Under drought conditions NaCl improves the nutritional status of the xerophyte *Zygophyllum xanthoxylum* but not of the glycophyte *Arabidopsis thaliana*

Wen-Ying Wang[1§], Wei-Wei Chai[1§], Chang-Yu Zhao[1§], Owen Rowland[1,2], Bao-Shan Wang[3], Xin Song[1], Ya-Qi Liu[1], Qing Ma[1], and **Suo-Min Wang[1]***

[1] State Key Laboratory of Grassland Agro-ecosystems; Key Laboratory of Grassland Livestock Industry Innovation, Ministry of Agriculture and Rural Affairs; College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou, 730020, P. R. China
[2] Department of Biology and Institute of Biochemistry, Carleton University, Ottawa, ON K1S 5B6, Canada
[3] Key Laboratory of Plant Stress Research, College of Life Science, Shandong Normal University, Jinan, 250014, P. R. China

Abstract

Zygophyllum xanthoxylum is a salt-accumulating xerophytic species with excellent adaptability to adverse environments. Previous studies demonstrated that *Z. xanthoxylum* absorbs a great quantity of Na^+ as an osmoregulatory substance under arid conditions. To investigate the nutritional status of *Z. xanthoxylum* in comparison with a typical glycophyte, *Arabidopsis thaliana*, seedlings were exposed to NaCl (50 mM for *Z. xanthoxylum* and 5 mM for *A. thaliana*), osmotic stress (–0.5 MPa), and osmotic stress combined with the NaCl treatment. Compared to the control, NaCl treatment or osmotic stress significantly increased Na^+ concentration in leaves and roots of *Z. xanthoxylum*, but not of *A. thaliana*. Under osmotic stress, the addition of NaCl significantly increased Na^+ concentration in leaves and roots of *Z. xanthoxylum*, resulting in improved biomass and tissue water content. However, such changes were not observed in *A. thaliana*. Compared to the control, K^+ concentrations in leaves and roots remained unchanged in *Z. xanthoxylum* when exposed to osmotic stress, with or without additional 50 mM NaCl. In contrast, significant reductions in shoot K^+ concentrations of *A. thaliana* were observed under osmotic stress alone or when combined with 5 mM NaCl. Moreover, NaCl alone or when combined with osmotic stress enhanced the accumulation of N, P, Fe, Si, Ca^{2+}, and Mg^{2+} in *Z. xanthoxylum*, but did not cause such nutritional changes in *A. thaliana*. Compared to the glycophyte *A. thaliana*, *Z. xanthoxylum* could accumulate Na^+ and maintain the stability of nutritional status at a relatively constant level to cope with drought stress.

Key words: K^+ homeostasis / potassium–sodium interaction / nutrients / water

Accepted March 31, 2019

1 Introduction

Drought is a major abiotic stress that threatens agricultural productivity all over the world (*Martínez* et al., 2003; *Bartels* and *Sunkar*, 2005; *Hassine* et al., 2010). About 25% of the world's agricultural land is affected by drought stress (*Jajarmi*, 2009). Global climatic change is predicted to alter growth-season precipitation-patterns, potentially increasing the risk of drought, and in particular extreme drought events during this century (*Anand* et al., 2003; *Luo* et al., 2018). Drought stress induces a set of physiological and biochemical reactions including reducing water use efficiency in plants, which impair normal growth and water status (*Farooq* et al., 2012; *Sahin* et al., 2018). Drought also generally results in inhibition of plant growth by disturbing the uptake of ions (*Farooq* et al., 2012; *Huang* et al., 2018). To mitigate the adverse effects of drought stress, plants have developed various adaptations which generally involve a mixture of stress tolerance and salt avoidance mechanisms (*Javadi* et al., 2017). In particular, xerophytes have evolved a range of adaptive mechanisms

that ensure their survival and reproduction in arid or semi-arid environments (*Farooq* et al., 2012; *Wu* et al., 2015a).

Zygophyllum xanthoxylum, which naturally grows in the desert areas of northwest China and Mongolia, is a salt-accumulating xerophytic species with strong adaptability to adverse environments (*Liu* et al., 1987; *Wang* et al., 2004; *Wu* et al., 2011; *Yuan* et al., 2015). Our previous studies showed that *Z. xanthoxylum* absorbs Na^+ from low-salt soils and accumulates Na^+ in leaves for osmotic adjustment (*Wang* et al., 2004; *Cai* et al., 2011; *Wu* et al., 2011; *Janz* and *Polle*, 2012; *Yuan* et al., 2015). Further investigations revealed that *Z. xanthoxylum* becomes more tolerant to drought in the presence of moderate salinity with improved photosynthesis and water status (*Ma* et al., 2012; *Yue* et al., 2012). Although the addition of 50 mM NaCl significantly increased the leaf Na^+ concentration in *Z. xanthoxylum* under drought stress, no significant change in K^+ concentration was observed (*Wu* et al.,

---

2   Wang, Chai, Zhao, Rowland, Wang, Song, Liu, Ma, Wang

J. Plant Nutr. Soil Sci. 2019, *000*, 1–10

2011; *Ma* et al., 2012; *Yue* et al., 2012). However, apart from Na^+ and K^+, other nutritional changes of *Z. xanthoxylum* exposed to salt or drought combined with salt have not yet been measured.

Generally, drought stress inhibits the uptake and translocation of nutrients including K^+ in plants, especially in glycophytes (*Hu* and *Schmidhalter*, 2005). In the Townsville stylo plant (*Stylosanthes humilis*), phosphorus (P) concentration was greatly reduced under drought stress (*Fisher*, 1980). Drought stress decreased nitrogen (N) concentration in several species, such as lettuce (*Lactuca sative*; *Ruiz-Lozano* and *Azcón*, 1996), maize (*Zea mays*; *Foyer* et al., 1998), and cowpea (*Vigna unguiculata*; *da Silveira* et al., 2001). A decreased level of K^+ and reduction in Mg^{2+} uptake were observed in banana (*Musa nana*) under drought conditions (*Mahouachi*, 2007). *Hu* et al. (2007) revealed that drought decreased the accumulation of N, P, K^+, Na^+, Ca^{2+}, Mg^{2+}, and Fe in blades of wheat (*Triticum aestivum*).

However, in *Beta vulgaris*, the addition of 50 mM NaCl improved resistance against osmotic stress with increased Na^+ concentrations, while the K^+ concentrations in shoots and roots were decreased (*Wu* et al., 2015a). Conversely, *Z. xanthoxylum* accumulates a large quantity of Na^+ and maintains the concentrations of K^+ in response to drought (*Ma* et al., 2012). Hence, we hypothesize that accumulating Na^+ and maintaining the stability of the nutritional status at a relatively constant level is a unique mechanism for *Z. xanthoxylum* in its response to drought. This was not predicted to occur with a glycophyte such as *Arabidopsis thaliana*. Therefore, in the present study, we analyzed nutrient accumulation in the salt-accumulating xerophyte *Z. xanthoxylum* in comparison with the glycophyte *A. thaliana* under drought stress and in the presence or absence of additional NaCl.

2 Material and methods

2.1 Plant growth conditions and treatments

Seeds of *Zygophyllum xanthoxylum* were collected from wild plants in the Alxa League (39°05′N, 105°34′E; elevation 1360 m) of Inner Mongolia Autonomous Region, China. The mean annual rainfall and temperature were 60–150 mm and 8°C, respectively (*Ma* et al., 2012). After removal of the bracts, seeds were sterilized for 1 min with 5% (v/v) sodium hypochlorite solution, rinsed six times with distilled water, soaked in distilled water at 4°C for 1 d, and then germinated on filter paper at 25°C in the dark for 2 d. The seedlings were transplanted to pots (5 cm × 5 cm × 5 cm; two plants per pot) containing silica sand, and irrigated with modified Hoagland nutrient solution containing 2 mM KNO_3, 0.5 mM $NH_4H_2PO_4$, 0.25 mM $MgSO_4$, 0.1 mM $Ca(NO_3)_2$, 0.5 mM Fe-citrate, 92 μM H_3BO_3, 18 μM $MnCl_2$, 1.6 μM $ZnSO_4$, 0.6 μM $CuSO_4$, and 0.7 μM $(NH_4)_6Mo_7O_{24}$, with a pH of 5.7 buffered with 1 M Tris. This solution was renewed every 3 d. Seedlings were grown in a greenhouse with mean temperatures of 28 ± 2°C/23 ± 2°C (16 h day/ 8 h night), light intensity of 600 μmol m^{-2} s^{-1}, and relative humidity of 65%.

Seeds of *Arabidopsis thaliana* (Col–0) were sterilized for 3 min with 75% (v/v) ethanol and 5% (v/v) sodium hypochlorite, rinsed 6 times with distilled water, and soaked in distilled water at 4°C for 2 d. The seedlings were transplanted to pots (5 cm × 5 cm × 5 cm; four plants per pot^{-1}) containing sand and irrigated with modified Hoagland nutrient solution as described above. The nutrient solution was renewed every 3 d. Seedlings were grown in a greenhouse with mean temperatures of 18 ± 2°C/16 ± 2°C (16 h day/ 8 h night), light intensity of 200 μmol m^{-2} s^{-1}, and relative humidity of 80%.

Z. xanthoxylum and *A. thaliana* were grown in modified Hoagland nutrient solution for 21 d and 40 d, respectively, to obtain similar-size plants. Plants of *Z. xanthoxylum* (21 d old) and *A. thaliana* (40 d old) were divided into four groups, respectively: control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum* because this concentration of NaCl enhances its growth, 5 mM NaCl for *A. thaliana* because 50 mM NaCl causes significant growth inhibition), and O+S (osmotic stress combined with NaCl treatment, total osmotic potential was –0.5 MPa). Prior to S and O+S treatments, the seedlings were preconditioned with the corresponding concentration of NaCl solution for 3 d. Plants were harvested 0, 24, 48, and 72 h after treatment for the measurement of biomass and the determination of nutrients. The treatment solutions were changed every day to maintain a constant concentration of NaCl and osmotic potential.

2.2 Tissue fresh weight, dry weight, and water content

Plants were separated into roots, stems, and leaves. The roots were washed twice for 8 min in ice-cold 20 mM $LiNO_3$ to exchange the cations in the apoplast, while the leaves and stems were rinsed with deionized water to remove any surface salts. The fresh weights were determined immediately and samples were dried in an oven at 80°C for 48 h to determine the dry weights. The tissue water contents were calculated using the equation:

$$Water\ content = (fresh\ weight - dry\ weight)/dry\ weight$$

(1)

2.3 Tissue Na^+ and K^+ concentrations

Na^+ and K^+ were extracted from 20 mg of dried plant tissues in 10 mL of 100 mM acetic acid at 90°C for 2 h, and ions assayed using a flame atomic absorption spectrophotometer (2655-00, Cole-Parmer Instrument Co., Vernon Hills, USA). The net Na^+ and K^+ uptake rates were calculated using the equation described by *Wang* et al. (2007, 2009).

2.4 Nitrogen (N) and phosphorus (P) concentrations

Nitrogen and P concentrations were determined in the dried plant material after acid digestion. For digestion, the dried powdered plant sample was put into a 100 mL tube containing concentrated 5 mL H_2SO_4 and a Kjeltab tablet (3.5 g K_2SO_4/

0.4 g CuSO$_4$; FOSS Analytical AB, Höganäs, Sweden) at 420°C for 1 h. The solution was cooled and diluted with distilled water to 50 mL. Nitrogen and P contents were determined using the flow-injection analysis method (FIAstar 5000) described by *Scharfy* et al. (2010).

2.5 Calcium (Ca^{2+}), magnesium (Mg^{2+}), and iron (Fe) concentrations

Twenty mg of dried tissue were digested in 10 mL of 100 mM acetic acid at 90°C for 2 h. After the liquid had cooled and had been filtered, ion analysis was performed using an atomic absorption spectrophotometer (2655-00, Cole-Parmer Instrument Co., Vernon Hills, USA) as described by *Song* et al. (2017).

2.6 Silicon (Si) concentration

Si content was determined using the colorimetric method of molybdate-blue described by *Dakora* and *Nelwamondo* (2003). Briefly, 0.1 g samples were heated to ash in porcelain crucibles for 3 h at 550°C. The ash was dissolved in 1.3% hydrogen fluoride, and then Si concentrations were measured using the colorimetric method of molybdenum blue at 630 nm with a spectrophotometer (UV-6100 Pcs Double Beam, JAPAN). A control (no sample) was added to eliminate porcelain crucible errors.

2.7 Data analysis

Data were analyzed with one-way analysis of variance (ANOVA) using SPSS 18.0 (SPSS Inc., Chicago, IL, USA). Duncan's multiple range test was used to detect significant differences among the means at a significance level of $P < 5\%$.

3 Results

3.1 Growth of *Z. xanthoxylum* and *A. thaliana* under osmotic and salt treatments

We chose 50 mM NaCl as the salt concentration for *Z. xanthoxylum* because this concentration does not cause obvious growth inhibition of this species but rather enhances its growth (*Ma* et al., 2012; *Yue* et al., 2012). For *A. thaliana*, 5 mM NaCl were selected for the salt treatment because we found it does not inhibit growth whereas 50 mM NaCl causes significant growth inhibition. Therefore, this concentration of NaCl for *A. thaliana* is comparable to 50 mM NaCl for *Z. xanthoxylum*.

As shown in Fig. 1, drought induced by –0.5 MPa osmotic stress (O) using sorbitol severely inhibited the growth of *Z. xanthoxylum* and *A. thaliana*. The addition of 50 mM NaCl significantly alleviated the deleterious impacts of drought on the growth of *Z. xanthoxylum*, whereas 5 mM NaCl did not improve the growth of *A. thaliana* under osmotic conditions (Fig. 1). In comparison to osmotically stressed *Z. xanthoxy-*
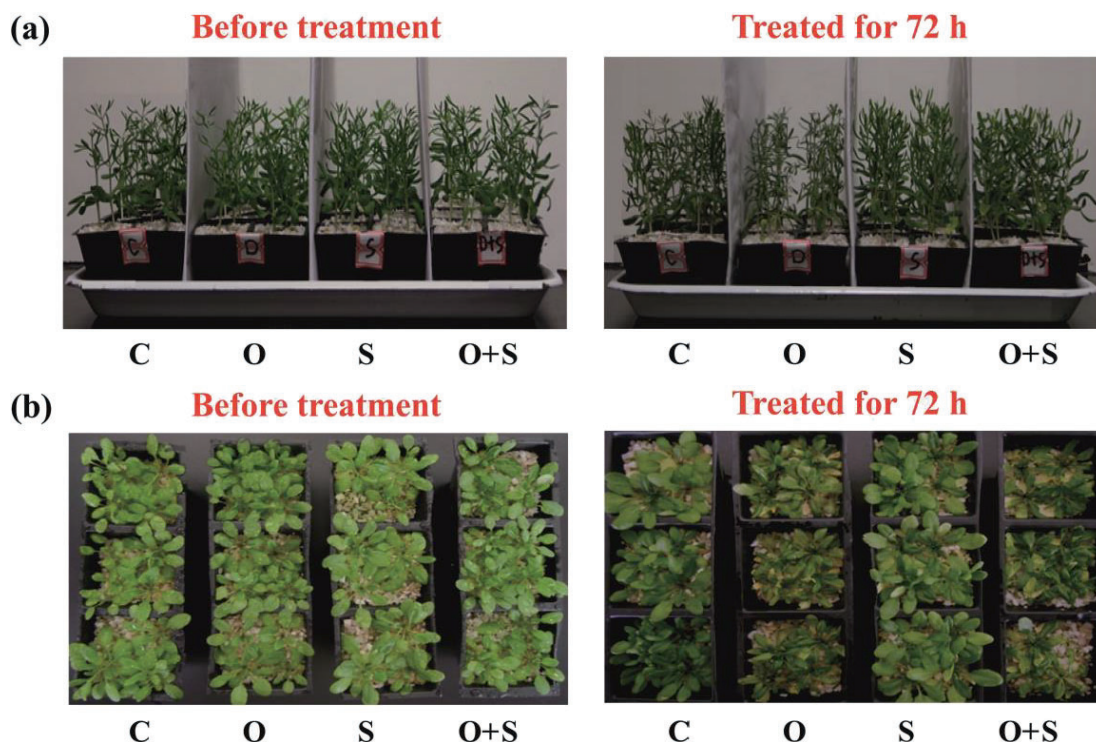
Figure 1: Growth status of *Z. xanthoxylum* (a) and *A. thaliana* (b) seedlings under various treatments (C, O, S, O+S) for 72 h. Control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum*, and 5 mM NaCl for *A. thaliana*), and osmotic stress with the corresponding concentration of NaCl (O+S) (total osmotic potential –0.5 MPa).

4   Wang, Chai, Zhao, Rowland, Wang, Song, Liu, Ma, Wang

J. Plant Nutr. Soil Sci. 2019, *000*, 1–10

lum with no added salt, the addition of 50 mM NaCl significantly increased the leaf fresh weight, leaf dry weight and tissue water content of osmotically stressed *Z. xanthoxylum* by 189%, 23% and 180%, respectively (Fig. 2a–c). The addition of 5 mM NaCl had no such effects on osmotic stressed *A. thaliana* (Fig. 2d–f).

3.2 Na$^+$ and K$^+$ concentrations in *Z. xanthoxylum* and *A. thaliana* seedlings exposed to osmotic and salt treatments

Although modified Hoagland nutrient solution only contains trace amounts of Na$^+$, the Na$^+$ concentrations in stems and leaves of osmotically stressed *Z. xanthoxylum* were about 1.1 times higher those that under control (Fig. 3a). Under O+S, Na$^+$ concentrations of *Z. xanthoxylum* increased significantly in the various tissues (leaf, stem and root), especially in leaves, which were 12, 5.2, and 0.5 times higher than those under C, O and S treatments, respectively (Fig. 3a). Under O+S treatment, the net Na$^+$ uptake rate of *Z. xanthoxylum* was 7.7 times higher than seedlings under osmotic conditions

only after 72 h (Fig. 4a). In contrast, in comparison to C, both O and O+S significantly decreased the Na$^+$ concentration in shoots (stems + leaves) of *A. thaliana* by 21% (Fig. 3c). The net Na$^+$ uptake rate of *A. thaliana* was reduced significantly under O or O+S, and the extent of decreased rate of net Na$^+$ uptake became more severe with the increasing treatment duration (Fig. 4c). These results indicate that the enhancement of drought resistance in *Z. xanthoxylum* was related to the increase of tissue Na$^+$ accumulation, as previously reported (*Ma* et al., 2012; *Yue* et al., 2012), but such an effect was not observed with Arabidopsis under moderate (no growth inhibition) saline conditions.

Compared with control, the K$^+$ concentrations in roots and leaves remained stable in *Z. xanthoxylum* exposed O or O+S (Fig. 3b). Moreover, compared with O, the addition of salt (O+S) increased the net K$^+$ uptake rate of *Z. xanthoxylum* by 40% after 72 h (Fig. 4b). In contrast to *Z. xanthoxylum*, the shoot K$^+$ concentrations of *A. thaliana* exposed to O or O+S significantly decreased by 36% (Figs. 3d and 4d).

3.3 The characteristics of N, P, Ca^{2+}, and Mg^{2+} accumulation in *Z. xanthoxylum* and *A. thaliana* seedlings exposed to osmotic and salt treatments

In comparison to the control, 50 mM NaCl increased the N and P concentrations in *Z. xanthoxylum* at the whole-plant level (roots and aerial tissues combined) by 16% and 33%, respectively (Fig. 5a, b). Nitrogen and P concentrations in *Z. xanthoxylum* under –0.5 MPa osmotic stress (O) decreased significantly. However, compared to O, O+S greatly increased the N and P concentrations by 58% and 121% in *Z. xanthoxylum*, respectively (Fig. 5a, b). Five mM NaCl had no effect on the N and P concentrations in *A. thaliana* (Fig. 5c, d). Under drought stress, the N and P concentrations in *A. thaliana* were significantly lower, and adding 5 mM NaCl (O+S) had no alleviating effect of osmotic stress on the N and P concentrations in *A. thaliana* (Fig. 5c, d).

Ca^{2+} and Mg^{2+} concentrations in leaves increased by 58% and 121% in *Z. xanthoxylum* exposed to 50 mM NaCl, respectively (Fig. 6a, b). Compared to O, O+S increased the Ca^{2+} and Mg^{2+} concentrations in the leaves of *Z. xanthoxylum* by 167% and 100%, respectively (Fig. 6a, b). Compared with C, addition of 5 mM NaCl had no effect on Ca^{2+} and Mg^{2+} concentrations in *A. thaliana* shoots or roots (Fig. 6c, d). Shoot Ca^{2+} and Mg^{2+} concentrations of *A. thaliana* decreased under O treatment, and the addition of 5 mM NaCl made no difference to the Ca^{2+} and Mg^{2+} concentrations (Fig. 6c, d).
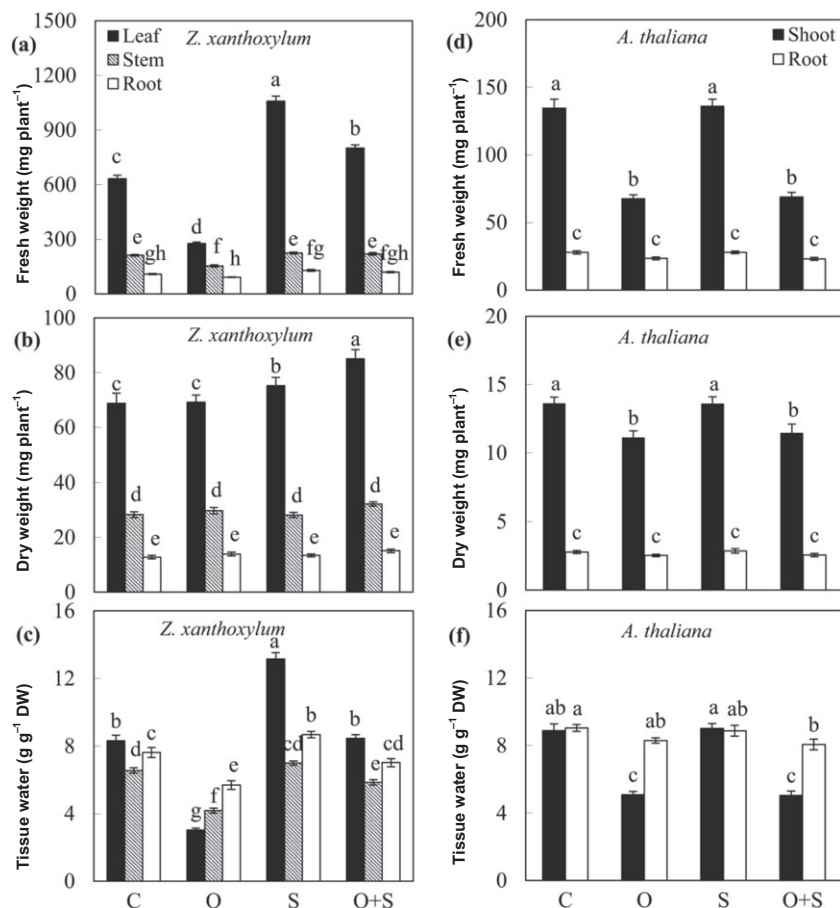
Figure 2: Fresh weight, dry weight, and tissue water content of *Z. xanthoxylum* (a, b, and c) and *A. thaliana* (d, e, and f) under different treatments (C, O, S, O+S) for 72 h. Control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum*, and 5 mM NaCl for *A. thaliana*), and osmotic stress with corresponding concentrations of NaCl (O+S) (total osmotic potential –0.5 MPa). Values are means ± standard errors (SE) (*n* = 8) and bars indicate SE. Columns with different letters indicate significant differences at P < 5% (Duncan's test).
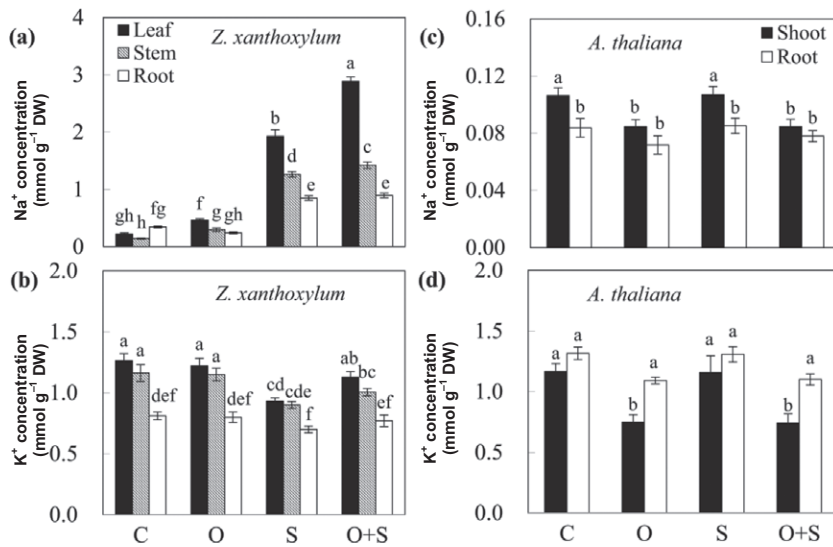
Figure 3: Na$^+$ and K$^+$ concentrations of *Z. xanthoxylum* (a, b) and *A. thaliana* (c, d) under various treatments (C, O, S, O+S) for 72 h. Control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum* and 5 mM NaCl for *A. thaliana*), and osmotic stress with corresponding concentrations of NaCl (O+S) (total osmotic potential –0.5 MPa). Values are means ± SE (*n* = 8) and bars indicate SE. Columns with different letters indicate significant differences at P < 5% (Duncan's test).
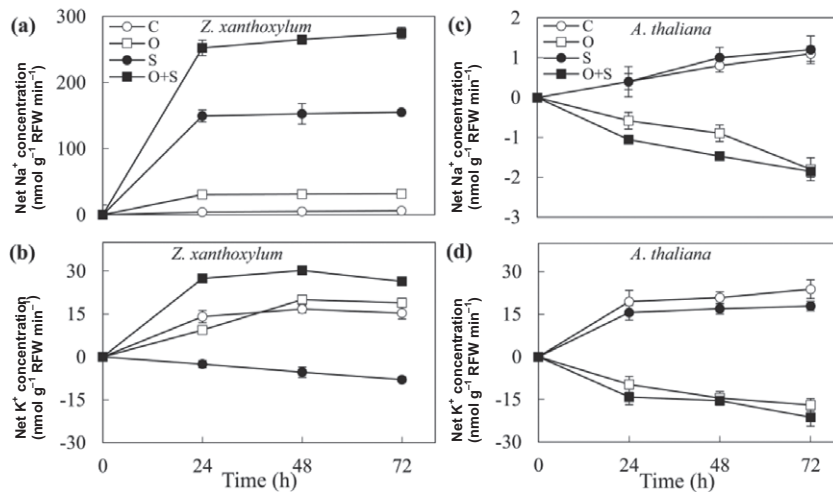
Figure 4: Net Na$^+$ and K$^+$ uptake rates of *Z. xanthoxylum* (a, b) and *A. thaliana* (c, d) under various treatments (C, O, S, O+S) for 24 h, 48 h, and 72 h. Control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum* and 5 mM NaCl for *A. thaliana*), and osmotic stress with corresponding concentration of NaCl (O+S) (total osmotic potential –0.5 MPa). Values are means ± SE (*n* = 8) and bars indicate SE.

3.4 The characteristics of Fe and Si accumulation in *Z. xanthoxylum* and *A. thaliana* seedlings exposed to osmotic and salt treatments

The concentration of Fe was increased 2.4 times in roots of *Z. xanthoxylum* under S treatment compared with the control (Fig. 7a). Compared with control, the Fe concentrations in leaves, stems, and roots remained stable in *Z. xanthoxylum*

exposed osmotic stress (Fig. 7a). Furthermore, Fe concentrations in leaves, stems and roots of *Z. xanthoxylum* exposed to O+S were 0.9, 1.9 and 5.3-fold higher than those of plants under drought stress, respectively (Fig. 7a). However, compared to the control, 5 mM NaCl had no such effects on Fe concentration in *A. thaliana* (Fig. 7b). Also, the addition of 5 mM NaCl did not affect the concentration of Fe in *A. thaliana* under osmotic stress compared with either C or O (Fig. 7b).

In comparison to the control, 50 mM NaCl increased the concentration of Si by 27% in *Z. xanthoxylum* (Fig. 8a). Under O+S, the Si concentration of *Z. xanthoxylum* was increased by 45% compared to O (Fig. 8a). The cumulative Si remained the same in *A. thaliana* under the various treatments (Fig. 8b).
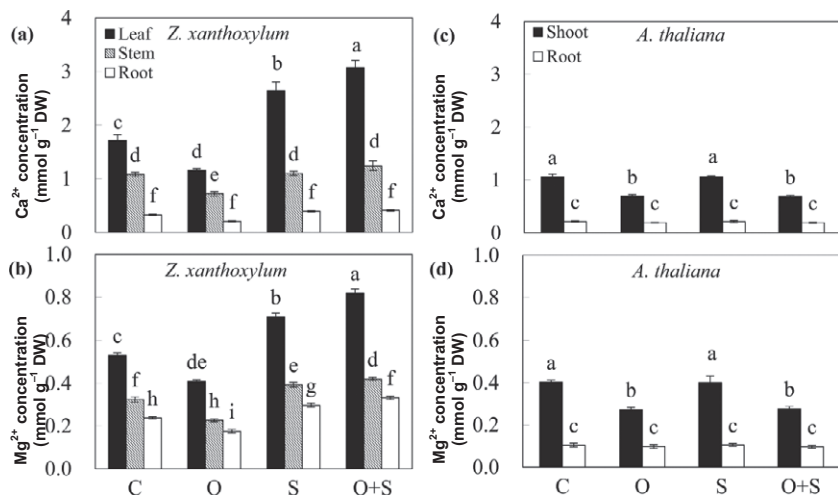
4 Discussion

4.1 In contrast to *A. thaliana*, *Z. xanthoxylum* accumulates Na$^+$ to improve the growth

Z. xanthoxylum is a salt-accumulating xerophytic species native to the desert regions of northwest China and Mongolia (*Liu* et al., 1987; *Wang* et al., 2004). In this study, we confirmed that *Z. xanthoxylum* accumulated more Na$^+$ in leaves under osmotic stress when growing in a low-Na$^+$ environment (Fig. 3a). *Z. xanthoxylum* accumulated more Na$^+$ in leaves under O+S than under S (Fig. 3a), resulting in increasing leaf turgor pressure, chlorophyll concentrations, and plant photosynthetic activity (*Ma* et al., 2012). In this study, increases of relative water content and leaf fresh and dry weights were also observed for *Z. xanthoxylum* exposed to O+S, accompanied by the accumulation of Na$^+$. Similar results were also obtained in other salt-accumulating species, such as *Atriplex halimus* (*Martínez* et al., 2005), *Atriplex canescens* (*Pan* et al., 2016), and *Populus euphratica* (*Ottow* et al., 2005). For *A. thaliana*, the growth was severely inhibited by 50 mM NaCl but was not inhibited by 5 mM NaCl (not shown). In contrast to *Z. xanthoxylum*, compared to O the O+S (osmotic stress combined with 5 mM NaCl treatment) did not increase the Na$^+$ concentration, the relative water content, or the fresh or dry weights of *A. thaliana* (Figs. 2 and 3). This finding is consistent with the observations found in other glycophytes such as rice (*Oryza sativa*; *Lutts* et al., 1996), cotton (*Gossypium hirsutum*; *Ashraf* and *Ahmad*, 2000), and tobacco
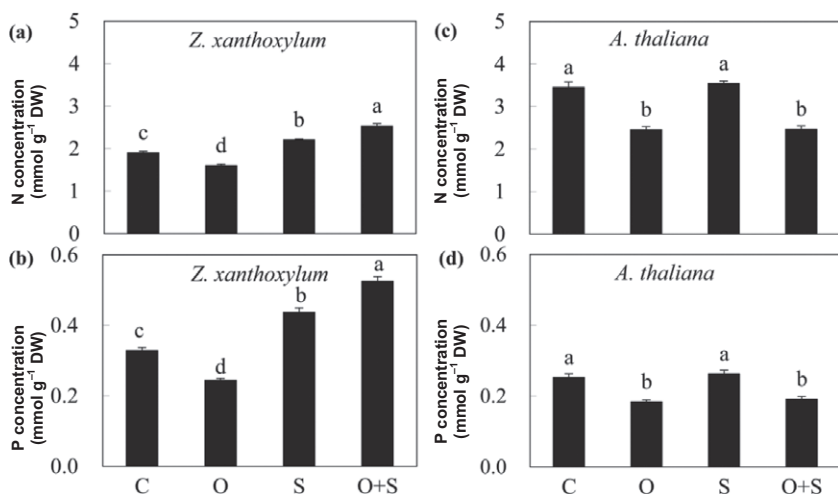
Figure 5: N and P concentrations of *Z. xanthoxylum* (a, b) and *A. thaliana* (c, d) under various treatments (C, O, S, O+S) for 72 h. Control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum* and 5 mM NaCl for *A. thaliana*), and osmotic stress with corresponding concentrations of NaCl (O+S) (total osmotic potential –0.5 MPa). Values are means ± SE (*n* = 8) and bars represent SE. Columns with different letters indicate significant differences at P < 5% (Duncan's test).

Figure 6: Ca^{2+} and Mg^{2+} concentrations of *Z. xanthoxylum* (a, b) and *A. thaliana* (c, d) under various treatments (C, O, S, O+S) for 72 h. Control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum* and 5 mM NaCl for *A. thaliana*), and osmotic stress with corresponding concentrations of NaCl (O+S) (total osmotic potential –0.5 MPa). Values are means ± SE (*n* = 8) and bars represent SE. Columns with different letters indicate significant differences at P < 5% (Duncan's test).

4.2 Maintenance of K^+ concentration is one of the key strategies of *Z. xanthoxylum* in response to drought

Potassium plays a key role in activating enzymes, regulating stomatal movement and balancing turgor pressure, and responding to major abiotic stresses (*Lebaudy* et al., 2007; *Tang* et al., 2014; *Wu* et al., 2015b). Potassium was reported to decrease different stress effects such as drought (*Hasanuzzaman* et al., 2018). Under drought stress, K^+ facilitates osmotic adjustment in both the vacuoles and cytosol of numerous species (*Shabala*, 2011). In *B. vulgaris*, the addition of 50 mM NaCl improved resistance against osmotic stress with increased Na^+ concentrations, but the K^+ concentrations in shoots and roots were decreased by 14% and 27%, respectively (*Wu* et al., 2015a). Commonly, over-accumulation of Na^+ in leaves and roots leads to a decline in K^+ concentration in glycophytes (*Yamaguchi* and *Blumwald*, 2005; *Silva* et al., 2015; *Song* et al., 2017). Our results with *A. thaliana* confirm that K^+ concentration in shoots was reduced significantly under O+S. Interestingly, although the concentration of Na^+ in leaves of *Z. xanthoxylum* increased tremendously under O or O+S, the concentration of K^+ did not significantly decrease (Fig. 3b). Na^+ and K^+ uptake are competitive processes in most higher plants (*Maathuis*, 2014), but such a competition did not occur in *Z. xanthoxylum*. One possible reason is that *Z. xanthoxylum* sequesters Na^+ into the vacuoles in the leaf under osmotic stress (when moderate levels of Na^+ are present), which would require the coordinated upregulation of other osmoticum levels such as K^+ in the cytoplasm to maintain the osmotic potential balance (*Møller* and *Tester*, 2007).

4.3 NaCl increases the accumulation of important nutrient elements in *Z. xanthoxylum*

Nitrogen and P concentrations in *Z. xanthoxylum* were increased by 50 mM NaCl treatment, suggesting that NaCl upregulates N and P uptake. *Jia* et al. (2017) found that the total N content of the halophyte *Suaeda salsa* was stable with increasing salinity levels. *Keutgen* and *Pawelzik* (2009) have demonstrated that N concentration in the plant organs of salt-tolerant strawberry (*Fragaria ananassa*) cultivar significantly increased under salt conditions. Sodium increased the P concentration in *Carthamus tinctorius* (*Patil*, 2012) and the utilization of P in *Saccharum officinarum* with increased inorganic P
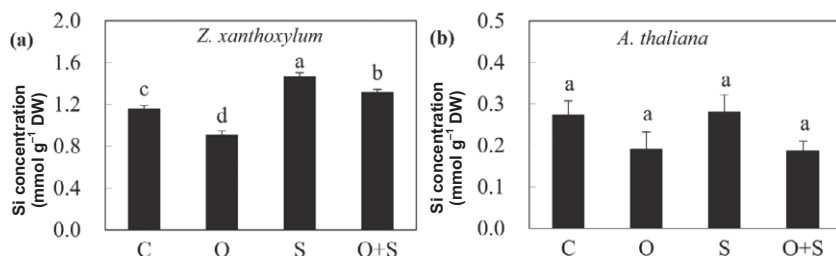
(*Nicotiana tabacum*; *Hajiboland* et al., 2012). Taken together, our results confirm that the drought resistance of *Z. xanthoxylum* is enhanced by the presence of moderate concentrations of Na^+. The likely mechanism is that *Z. xanthoxylum* compartmentalizes Na^+ in the vacuoles and uses Na^+ as an osmoregulatory substance to cope with drought stress (*Wu* et al., 2011; *Ma* et al., 2012; *Yuan* et al., 2015).

Figure 7: Fe concentration of *Z. xanthoxylum* (a) and *A. thaliana* (b) under various treatments (C, O, S, O+S) for 72 h. Control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum* and 5 mM NaCl for *A. thaliana*), and osmotic stress with corresponding concentrations of NaCl (O+S) (total osmotic potential –0.5 MPa). Values are means ± SE (*n* = 8) and bars represent SE. Columns with different letters indicate significant differences at P < 5% (Duncan's test).
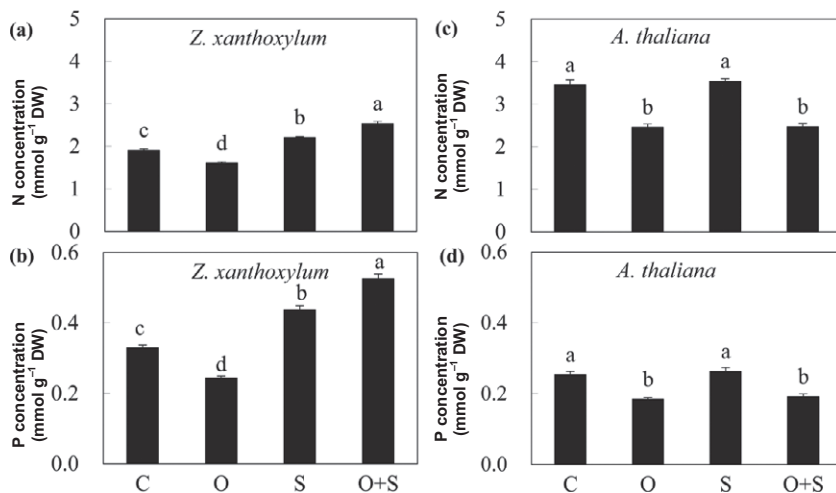
Figure 8: Si concentration of *Z. xanthoxylum* (a) and *A. thaliana* (b) under various treatments (C, O, S, O+S) for 72 h. Control (C), osmotic stress (O) (–0.5 MPa osmotic potential induced by sorbitol), salt treatment (S) (50 mM NaCl for *Z. xanthoxylum* and 5 mM NaCl for *A. thaliana*), and osmotic stress with corresponding concentrations of NaCl (O+S) (total osmotic potential –0.5 MPa). Values are means ± SE (*n* = 8) and bars represent SE. Columns labelled different letters indicate significant differences at P < 5% (Duncan's test).

and residual P fractions (*Rai* and *Singh*, 2013). *Song* et al. (2017) found that the P accumulation in the moderately resistant and sensitive perennial ryegrass (*Lolium perenne*) cultivars decreased under salinity, but the salinity-resistant cultivars accumulated more P.

Sodium can negatively affect plant Ca^{2+} relations (*Maathuis*, 2005) because Na^+ may replace electrostatically bound Ca^{2+} in cell walls and cell membranes. However, the compartmentation of Na^+ in vacuoles may instead facilitate Ca^{2+} uptake (*Zhao* et al., 2006). Our data show an increased Ca^{2+} concentration in leaves of Na^+-accumulating *Z. xanthoxylum*. Other investigators have also shown that salt-resistant plants have the capability to maintain Ca^{2+} uptake under moderate salt conditions (*Koyro*, 2000; *Zheng* et al., 2009), for example in *Kochia sieversiana*, a naturally alkali-resistant halophyte (*Yang* et al., 2007). Magnesium is important for plant health via Mg^{2+}-driven photosynthesis (*Gerendás* and *Führs*, 2013). Soil salinity causes a drastic decrease in Mg^{2+} concentration

in the roots and leaves of non-salt-resistant barley (*Hordeum vulgare*) (*Wu* et al., 2013), whereas a salt-resistant barley cultivar had less reduced Mg^{2+} (*Tavakkoli* et al., 2011). Our results in *Z. xanthoxylum* show a markedly increased Mg^{2+} concentration in leaves under 50 mM NaCl (Fig. 6b), which could be directly related to more efficient photosynthetic capacity (*Ma* et al., 2012).

In the current study, 50 mM NaCl caused a 2.4-fold increase of Fe concentration in roots of *Z. xanthoxylum*, which was similar to the finding that Fe was significantly increased in the roots of peanut (*Arachis hypogea*) by 50 mM NaCl (*Chavan* and *Karadge*, 1980). Silicon is clearly beneficial to plant growth and development (*Liang* et al., 2003; *Lee* et al., 2010; *Shi* et al., 2013; *Xu* et al., 2015). The increased Si concentration in *Z. xanthoxylum* after exposure to 50 mM NaCl suggests a positive role of Si on *Z. xanthoxylum* growth under salt stress. However, 5 mM NaCl had no influence on the nutrient levels of *A. thaliana*. In short, *Z. xanthoxylum* displayed improved nutritional status under moderate salt treatment, which was not the case with *A. thaliana*.

4.4 Moderate NaCl mitigates the deleterious impacts of drought stress on *Z. xanthoxylum* by improving its nutritional status

Drought stress inhibits the flow of nutrients within the soil, the absorption of elements, and their uptake by roots, leading to reduced plant productivity (*Fageria* et al., 2002). Adequate absorption of minerals is important for the maintenance of plant structural integrity and key physiological processes (*Liang* et al., 2018). In the current study, drought stress caused a significant decrease in the concentrations of N, P, Ca^{2+}, Mg^{2+}, and Si in *Z. xanthoxylum* and *A. thaliana*. It has been reported that Na^+ reduces the uptake of nutrients, such as N (*Rubinigg* et al., 2003), P (*Loupassaki* et al., 2002), Ca (*Kopittke*, 2012), Mg (*Ali* et al., 2012; *Wu* et al., 2013), and Fe (*Yousfi* et al., 2007). However, compared to O, the addition of 50 mM NaCl significantly increased the concentrations of N, P, and Si of whole plants and Ca^{2+} and Mg^{2+} in leaves of *Z. xanthoxylum*. The Fe concentration in roots of *Z. xanthoxylum* under osmotic stress was maintained while it increased significantly under O+S treatment, compared to O treatment in roots of *Z. xanthoxylum* (Fig. 7a). Such results were not observed in *A. thaliana*.

A high level of nutritional status could ameliorate the effects of drought on plant growth. Also, accumulation of ions promotes turgor maintenance, which contributes to increased ab-

sorption of water in water-stressed plants and thereby results in improving drought resistance (*da Silva* et al., 2011). Furthermore, N being an important component of chlorophyll and Rubisco affects the metabolism of the plant under drought stress (*Abid* et al., 2016). Functional activity of the photosynthetic apparatus of leaf largely depends on the availability of N in plants (*Brennan*, 1992). Phosphorus also contributes to an increase in photosynthesis and stomatal conductance (*Ackerson*, 1985; *Brück* et al., 2000) under drought stress. High Fe is required for the structural and functional integrity of the thylakoid membranes, and additional Fe is required by ferredoxin and for the biosynthesis of chlorophyll (*Bhatt* et al., 2008). A recent study has confirmed that increasing Si concentration improves photosynthesis and strengthens enzyme activities in *Z. xanthoxylum* under drought stress (*Kang* et al., 2016). In addition, accumulation of Mg^{2+} in leaves may reduce photo-oxidative damage and ROS generation in chloroplast (*Hanstein* et al., 2011; *Waraich* et al., 2011). Calcium may maintain membrane stability and regulate H_2O_2 homeostasis to help plants adapt to drought (*Hirschi*, 2004; *Gu* et al., 2016). Therefore, we speculate that the increased nutritional status under O+S treatment may contribute to maintain leaf turgor, photosynthetic activities, and the antioxidative defense system in *Z. xanthoxylum* (*Cai* et al., 2011; *Ma* et al., 2012).

5 Conclusions

Sodium plays an important role in the response of *Z. xanthoxylum* to drought, even under non-saline conditions. However, moderate sodium does not mitigate deleterious impacts of drought on the glycophyte *A. thaliana*. The molecular mechanisms underlying nutrient uptake and distribution in *Z. xanthoxylum* exposed to drought deserve further investigation. Elucidating these molecular mechanisms of xero-halophytes may contribute to breeding new drought-tolerant crop varieties.

Acknowledgments

References

Abid, M., *Tian, Z.*, *Ata-Ul-Karim, S. T.*, *Cui, Y.*, *Liu, Y.*, *Zahoor, R.*, *Jiang, D.*, *Dai, T.* (2016): Nitrogen nutrition improves the potential of wheat (*Triticum aestivum* L.) to alleviate the effects of drought stress during vegetative growth periods. *Front. Plant Sci.* 7. DOI: https://doi.org/10.3389/fpls.2016.00981.

Ackerson, R. C. (1985): Osmoregulation in cotton in response to water stress III. Effects of phosphorus fertility. *Plant Physiol.* 77, 309–312.

Ali, S., *Cai, S.*, *Zeng, F. R.*, *Qiu, B. Y.*, *Zhang, G. P.* (2012): Effect of salinity and hexavalent chromium stresses on uptake and accumulation of mineral elements in barley genotypes differing in salt tolerance. *J. Plant Nutr.* 35, 827–839.

Anand, A., *Trick, H. N.*, *Gill, B. S.* (2003): Stable transgene expression and random gene silencing in wheat. *Plant Biotechnol J.* 1, 241–251.

Ashraf, M., *Ahmad, S.* (2000): Genetic effects for yield components and fibre characteristics in upland cotton (*Gossipium hirsutum* L.) cultivated under salinized (NaCl) conditions. *Agronomie* 20, 917–926.

Bartels, D., *Sunkar, R.* (2005): Drought and salt tolerance in plants. *Crit. Rev. Plant Sci.* 24, 23–58.

Bhatt, M. J., *Patel, A. D.*, *Bhatti, P. M.*, *Pandey, A. N.* (2008): Effect of soil salinity on growth, water status and nutrient accumulation in seedlings of *Ziziphus mauritiana* (Rhamnaceae). *J. Fruit Ornam. Plant Res.* 16, 383–401.

Brennan, R. F. (1992): The role of manganese and nitrogen nutrition in the susceptibility of wheat plants to take-all in Western Australia. *Fertil. Res.* 31, 35–41.

Brück, H., *Payne, W. A.*, *Sattelmacher, B.* (2000): Effects of phosphorus and water supply on yield, transpirational water-use efficiency, and carbon isotope discrimination of pearl millet. *Crop Sci.* 40, 120–125.

Cai, J., *Ma, Q.*, *Zhou, X.*, *Zhang, J.*, *Wang, S.* (2011): Physiological role of Na^+ in adaption of *Zygophyllum xanthoxylum* to osmotic stress. *Acta Pratacult. Sin.* 20, 89–95.

Chavan, P. D., *Karadge, B. A.* (1980): Influence of salinity on mineral-nutrition of peanut (*Arachis hypogea* L.). *Plant Soil* 54, 5–13.

Dakora, F. D., *Nelwamondo, A.* (2003): Silicon nutrition promotes root growth and tissue mechanical strength in symbiotic cowpea. *Funct. Plant Biol.* 30, 947–953.

da Silva, E. C., *Nogueira, R. J. M. C.*, *da Silva, M. A.*, *de Albuquerque, M. B.* (2011): Drought stress and plant nutrition. *Plant Stress* 5, 32–41.

da Silveira, J. A. G., *da Costa, R. C. L.*, *Oliveira, J. T. A.* (2001): Drought-induced effects and recovery of nitrate assimilation and nodule activity in cowpea plants inoculated with *bradyrhizobium* spp. under moderate nitrate level. *Braz. J. Microbiol.* 32, 187–194.

Fageria, N. K., *Baligar, V. C.*, *Clark, R. B.* (2002): Micronutrients in crop production. *Adv. Agron.* 77, 185–268.

Farooq, M., *Hussain, M.*, *Wahid, A.*, *Siddique, K. H. M.* (2012): Drought Stress in Plants: An Overview: in Aroca, R. (ed.): Plant Responses to Drought Stress. Springer, Berlin, Germany, pp. 1–33.

Fisher, M. J. (1980): The influence of water stress on nitrogen and phosphorus uptake and concentrations in Townsville stylo (*Stylosanthes humilis*). *Aust. J. Exp. Agric.* 20, 175–180.

Foyer, C. H., *Valadier, M. H.*, *Migge, A.*, *Becker, T. W.* (1998): Drought-induced effects on nitrate reductase activity and mRNA and on the coordination of nitrogen and carbon metabolism in maize leaves. *Plant Physiol.* 117, 283–292.

Gerendás, J., *Führs, H.* (2013): The significance of magnesium for crop quality. *Plant Soil* 368, 101–128.

Gu, M. F., *Li, N.*, *Shao, T. Y.*, *Long, X. H.*, *Brestič, M.*, *Shao, H. B.*, *Li, J. B.*, *Mbarki, S.* (2016): Accumulation capacity of ions in cabbage (*Brassica oleracea* L.) supplied with sea water. *Plant Soil Environ.* 62, 314–320.

Hajiboland, R., *Ebrahimi, N.*, *Poschenrieder, C. H.* (2012): Bound putrescine a distinctive player under salt stress in the natrophilic sugar beet in contrast to glycophyte tobacco. *J. Sci. Islamic Rep. Iran* 23, 105–114.

Hanstein, S., Wang, X. Z., Qian, X. Q., Friedhoff, P., Fatima, A., Shan, Y. H., Feng, K., Schubert, S. (2011): Changes in cytosolic Mg^{2+} levels can regulate the activity of the plasma membrane H^+-ATPase in maize. *Biochem J.* 435, 93–101.

Hasanuzzaman, M., Bhuyan, M. H. M., Nahar, K., Hossain, M. S., Mahmud, J. A., Hossen, M. S., Masud, A. A. C., Moumita, Fujita, M. (2018): Potassium: A vital regulator of plant responses and tolerance to abiotic stresses. *Agronomy* 8. DOI: https://doi.org/10.3390/agronomy8030031.

Hassine, A. B., Bouzid, S., Lutts, S. (2010): Does habitat of *Atriplex halimus* L. affect plant strategy for osmotic adjustment? *Acta Physiol. Plant.* 32, 325–331.

Hirschi, K. D. (2004): The calcium conundrum: both versatile nutrient and specific signal. *Plant Physiol.* 136, 2438–2442.

Hu, Y., Burucs, Z., von Tucher, S., Schmidhalter, U. (2007): Short-term effects of drought and salinity on mineral nutrient distribution along growing leaves of maize seedlings. *Environ. Exp. Bot.* 60, 268–275.

Hu, Y., Schmidhalter, U. (2005): Drought and salinity: a comparison of their effects on mineral nutrition of plants. *J. Plant Nutr. Soil Sci.* 168, 541–549.

Huang, L., Li, M., Shao, Y., Sun, T., Li, C., Ma, F. (2018): Ammonium uptake increases in response to PEG-induced drought stress in *Malus hupehensis* Rehd. *Environ. Exp. Bot.* 151, 32–42.

Jajarmi, V. (2009): Effect of water stress on germination indices in seven wheat cultivar. *World Acad. Sci. Eng. Technol.* 49, 105–106.

Janz, D., Polle, A. (2012): Harnessing salt for woody biomass production. *Tree Physiol.* 32, 1–3.

Javadi, T., Rohollahi, D., Ghaderi, N., Nazari, F. (2017): Mitigating the adverse effects of drought stress on the morpho-physiological traits and anti-oxidative enzyme activities of *Prunus avium*, through β-amino butyric acid drenching. *Sci. Hortic.* 218, 156–163.

Jia, J., Huang, C., Bai, J., Zhang, G., Zhao, Q., Wen, X. (2017): Effects of drought and salt stresses on growth characteristics of euhalophyte *Suaeda salsa* in coastal wetlands. *Phys. Chem. Earth.* 103, 68–74.

Kang, J., Zhao, W., Zhu, X. (2016): Silicon improves photosynthesis and strengthens enzyme activities in the C_3 succulent xerophyte *Zygophyllum xanthoxylum* under drought stress. *J. Plant Physiol.* 199, 76–86.

Keutgen, A. J., Pawelzik, E. (2009): Impacts of NaCl stress on plant growth and mineral nutrient assimilation in two cultivars of strawberry. *Environ. Exp. Bot.* 65, 170–176.

Kopittke, P. M. (2012): Interactions between Ca, Mg, Na and K: alleviation of toxicity in saline solutions. *Plant Soil* 352, 353–362.

Koyro, H. W. (2000): Effect of high NaCl-salinity on plant growth, leaf morphology, and ion composition in leaf tissues of *Beta vulgaris* ssp. maritima. *Angew. Bot.* 74, 67–73.

Lebaudy, A., Véry, A. A., Sentenac, H. (2007): K^+ channel activity in plants: genes regulations and functions. *FEBS Lett.* 581, 2357–2366.

Lee, S. K., Sohn, E. Y., Hamayun, M., Yoon, J. Y., Lee, I. J. (2010): Effect of silicon on growth and salinity stress of soybean plant grown under hydroponic system. *Agroforest Syst.* 80, 333–340.

Liang, B., Ma, C., Zhang, Z., Wei, Z., Gao, T., Zhao, Q., Ma, F., Li, C. (2018): Long-term exogenous application of melatonin improves nutrient uptake fluxes in apple plants under moderate drought stress. *Environ. Exp. Bot.* 155, 650–661.

Liang, Y., Chen, Q., Liu, Q., Zhang, W., Ding, R. X. (2003): Exogenous silicon (Si) increases antioxidant enzyme activity and reduces lipid peroxidation in roots of salt-stressed barley (*Hordeum vulgare* L.). *J. Plant Physiol.* 160, 1157–1164.

Liu, J.-Q., Pu, J.-C., Liu, X.-M. (1987): Comparative studies on water relations and xeromorphic structures of some plant species in the middle part of the desert zone in China. *Acta. Bot. Sin.* 29, 314–319.

Loupassaki, M. H., Chartzoulakis, K. S., Digalaki, N. B., Androulakis, I. I. (2002): Effects of salt stress on concentration of nitrogen, phosphorus, potassium, calcium, magnesium, and sodium in leaves, shoots, and roots of six olive cultivars. *J. Plant Nutr.* 25, 2457–2482.

Luo, W., Xu, C., Ma, W., Yue, X., Liang, X., Zuo, X., Knapp, A. K., Smith, M. D., Sardans, J., Dijkstra, F. A., Peñuelas, J., Bai, Y., Wang, Z., Yu, Q., Han, X. (2018): Effects of extreme drought on plant nutrient uptake and resorption in rhizomatous *vs* bunchgrass-dominated grasslands. *Oecologia* 188, 633–643.

Lutts, S., Kinet, J. M., Bouharmont, J. (1996): Effects of salt stress on growth mineral nutrition and proline accumulation in relation to osmotic adjustment in rice (*Oryza sativa* L.) cultivars differing in salinity resistance. *Plant Growth Regul.* 19, 207–218.

Maathuis, F. J. M. (2014): Sodium in plants: perception signalling and regulation of sodium fluxes. *J. Exp. Bot.* 65, 849–858.

Maathuis, F. J. M. (2005): The role of monovalent cation transporters in plant responses to salinity. *J. Exp. Bot.* 57, 1137–1147.

Mahouachi, J. (2007): Growth and mineral nutrient content of developing fruit on banana plants (*Musa acuminata* AAA, 'Grand Nain') subjected to water stress and recovery. *J. Pomol. Hortic. Sci.* 82, 839–844.

Ma, Q., Yue, L.-J., Zhang, J.-L., Wu, G.-Q., Bao, A.-K., Wang, S.-M. (2012): Sodium chloride improves photosynthesis and water status in the succulent xerophyte *Zygophyllum xanthoxylum*. *Tree Physiol.* 32, 4–13.

Martínez, J. P., Ledent, J. F., Bajji, M., Kinet, J. M., Lutts, S. (2003): Effect of water stress on growth Na and K accumulation and water use efficiency in relation to osmotic adjustment in two populations of *Atriplex halimus* L. *Plant Growth Regul.* 41, 63–73.

Martínez, J. P., Kinet, J. M., Bajji, M., Lutts, S. (2005): NaCl alleviates polyethylene glycol-induced water stress in the halophyte species *Atriplex halimus* L. *J. Exp. Bot.* 56, 2421–2431.

Møller, I. S., Tester, M. (2007): Salinity tolerance of *Arabidopsis*: a good model for cereals? *Trends Plant Sci.* 12, 534–540.

Ottow, E. A., Brinker, M., Teichmann, T., Fritz, E., Kaiser, W., Brosché, M., Kangasjarvi, J., Jiang, X., Polle, A. (2005): *Populus euphratica* displays apoplastic sodium accumulation, osmotic adjustment by decreases in calcium and soluble carbohydrates, and develops leaf succulence under salt stress. *Plant Physiol.* 139, 1762–1772.

Pan, Y.-Q., Guo, H., Wang, S.-M., Zhao, B., Zhang, J.-L., Ma, Q., Yin, H.-J., Bao, A.-K. (2016): The photosynthesis Na^+/K^+ homeostasis and osmotic adjustment of *Atriplex canescens* in response to salinity. *Front. Plant Sci.* 7. DOI: https://doi.org/10.3389/fpls.2016.00848.

Patil, N. M. (2012): Adaptations in response to salinity in safflower cv.Bhima. *Asian J. Crop Sci.* 4, 50–62.

Rai, R. K., Singh, P. (2013): Sodium salt induced utilization of phosphorus in sugarcane leaf laminae reduces sucrose contents. *Sugar Tech.* 15, 165–176.

Rubinigg, M., Posthumus, F., Ferschke, M., Elzenga, J. T. M., Stulen, I. (2003): Effects of NaCl salinity on ^{15}N-nitrate fluxes and specific root length in the halophyte *Plantago maritima* L. *Plant Soil* 250, 201–213.

Ruiz-Lozano, J. M., Azcón, R. (1996): Mycorrhizal colonization and drought stress as factors affecting nitrate reductase activity in lettuce plants. *Agric. Ecosyst. Environ.* 60, 175–181.

Sahin, U., *Ekinci, M.*, *Ors, S.*, *Turan, M.*, *Yildiz, S.*, *Yildirim, E.* (2018): Effects of individual and combined effects of salinity and drought on physiological, nutritional and biochemical properties of cabbage (*Brassica oleracea*, var. capitata). *Sci. Hortic.* 240, 196–204.

Scharfy, D., *Eggenschwiler, H.*, *Holde, V.*, *Edwards, P. J.*, *Güsewell, S.* (2010): The invasive alien plant species *Solidago gigantea* alters ecosystem properties across habitats with differing fertility. *J. Veg. Sci.* 20, 1072–1085.

Shabala, S. (2011): Physiological and cellular aspects of phytotoxicity tolerance in plants: the role of membrane transporters and implications for crop breeding for waterlogging tolerance. *New Phytol.* 190, 289–298.

Shi, Y., *Wang, Y.*, *Flowers, T. J.*, *Gong, H.* (2013): Silicon decreases chloride transport in rice (*Oryza sativa* L.) in saline conditions. *J. Plant Physiol.* 170, 847–853.

Silva, E. N., *Silveira, J. A. G.*, *Rodrigues, C. R. F.*, *Viégas, R. A.* (2015): Physiological adjustment to salt stress in *Jatropha curcas* is associated with accumulation of salt ions transport and selectivity of K^+ osmotic adjustment and K^+/Na^+ homeostasis. *Plant Biol.* 17, 1023–1029.

Song, X., *Wang, S. M.*, *Jiang, Y.* (2017): Genotypic variations in plant growth and nutritional elements of perennial ryegrass accessions under salinity stress. *J. Am. Soc. Hortic. Sci.* 142, 476–483.

Tang, X., *Mu, X.*, *Shao, H.*, *Wang, H.*, *Brestic, M.* (2014): Global plant-responding mechanisms to salt stress: physiological and molecular levels and implications in biotechnology. *Crit. Rev. Biotechnol.* 35, 425–437.

Tavakkoli, E., *Fatehi, F.*, *Coventry, S.*, *Rengasamy, P.*, *McDonald, G. K.* (2011): Additive effects of Na^+ and Cl^- ions on barley growth under salinity stress. *J. Exp. Bot.* 62, 2189–2203.

Wang, C.-M., *Zhang, J.-L.*, *Liu, X.-S.*, *Li, Z.*, *Wu, G.-Q.*, *Cai, J.-Y.*, *Flowers, T. J.*, *Wang, S.-M.* (2009): *Puccinellia tenuiflora* maintains a low Na^+ level under salinity by limiting unidirectional Na^+ influx resulting in a high selectivity for K^+ over Na^+. *Plant Cell Environ.* 32, 486–496.

Wang, S., *Wan, C.*, *Wang, Y.*, *Chen, H.*, *Zhou, Z.*, *Fu, H.*, *Sosebee, R. E.* (2004): The characteristics of Na^+, K^+ and free proline distribution in several drought-resistant plants of the Alxa Desert, China. *J. Arid Environ.* 56, 525–539.

Wang, S.-M., *Zhang, J.-L.*, *Flowers, T. J.* (2007): Low-affinity Na^+ uptake in the halophyte *Suaeda maritima*. *Plant Physiol.* 145, 559–571.

Waraich, E. A., *Ahmad, R.*, *Ashraf, M. Y.* (2011): Role of mineral nutrition in alleviation of drought stress in plants. *Aust. J. Crop Sci.* 5, 764–777.

Wu, D., *Shen, Q.*, *Cai, S.*, *Chen, Z.*, *Dai, F.*, *Zhang, G.* (2013): Ionomic responses and correlations between elements and metab-olites under salt stress in wild and cultivated barley. *Plant Cell Physiol.* 54, 1976–1988.

Wu, G.-Q., *Feng, R.-J.*, *Liang, N.*, *Yuan, H.-J.*, *Sun, W.-B.* (2015a): Sodium chloride stimulates growth and alleviates sorbitol-induced osmotic stress in sugar beet seedlings. *Plant Growth Regul.* 75, 307–316.

Wu, G.-Q., *Xi, J.-J.*, *Wang, Q.*, *Bao, A.-K.*, *Ma, Q.*, *Zhang, J.-L.*, *Wang, S.-M.* (2011): The *ZxNHX* gene encoding tonoplast Na^+/H^+ antiporter from the xerophyte *Zygophyllum xanthoxylum* plays important roles in response to salt and drought. *J. Plant Physiol.* 168, 758–767.

Wu, H., *Zhu, M.*, *Shabala, L.*, *Zhou, M.*, *Shabala, S.* (2015b): K^+ retention in leaf mesophyll an overlooked component of salinity tolerance mechanism: a case study for barley. *J. Integr. Plant Biol.* 57, 171–185.

Xu, C. X., *Ma, Y. P.*, *Liu, Y. L.* (2015): Effects of silicon (Si) on growth, quality and ionic homeostasis of aloe under salt stress. *S. Afr. J. Bot.* 98, 26–36.

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

Yamaguchi, T., *Blumwald, E.* (2005): Developing salt-tolerant crop plants: challenges and opportunities. *Trends Plant Sci.* 10, 615–620.

Yousfi, S., *Wissal, M.*, *Mahmoudi, H.*, *Abdelly, C.*, *Gharsalli, M.* (2007): Effect of salt on physiological responses of barley to iron deficiency. *Plant Physiol. Biochem.* 45, 309–314.

Yuan, H. J., *Ma, Q.*, *Wu, G. Q.*, *Wang, P.*, *Hu, J.*, *Wang, S. M.* (2015): ZxNHX controls Na^+ and K^+ homeostasis at the whole-plant level in *Zygophyllum xanthoxylum* through feedback regulation of the expression of genes involved in their transport. *Ann. Bot.* 115, 495–507.

Yue, L. J., *Li, S. X.*, *Ma, Q.*, *Zhou, X. R.*, *Wu, G. Q.*, *Bao, A. K.*, *Zhang, J. L.*, *Wang, S. M.* (2012): NaCl stimulates growth and alleviates water stress in the xerophyte *Zygophyllum xanthoxylum*. *J. Arid Environ.* 87, 153–160.

Zhao, F. Y., *Zhang, X. J.*, *Hua, L. P.*, *Zhao, Y. X.*, *Zhang, H.* (2006): Coexpression of the *Suaeda salsa SsNHX1* and *Arabidopsis AVP1* confer greater salt tolerance to transgenic rice than the single *SsNHX1*. *Mol. Breed* 17, 341–353.

Zheng, Q., *Liu, L.*, *Liu, Z.*, *Chen, J.*, *Zhao, G.* (2009): Comparison of the response of ion distribution in the tissues and cells of the succulent plants *Aloe vera* and *Salicornia europaea* to saline stress. *J. Plant Nutr. Soil Sci.* 172, 875–883.