

NaCl and NaHCO₃ mediate tradeoffs in growth, leaf traits, and clonal reproduction of reed (*Phragmites communis*) under saline-alkali stress

Zhan-Wu GAO^{1†*}, Jing LIU^{2†}, Xiao-Ling LU¹, Xin LI¹, Ying-Qi QIN¹, Ge GAO¹, Li-Jie HE¹, Meng-Zhu CAI¹, Chen CHEN¹, Ji-Tao ZHANG³, Chun-Sheng MU^{4*}, Mohamed MOHANY⁵

¹Jilin Provincial Key Laboratory of Western Jilin's Clean Energy, Baicheng Normal University, Baicheng 137000, China; gaozw261@nenu.edu.cn (*corresponding author); lxl7302@163.com; 3551320967@qq.com; 1441884409@qq.com; 3327768955@qq.com; 2749784136@qq.com; c13630342480@163.com; 2980823866@qq.com

²Agricultural Technology Extension Station of Dongliao County, Liaoyuan, 136600, China; liujing20221129@163.com

³Chinese Academy of Sciences, Northeast Institute of Geography and Agroecology, Changchun, 130000, China; zhangjitaotao@iga.ac.cn

⁴Northeast Normal University, College of Life Sciences, Institute of Grassland Science, Changchun, 130024, China; mucs821@163.com (*corresponding author)

⁵King Saud University, College of Pharmacy, Department of Pharmacology and Toxicology, P.O. Box 55760, Riyadh, 11451, Saudi Arabia; mmohany@ksu.edu.sa

Abstract

Salinity stress is a serious constraint for crop productivity, and its extent is continuously across the globe. Therefore, it is direly necessary to develop appropriate measures to mitigate the toxic effects of salinity to meet rising food needs. The present study determined the impact of diverse concentrations of neutral salt (NaCl: 0, 200, 400 mM) and alkaline salt (Na₂CO₃: 0, 25, 50 mM) on the growth status, leaf traits, and clonal component characteristics of reed (*Phragmites communis* Trin.). The results indicated that increasing the intensity of salt and alkali stress markedly reduced growth (> 30%) and biomass production (> 35%). The impact of alkali stress was more significant as compared to salt stress, and it significantly decreased leaf area and dry matter production and increased the N concentration and N:P ratio. Further, stomata conductance and CO₂ concentration showed a decrease under stress conditions. While water use efficiency (WUE) also showed a decreasing trend under saline conditions, it first showed an increasing trend under alkali stress and then a decreasing trend. Further, plant tiller, rhizome, and seeds were markedly reduced by stresses. Moreover, the concentration of Na⁺ was increased under saline conditions while the concentration of K⁺ and NO₃⁻ showed a marked decrease, Na⁺/K⁺ showed a substantial increase. Therefore, salinity and alkaline stress can reduce the growth of reeds by disturbing plant physiological and biochemical functioning and nutrient homeostasis.

Keywords: abiotic stresses; individual growth; leaf traits; *Phragmites australis*; plant response

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Introduction

Soil salinity is a serious global challenge, negatively affecting crop productivity (Arzani and Ashraf, 2016). Globally, around 1 billion hectares are salt-affected, representing 8.7% of the world's land area, and causing more than 27.3 billion USD in losses (Ha-Tran *et al.*, 2021). Every year, around 10 million hectares are affected by salt stress, which is a serious challenge and needs dire attention to tackle this problem (Ould Ouali *et al.*, 2024). Songnen Plain in northeast China is the most critical commercial grain base with high economic and ecological value. China's agriculture will continue to develop this century, but the continuous improvement and effective utilization of soil salinization is still a problem (Singh, 2021). The total area of saline soil in social and economic development in China is 520 million mu, of which alkaline soil occupies 12.991 million mu and saline soil is 240 million mu (Wang *et al.*, 2018). Salinization has seriously restricted grassland productivity in this area and gradually reduced some grassland with high quality and high yield to saline-alkali bare land with very low productivity, which not only affects the sustainable development of grassland animal husbandry production. Moreover, it has seriously damaged the ecological environment (Cuevas *et al.*, 2019).

Plants can sense environmental stimuli and modulate defence mechanisms via various regulatory networks to mitigate abiotic stresses, including salt and alkali stress (Arzani *et al.*, 2023). Over time, rising salt concentrations cause primary damage in two stages: osmotic stress and ion toxicity. These trigger secondary stresses like oxidative stress and nutrient imbalances, ultimately stunting plant growth. This decline stems from impaired water and nutrient uptake, membrane dysfunction, and disruptions to photosynthesis, respiration, and protein synthesis (Arzani and Ashraf, 2016; Arzani *et al.*, 2023). Reed (*Phragmites communis* Trin) is an essential hydrophytic species thriving across the globe with an appreciable ability to grow in riverbanks, lakesides, and fresh and brackish swamps (Li *et al.*, 2021). It can also adapt well to adverse habitats and its different ecotypes showing genetic differences have developed resistance against drought and salinity stresses (Eller *et al.*, 2017; Li *et al.*, 2021). It has an extensive ecological amplitude and a great ability to acclimatize in adverse conditions owing to higher intra-specific diversity and phenotypic plasticity (Eller *et al.*, 2017). It can tolerate a wide range of salinity; however, different genotypes of different origins are different in their ability to tolerate salinity (Achenbach and Brix, 2014) owing to their diverse bio-climatic origins (Chambers *et al.*, 1998; Lissner *et al.*, 1999; Lambertini *et al.*, 2020). The genetic diversity of *Phragmites australis* could be decreased with increasing salinity stress in some areas. For instance, Yellow River Delta of China the genetic diversity of the reed decreased with increasing salinity and only particular phenotypes occurred in the saltiest areas of the delta (Gao *et al.*, 2012). Salinity stress significantly affects rhizome growth, and differentiation of plant tissues and organs, thereby causing a reduction in reed plant growth (Lata *et al.*, 2022). The increasing salt concentration reduces germination, and morphological growth and disturbs the plant functioning (Zhang *et al.*, 2022).

Driven by economic construction, human and socio-economic activities directly impact the global environment and ecosystem (Shi *et al.*, 2022). Thus, it is essential to investigate the growth, reproduction, and clonal components of reed (*P. communis*) a common clonal plant in Songnen Plain. It can provide essential data and theoretical support for the reed salt-alkali tolerance mechanism and ecological adaptability, and it can be applied in practice to maintain and improve the ecological environment. In this experiment, the common species reed of Songnen grassland was used as the genetic material to simulate the local salinization background for testing different concentrations of salt-alkaline stress treatment. We hypothesized that neutral salt stress may have a more detrimental impact on reed growth and biomass production than alkaline salt stress. This study determined the impact of saline and alkali stresses on growth, leaf traits and reproduction traits of reed.

Materials and Methods

Test materials and experiment site

The present study was conducted in 2023 at Northeast Normal University, and the plant material (seed) was taken from Changling, Songyuan City, Jilin Province. The fresh and vigorous seedlings selected were transplanted into plastic pots (diameter of 28 cm and length of 35 cm), and twenty seedlings were placed in each pot.

Experiment treatments

The treatments were applied to seedlings at earlier growth stages (30 days old); and Hoagland nutrient solution was applied every four days. The salt stress treatments were started in July, where-two salt stress treatments (100 and 200 mM) were imposed. Each treatment had three replicates, and treatments were performed from 17:00 to 18:00 daily. Every basin was irrigated with one-litre solution according to treatments on the first day. Following this, in the remaining three days, the same amount of water was applied. The pots were placed under the shed to avoid rain.

Growth and photosynthetic traits

Fifteen seedlings were marked in each pot to determine leaf length and plan, while standard methods of Blackman were used to determine the relative height growth rate by the following formula:

$$RHGR(H_i) = \frac{\ln(H_{i+1}) - \ln(H_i)}{T_{i+1} - T_i}$$

Specifically, H_i and H_{i+1} indicated the height of plants at T_i and T_{i+1} , respectively, and the formula indicates the high growth amount of plant strains in time from T_i and T_{i+1} . The leaf photosynthetic traits were measured in July and August using the CIRAS-3 portable photosynthesizing apparatus (PP SYSTEMS, USA). We selected the first unfolded leaf to test the photosynthetic traits.

Determination of leaf and root characteristics

Ten leaves were taken from every pot and weighed immediately after cutting to determine the fresh weight (FW). Then these leaves were oven-dried (80 °C) until constant weight to determine the dry weight (DW), and leaf water concentration was determined as $FW-DW/FW \times 100\%$

The samples were carefully washed to remove sand attached to the roots around the laboratory experiment. Further, seed plants and buds were manually counted, and an average was taken. Moreover, fifteen root samples were collected to determine their length, area, volume, and tip count. The various parts of sheepgrass (root, bud, rhizome, and stem) were taken and oven-dried to determine their DW.

Element concentration

The plant samples were dried and ground to make powder, and concentration of carbon and nitrogen was assessed by Elementary various EL III, UK. During the measurement, about 3 mg (0.001 mg) of each organ sample of sheepgrass was accurately weighed with a balance with an accuracy of one-thousandth of a milligram and put into a tin foil cup. The air in the tin foil bag was emptied as far as possible to reduce the error of the experimental instrument. In addition, total phosphorus concentration was assessed by the molybdenum resistance colorimetric technique.

Data Analysis

The data of the different collected traits were analyzed using SPSS26.0 software (SPSS, Chicago, IL, USA). The data were also subjected to a homogeneity test before analysis, and the differences between diverse treatments were sorted with Tukey's test (Steel *et al.*, 1997).

Results

Impact of salt and alkali stress on reed plant height, total biomass per plant

The increase in salts concentration caused a marked reduction in plant height. Under salt stress treatment, reed plant height decreased by 10.28% and 34.98% under 200 and respectively for 400 mM salt stress. Under alkali stress treatment, reed plant height decreased by 34.41% and 42.39% under 25 and respectively at 50 mM alkaline stress (Figure 1A). The total reed biomass was reduced by 7.56% at 200 mM and 17.59% at 400 mmol·L⁻¹. Under alkali stress treatment, the total reed biomass decreased by 16.19% at 25 mM and 49.91% at 50 mM alkali concentration (Figure 1B). With time, the growth rate of relative plant height showed a marked reduction, and the maximum value appeared in early June and approached 0 around mid-July.

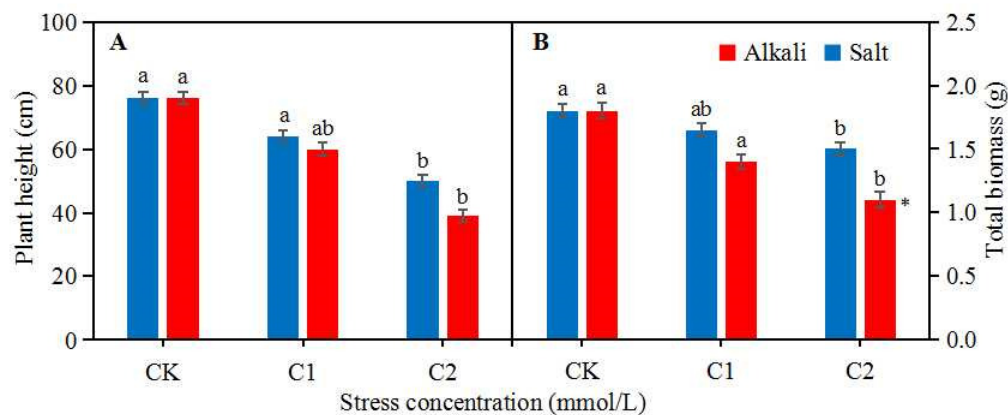


Figure 1. Impacts of salinity and alkaline stresses on plant height and total biomass of *P. australis*

Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Effects of salt-alkali stress on relative height growth rate of *Phragmites australis*

As shown in Figure 2 the growth rate relative to plant height generally shows a downward trend over time. Under the treatment of salt stress and alkali stress, it showed an upward trend from mid-May to early June, then dropped sharply, with the maximum value occurring in early June. It approached zero around mid-July and then stopped growing.

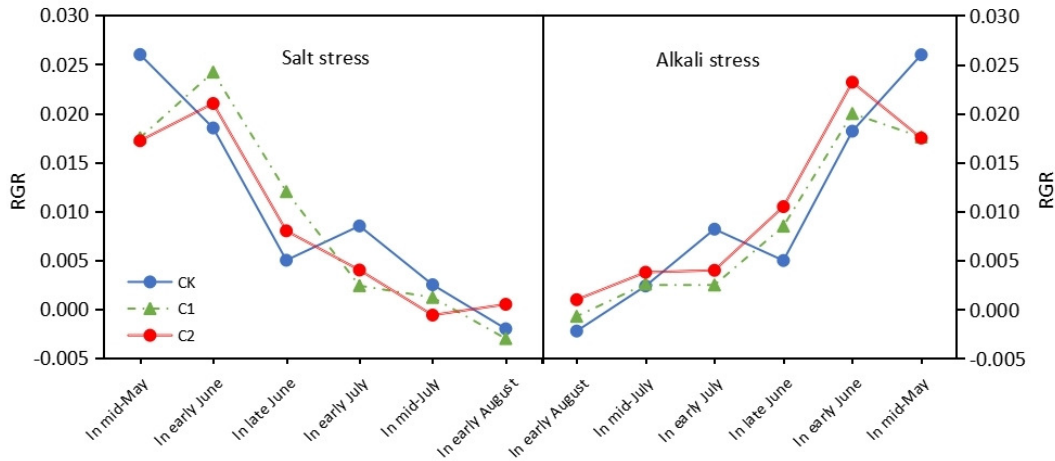


Figure 2. Effects of salt-alkali stress on relative height growth rate of *Phragmites australis*
 Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Impacts of salt-alkali stress on stem and leaf biomass of single plants under salinity stress treatment

Stem biomass per reed plant was decreased by 2.02% and 8.64% at 200 and at respectively 400 mM salt stress. The stem biomass per reed plant under alkali stress treatment decreased by 4.12% and 47.42% at moderate and higher alkaline stress (Figure 3A). The increasing intensity of salts and alkali stress markedly reduced leaf biomass, and leaf biomass per reed plant was significantly different under alkali stress treatment ($P < 0.05$). The leaf biomass per reed plant was 4.28% and 11.77% for 200 and respectively 400 mM salt stress. The leaf biomass per reed plant decreased by 6.53% and 49.96% by imposing alkaline stress of 25 and respectively 50 mM (Figure 3B).

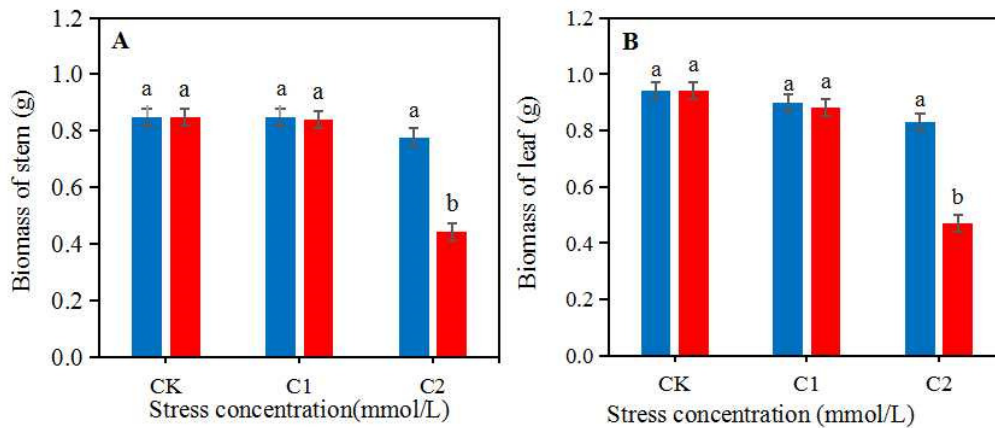


Figure 3. Impacts of salinity and alkaline stresses on stem and leaf biomass of single plants under salinity stress treatment
 Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Impacts of saline-alkali stress on stem length and root length of reed

The results indicate that under salt stress treatment, reed stem length decreased by 11.11% and 25.93% under 200- and 400-mM salt stress. Under alkali stress treatment, reed stem length decreased by 20.37% and 29.62% under moderate and higher alkaline stress (Figure 4A). The reed root length decreased by 17.28% at 200 mmol·L⁻¹ salt concentration and 34.88% at 400 mM salt concentration. The root length of the reed decreased by 22.31% at 25 mM and decreased at 50 mM alkali by 40.21% (Figure 4B).

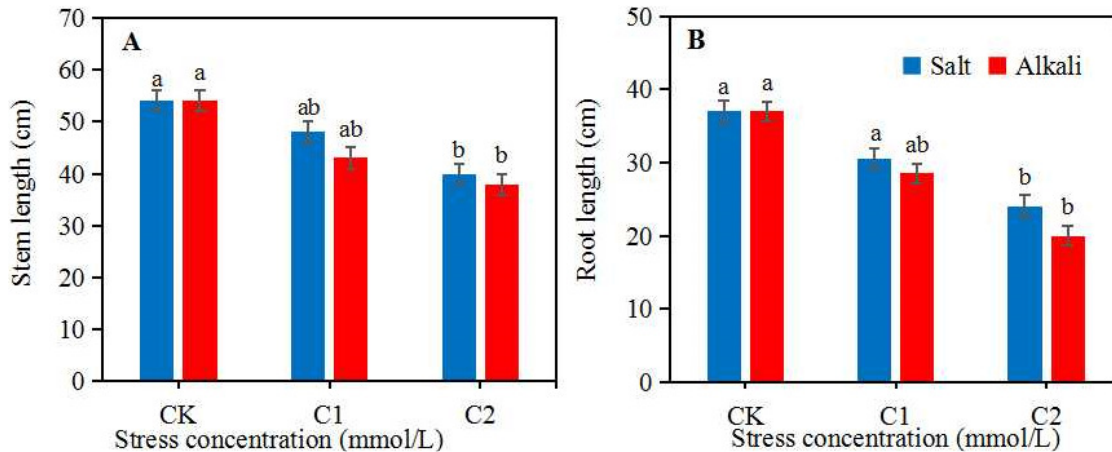
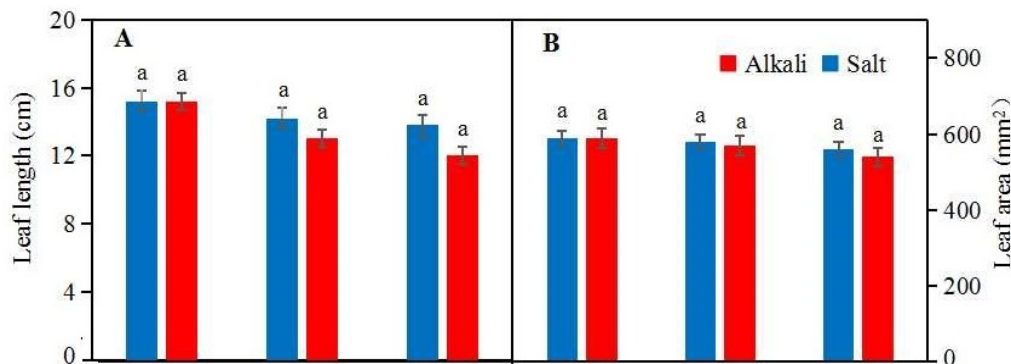


Figure 4. Impact of salinity and alkaline stress on root length and steam lengths of *P. australis*

Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Compared with the control under salt stress treatment, reed leaf area was decreased by 2.52% and 5.97% under salt concentrations of 200 and 400 mM. Leaf area was also significantly reduced by 3.38% and 7.99% at 25 and mM alkaline stress (Figure 5B). Under salt stress treatment, the specific leaf area of the reed was decreased by 8.98% at lower salinity stress and increased by 4.31% at 400 mM salt concentration. Under alkali stress treatment, the specific leaf area of the reed decreased by 6.67% and 5.01% at moderate and higher stress levels (Figure 5C). The reed leaves' dry matter content (LDMC) decreased under salt and alkali stress. The LDMC was reduced by 1.36% and 5.21% under 200 and 400 mM salt stress, while LDMC was decreased by 3.74% and 4.94% under 25 and 50 mmol·L⁻¹ alkaline stress (Figure 5D).



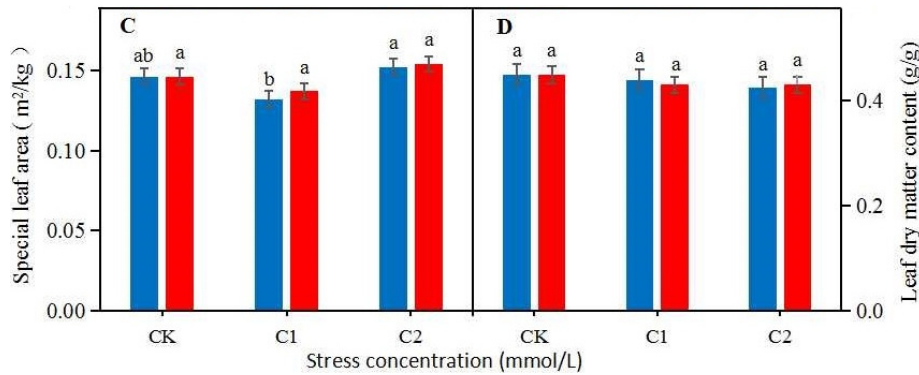


Figure 5. Impacts of salinity and alkaline stresses leaf length, leaf area, specific leaf area, and leaf dry matter content of *P. australis*

Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Impact of salinity and alkaline stresses on element concentration

The carbon content of reed leaves is enhanced with increasing intensity of both stresses. The carbon content of reed leaves increased by 8.98% when the salt concentration was 200 mmol·L⁻¹ and 3.89% when the salt concentration was 400 mM. The carbon content of reed leaves increased by 2.84% when the alkali concentration was 25 mmol·L⁻¹ and 3.64% when the alkali concentration was 50 mmol·L⁻¹ (Figure 6A). The nitrogen was decreased by 36.62% and 52.42% under 200 and 400 mM salt stress, while nitrogen contents were decreased by 29.31% and 47.37% under moderate and higher stress levels (Figure 6B).

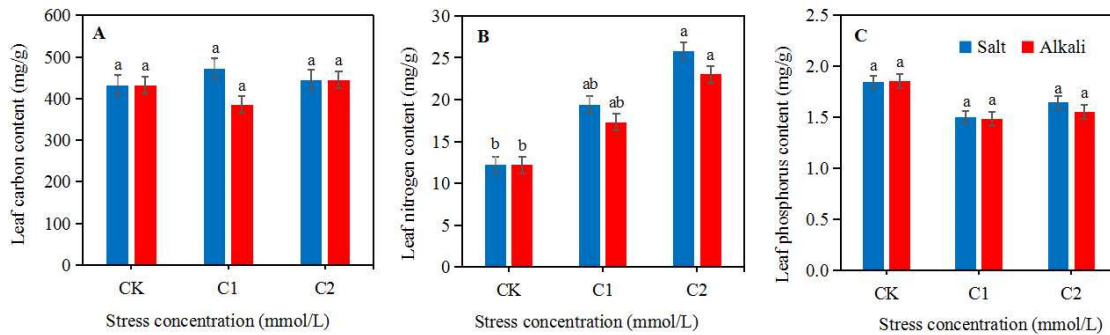


Figure 6. Effects of salt-alkali stress on leaf carbon content, nitrogen content and phosphorus content of *P. australis*

Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Phosphorus content in reed leaves decreased first and then increased but was lower than control. The phosphorus content was reduced by 11.26% and 19.08% under 200 and 400 mM salt stress, while phosphorus contents was decreased by 19.96% and 15.93% under 25 and 50 mM alkaline stress (Figure 6C). Plant C/N ratio was decreased by 30.64% and 51.03% at moderate and higher salinity stress, while it decreased by 28.9% and 45.93% at moderate and higher alkaline stress (Figure 7A). Compared with the control, under salt stress treatment, the C/P ratio of reed leaves increased by 16.04% at 200 mmol·L⁻¹ salt concentration and 9.78% at 400 mM salt concentration. Further, C/P was increased by 13.43% and 10.17% moderate and higher stress levels (Figure 7B). The N:P was increased by 48.71% and 57.78% under 200 and 400 mM salt stress, while N:P was increased by 43.42% and 55.75% under 25 and 50 mmol·L⁻¹ alkaline stress (Figure 7C).

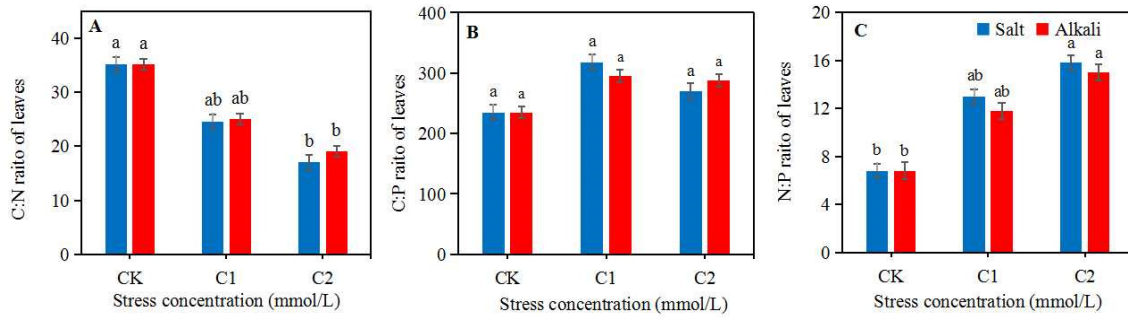


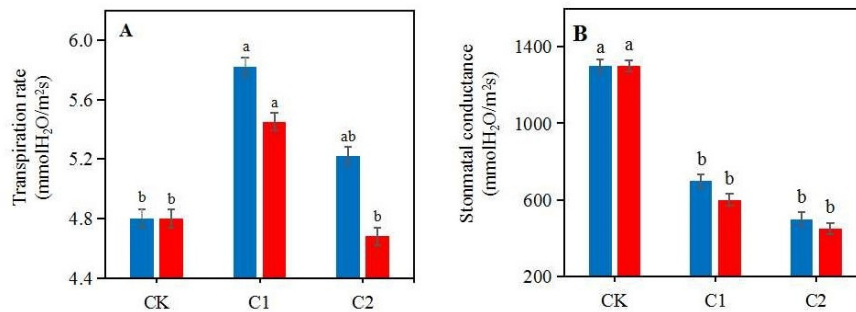
Figure 7. Impacts of salinity and alkaline stresses ratio relationship between carbon, nitrogen and phosphorus in reed

Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Effects of salt and alkali stress on photosynthetic physiological characteristics of reed

Under salinity treatments, the transpiration rate increased by 21.35% and 8.65% at moderate (200 mM L⁻¹) and higher salinity stress (400 mM L⁻¹). Under alkali stress treatment, the transpiration rate increased by 13.46% and 2.54% at lower and higher alkaline stress levels (Figure 8A). The stomata conductance was decreased by 41.94% and 56.42% under 200 and 400 mmol·L⁻¹ salt stress, while stomata conductance was reduced by 51.54% and 62.31% at both levels of alkaline stress (Figure 8B).

The water use efficiency of reed leaves under salt stress treatment increased by 13.21% at mM and 22.03% at 400 mM. Under alkali stress treatment, the water use efficiency of reed leaves increased by 20.68% and 14.81% at both levels of alkaline stress (Figure 8C). Under salt stress treatment, the intercellular carbon dioxide concentration of reed leaves at 200 mM decreased by 13.39%, and that at 400 mM decreased by 21.86%. Under alkali stress treatment, the intercellular carbon dioxide concentration of reed leaves decreased by 21.98% when the alkali concentration was 25 mmol·L⁻¹ and 30.47% when the alkali concentration was 50 mmol·L⁻¹ (Figure 8D). Under salt stress treatment, the net photosynthetic rate of the reed increased by 1.49% when the salt concentration was 200 mmol·L⁻¹ and 11.56% when the salt concentration was 400 mM. Under alkali stress treatment, the net photosynthetic rate of the reed increased by 13.08% and 29.62% with moderate and higher alkaline stress (Figure 8E).



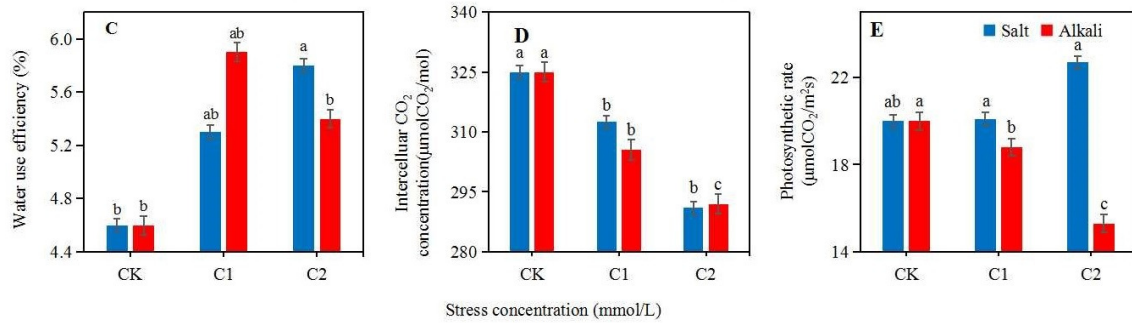


Figure 8. Impacts of salinity and alkaline stresses on photosynthetic traits of *P. australis*

Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Impacts of salt and alkali stress on component traits of reed clones

The total number of reed seeds decreased by 15.22% under salt concentration of 200 mM and 18.48% under salt concentration of 400 mM. A total number of reed seeds decreased by 51.09% and 65.22% at moderate (25 mM L⁻¹) and higher salinity stress (50 mM L⁻¹) alkaline stress. The total number of bud was decreased by 5% and 11.47% under 200 and 400 mM salt stress, while phosphorus contents were decreased by 11.67% and 31.67% under 25 and 50 mM alkaline stress (Figure 9B).

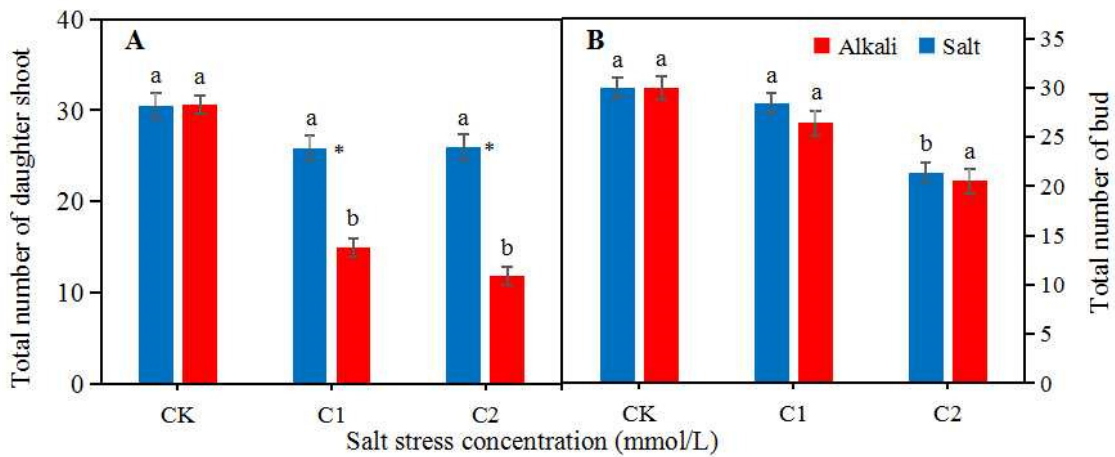


Figure 9. Effects of salinity and alkaline stress on total number of daughter shoots and total number of buds per plant of *P. australis*

Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Different letters showed significance among means

Under salt stress, the number of tiller plants of reed was decreased by 24.57% and 25.66% at moderate (200 mM) and higher salinity stress (400 mM). Rhizomes and stems decreased by 11.89% and 30.55%, respectively, at moderate (200 mM) and higher salinity stress (400 mM L⁻¹). The tiller buds and internode buds first depicted a substantial reduction and then increased with increasing intensity of salts. The number of tiller plants of reed was reduced by 41.82% and 63.33% under alkali concentrations of 25 and 50 mM. The number of rhizomes and stems decreased by 13.79% and 31.03%, respectively.

Number of different types of sub plants and buds of reed

With the increase of salt and alkali stress concentration, the tiller plant and rhizome plant of reed decreased significantly under alkali stress, and showed a downward trend under salt stress. Salt and alkali stress had different effects on the number of different sub strains and buds of different types of reeds (Table 1).

Table 1. Clonal growth characteristics of reed under salt and alkali stress

Clonal growth	Treatments	Control	200 mM NaCl stress	400 mM NaCl stress
Tiller plant	Salt treatment	2.5001 ± 0.19a	1.7857 ± 0.21a	1.7667 ± 0.24b
	Alkali treatment	2.5001 ± 0.19a	1.4545 ± 0.15b	0.6667 ± 0.22c
Rhizomes	Salt treatment	2.9995 ± 0.45a	2.6428 ± 0.36a	2.0833 ± 0.29a
	Alkali treatment	2.9995 ± 0.45a	2.5345 ± 0.45a	2.00 ± 0.28b
Tiller bud	Salt treatment	0.0978 ± 0.09b	0.0838 ± 0.05a	0.0901 ± 0.05a
	Alkali treatment	0.0978 ± 0.09b	0.1401 ± 0.03a	0.0012 ± 0.13b
Internal bud	Salt treatment	0.4891 ± 0.34a	0.1923 ± 0.36a	0.2608 ± 0.37a
	Alkali treatment	0.4891 ± 0.34c	0.1571 ± 0.23b	0.1249 ± 0.12a
Rhizome terminal bud	Salt treatment	0.4239 ± 0.12a	0.5384 ± 0.15a	0.3782 ± 0.09a
	Alkali treatment	0.4239 ± 0.12c	0.3891 ± 0.15b	0.3662 ± 0.14a

Note: Different letters in each row showed significance among means

Compared with the control group, under salt stress treatment, the number of tiller plants of reed was decreased by 24.57% under salt concentration of 200 mmol·L⁻¹, and 25.66% under salt concentration of 400 mmol·L⁻¹. The number of rhizomes and stems decreased by 11.89% and 30.55%, respectively. With the increase of salt stress concentration, the number of tillering buds and the number of internode buds first decreased and then increased with the increase of salt concentration, and the number of terminal buds first increased and then decreased.

Compared with the control group, under alkali stress treatment, the number of tiller plants of reed was reduced by 41.82% under alkali concentration of 25 mmol·L⁻¹, and decreased by 63.33% under alkali concentration of 50 mmol·L⁻¹. The number of rhizomes and stems decreased by 13.79% and 31.03%, respectively. With the increase of alkali stress concentration, the number of internode buds and terminal buds of rhizomes decreased, and the number of tillering buds increased first and then decreased

Impacts of salt and alkali stress on cation content of reed underground bud

The K content was decreased by 0.83% and 19.01% under 200 and 400 mM salt stress, while K contents was reduced by 22.89% and 38.24% under moderate (25 mM) and higher (50 mM L⁻¹) alkaline stress (Figure 10A). The Na content was increased by 89.64% and 128.13% under 200 and 400 mM salt stress, while Na contents was decreased by 121.56% and 109.14% at moderate (25 mM) and higher (50 mM) alkaline stress (Figure 10B). Na⁺/K⁺ of underground reed bud increased by 79.57% at 200 mM salt concentration and 146.42% at 400 mM salt concentration. Under alkali stress treatment, Na⁺/K⁺ increased by 172.04% when the alkali concentration was 25 mM and by 203.42% when the alkali concentration was 50 mmol·L⁻¹ (Figure 10C).

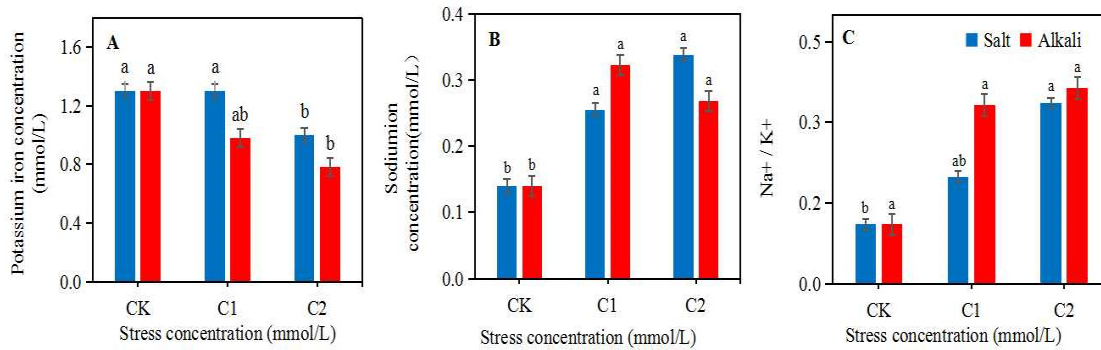


Figure 10. Impacts of salinity and alkaline stresses on cation content in underground sprouts of *P. australis*. Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Moreover, different letters showed significance among means

Effects of salt and alkali stress on anion content of reed underground bud

The content of Cl⁻ in underground buds of reed increased by 33.38% and 45.82% at moderate (25 mM) and higher (50 mM) salinity stress. Cl⁻ in underground reed buds decreased by 3.04% and 3.87% at moderate (25 mM) and higher (50 mM) alkaline stress (Figure 11A). The content of NO₃⁻ in underground reed buds decreased significantly under stress conditions ($p < 0.05$). NO₃⁻ in reed decreased by 24.59% and 49.77% under both stresses. NO₃⁻ content of underground reed buds decreased by 49.41% and 75.6% at moderate (25 mM) and higher (50 mM) alkaline stress (Figure 11B). The H₂PO₄⁻ content in underground reed buds increased by 4.12% at 200 mmol·L⁻¹ salt concentration and 9.03% at 400 mmol·L⁻¹ salt concentration. Under alkali stress treatment, the content of H₂PO₄⁻ in the underground bud of reed was decreased by 22.04% when the alkali concentration was 25 mM and by 43.26% when the alkali concentration was 50 mM (Figure 11C).

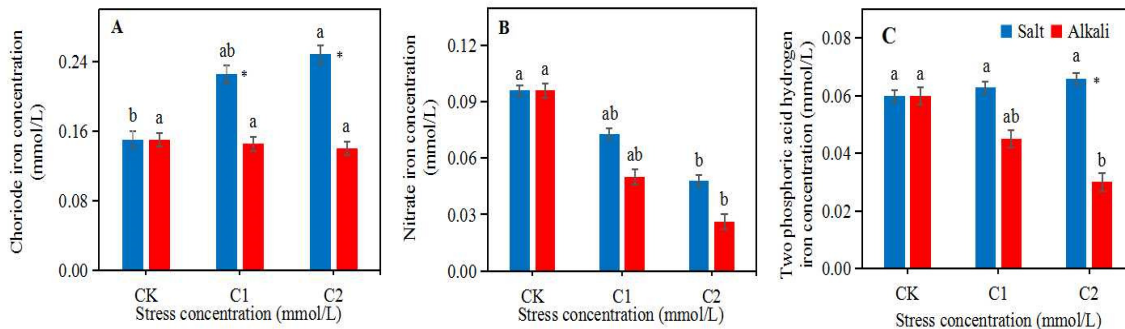


Figure 11. Impacts of salinity and alkaline stresses on anion content in underground sprouts of *P. australis*. Note: CK indicates control, C1, indicates 200 mM salinity stress and 25 mM alkaline stress while C2 indicates 400 mM salinity stress and 50 mM alkaline stress. Moreover, different letters showed significance among means

Discussion

Effects of salt and alkali stress on individual characteristics of reed

In the present study, salinity, and alkaline stress markedly reduced growth and biomass; however, alkaline stress imposed more negative impacts than salinity stress (Zhao *et al.*, 2023). The decrease in plant height and some above-ground biomass is a significant functional characteristic of plants under saline-alkali stress (Brant and Chen, 2015; Balasubramaniam *et al.*, 2023). Reeds distribute nutrients to the leaves of plants to ensure that the plants can produce the appropriate substances and then regulate stem growth to make effective use of environmental pressures

(Brant and Chen, 2015). In the practical research, the paper found that reed growth would produce a significant inhibition under salt-alkali stress. In increasing stress, the research results are the same as those of previous experts in the academic field. The expansion of plant leaves under salt-alkali stress is inhibited to a certain extent so that the plant will not lose water seriously (Balasubramaniam *et al.*, 2023). The reed will be seriously damaged by salt and alkali stress. The increasing intensity of both stresses increased N and N/P and decreased C, P, C/P, and C/N.

In recent years, with the in-depth study of ecological stoichiometry, the hypothesis of plant growth rate has become a typical theory (Yuan *et al.*, 2022). Suppose you take the ratio C: N: P, and it is integrated with the study of rRNA distribution and the rDNA composition of different biota so as to correlate the distribution of nutrient elements, the functional characteristics of organisms at this time, and ecological dynamics. The changes in plant history can induce a change in C: N:P values (Elser *et al.*, 2010; Sulpice *et al.*, 2014; Zhang *et al.*, 2023c). The N/P ratio of reed leaves was higher with increased salt and alkali concentrations. This is consistent with the typical “growth rate theory” mentioned above, and the C/N ratio decreased with increasing intensity of stresses.

The photosynthetic index of plants is an essential and obvious index for measuring plant response to stress (Kanai *et al.*, 2007; Takahashi *et al.*, 2007; Hnilickova *et al.*, 2021). In many other studies, the reduction of photosynthetic rate is directly related to the inhibition of plant growth to a certain extent (Lu *et al.*, 2023), which further reflects that plant growth is constrained by related factors, which is caused by the reduction of C assimilation rate of plants under stress (Zahra *et al.*, 2022). Stomatal conductance decreases continuously under salt and alkali stress, and the direction of intercellular CO₂ concentration C_i is the main index to analyze the decline of plant photosynthetic rate accurately. The intercellular CO₂ concentration (C_i) was decreased under increasing salt and alkali stress. These findings are aligning with previous findings indicating that salinity stress caused a significant reduction in plant photosynthesis (Rezaei *et al.*, 2017; Ebrahim *et al.*, 2019). The salt stress increases the production of reactive oxygen species (ROS) which damage the photosynthetic apparatus, and decreases the stomata conductance and intercellular CO₂ concentration leading to a substantial reduction in photosynthesis (Rezaei *et al.*, 2017; Ebrahim *et al.*, 2019). Further, other researchers also found salinity stress also decreases leaf and root potassium concentration and increases salinity-induced oxidative damage to photosynthetic apparatus, thereby reducing photosynthetic efficiency and overall plant performance (Kiani *et al.*, 2015; Hoseini *et al.*, 2024).

Effect of salinity and alkaline stress on tillers, rhizomes, and seed production

The total bud number showed a decreasing trend under salt and alkali stress. In this stage, plant buds will pre-generate the main characteristics of perennial clones (Müller *et al.*, 2022). These buds can effectively differentiate into leaf primordium and then smoothly form complete sub-strains, thus promoting the continuous reproduction of the population (Shen *et al.*, 2020). The reproductive resources required for plant growth have specific heterogeneity with the environmental conditions of plants (Zhang *et al.*, 2023b). This kind of strong selective pressure makes plants need to obtain adequate resources for ecological environment adaptation (Chen 2004; Zhang *et al.*, 2023b). The results showed that the reed was disturbed by salt and alkali stress, and the bud bank was expanded to prepare for reproduction. Still, the nutrients and energy were not enough to support the development of daughter plants, which was a kind of growth mode of reed growth and reproduction under limited and harsh environment. Under salt stress, the number of tillering buds and rhizome internode buds showed a reduction with increasing intensity of salts. The number of rhizome apex buds increased first and then decreased. This is similar to Ba *et al.* (2024) comprehensive comparative analysis of the elemental composition and change rules of reed bud banks in the two habitats of meadow grassland soil and saline-alkali soil in Northeast China (Ba *et al.*, 2024). Soil pH has a severe impact on soil chemical reactions and chemical processes and then effectively restricts the nutrients in plants. This link has a direct constraint on the decomposition rate of mineral elements. Soil pH value in the range of 6 to 7 is a slightly acidic state, at which time soil nutrients have the highest availability. Ten points are suitable for the healthy growth of plants (Penn and Camberato, 2019). Suppose the pH value of the saline-alkali soil habitat is the highest. In that case, it will significantly inhibit the reed bud bank and the bud formation in the whole life cycle. Under alkali stress conditions, the

reproduction of the reed was seriously affected. Tillering plants, rhizomes, rhizomes internode buds, and rhizomes apex buds all decreased with increased intensity of salts, and tillering buds increased first and then decreased. When the pH ratio of soil is high, the reed bud bank has a noticeable inhibition effect, which has a certain degree of unfavorable influence on the bud formation in the whole life cycle of the reed, resulting in a decrease in the number of buds in saline-alkali soil.

Under the influence of NaCl, the content of Na⁺ and Cl⁻ in underground buds increased significantly, and the harmful ion Na⁺ required less energy. It was first ingested, thus inhibiting the absorption of K⁺. The balance of the ratio of Na⁺/K⁺ was damaged, resulting in the change of osmotic potential in plant cells and abnormal accumulation of H₂PO₄⁻ content. Under alkali concentration treatment, Na⁺ content in underground reed buds increased first and then decreased with increased intensity of salts, which was greater than that in the control group. K⁺ content decreased significantly, NO₃⁻ and H₂PO₄⁻ contents decreased significantly, and the imbalance of cations and ions greatly inhibited each type of enzymatic reaction, resulting in metabolic disorders in cells. The growth and development of plants are greatly affected. This indicates that the normal asexual reproduction of the reed can no longer be maintained, and even the individual is on the verge of death.

Conclusion

In conclusion, increased salt and alkaline stress concentration markedly reduced the root length, plant height, and growth parameters. However, alkaline stress's impact was greater than salinity stress. Further, the concentration of K⁺ and NO₃⁻ was significantly decreased while Na⁺, Cl⁻, and Na⁺/K⁺ ratio concentration was increased under both stresses. Moreover, both stresses decreased stomata conductance, CO₂ concentration, and water use efficiency. However, more reduction was observed under salinity stress. The current study was conducted in controlled conditions; therefore, field studies are conducted to determine the toxicity of both salinity and alkaline stress on reed.

Authors' Contributions

Conceptualization: ZWG; Data curation: ZWG; Formal analysis: ZWG, JL; Funding acquisition: ZWG; Investigation: ZWG, JL; Methodology: ZWG, JL; Project administration: ZWG, JL; Resources: XLL, XL, YQQ, GG, LLH, MZC; Software: CC; Supervision: CSM; Validation: JTZ; Visualization: MH; Roles/Writing - original draft: ZWG, JL; and Writing - review & editing: GZW, JL.

All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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