How soil ion stress and type influence the flooding adaptive strategies of *Phragmites australis* and *Bolboschoenus planiculmis* in temperate saline–alkaline wetlands?

Zhi Ding [a,b,c,d], Ying Liu [a,*], Yanjing Lou [e,*], Ming Jiang [e], He Li [f], Xianguo Lü [e]

[a] *The Three Gorges Institute of Ecological Environment, Chongqing Institute of Green and Intelligent Technology, Chinese Academy of Sciences, Chongqing 400714, China*
[b] *Key Laboratory of Geospatial Technology for the Middle and Lower Yellow River Regions, Henan University, Kaifeng 475004, China*
[c] *State Cultivation Base of Eco-agriculture for Southwest Mountainous Land, Southwest University, Chongqing 400715, China*
[d] *Chongqing Jinfo Mountain Field Scientific Observation and Research Station for Kast Ecosystem, Ministry of Education, School of Geographical Sciences, Southwest University, Chongqing 400715, China*
[e] *Key Laboratory of Wetland Ecology and Environment, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130012, China*
[f] *State Key Laboratory of Resources and Environmental Information System, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China*

HIGHLIGHTS

- *P. australis* escaped but *B. planiculmis* kept quiescent from flooding.
- High soil ion stress changed the strategy of *P. australis* to quiescence.
- High alkaline ion stress induced *P. australis* to stay quiescent with flooding.
- However, low alkaline ion stress promoted *B. planicumis* to escape from below water.
- The two marshes may degrade severely under high GHG emissions in the future.

GRAPHICAL ABSTRACT
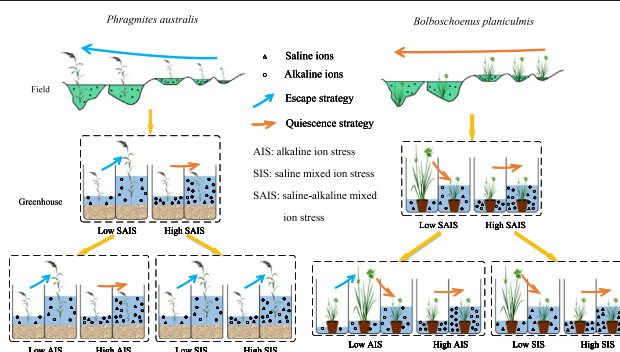
ARTICLE INFO

ABSTRACT

Soil saline–alkaline stress and flooding extremes have been projected to be the main factors influencing the degradation of marsh plants in wetlands worldwide, which would affect their ecological functions (i.e. food source for migrating birds). Plants cope with flooding either by escaping from below water through shoot elongation or by remaining quiescent until water subsides. However, little is known about the adaptive strategies of *Phragmites australis* and *Bolboschoenus planiculmis* to flooding combined with salinity–alkalinity, which are the key environmental filters in Western Songnen Plain, China. Accordingly, this study investigated the adaptive strategies of *P. australis* and *B. planiculmis* subjected to the interacting effects of flooding and soil ion stress under field and greenhouse conditions. Results showed that the two species adopted different strategies to survive flooding. *P. australis* exhibited an escape strategy because of leaf and shoot elongation with increasing flooding depth whereas *B. planiculmis* became quiescent with no or deceased leaf and shoot elongation and biomass accumulation. High soil ion stress changed the flooding adaptive strategy of *P. australis* to a quiescence strategy, whereas *B. planiculmis* remained quiescent with increasing flooding depth at each soil ion content. The strategies of the two species were changed by alkaline ion stress but not by saline ion stress, and they exhibited different adaptive responses. High alkaline ion stress induced *P. australis* to remain quiescent with increasing flooding depth, whereas low alkaline ion stress promoted *B. planicumis* to escape from below water, probably due to the buffer effect of low alkaline ion contents outside the roots probably. Hence, *P. australis* and *B. planicumis* might adopt

* Corresponding authors.
E-mail addresses: liuying311@mails.ucas.ac.cn (Y. Liu), louyj@iga.ac.cn (Y. Lou).

the quiescence strategy with increasing degree of soil salinization and alkalization under high greenhouse gas emissions scenarios in Western Songnen Plain, which may lead to severe degradation of the two kinds of marshes in the future.

1. Introduction

Increasing area and degree of soil salinization and alkalization resulting from intensive farming activities and increasing evaporation rates (Holland et al., 2009; Jolly et al., 2008) have been projected to threaten the ecological function in wetlands worldwide (Xu et al., 2014). Marsh plants, a dominating part of wetland ecosystems, play an irreplaceable role in maintaining ecological functions of wetlands, including water purification, food source for migrating birds and soil structure improvement (Halls, 1997; Keddy, 2010). However, inland saline–alkaline wetlands cannot acquire water supply from the ocean (Wan et al., 2003; Wang et al., 2009). Hence, the plant species in these ecosystems are vulnerable to soil salinization and alkalization, especially those distributed in arid or semi-arid regions (Sun et al., 2000). Understanding the adaptive strategies of salt marsh species to soil salinization and alkalization is important to elucidate the driving mechanism of wetland degradation and protect and manage these vulnerable wetland ecosystems in the future of environmental change.

Flooding regime is a major determining factor affecting wetland plant growth by reducing oxygen availability (Lou et al., 2016; Vervuren et al., 2003; Voesenek et al., 2004). Escape and quiescence are flooding adaptive strategies which allow plants to cope with low oxygen stress (Bailey-Serres and Voesenek, 2008, 2010). The escape strategy involves shoot elongation to restore leaf contract with the atmosphere, but it is costly under low-oxygen conditions (Bailey-Serres and Voesenek, 2008). By contrast, the quiescence strategy is characterized by steady energy conservation without shoot elongation (Bailey-Serres and Voesenek, 2008; Setter and Laureles, 1996). However, flooding accompanied by salinity–alkalinity in saline–alkaline wetlands is a common double source of stress encountered by plants (Li et al., 2017; Liu et al., 2018). Oxygen deficiency caused by flooding may exacerbate ion imbalance (increase Na^+ uptake but prevent K^+ uptake) in tissues due to soil salinity–alkalinity and lead to severe root necrosis or even death (Bazihizina et al., 2012; Munns and Tester, 2008). Although concern about the two flooding strategies has increased, most studies have been focusing on freshwater marsh species, such as Rumex, Lotus and Oryza (Chen et al., 2011; Hattori et al., 2009; Striker et al., 2012). Therefore, whether or not salt marsh plants change their flooding strategies in response to the interacting effects of flooding and salinity–alkalinity remains unclear.

Different from coastal salt marshes suffering from saline ion stress (i.e. Na^+, Cl^-) (Marcum and Murdoch, 1992; Rogel et al., 2000), inner saline–alkaline wetlands are mainly characterized by alkaline ion stress (i.e. HCO_3^-; (Deng, 2011, Liu et al., 2018). Furthermore, besides oxygen deficit, osmotic stress and ionic toxicity that are already exerted by saline stress (Ahmad et al., 2011; Smirnoff, 1993), alkaline stress also exerts high pH stress, which decreased availability of mineral nutrients in plants (Li et al., 2008; Yang et al., 2006; Zhang et al., 2008). Therefore, the toxic effect of alkaline ion stress on plants is more severe than that of saline ion stress (Liu et al., 2018; Shi and Wang, 2005; Yang et al., 2007). Thus, the two ion stresses may have different influences on the flooding adaptive strategy of species. However, few studies have tested this hypothesis.

The Western Songnen Plain is a typical area that has developed inland saline–alkaline wetlands. However, the marshes in this area suffer from severe degradation due to increasing soil saline–alkaline stress and flooding/drought extremes (Cañedo-Argüelles et al., 2014; Garssen et al., 2015). Phragmites australis and Bolboschoenus planiculmis are the dominant species in the Western Songnen Plain. The marshes dominated by these two species are the main stopover for some scarce and critically endangered cranes such as Grus japonensis, G. monacha

and G. leucogeranus (BirdLifeInternational, 2018; Zou et al., 2018). However, little is known about the adaptive strategies of P. australis and B. planiculmis to flooding combined with salinity–alkalinity. Therefore, we examined the adaptive strategies of P. australis and B. planiculmis to the interacting effects of different types and severities of soil ion stress and flooding depth under field and greenhouse conditions. Specific objectives of this study are to answer the following questions: (1) which flooding adaptive strategy (escape or quiescence) P. australis and B. planiculmis show, respectively, (2) whether soil ion stress changes the flooding adaptive strategy of the two species, and (3) whether alkaline ion stress and saline ion stress have different effects on the flooding adaptive strategy of the two species.

2. Materials and methods

2.1. Study area

The Western Songnen Plain, which is located in the central part of Northeast China, is an alluvial plain of the Songhua, Second Songhua and the Nen Rivers (121°32′3″–126°34′24″ E, 43°57′27″–48°32′57″ N, 110–140 m a.s.l). It has a semi-humid and semi-arid temperate continental monsoon climate with an annual mean air temperature of 2–6 °C, an annual mean precipitation of 350–460 mm and an annual mean evaporation of 1200–1900 mm. The dominant marsh species are Phragmites australis, Deyeuxia angustifolia, Bolboschoenus planiculmis, Typha orientalis and Scirpus validus. The soil types include solonetzic soil, salinized soil, meadow soil, aelian soil, etc. The soil ion content ranges from 0.66 g kg^{-1} to 10.44 g kg^{-1} and HCO_3^-, Na^+, Cl^- and Ca^{2+} are the most abundant ions (Liu et al., 2018).

2.2. Experimental design

2.2.1. Field study

The field work was conducted in 15 marsh sites dominated by P. australis (10 sites) and B. planiculmis (3 sites) or co-dominated by both species (2 sites) in August 2015 (Table A1). Mature leaves (for the measurement of leaf traits), aboveground whole plants (for the measurement of shoot height and shoot biomass), flooding depth and soil samples from the top 20 cm were collected in three plots (0.5 m × 0.5 m) at each site.

2.2.2. Pot experiment

Rhizomes of P. australis and tubers of B. planiculmis were collected in May 2015 from Momoge National Nature Reserve in the Western Songnen Plain (123°39′ E, 45°55′ N), Jilin Province, China. Rhizomes and tubers were soaked in tap water to promote sprouting prior to treatments. Shoots of P. australis with a uniform morphology, specifically 10 cm in height, were transplanted into pots (40 cm in diameter and 55 cm in height) with 20 cm-high washed sand. Similarly, for B. planiculmis, 2–5 cm-high shoots of B. planiculmis were transplanted into pots (14 cm in diameter and 13 cm in height) containing 12.5 cm-high of washed sand. Five shoots were planted in each pot.

Our treatments included three or four flooding depths and five ion contents of three ion types with three replications (Table 1). The treatment of saline–alkaline mixed ion contents was used to compare the flooding adaptive strategies under field and greenhouse conditions. The shoots were watered to maintain the required flooding depths with a modified Hoagland half-strength nutrient solution (see Liu et al., 2018 for detailed information). The nutrient solutions were renewed weekly.

Table 1

Layout of treatments.

Ion stress type	Ion content (g kg^{-1})	Flooding depth (cm)	
P. australis/B. planiculmis	*P. australis/B. planiculmis*	*P. australis*	*B. planiculmis*
Alkaline ion stress (AIS): NaHCO$_3$	0, 2.5, 5, 10, 20	0, 15, 30	−5, 0, 10, 20
Saline ion stress (SIS): NaCl	0, 2.5, 5, 10, 20	0, 15, 30	−5, 0, 10, 20
Saline-alkaline mixed ion stress (SAIS): NaHCO$_3$ + NaCl (mass ratio 3:1)	0, 2.5, 5, 10, 20	0, 15, 30	−5, 0, 10, 20

Mature leaves and aboveground whole plants were sampled for further analyses at the end of the experiments (6 weeks later for *P. australis* and 4 weeks later for *B. planiculmis*). The total number of pots was 315 (5 ion content treatments × 3 ion stress type treatments × (3 + 4) flooding depth treatments × 3 replicates).

2.3. Measurements

The area (LA, cm^2 per leaf) and length (cm per leaf) of the mature leaves and shoot height (cm) were measured before being oven-dried at 70 °C for 72 h. The corresponding leaf dry weight (g per leaf) was measured to calculate the specific leaf area (SLA, LA/LDW, cm^2 g^{-1}). Shoot biomass (g per plant) was measured. Leaf total organic carbon content (LOC, g kg^{-1}) was measured using the K$_2$Cr$_2$O$_7$-H$_2$SO$_4$ oxidation method and leaf total nitrogen content (LTN, g kg^{-1}) was analyzed using the Kjeldahl acid–digestion method (Sparks et al., 1996).

Soil HCO$_3^-$, CO$_3^{2-}$, Cl$^-$, SO$_4^{2-}$, K$^+$, Na$^+$, Ca^{2+} and Mg^{2+} were measured after air drying. The soil ion content per site in the field was the sum of the above eight ions. HCO$_3^-$, CO$_3^{2-}$ and Cl$^-$ were measured using the titrimetric method. K$^+$, Na$^+$, Ca^{2+}, and Mg^{2+} were analyzed using inductively coupled plasma atomic emission spectrometry (ICPS-7500, Shimadzu Corporation, Japan). SO$_4^{2-}$ was measured via ultraviolet spectrophotometry (UV-2550, Shimadzu Corporation, Japan).

2.4. Statistical analyses

The relationships between leaf length/shoot biomass and flooding depth and between SLA/shoot biomass/LOC/LTN and leaf length/shoot biomass in the field and greenhouse were tested separately with linear models. Tukey's *post-hoc* test was used to determine differences between flooding depth within each soil ion content ($P < 0.05$). For the field study, linear mixed-effects models were used to examine the interactions of soil ion content and flooding depth on leaf length/shoot biomass. Soil ion content, flooding depth and species were treated as fixed effects and site was treated as a random effect to account for the spatial variation among different sites. Linear models were used to test the interaction of soil ion content, flooding depth and soil ion type on leaf length/shoot biomass in the greenhouse. All analyses were conducted using R (RDevelopmentCoreTeam, 2017).

3. Results

3.1. Growth responses of P. australis and B. planiculmis to flooding depth

In both the field and greenhouse, leaf length and shoot height of *P. australis* increased significantly with higher flooding depth
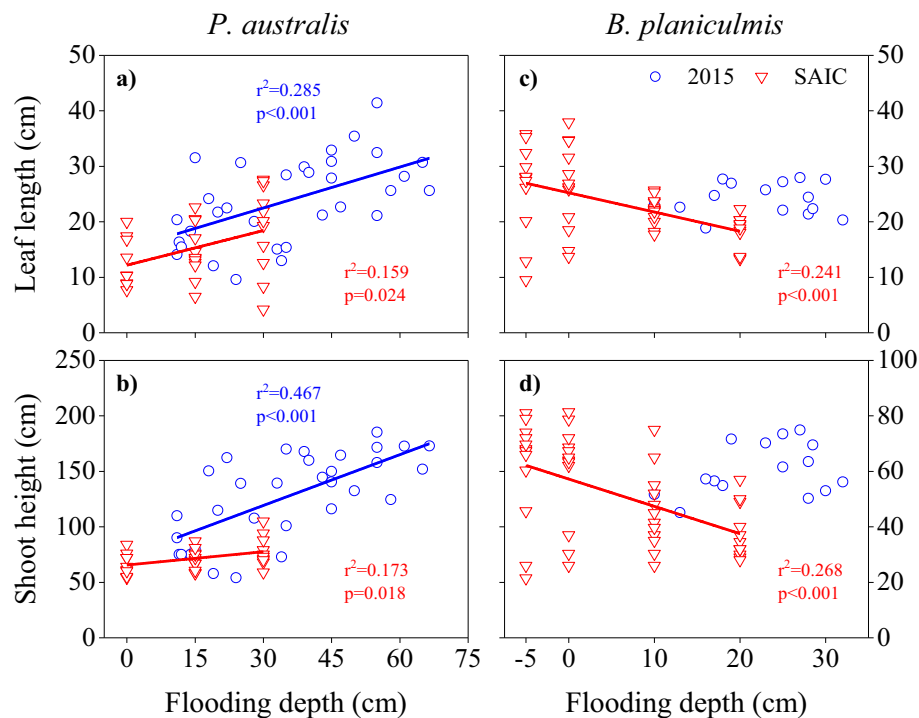

Fig. 1. Leaf length and shoot height of *P. australis* (a–b) and *B. planiculmis* (c–d) in relation to flooding depth in both field of 2015 (blue circles) and greenhouse under saline–alkaline mixed ion contents (SAIC, red triangles). r^2: regression coefficient. (More specific details on the equations of lines are in Table A2).

(Fig. 1a–b, Table A4–5). However, for *B. planiculmis*, leaf length and shoot height were similar in the plants grown in soils of different flooding depth in the field but decreased significantly with increasing flooding depth in the greenhouse (Fig. 1c–d, Table A4–5).

In *P. australis*, SLA, shoot biomass, LOC and LTN increased significantly with increasing leaf length in the field and greenhouse, but no significant relationship was found between leaf length and LOC in the greenhouse (Fig. 2a–d). SLA, shoot biomass, LOC and LTN increased significantly with higher shoot biomass in the field, whereas only shoot biomass and LTN significantly increased with increasing shoot biomass in the greenhouse (Fig. 2e–h). In *B. planiculmis*, SLA, shoot biomass, LOC and LTN exhibited no significant correlations with leaf length and shoot height in the field, whereas SLA, shoot biomass, LOC and LTN increased significantly with increasing leaf length and shoot height in the greenhouse (Fig. 3).

3.2. Flooding adaptive responses to soil ion contents

In the greenhouse, the interaction between high soil ion content (e.g. 20 g kg^{-1}) and low flooding depth (e.g. 0 cm) exerted a negative synergistic effect on the leaf length and shoot height elongation of *P. australis* (Fig. 4a–d, Table A5). In particular, *P. australis* treated at 10 g kg^{-1} saline–alkaline mixed ion stress showed no growth at 0 cm flooding depth and no significant difference in leaf length and shoot height was found between 15 and 30 cm flooding depths (Fig. 4b, d). Similar to those in no ion stress treatment, leaf length and shoot height of *P. australis* at high flooding depth (30 cm) were markedly higher than those at low flooding depth (0 or 15 cm) in 2.5–5 g kg^{-1} saline–alkaline mixed ion stress treatment (Fig. 4a–d).

For *B. planiculmis*, the combination of high soil ion content (e.g. 20 g kg^{-1}) and high flooding depth (e.g. 10 or 20 cm) caused a negative
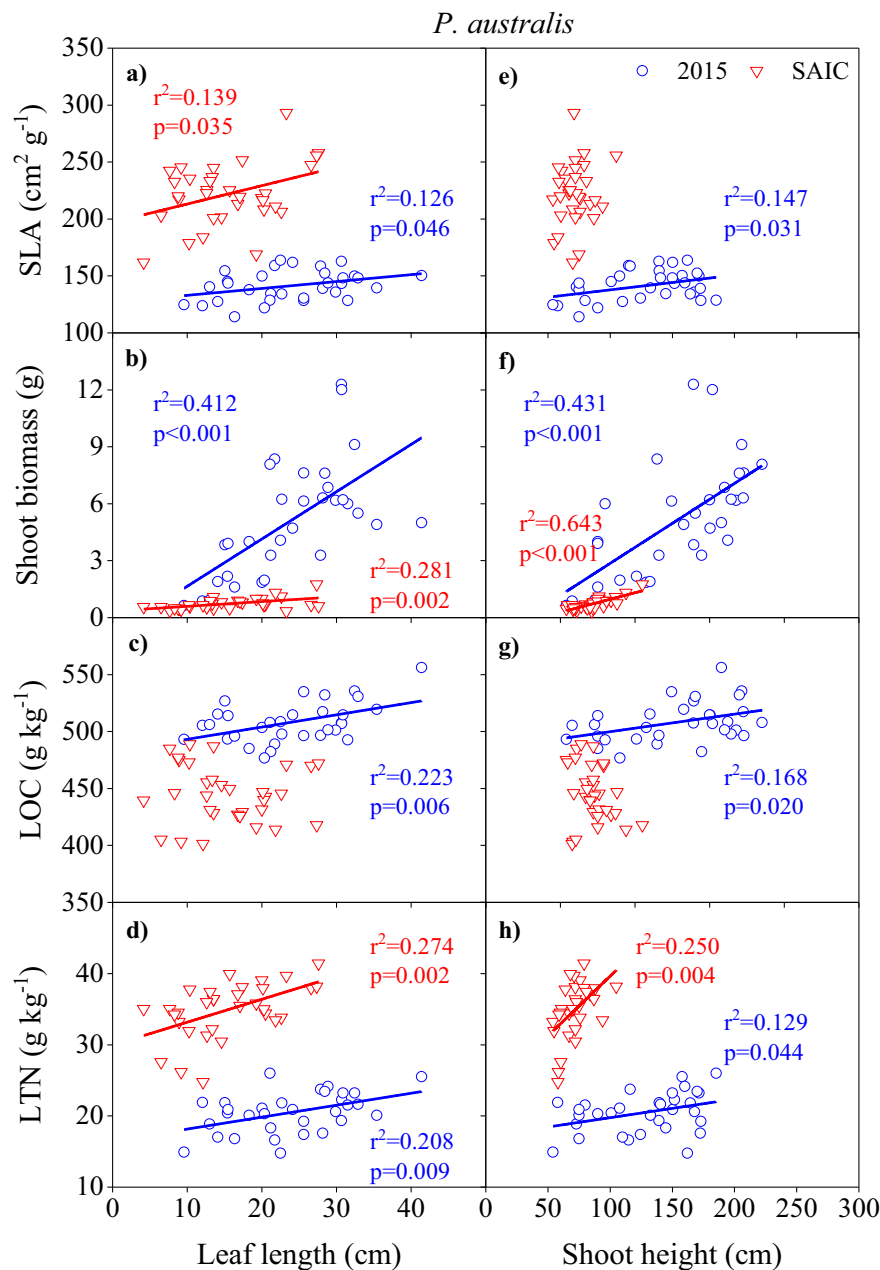

Fig. 2. Specific leaf area (SLA), single shoot biomass, leaf organic carbon content (LOC) and leaf total nitrogen content (LTN) of *P. australis* in relation to leaf length and shoot height in both field of 2015 (blue circles) and greenhouse under saline–alkaline mixed ion contents (SAIC, red triangles). r^2: regression coefficient. (More specific details on the equations of lines are in Table A3).
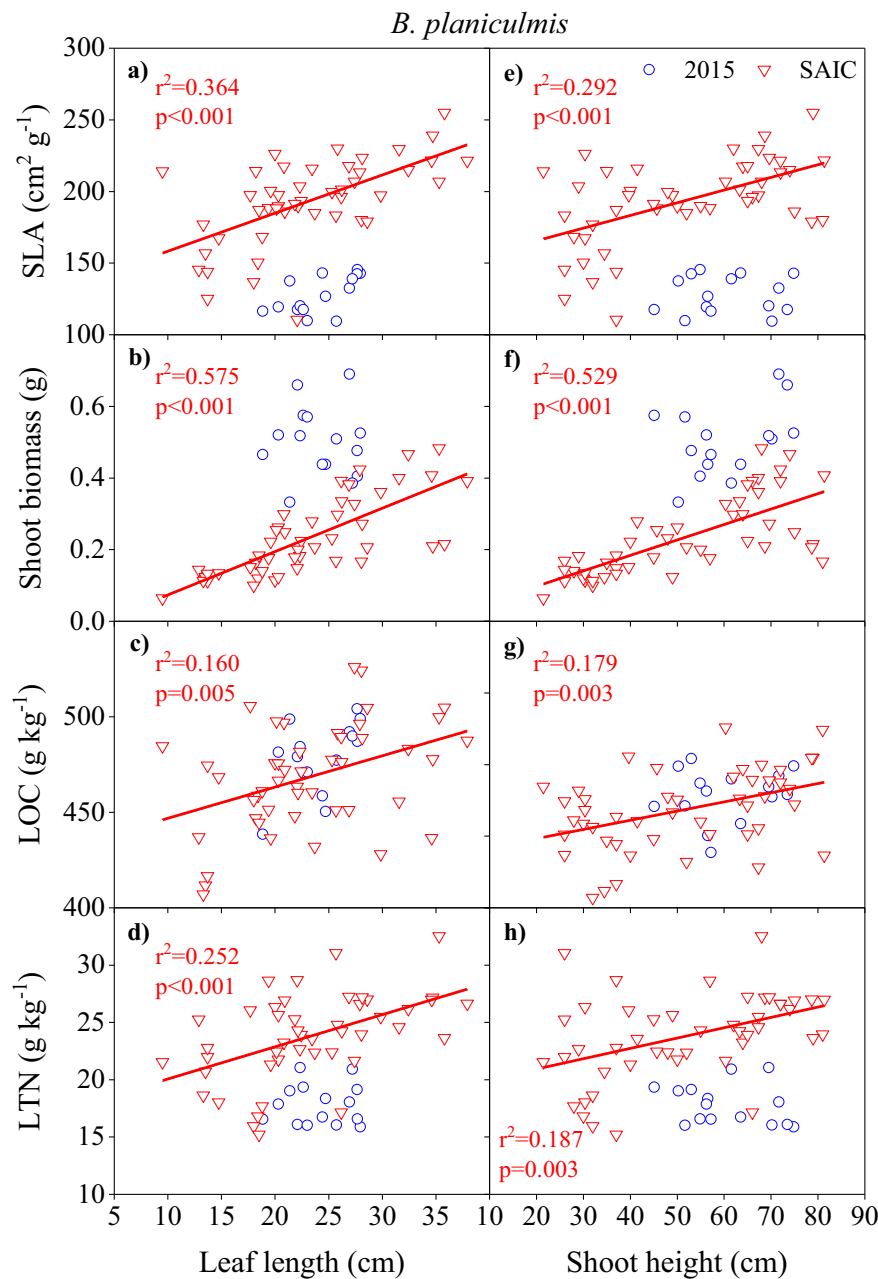
Fig. 3. Specific leaf area (SLA), single shoot biomass, leaf organic carbon content (LOC) and leaf total nitrogen content (LTN) of *B. planiculmis* in relation to leaf length and shoot height in both field of 2015 (blue circles) and greenhouse under saline–alkaline mixed ion contents (SAIC, red triangles). r²: regression coefficient. (More specific details on the equations of lines are in Table A3).

synergistic effect on leaf length and shoot height elongation (Fig. 4f, h, Table A5). *B. planiculmis* treated with 20 g kg⁻¹ saline–alkaline mixed ion stress showed no growth. Leaf length and shoot height at low flooding depth (−5 or 0 cm) were markedly higher than those at high flooding depth (10 or 20 cm) in 2.5–5 g kg⁻¹ saline–alkaline mixed ion stress treatment, similar to those in no ion stress treatment. However, no significant difference in leaf length and shoot height was observed among different flooding depths in 10 g kg⁻¹ saline–alkaline mixed ion stress treatment (Fig. 4e–h).

3.3. Flooding adaptive responses to soil ion types

The interaction of soil ion content, flooding depth and soil ion type exerted significant effects on the growth of *P. australis* and *B. planiculmis* (Table A5). Similar to those in no ion stress treatment,

leaf length and shoot height of *P. australis* increased with increasing flooding depth in 2.5 g kg⁻¹ alkaline ion stress treatment and in 2.5–20 g kg⁻¹ saline ion stress treatment, (Fig. 5a–f). In 5 and 10 g kg⁻¹ alkaline ion stress treatment, *P. australis* died at 0 cm flooding depth and had similar leaf length and shoot height between 15 and 30 cm flooding depth, except that shoot biomass was significantly higher at 30 cm than at 15 cm flooding depth in 5 g kg⁻¹ alkaline ion stress treatment (Fig. 5b, e).

For *B. planiculmis*, leaf length and shoot height decreased with increasing flooding depth in 2.5–5 g kg⁻¹ saline ion stress treatment (Fig. 6a, c, d, f), similar to those in no ion stress treatment. However, no significant difference in leaf length and shoot height was found among different flooding depths in 5 g kg⁻¹ alkaline ion stress treatment and 10–20 g kg⁻¹ saline ion stress treatment (Fig. 6b–c, e–f). *B. planiculmis* died at 20 cm flooding depth in 10–20 g kg⁻¹ saline ion
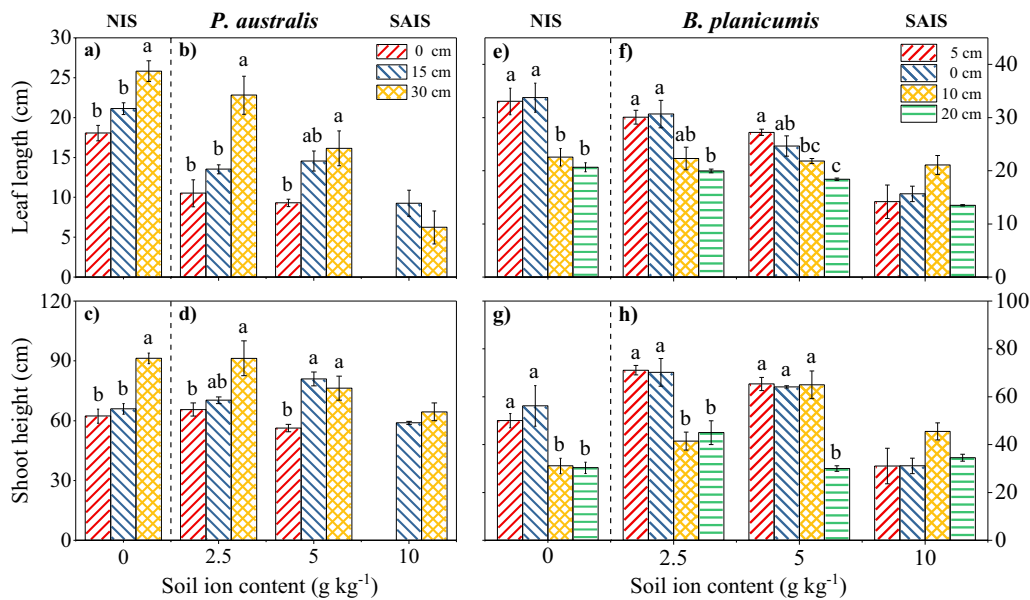
Fig. 4. Effects of flooding stress, no ion stress (0 g kg^{-1}, NIS) and saline–alkaline ion mixed stress (2.5, 5 and 10 g kg^{-1}, SAIS) on leaf length and shoot height of *P. australis* (a–d) and *B. planiculmis* (e–h) grown at different flooding depths (colored bars) in the greenhouse (means ± 1 s.e., n = 3). Different lowercase letters indicate significant differences between flooding depth within each soil ion content ($P < 0.05$). A Tukey *post-hoc* test was used for multiple comparisons.

stress treatment (Fig. 6c, f). In 2.5 g kg^{-1} alkaline ion stress treatment, leaf length and shoot height were the highest at 0 cm flooding depth.

4. Discussion

4.1. Differences in strategies of P. australis and B. planiculmis to deal with flooding depth

Submerged shoots of *P. australis* elongated their shoot height and leaf length with increasing flooding depth (Fig. 1a), indicating that *P. australis* exhibited an apparent escape strategy to cope with flooding. Leaf and shoot elongation is a key attribute in the escape strategy, and an efficient approach that enables plants to survive prolonged flooding (Chen et al., 2009) in the natural habitats of *P. australis* (Liu et al., 2015). However, elongation growth needs carbon and nitrogen to supply energy for basic metabolic processes of plants during complete

submergence (Ram et al., 2002; Sauter, 2000). Thus, increased LOC and LTN with leaf and shoot elongation (Fig. 2c–d, g–h) helped provide more material basis and energy for the growth of *P. australis* under flooding conditions. Furthermore, high LTN indicates a rapid growth rate (Reich et al., 2008), and large SLA improves the photosynthetic rate (Cornelissen et al., 2003) and increases shoot biomass, thereby inducing more organic matter accumulation and promoting the leaves and shoots of *P. australis* to surpass above the water to restore contact with the atmosphere. These results suggest that *P. australis* copes with flooding by using the escape strategy.

Differing from those of *P. australis*, leaf length and shoot height of *B. planiculmis* did not differ along the flooding gradient in the field (Fig. 1b), representing typical responses of the 'quiescence' syndrome. Therefore, the quiescence strategy was employed by *B. planiculmis*. This result is in line with the natural habitats of shallow water that
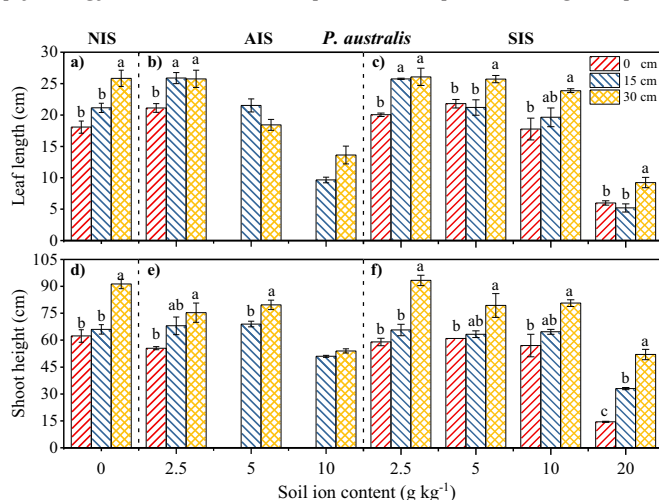

Fig. 5. Effects of flooding stress, no ion stress (0 g kg^{-1}, NIS, a, d), alkaline ion stress (2.5, 5 and 10 g kg^{-1}, AIS, b, e) and saline ion stress (2.5, 5, 10 and 20 g kg^{-1}, SIS, c, f) on leaf length and shoot height of *P. australis* grown at different flooding depths (colored bars) in the greenhouse (means ± 1 s.e., n = 3). Different lowercase letters indicate significant differences between flooding depth within each soil ion content ($P < 0.05$). A Tukey *post-hoc* test was used for multiple comparisons.
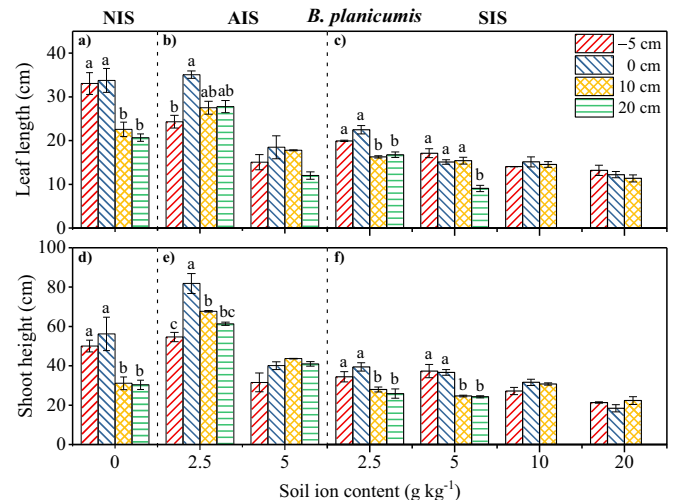

Fig. 6. Effects of flooding stress, no ion stress (0 g kg^{-1}, NIS, a, d), alkaline ion stress (2.5, 5 and 10 g kg^{-1}, AIS, b, e) and saline ion stress (2.5, 5, 10 and 20 g kg^{-1}, SIS, c, f) on leaf length and shoot height of *B. planiculmis* grown at different flooding depths (colored bars) in the greenhouse (means ± 1 s.e., n = 3). Different lowercase letters indicate significant differences between flooding depth within each soil ion content ($P < 0.05$). A Tukey *post-hoc* test was used for multiple comparisons.

B. planiculmis usually inhabits (Li and Li and Zhang, 2013, Liu et al., 2016), of which sporadic events of water excess could generate deep but temporary floods (Hroudová et al., 2014). However, differing from the results in the field, both leaf length and shoot height decreased with increasing flooding depth in the greenhouse (Fig. 1b). This result is similar to the findings of other studies (Ding, 2019; Liu, 2017). The different results between the field and the greenhouse may be related to the fact that *B. planiculmis* grew in deep and prolonged flooding in the greenhouse that its leaf length and shoot height was reduced because of insufficient energy supply, which was evidenced by decreasing shoot biomass with increasing flooding depth (Fig. 7). Conversely, the results of *P. australis* in the field and the greenhouse were consistent (Fig. 1a). The different responses of the two species may be related to their different abundance levels of aerenchyma, a system of interconnected gas conduits which resist the hypoxic environment (Colmer, 2003; Evans, 2004). Compared with *B. planiculmis*, *P. australis* usually grows in deep water, and its aerenchyma is more abundant in the stems, rhizomes and roots than in other organs (Armstrong et al., 1999; Mal and Narine, 2004). As a consequence, *P. australis* has a much more efficient pathway to provide oxygen to roots for respiration and oxidation (Ailstock and Center, 2000; Bailey-Serres and Voesenek, 2008), and *B. planiculmis* is inhibited or even died in deep and long-lasting flooding because of inefficient oxygen supply.

4.2. Effects of soil ion stress and type on the flooding adaptive strategies of P. australis and B. planiculmis

Overall, soil ion stress changed the flooding adaptive strategy of *P. australis* from escape to quiescence. In specific, 10.0 g kg^{-1} saline–alkaline mixed ion content severely inhibited the leaf and shoot elongation, that is, *P. australis* died when suffered drought (0 cm flooding depth) and showed the 'quiescence' syndrome at high flooding depth (15 and 30 cm, Fig. 4a–d). These phenomena appeared from 5.0 g kg^{-1} AIS (Fig. 5b, e). However, *P. australis* retained the 'escape' syndrome at each saline ion content (Fig. 5c, f). This result indicates that high alkaline ion stress changes the escape strategy of *P. australis* to quiescence strategy and the content should be higher than 3.75 g kg^{-1}. In specific, 5 g kg^{-1} saline–alkaline mixed ion content (of which 3.75 g kg^{-1} alkaline ion content) did not change the flooding adaptive strategy of *P. australis*, but 5 g kg^{-1} alkaline ion content did. In general, saline ion stress generates low-oxygen stress, osmotic stress and ionic toxicity on plants (Agarwal and Pandey, 2004; Ghoulam et al., 2002;

Upadhyay and Panda, 2005), which can exacerbate flooding stress and lead to severely restricted growth of plants or even death. However, pseudo-halophytes could intercept salt ions in the parenchyma of the roots and minimize their transport to the shoots to protect against metabolic tissue (Wang et al., 2013; Zhang et al., 2019). *P. australis* is a pseudo-halophyte with much aerenchyma which can reduce the toxicity (i.e. Na$^+$, Cl$^-$) (Adams and Bate, 1999; Kefu et al., 2002) and low oxygen stress (Vervuren et al., 2003) from flooding. Thus, saline ion stress did not change the escape strategy of *P. australis* but inhibited its growth. Aside from the detrimental effects of saline ion stress (Ahmad et al., 2011; Smirnoff, 1993), alkaline ion stress also exerts additional high pH stress which is the most toxic effect on plants (Li et al., 2008; Yang et al., 2006; Zhang et al., 2008). *P. australis* might lose the ability to adjust the pH around its rhizosphere and changes to quiescence strategy for energy saving under high alkaline ion stress. This result also indicates that *P. australis* is saline tolerant but not alkaline tolerant.

Different from its effect on *P. australis*, soil ion stress did not change the quiescence strategy of *B. planiculmis*. That finding may be ascribed to the fact that *B. planiculmis* is neither a halophyte nor has as much aerenchyma as *P. australis* (Huang, 2013). Therefore, *B. planiculmis* cannot mitigate the ionic toxicity and osmotic stress from soil ion stress and the oxygen deficit from flooding. *B. planiculmis* remained stable or deceased functional traits to save energy and survive under both stresses. However, low alkaline ion stress (2.5 g kg^{-1}) changed the flooding adaptive strategy of *B. planiculmis* to escape strategy from −5 to 0 cm flooding depth. This result is probably related to the buffer effect of low alkaline ion contents outside the roots (Bailey, 1996) and the optimum water level for the growth of *B. planiculmis*. High alkalinity in soil solution may be harmful, but soil solution with zero alkalinity is not necessarily recommended (Roosta, 2011). The buffer capacity of alkalinity prevents sudden pH changes in growing medium solution, which may cause nutrient unbalances, especially Fe availability (Alhendawi et al., 1997; Bailey, 1996; Bertoni et al., 1992). Thus, a low level of alkalinity in soil solution is desirable and promotes the growth of *B. planiculmis*. Furthermore, the optimum water levels are 0–5 cm for the shoot elongation of *B. planiculmis* (Ding, 2019; Liu et al., 2016). Hence, the double positive effects and optimum water levels (0 cm) coupled with the promotion of low alkaline ion contents (2.5 g kg^{-1}) promote *B. planicumis* to escape from below water.

The Western Songnen Plain will became drier in the mid-late 21th century under middle/high greenhouse gas (GHG) emissions scenarios (RCP4.5/8.5) (Tao et al., 2016; Wang and Chen, 2014; Zhang et al., 2020; Zhang et al., 2017). This will aggravate the degree of soil salinization and alkalization in our study area (Liu et al., 2018), which may cause *P. australis* and *B. planicumis* to adopt the quiescence strategy with short leaves, small plants and low aboveground biomass, and the two kinds of marshes might degrade severely in the future. Therefore, a reduction of GHG emissions or adequate water supply would be effective ways to alleviate the degradation of *P. australis* and *B. planicumis* marshes caused by climate change.

5. Conclusions

P. australis exhibits an escape strategy, whereas *B. planiculmis* adopts a quiescent strategy. High soil ion stress changes the flooding adaptive strategy of *P. australis* to quiescent strategy but not that of *B. planiculmis*. The strategies of the two species are changed by alkaline ion stress, but they show different responses. High alkaline ion stress compels *P. australis* to remain quiescent with increasing flooding depth, whereas low alkaline ion stress promotes *B. planicumis* to escape from below water. Hence, increasing soil salinization and alkalization resulting from high GHG emissions might cause *P. australis* and *B. planicumis* to adopt the quiescence strategy in Western Songnen Plain and this may lead to severe degradation of the two kinds of marshes in the future.
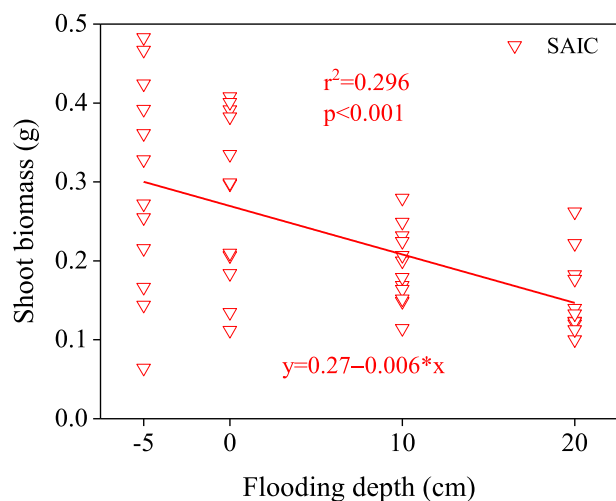

Fig. 7. Shoot biomass in relation to flooding depth of plant grown in the greenhouse under saline-alkaline mixed ion contents (SAIC). r^2: regression coefficient.

CRediT authorship contribution statement

Zhi Ding: Conceptualization, Methodology, Software, Data curation, Writing – original draft, Visualization, Investigation. **Ying Liu:** Conceptualization, Methodology, Software, Data curation, Writing – original draft, Visualization, Investigation, Writing – review & editing. **Yanjing Lou:** Software, Validation, Writing – review & editing. **Ming Jiang:** Supervision. **Xianguo Lü:** Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.144654.

References

Adams, J., Bate, G., 1999. Growth and photosynthetic performance of *Phragmites australis* in estuarine waters: a field and experimental evaluation. Aquat. Bot. 64 (3–4), 359–367.

Agarwal, S., Pandey, V., 2004. Antioxidant enzyme responses to NaCl stress in *Cassia angustifolia*. Biol. Plant. 48 (4), 555–560.

Ahmad, P., Nabi, G., Jeleel, C., Umar, S., 2011. Free Radical Production, Oxidative Damage and Antioxidant Defense Mechanisms in Plants under Abiotic Stress. Oxidative Stress: Role of Antioxidants in Plants. Studium Press, New Delhi, pp. 19–53.

Ailstock, M.S., Center, E., 2000. Adaptive strategies of common reed *Phragmites australis*. Proceedings: The Role of *Phragmites* in the Mid-Atlantic Region, April 17.

Alhendawi, R.A., Römheld, V., Kirkby, E.A., Marschner, H., 1997. Influence of increasing bicarbonate concentrations on plant growth, organic acid accumulation in roots and iron uptake by barley, sorghum, and maize. J. Plant Nutr. 20 (12), 1731–1753.

Armstrong, J., Afreen-Zobayed, F., Blyth, S., Armstrong, W., 1999. *Phragmites australis*: effects of shoot submergence on seedling growth and survival and radial oxygen loss from roots. Aquat. Bot. 64 (3–4), 275–289.

Bailey, D., 1996. Alkalinity, pH, and acidification. Water, Media, and Nutrition for Greenhouse Crops. Ball Publishing, Batavia.

Bailey-Serres, J., Voesenek, L.A.C.J., 2008. Flooding stress: acclimations and genetic diversity. Annu. Rev. Plant Biol. 59 (1), 313–339.

Bailey-Serres, J., Voesenek, L.A.C.J., 2010. Life in the balance: a signaling network controlling survival of flooding. Curr. Opin. Plant Biol. 13 (5), 489–494.

Bazihizina, N., Barrett-Lennard, E.G., Colmer, T.D., 2012. Plant growth and physiology under heterogeneous salinity. Plant Soil 354 (1), 1–19.

Bertoni, G.M., Pissaloux, A., Morard, P., Sayag, D.R., 1992. Bicarbonate-pH relationship with iron chlorosis in white lupine. J. Plant Nutr. 15 (10), 1509–1518.

BirdLifeInternational, 2018. Leucogeranus leucogeranus. The IUCN Red List of Threatened Species. vol. 2018 (e.T22692053A134081990).

Cañedo-Argüelles, M., Bundschuh, M., Gutiérrez-Cánovas, C., Kefford, B.J., Prat, N., Trobajo, R., Schäfer, R.B., 2014. Effects of repeated salt pulses on ecosystem structure and functions in a stream mesocosm. Sci. Total Environ. 476, 634–642.

Chen, X., Huber, H., de Kroon, H., Peeters, A.J.M., Poorter, H., Voesenek, L.A.C.J., Visser, E.J.W., 2009. Intraspecific variation in the magnitude and pattern of flooding-induced shoot elongation in *Rumex palustris*. Ann. Bot. 104 (6), 1057–1067.

Chen, X., Visser, E.J.W., de Kroon, H., Pierik, R., Voesenek, L.A.C.J., Huber, H., 2011. Fitness consequences of natural variation in flooding-induced shoot elongation in *Rumex palustris*. New Phytol. 190 (2), 409–420.

Colmer, T.D., 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. Plant Cell Environ. 26 (1), 17–36.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.T., Morgan, H.D., Heijden, M.G.A.V.D., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51 (4), 335–380.

Deng, C., 2011. Eco-Physiological Responses of *Phragmites australis* to Different Water Regime and Water Quality Conditions in Momoge Wetland (in Chinese with English Abstract). University of China Science Academy.

Ding, S., 2019. The Responses of Typical Plant-*Scirpus planiculmis* to the Coupling Effects of Freeze Thawing-Water-Salt in Saline-Alkali Wetland (in Chinese with English Abstract). Master. University of Chinese Academy of Sciences.

Evans, D.E., 2004. Aerenchyma formation. New Phytol. 161 (1), 35–49.

Garssen, A.G., Baattrup-Pedersen, A., Voesenek, L.A.C.J., Verhoeven, J.T.A., Soons, M.B., 2015. Riparian plant community responses to increased flooding: a meta-analysis. Glob. Chang. Biol. 21 (8), 2881–2890.

Ghoulam, C., Foursy, A., Fares, K., 2002. Effects of salt stress on growth, inorganic ions and proline accumulation in relation to osmotic adjustment in five sugar beet cultivars. Environ. Exp. Bot. 47 (1), 39–50.

Halls, A.J., 1997. Wetlands, biodiversity and the Ramsar convention: the role of the convention on wetlands in the conservation and wise use of biodiversity. Hails. A.J. (ed, Ramsar Convention Bureau.

Hattori, Y., Nagai, K., Furukawa, S., Song, X.-J., Kawano, R., Sakakibara, H., Wu, J., Matsumoto, T., Yoshimura, A., Kitano, H., Matsuoka, M., Mori, H., Ashikari, M., 2009. The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. Nature 460 (7258), 1026–1030.

Holland, K.L., Charles, A.H., Jolly, I.D., Overton, I.C., Gehrig, S., Simmons, C.T., 2009. Effectiveness of artificial watering of a semi-arid saline wetland for managing riparian vegetation health. Hydrol. Process. 23 (24), 3474–3484.

Hroudová, Z., Zákravský, P., Flegrová, M., 2014. The tolerance to salinity and nutrient supply in four European *Bolboschoenus* species (*B. maritimus*, *B. laticarpus*, *B. planiculmis* and *B. yagara*) affects their vulnerability or expansiveness. Aquat. Bot. 112, 66–75.

Huang, L., 2013. Responses of Riparian Plants to Environmental Stresses: A Multi-Species Comparison (in Chinese with English Abstract). Beijing Forest University, Master.

Jolly, I.D., McEwan, K.L., Holland, K.L., 2008. A review of groundwater–surface water interactions in arid/semi-arid wetlands and the consequences of salinity for wetland ecology. Ecohydrology 1 (1), 43–58.

Keddy, P.A., 2010. Wetland Ecology: Principles and Conservation. Cambridge University Press, Cambridge.

Kefu, Z., Hai, F., Ungar, I., 2002. Survey of halophyte species in China. Plant Sci. 163 (3), 491–498.

Li, H., Zhang, G., 2013. Influence of water depth and salinity coupling on growth of *Scirpus planiculmis* seedlings in Momoge National Nature Reserve. Wetland Science 11 (2), 173–177.

Li, B., Wei, A., Song, C., Li, N., Zhang, J., 2008. Heterologous expression of the TsVP gene improves the drought resistance of maize. Plant Biotechnol. J. 6 (2), 146–159.

Li, X., Wen, B., Yang, F., Hartley, A., Li, X., 2017. Effects of alternate flooding–drought conditions on degenerated *Phragmites australis* salt marsh in Northeast China. Restor. Ecol. 25 (5), 810–819.

Liu, B., 2017. Control for Echinochloa caudata and restoration for *Bolboschoenus planiculmis* in wetlands of Songnen Plain (in Chinese with English abstract). PhD. University of Chinese Academy of Sciences.

Liu, Y., Jiang, M., Lu, X.G., Zhang, Z.S., Lou, Y.J., 2015. Leaf carbon, nitrogen and phosphorus stoichiometry of *Phragmites Australis* in northeastern China. Fresenius Environ. Bull. 24 (12C), 4711–4719.

Liu, B., Jiang, M., Tong, S., Zhang, W., Zou, C., Wang, B., Lu, X., 2016. Effects of burial depth and water depth on seedling emergence and early growth of *Scirpus planiculmis* Fr. Schmidt. Ecol. Eng. 87, 30–33.

Liu, Y., Ding, Z., Bachofen, C., Lou, Y., Jiang, M., Tang, X., Lu, X., Buchmann, N., 2018. The effect of saline-alkaline and water stresses on water use efficiency and standing biomass of *Phragmites australis* and *Bolboschoenus planiculmis*. Sci. Total Environ. 644, 207–216.

Lou, Y., Pan, Y., Gao, C., Jiang, M., Lu, X., Xu, Y.J., 2016. Response of plant height, species richness and aboveground biomass to flooding gradient along vegetation zones in floodplain Wetlands, Northeast China. PLoS One 11 (4), e0153972.

Mal, T.K., Narine, L., 2004. The biology of Canadian weeds. 129. *Phragmites australis* (Cav.) Trin. ex Steud. Can. J. Plant Sci. 84 (1), 365–396.

Marcum, K.B., Murdoch, C.L., 1992. Salt tolerance of the coastal salt marsh grass, *Sporobolus virginicus* (L.) kunth. New Phytol. 120 (2), 281–288.

Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 59, 651–681.

Ram, P.C., Singh, B.B., Singh, A.K., Ram, P., Singh, P.N., Singh, H.P., Boamfa, I., Harren, F., Santosa, E., Jackson, M.B., Setter, T.L., Reuss, J., Wade, L.J., Pal Singh, V., Singh, R.K., 2002. Submergence tolerance in rainfed lowland rice: physiological basis and prospects for cultivar improvement through marker-aided breeding. Field Crop Res. 76 (2), 131–152.

RDevelopmentCoreTeam, 2017. R: A Language and Environment for Statistical Computing.

Reich, P.B., Tjoelker, M.G., Pregitzer, K.S., Wright, I.J., Oleksyn, J., Machado, J.-L., 2008. Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. Ecol. Lett. 11 (8), 793–801.

Rogel, J.A., Ariza, F.A., Silla, R.O., 2000. Soil salinity and moisture gradients and plant zonation in Mediterranean salt marshes of Southeast Spain. Wetlands 20 (2), 357–372.

Roosta, H.R., 2011. Interaction between water alkalinity and nutrient solution ph on the vegetative growth, chlorophyll fluorescence and leaf magnesium, iron, manganese, and zinc concentrations in lettuce. J. Plant Nutr. 34 (5), 717–731.

Sauter, M., 2000. Rice in deep water: "how to take heed against a sea of troubles". Naturwissenschaften 87 (7), 289–303.

Setter, T.L., Laureles, E.V., 1996. The beneficial effect of reduced elongation growth on sub-mergence tolerance of rice. J. Exp. Bot. 47 (10), 1551–1559.

Shi, D., Wang, D., 2005. Effects of various salt-alkaline mixed stresses on *Aneurolepidium chinense* (Trin.) Kitag. Plant Soil 271 (1), 15–26.

Smirnoff, N., 1993. The role of active oxygen in the response of plants to water deficit and desiccation. New Phytol. 125 (1), 27–58.

Sparks, D.L., Page, A., Helmke, P., Loeppert, R., Soltanpour, P., Tabatabai, M., Johnston, C., Sumner, M., 1996. Methods of Soil Analysis. Part 3-Chemical Methods. Soil Science Society of America Inc.

Striker, G.G., Izaguirre, R.F., Manzur, M.E., Grimoldi, A.A., 2012. Different strategies of *Lotus japonicus*, *L. corniculatus* and *L. tenuis* to deal with complete submergence at seedling stage. Plant Biol. 14 (1), 50–55.

Sun, G., Luo, X., Yi, F., Zhang, X., 2000. Concept, distribution law and formation mechanism of inland saline alkaline wetland-taking Songliao plain as an example. Chin. Geogr. Sci. 3, 44–47.

Tao, C.W., Jiang, C., Sun, J.X., 2016. Projection of future changes in climate in Northeast China using a CMIP5 multi-model ensemble. Chinese Journal of Geophysics.

Upadhyay, R., Panda, S., 2005. Salt tolerance of two aquatic macrophytes, *Pistia stratiotes* and *Salvinia molesta*. Biol. Plant. 49 (1), 157–159.

Vervuren, P.J.A., Blom, C.W.P.M., De Kroon, H., 2003. Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. J. Ecol. 91 (1), 135–146.

Voesenek, L., Rijnders, J., Peeters, A., Van de Steeg, H., De Kroon, H., 2004. Plant hormones regulate fast shoot elongation under water: from genes to communities. Ecology 85 (1), 16–27.

Wan, Z., Yu, S., Wang, H., 2003. The types and characteristics of inland saline-alkaline wet-land in Songnen Plain. Wetland Science (in Chinese with English abstract) 1 (2), 141–146.

Wang, L., Chen, W., 2014. A CMIP5 multimodel projection of future temperature, precip-itation, and climatological drought in China. Int. J. Climatol. 34 (6), 2059–2078.

Wang, L., Seki, K., Miyazaki, T., Ishihama, Y., 2009. The causes of soil alkalinization in the Songnen Plain of Northeast China. Paddy Water Environ. 7 (3), 259–270.

Wang, L.-L., Chen, A.-P., Zhong, N.-Q., Liu, N., Wu, X.-M., Wang, F., Yang, C.-L., Romero, M.F., Xia, G.-X., 2013. The *Thellungiella Salsuginea* tonoplast aquaporin TsTIP1;2 func-tions in protection against multiple abiotic stresses. Plant Cell Physiol. 55 (1), 148–161.

Xu, H., Huang, X., Zhong, T., Chen, Z., Yu, J., 2014. Chinese land policies and farmers' adop-tion of organic fertilizer for saline soils. Land Use Policy 38, 541–549.

Yang, C., Jianaer, A., Shi, D., 2006. Effects of complex salt and alkali conditions on the ger-mination of seeds of *Puccinellia tenui* flora. Acta Prataculturae Sinica (in Chinese with English abstract) 15 (5), 45.

Yang, C., Chong, J., Li, C., Kim, C., Shi, D., Wang, D., 2007. Osmotic adjustment and ion bal-ance traits of an alkali resistant halophyte *Kochia sieversiana* during adaptation to salt and alkali conditions. Plant Soil 294 (1–2), 263–276.

Zhang, D., Cao, B., Jia, B., Tang, Q., 2008. Germination and physiological response of *Albizia julibrissin* seeds under alkali-salt stress. Scientia Silvae Sinicae (in Chinese with En-glish abstract) 44 (9), 157–161.

Zhang, X., Xiong, Z., Zhang, X., Shi, Y., Liu, J., Shao, Q., Yan, X., 2017. Simulation of the cli-matic effects of land use/land cover changes in eastern China using multi-model en-sembles. Global & Planetary Change 154.

Zhang, Y., Shi, S.H., Li, F.L., Zhao, C.Z., Li, A.Q., Hou, L., Xia, H., Wang, B.S., Baltazar, J.L., Wang, X.J., Zhao, S.Z., 2019. Global transcriptome analysis provides new insights in *Thellungiella salsuginea* stress response. Plant Biol. 21 (5), 796–804.

Zhang, T., He, W., Zheng, H., Cui, Y., Song, H., Fu, S., 2020. Satellite-based ground PM2. 5 estimation using a gradient boosting decision tree. Chemosphere https://doi.org/10.1016/j.chemosphere.2020.128801, 128801.

Zou, H., Huang, H., Song, Y., Wu, Q., 2018. Research progress on cranes in Songnen Plain, China. Chinese Journal of Wildlife 39 (2), 225–229.