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Fluctuating saline conditions favor competition of *Bolboschoenus planiculmis*, a dominant species in inland salt marshes

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Abstract

Background The changing hydrological conditions in wetland ecosystems are often accompanied by salt fluctuations. However, how fluctuating salt conditions affect growth and interspecific competition of dominant plants in wetlands remains unclear. This study aims to investigate the response of growth and competitive ability of a dominant species in inland salt marshes, *Bolboschoenus planiculmis*, under different salt conditions and test if *B. planiculmis* is more adapted to the fluctuating salt environments.

Methods We quantified the growth indices and competitive response of *B. planiculmis* and two other dominant species *Phragmites australis* and *Suaeda salsa* under five salt treatments (control, constant NaCl, constant mixed salt, pulsed increase of mixed salt, and fixed increase of mixed salt) and two competition treatments (no competition and interspecific competition) in a greenhouse experiment.

Results We found that the total biomass of *B. planiculmis* was significantly higher under the mixed salt treatments compared to the NaCl treatment, and was more advantageous than *S. salsa* in the mixed salt treatments when competing with it. Fluctuating mixed salt treatments significantly increased the total biomass of *B. planiculmis* more than the constant mixed salt treatment. Particularly, *B. planiculmis* benefited more than *P. australis* or *S. salsa* in competition. Moreover, the competitive response of *B. planiculmis* was stronger than the other two species in the fluctuating mixed salt treatments, although the biomass of *B. planiculmis* was lower than the other two species.

Conclusion Our results demonstrated that fluctuating salt conditions prioritized interspecific competition of *B. planiculmis*. We support the competition-to-stress hypothesis that the competition ability rather than salt stress tolerance was the main determinant of species survival in fluctuating salt with a less stressful survival condition. Our study provides important information in understanding community composition changes and restoration of degraded salt marshes.

Keywords Competition-to-stress hypothesis, Competitive response, Fluctuating salt, *Phragmites australis*, *Suaeda salsa*, Wetland

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Introduction

Salinization is an increasingly serious problem due to the superimposed effects of human activities and global climate change (Hassani et al. 2021; Ondrasek and Rengel 2021). Wetland ecosystems are affected by salinization as climate change leads to more frequent flooding and drought events. Concurrently, human interventions, particularly unsustainable agricultural water management practices (Jolly et al. 2008; Short et al. 2016) and the extraction of freshwater resources (Herbert et al. 2015), significantly disrupt natural hydrological regimes in wetlands. These combined climatic and anthropogenic drivers have resulted in pronounced fluctuations in wetland salinity which greatly affect plant growth and community composition.

In general, it is difficult for plants to survive in high salinity environments, although adaptation over time is possible, as long as the plants are growing within their tolerance range (Flowers and Colmer 2008; Fang et al. 2021). Fluctuating salt conditions may provide opportunities for plants to buffer and adapt to environmental stress (Bompy et al. 2014). It has been found that daily fluctuating salt levels can be beneficial to the growth of salt marsh plants (Ma et al. 2022; Wang et al. 2020), e.g. the significant increases in the stem, leaf, and total biomass of *Bruguiera gymnorhiza* seedlings by adding 0–30 PSU fluctuation of natural sea salt (Wang et al. 2020). Plants may also optimize their biomass allocation to maintain basic growth under environmental stress conditions (Thornley 1972; Gedroc et al. 1996; Wright and McConnaughay 2002; McCarthy and Enquist 2007; Liu et al. 2021). Nonetheless, the response of wetland plants in terms of growth and biomass allocation under fluctuating salt conditions remains poorly understood.

The interaction of abiotic stress such as flood and high salt with biotic stresses such as competition defined the distribution of wetland plants (Crain et al. 2004; Engels and Jensen 2010). Growth and community composition of species in salt marsh ecosystems are determined not only by changes in saline-alkaline conditions but also by interspecific competition. For instance, *Crinum americanum* can grow in high salinity (about 4–24 ppt), but its growth was reduced by the presence of competitor *Spartina alterniflora* (Nunes and Camargo 2018; Ma et al. 2020). Obligate halophytes, characterized by their inability to compete with glycophytes in non-saline habitats, are exemplified by *Suaeda salsa* (Ungar 1998; He et al. 2017). This species has the capacity to grow alone in low salt habitats, but suffers a clear competitive disadvantage in the presence of *Phragmites australis* or other competitors; therefore, in natural environments *S. salsa* is mainly found in high salt environment (Qi et al. 2018). This leads to the conclusion that the competitive relationship of salt

marsh plants is a function of environmental conditions, where altered salinity regimes can drive shifts in community composition and spatial distribution (Pennings et al. 2005; Engels 2010). This statement is consistent with the competition-to-stress hypothesis, which suggests that only a small set of species has developed physiologic strategies to helping them live in higher salinity and flooding, whereas competition excludes them from the low abiotic stress (Crain et al. 2004; Engels and Jensen 2010). However, the fluctuations in environmental stress may allow pressure release, providing an opportunity for some plant species to improve their competitive ability. Ma et al. (2022) found no significant effects of fluctuating salt on intraspecific competition, but its impact on interspecific competition remains unclear. The previous study has showed that fluctuating conditions alter interspecific competition (Javed et al. 2020), for example, invasive *Wedelia trilobata* under fluctuating water levels outperformed native *W. chinensis* despite both being inhibited by high water. This led us to hypothesize that fluctuating salt conditions may similarly boost the competitive ability of some species, leading to changes in interspecific competition between wetland species. Especially, to date, the competition-to-stress hypothesis under fluctuating salinity-alkaline conditions has not been tested.

Wetland ecosystem salinization can be divided into various classes, including neutral salt and mixed salt situations (Hassani et al. 2021). NaCl is the dominant form of salt in most coastal wetlands, while inland salt marshes are generally typified by a mixture of different salts (e.g. NaHCO₃, Na₂CO₃, Na₂SO₄; Wan et al. 2003; Wang et al. 2009; Pratolongo et al. 2019; An et al. 2021). Plants inhabiting in saline-alkaline marshes face not only the ion stress of high salt concentration, but also the toxic effects of high pH (Ding et al. 2021; An et al. 2021). Plants grown under high salt environment usually exhibit a range of stress-associated traits, such as thicker stalks, lower plant height and limited roots, along with reduced biomass accumulation (Gorai et al. 2007; Pagter et al. 2009; Xiao et al. 2016; Zhou et al. 2015; Liu et al. 2018; Rahman et al. 2021). High alkalinity affects the availability of some mineral nutrients in soil and suppress ion absorption in plants cells, resulting in nutrient deficiency for plants (Li et al. 2010). Therefore, the responses of wetland species to salt stress is highly dependent on the characteristics of their habitats.

Momoge National Nature Reserve located in the Western Songnen Plain of China is a typical inland salt marsh for the region (Liu et al. 2018). Momoge wetland has large annual water depth fluctuations and the degree of salinity changes with the receding and rising of the water level. *Bolboschoenus planiculmis* is a dominant glycophytic species in Momoge and often coexists with *P. australis*

or *S. salsa*. Previous studies found that *B. planiculmis* thrives in the intermediate transitional habitat between *P. australis* and *S. salsa* communities (Zheng 2008; Wang et al. 2023), suggesting *B. planiculmis* may have a strong adaptability to fluctuating salt conditions. In contrast, *P. australis* with the salt-excreting traits (Anjum et al. 2014; Zhang et al. 2023), and *S. salsa* with the salt-tolerant characteristics have evolved specific adaptations to stable salt environments (Song et al. 2022). These properties enable them more susceptible to disturbances caused by frequent changes in salt levels (Ma et al. 2022; Yu et al. 2022). Therefore, we aim to answer the following questions: (a) does fluctuating salt conditions promote the growth of *B. planiculmis* and enhance its competitive ability compared with *P. australis* and *S. salsa* in inland salt marsh ecosystems? (b) does the competition-to-stress hypothesis also exist under fluctuating salt conditions, and if so, what is the driving factor for species survival, interspecific competition or salt tolerance?

Materials and methods

Study area and plant materials

Momoge National Nature Reserve is located at the confluence of the Songhua River and the Nen River in the Western Songnen Plain, China (123°27'0" to 124°4'33.7" E, 45°42'25" to 46°18'0" N, Fig. S1). It has a semi-arid temperate continental monsoon climate. The average annual temperature is 4.6 °C and the average annual precipitation is 393.8 mm. The soil salt content ranges from 0.66 g kg⁻¹ to 10.44 g kg⁻¹ (Liu et al. 2018). The average pH was 10.65 and the electrical conductivity (EC) was 2441 µS cm⁻¹. The average total nitrogen was 0.39 g kg⁻¹ and total phosphorus was 0.24 g kg⁻¹ (Zhang et al. 2022). The Nen River flows through for 111.5 km, and the basin area is 30000 km². Reflecting the seasonal interplay of precipitation and river flow, the optimal water levels for wetland vegetation growth are 1.23 m in wet periods, 0.99 m in normal periods, and 0.81 m in dry periods (Liu et al. 2018, 2020). Water depth was 10 cm or less during the spring and autumn dry periods, with *S. salsa* as the dominant species. *P. australis* was the dominant species when the water depth increased to more than 30 cm during the rainy summer. *B. planiculmis* is a dominant glycophytic species when the water level was in 10 to 30 cm at the alternate seasons in Momoge and often coexists with *P. australis* or *S. salsa* (Liu et al. 2018; Zhang et al. 2020, 2022; An et al. 2022). *P. australis* is a recretohalophyte (plant which eliminates excess salts via salt glands) that tends to dominate high water level and low salt environments, while *S. salsa* is a halophytic species that tends to inhabit low water and high salt environments (An et al. 2019).

Three dominant species *B. planiculmis*, *P. australis* and *S. salsa* were used in this study. Over 100 g seeds of *S. salsa* were collected from the dominant communities in the Momoge wetland in Autumn 2019. Seeds with full grain were selected for seedling cultivation in plastic trays with peat soil. Bulbs of *B. planiculmis* and rhizomes of *P. australis* were excavated from Momoge wetland in June 2020. Similar size of *B. planiculmis* bulbs and *P. australis* rhizomes were selected and planted into trays to cultivate seedlings from 14 July to 4 August 2020. We propagated the species on different dates to ensure that the seedlings were of a similar developmental stage at the start of the experiment. The cultivated seedlings were watered twice a day to provide enough soil moisture. The experiment was carried out in the greenhouse of Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences (43°59'49.3" N, 125°24'03.6" E).

Experimental design and implementation

To test the responses of the three species to competition and fluctuating salt conditions, two competition treatments and five salt treatments were used. The competition treatments included the three species under conditions of either no competition or interspecific competition between *B. planiculmis* and *S. salsa*, or between *B. planiculmis* and *P. australis* (each as target species and competitor for statistical purpose, Fig. 1a). The interspecific competition of *S. salsa* and *P. australis* was excluded because the two species do not coexist in the natural ecosystems of the Momoge wetland. We set up five salt treatments for *B. planiculmis* based on its habitat with dynamic salinity and alkalinity, focusing on the types and addition way of salt. The salt treatments included: (a) control (CK), (b) constant NaCl (NaCl), (c) constant mixed salt (CMS), (d) pulsed increase of mixed salt (PIMS), and (e) fixed increase of mixed salt (FIMS; Fig. 1b). In the mixed salt treatments, we used a 2:1 molar ratio of NaHCO₃ and NaCl, based on the composition of the highest soil salt conditions in the Momoge wetland (Liu et al. 2018). There were six replicates for each treatment.

On 16 August 2020, 150 seedlings of *B. planiculmis* and 90 seedlings of *S. salsa* and *P. australis* with similar-size were selected and transplanted into 2.5 L circular plastic pots with a 1:1 mixture of sand and fine vermiculite mixed with 6 g slow-release fertilizer (Osmocote Exact Standard; 15% N+9% phosphorus pentoxide+12% potassium oxide+2% magnesium oxide+0.02% B+0.05% Cu+0.45% Fe+0.09% chelated by EDTA+0.06% Mn+0.02% Mo+0.015% Zn; Everris International B.V., Geldermalsen, The Netherlands). There was one seedling in each pot in the no competition treatments and two seedlings in each pot in the interspecific competition

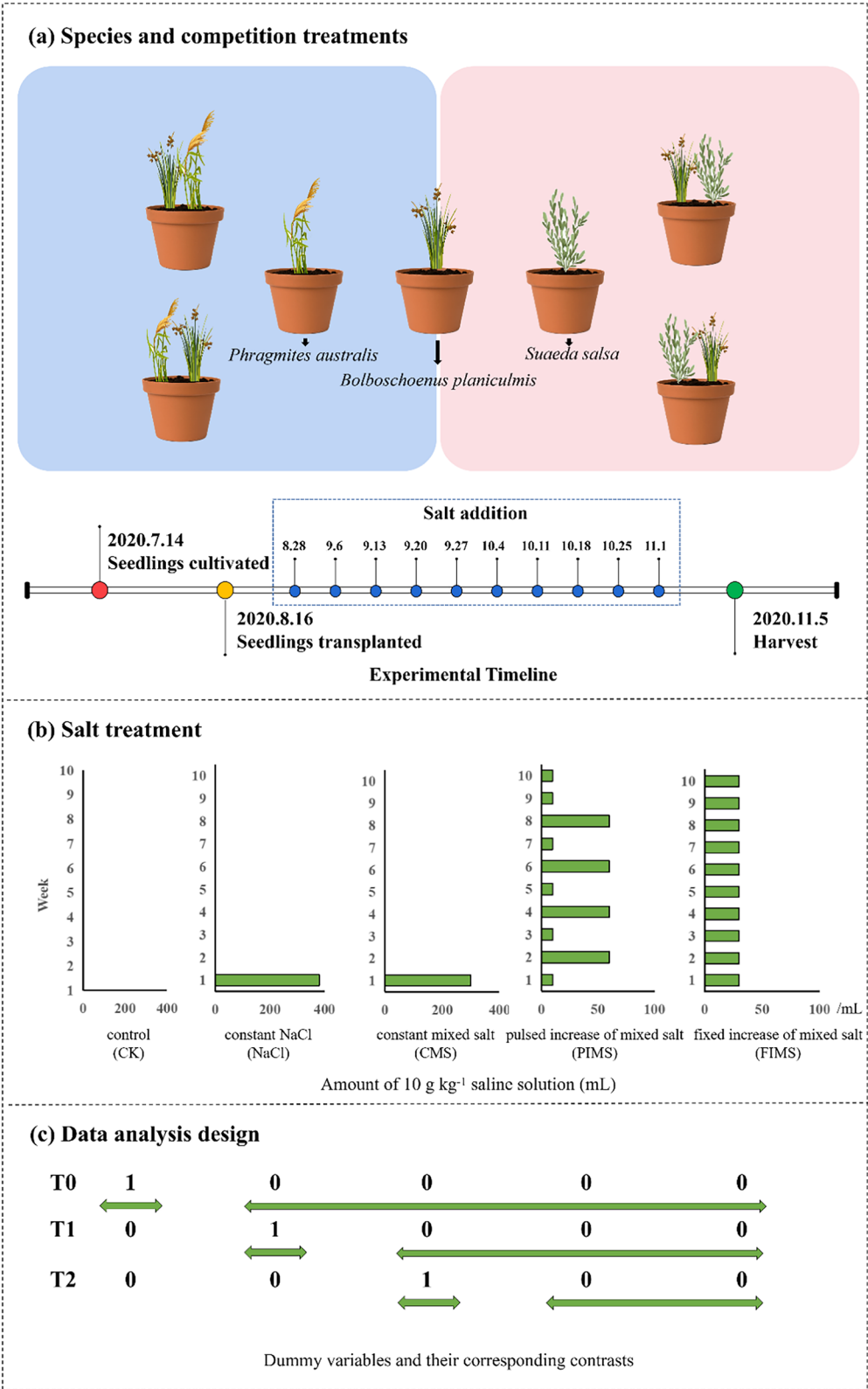


Fig. 1 Graphical illustration of the experimental design and data-analysis design

treatments (Fig. 1a). As *B. planiculmis* and *P. australis* are clonal and produce ramets, the mother plants were tagged in each pot. The pots were also tagged with different treatments and randomly assigned to positions on a greenhouse bench in a fully randomized design. The position of the pots was randomly changed again on 15 October. To avoid the leakage of nutrient and salt from the pots after watering, we put a plastic dish underneath each pot and poured excess water back into the pot.

The salt solution was applied to the seedlings from the second week after transplanting. In order to keep the same amount of total salt contents in all salt treatments, we applied a total of 10 g kg⁻¹ salt content in each pot, the specific applied schedule was shown in supplementary material and Table S1. Salt solutions of 380 mL and 300 mL were added in four times to the pots of NaCl and CMS treatments in the first 2 days of the first salt application week. Changed amount of salt solutions (10/60 mL) was added to the pots of PIMS treatment and the same amount of salt solutions (30 mL) was added to the pots of FIMS treatment each week for 10 weeks, totally 300 mL mixed salt solutions (Fig. 1b, Table S1). Each time we applied salt solutions, water was supplemented to the largest amount of the applying salt solutions for all pots. For example, for the week of 60 mL mixed salt added to pots of PIMS treatment, 30 mL additional water was added for FIMS treatment and 60 mL water was added for CK, NaCl and CMS treatments. Water was supplied as necessary throughout the experimental period, and supplemental light was supplied to ensure a 14 h light period per day for plants. Soil was sampled from each pot on 24 September and on 5 November to measure pH values and EC in order to better understand soil salt dynamics (Fig. S2).

Measurements

Plant height was measured during the experimental period as a measure of plant growth. In order to obtain the growth of plant height during the experimental period, we measured the initial absolute plant height on the second day after the experiment began. The experiment lasted for 80 d and was terminated on 5 November (Fig. 1a timeline). Immediately prior to harvest, we measured the absolute plant height and base stem diameter with vernier calipers and recorded the number of ramets for *B. planiculmis* and *P. australis*. Above-ground parts of the three species in all treatments were harvested and put into envelopes. The below-ground parts of all plants were washed from the soil and stored in plastic bags with distilled water in a 4 °C refrigerator. Since the below-ground part of *B. planiculmis* includes the bulbs, rhizomes and roots, and that of *P. australis* includes the rhizomes and roots, we separated them to each part to

obtain their dry mass. It was not difficult to separate the below-ground parts of the two plants in competition treatments because the below-ground morphology of the three plants differed greatly. The samples were dried at 65 °C for 72 h and then weighed. The above-ground biomass, biomass of bulb, rhizome and root were measured and below-ground biomass (bulb biomass + rhizome biomass + root biomass) and total biomass (above-ground biomass + below-ground biomass) were calculated.

The competitive response (CR) was used to quantify the ability of a species to withstand the limiting effects of competition from its neighbors (Goldberg and Landa 1991; Weigelt and Jolliffe 2003; Wang et al 2010). It was calculated as:

$$CR_T = \ln(TB_{\text{comp}}/TB_{\text{no comp}})$$

where TB_{comp} and $TB_{\text{no comp}}$ are the total biomass of plant in the competition and no competition treatments, respectively, and CR_T is the competitive response of plant total biomass. Smaller values of CR_T indicate a greater negative effect of competition (Weigelt and Jolliffe 2003; Wang et al. 2014).

Statistical analysis

To test for differences in growth performance and competitive response between species in different salt treatments, we fitted general linear models and generalized linear models using the *lm* and *glm* function in the R package “lme 4” (Pinheiro et al. 2023) in R 4.0.3 (R Core Team 2020). Above-ground biomass, below-ground biomass, total biomass, height increment, stem diameter and competitive response were the response variables in the *lm* model. The number of ramets was the response variable in the *glm* model. To satisfy the assumption of normality, all biomass data were natural-log transformed. Poisson (*B. planiculmis* vs *P. australis*) and negative binomial distribution (*B. planiculmis* vs *S. salsa*) was used for number of ramets. In all models, we included species (*B. planiculmis* vs *P. australis* or *B. planiculmis* vs *S. salsa*), salt level (control vs salt stress), salt type (NaCl vs mixed salt), salt variation (constant salt vs fluctuating salt), competition treatment (no competition vs competition) and their interactions as fixed effects. Because salt type and salt variation were nested within the salt level, with the salt supply patterns coded as dummy variables T0–T2 (Fig. 1c) in all models to obtain treatment contrasts (Schieleth 2010). As there was no significant difference between the PIMS and FIMS treatments (Table S4), we combined them in the statistical analysis representing fluctuating salt treatment. The significance of each response variable under different salt comparisons was analyzed by ANOVA (type=3) in the package “car” (Fox and Weisberg 2018) with the significance level set at 0.05.

We drew the figures in the package “ggplot2” in R (Wickham 2016).

Results

Species biomass under competition and different salt treatments

In the competitive combination of *B. planiculmis* and *P. australis*, the total biomass of *P. australis* was significantly higher than that of *B. planiculmis*, regardless of treatment ($P < 0.05$; Table 1; Fig. 2a, b, and c). However, the biomass of *P. australis* decreased by 31.2% and that of *B. planiculmis* increased by 25.1% in the competition treatment, leading to significant biomass differences between the two species under the competition treatments (Table 1). Salt treatments reduced total biomass by an average of 51.3% for both species compared with controls (Table 1; Fig. 2a), whereas the fluctuating mixed salt treatment resulted in an average increase of 97.6% in total biomass compared with the constant treatment, this was especially evident in the below-ground organs with a 99.5% increase (Table 1; Fig. 2c and Fig. S3f).

In the competitive combination of *B. planiculmis* and *S. salsa*, the above-ground and total biomass achieved

by *S. salsa* was significantly higher than that of *B. planiculmis*, but its below-ground biomass was significantly lower than that of *B. planiculmis*, regardless of treatments (Table 1 and Table S2; Fig. 2d, e, f and Fig. S3j, k, l). The salt treatment significantly increased the total biomass of *S. salsa* by 7.9%, but it decreased *B. planiculmis* by 38.2% (Table 1; Fig. 2d). Compared with the NaCl treatment, the mixed salt treatment significantly increased the total biomass of *B. planiculmis* in no competition by 35.7% and competition caused 91.8% more biomass increases, whereas total biomass of *S. salsa* decreased under mixed salt compared with NaCl treatment much smaller in competition treatment by 10.6% than no competition treatment by 49.5%. Compared with the constant salt treatment, the fluctuating salt treatment significantly increased the total biomass of *B. planiculmis* and *S. salsa* in no competition by 67.1% and 214.6%, respectively, and the interspecies competition caused more total biomass increases in *B. planiculmis* by 262.7% than *S. salsa* by 24.9% (Table 1; Fig. 2f).

Table 1 The results of the general linear model testing the effects of different salt treatments and competition on the total biomass (natural-log transformed) of target species in *Bolboschoenus planiculmis* and *Phragmites australis* competition group and *B. planiculmis* and *Suaeda salsa* competition group

Fixed effects	Total biomass of target species in <i>B. planiculmis</i> and <i>P. australis</i> group			Total biomass of target species in <i>B. planiculmis</i> and <i>S. salsa</i> group		
	df	F	P	df	F	P
Species (S)	1	49.732	< 0.001	1	26.544	< 0.001
Com (C)	1	2.768	0.099	1	3.691	0.057
CK vs Salt (T0)	1	11.368	0.001	1	9.948	0.002
NaCl vs Mixed salt (T1)	1	0.382	0.538	1	0.334	0.565
Constant salt vs Fluctuating salt (T2)	1	6.607	0.012	1	5.782	0.018
S × C	1	16.456	< 0.001	1	4.714	0.032
S × T0	1	1.008	0.318	1	4.656	0.033
S × T1	1	0.379	0.539	1	14.723	< 0.001
S × T2	1	0.002	0.967	1	5.694	0.019
C × T0	1	0.143	0.707	1	0.309	0.580
C × T1	1	0.004	0.950	1	0.001	0.973
C × T2	1	0.356	0.552	1	9.900	0.002
S × C × T0	1	0.147	0.702	1	0.248	0.619
S × C × T1	1	1.734	0.191	1	4.092	0.046
S × C × T2	1	0.126	0.724	1	21.345	< 0.001
	SD			SD		
Residuals	0.4074			0.4361		
R ² of the model	0.6150			0.6734		

The model performance is characterized by the residual standard deviation (SD) and the coefficient of determination (R^2). The degrees of freedom (df) indicate the independent information used in statistical tests. The F-value represents the ratio of between-group variance to within-group variance. The P-value quantifies the statistical significance of the treatment effect. Significant effects ($P < 0.05$) are in bold

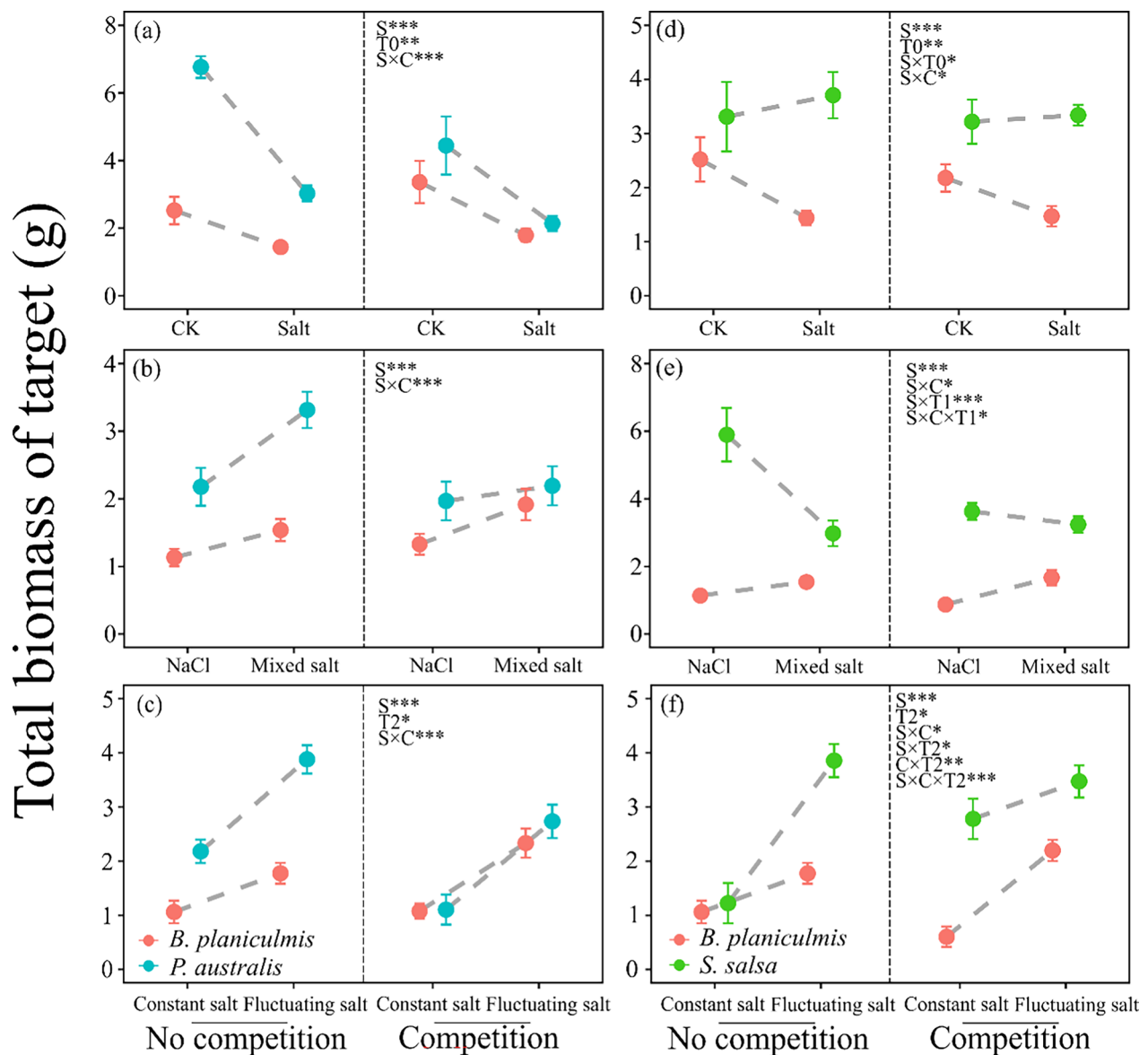


Fig. 2 Mean ($\pm$ SE) values of total biomass of target species in *Bolboschoenus planiculmis* and *Phragmites australis* competition group and *B. planiculmis* and *Suaeda salsa* competition group influenced by competition and different salt treatment comparisons. Significant effects are presented as follows: $0.01 < P < 0.05$ (*), $0.001 < P < 0.01$ (**), $P < 0.001$ (***)

Competitive ability of species under different salt treatments

There were no significant salt or species $\times$ salt interactive effects on the competitive responses of *B. planiculmis* and *P. australis* (Table 2). However, the species effect was significant, with the competitive response of *B. planiculmis* being significantly higher than that of *P. australis* (Table 2; Fig. 3a, b, c). *B. planiculmis* and *S. salsa* showed complex responsive pattern in different salt modes. The competitive response of *B. planiculmis* and *S. salsa* were both increased in the mixed salt treatment compared with the NaCl

treatment, and the *S. salsa* increased more than that of *B. planiculmis* (Table 2; Fig. 3e). The competitive response of *B. planiculmis* increased in the fluctuating mixed salt treatment compared with the constant mixed salt treatment, but that of *S. salsa* decreased (Table 2; Fig. 3f).

Discussion

The greater tolerance of *B. planiculmis* to alkaline salt promotes its growth in competitive condition

Salt stress, especially salt type, can significantly influence the growth and competition of different plant

Table 2 The results of the general linear model testing the effects of different salt treatments on the competitive response calculated by total biomass in *Bolboschoenus planiculmis* and *Phragmites australis* competition group and *B. planiculmis* and *Suaeda salsa* competition group

Fixed effects	Competitive response of target species in <i>B. planiculmis</i> and <i>P. australis</i> group			Competitive response of target species in <i>B. planiculmis</i> and <i>S. salsa</i> group		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Species (S)	1	19.894	< 0.001	1	6.615	0.013
T0	1	0.216	0.645	1	0.632	0.430
T1	1	0.025	0.875	1	0.097	0.757
T2	1	0.849	0.361	1	20.615	< 0.001
S × T0	1	0.181	0.673	1	0.906	0.346
S × T1	1	1.684	0.200	1	7.591	0.008
S × T2	1	0.049	0.826	1	33.771	< 0.001
	SD			SD		
Residuals	0.4799			0.4506		
<i>R</i> ² of the model	0.3690			0.4715		

The model performance is characterized by the residual standard deviation (SD) and the coefficient of determination (*R*²). The degrees of freedom (*df*) indicate the independent information used in statistical tests. The *F*-value represents the ratio of between-group variance to within-group variance. The *P*-value quantifies the statistical significance of the treatment effect. Significant effects (*P* < 0.05) are in bold

species (Liu et al. 2019; Guo et al. 2023). *B. planiculmis* is beneficial in mixed alkaline salts, compared with the same salt content, especially competing with *P. australis* or *S. salsa* (Fig. 2b, e). It is well documented that salts have a negative effect on glycophytic species like *B. planiculmis* and *P. australis* that do not often grow in high-salt environments (West et al. 2004; Yang et al. 2011; Arif et al. 2020; Basu et al. 2021; Rahman et al. 2021). Previous study found that both species *B. planiculmis* and *P. australis* can inhabit low saline and alkaline soils, but *B. planiculmis* seems more alkaline salt tolerate than *P. australis* (Hroudová et al. 2014). There was some evidence showing that *P. australis* will die when the mixed salt content exceeded 10 g kg⁻¹ with a molar ratio of NaHCO₃ and NaCl of 3:1 in soils, whereas *B. planiculmis* can still survive in such high saline-alkaline conditions (Liu et al. 2018; An et al. 2021). This suggests that *B. planiculmis* has a higher tolerance to alkaline salts than *P. australis*. As to *S. salsa*, it can thrive well in high salinity environments (Song and Wang 2015), but alkaline salt ions (e.g. HCO₃⁻) do great harm to this species (Li et al. 2019). Our results are consistent with this finding, showing that the biomass of *S. salsa* greatly reduced in the alkaline salt treatment. Therefore, although the biomass of *B. planiculmis* is still lower than that of the other two species under saline-alkaline stress, its stronger tolerance to alkaline stress confers an advantage in competitive conditions.

***B. planiculmis* has a competitive advantage under fluctuating mixed salt conditions**

The results of fluctuating salt in the study represent the combination of pulsed increase (PIMS) and fixed increase of mixed salt (FIMS), because there was no significant difference between the two fluctuation conditions of PIMS and FIMS (Table S4). One possible reason is that the pulsed amount (10–60 mL, equivalent to soil salt content from 0.3 to 2 g kg⁻¹) and fixed amount (30 mL, equivalent to soil salt content 1 g kg⁻¹) used in PIMS and FIMS was not enough to create a noticeable difference over the 10 weeks (Table S1; Fig. S2). Additionally, with a pulsed frequency of 1 week, the stress from the previous week was only partially re-established by the second week. For instance, plants that had adapted to high salt stress during a peak pulse may not fully adjust their growth response to the stress of the current pulse due to the short interval between pulses. As a result, they may enter the next pulse peak before their new adaptation strategy occurred, meaning the effects of different pulses were not fully manifested.

Although there are many studies addressing natural salt and mixed salt effects on plants, our understanding of how the fluctuating saline-alkali stress may affect plant growth and competition remains weak (Ondrasek et al. 2022; Hao et al. 2021). Our results showed that the biomass of the three species all increased in the fluctuating mixed salt treatment, compared with the constant mixed salt treatment (Fig. 2c, f). This was likely due to the

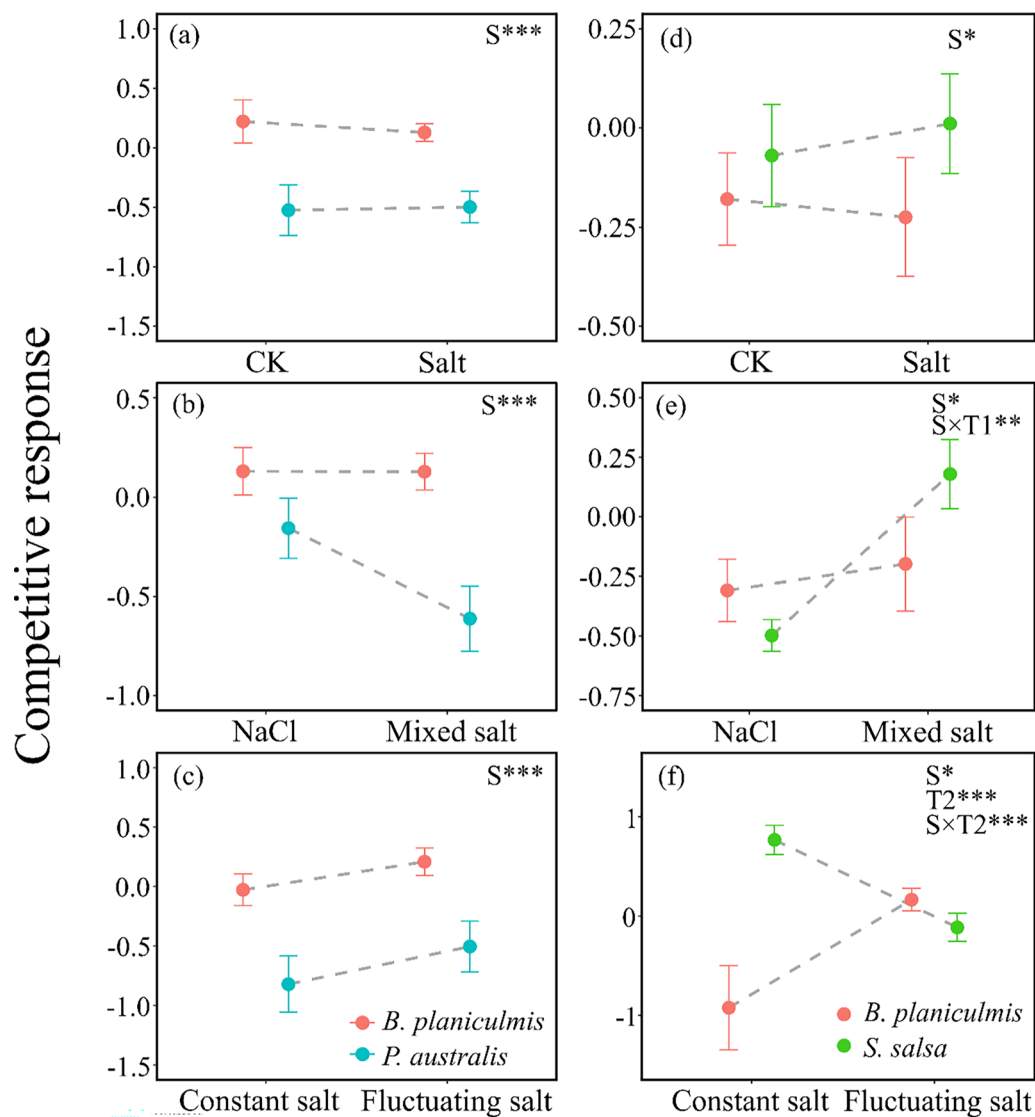


Fig. 3 Mean ($\pm$ SE) values of competitive response of target species calculated by total biomass in *Bolboschoenus planiculmis* and *Phragmites australis* competition group and *B. planiculmis* and *Suaeda salsa* competition group under different salt treatment comparisons. Significant effects are presented as follows: $0.01 < P < 0.05$ (*), $0.001 < P < 0.01$ (**), $P < 0.001$ (***)

negative “salt shock” effect of a one-time addition of salt to the entire growth system by constant mixed salt treatment (Shavrukov 2013). However, the salt content of the whole system was not in the state of high salt in the fluctuating salt conditions, therefore, the fluctuating mixed salt treatment can bring the plant a gradual adaptation of salts, allowing the plant to become gradually accustomed to it and grow better. But different species have different response extent to the fluctuating mixed salts when grow in mixture (Figs. 2c, f, 3c, f). As shown in our results, *B. planiculmis* gained a competitive benefit in fluctuating mixed salt conditions when competing either *P. australis* or *S. salsa* (Figs. 2c, f, 3c, f). The competitive advantage of

B. planiculmis was related to greater stem diameter in the above-ground part (Table S3; Fig. S4f, S5f; Álvarez et al. 2012) and higher biomass of bulbs and rhizomes in the below-ground part (Fig. S6; Ding et al. 2021) than those parameters of *P. australis* and *S. salsa* under competition in the fluctuating mixed salt treatments. These strategies can help to explain why *B. planiculmis* performed better than the other two species in fluctuating mixed salt conditions. Therefore, the fluctuating saline-alkaline environment is beneficial for the growth of *B. planiculmis*, although the biomass was lower than that of other competitor, the competitive ability of *B. planiculmis* was dramatically improved when grown in the mixture.

Plants follow the competition-to-stress hypothesis under fluctuating salt conditions

Our results are consistent with the competition-to-stress hypothesis which states that most species are excluded from high abiotic stress environments by their lack of adaptation to that stress, whereas competition may exclude other species from low abiotic stress systems (Crain et al. 2004; Engels and Jensen 2010). In our study, the fluctuating salt provided a less stressful survival condition for plants. This means that competition ability rather than salt stress tolerance was the main determinant of species survival. Our results demonstrated that *B. planiculmis* exhibited a stronger competitive response compared to the other two species in the fluctuating salt conditions (Fig. 3c, f). However, there are conflicting opinions on this hypothesis. For example, Nunes and Camargo (2018) found that the salt-tolerant plant *S. alterniflora* did not live in low-salt environments due to low nutrient availability, rather than competitive pressure. Similarly, Guo and Pennings (2012) found that several halophytes struggled to grow in freshwater habitats even in the absence of competition. These contrasting results suggest that the competition-to-stress hypothesis still remains controversial, but our findings support this hypothesis and provide the experimental evidence under the different saline-alkaline scenarios.

Conclusion

Our results indicated that fluctuating saline conditions favored the growth and competitive ability of *B. planiculmis*. This enhancement was likely due to the positive responses in biomass of bulbs, rhizomes, and stem diameter, as well as a strong competitive response of *B. planiculmis* in fluctuating salt environment. Our study demonstrated that salt stress tolerance was more dominant under high stress conditions (e.g. constant salt), whereas competition ability was the main determinant of species survival in a less stressful survival condition (e.g. fluctuating salt). Therefore, our results support the competition-to-stress hypothesis under different saline-alkaline modes. This study also provides new data for the fluctuating salt studies and important information in understanding the community composition dynamics of coastal wetlands and salt marshes under climate change.

Abbreviations

CK	Control
NaCl	Constant NaCl
CMS	Constant mixed salt
PIMS	Pulsed increase of mixed salt
FIMS	Fixed increase of mixed salt
CR	Competitive response
S	Species
C/Com	Competition
T0	CK vs Salt

T1	NaCl vs mixed salt
T2	Constant salt vs fluctuating salt

Supplementary Information

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Supplementary material 1.

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Author contributions

HZ, YG and CH conceived the idea and designed the experiment. LW and XL performed the experiment. LW and HZ analyzed the data. LW, HZ and YG wrote the manuscript. TZ, AY and WZ reviewed and revised the manuscript. XY and YT performed data verification and analysis.

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Data availability

The data sets used in this study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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