

BELOWGROUND RESPONSES OF PHRAGMITES AUSTRALIS AND SUAEDA SALSA TO SALINITY AND WATER DEPTH CHANGES

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Abstract

Mesocosm experiments were conducted to examine belowground responses of *Phragmites australis* and *Suaeda salsa* to the combined stresses of increased salinity and water depth. The results demonstrated that: (1) belowground biomass of *P. australis* responded negatively to both increased salinity and water depth, whereas belowground biomass of *S. salsa* mainly responded negatively to increased water depth; (2) belowground biomass of *S. salsa* negatively responded to increased water depth more strongly than that of *P. australis*, thus *S. salsa* might disappear before *P. australis* in wetlands experiencing prolonged water-logging; (3) *P. australis* and *S. salsa* responded to increased salinity and/or water-logging by shifting their resource allocations towards aboveground biomass; (4) belowground biomass of *P. australis* tended to have more negative responses to increased salinity and water depth at deeper versus shallower soil depths, hindering *P. australis* from utilizing resources in deeper soil; in contrast, belowground biomass of *S. salsa* tended to have more negative responses to increased water depth at shallower versus deeper soil depths, greatly decreasing the overall root density and thereby increasing the chance of uprooting disturbance to *S. salsa*. These responses would accelerate sediment loss due to compromised sediment-binding abilities of *P. australis* and *S. salsa*, leading to an adverse positive feedback between environmental changes associated with sea level rise and performance of *P. australis* and *S. salsa*, resulting in faster deterioration of coastal wetlands than might otherwise be expected.

Key words: Belowground responses; *Phragmites australis*; Salinity; Sea level rise; *Suaeda salsa*; Water-logging.

Introduction

Sea level rise induced by global warming has become a serious challenge to coastal areas (Nicholls & Cazenave, 2010; Cazenave & Cozannet, 2014; Anon., 2014). Sea level rise may cause saltwater intrusion into low salinity coastal wetlands, and consequent increased salinity (FitzGerald *et al.*, 2008; Craft *et al.*, 2009) and water-logging (Day *et al.*, 2008; Peterson & Li, 2015). Understanding the responses of plant species in low salinity coastal wetlands to stressors such as increased salinity and water-logging is critical for predicting sea level rise impacts on plant species distributions and functions within coastal wetlands (Cazenave & Cozannet, 2014).

Phragmites australis is a perennial and widespread wetland plant species, and is one of the dominant species in coastal wetlands worldwide (Koppitz, 1999; Engloner, 2009; Jiao *et al.*, 2017). *Suaeda salsa* is an annual succulent halophyte, and is commonly distributed in coastal wetlands in eastern China (He *et al.*, 2009; Mao *et al.*, 2014). *P. australis* and *S. salsa* both play important roles in wetland ecosystem functions, such as carbon sequestration (Adams & Bate, 1999; Brix *et al.*, 2001; Olsson *et al.*, 2015), decomposition (Zhang *et al.*, 2014; Fan *et al.*, 2015), nutrient cycling (Mao *et al.*, 2014; Huang *et al.*, 2015; Liu *et al.*, 2015), and trophic interactions (Lenssen *et al.*, 2004; He *et al.*, 2015). Thus, both *P. australis* and *S. salsa* are fairly important for wetland ecosystem conservation.

Several previous studies have examined the responses of *P. australis* and *S. salsa* to salinity (e.g.

Lissner & Schierup, 1997; Moore *et al.*, 2012; Song & Wang, 2015) or water-logging stress (e.g. Mauchamp *et al.*, 2001; He *et al.*, 2009; Zhao *et al.*, 2013), respectively. But only a few studies investigated the combined effects of salinity and water-logging on the performances of *P. australis* and *S. salsa* (Hellings & Gallagher, 1992; Guan *et al.*, 2011; Song *et al.*, 2011; Yu *et al.*, 2012; Yang *et al.*, 2014b). Although these studies shed light on how *P. australis* and *S. salsa* respond to the combined influences of salinity and water-logging stresses, they mainly focused on physiological and aboveground parameters (Fahey & Knapp, 2007). Thus, belowground responses of wetland plant species to the combined stress of salinity and water-logging remains unclear. This knowledge is critical for understanding coastal wetland vulnerability to sea level rise because roots form and bind soils (Casper *et al.*, 2003; Tripathee & Schafer, 2015), which influence vertical accretion rates and elevations.

In this study, we examined the responses of belowground biomass of *P. australis* and *S. salsa* to the combined stresses of moderately increased salinity and water depth associated with early-stage sea level rise, using mesocosm experiments in a glasshouse. Previous studies on physiological and aboveground parameters of *P. australis* and *S. salsa* have shown that *P. australis* responded negatively to salinity and water-logging (Gorai *et al.*, 2010; Yu *et al.*, 2012; Yang *et al.*, 2014a); and that *S. salsa* has relatively high tolerance to salinity (Song *et al.*, 2009; Guan *et al.*, 2011), but tends to respond negatively to water-logging stress (He *et al.*, 2009; Alhdad *et al.*, 2015). We therefore hypothesized that belowground biomass of *P. australis* would respond negatively to the combined

stresses of increased salinity and water depth, and that belowground biomass of *S. salsa* would respond more negatively to increased water depth than to increased salinity. We tested these hypotheses by conducting mesocosm experiments with *P. australis* ramets and *S. salsa* seedlings under six combinations (full factorial design) of salinity (fresh (0 PSU) and brackish (10 PSU) water) and water depths (drained, 5 cm, and 10 cm), and we examined the belowground biomass of the plants at three soil depth ranges.

Materials and Methods

Mesocosm experiments: We grew *P. australis* ramets and *S. salsa* seedlings in different combinations of salinities (fresh (0 PSU) and brackish (10 PSU) water), and water depths (drained, 5 cm and 10 cm). *P. australis* ramets were grown from spring buds with associated rhizomes attached and *S. salsa* seedlings were grown from seeds. In December 2013, we collected healthy *S. salsa* seeds (similar in size within the medium size range) from Qilihai wetland, Tianjin, China (N 39.30, E 117.52), and these seeds were stored at 4 °C in the laboratory over the winter. In April 2014, healthy spring buds of *P. australis* with associated rhizomes attached from *P. australis* plants in Qilihai wetland, Tianjin, China were collected. Rhizomes were: ~3cm long and ~0.5cm in diameter. Rhizomes were collected more than 5m apart to reduce the chance of collecting multiple spring buds from the same clone.

The experiments were conducted in a glasshouse at Tianjin Normal University. The glasshouse is open to ambient air which allowed sunlight and temperature conditions within to be similar to the ambient environment (25 ± 5 °C during the course of the experiments) and its glass roof blocked natural precipitation. PVC pots (diameter: 20 cm, height: 50 cm, and bottom sealed) were used to grow *P. australis* ramets and *S. salsa* seedlings (initially 50 pots/species). Each pot was filled with ~10 kg soil collected from a fresh wetland habitat in Qilihai wetland (soil salinity: ~0 PSU, pH: ~7.1, organic matter content: ~4.6%) to 35 cm soil height. In April 2014, we placed *P. australis* spring buds with associated rhizomes attached or *S. salsa* seeds in the pots (one *P. australis* bud or *S. salsa* seed in each pot). *P. australis* buds or *S. salsa* seeds were placed at ~2 cm below the soil surface. The pots were irrigated with fresh water to ensure the development of *P. australis* rhizome buds and the germination of *S. salsa* seeds. In early May 2014, we selected 30 healthy individuals of each plant species that were similar in size to minimize variation in initial size at the beginning of the experiments.

We applied the experimental treatments to the *P. australis* and *S. salsa* seedlings (heights of *P. australis* and *S. salsa* seedlings were ~65 cm and ~35 cm, respectively) starting on May 15, 2014. Fresh water (0 PSU) was added to the pots in the fresh treatment, and brackish water (10 PSU) to the pots in the brackish treatment. A drain hole was made at 5 cm below the soil surface on the side of each pot in the drained treatment, and at 5 or 10 cm above the soil surface on the side of each pot in the 5 or 10 cm water depth treatment,

respectively. Adequate fresh water or brackish water was added to each pot accordingly, and then water level in each pot relatively quickly reached the position where the drain hole was (5 cm below the soil surface in the drained treatment, 5 cm above the soil surface in the 5 cm water depth treatment, 10 cm above the soil surface in the 10 cm water depth treatment). In the 5 and 10 cm water depth treatments, after adding water, the water level in each pot was allowed to decrease naturally (by evaporation and transpiration) to soil surface (generally within two weeks), and then appropriate amount of fresh water or brackish water was added (to 5 or 10 cm water depth) to mimic the situation of water level dynamics in natural wetland habits to some extent. In the drained treatment, fresh water or brackish water was added to each pot accordingly daily. Salinity and water depth status were monitored daily during the course of the experiments.

There were 5 replicates of each combination of salinity and water depth (5 replicates × 2 salinities × 3 water depths = 30 pots in total for each species). For each plant species, pots were randomly assigned to each combination of salinity and water depth, and the pots were separated by ~0.5 m to ensure minimal shading from plants in adjacent pots. At the end of growing season (October 10, 2014), we harvested plant above- and belowground biomass. When we harvested the belowground biomass, we removed the soil from each pot as a whole monolith and then cut the soil into sections of 0-10 cm, 10-20 cm and 20-30 cm depth. These sections were thoroughly rinsed with freshwater and through a sieve (mesh size 0.25mm) to remove soil from roots and rhizomes. When we harvested belowground biomass, almost all roots and rhizomes were fresh and live. All biomass was dried for 3 days at 60 °C (Pennings *et al.*, 2005; Guo & Pennings, 2012) to constant weight and weighed.

Data analysis: Data analyses were performed with JMP 9 statistical software (SAS Institute, 2010). We used two-way ANOVA to analyze the effects of salinity, water depth and the interaction between them on belowground biomass and the ratio of belowground to total biomass of *P. australis* and *S. salsa*. The significance level for each ANOVA was set at $P=0.05$. We also calculated the response ratio of *P. australis* and *S. salsa* belowground biomass (for total belowground biomass and belowground biomass within each soil depth range) to salinity and water depth. Response ratio (RR) to salinity was calculated for each water depth treatment as: $RR \text{ to salinity} = \ln [(mean \text{ belowground biomass under brackish treatment}) / (mean \text{ belowground biomass under fresh treatment})]$; RR to water depth (5 cm or 10 cm water depth) was calculated for each salinity treatment respectively as: $RR \text{ to water depth} = \ln [(mean \text{ belowground biomass under 5 cm or 10 cm water depth treatment}) / (mean \text{ belowground biomass under drained treatment})]$. Positive values of the RR indicate positive responses to the treatment (salinity or water depth), while negative values of the RR indicate negative responses to the treatment (Hedges *et al.*, 1999; Lajeunesse, 2011).

Results

Responses of belowground biomass and ratio of belowground to total biomass: The belowground biomass of *P. australis* negatively responded to both increased salinity and water depth ($p < 0.05$, Table 1, Fig. 1a), with the highest belowground biomass occurring in the combination of fresh and drained treatments (Fig. 1a), and the lowest belowground biomass occurring in the combination of brackish and 10 cm water depth treatments (Fig. 1a). The ratio of belowground to total biomass of *P. australis* also negatively responded to both increased salinity and water depth ($p < 0.05$, Table 1, Fig. 1b). The total biomass of *P. australis* negatively responded to increased salinity, regardless of water depth ($p < 0.05$, Table 2, Fig. 2).

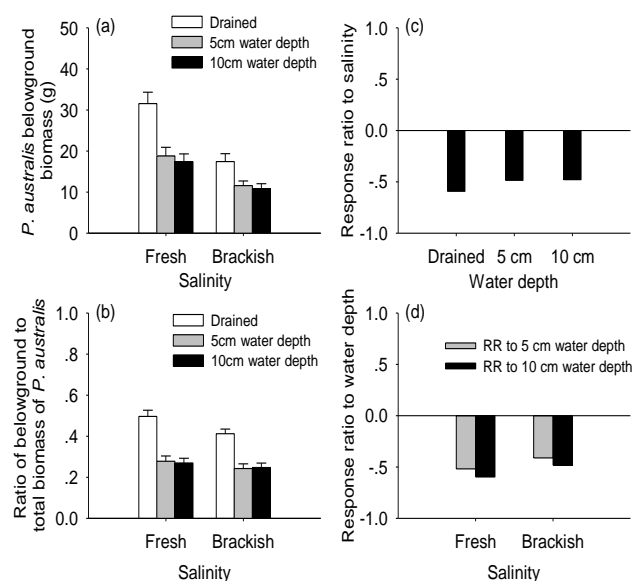


Fig. 1. *P. australis* belowground biomass (Panel a; means +SE), ratio of belowground to total biomass (Panel b; means +SE) under different salinity and water depth treatments, response ratio (RR) of *P. australis* belowground biomass to salinity (Panel c; RR to salinity was calculated for each water depth treatment respectively), and RR to water depth (Panel d; RR to water depth (5 cm or 10 cm water depth) was calculated for each salinity treatment).

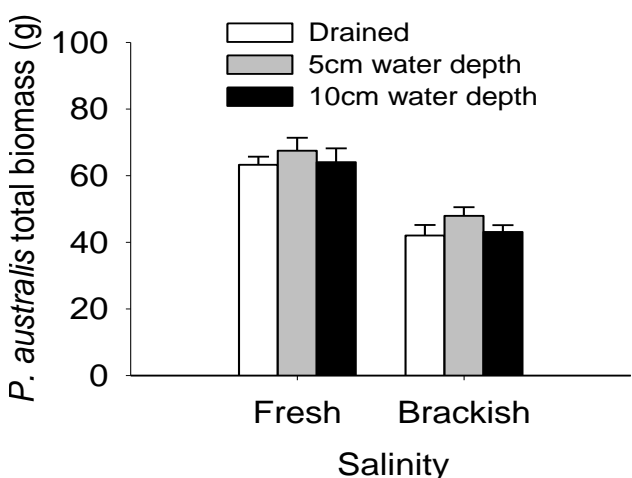


Fig. 2. Total biomass of *P. australis* under different salinity (fresh (0PSU) and brackish (10 PSU)) and water depth (drained, 5 cm and 10 cm water depths) treatments. Data are means +SE (n=5).

Under all the water depth treatments, the response ratios (RR) of *P. australis* belowground biomass to increased salinity were negative, with RR_{salinity} values of -0.59 to -0.48, and there was a tendency for the RR_{salinity} to decrease in intensity (decrease in absolute value) as water depth increased (Fig. 1c). Under both fresh and brackish treatments, the RR of *P. australis* belowground biomass to increased water depths were also negative, with $RR_{\text{water-depth}}$ values of from -0.60 to -0.41, and there was a tendency that under each salinity treatment, the $RR_{\text{water-depth}}$ was increased in intensity (increase in absolute values) as water depth increased (Fig. 1d).

The belowground biomass of *S. salsa* did not respond to salinity ($p > 0.05$, Table 1, Fig. 3a), but did respond to increased water depth ($p < 0.05$, Table 1, Fig. 3a), with the belowground biomass of *S. salsa* in the drained treatment being ~5-fold greater than that in the 5 cm and 10 cm water depth treatments (Fig. 3a). The ratio of belowground to total biomass of *S. salsa* did not respond to salinity significantly ($p > 0.05$, Table 1, Fig. 3b), but negatively responded to increased water depth ($p < 0.05$, Table 1, Fig. 3b). The total biomass of *S. salsa* negatively responded to increased water depth, regardless of salinity ($p < 0.05$, Table 2, Fig. 4).

Under all water depth treatments, the RR values of *S. salsa* belowground biomass to increased salinity were close to zero (-0.03 to 0.09, Fig. 3c), about a magnitude less than RR_{salinity} values for *P. australis* (Fig. 1c and Fig. 3c). Under both the fresh and brackish treatments, the RR values of *S. salsa* belowground biomass to increased water depth were sharply negative, with $RR_{\text{water-depth}}$ values of -2.00 to -1.72 (Fig. 3d), ~3-4 fold greater than $RR_{\text{water-depth}}$ values for *P. australis* (Fig. 1d and Fig. 3d).

Responses of vertical distributions of belowground biomass:

In the fresh treatment, belowground biomass of *P. australis* in the drained treatment tended to increase with soil depth (Fig. 5a). In contrast, belowground biomass in the 5 cm and 10 cm water depth treatments tended to decrease with soil depth (Fig. 5a). In the brackish treatment, belowground biomass of *P. australis* in all the water depth treatments tended to decrease with soil depth (Fig. 5b). Belowground biomass of *P. australis* negatively responded to increased salinity within 0-10cm soil depth range ($p < 0.05$, Table 3, Fig. 5), negatively responded to increased salinity and water depth within 10-20cm soil depth range ($p < 0.05$, Table 3, Fig. 5), and negatively responded to increased salinity and water depth within 20-30cm soil depth range ($p < 0.05$, Table 3, Fig. 5). The RR_{salinity} values of *P. australis* belowground biomass were negative and tended to increase in magnitude as soil depth increased (Fig. 6a). The $RR_{\text{water-depth}}$ of *P. australis* were also negative and tended to increase in magnitude as soil depth increased (Fig. 6b). These results showed that belowground organs of *P. australis* tended to have more strongly negative responses to increased salinity and water depth at deeper versus shallower soil depths.

Table 1. Summary of ANOVAs examining the effects of salinity (fresh (0PSU) and brackish (10 PSU)), water depth (drained, 5 cm and 10 cm) and the interaction between them on belowground biomass and the ratio of belowground to total biomass of *P. australis* and *S. salsa*. Significant level: $p < 0.05$.

Source of variance	df	F	P
Belowground biomass of <i>P. australis</i>			
Salinity	1, 24	34.823	<0.001
Water depth	2, 24	17.575	<0.001
Salinity × Water depth	2, 24	2.322	0.120
Ratio of belowground to total biomass of <i>P. australis</i>			
Salinity	1, 24	5.420	0.029
Water depth	2, 24	42.066	<0.001
Salinity × Water depth	2, 24	0.721	0.496
Belowground biomass of <i>S. salsa</i>			
Salinity	1, 24	< 0.001	0.978
Water depth	2, 24	162.404	<0.001
Salinity × Water depth	2, 24	0.003	0.997
Ratio of belowground to total biomass of <i>S. salsa</i>			
Salinity	1, 24	0.552	0.465
Water depth	2, 24	63.857	<0.001
Salinity × Water depth	2, 24	0.187	0.831

Table 2. Summary of ANOVAs examining the effects of salinity (fresh (0PSU) and brackish (10 PSU)), water depth (drained, 5 cm and 10 cm) and the interaction between them on total biomass of *P. australis* and *S. salsa*, respectively. Significant level: $p < 0.05$.

Source of variance	df	F	P
Total biomass of <i>P. australis</i>			
Salinity	1, 24	63.817	<0.001
Water depth	2, 24	1.447	0.255
Salinity × Water depth	2, 24	0.039	0.962
Total biomass of <i>S. salsa</i>			
Salinity	1, 24	< 0.001	0.978
Water depth	2, 24	162.404	<0.001
Salinity × Water depth	2, 24	0.003	0.997

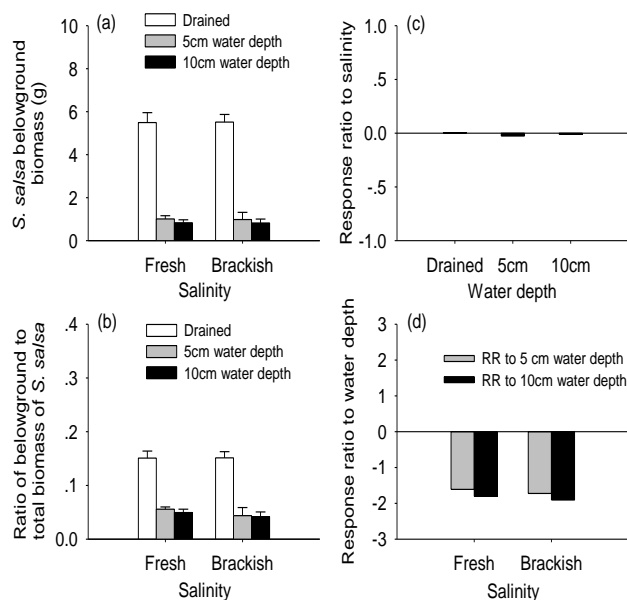


Fig. 3. *S. salsa* belowground biomass (Panel a; means +SE), ratio of belowground to total biomass (Panel b; means +SE) under different salinity and water depth treatments, response ratio (RR) of *S. salsa* belowground biomass to salinity (Panel c; RR to salinity was calculated for each water depth treatment respectively), and RR to water depth (Panel d; RR to water depth (5 cm or 10 cm water depth) was calculated for each salinity treatment).

For *S. salsa*, belowground biomass in all the combinations of salinity and water depth treatments tended to decrease with soil depth (Fig. 7). *S. salsa* belowground biomass within each soil depth range did not respond significantly to increased salinity ($p > 0.05$, Table 3), but negatively responded to increased water depth ($p < 0.05$, Table 3), with relatively stronger decreases in biomass under water-logging within 0-10 cm soil depth versus deeper soil depths (Fig. 7). The RR_{salinity} values of *S. salsa* were close to zero (-0.12 to 0.14, Fig. 8a), which was consistent with the ANOVA results showing the non-significant responses of *S. salsa* to increased salinity (Tables 1 and 3). In contrast, the $RR_{\text{water-depth}}$ values of *S. salsa* were negative and tended to be greater for the 0-10 cm versus deeper soil depths (Fig. 8b). These results showed that the belowground organs of *S. salsa* tended to have more strongly negative responses to increased water depth at shallower versus deeper soil depths.

Discussion

Responses of belowground biomass of *P. australis* and *S. salsa*: The results indicated that belowground biomass of *P. australis* negatively responded to increased salinity, whereas belowground biomass of *S. salsa* did not respond significantly to increased salinity within the salinity range tested. Our results were consistent with previous studies that *P. australis* was relatively sensitive to high salinities

(Adams & Bate, 1999; Asaeda *et al.*, 2003) and would decrease growth rate under high salinity conditions (Soetaert *et al.*, 2004). However, *S. salsa* was relatively tolerant to salinity stress (Tessier *et al.*, 2000). Furthermore, the different belowground responses of *P. australis* and *S. salsa* to salinity are also consistent with the distribution patterns of these two species across the salinity gradient in Qilihai wetland. *S. salsa* tends to occur in saltier areas than does *P. australis* (authors' unpublished data). Our findings suggested that even a moderate increase in salinity would likely have significant negative effects on belowground growth of *P. australis*.

On the other hand, belowground biomass of both *P. australis* and *S. salsa* negatively responded to increased water depth, but with a much higher $RR_{\text{water-depth}}$ for *S. salsa* versus *P. australis*. It has been shown that *P. australis* performs poorly in relatively deep water (Squires & Valk, 1992; Weisner *et al.*, 1993; Vretare *et al.*, 2001), and that *S. salsa* grows poorly under water-logged conditions (Song *et al.*, 2011), probably both due to anoxia (Weisner & Strand, 1996; He *et al.*, 2009). Our results were consistent with these studies, and the different belowground responses (in term of intensity) of *P. australis* and *S. salsa* to increased water depth were also consistent with the distribution patterns of these two species across the elevation gradient (associated with water-logging stress gradient) in Qilihai wetland. *P. australis* tends to occur at lower marsh elevations than does *S. salsa* (authors' unpublished data). Our results demonstrated that the belowground biomass of the annual species *S. salsa* would be more sensitive than that of the perennial species *P. australis* to increased water depth, indicating that *S. salsa* might be lost earlier than *P. australis* in wetlands experiencing prolonged water-logging due to sea level rise.

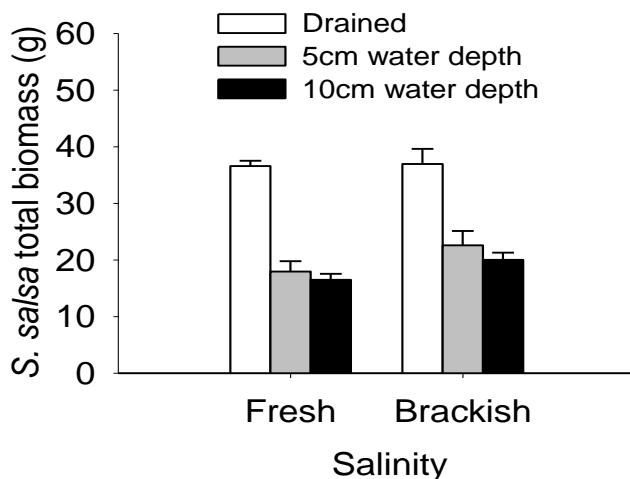


Fig. 4. Total biomass of *S. salsa* under different salinity (fresh (0PSU) and brackish (10 PSU)) and water depth (drained, 5 cm and 10 cm water depths) treatments. Data are means +SE (n=5).

For *P. australis*, the ratio of belowground to total biomass decreased as salinity and water depth increased; while for *S. salsa*, this ratio decreased only when *S. salsa* experienced increased water depth. These results suggested that *P. australis* and *S. salsa* will shift their resource allocations away from belowground biomass under salinity and/or water-logging stresses, both of which make belowground biomass costly to maintain. Increased proportions of aboveground parts could potentially improve oxygen-transport through shoots or stems to belowground

parts (Weisner & Strand, 1996; Vretare *et al.*, 2001), which could benefit these two species under anaerobic conditions to some extent. Similar results were also found in other wetland plant species. For example, Janousek and Mayo (2013) investigated responses of six marsh plant species to salinity exposure, and found that most species in the study had relatively greater loss of belowground than aboveground biomass under greater salinity exposure. Naidoo & Naidoo (2015) found that the belowground to aboveground biomass ratios of *Schoenoplectus scirpoides* were lower in water-logged treatments than in the drained treatment. Similarly, the results from our study indicated that belowground organs of *P. australis* and *S. salsa* would be suppressed greatly by increased salinity and/or water-logging associated with sea level rise.

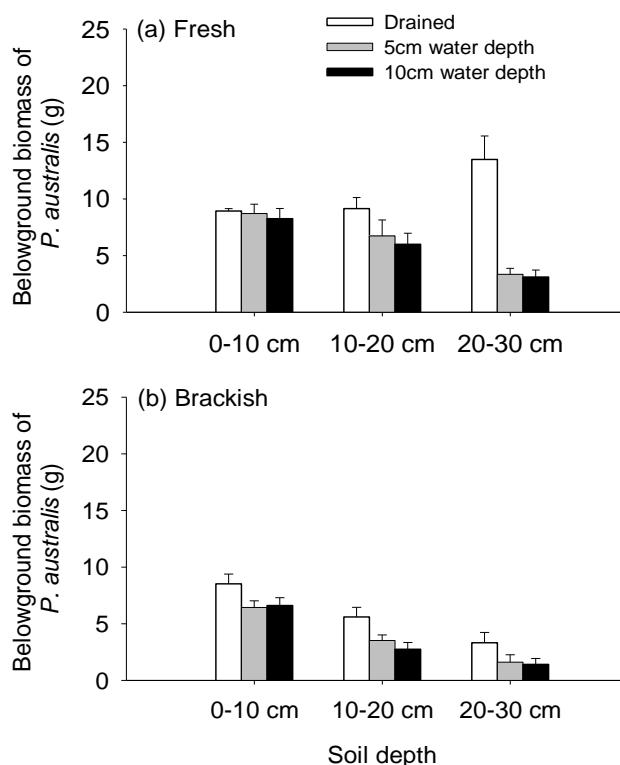


Fig. 5. Vertical distribution of *P. australis* belowground biomass (means +SE) within different soil depth ranges under different salinity and water depth treatments.

Responses of the vertical distributions of belowground biomass: Our results indicated that the effect of salinity or water-logging on the belowground organs of *P. australis* was greater at deeper versus shallower soil depths. It has been shown that *P. australis* rhizomes penetrated relatively less deep into the substrate in deep versus shallow water (Weisner & Strand, 1996). Some other studies have shown that stresses of increased salinity or water depth could suppress the growth and development of *P. australis* belowground organs (Vretare *et al.*, 2001; Soetaert *et al.*, 2004). The shallower distribution of belowground biomass of *P. australis* under increased salinity and water depth may hinder *P. australis* from utilizing resources (such as nutrients) in deeper soil (Burdick *et al.*, 2001; Moore *et al.*, 2012), further limiting *P. australis* growth; and may also reduce oxygenation via *P. australis* roots and rhizomes in deeper soil (Armstrong

et al., 2006), decreasing the activities of aerobic microorganisms or reactions of direct chemical oxidation (Begg *et al.*, 1994; Kirk & Bajita, 1995) within this layer of soil, and thereby influencing the biogeochemistry characteristics (Lee *et al.*, 1999).

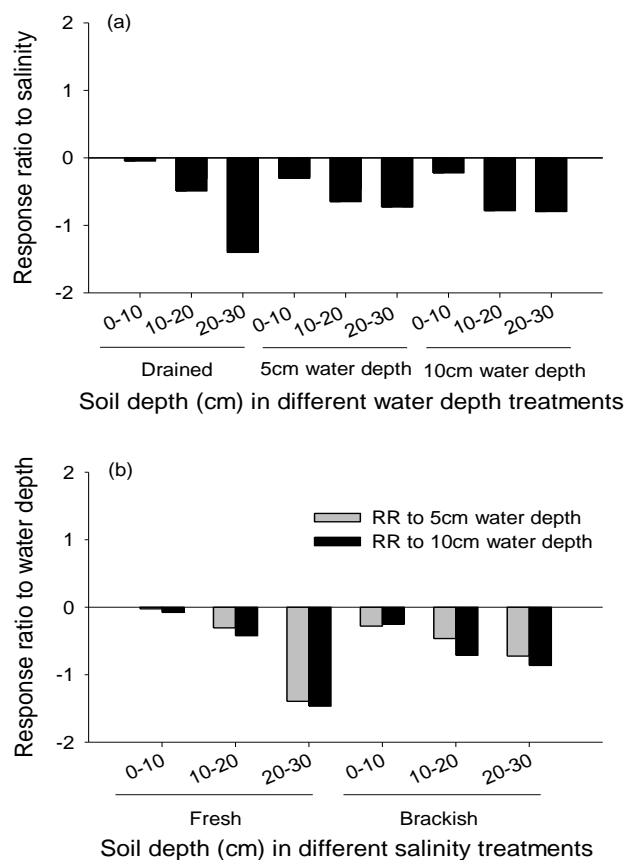


Fig. 6. Response ratio (RR) of *P. australis* belowground biomass within different soil depth ranges to salinity (Panel a; under each water depth treatment and within each soil depth range) and RR to water depth (Panel b; under each salinity treatment and within each soil depth range).

Although salinity did not affect the belowground biomass profile of *S. salsa*, *S. salsa* belowground biomass responded to increased water depth more strongly at shallower versus deeper soil depths. When soil experiences water-logging, soil redox potential (associated with oxygen availability) is reduced more dramatically in shallow versus deep soils (Colmer *et al.*, 2013; Uteau *et al.*, 2015). As *S. salsa* species mainly rely on an external oxygen supply from the soil for root growth (Wetson & Flowers, 2011; Colmer *et al.*, 2013) due to low root porosity (Justin & Armstrong, 1987), the dramatic reduction of oxygen availability in shallower soil depths might have contributed to the relatively greater decrease of belowground biomass of *S. salsa* in shallower soil depths under water-logging stress. Because the majority of belowground biomass of *S. salsa* was located at relatively shallower soil depths (0-10 cm), the strong negative belowground responses of *S. salsa* to increased water depth within this soil depth range would greatly decrease overall root density, and thus lead to reductions in soil shear strength and erosion resistance (Simon *et al.*, 2006; Howes *et al.*, 2010; Snedden *et al.*, 2015), thereby

increasing the chance of uprooting disturbance to *S. salsa* (Tessier *et al.*, 2000), which would increase the mortality of *S. salsa* under sea level rise.

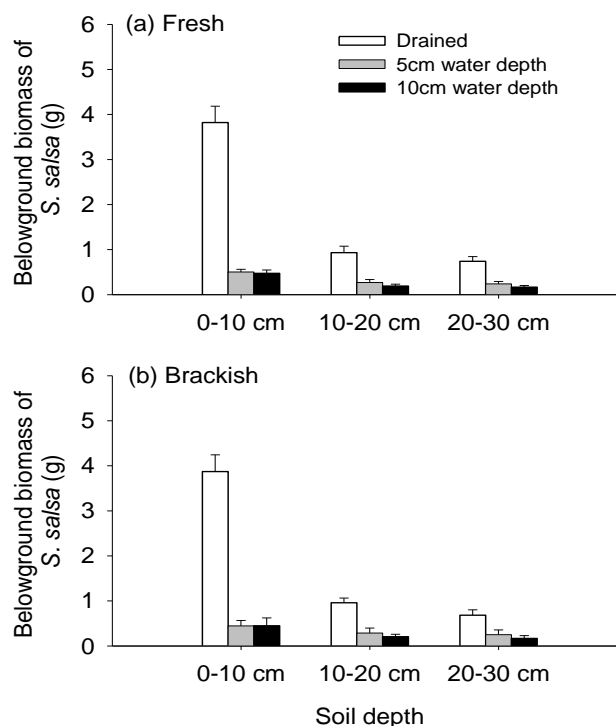


Fig. 7. Belowground biomass distribution of *S. salsa* (means +SE) within different soil depth ranges under different salinity and water depth treatments.

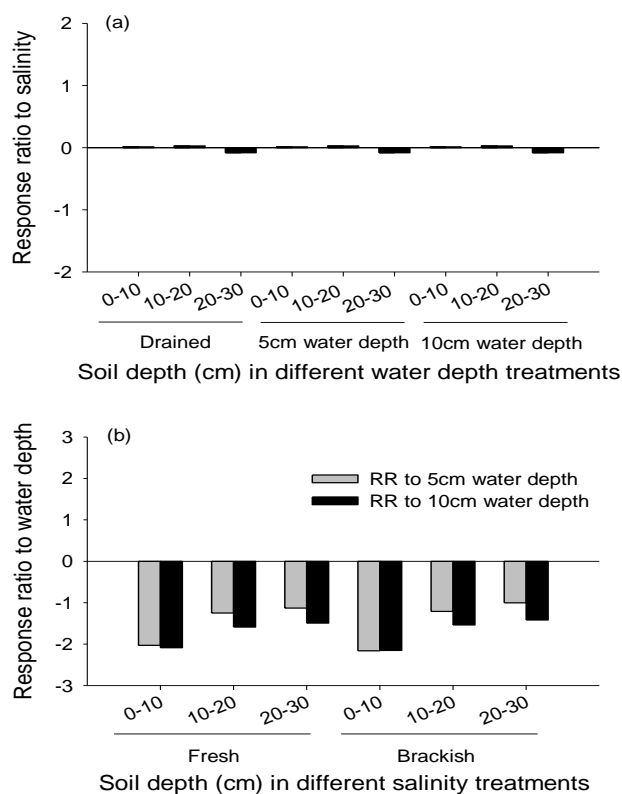


Fig. 8. Response ratio (RR) of *S. salsa* belowground biomass within different soil depth ranges to salinity (Panel a; under each water depth treatment and within each soil depth range) and RR to water depth (Panel b; under each salinity treatment and within each soil depth range).

Table 3. Summary of ANOVAs examining the effects of salinity (fresh (0PSU) and brackish (10 PSU)), water depth (drained, 5cm and 10cm) on belowground biomass of *P. australis* and *S. salsa* within different soil depth ranges (0-10 cm,10-20 cm and 20-30 cm). Significant level: $p < 0.05$.

Source of variance	df	F	P
<i>P. australis</i> , 0-10cm soil depth			
Salinity	1, 24	6.077	0.021
Water depth	2, 24	1.941	0.166
Salinity × Water depth	2, 24	0.878	0.429
<i>P. australis</i> , 10-20cm soil depth			
Salinity	1, 24	19.429	<0.001
Water depth	2, 24	5.669	0.010
Salinity × Water depth	2, 24	0.020	0.981
<i>P. australis</i> , 20-30cm soil depth			
Salinity	1, 24	28.229	<0.001
Water depth	2, 24	22.294	<0.001
Salinity × Water depth	2, 24	10.891	<0.001
<i>S. salsa</i> , 0-10cm soil depth			
Salinity	1, 24	0.002	0.963
Water depth	2, 24	141.371	<0.001
Salinity × Water depth	2, 24	0.029	0.972
<i>S. salsa</i> , 10-20cm soil depth			
Salinity	1, 24	0.063	0.804
Water depth	2, 24	38.501	<0.001
Salinity × Water depth	2, 24	0.002	0.999
<i>S. salsa</i> , 20-30cm soil depth			
Salinity	1, 24	0.054	0.818
Water depth	2, 24	23.317	<0.001
Salinity × Water depth	2, 24	0.093	0.912

Conclusions

Our experimental results demonstrated that: (1) belowground organs of *P. australis* responded negatively to both increased salinity and water depth, whereas belowground organs of *S. salsa* mainly responded negatively to increased water depth; (2) belowground biomass of *S. salsa* responded to increased water depth more strongly than that of *P. australis*, thus *S. salsa* might disappear before *P. australis* in wetlands experiencing prolonged water-logging due to sea level rise; (3) *P. australis* and *S. salsa* responded to increased salinity and/or water-logging by shifting their resource allocations towards aboveground biomass; (4) belowground organs of *P. australis* tended to have more negative responses to increased salinity and water depth at deeper soil depths, which would hinder *P. australis* from utilizing resources in deeper soil, resulting in further suppression of below- and aboveground growth of *P. australis*; in contrast, belowground organs of *S. salsa* tended to have more negative responses to increased water depth at shallower versus deeper soil depths, which would greatly decrease the overall root density and thereby increasing the chance of uprooting disturbance to *S. salsa*.

Our results suggest that different coastal wetland plant species may or may not be sensitive to increased salinity and water-logging, and the magnitude of these stressor's impacts on plant species may vary. Thus, predictions of sea level rise impacts on coastal wetlands should take into account the specific characteristics of different plant species and their responses to stressors. Our study also indicated that even moderate increases in

salinity and water depth, which likely occurs in early-stage sea level rise, would significantly suppress the growth of belowground organs of *P. australis* and *S. salsa*, and thus their abilities to build and bind sediments would likely be compromised (Deegan *et al.*, 2012). This in turn might accelerate sediment erosion and loss, making it even more difficult for *P. australis* and *S. salsa* to keep pace with sea level rise, which would lead to an adverse positive feedback between sea level rise and performance of *P. australis* and *S. salsa*, resulting in faster deterioration of coastal wetlands under sea level rise than otherwise expected.

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