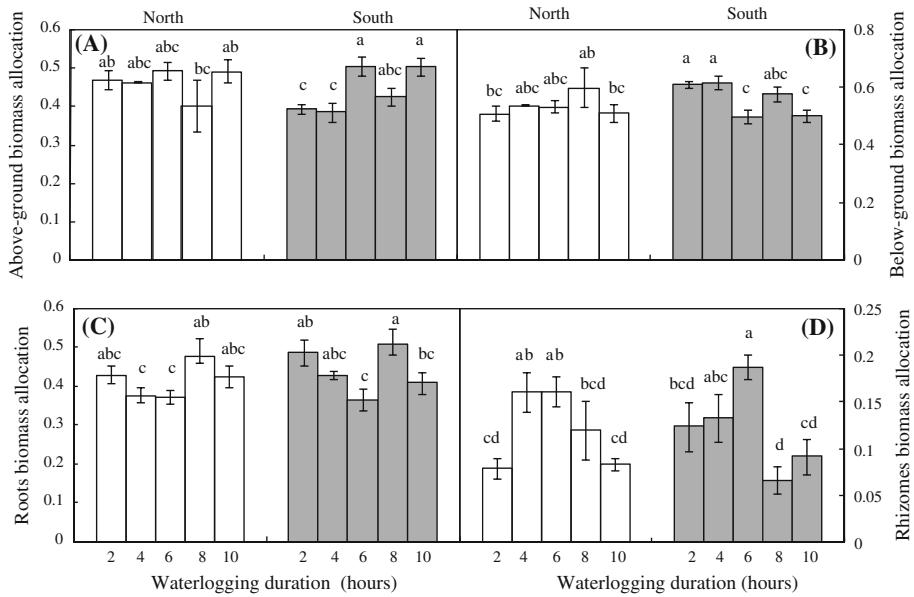


waterlogging treatments than that at 8-h waterlogging treatment (Fig. 4c). The inverse was the case for biomass allocation to rhizomes (Fig. 4d). Biomass allocation to above-ground and below-ground structures did not differ among the treatments (Fig. 4a, b).

When the plants were from the south, above-ground biomass allocations in the 6- and 10-h water-

logging treatments were significantly greater than those in the 2- and 4-h treatments (Fig. 4a). This tendency was reversed for below-ground biomass allocation (Fig. 4b). Biomass allocation to roots in the 6-h treatment was smaller than that in the 8-h treatment, but biomass allocation to rhizomes was the greatest (Fig. 4c, d).

Fig. 4 Biomass allocation of the *Spartina anglica* plants from the two provenances under the five waterlogging duration treatments. Bars sharing the same letters are not different at $p = 0.05$ (by Duncan tests). Numbers represent proportions of total biomass



Discussion

Provenance of the *S. anglica* plants (north and south site) did not affect any of the traits except height, stalk diameter, and leaf area. However, all traits measured were affected by waterlogging duration (Table 1), suggesting that *S. anglica* can tolerate waterlogging to some extent. These results agree with previous findings for various wetland species (Etherington and Thomas 1986; Fagerstedt and Crawford 1987; Waldren et al. 1988; Lentz and Dunson 1998). Similar to our finding regarding plant source, Heathcote et al. (1987) showed that populations of *Carex flacca* collected from sites with a wide range of water content showed no variation to various levels of flooding.

Although *S. anglica* can tolerate waterlogging, the measured traits varied among different waterlogging treatments. In general, *S. anglica* plants grew the best when subjected to 6 h of waterlogging, with shorter or longer waterlogging durations inhibiting growth. Other studies have found that waterlogging may affect plant growth compared to drained conditions or according to different levels of flooding (Waldren et al. 1987, 1988; Mendoza et al. 2005). Longer durations of waterlogging have been shown to inhibit leaf area expansion (Dale and Causton 1992; Lenssen et al. 2002) and reduce biomass allocation to below-ground resources (Rubio and Lavado 1999). It was correlated with some chemical change in waterlogging condition, such as redox potential of the soil, exchangeable ferric iron and manganese considerably decreasing (Etherington 1984; Waldren et al. 1987, 1988). Many of these reduced chemical forms were potentially phytotoxic and may inhibit plant growth in flooded soils (Waldren et al. 1987; Mendelsohn and McKee 1988; Rengel 1992). Other results were a decrease in the uptake of essential nutrients by plants

(Koch et al. 1990; Rengel 1992), for example a reduction in the uptake of NH₄-N shown by (Bradley and Morris 1990; Rengel 1992; Fitter and Hay 2002).

S. anglica possesses specialized internal structures and physical responses to chemical changes in waterlogged soil. It forms root aerenchyma that can facilitate oxygen transportation within the plants (Jackson and Armstrong 1999; Maricle and Lee 2002; Shiono et al. 2008). Moreover, porous leaves, shoots, and roots as well as root adaptations (i.e., thickened hypodermis) and the internal and external ability to oxidize phytotoxins and sulphides have all contributed to the superior waterlogging tolerance of *Spartina* (Howarth 1979; Carlson and Forrest 1982; Armstrong et al. 1985). For *Bruguiera gymnorhiza* seedlings, leaf anatomical characteristics such as palisade parenchyma and spongy parenchyma thickness varied with waterlogging time (Wang et al. 2007). In another study, *S. anglica* adapted more easily to 6-h waterlogging duration by changes in physical parameters such as free proline content, soluble sugar content, and the photosynthetic rate of leaf than those of other treatment under different waterlogging treatments of simulated tides (Li et al. 2010).

Tide and the geomorphic construct of the marsh are the most important factors determining the composition and distribution of species in salt marshes (Brewer and Grace 1990; Bridgewater and Cresswell 1999; Sanderson et al. 2000). Duration of waterlogging on *Spartina* plants in the field is driven by tidal action, which can bring about nutrient exchange between macrophyte stands and open water (Adams and Bate 1995; Rybicki et al. 1997). The flux of organic and inorganic compounds between the sediment and the water may be affected by low tide. Rybicki et al. (1997) found that diurnal distribution was influenced by the physical and biochemical fluctuations. For growth and asexual reproduction,

S. anglica plants would appear best situated for nutrient exchange and environmental factors at 6 h of waterlogging. *Kandelia candel* (a mangrove species) tolerates tidal immersion by seawater up to about 8 h in each cycle, a time frame that matched the tidal cycle in its natural distributional zone and induced the optimum interaction between physiological responses and environmental factors (Ye et al. 2003; Chen et al. 2005).

Waterlogging duration is determined by tidal marsh geomorphology (e.g., elevation) and distance from the sea (Armstrong et al. 1985; Brewer and Grace 1990). Interactions between the flooding regime and elevation gradients contribute to vegetation structure (Brewer and Grace 1990). During high tides, water levels can rise about 1.5 m, but only about 1.0 m in neap tides. The elevational niche of *S. anglica* has changed greatly compared to 40 years ago. *S. alterniflora* has accelerated new land formation by sediment accretion; during a period of 11–13 years, it accreted an area of 29 km², with 48–52 cm vertical accretion rates over 3–4 years (Chung et al. 2004). At present, the niche elevation of *S. anglica* is about 1.5 m, and thus only the highest tides can reach it. Therefore, the interval between tidal immersions is longer and the immersion duration is shorter, and the exchanges of nutrients and water are less than that of 40 years before. The *S. anglica* populations currently rely mainly on asexual reproduction because few viable seeds are produced due to poor pollen growth and irregular pollen tubes (Li et al. 2008). This may greatly restrict its ability to adapt to environmental changes such as changes in tidal immersion (Gray et al. 1991; Ayres and Strong 2001).

In conclusion, a shorter duration of tidal waterlogging induced by geomorphic changes may have inhibited the growth of *S. anglica* in coastal China. Also, the ability of *S. anglica* to adapt to environmental changes may be greatly reduced because sexual reproduction was also inhibited, as shown in a prior study (Li et al. 2008). These factors together appear to have resulted in the decline of *S. anglica* in coastal China. We propose that manipulation of tidal immersion periodicity may be useful for the control and management of the species (Fragoso and Spencer 2008) where it has become an aggressive invader.

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