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PRIMARY RESEARCH PAPER

Trade-offs among growth, clonal, and sexual reproduction in an invasive plant *Spartina alterniflora* responding to inundation and clonal integration

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Abstract The purpose of this article was to study the trade-offs among vegetative growth, clonal, and sexual reproduction in an aquatic invasive weed *Spartina alterniflora* that experienced different inundation depths and clonal integration. Here, the rhizome connections between mother and daughter ramets were either severed or left intact. Subsequently, these clones were flooded with water levels of 0, 9, and 18 cm above the soil surface. Severing rhizomes decreased growth and clonal reproduction of daughter ramets, and increased those of mother ramets grown in shallow and deep water. The daughter ramets disconnected from mother ramets did not flower, while sexual reproduction of mother ramets was not affected by severing. Clonal integration only benefited the total rhizome length, rhizome biomass, and number of rhizomes of the whole clones in non-inundation conditions. Furthermore, growth and clonal reproduction of mother, daughter ramets, and the whole clone decreased with inundation depth, whereas sexual reproduction of mother ramets and the whole clones increased. We concluded that the trade-offs among growth, clonal, and sexual reproduction of *S. alterniflora* would be affected by inundation depth, but not by clonal integration.

Keywords Clonal reproduction · Growth · Inundation · Invasive plant · Reproductive strategy · Sexual reproduction · *Spartina alterniflora*

Introduction

Most perennial clonal plants possess the capacity for both sexual reproduction through seeds and clonal reproduction through vegetative propagation (Klimes et al., 1997). In general, clonal reproduction benefits rapid, short-distance spread, while sexual reproduction increases long-distance dispersal (Rautiainen et al., 2004). The relative importance of these two reproductive modes can vary widely within species in response to ecological factors (Eckert, 2002). Such trade-offs between sexual and clonal reproduction have been demonstrated in many species and have been found to be influenced by plant size (Worley & Harder, 1996; Gardner & Mangel, 1999), competition (Rautiainen et al., 2004), nutrient levels (Liu et al., 2009), successional stages (Sun et al., 2001; Weppler & Stöcklin, 2005), and population age (Piquot et al., 1998; Weppler et al., 2006). However, they have rarely been quantified for invasive species associated with their favorable environmental conditions (Ronsheim & Bever, 2000; Lui et al., 2005).

It has been suggested that a high degree of integration between the ramets at the ramet level in clonal species

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may obscure trade-offs that are occurring at the whole clone (genet) level (Delph et al., 1993). Maintenance of ramet connections of clonal plant enables resource translocations between ramets (Abrahamson et al., 1991; Alpert et al., 2002; D'Hertefeldt & Falkengren-Grerup, 2002). Previous studies found that physiological integration benefited clonal plants, especially in environments that were heterogeneous at small spatial scales (Hutchings & Wijesinghe, 1997; van Kleunen et al., 2000). Consequently, clonal integration sometimes increases plant performance of the whole clone (Alpert, 1999). Nevertheless, physiological integration has potential costs, such as the cost of maintaining the connections between the ramets, or the cost resulting from facilitation of pathogen infection that may make disintegration beneficial (Kelly, 1995; van Kleunen et al., 2000). Therefore, clonal integration may not always benefit the genet as a whole (Alpert, 1999; Wang et al., 2009). Nevertheless, little is known about how the reproductive strategy of clonal plants associated with clonal integration responds to environment.

Native to the Atlantic and Gulf coast marshes of North America, the clonal plant *Spatina alterniflora* monocultures have dominated the lower marsh habitats that were flooded daily by tides (Bertness, 1991). Previous experiments showed that *S. alterniflora* had stronger tolerance to inundation when compared with other marsh plants (Mendelssohn & Patrick, 1981; Wang et al., 2006). In this article, we hypothesized that clonal integration would influence the trade-offs among vegetative growth, clonal, and sexual reproduction of *S. alterniflora* grown in different water depths. Specifically, the following specific questions have been addressed: (1) Are the growth, clonal, and sexual reproduction of mother, daughter ramets, and the whole clone affected by rhizome severing and inundation? (2) Do the three components of allocation, vegetative growth, clonal propagation, and sexual reproduction correlate negatively with one another? and (3) Does clonal integration affect these trade-offs under inundation conditions?

Materials and methods

Study species

Spartina alterniflora, a monocotyledonous halophyte of the family Poaceae, is a tall perennial species. It dominates the lower marsh habitats and has high tolerance to salinity and waterlogging (Bertness, 1991; Wijte & Gallagher, 1996). The general view on *S. alterniflora* population expansion is that it disperses by seeds and clonal fragments carried by the tides (Proffitt et al., 2003). Following initial colonization by either vegetative propagules or seeds, the populations of *S. alterniflora* that develop on bare flats often consist of a large number of circular patches of grass produced by clonal growth (Davis et al., 2004). *S. alterniflora* has become an invasive plant, either by itself or by hybridizing with native species and preventing propagation of the pure native strain. In China, this species can be found in most of the tidal marshes, from Beihai at the south (21°36′N, 109°42′E) to Tianjin (38°56′N, 121°35′E) at the north coasts, and now covers a total area of 112000 ha (An et al., 2007).

Plant material and precultivation

The experiment was conducted in the greenhouse of Nanjing University, China (118°41′E, 32°10′N). In April 2008, 100 individuals of *S. alterniflora* consisting of a single tiller with 31.5 ± 0.43 cm in height (mean ± s.e., $n = 15$) were taken from low marsh at Xinyang Harbor (33°42′N, 120°18′E) in Jiangsu Province, China, where the average salinity is approximately 30‰. These plants were cultivated separately in quadrate plastic tanks (50 cm in length, 40 cm in breadth, and 30 cm in height; 50 l in volume) containing 12-cm deep fine sand. To make the severing process easier, fine sand substrate was used in this experiment. To reduce osmotic shock, salinity was increased every 3 days by 3‰ increments until the final concentration of 15‰ was reached and kept. The water level was maintained 2 cm above the soil surface. To maintain the environmental conditions throughout the experiments, salinity and water levels were monitored twice a week and adjusted to initial conditions, either by adding freshwater or saline water. All the seedlings were grown in a greenhouse with an air temperature of 20–37°C, where the irradiance level was approximately 1000–1200 μmol m^{-2} s^{-1} at full sun. These plants that produced new daughter ramets consisting of one tiller were prepared for the following experiment.

Experimental design

The experiments included two severing (clonal integration) treatments and three water-depth treatments. On July 19, the rhizomes of *S. alterniflora* between original plants (mother plants) and tagged daughter plants were severed by inserting a sharp blade perpendicular to the sand surface. The average initial shoot height of the daughter ramets was 26.73 ± 0.97 cm (mean ± s.e., $n = 48$). After harvest, we observed that all the rhizomes were severed completely. Numerous studies have found no effect of severing connections under control conditions (Hartnett & Bazzaz, 1983; Evans, 1992; Peltzer, 2002). In addition, we did not observe any patterns of sudden death or increased disease, indicating that severing treatment did not result in severe damage. After severing, the plants were flooded to water levels of 0 cm (control), 9 cm (shallow water), and 18 cm (deep water) above the soil surface. The plants were fertilized biweekly with 50 ml of 10-strength Hoagland's nutrient solution. The solutions were renewed biweekly, and eight replicate tanks were allocated for each treatment.

Measurement

All the plants were harvested after 3 months on October 24, 2008, and we counted the numbers of tillers, leaves, rhizomes, and flowering tillers. The total rhizome length and shoot length were measured by a ruler, and leaf area was measured by LI-3000C portable area meter. The total shoot length was estimated using the sum of the heights of all the shoots in an experiment tank (Pennings & Callaway, 2000). Dry mass was determined after drying at 70°C for 48 h. The number of flowering shoots, proportion of flowering shoots, and inflorescence biomass were used to quantify the investment in sexual reproduction. The number of tillers and rhizomes, total rhizome length, and rhizome biomass were used to quantify the investment in clonal reproduction. The total shoot length, shoot biomass, number of leaves, and leaf area were used for growth.

Data analysis

We employed two-way ANCOVA to investigate the effects of severing, water depth, and their interactions on growth, clonal, and sexual reproduction. The tiller number of the mother ramets and whole clone measured on 19 July was considered as covariates of the mother ramets and whole clones, respectively. As all daughter ramets consisted of a single tiller at the start of severing treatments, the shoot height was used as covariates of daughter ramets. If necessary, the data were square-root transformed to meet the homogeneity of variance and normality. The severed daughter ramets did not flower, and this category was excluded from two-way ANCOVA. The daughter ramets connected with mother ramets also failed to flower in control treatments, resulting in dissatisfaction of homogeneity of variance. Consequently, Kruskal–Wallis rank test was performed to determine the differences of sexual production in daughter ramets with clonal integration among three water-depth treatments. One-way ANCOVAs were used to assess whether the number of rhizomes and total rhizome length differed among the three water-depth treatments and between two severing treatments. Linear regression analysis was applied to estimate the relationships between water depth and all morphological parameters with pooled severing and connected treatments, and among growth, clonal, and sexual reproductive characters. SPSS 13.0 was used for all analyses.

Results

Effects of clonal integration on mother, daughter ramets, and the whole clones

Severing significantly decreased the total shoot length, shoot biomass, number of leaves, and leaf area of the daughter ramets, but significantly increased the growth parameters of the mother ramets. The growth characters of the whole clones were not influenced by rhizome severing (Fig. 1; Table 1).

With regard to clonal reproduction characters, the number of tillers showed a similar response to clonal integration as growth characters. The number of tillers of the daughter ramets was inhibited, and that of the mother ramets was stimulated by rhizome severing, and thus that of the whole clones did not change (Fig. 2). It was noted that the rhizome characters, including the total rhizome length, rhizome biomass, and the number of rhizomes of the daughter ramets were decreased by rhizome severing, except a slight increase in the number of rhizomes of the daughter ramets grown in control treatments (Fig. 2; Table 2). Separate ANOVAs showed that severing resulted in no significant reductions in the rhizome biomass, total rhizome length, and the number of rhizomes of the daughter ramets in control treatments. On the other hand, when compared with the connected mother ramets, the total rhizome length, rhizome biomass, and number of rhizomes of the disconnected mother ramets increased by 83.3, 75.8, and 80.0% in control treatments, respectively. Consequently, the rhizome biomass, total rhizome length, and number of rhizomes of the whole clones were increased by rhizome severing (Table 2). However, when the plants grew in shallow and deep water, severing did not affect the rhizome characters of the whole clones.

Daughter ramets with clonal integration flowered in shallow and deep water treatments, while those ramets that disconnected from the mother ramets did not flower in any treatment (Fig. 3). The number of flowering shoots, proportion of flowering shoots, and inflorescence biomass of the mother ramets and the whole clones were not affected by clonal integration (Table 3).

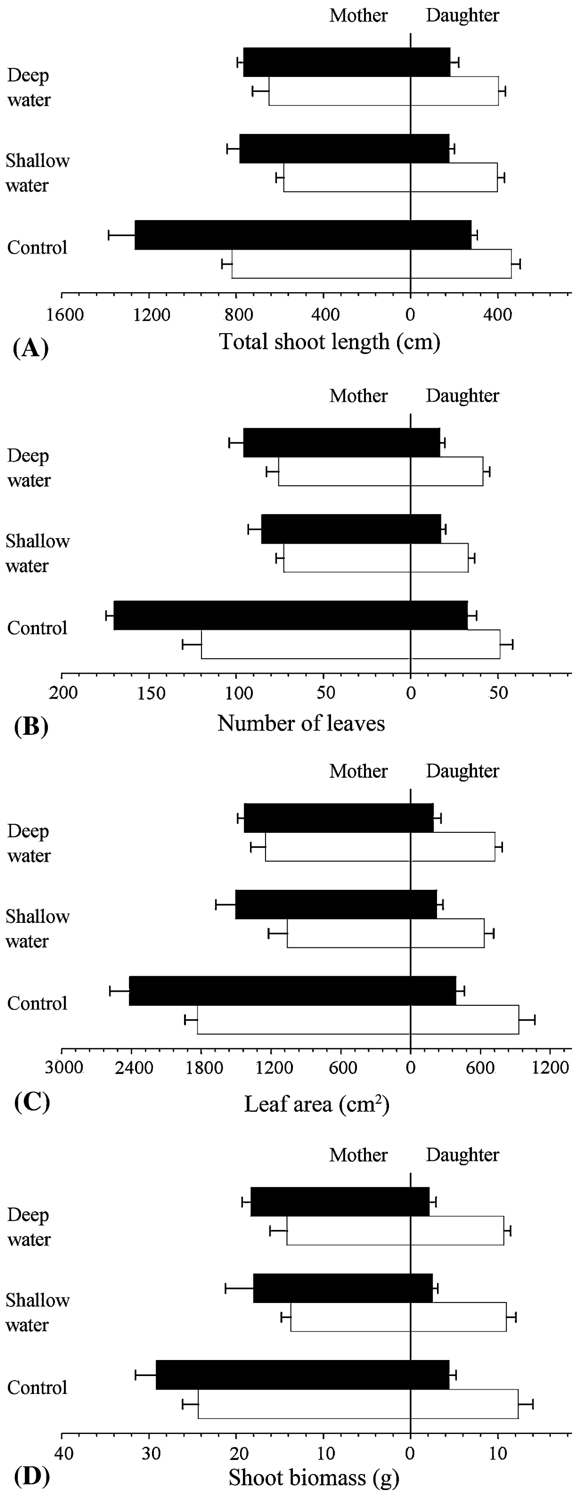

Fig. 1 Growth characters of *S. alterniflora* under combinations of three water depth and two rhizome-severing treatments (*open bars* originally integrated ramet pairs, *black bars* severed ramet pairs)

Effects of inundation on growth, clonal, and sexual reproductive characters and their relationships

In two rhizome-severing treatments, higher water level reduced the growth and clonal reproductive parameters of the mother, daughter ramets, and the whole clones (Figs. 1, 2; Tables 1, 2). The daughter ramets that disconnected from the mother ramets failed to flower in three inundation treatments. In the connected treatments, the daughter ramets did not flower in control treatments, and inundation had no significant effect on the number of flowering shoots, proportion of flowering shoots, and inflorescence biomass of the daughter ramets ($P > 0.05$, $P > 0.05$, $P > 0.05$; Kruskal–Wallis rank test). However, the sexual reproductive characters of the mother ramets and whole clones in both connected and severed treatments increased with increasing water depth (Fig. 3; Table 3). For the whole clone, linear regression analysis showed that the sexual productive characters were negatively correlated with both growth and clonal reproductive characters, whereas

Table 1 Results of ANCOVA for effects of water depth and rhizome severing on growth characters of *S. alterniflora*

Source	d.f.	Total shoot length			Number of leaves			Leaf area			Shoot biomass		
		Mother ramets	Daughter ramets	Whole clone	Mother ramets	Daughter ramets	Whole clone	Mother ramets	Daughter ramets	Whole clone	Mother ramets	Daughter ramets	Whole clone
Co1	1	0.118†	–	–	1.475†	–	–	1.114†	–	–	4.826*	–	–
Co2	1	–	21.635***	–	–	6.751*	–	–	14.132**	–	–	13.140**	–
Co3	1	–	–	0.269†	–	–	2.860†	–	–	1.703†	–	–	7.874**
Severing (S)	1	20.105***	94.622***	0.734†	21.699***	33.873***	2.644†	13.864**	71.766***	0.455†	9.843**	145.395***	2.535†
Water depth (W)	2	14.862***	6.277**	19.647***	39.061***	8.990**	58.974***	19.125***	6.264**	25.605***	14.693***	3.959*	17.302***
S × W	2	3.104†	0.220†	3.534*	3.889*	0.361†	4.397*	0.286†	0.511†	0.894†	0.146†	0.709†	0.305†

Covariates 1 (Co1), 2 (Co2), and 3 (Co3) are tiller number of mother ramets, shoot height of daughter ramets, and tiller number of whole clone measured at the start of the severing experiment

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, † $P > 0.05$

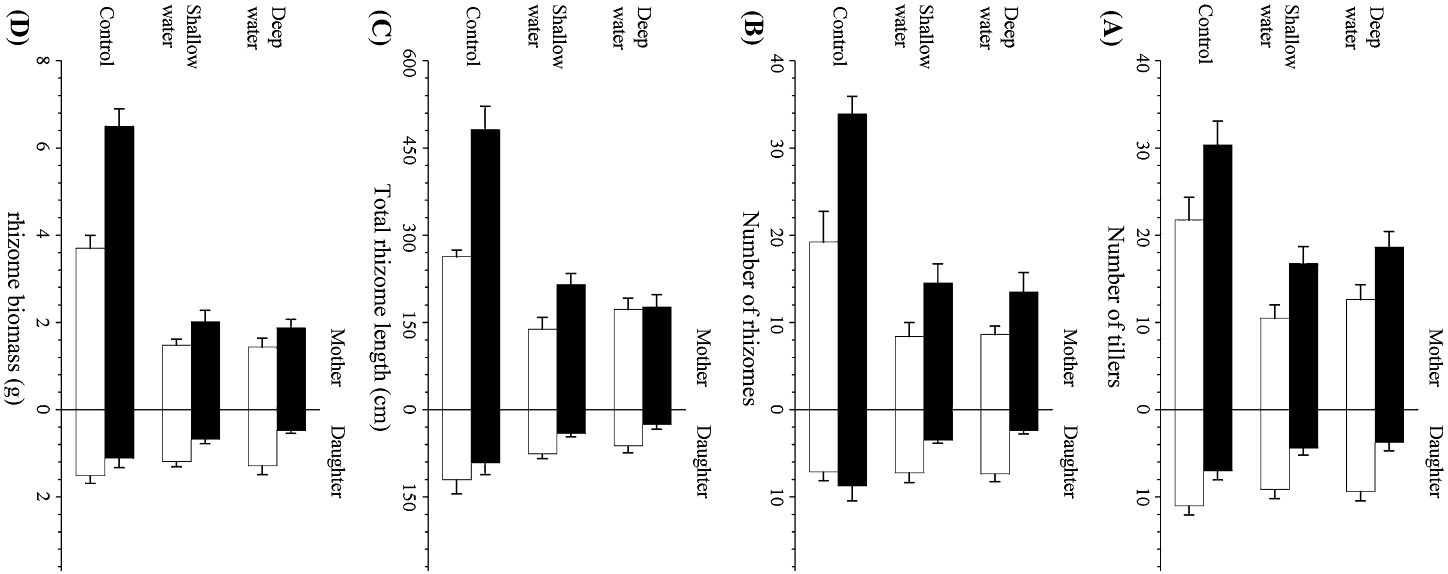

Fig. 2 Clonal reproduction characters of *S. alterniflora* under combinations of three water depth and two rhizome-severing treatments (*open bars* originally integrated ramet pairs, *black bars* severed ramet pairs)

Table 2 Results of ANCOVA for effects of water depth and rhizome severing on clonal reproduction characters of *S. alterniflora*

Source	d.f.	Number of tillers			Number of rhizomes			Total rhizome length			Rhizome biomass		
		Mother ramets	Daughter ramets	Whole clone	Mother ramets	Daughter ramets	Whole clone	Mother ramets	Daughter ramets	Whole clone	Mother ramets	Daughter ramets	Whole clone
Co1	1	0.078†	–	–	0.996†	–	–	0.195†	–	–	0.110†	–	–
Co2	1	–	18.211***	–	–	7.268*	–	–	25.929***	–	–	11.384**	–
Co3	1	–	–	0.371†	–	–	0.133†	–	–	0.000†	–	–	0.074†
Severing (S)	1	15.862***	49.684***	1.696†	18.949***	9.778**	6.911*	23.414***	12.494**	6.836*	31.222***	29.878***	5.599*
Water depth (W)	2	17.863***	5.487**	22.215***	31.052***	6.335**	28.226***	41.978***	15.887***	43.058***	101.054***	5.931**	68.992***
S × W	2	0.258†	0.136†	0.563†	2.387†	6.155**	4.934*	9.675***	0.074†	6.827**	11.924***	0.880†	8.729**

Covariates 1 (Co1), 2 (Co2), and 3 (Co3) are tiller number of mother ramets, shoot height of daughter ramets, and tiller number of whole clone measured at the start of the severing experiment

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, † $P > 0.05$

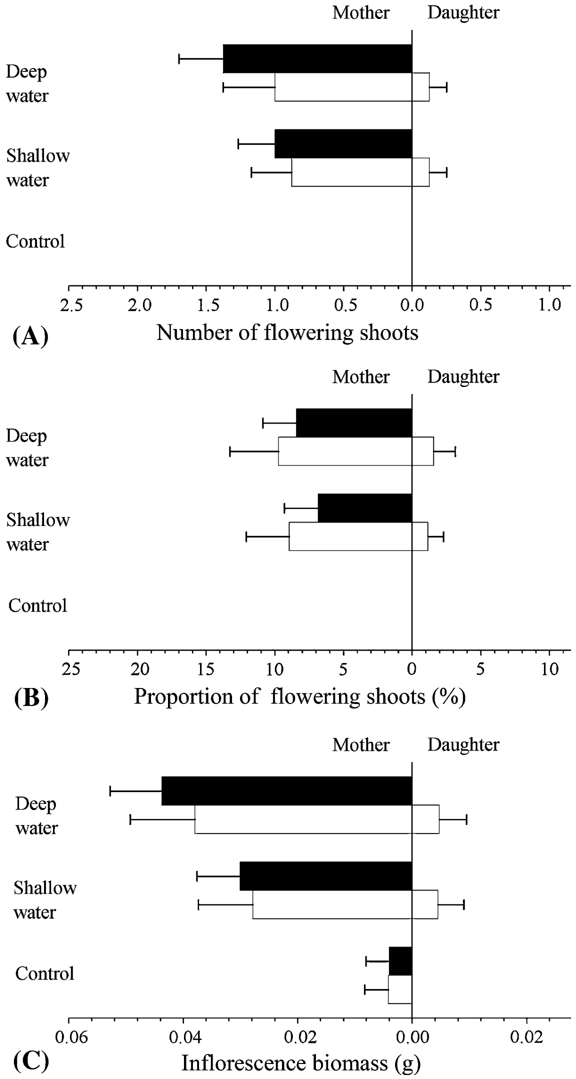

Fig. 3 Sexual reproduction characters of *S. alterniflora* under combinations of three water depth and two rhizome-severing treatments (*open bars* originally integrated ramet pairs, *black bars* severed ramet pairs)

positive correlations were found between growth and clonal reproductive characters (Table 4).

Discussion

Cost–benefit analysis of clonal integration in terms of growth, clonal, and sexual reproduction

As predicted, severing rhizomes markedly decreased the growth parameters and number of tillers of

Table 3 Results of ANCOVA for effects of water depth and rhizome severing on sexual reproduction characters of *S. alterniflora*

Source	d.f.	Number of flowering shoots			Proportion of flowering shoots			Inflorescence biomass		
		Mother ramets	Daughter ramets	Whole clone	Mother ramets	Daughter ramets	Whole clone	Mother ramets	Daughter ramets	Whole clone
Co1	1	1.222†	–	–	2.144†	–	–	0.910†	–	–
Co2	1	–	–	–	–	–	–	–	–	–
Co3	1	–	–	1.652†	–	–	2.785†	–	–	1.368†
Severing (S)	1	0.495†	–	0.122†	0.631†	–	0.982†	0.251†	–	0.003†
Water depth (W)	2	9.746***	–	12.241***	11.330***	–	11.232***	10.780***	–	14.041***
S × W	2	0.017†	–	0.128†	0.391†	–	0.062†	0.023†	–	0.184†

Covariates 1 (Co1), 2 (Co2), and 3 (Co3) are tiller number of mother ramets, shoot height of daughter ramets, and tiller number of whole clone measured at the start of the severing experiment

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, † $P > 0.05$

daughter ramets, but increased those of mother ramets (Figs. 1, 2). These results agreed with the previous study on *Alternanthera philoxeroides* suffering from submergence (Wang et al., 2009). Thus, the growth and clonal reproduction of the whole clones was not affected by clonal integration (Tables 1, 2). However, no reductions in the total rhizome length, rhizome biomass, and the number of rhizomes of daughter ramets and increase in those of the mother ramets induced by rhizome severing contributed to the increased rhizome characters of the whole clones in non-inundation conditions (Fig. 2B, C). Under such circumstances, greater potential expansion capacity through clonal reproduction would be stimulated by rhizome severing.

Failure of flowering of the disconnected daughter ramets in all treatments indicated that the resource transported from mother ramets might play an important role in affording sexual production of their offspring. Mendoza & Franco (1998) also suggested that resource movement within plants owing to clonal integration favors an increase in the probability of producing a flower. Sexual production was considered to be more nutrient-demanding than vegetative production (Watson, 1984). In general, mother ramets usually specialized in sexual reproduction, whereas daughter ramets specialized in vegetative reproduction (van Kleunen et al., 2000). Reproductive specialization between plant ramets could represent an evolved ontogenetic pattern to increase its fitness (Schmid, 1992). Due to this reproductive specialization between parent ramets and their offspring, the sexual productions of the whole clones mainly depended on those of the mother ramets. Thus, the sexual reproduction of mother ramets remained unchanged after severing rhizomes.

It has been suggested that resource-sharing between ramets within the clones is likely to be disadvantageous in uniform habitats resulting from metabolic costs of resource transport, and advantageous in patchy ones (Alpert, 1999). Our results showed that clonal integration did not influence growth characters, number of tillers, and sexual reproduction of *S. alterniflora* of the whole clones in homogeneous inundation conditions. Nevertheless, in non-inundation conditions, rhizome production of the whole clones would be promoted.

Trade-offs among three components associated with inundation

Although *S. alterniflora* exhibited strong tolerance to flooding, this species was negatively influenced by excessive flooding and subsequent oxygen deficiencies (Mendelssohn & Patrick, 1981). Increasing degree of inundation induced reductions in both growth and clonal reproduction of *S. alterniflora* (Figs. 1, 2), which is in accordance with a previous study on this species and other *Spartina* species (Wang et al., 2006; Mateos-Naranjo et al., 2007). This would be responsible for the positive correlation between clonal reproduction and growth (Table 4).

On the contrary, negative phenotypic correlations between sexual reproduction and clonal reproduction and growth have been demonstrated in *S. alterniflora* (Table 4). Similar reduced growth in response to

Table 4 Summaries of linear regressions indicating correlation coefficient among water depth, total shoot length, number of leaves, leaf area, shoot biomass, number of tillers, number of rhizomes, total rhizome length, rhizome biomass, number of flowering shoots, proportion of flowering shoots, and inflorescence biomass in *S. alterniflora*

	Inflorescence biomass	Proportion of flowering shoots	Number of flowering shoots	Rhizome biomass	Total rhizome length	Number of rhizomes	Number of tillers	Shoot biomass	Leaf area	Number of leaves	Total shoot length
Water depth	0.631***	0.528***	0.582***	−0.738***	−0.691***	−0.626***	−0.593***	−0.587***	−0.631***	−0.685***	−0.579***
Total shoot length	−0.437**	−0.503***	−0.418**	0.834***	0.811***	0.751***	0.877***	0.723***	0.546***	0.507***	
Number of leaves	−0.536***	−0.527***	−0.514***	0.643***	0.515***	0.527***	0.578***	0.541***	0.789***		
Leaf area	−0.481**	−0.476**	−0.470**	0.635***	0.470**	0.435**	0.558***	0.600***			
Shoot biomass	−0.393**	−0.473**	−0.395**	0.703***	0.656***	0.509***	0.705***				
Number of tillers	−0.410**	−0.516***	−0.390**	0.794***	0.779***	0.785***					
Number of rhizomes	−0.362*	−0.358*	−0.317*	0.866***	0.861***						
Total rhizome length	−0.465**	−0.442**	−0.430**	0.878***							
Rhizome biomass	−0.501***	−0.472**	−0.468**								
Number of flowering shoots	0.973***	0.912***									
Proportion of flowering shoots	0.890***										

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

elevated sexual production has been known for many species (reviewed in Snow & Whigham, 1989). It was indicated that environmental factors (e.g., mineral starvation and drought) could induce flowering in strawberries (Gardner & Mangel, 1999). Waxapple (*Syzygium samarangense*) plants receiving up to 40 days of continuous flooding treatment showed early flowering (Lin & Lin, 1992). In addition, a study on starfruit (*Averrhoa carambola*) plants also reported an increase in flower number associated with soil flooding (Ismail & Noor, 1996). Volder et al. (1997) found that continuous flooding induced an amphibious plant *Ranunculus peltatus* to flower in a shorter period than plants grown under terrestrial circumstance. Watson (1984) has shown that inflorescence production may limit ramet production by limiting the number of meristems available to become rhizomes. Guttridge (1989) suggested that the inhibition of flowering may be related to stimulation of vegetative growth rather than to the supply of any one of these major elements specifically. In this study, we speculated that the reduced vegetative growth with increasing water depth would be one of the possible explanations for the switch toward sexual reproductive development.

Sexual reproduction via seed is better for creating new population because of their small size and adaptation to dispersal, while clonal propagation via bulbils, corms, or rhizomes is considered to be more successful in stable habitats (Eriksson, 1997). Long-distance movement of species associated with biological invasion is considered to have significant ecological and evolutionary consequences for both the species being invaded as well as the invasive species themselves (Brown & Eckert, 2005). Frequent colonization and population expansions are considered to increase the proportional allocation of resources to reproduction and dispersal (Barrett & Pannell, 1999). Our results indicated that once the clonal production of *S. alterniflora* associated with short-distance spread was inhibited by the surrounding physical environmental stress, the sexual production would be promoted to benefit long-distance dispersal, which would increase the probability to occupy more suitable habitats. However, similar to an earlier study in a rhizome clonal grass *Leymus chinensis* (Bai et al., 2009), we observed that rhizome fragmentation did not affect the reproductive strategy.

Conclusion

Clonal integration enhanced the growth, clonal, and sexual reproduction of *S. alterniflora* daughter ramets suffering from inundation. The resource transports to daughter ramets decreased the growth and clonal reproduction of mother ramets, but not the sexual reproduction. Furthermore, cost-benefit analysis showed that rhizome fragmentation only increased the rhizome production of the whole clones in non-inundation conditions. The inundation depth was found to modify the trade-off among growth, clonal, and sexual reproduction, but clonal integration did not change this trade-off. However, some physiological experiments should be carried out in future, which might help to explain the effect that salt-water flooding promotes flowering.

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