

THE EFFECTS OF SALT AND ALKALINE STRESS ON THE FOURWING SALTBUSH (*ATRIPLEX CANESCENS* (PURSH) NUTT.) STRESS

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Abstract. *Atriplex canescens* is a C₄ fodder shrub that is excellent for phytore-mediation in saline-alkali environments. However, little is known about the response of this shrub species to salt and alkaline stress and its underlying physiological adaptive mechanisms. In this study, we treated 8-week-old *A. canescens* seedlings in the lab with neutral salt (NS) (1:1 molar ratio of NaCl to Na₂SO₄, pH 6.65-6.95) and alkali salt (AS) (1:1 molar ratio of NaHCO₃ to Na₂CO₃, pH 9.75-10.12) at five concentrations (0-400 mM). Our results showed that individual *A. canescens* seedlings could maintain growth under certain ranges of both NS stress and AS stress. These findings suggest that AS can more strongly inhibit *A. canescens* seedlings than can NS. This result was attributed to a decrease in photosynthetic ability and damage to Na⁺/K⁺ homeostasis under alkali salinity. Differences were evident in the NS and AS treatments for almost all of the considered parameters.

Keywords: *adaptive mechanism, concentration, chlorophyll, photosynthesis, environmental science*

Introduction

Primary and secondary soil salinization and alkalization are well-known constraints against the sustainable development of agriculture and land conservation, as they are critical environmental factors that can inhibit plant productivity (Flowers, 2004; Kalaji et al., 2016; Ogonye et al., 2018). Natural salt-alkalinized soils are driven by various cations, such as Na⁺, K⁺, Ca²⁺ and Mg²⁺, and various anions, such as Cl⁻, SO₄²⁻, HCO₃⁻ and CO₃²⁻ (Läuchli and Lüttge, 2002; Nwankwo and Nwankwoala, 2018). Based on salt characteristics, two types of stresses can be incurred from salt-alkalinized soils. Neutral salt (NS) stress, which is induced by a high amount of NS such as NaCl and Na₂SO₄. And alkali salt (AS) stress, which is caused by NaHCO₃ and Na₂CO₃ (Shi and Yin, 1993; Jamil et al., 2018). AS stress can impact plants more severely than deleted NS stress (Shi and Yin, 1993; Gong et al., 2014; Nkwuda et al., 2019). Furthermore, plants growing in salt-alkalinized soils are affected by both NS and AS.

Salinity can exert osmotic and toxic effects on plants, consequently damaging the photosynthetic process and impeding plant growth (Benzart Maali et al., 2012; Kumar, 2018). High-salt environments can disrupt ionic homeostasis in plant tissues. The re-establishment of both ionic balance and osmotic adjustment is a key functional mechanism for plant survival under NS stress (Li et al., 2003; Tianlei, 2019). Compared to that of NS stress, the higher pH value of AS stress can impose greater effects on plants, probably because the alkalinity of saline soils can severely disrupt both ionic and pH homeostases in plant tissues (Yang et al., 2008; Rajendran and Mohsin, 2018).

Therefore, plants under AS stress may suffer not only from ion toxicity and physiological drought but also from alkaline stress in high-pH environments. To resist AS stress, plants must allocate higher amounts of energy to regulate the pH in their roots to maintain intracellular ionic balance (Yang et al., 2007; Sufiyan et al., 2018).

Due to the high adaptability of halophytes to saline and alkaline environments, many studies have examined the physiological responses of these types of plants to salt stress (Maali Benzart et al., 2014). Many studies have found that moderate salt solutions can stimulate net photosynthetic rates (Pns) (i.e., the highest rates of net photosynthesis are found in plants under moderate salt concentrations). For example, the growth rate of the C₃ perennial halophyte shrub *Atriplex portulacoides* peaked at 200 mM NaCl concentrations (Redondo-Gómez et al., 2007; Madhav et al., 2018). Halophytes can survive in saline environments by employing the following mechanisms: enhancing photosynthetic ability, reducing Na⁺ concentrations in the cytosol and using Na⁺ as an osmoregulator to maintain cellular ion homeostasis, as well as improving water status via osmotic adjustment by producing compatible solutes (Shabala et al., 2014; Flowers et al., 2015). For instance, *Puccinellia tenuiflora* can limit Na⁺ influx to maintain a high K⁺/Na⁺ ratio in the shoots (Niu et al., 2016; Raj and Prabhakaran, 2018). However, studies on the effects of salt stress on plants have mainly focused on NS environments dominated by NaCl. Few studies have investigated the impact of alkaline stress on halophytes and their underlying mechanisms, which may have implications for better utilization and restoration of salt-alkalinized soil.

Furthermore, recent studies have typically used herbs and crops, including *Chloris virgate*, *P. tenuiflora*, *Kochia sieversiana*, wheat, oats and tomato, to investigate the effects of salt and alkaline stress on plants (Yang et al., 2008). However, how halophytes are affected by salt and alkaline stress and the way they physiologically respond in saline and alkaline environments are not well understood. The saline-alkali region in Northwest China also experiences long periods of drought, gale-force winds and dust. Therefore, shrubs have great implications in land restoration and local economies, as shrubs cannot be replaced by herbs and crops due to the lack of ecological functions, such as disrupting wind and preventing erosion, of those two plant types. The C₄ perennial evergreen shrub *Atriplex canescens*, which belongs to the Chenopodiaceae family, is native to xeric and saline deserts in North America. Due to its strong resistance to drought (annual rainfall of 90-350 mm), salinity (soil salinity of 0.5-1.5%, and cold (elevation of 500-3500 m) (Glenn and Brown, 1999; Kong, 2013), this species is well naturalized and adapted to a wide range of environments. It is widely used as fodder and screens and for preventing soil erosion and soil recovery (Peterson et al., 1987; Benzarti et al., 2013). This shrub species was introduced to China in 1990 and has shown the ability to maintain high levels of photosynthesis and growth rates throughout a wide range of NaCl concentrations (Pan et al., 2016). Therefore, *A. canescens* represents an excellent phytoremediation plant in saline-alkali environments (Benzarti et al., 2013). However, it is not clear whether the photosynthesis and growth of *A. canescens* differ between AS and NS environments. In this study, we conducted a controlled experiment by simulating neutral and alkali soil salt conditions along a concentration gradient from 0 to 400 mM in order to compare the different effects of NS and AS on the growth and physiological response of *A. canescens*. To understand the different impact of salt and alkaline stress on their plants and their physiological response traits, we tested the following three hypotheses:

1. AS more strongly inhibits plant growth than does NS.

2. AS more strongly inhibits plant photosynthetic ability than does NS.
3. The Na⁺ and K⁺ contents in *A. canescens* seedlings are more strongly influenced by AS than by NS.

Materials and methods

Experimental treatments

Plant materials

We collected seeds of *A. canescens* from the Academy of Agriculture and Forestry Sciences, Qinghai University, China. The seeds were treated with H₂SO₄ and distilled water and then were germinated in washed sand under dark conditions for 8 days in a greenhouse. A total of 100 plastic pots were used to house the germinated *A. canescens* seeds; the size of each pot was 10 cm × 10 cm × 10 cm. Each pot was filled with 1 kg of washed soil (1.36 g/cm³ of soil bulk density) and contained 2 seedlings. The seedlings were watered with 1/2-strength Hoagland nutrient solution at 2-day intervals until a suitable soil moisture content (19.96 ± 1.32%, 79.64% percentage of field capacity) was reached. We examined the relationship between the diurnal variation in soil water and seedling growth and defined the suitable soil moisture content as that at which the highest plant growth rates occurred. The climatic conditions of the greenhouse included a temperature of 27.5 ± 1.5 °C/19.0 ± 1.5 °C (day/night) and a photoperiod of 16 h/8 h (light/dark). We controlled the photosynthetically active radiation (PAR) to be 800 μmol m⁻² s⁻¹ and the relative humidity to be 60 ± 2.5%.

Design of simulated salt and alkali conditions

The northwestern inland saline-alkali area in China is characterized by a low annual precipitation (43.5 mm) and a very high intensity of solar radiation (2940 KJ cm⁻²). The soil salts are mainly composed of NaCl, Na₂SO₄, NaHCO₃ and Na₂CO₃. Accordingly, we simulated the NS conditions by mixing NaCl and Na₂SO₄ at a molar ratio of 1:1. To simulate the AS conditions, we mixed NaHCO₃ and Na₂CO₃ at a molar ratio of 1:1. Under each salt condition, five levels of soil solution salt concentrations were applied: 80, 160, 240, 320, and 400 mmol L⁻¹ (mM).

Stress treatment

A total of 72 uniform 8-week-old seedlings (36 pots) were selected and randomly divided into 12 sets. Each set consisted of 3 pots, and each pot contained two plants. One set was used to measure the initial size of the seedlings at the beginning of the treatment, and one set was used as a control group during the whole treatment. Five sets were used for AS stress treatments, while the other five sets were used for NS stress treatments.

By using the soil solution's salt concentrations, soil bulk density and soil moisture content data, we calculated the quantity of the four different salts added to each treatment. One fifth of the salt quantity were added to the plants along with 200 mL 1/2-strength Hoagland nutrient solution between 17:30 and 18:30 every day for five days until the salt quantity reached the desired level. After the desired salt concentrations in the soil were met, the treatments continued for 20 days in the greenhouse. And the soil

moisture contents in all pots were kept constant at $19.96 \pm 1.32\%$ throughout the whole experiment.

Measurement of parameters

Growth

Shoot and root relative growth rates (RGRs) were measured. After the experiment, we harvested the whole plants, separated the shoots from the roots and then dried the tissue at 80 °C for 48 h. We calculated the RGR of both the shoots and roots in accordance with the methods of Kingsbury et al. (1984) as follows: $RGR = (\ln DM_1 - \ln DM_0) / D$, where DM_1 denotes the dry mass at the end of the stress treatment, DM_0 refers to the initial dry mass at the beginning of the stress treatment, and DM is the total treatment duration in days.

Photosynthesis

To measure the photosynthetic ability of the plants, the P_n , stomatal conductance (G_s), transpiration rate (Tr) and chlorophyll (chl) content were measured. Before harvesting the plants, we selected a total of three fully expanded leaves on the upper, middle and lower parts of the seedlings for measuring their P_n , G_s and Tr under a light intensity of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ by using an Li-6400 portable photosynthesis system (LiCor, Lincoln, NE, USA) between 10:00 and 11:00. For each leaf, three replicate measurements were performed for each parameter. The same leaves used for measuring P_n were used for measuring leaf area and chl content. We used a photo scanner (CS4200F; Canon, Inc., Tokyo, Japan) to estimate the leaf area. The water use efficiency (WUE) was calculated as the P_n/Tr ratio. The chl a (Chla), chl b (Chlb) and carotenoids (Car) were extracted by using acetone, and their contents were determined with a spectrophotometer (UV-6100PCS; Mapada Instruments, Co., Ltd., Shanghai, China) at 440-, 654-, and 663-nm wavelengths, respectively. Their concentrations were calculated in accordance with the equations (Lichtenthaler, 1987).

Na⁺, K⁺ concentrations

The roots, stems and leaves were carefully separated and rinsed with deionized water, after which they were dried in an oven at 80 °C for 72 h. The Na^+ and K^+ ions were extracted from the dried tissues by using 100 mM acetic acid at 90 °C for at least 2 h. The extractions were then transferred to a water bath, cooled and filtered, after which the cation accumulation was determined by using a flame spectrophotometer (Model 410 Flame; Sherwood Scientific, Ltd., Cambridge, UK) (Bao et al., 2016). Three replicates were used per measurement.

Statistical analysis

One-way analysis of variance (ANOVA) was performed for each measurement by using SPSS statistical software (Ver. 19.0, SPSS, Inc., Chicago, IL, USA). Duncan's multiple range test (DMRT) was used to identify significant differences among the means at a significance level of $P < 0.05$. All the acquired data were presented as the average values and their standard errors (SEs).

Results

In total, 66 seedlings (1 set of control treatment, 5 sets of NS treatment and 5 sets of AS treatment) were analysed. The mean height of the *A. canescens* seedlings was 12.26 ± 1.90 cm and 10.43 ± 1.21 cm under NS and AS conditions (0-400 mM), respectively, after 20 days.

Effects of NS and AS on the growth of A. canescens seedlings

The growth of *A. canescens* seedlings under the AS treatment differed from that under the NS treatment at the same level of salinity (Fig. 1). A moderate NS concentration (i.e., 160 mM) caused a growth peak for both the shoots and roots. When the NS concentration reached 240 mM or greater (< 400 mM), the shoot growth rates did not significantly differ from those under the non-saline conditions. Under AS conditions, the peak growth of the both the shoots and roots occurred at the lowest AS concentration (80 mM). Further increases in the AS concentrations considerably reduced the growth rates, especially for the root RGR above the AS concentration of 240 mM, which had already significantly inhibited root growth.

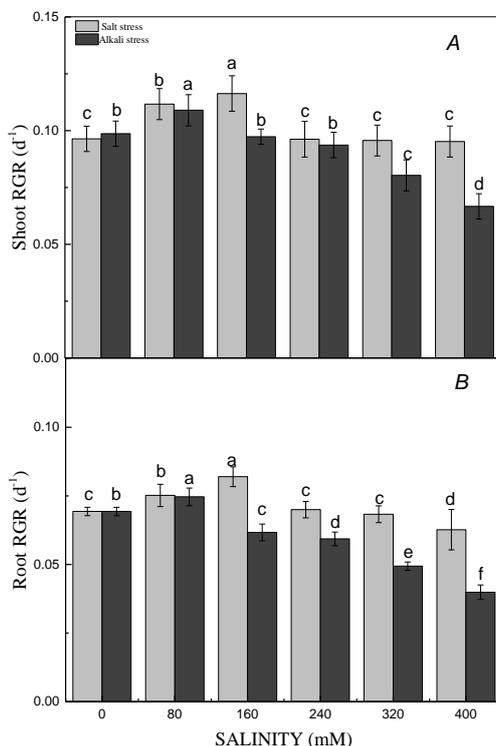


Figure 1. The mean relative growth rates (RGRs) of the shoots (A) and roots (B) of *A. canescens* seedlings under different neutral salt (NS) and alkali salt (AS) concentrations (0-400 mM) after 20 days. The error bars indicate the 95% confidence intervals of the means. Different letters in the same panel indicate significant differences at $P < 0.05$ according to the Duncan test

Effects of NS and AS on photosynthetic ability of A. canescens seedlings

The variation in leaf Pn as salinity increased under AS conditions differed from that under NS conditions (Fig. 2). The Pn significantly and continuously increased as

salinity increased under NS conditions. Moderate AS concentrations increased the Pn; however, compared with that of the control, the Pn decreased dramatically when the AS concentration reached 320 mM or above. NS concentrations of 160 mM and AS concentrations of 80 mM resulted in highest leaf Gs values. The leaf Gs gradually decreased as salinity further increased. However, *A. canescens* seedlings subjected to NS and AS conditions presented different leaf Ci contents. When exposed to NS, the Ci continuously decreased as the salt concentration increased in NS treatment, and similar trend was observed under AS conditions. Furthermore, under AS conditions, after reaching the lowest content at 240 mM, the Ci sharply increased at 320 mM. Correspondingly, leaf WUE was significantly reduced at 160 mM but gradually increased as the salinity concentration increased. At salinity concentrations of 320 mM, the leaf WUE was higher under NS conditions than under AS conditions.

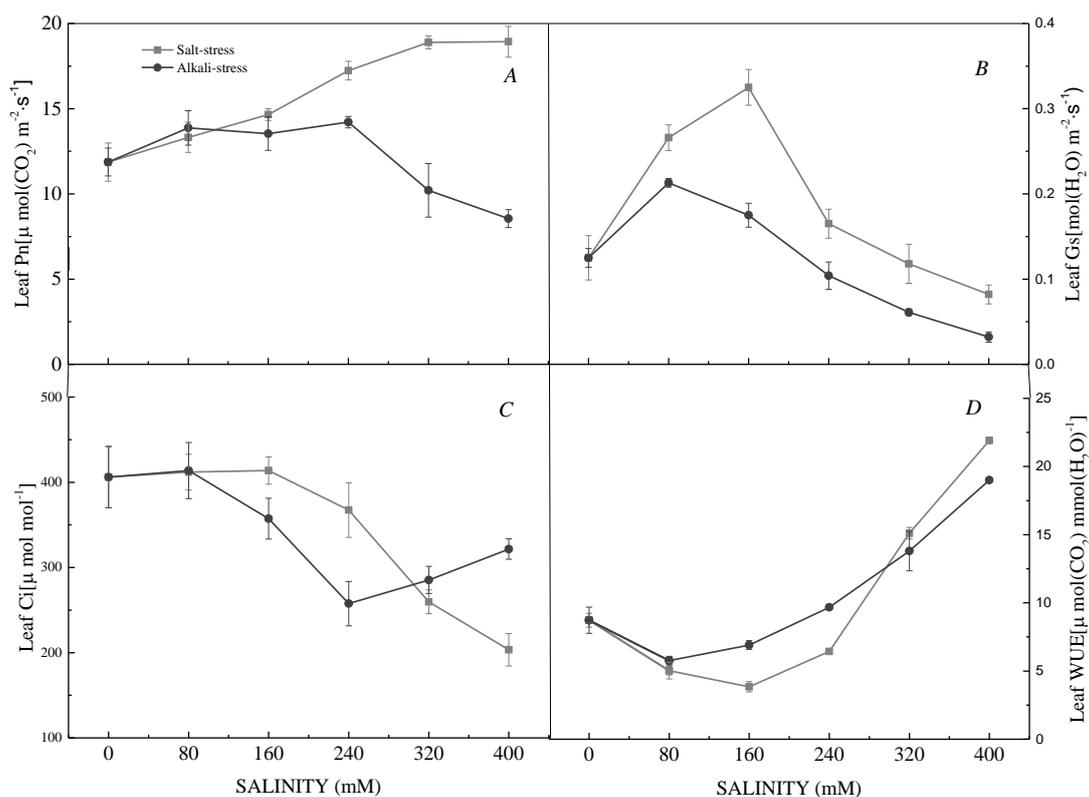


Figure 2. Mean leaf net photosynthetic rate (Pn) (A), leaf stomatal conductance (Gs) (B), leaf intercellular CO₂ concentration (Ci) (C), and leaf water use efficiency (WUE) (D) of *A. canescens* seedlings under different NS and AS concentrations (0-400 mM) after 20 days. The error bars indicate the 95% confidence intervals of the means

The leaf chl contents of the *A. canescens* seedlings under AS conditions were lower than those under NS conditions ($P < 0.05$) (Table 1). Leaves produced more Chla, Chlb and Car as the NS concentration increased (Table 1). At 400 mM NS, the leaf Chla and Chlb contents were 52% and 44% higher than those under non-saline soil conditions, respectively. However, the Chla, Chlb and Car of leaves responded differently to AS stress than to NS stress. The leaf chl content slightly increased as the AS concentration increased but significantly decreased at the AS concentration of 320 mM. Leaf Car were

not affected by AS concentrations less than 320 mM; however, the Car increased at AS concentrations of 400 mM. The ratio of leaf Chla and Chlb increased as NS concentrations increased but decreased as AS concentrations increased.

Table 1. The mean contents of photosynthetic pigments (Chl – chlorophyll, Car – carotenoids) [g kg^{-1} of fresh matter (FM)] in *A. canescens* seedlings under different NS and AS concentrations (0-400 mM) after 20 days

Treatment	Salinity concentration [mM]	Chla [mg g^{-1} of dry matter (DM)]	Chlb [mg g^{-1} of DM]	Chla/Chlb	Car [mg g^{-1} of DM]
Control NS	0	1.42 ± 0.07 c	0.43 ± 0.01 b	3.30 ± 0.07 b	0.35 ± 0.01 b
	80	1.66 ± 0.21 c	0.47 ± 0.04 b	3.53 ± 0.12 b	0.35 ± 0.02 b
	160	1.85 ± 0.09 b	0.51 ± 0.02 b	3.62 ± 0.06 a	0.38 ± 0.06 a
	240	1.90 ± 0.14 b	0.54 ± 0.07 b	3.51 ± 0.11 b	0.39 ± 0.07 a
	320	1.99 ± 0.03 b	0.56 ± 0.06 a	3.55 ± 0.08 b	0.40 ± 0.05 a
	400	2.16 ± 0.12 a	0.62 ± 0.05 a	3.48 ± 0.05 b	0.41 ± 0.01 a
Control AS	0	1.42 ± 0.07 b	0.43 ± 0.01a	3.30 ± 0.07 a	0.35 ± 0.01b
	80	1.49 ± 0.05 b	0.44 ± 0.03a	3.38 ± 0.06 a	0.38 ± 0.06 b
	160	1.52 ± 0.06 a	0.45 ± 0.01 a	3.37 ± 0.11a	0.38 ± 0.07 b
	240	1.55 ± 0.11 a	0.43 ± 0.04 a	3.29 ± 0.03 a	0.39 ± 0.04 b
	320	1.29 ± 0.13 c	0.38 ± 0.07 b	3.14 ± 0.07 b	0.37 ± 0.01 b
	400	1.09 ± 0.01 c	0.35 ± 0.03 b	2.86 ± 0.08 c	0.47 ± 0.05 a

In each column, different letters indicate significant differences at $P < 0.05$ according to the Duncan test

Effects of NS and AS on the Na^+/K^+ of *A. canescens* seedlings

The Na^+ and K^+ contents in *A. canescens* seedlings were differently influenced by AS than by NS. The Na^+ content in the leaves, stems and roots under AS conditions was higher than that under NS conditions, with the exception of the roots in which the AS concentrations of 320 and 400 mM significantly inhibited root Na^+ absorption. At 400 mM NS, the leaf, stem, and root Na^+ contents were approximately 17.25-, 14.89- and 3.86-fold higher than those of the control plants, respectively. Compared with NS stress, AS stress had a more profound effect on reducing the K^+ content in all plant organs.

Under NS conditions, the K^+ content in shoot tissue remained relatively constant as salinity increased, whereas the root K^+ content decreased as salinity increased. Similarly, the K^+ content significantly decreased in the leaves and the roots as the AS concentration increased (Fig. 3D-F). The Na^+/K^+ ratios in the leaves and stems significantly increased as salinity increased, and a larger magnitude of increase occurred under NS conditions than under AS conditions. However, in the roots, the Na^+/K^+ ratio peaked at 240 mM under both NS and AS conditions, but the ratio decreased thereafter as the NS concentration increased (Fig. 3G-I).

Discussion

The RGR reflects the life-sustaining activities of plants and how they respond to stress (Wang et al., 2015). Our results showed that *A. canescens* can adjust to NS stress and AS stress. However, higher AS stress more strongly inhibits plant growth, which confirms our first hypothesis. We found that the growth rates peaked at moderate NS concentrations (160 mM), and growth was maintained in non-saline environments at NS

concentrations up to 400 mM. Similarly, Pan et al. (Pan et al., 2016) reported that *A. canescens* grew better under 100 mM NaCl conditions than under non-saline conditions; however, the salinity level at which the peak growth occurred was lower than the level we recorded in our experiments (100 mM vs. 160 mM). This finding might be attributed to the salt mixtures (i.e., NaCl and Na₂SO₄) that we used (Qiu et al., 2003). In contrast, growth was inhibited by external AS treatment (> 320 mM). Previous reports have also shown greater deleterious effects from alkaline stress than salt stress on other plant species, such as *Aneurolepidium chinense*, *Chloris virgate*, *Suaeda corniculata*, (Shi and Wang, 2005; Yang et al., 2007, 2008). The different influence of both kinds of stress on plant growth might be due to the different underlying mechanisms. Plant survival in AS soil relies not only on the ability to address ion toxicity and low water potential but also on the ability to tolerate high pH (Shi and Wang, 2005; Yang et al., 2007, 2008). Adjustments of the pH outside the roots may represent another key physiological mechanism of alkalinity resistance. Under high AS conditions, a high pH around the roots could disrupt the governing ion balance and nutrient supplies; this disruption could lead to the inhibition of transmembrane electrochemical potential gradients in the root cells, which would negatively impact photosynthetic parameters and growth. Moreover, our results also demonstrated that the different responses of the photosynthetic ability (Shabala et al., 2014), ion homeostasis and osmotic adjustment capacity of the *A. canescens* seedlings represented the mechanisms that drove the stronger growth inhibition under AS conditions than under NS conditions (Fig. 1).

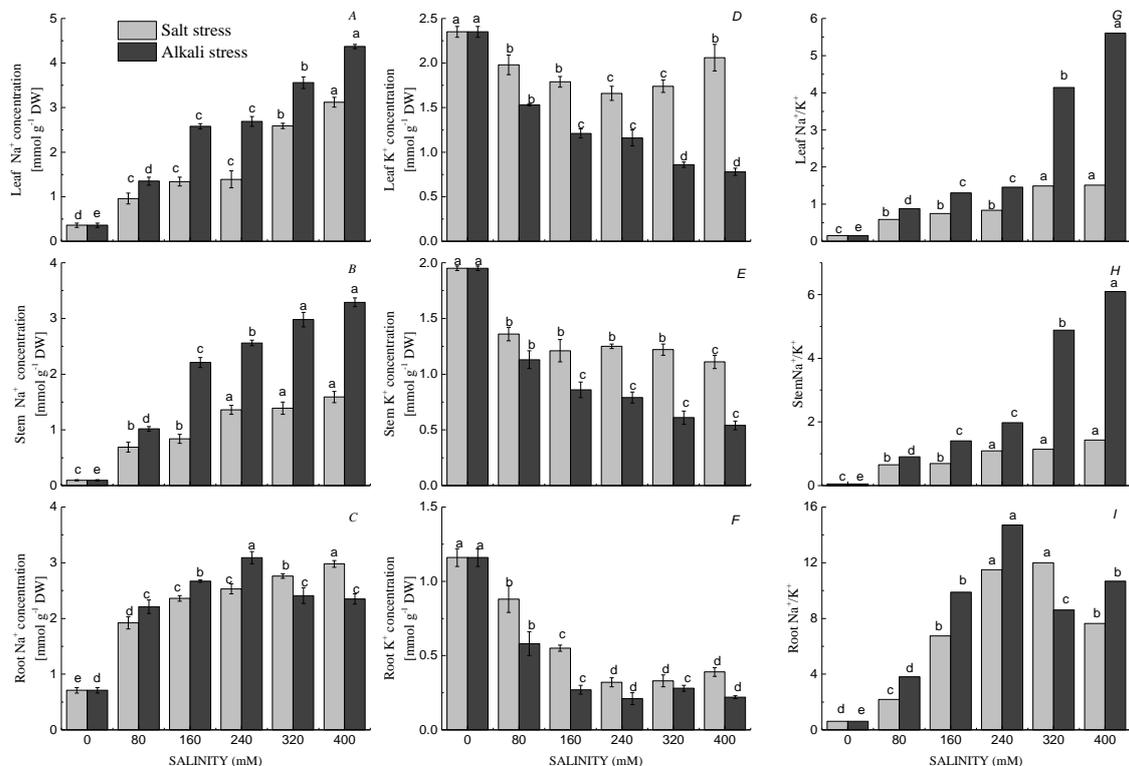


Figure 3. The mean Na⁺ and K⁺ contents and Na⁺/K⁺ ratios in the leaves (A, D, G), stems (B, E, H) and roots (C, F, I) of *A. canescens* seedlings under different NS and AS concentrations (0-400 mM) after 20 days. The error bars indicate 95% confidence intervals of the means. Different letters in the same panel indicate significant differences at $P < 0.05$ according to the Duncan test

Plants must spend energy to adapt and exhibit resistance to stressful environments. The amount of energy spent directly depends on the photosynthetic ability (Wellburn and Lichtenthaler, 1984). The different growth rates of the *A. canescens* seedlings under the different treatments were basically the result of the Pn (Wang et al., 2004). In the present study, the Pn of the *A. canescens* seedlings significantly increased as both NS and AS concentrations increased, with the exception of that at 320 and 400 mM AS (Tsutsumi et al., 2015). This finding indicated that the *A. canescens* seedlings strongly tolerated more than just salt and alkaline stress (Shi and Wang, 2015). However, the AS more strongly inhibited the Pn of the plants than did the NS, which is in line with our second hypothesis.

The responses of the Pn might be mediated by the photochemical process, resistance to gas exchange and the assimilatory system. Under moderate stress, *A. canescens* seedlings can increase cyclical electron transport (Bukhov and Carpentier, 2004) and photorespiration (Parida and Das, 2005) as mechanisms for protection against salinity. Furthermore, *A. canescens* seedlings can cope with excessive salt by decreasing their stomatal aperture to increase leaf WUE and carboxylation (Guy et al., 1980; Megdiche et al., 2008). Our results showed that the Gs first increased but then decreased as salinity increased. In contrast (Ma et al., 2012) reported that the Pn and Gs of *Zygophyllum xanthoxylum* were positively correlated. This correlation might be due to the different properties of C₃ and C₄ plants (Yang et al., 2017). Moderate Na⁺ concentrations may promote the C₄ photosynthesis of *A. canescens* by facilitating the activity of photosystem II (PSII), converting pyruvate to phosphoenolpyruvate, as well as other biochemical processes in the photosynthetic pathway (Chaves et al., 2011; Kronzucker et al., 2013). In this study, we also found that the contents of Chla, Chlb and Car increased as the NS concentration increased. Under moderate stress, the *A. canescens* seedlings might accumulate photosynthetic pigments and metabolically regulate chl to adapt to NS or AS conditions. In addition, Car are not only photosynthetic pigments but also endogenous antioxidants. Apart from the photosynthetic function of Car, they can also prevent membrane lipid peroxidation (Yang et al., 2008). In contrast to the stimulating effects of the high levels of neutral salinity on the Pn, high concentrations of AS significantly reduced the Pn. This result might be due to the dual effects of stimulation and inhibition caused by the AS (Zhao et al., 2013). At AS concentrations of 320 mM, the inhibitory effects gradually strengthened as salinity increased and exceeded the stimulatory effects. High pH values may injure the photosynthetic system, possibly inhibiting the transmembrane electrochemical potential of PSII. The sudden increase in Ci also indicated a damaged photosynthetic system when the AS concentrations reached 320 mM or greater (Yang et al., 2012). This Ci enhancement at AS concentrations of 320 mM was probably caused by non-stomatal limitations in accordance with the Farquhar gas exchange model. For example, limiting Rubisco carboxylase activity and destroying chloroplast structure could explain the reductions in the Pn, causing Ci to increase (Bethke and Drew, 1992; James et al., 2006). Salinity induces a wide range of perturbations in terms of chl concentration and chloroplast structure (Abdelkader et al., 2007). In our study, the reduced chl content after an initial increase as the AS concentration increased might also indicate a stronger inhibitory impact of AS compared with NS on chl synthesis, and Mg²⁺ precipitation (Shi and Zhao, 1997). Furthermore, Chlb is an important component of the light-harvesting complex. The decrease in Chlb in our results might also impair the light-harvesting complex structure and function, consequently weakening the light

absorption ability of the chloroplasts. To summarize the above results, the inhibition of *A. canescens* seedling growth under AS conditions might result from a decrease in the Pn, which might be due to non-stomatal limitations and lower chl concentrations caused by a high pH (Zhao et al., 2014).

In saline soil, Na⁺ is considered a major toxic ion. Low Na⁺ and high K⁺ contents in plant cells are preconditions to the maintenance of enzymatic processes (Munns and Tester, 2008). Thus, maintaining a relatively constant intracellular Na⁺/K⁺ homeostasis is crucial for plants to acclimate to salinity stress conditions (Zhu, 2003; Tang et al., 2014). In the present study, the Na⁺ content was higher and the K⁺ content was lower under AS conditions than under NS conditions (Volkov, 2015). The Na⁺/K⁺ ratios increased along the salinity gradient. However, compared with the AS treatment, the NS treatment resulted in Na⁺/K⁺ ratios that remained relatively constant as salinity increased. This finding confirmed our third hypothesis that AS more strongly influenced the Na⁺ and K⁺ contents in *A. canescens* seedlings than did NS (Zhang, 2013). The increased accumulation of Na⁺ and decreased accumulation of K⁺ represent mechanisms for adapting to salinity in *Atriplex* (Bajji et al., 1998; Bose et al., 2015; Ma et al., 2016). In the present study, the growth of *A. canescens* seedlings was positively affected by NS despite the increased Na⁺ content, which might be attributed to two physiological processes. First, ion compartmentation enables plants to sequester a large quantity of excess Na⁺ into epidermal bladder cells to avoid ion toxicity in organelles (Flowers and Colmer, 2008; Ding et al., 2010; Shabala, 2011, 2014). Second, *A. canescens* is capable of transporting K⁺ instead of Na⁺ from the roots to the stem or from the stem to the leaves to maintain a relatively constant cytosolic Na⁺/K⁺ ratio in the shoots (Flowers and Colmer, 2008; Pan et al., 2016). In contrast, under AS conditions, the over-accumulation of Na⁺ had adverse impact on the *A. canescens* seedlings. This finding might be related to reduced Na⁺ sequestration within vacuoles and weakened control over Na⁺ transport within plant tissues driven by high pH values (Chen et al., 2009). These phenomena can thus lead to a significant increase in Na⁺ concentration and can disrupt ionic balance in tissues. Furthermore, AS can also neutralize the number of protons and weaken the establishment of Na⁺/H⁺ antiporters in the plasma membrane, leading to the failure of Na⁺ compartmentation (Munns and Tester, 2008; Pan et al., 2016). Our results further showed that the AS environment more strongly impeded the ability of plants to maintain K⁺ uptake than did the NS environment. Similarly, excess Na⁺ competes with K⁺ uptake in many species. This phenomenon can inhibit K⁺-dependent metabolic process, such as the induction of the photosynthetic ATPase enzyme, and can inhibit the participation of K⁺ during carbohydrate biosynthesis, consequently resulting in oxidative stress (Munns and Tester, 2008; Flowers et al., 2015; Volkov, 2015). We demonstrated that the disrupted K⁺ and Na⁺ homeostasis due to the high pH value is probably responsible for the inhibited growth and reduced Pn of *A. canescens* seedlings in AS environments.

Conclusion

Our results indicated that *A. canescens* seedlings can adapt to NS stress and AS stress though strengthening the photosynthetic ability and maintaining ionic homeostasis capacity. However, at higher concentrations (> 240 mM), alkali salinity more strongly inhibited plant performance than did neutral salinity, and the change was associated with a decrease in photosynthetic ability and damage to Na⁺/K⁺ homeostasis under

alkali salinity. *A. canescens* as an exotic tree species can be used to achieve the ecological recovery and city afforestation for moderate salinization areas of northwest China. In this study, we compared the growth responses of *Atriplex canescens* to salt and alkaline stress under an optimal soil water condition. In the future, experiments may be conducted under different soil water conditions.

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Conflict of interests. The authors declare that they have no conflict of interest.

Compliance with ethical standards. This article does not contain any studies with human participants or animals performed by any of the authors. Informed consent was obtained from all individual participants included in the study.

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