Plant Physiology and Biochemistry 135 (2019) 489–498

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

The synergistic effects of sodium and potassium on the xerophyte *Apocynum venetum* in response to drought stress

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ARTICLE INFO

Keywords:
Apocynum venetum
Potassium efficiency
Osmotic stress
Sodium
Osmotic adjustment
Photosynthesis

ABSTRACT

Apocynum venetum is an eco-economic plant species with high adaptability to saline and arid environments. Our previous work has found that *A. venetum* could absorb large amount of Na^+ and maintain high K^+ level under saline conditions. To investigate whether K^+ and Na^+ could simultaneously enhance drought resistance in *A. venetum*, seedlings were exposed to osmotic stress (−0.2 MPa) in the presence or absence of additional 25 mM NaCl under low (0.01 mM) and normal (2.5 mM) K^+ supplying conditions, respectively. The results showed that *A. venetum* should be considered as a typical K^+-efficient species since its growth was unimpaired and possessed a strong K^+ uptake and prominent K^+ utilization efficiency under K^+ deficiency condition. Leaf K^+ concentration remained stable or was even significantly increased under osmotic stress in the presence or absence of NaCl, compared with that under control condition, regardless of whether the K^+ supply was sufficient or not, and the contribution of K^+ to leaf osmotic potential consistently exceeded 37%, indicating K^+ is the uppermost contributor to osmotic adjustment of *A. venetum*. Under osmotic stress, the addition of 25 mM NaCl significantly increase Na^+ accumulation in leaves and the contribution of Na^+ to osmotic adjustment, thus improving the relative water content, concomitantly, promoting the photosynthetic activity resulting in an enhancement of overall plant growth. These findings suggested that, K^+ and Na^+ simultaneously play crucial roles in the osmotic adjustment and the maintenance of water status and photosynthetic activity, which is beneficial for *A. venetum* to cope with drought stress.

1. Introduction

Drought is among the most severe environmental stresses that seriously inhibits plant growth by disrupting various physiological and biochemical processes such as nutrition uptake, photosynthesis, cellular metabolism and turgor maintenance (Yordanov et al., 2000; Rampino et al., 2006; Rivero et al., 2007; Farooq et al., 2009; Jaleel et al., 2009; Carmo-Silva et al., 2012). Due to global climate change and expansion of human activities, drought has been much more frequent and severe in recent years (Mishra and Singh, 2010) and thereby, triggers large scale desertification coupled with a rapid reduction of vegetation coverage and crop yield in arid and semi-arid regions (Martínez et al., 2005; Slama et al., 2007; Ben Hassine et al., 2010; Ma et al., 2012a). Some wild plant species such as xerophytes, however, have evolved multiple protective mechanisms to successfully survive in these harsh environments (McDowell et al., 2008; Ashraf, 2010; Ma et al., 2012a; Yue et al., 2012). Therefore, investigating and clarifying the drought-resistance mechanisms of these unique plant species are of great values for settling drought crisis on environment restoration and agriculture development (Chaves and Oliveira, 2004; Sambatti and Caylor, 2007; Ashraf, 2010).

Apocynum venetum, a C_3 perennial shrub belonging to Apocynaceae, is widely distributed throughout the salt-barren zones, desert steppes and alluvial flats of Mediterranean area and northwestern China. This species plays an important role in sand-fixing as well as soil and water conservation in local areas (Kim et al., 2000; Xie et al., 2012). Meanwhile, the medical properties and high fiber utilization value make it attractive as a traditional Chinese herb and textile raw material (Wang et al., 2007a; Li et al., 2010; Zheng et al., 2012; Jiang et al., 2014). *A. venetum* could well cope with various abiotic stresses including drought and salinity and thereby, be flourish in desert environments (Ma et al., 2000; Ning et al., 2010). Our previous work has preliminarily found

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https://doi.org/10.1016/j.plaphy.2018.11.011
Received 26 September 2018; Received in revised form 27 October 2018; Accepted 8 November 2018
Available online 10 November 2018

that *A. venetum* should possess strong potassium (K^+) uptake ability as tissue K^+ concentrations maintained stable under low K^+ treatment for 5 weeks; moreover, its growth was unimpaired and tissue K^+ concentration was unaffected under 50 mM NaCl treatment for over one month, accompanyied with a drastically increased sodium (Na^+) concentration in leaves (Xia et al., 2014). Therefore, the simultaneous absorption of K^+ and Na^+ from external surroundings might be an important physiological mechanism of *A. venetum* to survive in desert environments.

As an essential macronutrient and the most abundant cation in plant cells (Lebaudy et al., 2007; Szczerba et al., 2009; Coskun et al., 2013; Zörb et al., 2014), K^+ plays crucial roles in many fundamental processes in plants, such as enzyme activation, protein biosynthesis, electrical neutralization for anionic groups, cell expansion, and consequently affects overall plant growth and development (Cakmak, 2005; Lebaudy et al., 2007; Marschner, 2012; Wang et al., 2013; Benito et al., 2014; Martineau et al., 2017). Moreover, increasing studies have proven that the accumulation of K^+ in both vacuole and cytosol could promote water acquisition of plants by enhancing osmotic adjustment (OA) (Egilla et al., 2005; Wang et al., 2013). Therefore, K^+ is thought to be one of the most prominent osmoticum for plants under drought conditions (Shabala and Shabala, 2011; Anschütz et al., 2014). Na^+ is the major cation existing in most saline soils (Munns, 2005; Britto and Kronzucker, 2015; Tang et al., 2015a,b), which is commonly recognized to be the principal factor restricting plant growth caused by salinity (Munns and Tester, 2008). However, according to Glenn and Brown (1998) and Slama et al. (2007), absorbing large amount of Na^+ and directly using it for OA is an effective physiological strategy of halophytes *Atriplex canescens* and *Sesuvium portulacastrum* to cope with water deficit; meanwhile, in the xerophyte *Zygophyllum xanthoxylum*, Na^+ is the most important osmoticum that contributes to improving leaf photosynthesis and tissue hydration under drought stress (Ma et al., 2012a). Therefore, Na^+ is classified as a functional nutrient element for certain plant species that is actively involved in stress resistances (Subbarao et al., 2003; Pilon-Smits et al., 2009). In recent years, the positive effects of K^+ together with Na^+ supply on growth and drought adaptability in plants have gradually been assessed (Battie-Laclau, 2014a and b). However, comprehensive studies on the synergistic impacts of K^+ and Na^+ on drought resistance in xerophytic desert plants are still scarce.

Despite the high ecological and economic value of *A. venetum* for regions that undergo severe drought, the mechanisms developed by *A. venetum* to cope with water deficit are still poorly documented. Considering that K^+ and Na^+ both are osmoticum for plants and *A. venetum* could absorb and accumulate large amount of these two cations, we may hypothesize that K^+ and Na^+ simultaneously play positive roles in drought resistance of *A. venetum*. Therefore, in this study, *A. venetum* seedlings were subjected to osmotic stress in the presence or absence of additional NaCl under both low and normal K^+ supplying conditions, and various parameters related to growth, photosynthesis, water status, ion accumulation and osmotic adjustment were assessed.

2. Materials and methods

2.1. Plant growth and treatments

Seeds of *A. venetum* were collected from Altay City (47°43′N, 87°23′E; elevation 493 m) in Xinjiang Uygur Autonomous Region, China. After removal of the bracts, seeds were surface sterilized in 0.5% potassium permanganate (w/v) for 10 min, rinsed 6 times with distilled water, and soaked in distilled water at 25 °C for 24 h. Then seeds were sown in seed containers (5 cm × 5 cm × 5 cm, four seeds/container) filled with vermiculite, and irrigated with Hoagland solution containing 2 mM KNO_3, 0.5 mM KH_2PO_4, 0.5 mM $MgSO_4$, 0.5 mM $Ca(NO_3)_2$, 60 μM Fe-citrate, 50 μM H_3BO_3, 10 μM $MnCl_2$, 1.6 μM $ZnSO_4$, 0.6 μM $CuSO_4$, 0.05 μM Na_2MoO_4. Solutions were renewed every 3 days. At the fourth leaf stage, the seedlings were thinned out to two uniform plants in each container. All seedlings were grown in a greenhouse with photoperiod of 16 h light at 25 °C/8 h dark at 18 °C, light flux density was about 500 μmol m^{-2} s^{-1} during the light period, and relative humidity was about 70%. After 5 weeks, uniform seedlings were used for experimental treatments.

All seedlings used in this study were firstly confronted with K^+-starvation treatment. To achieve this, the vermiculite in containers was rinsed with modified Hoagland solution containing 0.01 mM K^+ (2 mM KNO_3 and 0.5 mM KH_2PO_4 in Hoagland solution was substituted by 2 mM HNO_3 and 0.5 mM H_3PO_4, respectively, and 0.01 mM K^+ was provided by 0.01 mM KCl) from top to bottom thoroughly to remove surplus K^+ in vermiculite as much as possible. Then seedlings were subjected to modified Hoagland solution containing 0.01 mM K^+ as K^+-starvation treatment for 7 days. After that, they were randomly divided into two groups: low K^+ supplying (Low K) and normal K^+ supplying (Normal K) group. The K^+ supplement was returned to 2.5 mM by adding KCl in Normal K group, whereas maintained at 0.01 mM in Low K group. In each group, there were three treatments: control (C, neither sorbitol nor salt), osmotic stress alone (O, seedlings were irrigated by Hoagland solution containing sorbitol with the final osmotic potential of −0.2 MPa) and osmotic stress together with salt (O + S, seedlings were irrigated by Hoagland solution containing 25 mM NaCl and a certain amount of sorbitol with the final osmotic potential of −0.2 MPa). The pH of all solutions used in this study was adjusted to 5.7 using Tris [(hydroxymethyl) aminomethane] according to Zhu et al. (2013) and Teaster et al. (2015). Tris is an alkaline organic compounds without the components of K^+ or Na^+ that has no effect on final concentrations of K^+ and Na^+ in treatment solutions. All solutions were renewed every day. To minimize the effects of possible environmental gradients in the greenhouse, seedlings were randomly reassigned to new positions every day as well. After 7 days, the leaves of *A. venetum* seedlings under osmotic stress alone in Low K group primarily began to wilt, the photosynthesis-related parameters under all treatments were firstly determined. Then all seedlings were harvested for measurement and analysis of other physiological parameters. Each treatment was repeated 6 times independently containing 2 plants in each replicate.

2.2. Determination of photosynthesis and leaf gas-exchange parameters

An open infrared portable gas exchange fluorescence system (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany) was used to measure net photosynthesis rate (Pn), transpiration rate (Tr) and stomatal conductance (Gs). Parameters were measured on middle-upper part of fully expanded mature leaves from 9:00 a.m. to 11:30 a.m. in bright sunlight on a clear, cloudless day. During the measurement, the temperature, relative air humidity, photosynthetic photon flux density and CO_2 concentration in the leaf chamber of the apparatus were constantly maintained at 25 °C, 50%, 1000 ± 50 μmol m^{-2} s^{-1} and 420 ± 20 μmol mol^{-1}, respectively. The intrinsic water use efficiency (WUEi) = Pn/Gs (Ran et al., 2010).

2.3. Determination of plant biomass, relative growth rate and relative water content

Plant height (PH) was measured at first, and then roots, stems and leaves were separated gently. Fresh weight (FW) of different tissues was determined immediately, then leaves were soaked in deionized water in test tubes at 4 °C overnight in the dark to obtain turgid weight (TW). After that, samples were oven dried at 80 °C for 3 days for dry weight (DW) measurements.

The relative growth rate (RGR) of whole plants was calculated using the formula: RGR (g kg^{-1} d^{-1}) = ($\ln W_f$ - $\ln W_i$)/Δt × 1000, where W_f and W_i are final (after 7 days of treatment) and initial (before treatment) dry weights (g), respectively, andΔt is the time elapsed (7 days) between the two measurements (Martínez et al., 2005).

The relative water content (RWC) was estimated using the following formula: RWC (%) = 100 × (FW - DW)/(TW - DW) (Slama et al., 2007).

2.4. Measurement of K^+, Na^+ and Ca^{2+} concentrations

K^+, Na^+ and Ca^{2+} concentrations were measured as described by Wang et al. (2007b). Briefly, K^+, Na^+ and Ca^{2+} were extracted from oven dried leaves, stems and roots in 100 mM acetic acid at 90 °C for 2 h, then K^+ and Na^+ analysis was performed using a flame spectrophotometer (Model 410 Flame; Sherwood Scientific, Ltd., Cambridge, UK), and Ca^{2+} was determined with atomic absorption spectrophotometer (AAS, AA-670, Shimadzu, Kyoto, Japan).

The selective absorption (SA) and selective transport (ST) for K^+ over Na^+ were estimated according to the following equations, respectively, as described by Wang et al. (2002):

SA = (K^+ content/Na^+ content in whole plant)/(K^+ concentration/Na^+ concentration in medium);

ST_1 (Root to Stem) = (K^+ concentration/Na^+ concentration in stems)/(K^+ concentration/Na^+ concentration in roots);

ST_2 (Stem to Leaf) = (K^+ concentration/Na^+ concentration in leaves)/(K^+ concentration/Na^+ concentration in stems).

2.5. Measurement of K^+-uptake and -utilization efficiency parameters

K^+ net uptake rate (KNUR) was calculated using the equation described by Wang et al. (2009): KNUR (nmol g^{-1} RFW min^{-1}) = (C_2 - C_1)/[RFW × (t_2 - t_1)], where C_2 and C_1 is K^+ accumulation amount in whole plant after treatment and before treatment, respectively. RFW is the root fresh weight (g), and Δt is the time elapse (7 days).

K^+ accumulation amount (KAA) and K^+ use efficiency (KUE) were calculated as the following formula according to Yang et al. (2003) and Damon et al. (2007):

K^+ accumulation amount (KAA) = K^+ accumulated per plant (mg);

K^+ use efficiency (KUE) = dry weight per plant (g)/K^+ accumulated in shoot (g).

2.6. Determination of leaf chlorophyll concentration

Chlorophyll concentrations were estimated according to Hong et al. (2005). Chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and total chlorophyll (total Chl) in fresh leaf samples (about 0.1 g) were extracted with 80% acetone and 95% ethanol (v/v = 1:1) for 24 h in the dark, then centrifuged at 9000 g for 10 min at 4 °C. After that, the supernatant was taken to measure the absorbance at 645 and 663 nm with a UV spectrophotometer (UV-2102C, Unico Instrument Co., Ltd, Shanghai, China). Chl *a*, Chl *b* and total Chl concentrations were calculated by using the formulas as Inskeep and Bloom (1985) described.

2.7. Determination of leaf osmotic potential and the contributions of K^+ and Na^+ to leaf osmotic potential

Leaf osmotic potential (Ψs) was estimated according to the method described by Ma et al. (2012a). Fresh leaf samples were transiently frozen in liquid nitrogen and then thawed to extrude sap by a syringe. Cell sap was centrifuged at 9000 g for 5 min, and the osmolality of the supernatant was analyzed with a cryoscopic osmometer (Osmomat-030, Gonotec GmbH, Germany) at 25 °C. The readings (n, mmol kg^{-1}) were used to calculate the solute potential with the Van't Hoff equation: Ψs (MPa) = -n × R × T; here R is gas constant (0.008314 m^3 MPa mol^{-1} K^{-1}) and T is the thermodynamic temperature (298.8 K). The Ψs values of Na^+ and K^+ (calculated osmotic potential; COP) were estimated by the Van't Hoff equation as described by Guerrier (1996) and Ma et al. (2012a). The contributions of solute to leaf osmotic potential were estimated by the formula: C = COP/Ψs × 100%.

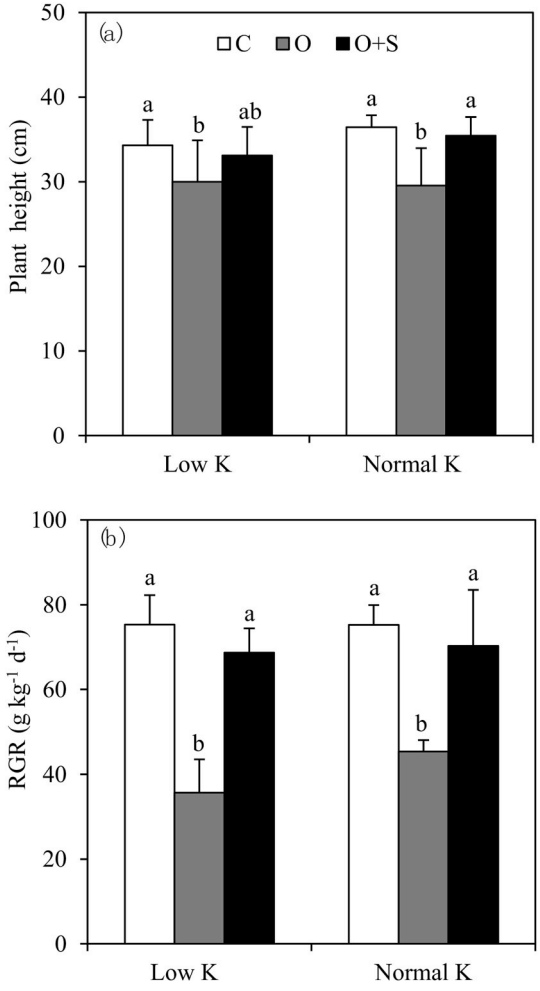

Fig. 1. Plant height (PH) (a) and relative growth rate (RGR) (b) of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate (n = 6). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

2.8. Data analysis

Above mentioned parameters were all presented as means with standard error (n = 6). All the data were subjected to one-way analysis of variance (ANOVA) using SPSS 23.0 (SPSS Inc., Chicago, IL, USA). Duncan's multiple range tests were used to detect significant differences between means at a significance level of $P < 0.05$.

3. Results

3.1. The growth of A. venetum exposed to osmotic stress in the presence or absence of 25 mM NaCl under different K^+ supplying levels

When plants were grown under control condition (C, neither sorbital nor salt), no significant difference on plant height (PH), relative growth rate (RGR), tissue fresh weight (FW) and dry weight (DW) (except for leaf DW) was observed between Low K (0.01 mM K^+) and Normal K (2.5 mM K^+) group (Fig. 1, Fig. 2, Fig. S1 and Fig. S2), indicating that K^+-deficiency had no adverse effects on the growth of *A. venetum*. Osmotic stress severely inhibited the growth of *A. venetum*: compared with corresponding control, osmotic stress alone (O) respectively decreased PH, RGR, leaf FW and DW by 13, 53, 28 and 31% in Low K group, and by 19, 40, 31 and 29% in Normal K group (Figs. 1

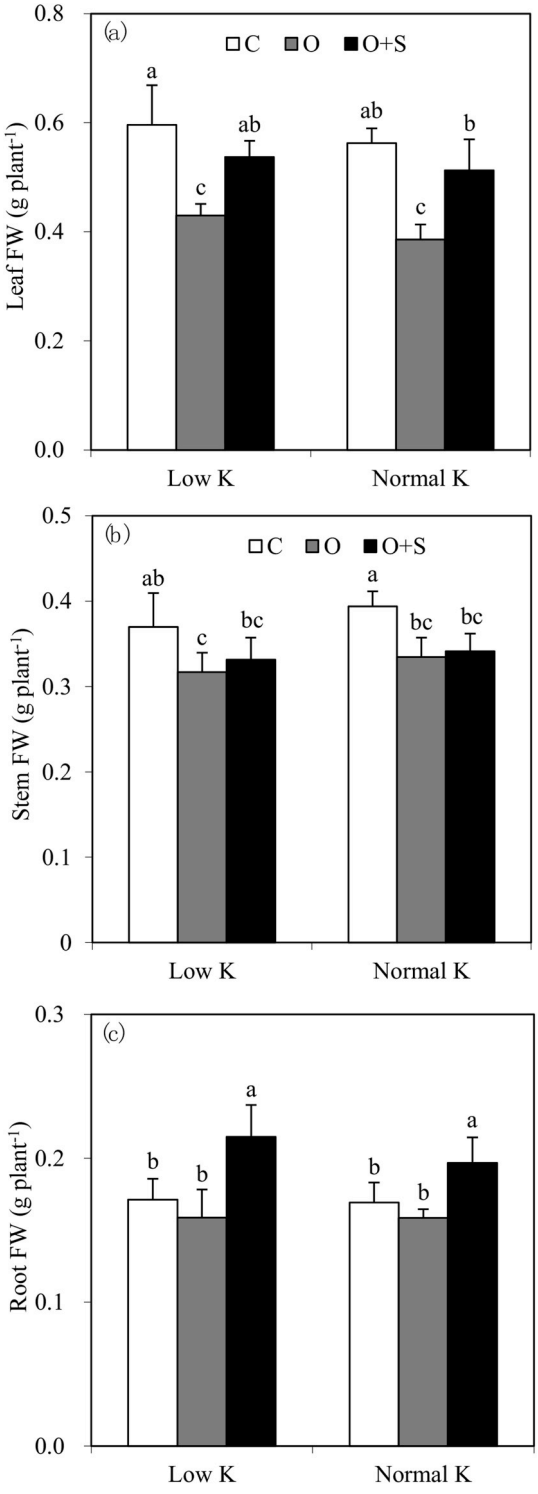

Fig. 2. Leaf (a), stem (b) and root (c) fresh weight (FW) of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate ($n = 6$). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

and 2, Fig. S1 and Fig. S2). However, the addition of 25 mM NaCl in osmotic stress (O + S) substantially mitigated the detrimental effects of osmotic stress on the growth of *A. venetum*: in both Low and Normal K groups, PH, RGR, leaf FW and DW, and root FW under O + S treatment were all significantly higher than those under corresponding O treatment (Figs. 1 and 2a, c, Fig. S1 and Fig. S2).

Table 1
Leaf relative water content (RWC) and intrinsic water use efficiency (WUEi) of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate ($n = 6$). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

Treatments		RWC (%)	WUEi (μmol CO_2 mmol H_2O^{-1})
Low K	C	90.42 ± 2.14 a	0.146 ± 0.003 d
	O	85.16 ± 4.00 b	0.147 ± 0.006 d
	O + S	92.32 ± 1.51 a	0.155 ± 0.001 c
Normal K	C	94.14 ± 1.55 a	0.173 ± 0.004 ab
	O	91.66 ± 5.78 a	0.172 ± 0.007 b
	O + S	94.71 ± 1.13 a	0.178 ± 0.001 a

3.2. Moderate NaCl improves leaf hydration of *A. venetum* exposed to osmotic stress

As shown in Table 1, under control condition, no obvious difference on leaf relative water content (RWC) between Low and Normal K group was observed, indicating that K^+-deficiency did not deteriorate leaf water status of *A. venetum*. Compared with corresponding control, osmotic stress significantly reduced leaf RWC in Low K group, however, a significant higher leaf RWC by 8% under O + S treatment than that under O treatment was observed (Table 1). O + S treatment also significantly elevated intrinsic water use efficiency (WUE_i) in both Low and Normal K groups, compared with corresponding O treatment (Table 1).

3.3. Moderate NaCl enhanced photosynthetic performance of *A. venetum* exposed to osmotic stress

In comparison with corresponding control, osmotic stress significantly reduced net photosynthetic rate (Pn) by 42 and 44%, stomatal conductance (Gs) by 39 and 46%, as well as transpiration rate (Tr) by 39 and 48% in Low and Normal K group, respectively (Fig. 3). Compared with corresponding O treatment, O + S treatment respectively increased Pn, Gs and Tr by 22, 17 and 33% in Low K group, and by 81, 76 and 76% in Normal K group (Fig. 3).

As shown in Table 2, when plants were grown under normal condition, no obvious differences on chlorophyll (Chl) concentrations between Low and Normal K group were observed. Compared with corresponding control, osmotic stress respectively reduced Chl *a* and total Chl concentration by 17 and 11% in Low K group, while had no effect on Chl *a*, Chl *b* and total Chl concentrations in Normal K group (Table 2). Therefore, under O treatment, Chl *a* and total Chl concentrations in Low K group were significantly lower than those in Norma K group (Table 2). O + S treatment noticeably increased Chl *a* and total Chl concentrations in Low and Normal K groups, compared with corresponding O treatment, and even led these two parameters to distinctly exceed the control level in Normal K group (Table 2).

3.4. Ions accumulation and distribution in *A. venetum* exposed to osmotic stress in the presence or absence of 25 mM NaCl under different K^+ supplying levels

When plants were grown under control condition, leaf and root K^+ concentrations maintained stable, and stem K^+ concentration was even obviously increased in Low K group, compared with those in Normal K group (Fig. 4a, b and c). Under osmotic stress, root K^+ concentrations in Low and Normal K group were respectively 49 and 40% lower than those under corresponding control condition, but K^+ concentration in shoots, especially in leaves, consistently maintained stable, or even

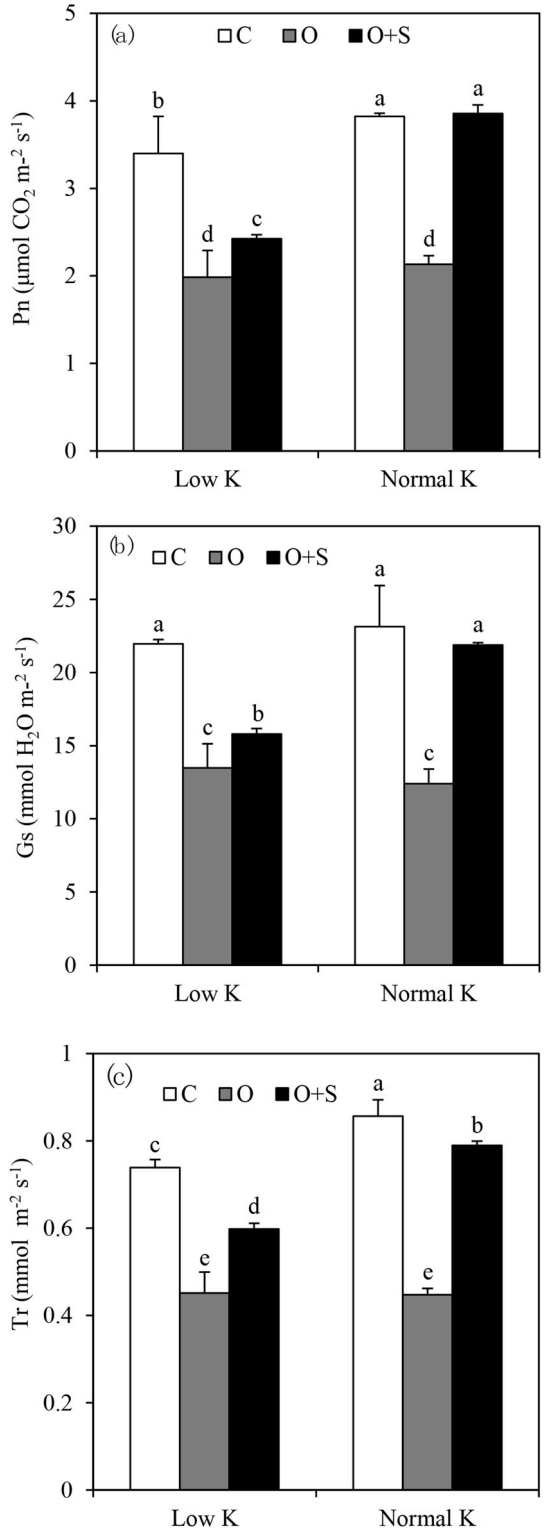

Fig. 3. Net photosynthesis rate (Pn) (a), stomatal conductance (Gs) (b) and transpiration rate (Tr) (c) in leaf of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate ($n = 6$). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

showed apparent increase (Fig. 4a, b and c), indicating that *A. venetum* could transport large amount of K^+ into shoots to maintain K^+ homeostasis under osmotic stress. Because of the additional NaCl, Na^+

Table 2
Chlorophyll concentrations in leaf of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate ($n = 6$). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

Treatments		Chlorophyll *a* (μg g^{-1} FW)	Chlorophyll *b* (μg g^{-1} FW)	Total chlorophyll (μg g^{-1} FW)
Low K	C	307.4 ± 10.9 b	201.3 ± 5.2 ab	509.6 ± 12.6 b
	O	254.6 ± 6.7 c	198.0 ± 6.5 b	452.5 ± 8.6 c
	O + S	309.3 ± 9.5 b	192.2 ± 4.1 b	501.4 ± 10.0 b
Normal K	C	288.5 ± 10.5 b	197.7 ± 3.2 b	485.8 ± 12.2 bc
	O	293.0 ± 6.5 b	215.6 ± 6.9 a	499.6 ± 15.4 b
	O + S	350.7 ± 7.7 a	199.4 ± 6.4 ab	549.9 ± 11.9 a

concentration in all tissues under O + S treatment condition were dramatically increased in both Low and Normal K groups (Fig. 4d, e and f). Unexpectedly, O + S treatment didn't affect leaf and stem K^+ concentrations, and even obviously increased root K^+ concentration by 30 and 93% in Low and Normal K group, respectively, compared with corresponding O treatment (Fig. 4a, b and c). In addition, it is also observed that K^+ concentration was constantly much higher than Na^+ under all growing conditions, resulting in extremely high K^+/Na^+ ratio in all tissues (Fig. S3). Besides, the K^+/Na^+ ratio in leaves were much higher than that in stems and roots (Fig. S3).

In both Low and Normal K groups, osmotic stress significantly reduced leaf Ca^{2+} concentration, in comparison with corresponding control; however, it's obvious that leaf Ca^{2+} concentration under O + S treatment were higher than that under corresponding O treatment (Fig. 4g). Both O and O + S treatments had no effect on stem Ca^{2+} concentrations, but significantly elevated root Ca^{2+} concentration, compared with corresponding control (Fig. 4h and i).

SA and ST values were calculated to respectively reflect the selective absorption and transport ability for K^+ over Na^+ in *A. venetum*. As shown in Table 3, when plants were grown under either control condition or O treatment, SA values in Low K group were much higher than those in Normal K group. Moreover, compared with corresponding control, osmotic stress sharply increased SA value by 68% in Low K group (Table 3). In comparison with corresponding control, O treatment significantly improved ST_1 value (selective transport for K^+ over Na^+ from root to stem) by 55% in Normal K group, and ST_2 value (selective transport for K^+ over Na^+ from stem to leaf) by 41% in Low K group (Table 3). ST_1 value under O + S treatment was significantly decreased by 25% in Normal K group, while increased by 23% in Low K group, compared with that under corresponding O treatment (Table 3). Furthermore, it's also observed that ST_1 values under all growing conditions were much higher than corresponding ST_2 values (Table 3).

3.5. Leaf osmotic potential and the contribution of K^+, Na^+ to osmotic potential of A. venetum grown in osmotic stress in the presence or absence of 25 mM NaCl under different K^+ supplying levels

Total leaf osmotic potential (Ψ_s) and the contributions of K^+ and Na^+ to Ψ_s were shown in Table 4. Leaf Ψ_s was declined consistently under O and O + S treatments in both Low and Normal K groups, in comparison with that under corresponding control condition. The contribution of K^+ to leaf Ψ_s under control condition was about 49 and 45% in Low and Normal K group, respectively, which was much higher than the contribution of Na^+ to leaf Ψ_s (Table 4). In comparison with corresponding control, osmotic stress significantly decreased the contribution of K^+ to Ψ_s in Low K group, however, its value was still over 37%. Compared with corresponding O treatment, O + S treatment dramatically increased the contribution of Na^+ to Leaf Ψ_s by 4.7 and

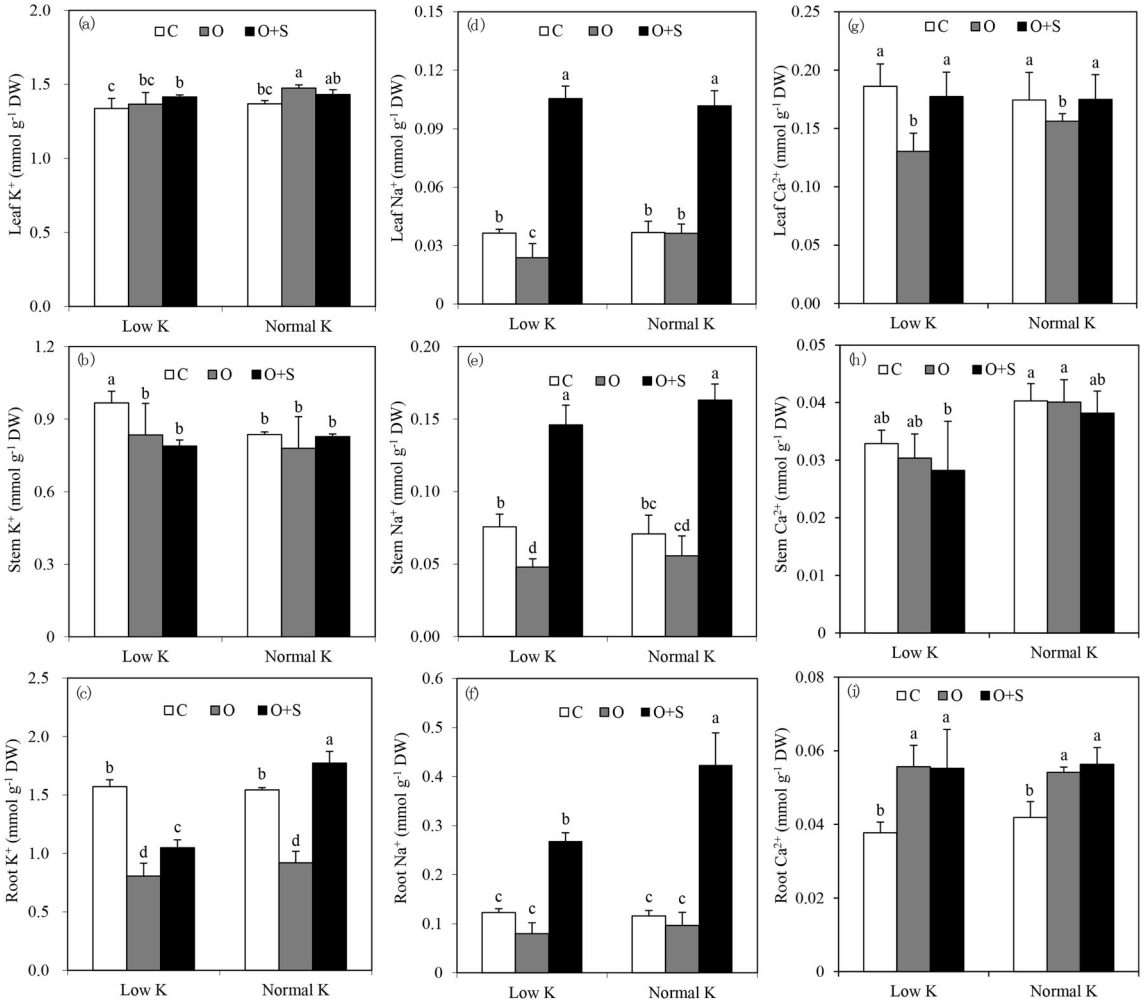

Fig. 4. K^+ (a, b, c), Na^+ (d, e, f) and Ca^{2+} (g, h, i) concentration in leaf, stem and root of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate ($n = 6$). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

Table 3
Selective absorption (SA) and selective transport (STn) capacity for K^+ over Na^+ of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate ($n = 6$). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

Treatments		SA value	ST_1 (Root to Stem) value	ST_2 (Stem to Leaf) value
Low K	C	38.47 ± 3.16 b	1.10 ± 0.05 bc	2.32 ± 0.25 b
	O	64.67 ± 1.22 a	1.27 ± 0.12 b	3.27 ± 0.13 a
	O + S	–	1.55 ± 0.06 a	2.63 ± 0.22 ab
Normal K	C	0.14 ± 0.01 a	0.98 ± 0.06 c	3.07 ± 0.36 ab
	O	0.15 ± 0.01 a	1.52 ± 0.14 a	2.84 ± 0.23 ab
	O + S	–	1.17 ± 0.03 bc	2.98 ± 0.16 ab

Table 4
Leaf osmotic potential (Ψs) and the contribution of K^+ and Na^+ to Ψs of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate ($n = 6$). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

Treatments		Leaf Ψs (MPa)	Contribution of K^+ to Ψs (%)	Contribution of Na^+ to Ψs (%)
Low K	C	−1.12 ± 0.08 a	48.51 ± 2.50 a	1.32 ± 0.06 b
	O	−1.67 ± 0.12 c	37.20 ± 3.37 d	0.53 ± 0.03 d
	O + S	−1.42 ± 0.09 b	41.18 ± 1.10 c	3.04 ± 0.18 a
Normal K	C	−1.16 ± 0.02 a	44.56 ± 2.33 b	1.17 ± 0.18 bc
	O	−1.46 ± 0.04 b	42.58 ± 1.25 bc	1.02 ± 0.12 c
	O + S	−1.39 ± 0.09 b	39.72 ± 1.34 cd	2.84 ± 0.19 a

1.8 times in Low and Normal K group, respectively (Table 4), indicating that Na^+ also actively participated in osmoregulation of *A. venetum* under osmotic stress.

3.6. K^+ uptake and utilization efficiency of A. venetum grown in osmotic stress in the presence or absence of 25 mM NaCl under different K^+ supplying levels

To assess K^+ uptake and K^+ utilization efficiency of *A. venetum*, K^+ net uptake rate (KNUR), K^+ accumulation amount (KAA) and K^+ utilization efficiency (KUE) were calculated in this study. As shown in Table 5, under control condition, KNUR, KAA and KUE in Low K group were all unaltered, compared with those in Normal K group. O and O + S treatments significantly decreased KNUR and KAA, but had no effects on KNUR in both Low and Normal K groups, compared with corresponding control (Table 5).

Table 5
K^+ net uptake rate (KNUR), K^+ accumulation amount (KAA), and K^+ utilization efficiency (KUE) of *A. venetum* seedlings exposed to control (C), osmotic stress (O) and osmotic stress together with salt (O + S) for 7 days under low or normal K^+ condition. Two plants were pooled in each replicate ($n = 6$). Values indicate the means ± SE and bars indicate SE. Columns with different lowercase letters indicate significant differences at $P < 0.05$ (Duncan's test).

Treatments		KNUR (nmol g^{-1} RFW min^{-1})	KAA (mg)	KUE (g g^{-1})
Low K	C	22.56 ± 3.97 a	7.26 ± 0.63 a	24.70 ± 0.72 a
	O	17.32 ± 2.81 b	6.21 ± 0.25 b	26.95 ± 1.70 a
	O + S	15.94 ± 1.48 b	6.75 ± 0.12 b	26.28 ± 0.32 a
Normal K	C	23.71 ± 2.97 a	7.34 ± 0.20 a	25.32 ± 0.28 a
	O	15.33 ± 1.76 b	5.69 ± 0.12 b	26.32 ± 0.68 a
	O + S	18.92 ± 4.17 b	6.81 ± 0.52 b	25.06 ± 0.18 a

4. Discussion

4.1. A. venetum is a typical K^+-efficient species that possesses prominent K^+ uptake and utilization efficiency under K^+-deficiency condition

Potassium (K^+) plays a vital role as macronutrient in plant growth and sustainable crop production (Yang et al., 2003; Pettigrew, 2008; Oosterhuis et al., 2014). K^+ availability at the interface of roots and soils is commonly low as K^+ is easily enclosed to silicates or clay particles (Britzke et al., 2012). Moreover, due to intensive cropping and increased application of nitrogen and phosphorus fertilizers, the soils are getting depleted in reserve K^+ at a faster rate and thereby, K^+ deficiency in soils is becoming a severe constraint for crop production (Yang et al., 2003; Amtmann and Armengaud, 2007). K^+-efficient plant species could grow and yield well in soils with limited K^+ availability (Baligar et al., 2001; Yang et al., 2003). Hence, exploring K^+-efficient species or crop genotypes and understanding their adaptation mechanisms to barren soils would be valuable for maintaining sustainable intensification of agriculture systems (Rengel and Damon, 2008; Abbadi, 2017). In the present study, the growth (e.g. PH, RGR, tissue biomass), leaf hydration and photosynthesis of *A. venetum* were all unaffected by low K^+ treatment (0.01 mM K^+ supplement) for 7 days (Figs. 1, Fig. 2, Fig. 3, Table 1, Table 2, Fig. S1 and Fig. S2), indicating that *A. venetum* is remarkably tolerant to low K^+ supplement and could grow well in K^+ deficient condition. By contrast, the growth of *Arabidopsis thaliana* under 0.01 mM K^+ treatment for 7 days and *Oryza sative* under K^+-free treatment for 5 days are severely inhibited (Kang et al., 2004; Ma et al., 2012b). Therefore, we propose that *A. venetum* should be considered as a K^+-efficient species.

Although the supplement of K^+ for *A. venetum* was extremely low under K^+-deficiency condition (0.01 mM K^+ supplement), both K^+ accumulation amount (KAA) in whole plant and K^+ concentration in leaves sustained at the same level as that under K^+-sufficiency condition (2.5 mM K^+ supplement; Fig. 4a, Table 5). Differently, in *O. sativa* grown under K^+-deficiency condition for only one day, tissue K^+ concentration are drastically decreased (Ma et al., 2012b). Hence, *A. venetum* possesses a strong ability to acquire K^+ from low K^+ available surroundings. K^+ uptake efficiency is crucial for K^+-efficient species/genotypes to acquire higher K^+ from soils with low K^+ availability (Zhang et al., 1999; George et al., 2002), which is a complex trait determined by mechanisms relying on root architecture, the capacity to mobilize non-exchangeable K^+ by root exudates and the uptake capacity at the root surface (Rengel and Damon, 2008). Previous research has demonstrated that the K^+ uptake efficiency in K^+-efficient tomato genotypes (*Lycopersicon esculentum*) is mainly due to high K^+ net uptake by roots (Chen and Gabelman, 2000). Similarly, in the present study, K^+ net uptake rate (KNUR) maintained unaffected under K^+-deficiency condition (Table 5). Plants can maintain constant concentrations of nutrients in tissues, despite the concentrations of nutrients in soils are dynamically varied (Wang and Wu, 2010). It is recognized that high-affinity K^+ uptake system at root plasma membrane including some inward-rectifying K^+ channels and high-affinity K^+ transporters governs the K^+ uptake from low K^+ (less than 1 mM) available soils (Hirsch et al., 1998; Gierth et al., 2005; Britto and Kronzucker, 2006; Wang and Wu, 2010). Therefore, *A. venetum* should have evolved superior ability to largely absorb K^+ from barren soils in arid and semi-arid areas via high-affinity K^+ uptake system.

K^+ utilization efficiency (KUE, higher dry matter production per unit of K^+ taken up) is another advancing trait of K^+-efficient species/genotypes (Zhang et al., 1999; Yang et al., 2003; Damon et al., 2007; Tang et al., 2015b). As K^+ is a highly mobile solute in plants, the capacity to translocate K^+ between tissues predominately affects the efficient utilization of K^+ in plants (Rengel and Damon, 2008). Our results showed that K^+ concentration in shoots especially in leaves of *A. venetum* under normal K^+ supplying condition was much higher than that in roots (Fig. 4a, b and c), which is highly consistent with previous viewpoint that K^+-efficient species are inclined to translocate more K^+ absorbed by roots into shoots or functional leaves (George et al., 2002; Xia et al., 2013). It's also observed that leaf K^+ concentration (1.4 mmol/g DW) under K^+-deficiency condition sustained at the same level as that under K^+-deficiency condition, and was much higher than that (less than 0.8 mmol/g DW) in the K^+-rich species *Alternanthera philoxeroides* grown under K^+-deficiency condition (Song and Su, 2013); moreover, stem K^+ concentration was even significantly increased under K^+-deficiency condition, compared with that under K^+-sufficiency condition (Fig. 4a and b). These results indicate that *A. venetum* could transport the majority of K^+ into shoots under low K^+ supplying conditions. Therefore, we further investigated K^+ utilization efficiency (KUE) of *A. venetum*, which reflects relative ability to produce dry matter per unit of K^+ accumulated in shoots, and the results showed that K^+-deficiency in medium had no influence on KUE (Table 5), suggesting that *A. venetum* possesses a prominent capacity to efficiently utilize the K^+ accumulated in shoots to produce higher biomass under low K^+ available conditions. Taken together, these findings provide supporting evidences for the facticity that *A. venetum* is a typical K^+-efficient species with prominent K^+ uptake efficiency and K^+ utilization efficiency.

4.2. K^+ acts as the uppermost osmolyte playing a crucial role in osmotic adjustment for drought resistance in A. venetum

Osmotic adjustment (OA) allows the plant cells to decrease osmotic potential (Ψs) and as a consequence, generates high gradient for water influx and turgor maintenance (Farooq et al., 2009). In this study, leaf Ψs was substantially declined when *A. venetum* was exposed to osmotic stress (Table 4), suggesting that *A. venetum* possesses a strong OA capacity for water acquisition under drought conditions. Similar results were earlier reported in many plant species, such as *Beta vulgaris* (Chołuj et al., 2008; Wu et al., 2014), *Vitis vinifera* (Patakas and Nortsakis, 1999), *Gossypium hirsutum* (Oosterhuis and Wullschleger, 1987) and *Manihot esculenta* (Alves and Setter, 2004). It is well known that OA capacity is determined by the amount of solutes stored in plant cells, and inorganic ions especially K^+ act as efficient osmoticum for most plant species (Wright et al., 1997; Martínez et al., 2004; Shabala and Shabala, 2011; Anschütz et al., 2014). In the present study, K^+ concentration in all tissues of *A. venetum* was consistently much higher than Na^+ and Ca^{2+}; moreover, K^+ concentration in leaves was obviously higher than that in roots and stems under osmotic stress, regardless of whether the supply of K^+ was sufficient or not (Fig. 4), indicating that *A. venetum* could accumulate large amount of K^+ in leaves under drought conditions. Furthermore, it is noteworthy that leaf hydration (e.g. RWC and WUEi) in *A. venetum* exposed to osmotic stress was significantly suppressed in Low K group, while was unaltered in Normal K group (Table 1), indicating that water status of *A. venetum* was seriously deteriorated by osmotic stress when the K^+ supplement

was deficient. These results suggest that K^+ may play a crucial role in OA of *A. venetum* under drought environments. Indeed, when *A. venetum* was exposed to osmotic stress, the contribution of K^+ to leaf Ψs was up to 42% under normal K^+ supplying condition (Table 4), which is 3 times higher than that in salt-accumulating xerophyte *Z. xanthoxylum* subjected to drought stress (Ma et al., 2012a); moreover, this parameter was obviously declined as the K^+-deficiency in medium (Table 4), that is why leaf hydration in *A. venetum* exposed to osmotic stress was significantly lower under low K^+ supplying condition than that under normal K^+ supplying condition (Table 1); in addition, the minimum contribution of K^+ to leaf Ψs still exceeded 37% among all conditions (Table 4), which is much higher than the maximal contribution of K^+ to leaf Ψs (28%) in wheat genotypes grown under K^+-deficiency together with drought stress (Damon et al., 2011). The above mentioned results strongly demonstrate that K^+ is the uppermost osmoticum for *A. venetum* under drought conditions.

Water scarcity interferes nutrient uptake and transport mechanisms, as well as suppresses transpiration flow of plants and thereby, generally inhibits the absorption and translocation of inorganic nutrients in plants (Garg, 2003; McWilliams, 2003). It has been proven that, for most glycophytes with lower tolerance to environmental stresses such as citrus, cotton and sugar beet, K^+ absorption is severely hampered under drought stress resulting in decreased tissue K^+ concentrations (Syvertsen et al., 1988; McWilliams, 2003; Farooq et al., 2009; Wu et al. 2014, 2015). In the present study, KNUR was declined under osmotic stress, leading to lower KAA in *A. venetum* (Table 5). However, it's obvious that although root K^+ concentration was substantially decreased under osmotic stress alone, leaf K^+ concentration constantly maintained stable or even showed apparent increase, regardless of whether the K^+ supply was sufficient or not (Fig. 4a and c). These results suggest that K^+ acquisition is inhibited under drought stress, but *A. venetum* could transport abundant K^+ from roots into leaves, and consequently, assure higher K^+ accumulated in leaves using for OA. Our results also showed that leaf Na^+ concentration under osmotic stress in the presence of NaCl was drastically increased (Fig. 4d), however, the value of leaf K^+/Na^+ ratio was still exceeding 10 (Fig. S3a), leaf K^+ concentration and the contribution of K^+ to leaf Ψs constantly maintained stable, compared with those under osmotic stress alone, regardless of whether the K^+ supply was sufficient or not (Fig. 4a and Table 4). Moreover, in Low K group, although Na^+ supply for *A. venetum* under osmotic stress in the presence of NaCl was 2500 times higher than K^+, ST_2 value was unaffected and ST_1 value even significantly increased, compared with those in *A. venetum* under osmotic stress alone (Table 3), suggesting that, when supplied with excessive Na^+ but deficient K^+ under drought stress, *A. venetum* could selectively transport more K^+ over Na^+ from roots into leaves. These results sufficiently prove that accumulating abundant K^+ in leaves and then directly using K^+ in OA to maintain water status are principal adaptive mechanisms of *A. venetum* to cope with barren (especially K^+ deficiency) and saline soil in arid and semi-arid regions.

4.3. Moderate NaCl alleviates deleterious impacts of osmotic stress on A. venetum by improving osmotic adjustment ability and photosynthetic capacity

It has been proven that certain concentrations of NaCl could mitigate detrimental impacts of drought stress on the growth of some halophytes or xerophytes by improving water status, and then favorable water status will increase turgor pressure of plant cells, which further contributes to stimulating stomata opening and enhancing transpiration under drought stress (Heidecker et al., 2003; Zhu, 2003; Franks, 2006; Franks and Farquhar, 2007; Ma et al., 2012a; Wu et al., 2014). Our results also showed that leaf hydration in *A. venetum* under osmotic stress was significantly improved when 25 mM NaCl was further added in Low K group; meanwhile, optimal leaf RWC and WUEi was observed in *A. venetum* under osmotic stress together with 25 mM NaCl in Normal K group (Table 1). Correspondingly, the presence of NaCl substantial enhanced Pn, Gs and Tr in *A. venetum* under osmotic stress, regardless of whether the K^+ supply was sufficient or not (Fig. 3). These results suggest that moderate NaCl could improve water status of *A. venetum* under osmotic stress and, concomitantly, substantially enhance photosynthetic capacity, and as a consequence, improves the growth of *A. venetum* under osmotic stress. Increasing researches have demonstrated that the sequestration of Na^+ into vacuole is an effective mechanism of some plant species to enhance OA under saline or drought conditions (Wang et al., 2001; Zhu, 2001; Slama et al., 2007; Farooq et al., 2009; Ma et al., 2012a; Yue et al., 2012). In the present study, the addition of 25 mM NaCl dramatically elevated leaf Na^+ concentration in *A. venetum* under osmotic stress, regardless of whether the K^+ supply was sufficient or not (Fig. 4d), and correspondingly, the contribution of Na^+ to leaf Ψs under osmotic stress in the presence of NaCl was much higher than that under osmotic stress alone (Table 4), which indicate *A. venetum* could also absorb large amount of Na^+ to enhance OA under drought stress. Stomatal movement and transpiration are closely related to keeping leaf water status and improving biomass through providing transpiration stream for water transport from roots into shoots and acquiring more CO_2 for carbon assimilation (Giorio et al., 1999; Oosterhuis et al., 2014; Hedrich and Shabala, 2018). Thus the enhancement on water status by NaCl would in turn improve the long-distance transport of water and photosynthetic capacity, which could further enhance the growth of *A. venetum* under drought stress. Taken together, accumulating large amount of Na^+ in leaves to promote osmotic adjustment ability and photosynthetic capacity should be a vital strategy in drought resistance in *A. venetum*.

According to Brownell and Bielig (1996) and Subbarao et al. (1999), Na^+ is involved in chlorophyll biosynthesis by activating key enzymes and participating in proliferation of chloroplasts in plants. Our results showed that chl *a* and total chl concentrations in *A. venetum* subjected to osmotic stress were significantly increased as the addition of NaCl. Meanwhile, when *A. venetum* was exposed to osmotic stress alone, chlorophyll concentrations under low K^+ supplying condition were much lower than those under normal K^+ supplying condition (Table 2), which was highly consistent with the variation trend of corresponding Na^+ concentration in leaves (Fig. 4d). These results suggest that Na^+ could also enhance chlorophyll biosynthesis in *A. venetum* under osmotic stress, and consequently, contributes to the improvement of drought resistance of *A. venetum*.

Additionally, compared with osmotic stress alone, the presence of NaCl under osmotic stress also significantly increased leaf Ca^{2+} concentration in *A. venetum* (Fig. 4g). It has been reported that exogenous Ca^{2+} could promote the chlorophyll concentration and photosynthetic rate by improving chlorophyllase degradation in *Cyclocarya paliurus* (Yao et al., 2012). Moreover, Wei et al. (2015) proposed that Ca^{2+} could improve the utilization of light energy of PSII reaction center. Hence, NaCl induced the increase of Ca^{2+} in leaves could also be a meritorious action for the promotion of photosynthetic performance of *A. venetum* to cope with drought stress.

5. Conclusions

In conclusion, our results demonstrate that *A. venetum* is a typical K^+-efficient species that could grow well in low K^+ availability soils due to its prominent K^+-uptake and -utilization efficiency. Furthermore, absorbing large amount of Na^+ and maintaining stable K^+ absorption, and then simultaneously accumulating substantial Na^+ and K^+ in leaves for osmotic adjustment to improve leaf hydration and photosynthesis is a vital strategy for *A. venetum* to cope with drought environments. These findings provide further understanding on physiological mechanisms of desert plants to adapt to harsh environments.

CRediT authorship contribution statement

Yan-Nong Cui: Data curation, Formal analysis, Writing – original draft. **Zeng-Run Xia:** Data curation, Methodology, Writing – original draft. **Qing Ma:** Writing – review & editing. **Wen-Ying Wang:** Data curation. **Wei-Wei Chai:** Data curation. **Suo-Min Wang:** Supervision, Writing – review & editing.

Acknowledgements

This work was financially supported by the National Natural Science Foundation of China (Grant No. 31730093 and 31470503).

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.plaphy.2018.11.011.

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