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Effects of salinity and temperature on tuber sprouting and growth of *Schoenoplectus nipponicus*

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Abstract. In a scenario of climate change and intensive land-use change, the issue of salt marsh degradation caused by global warming and soil salinization is becoming more serious. A climate chamber experiment was conducted to examine the responses of tuber sprouting and seedling growth of *Schoenoplectus nipponicus* to variations in the temperature regimes (20/10, 25/15, 30/20 and 35/25°C; 12-h light/dark 12-h photoperiod) and different salt concentrations (0, 50, 75, and 100 mmol/L salinity). Results showed that the final sprouting percentage decreased with the increase in salinity and increased with the rising temperature. Salinity lower than 50 mmol/L was the most favorable for tuber sprouting. Under high salinity (75 and 100 mmol/L salinity), the inhibition of tuber sprouting at 20/10°C was greater than other temperature regimes. Along the temperature gradients, both plant height and leaf N content increased, and root length decreased under non-saline-alkali conditions, while plant height, leaf N content, and root length declined significantly under salt stress (50, 75, and 100 mmol/L salinity). With the increase in temperature, the production of tubers under the control treatments was enhanced significantly, but that under salt stress declined significantly. Under 0 mmol/L salinity, the accumulation of biomass in various organs increased with rising temperature. Biomass accumulation increased first and then declined for plants grown under salt stress, with a peak value of 25/15°C. Root: shoot ratio was reduced significantly under the combination of high salt stress (75 and 100 mmol/L salinity) and high temperatures (30/20°C and 35/25°C). Our study will contribute to a better understanding of the influence of climate warming and increasing serious human disturbances on this important wetland species.

Key words: biomass; bulbous sedge; climate warming; clonal reproduction; functional traits; propagation; salt marsh; soil salinization.

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INTRODUCTION

Climate change models indicate that extreme climatic events, such as salinization and temperature extremes, are likely to increase, not only in intensity but also in frequency (IPCC 2014). Salt marshes are among the most valuable ecosystems in the world, yet vulnerable to climate change and direct anthropogenic disturbance (Gedan et al. 2009, Kirwan and Mudd 2012). Salinity and temperature are two major abiotic stress factors affecting plant growth in inland salt marshes distributed in arid and semi-arid regions (Stenstrom et al. 2002, Munns and

Tester 2008). So a better understanding of the effect of temperature and salinity on the growth of salt marsh plants is of great significance in predicting the distribution pattern of salt marsh vegetation and is beneficial to the protection and management of degraded salt marsh.

Clonal reproduction is the main propagation mode of wetland plants (Sosnova et al. 2010). Tuber propagation is one of the modes of clonal reproduction, and tuber sprouting is a critical stage in life history for the growth and distribution of tuber plants (Luo et al. 2018). Many studies have shown that tuber sprouting is markedly influenced by salinity and temperature (Seneca 1969, Luque et al. 2013, Gu et al. 2018, Fos et al. 2020). For instance, higher salinity can suppress the tuber sprouting, affect sprouting kinetics, delay, and slow down the sprouting process (Munoz-Rodriguez et al. 2017, Santo et al. 2017). Meanwhile, the temperature can influence factors such as membrane permeability and enzyme activity, thus affecting the sprouting process (Gul and Weber 1999, Lin et al. 2011). And tuber sprouting is more rapid and complete with alternating temperatures than with constant temperatures (Miles et al. 2017). More importantly, the synergy of the two factors may aggravate or mitigate the influence of a single factor on tuber sprouting, because many physiological processes that are essential for tuber sprouting are subject to complex interactions of salinity and temperature (Gulzar et al. 2001, Al-Khateeb 2006). Unfortunately, little research has been done in this field.

Following the sprouting process, seedling growth is the most significant phenological event that affects the distribution area (Forcella et al. 2000). More researches have focused on seedling growth compared with the sprouting stage. The influence of salinity on plant growth generally showed that seedling growth is inhibited with the increase in salinity, which is mainly manifested by the reduction in growth traits and biomass accumulation (Pompeiano et al. 2016, MacTavish and Cohen 2017). Meanwhile, the biomass accumulation and clonal reproductive capacity of salt marsh plants would increase with the rising temperature (Johnson and Thornley 1985, Cao and Ruan, 2015, Zhang et al. 2018). Higher temperature may also enlarge or reduce the influence of salinity on plant growth, but the relevant evidence is still insufficient. More importantly, the joint research on sprouting and growth will provide clearer evidence for our prediction of plant distribution, and the related researches need to be strengthened urgently.

Schoenoplectus nipponicus is a perennial helophyte with tuber propagation (Eunsang et al. 2000). It is mainly distributed in North Korea, Russian Far East, and Northeast China. Its tubers are the major food source for a critically endangered bird species—the Siberian white crane (*Grus leucogeranus*; Cui et al. 2018). The distribution area of *S. nipponicus* in the Momoge National Nature Reserve has been gradually decreasing due to the impact of global climate change and human activities (Cui et al. 2018). However, the current research on *S. nipponicus* focuses on the effects of water depth, salt-alkaline stress, and nitrogen addition on its growth (Gu et al. 2019, 2020, Tang et al. 2020). It is therefore still unclear how *S. nipponicus* marshes respond to the interacting effects of temperature and salinity.

The present study aimed to investigate how tuber sprouting and seedling growth of *S. nipponicus* respond to salinity and temperature changes. We tested the tuber sprouting and seedling growth of *S. nipponicus* to different temperature and salinity treatment combinations under artificial climate chamber conditions to answer the following questions: (1) Do temperature changes result in changes in the effect of salinity on tuber sprouting of *S. nipponicus*? (2) Does rising temperature alleviate salt stress to the growth performance of *S. nipponicus*? (3) Does rising temperature promote the clonal reproductive traits of *S. nipponicus*, independently of the saline level? (4) Do salt stress and rising temperature change the biomass allocation pattern of *S. nipponicus*? We hypothesized that (1) changes in temperature will influence the response of tuber sprouting to salinity; (2) rising temperature will reduce the damage of salt stress on growth performance; (3) the high temperature will promote the production of ramets and tubers, and salinity and temperature have interactive effects on the clonal traits; (4) the high temperature will aggravate the adverse effects of salt stress on the root system and reduce the allocation to belowground biomass.

Materials and Methods

Study area

The Momoge National Nature Reserve (45°42′–46°18′ N, 123°27′–124°4′ E) is located in the northern part of the Songliao settlement zone and the western margin of the Songnen Plain (Xu et al. 2017, Ban et al. 2019). This area belongs to the semi-arid temperate continental monsoon climate, with an average annual temperature of 4.2°C and annual precipitation of 393.8 mm, which is mainly concentrated in the summer from July to August (Liu and Fan 2013). The elevation ranges from 128 to 167.7 m above sea level, and the relative height is 2–10 m between flat terrain and depressions. It covers an area of 1440 km^2, of which the wetland covers nearly 80% (Xu et al. 2017). Additionally, it is a wetland of international importance, mainly since this area provides stopover habitat for the Siberian crane (*Grus leucogeranus*) and plays an important role in preventing the saline-alkaline desertification of the Songnen Plains (Yu et al. 2014, Jiang et al. 2015).

Experimental design

Tubers of *S. nipponicus* were collected from the 30 cm deep silt in the study area in March 2019 and stored in a ziplock bag at 4°C. Tubers of similar size were selected and sterilized by NaClO solution for 5 min, and subsequently washed with distilled water and weighted before being used in the experiments. To evaluate the interactive effects of salinity and temperature on tuber sprouting and seedling growth, four salinities (0, 50, 75, and 100 mmol/L) were used, of which 0 mmol/L was used as a control. The salt solution was composed of $NaHCO_3$ and NaCl in a mass ratio of 2 to 1. Four diurnal temperature regimes (20/10, 25/15, 30/20, and 35/25°C) were used according to the preliminary test. The higher temperatures (20, 25, 30, and 35°C) coincided with the 12-h photoperiod, and the lower temperatures coincided with the 12-h dark period in the climate chamber.

The cleaned tubers were sown into pots (specification length × width × height: 10 × 10 × 10 cm) containing 8 cm of river sand (autoclave the river sand before use). Each pot was sown with a tuber at the same burial depth and added 200 mL test solution. The pots were then placed in four climate chambers. Three replicates of six tubers each were used for each treatment. An appropriate amount of water was added every morning and evening to maintain constant salinity in the river sand. Tubers were considered to have sprouted with the emergence of the radicle. No sprouting of new tubers for seven consecutive days was considered as the end of the sprouting experiment. The sprouting percentage was recorded every day until the end of the experiment.

After the tuber sprouting experiment was completed, seedlings with basically the same growth (plant heights were similar) were selected from the seedlings under the corresponding temperature and salinity treatment, and transplanted into large pots (specification length × width × height: 18 × 18 × 25 cm). One plant was planted in each pot filled with river sand. We had 48 observations of *S. nipponicus* (4 temperature regimes × 4 salinities, replicated 3 times). Watering was kept daily to keep the surface of the river sand moist, and the control experiment was officially started one week later. The pots were placed into solution tanks filled with 1/2 concentration of Hoagland solution with different salinities, and all treatments are maintained at a water level of 0. The solution tanks were then placed into the climate chamber. There were four salinity levels and four temperature treatments repeated three times. The relative humidity was set to 45%, and the Hoagland solution was replaced once every seven days. The seedling growth experiment lasted a total of 75 d.

Measurements

After the harvest, the plant height (cm height on the main plant) and root length (cm average root length pet pot) were determined. Following the completion of the growth traits measurements, mid-leaf sections of other young, fully expanded leaves of each individual were collected for the analysis of leaf N and P content. The leaves were oven-dried in an oven at 65°C for 48 h. The mass of the dried leaf samples was measured prior to grinding them to a powder using a Pica Blender Mill (Cianflone Scientific Instruments, Pittsburgh, Pennsylvania, USA). A 10.0 ± 0.5 mg portion of each sample was

packaged for the analysis of N and P content performed by the SmartChem300 Discrete Chemistry Analyzer (AMS Alliance, Graz, Italy). Leaf N and P contents were reported on a percentage basis (milligram per gram). Finally, all plant samples were oven-dried at 65°C to constant weight for at least 48 h and weighted. We recorded the tuber number (per pot) that had formed by the end of the experiment and the ramet number (per pot), and measured the root biomass (g dry weight per pot), tuber biomass (g dry weight per pot), and aboveground biomass (g dry weight per pot).

Statistical analysis

A two-way ANOVA was used for each of the treatment combinations to test the effects of factors and their interaction (salinity temperature) on the sprouting and growth. In order to meet the assumptions of homoscedasticity, part of the data has been transformed. Untransformed data are presented in figures. The mean values were further separated using Duncan's multiple range test (DMRT) for statistical significance levels ($P < 0.05$). All data were expressed as mean ± standard error (SE), and each mean value was calculated from three replicates.

Simple linear regression was then applied to estimate the relationship of growth traits and clonal traits at univariable level. Multiple linear regression was then applied to estimate the relationship of total biomass with functional traits. Variable selection for exploratory analyses was done by automatic backward stepwise procedure. The model assessment was done by checking the linearity assumptions, equal variance assumption, normality assumption, and outliers by using standardized residual plots. Variables with $P < 0.05$ were considered as statistically significant. The data were analyzed using SPSS 22.0 (SPSS, Chicago, Illinois, USA).

Results

Tuber sprouting

Significant effects of salinity ($F = 11.119$, $P < 0.001$) and temperature ($F = 13.976$, $P < 0.001$) were found on the tuber sprouting of *S. nipponicus*, whereas the effect of their interaction on the sprouting percentage has not been observed ($F = 0.452$, $P = 0.895$). For any of the temperature regimes, the final sprouting percentage declined as the salinity concentration increased. There is no significant difference in the final sprouting percentage between 0 and 50 mmol/L salinity at high temperatures (30/20°C and 35/25°C; Fig. 1). For any of the salinity levels, the final sprouting percentage increased as the temperature rose. The highest final sprouting percentage (94.4 ± 9.6%) was found in the treatments with 0 and 50 mmol/L salinity at 35/25°C (Fig. 1). The time to sprouting started and reach the maximum sprouting at 35/25°C was earlier than other temperature regimes. At high salt concentrations (75 and 100 mmol/L salinity), the initial sprouting time was delayed, and the sprouting period was also prolonged (Fig. 2).

Growth traits

A two-way ANOVA indicated that growth traits were significantly affected by salinity, temperature, and their interaction (Table 1). Plant height and root length significantly decreased with increasing salinity from 0 to 100 mmol/L

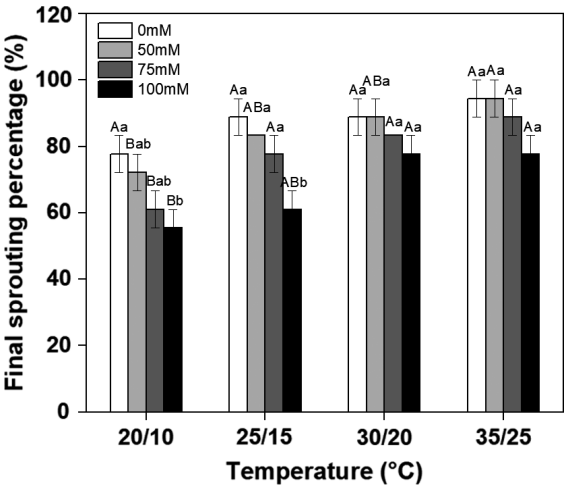


Fig. 1. Final sprouting percentage of *S. nipponicus* tubers under different temperature regimes and different saline concentrations. Different lowercase letters indicate significant differences between saline concentrations within each temperature ($P < 0.05$). Different capital letters indicate significant differences between temperature regimes within each saline concentration ($P < 0.05$). Error bars represent SE ($n = 3$). As the three replicates are the same at 25/15°C under 50 mmol/L salinity and 30/20°C under 75 mmol/L salinity, respectively, the standard error was 0.

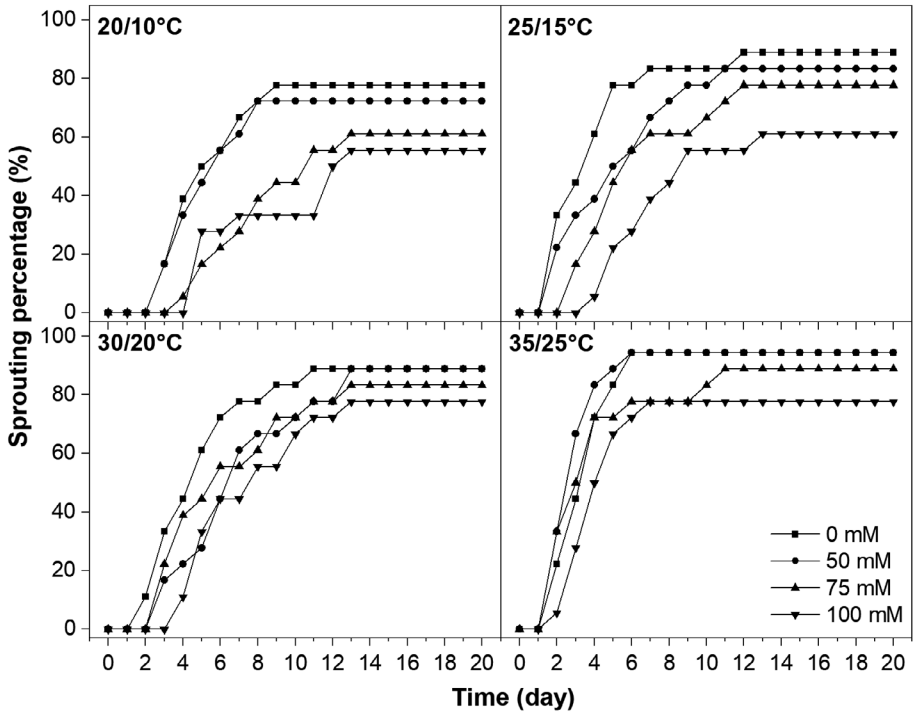


Fig. 2. Mean cumulative sprouting percentage of *S. nipponicus* tubers during 20 d under different temperature regimes and different salinity concentrations in 12-h light:12-h dark photoperiod.

under all temperature treatments (Fig. 3a, b). Under 0 mmol/L salinity, plant height was enhanced and root length was reduced at 30/20°C and 35/25°C compared with temperatures of 20/10°C and 25/15°C. With the increase in temperature, the plant height and root length increased slightly and then decreased under the salt stress treatments (50, 75, 100 mmol/L salinity; Fig. 3a, b). Leaf N content significantly declined with the increase in salinity at moderate and high temperatures (25/15°C, 30/20°C, and 35/25°C; Fig. 3c). Similar to plant height, leaf N content was significantly enhanced as temperature increased under 0 mmol/L salinity. Leaf N content significantly declined with higher temperatures from 20/10°C to 35/25°C, and the difference between 75 and 100 mmol/L was not significant (Fig. 3c). As the increase in salinity, leaf P content increased first and then declined at low temperatures (20/10°C and 25/15°C), with a peak value of 50 mmol/L salinity (Fig. 3d). As the temperature increased from 20/10°C to 35/25°C, leaf P content declined first and then increased under 50 and 75 mmol/L salinity, and the lowest at 30/20°C (Fig. 3d).

Clonal traits

Clonal traits of *S. nipponicus* were significantly affected by salinity, temperature, and their interaction (Table 1). Ramet number diminished as the salinity increased at the same temperature (Fig. 4a). Under low salinity (0 and 50 mmol/L salinity), ramet number increased first and then declined with the increase in temperature, with a peak value of 25/15°C (Fig. 4a). At moderate and low temperature (20/10°C, 25/15°C and 30/20°C), the production of tubers was promoted in the lower saline treatment (50 mmol/L salinity) than in the control treatment (Fig. 4b, c). Tuber number and tuber biomass showed a significant enhancement with rising temperature under 0 mmol/L salinity. However, as the increased temperature, the tuber number and tuber biomass increased first and then decreased under the salt stress treatments (50, 75, 100 mmol/L salinity; Fig. 4b, c). Tuber average mass declined as the salinity increased at 20/10°C and 35/25°C, whereas there was no significant difference in that at 25/15°C and 30/20°C in the four salinity treatments (Fig. 4d). At the salinity of 0 mmol/L,

Table 1. Analysis of variance (ANOVA) indicating effects of temperature, salinity, and their interactions on functional traits of *S. nipponicus*.

Source of variance	Salinity		Temperature		Salinity × temperature	
	F	*P*	*F*	*P*	*F*	*P*
Growth traits						
Plant height (cm)	567.298	<0.001***	125.197	<0.001***	62.074	<0.001***
Root length (cm)	120.747	<0.001***	186.089	<0.001***	5.299	<0.001***
Leaf N (mg/g)	351.370	<0.001***	252.798	<0.001***	83.626	<0.001***
Leaf P (mg/g)	77.967	<0.001***	40.840	<0.001***	42.951	<0.001***
Clonal traits						
Ramet number	150.750	<0.001***	150.750	<0.001***	11.583	<0.001***
Tuber number	19.447	<0.001***	64.730	<0.001***	25.535	<0.001***
Tuber biomass (g)	22.334	<0.001***	43.811	<0.001***	21.047	<0.001***
Average tuber mass (g)	4.344	0.011*	4.758	0.007**	3.006	0.010*
Biomass						
Aboveground biomass (g)	255.238	<0.001***	20.385	<0.001***	17.052	<0.001***
Belowground biomass (g)	379.382	<0.001***	145.792	<0.001***	33.758	<0.001***
Total biomass (g)	570.447	<0.001***	97.301	<0.001***	40.158	<0.001***
Root: shoot ratio	4.669	0.008**	38.371	<0.001***	11.357	<0.001***

Notes: The numbers in the table are *F* and *P* values. Data represent *F* values at 0.05 level.
*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

there was no significant difference in the tuber average mass at different temperatures. However, under high salt treatments (75 and 100 mmol/L salinity), tuber average mass at 20/10°C and 35/25°C was significantly lower than that at 25/15°C and 30/20°C (Fig. 4d).

Biomass accumulation and allocation

Significant effects of salinity, temperature, and their interactions were found on biomass accumulation and allocation of *S. nipponicus* (Table 1). Aboveground biomass, belowground biomass, and total biomass were significantly reduced as the increase in salt concentration at the same temperature (Fig. 5a, b, c). The accumulation of biomass in various organs was significantly enhanced with rising temperature under 0 mmol/L salinity. For plants grown under salt stress (50, 75 and 100 mmol/L salinity), biomass accumulation showed that increased first and then decreased, with a peak value of 25/15°C (Fig. 5a, b, c). The root: shoot ratio was significantly increased with increasing salinity from 50 to 100 mmol/L at 25/15°C and 30/20°C, whereas it declined with increasing salt stress at extreme temperatures (20/10°C and 35/25°C; Fig. 5d). Root: shoot ratio first increased and then declined with the increase in temperature under the salt stress treatments (50, 75, 100 mmol/L salinity; Fig. 5d).

Relationship among growth traits, clonal traits, and biomass

Five traits were chosen for simple linear regression analysis based on their statistical. Tuber number ($R^2 = 0.5209$, $P < 0.001$) and ramet number ($R^2 = 0.1616$, $P = 0.005$) were both significantly correlated with plant height, increasing with increasing plant height (Fig. 6a, b). Root length ($R^2 = 0.5182$, $P < 0.001$) and ramet number ($R^2 = 0.4621$, $P < 0.001$) were both significantly correlated with leaf N content, increasing with increasing leaf N content (Fig. 6c, d). Multiple linear regression analysis showed that for total biomass, only plant height and ramet number were included in the final model, with these variables explaining 70.6% and 17.8% of the variation in total biomass, respectively (Table 2).

Discussion

Responses of tuber sprouting to salinity and temperature

Our experiments indicated that increasing salinity significantly reduced the tuber sprouting percentage and prolonged the sprouting period. Similar results have been reported by others (Levy et al. 1993, Sanchéz-Bernal and Ortega-Escobar, 2011). That may be related to the result of the combined action of osmotic stress and ion

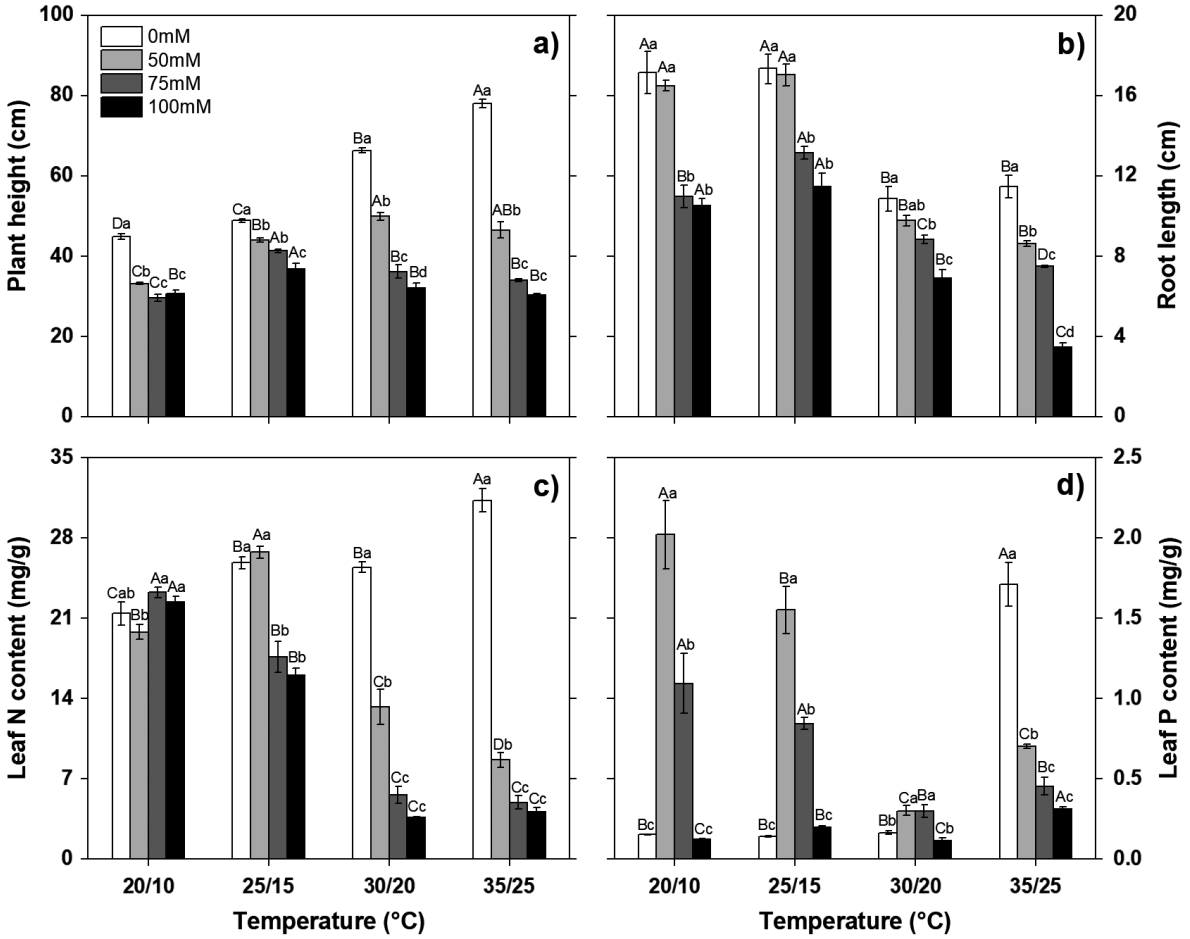


Fig. 3. The effect of salinity and temperature on plant height (a), root length (b), leaf N content (c), and leaf P content (d) of *S. nipponicus*. Different lowercase letters indicate significant differences between saline concentrations within each temperature ($P < 0.05$). Different capital letters indicate significant differences between temperature regimes within each saline concentration ($P < 0.05$). Error bars represent SE ($n = 3$).

toxicity (Song et al. 2005), such as the penetration effect of Na^+ (Bajji et al. 2002). This behavior could also be because salinity lowers the osmotic potential of the soil and slows down the hydration of the propagules (Melendo and Giménez 2018). Compared with the non-saline treatments, the sprouting percentage decreased by 28.6% at 100 mmol/L salinity at 20/10°C, whereas this value dropped to 17.6% at 35/25°C. This shows that the elevation in temperature in the sprouting stage has a certain compensation effect on the negative effect of salt (Yue et al. 2019).

We also observed that elevated temperature promoted tuber sprouting. The highest sprouting percentage values for any of the salinity concentrations tested also occurred when the temperature regime was 35/25°C, and the greater the difference with respect to this temperature, the greater the decline in the sprouting percentage. Therefore, this is the optimal temperature for the tuber sprouting. Our results are in accordance with previous studies of tuber sprouting response to elevated temperature (Huang et al. 2019). This may be because the temperature can change the content of plant hormones and regulate the dormancy and sprouting of tubers (Liu et al. 2015). Simultaneously, the temperature can affect either the initial processes of water uptake

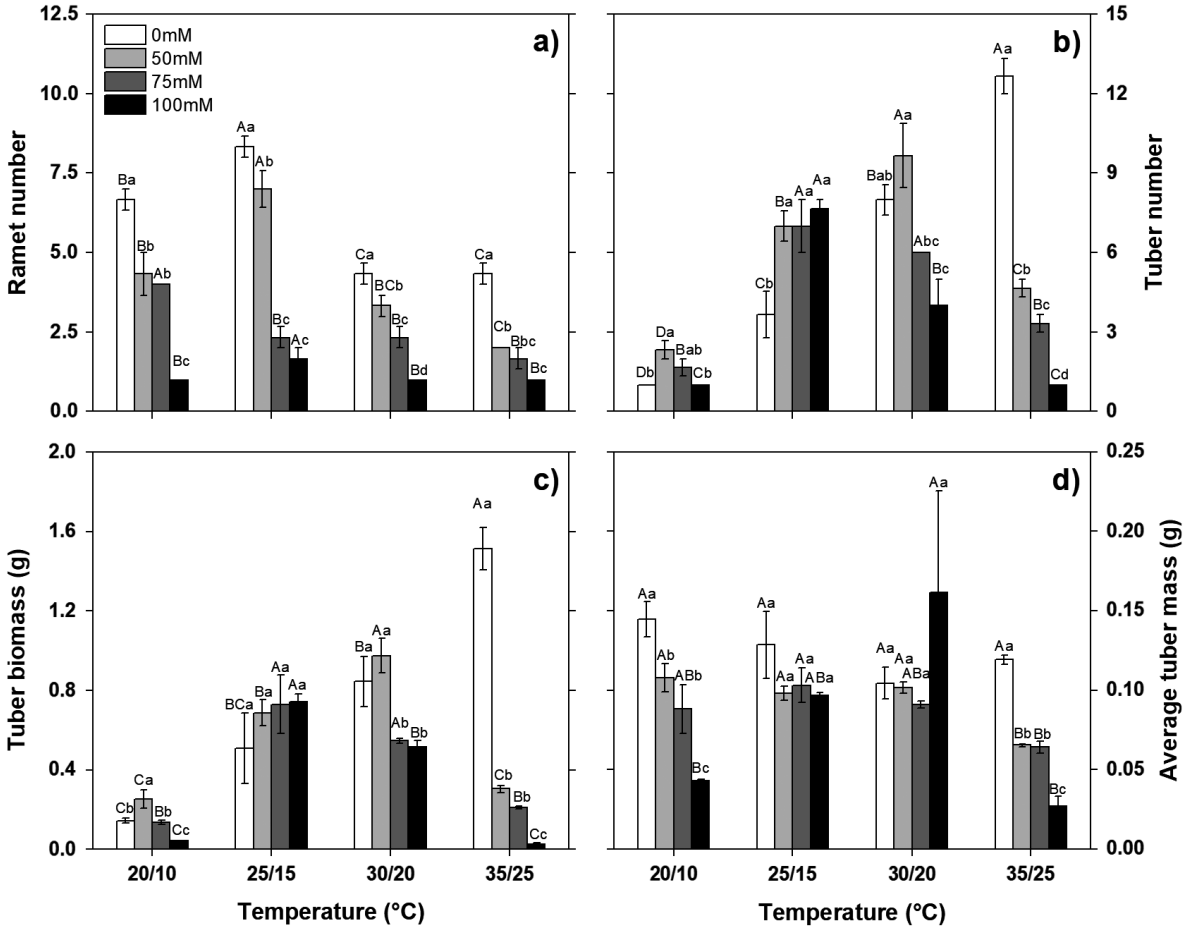


Fig. 4. The effect of salinity and temperature on ramet number (a), tuber number (b), tuber biomass (c), and average tuber mass (d) of *S. nipponicus*. Different lowercase letters indicate significant differences between saline concentrations within each temperature ($P < 0.05$). Different capital letters indicate significant differences between temperature regimes within each saline concentration ($P < 0.05$). Error bars represent SE ($n = 3$).

or the following physiological–biochemical processes that induce cell division within the propagules (Kermode 1990).

Counter to predictions, the interaction between salinity and temperature on the tuber sprouting was not significant, but we think temperature still affects the response of tuber sprouting to salinity gradients to a certain extent. The unremarkable effects of interaction in our experiment may be related to the salt concentration gradients. In general, sprouting in halophytes occurs with a certain combination of light (photoperiod), salinity, and temperature (Gul et al. 2013). But different plants have different responses to the combination of temperature and salt stress.

Responses of growth performance to salinity and temperature

In the present study, *S. nipponicus* showed substantially lower plant height with increasing salinity. Similar results have also been demonstrated by other studies (Abdel Latef et al. 2016, Rodrigues et al. 2019). Moreover, the leaves of the plant began to turn yellow, wilt, and shedding at 100 mmol/L salinity, which maybe since that the plants shed old leaves to avoid salt toxicity, and cannot effectively accumulate nutrients (Mishra and Tanna 2017). Rising temperature increased plant height in our experiment in the absence of salt, which has been previously observed in other wetland pants (Anastácio et al.

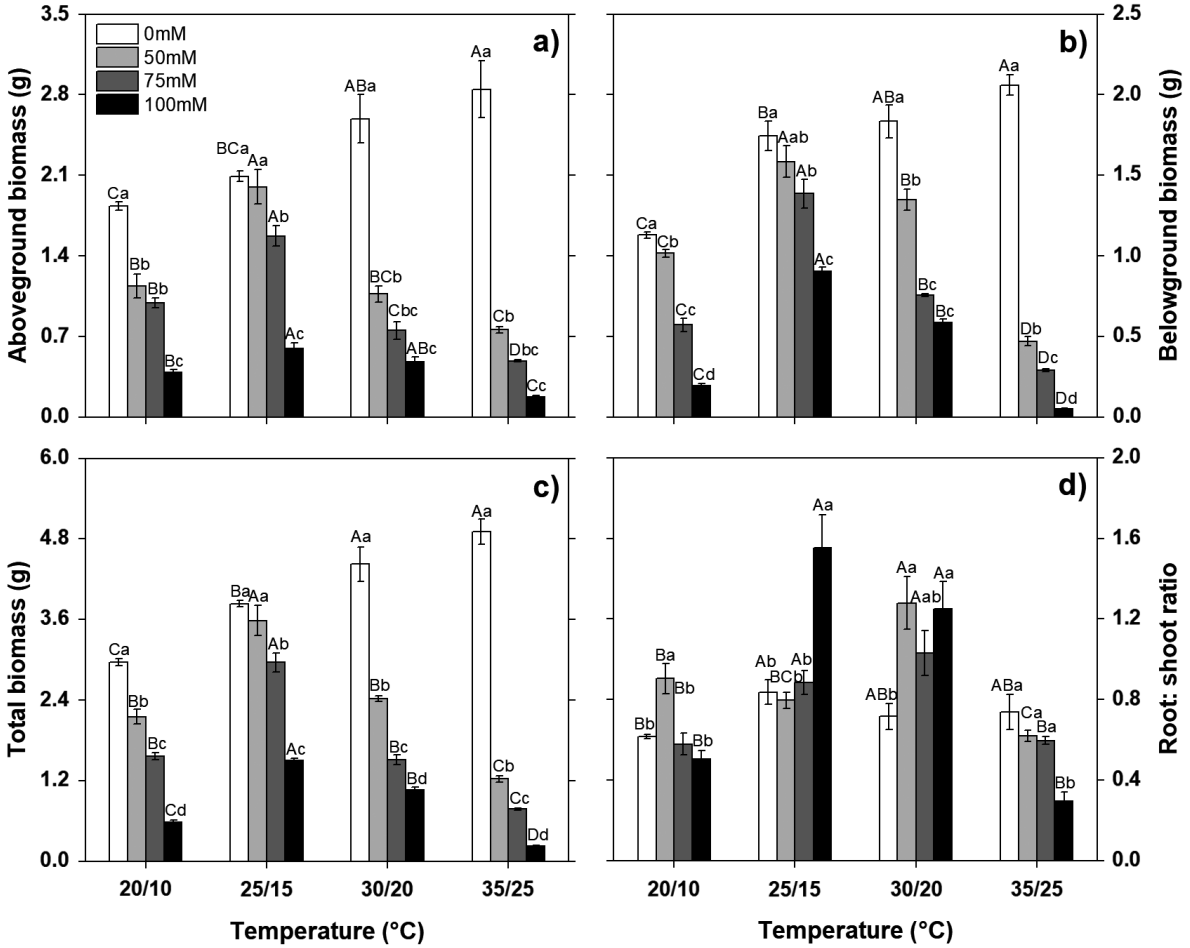


Fig. 5. The effect of salinity and temperature on aboveground biomass (a), belowground biomass (b), total biomass (c), and root: shoot ratio (d) of *S. nipponicus*. Different lowercase letters indicate significant differences between saline concentrations within each temperature ($P < 0.05$). Different capital letters indicate significant differences between temperature regimes within each saline concentration ($P < 0.05$). Error bars represent SE ($n = 3$).

2013, Zhang et al. 2013, 2018, Velthuis et al. 2017). Higher temperature causes increased photosynthesis in plant leaves, which in turn led to increased plant height (Yamori et al. 2005). Plant height of this species generally decreased in a concentration-dependent manner with increasing salinity at 25/15°C and above; however, when the temperature was below 25/15°C, this decrease was concentration-independent, with all the salt-treated seedlings exhibiting decreases in a similar magnitude, regardless of salt concentration. It seems that the positive effects of temperature are able to partially compensate for the negative effects of salinity.

Results obtained from statistical analyses in this study demonstrated that higher salinity led to lower leaf N and P content at higher temperatures. Similar results have been reported by others (Garcia-Caparros et al. 2017). This may be related to the higher salinity resulted in a negative value for net uptake and translocation rates from roots to shoots of N and P. For P, the reduction may be the result of the activity of antagonism between ions, such as Cl^-, which can reduce the activity of phosphate transporters (of both high and low affinity), which are necessary for the uptake of P (Kochian 2000). As the temperature increases, increasing the salinity significantly reduced the

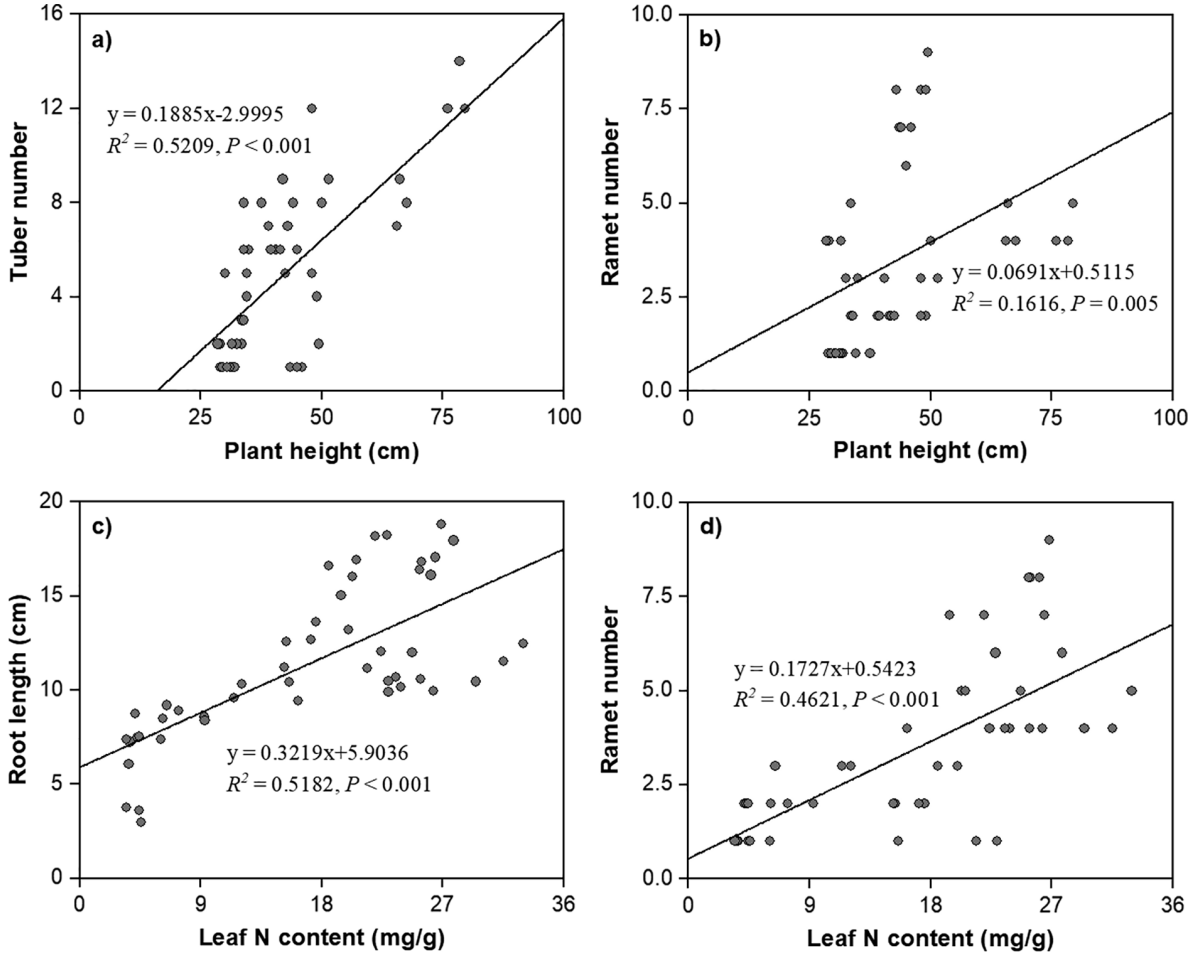


Fig. 6. Relationships between aboveground traits and belowground traits of *S. nipponicus* seedling. (a) tuber number vs. plant height; (b) ramet number vs. plant height; (c) root length vs. leaf N content; (d) ramet number vs. leaf N content. Solid lines are fit by an equation with $P < 0.05$.

Table 2. Summary of multiple linear regression model of total biomass with functional traits.

Factor	df	MS	SS%	*F*	*P*
Plant height	1	64.900	70.6%	273.539	<0.001
Ramet number	1	16.368	17.8%	68.989	<0.001
Residuals	45	0.237	11.6%		

Note: df, degrees of freedom; MS, mean squares; SS, proportion of variances explained by the variable.

nitrogen and phosphorus content of the leaves. This may be due to the increased adverse effects of salinity on plants after rising temperature (Wittyngham et al. 2019).

The belowground traits of the plant will be more sensitive to salt stress than the aboveground traits (Croser et al. 2001), and our results also confirm this view. With increasing salinity level, root length of *S. nipponicus* decreased significantly, which is consistent with the findings of related researchers using *Lupinus termis* (Abdel Latef et al. 2016). The plant root systems can respond to sodium chloride toxicity by changing structure, such as reducing root length (Mahajan and Tuteja 2005). Previous studies have shown that cell-wall peroxidase activity and H_2O_2 levels increased by sodium salt stress, while exogenous H_2O_2 and peroxidase inhibited plant root growth (Marius Assaha et al. 2015). When the temperature is lower than 25/15°C, the salinity has a significant effect on the root length,

and the temperature has little effect on it. However, root length generally decreased with increasing temperature at 25/15°C and above, and this decrease more significantly at high salt. Similar observations were made by Lopes et al. (2015) in *Montrichardia arborescens*. At the high saline treatments, the imbalance of ions around the plant roots reduces the effective absorption of external nutrients, inhibits the outward expansion of the root system, and higher temperature expands this adverse effect (Thompson et al. 2007).

Responses of clonal reproductive traits to salinity and temperature

It was found in this study that high saline treatments significantly reduced the ramet number, tuber number, tuber biomass, and tuber average mass of *S. nipponicus*. Similar to our results, Dias et al. (2016) observed that *Helianthus tuberosus,* L. grown in salt absence had better tuber yield, and Ding et al. (2011) also found that salt stress would significantly reduce ramet number of *Aeluropus sinensis*. Zhang et al. (2020) also found that high saline treatments inhibit the asexual reproduction of *Scirpus mariqueter*. Tillering capacity of *S. nipponicus* was significantly inhibited with the increase of salt concentration, which was beneficial to reducing the ion accumulation and alleviated saline injures in plants. Compared with 0 mmol/L saline treatment, the tuber number increased significantly under low salt condition (50 mmol/L salinity) except for 35/25°C. On the one hand, the tuber can store a large amount of salt ions to reduce the injures caused by salt stress to other organs of the plant (Mauchamp and Mésleard 2001). On the other hand, the transfer of plant matter is mainly from top to bottom under salt stress, and the aerial part is mainly a place to obtain resources.

In the present study, the ramet number was increased at 25/15°C and then diminished with the temperature rose in non-saline conditions. Similar to our results, an appropriate increase in temperature will increase the ramet number of submerged macrophyte *Vallisneria natans* (Cao and Ruan 2015). For one thing, temperature elevation can increase the activity of photosynthetic, enzymes, and carbonic anhydrase, which likely caused the increases in ramet number in our experiment (Olesen and Madsen 2000). For another thing, excessive elevated temperature caused a highly significant decrease in the abscisic content and an increase in the gibberellic acid hormones, which led to a decrease in tillering capacity (Morales-Coronado et al. 2019). Moreover, higher temperatures significantly reduced the clonal reproductive traits under salt stress. This may be caused by the combination of the negative effects of high temperature and salt stress.

Responses of biomass accumulation and allocation to salinity and temperature

Our statistical results displayed that total biomass and aboveground biomass were reduced with increasing salinity levels. A similar conclusion has been reached for the study of the wetland plants *Beckmannia syzigachne*, *Comarum palustre* L., *Myosotis scorpioides* L., and *Polygonum maritimum* L. (Stofberg et al. 2015, Glaeser et al. 2016, Rodrigues et al. 2019). Excessive salinity may hinder the normal metabolism of plant leaves through osmotic stress and ion poisoning, or by affecting the synthesis of chlorophyll, gas exchange, and stomatal conductance, thereby inhibiting the synthesis and accumulation of plant organic matter (Li et al. 2010, Xue et al. 2017). The results of this experiment showed that belowground biomass decreased significantly with increasing salinity when compared with the salt-free treatments. Our results are consistent with previous studies of root response to salt stress in *Spartina alterniflora* and *Paspalum paspaloides* (MacTavish and Cohen 2017, Xing et al. 2019). Our study also found that the biomass accumulation reached the maximum at 25/15°C under salt stress, and the greater the difference with respect to this temperature, the greater the decline in the biomass accumulation. That may be owing to the fact that low or high temperature will reduce stomatal conductance, enzyme activity, and electron transport under stress, which in turn cause lower photosynthetic rate, which will inhibit the growth of plants (Ge et al. 2014).

The plasticity response of the biomass allocation pattern is one of the important adaptation strategies of wetland plants in response to environmental changes (Wright and McConnaughay 2002). In this study, with the increased salinity, there was a trend toward lower root: shoot ratio at the highest temperature (35/25°C). Similar to

our result, salinity shifts from 5 to 20 parts per thousand considerably diminished root: shoot ratio of *Myriophyllum spicatum* L. *and Ruppia maritima* L. (Hillmann and La Peyre 2019). This may be related to the fact that individuals from high salinity treatments had less fine roots, and the remaining roots had a brown discoloration (Stofberg et al. 2015). Moreover, high temperature aggravated the damage of salt stress to the root system. Therefore, roots system may be more seriously damaged by high salinities than aboveground tissue.

Association among growth traits, clonal traits, and biomass

Plant height and leaf N content were significantly positively correlated with the clonal reproductive traits in our study by *S. nipponicus*. These showed that there is a very strong synergy between growth traits and clonal reproduction traits. Gaudet and Keddy (1988) believe that dominance and competitive ability among plants can be enhanced by certain traits such as individual plant biomass and height. Our results showed that both plant height and ramet number had positive effects on the total biomass. Similar results have also been found for saltmarsh plants, where canopy height exerted a positive influence on aboveground production (Minden and Kleyer 2015). This is mainly because plant height has a strong influence on light capture ability, and taller plants have high nutrient acquisition potential (Gustafsson et al. 2018). For wetland plants, clonal reproduction ability is an essential manifestation of their dominance and competitive ability. Clonal traits are closely related to the resource utilization, survival, and reproduction of clonal plants, and ramet traits determine the capacity of the plant to utilize photosynthetic products (Li et al. 2020).

Conclusions

The present study indicated that *S. nipponicus* is quite sensitive to changes in salinity. Salinity lower than 50 mmol/L is the most favorable for tuber sprouting, and increasing temperature can reduce the inhibitory effect of salt stress on tuber sprouting. However, high temperatures (30/20°C and 35/25°C) aggravate the adverse effects of salt stress on growth, reproduction, and biomass accumulation. This study provides baseline information on salt tolerance of *S. nipponicus* at different temperatures. Future studies will be conducted to discuss the effects of fluctuations of salt concentration and varying diel temperature ranges on the sprouting and growth of *S. nipponicus*.

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