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Contrasting water sources and water use efficiency in coexisting desert plants in two saline-sodic soils in northwestern China

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Running Head: Variation in the stable isotope composition of desert plants in two saline-sodic soils

Abstract:

- Soil degradation resulting from various types of salinity is a major environmental problem, especially in arid and semiarid regions. Exploring the water-related physiological traits of halophytes is useful for understanding the mechanisms of salt tolerance. This knowledge may be used to rehabilitate degraded arid lands.
- To investigate whether different types of salinity influence the water sources and water use efficiency of desert plants (*Karelinia caspia*, *Tamarix hohenackeri*, *Nitraria sibirica*, *Phragmites australis*, *Alhagi sparsifolia*, *Suaeda microphylla*, and *Kalidium foliatum*) in natural environments, we measured leaf gas exchange, leaf carbon and xylem oxygen isotope composition and soil oxygen isotope composition at neutral saline-sodic site (NSS) and alkaline saline-sodic site (ASS) in northwestern China.
- The studied plants had different xylem water oxygen isotope compositions ($\delta^{18}O$) and foliar carbon isotope compositions ($\delta^{13}C$), indicating that desert plants coexist through differentiation in water use patterns. Compared to that at the NSS site, the stem water in *K. caspia*, *A. sparsifolia* and *S. microphylla* was depleted in ^{18}O at the ASS site, which indicates that plants can switch to obtain water from deeper soil layers when suffering

environmental stress from both salinity and alkalinization. *A. sparsifolia* had higher $\delta^{13}C$ at the ASS site than at the NSS site, while *K. caspia* and *S. microphylla* had lower $\delta^{13}C$, which may have resulted from interspecific differences in plant alkali and salt tolerance ability.

- Our results suggest that under severe salinity and alkalinity, plants may exploit deeper soil water to avoid ion toxicity resulting from high concentrations of soluble salts in the superficial soil layer. In managed lands, it is vital to select and cultivate different salt-tolerant or alkali-tolerant plant species in light of the local conditions.

Key words: Saline-sodic, Stable isotopes, Water source, Water-use efficiency, Photosynthesis

Introduction

Salinity problems have drawn increasing attention in arid and semiarid regions, where the soil water availability is low, evaporation is high, and precipitation is deficient in terms of salt leaching (Biswas and Biswas, 2014; Cui et al., 2011; Kuznetsov and Shevyakova, 2010). Globally, More than 800 million ha of land are affected by salt, which accounts for more than 6% of the world's total land area (Munns and Tester, 2008). On the basis of their differences in pH value, electrical conductivity (EC) and sodium adsorption ratio (SAR), salt-affected soils can generally be divided into nine categories: saline, acidic-saline, alkaline-saline, saline-sodic, acidic saline-sodic, alkaline saline-sodic, sodic, acidic-sodic and alkaline-sodic soils (Rengasamy, 2010). These salt-affected soils have unique physical and chemical properties that have different effects on plants (Rengasamy, 2010), causing plant water

sources and water use efficiency (WUE) to differ among them. A better understanding of the physiological responses of halophytes to various types of salt-affected soils would facilitate the protection and management of arid and semiarid ecosystems.

Plants take up water that originates from different sources, i.e., soil water from varying depths, precipitation and groundwater, etc. Even some species shift soil depth of water uptake in response to changing environmental conditions. Moreover, differences in root distribution may contribute to the coexistence of various plant growth forms (Cui et al., 2017; Tiemuerbieke et al., 2018). For example, grasses rely on shallow soil water, and trees extract water from deeper regions of the soil profile, while herbs take up water from intermediate soil depths (Rossatto et al., 2013). Compared to neutral saline stress, which generally involves osmotic stress and ion injury (Munns, 2002), alkaline saline stress involves the additional influence of high pH. The high-pH environment that surrounds plant roots can directly inhibit the absorption of mineral elements (such as Ca^{2+} and Mg^{2+}) and disrupt the ion homeostasis of plant cells (Yang et al., 2007). Alkaline saline soils also have unique structural problems, such as surface crusting and hardening (Qadir et al., 2007). These problems can affect water movement, the holding capacity of plant-available water, and root penetration, which will subsequently influence plant water use (Oster and Jayawardane, 1998). Plants can modify their root distribution to acquire available resources and endure environmental stress (Xu et al., 2007; Zhou et al., 2015). Thus, plants may shift to use deeper soil water under increased salinity and alkaline stress in arid and semiarid environments.

High WUE is one of the most important physiological mechanisms conferring salinity tolerance in halophytes (Alla et al., 2011). An increase in WUE could be achieved via reduced stomatal conductance, which leads to a lower CO_2 assimilation rate and slower growth rate but an increase in the ratio of carbon fixed per unit of water transpired. Stable carbon isotope composition ($\delta^{13}C$) is routinely measured to assess plant WUE in C_3 plants (Farquhar et al., 1989; Farquhar et al., 1982), and previous studies have shown that $\delta^{13}C$ values are positively correlated with salinity (Brugnoli and Lauteri, 1991; Glenn et al., 2012; Yousfi et al., 2012) and alkalinity (Lu et al., 2018; Xu et al., 2013). The toxic effects of alkaline stress on some halophytes are more severe than those of salt stress (Yang et al., 2007); therefore, plants in alkaline saline-sodic soils are likely to have a higher WUE than plants in neutral saline-sodic soils. To date, few studies have been conducted on the water sources and WUE of desert plants in different saline-sodic soils (neutral vs alkaline saline-sodic), especially under field conditions.

We aimed to investigate the water sources and WUE of desert plants during the dry season in different saline-sodic soils in NW China. Two saline-sodic soils were selected: neutral saline-sodic (NSS, EC>4, SAR>6, 6<pH<8) and alkaline saline-sodic (ASS, EC>4, SAR>6, pH>8) soil (Rengasamy, 2010). We measured the xylem $\delta^{18}O$ (to study plant water sources), leaf $\delta^{13}C$ (to study plant WUE), and shoot water potentials and leaf gas exchange (to study plant physiological features) of the dominant species. Because of the differences in alkalinity between the studied soils and the ability of plants to modify their water use strategies to cope with environmental stress, we hypothesized that (1) compared to those at the NSS site, plants at the ASS site will adjust their root systems to decrease water uptake

from shallow soil and utilize deeper soil water and (2) plants at the ASS site will have higher WUE than those at the NSS site in response to the higher salinity and alkalinity.

Materials and methods

Study area

The study sites were located in the lower reaches of the Manas River in Shihezi City (44°18'18"N, 86°1'56"E), Xinjiang Uyghur Autonomous Region, northwest China. The study area has a typical continental arid climate. The mean annual temperature ranged from 6 to 8°C in 1949-2001, while the annual rainfall ranged from 110 to 200 mm during the same years. The potential evapotranspiration is 1600-2000 mm (Cheng et al., 2005). The soils are sierozems (Wang et al., 2016), and salt crusts occur on the soil surface. The vegetation is poor and sparse. The dominant species are *Karelinia caspia*, *Suaeda microphylla*, and *Alhagi sparsifolia*, and shrubs (*Nitraria sibirica* and *Tamarix hohenackeri*) are rare. Two saline sites differing in their degree of alkalinity (ASS: alkaline saline-sodic soil; NSS: neutral saline-sodic soil) were selected for the study. Detailed site information, including locations, elevations, and dominant species and life forms, is provided in Table 1.

Leaf gas exchange measurements

Leaf gas exchange measurements were conducted using a LI-6400 portable photosynthesis system (LI-6400, LI-COR Biosciences, Lincoln, Nebraska, USA) at 0900, 1200, 1500, 1800 and 2100 h (Beijing time) on *N. sibirica*, *T. hohenackeri*, *K. caspia*, *S. microphylla*, *A. sparsifolia* and *Kalidium foliatum* at the ASS site (July 23, 2009) and *K.*

caspia, *S. microphylla*, *A. sparsifolia* and *Phragmites australis* at the NSS site (July 24, 2009). Five individuals of each studied plant species were randomly selected for repeated measurements. Leaf gas exchange was conducted 5 times for each plant in the two studied sites. However, we only used the measurements at 12:00 o' clock to represent daily maximum leaf carbon assimilation. Young, fully expanded leaves from near the top of the canopy in fully illuminated locations were measured for CO_2 and H_2O exchanges. For each measurement, the environmental conditions inside the leaf chamber (i.e., photosynthetically active radiation, chamber block temperature, relative humidity, and CO_2 concentration) were set to match the ambient conditions. The leaf area was determined by scanning the leaves enclosed in the gas exchange chamber using a scanner.

Leaf water potential measurements

The predawn leaf water potential (Ψ_{pd}) and midday leaf water potential (Ψ_{md}) were measured with an HR-33T Dew Point Microvoltmeter (Wescor, Logan, UT, USA) at 0600 h and 1500 h (Beijing time), respectively. For each species, the Ψ_{pd} and Ψ_{md} measurements were repeated three times.

Soil and plant sampling

Soils at 0-5, 5-10, 10-20, 20-40, 40-60, 60-80 and 80-100 cm depth were collected from five randomly selected locations at each sampling site. Five soil cores were collected at each location and mixed together to form a single soil sample. We separated the soils from each depth into three parts, which were used for measurements of the soil water content (SWC),

the pH, EC, and ion content and the isotopic composition, respectively. For the determination of the SWC, the fresh soils were stored in an aluminum box and oven dried to a constant weight. The SWC was then calculated as the difference in weight between the fresh and dry soil samples. The soil used for the measurements of pH, EC and ion content were sieved and air dried, while those used for the hydrogen and oxygen isotope analyses were stored in a 12 mL vial. The vials were sealed with parafilm to prevent water loss and kept in a cooler on ice. The soil samples for the isotope analysis were collected during the morning period and stored in a -20°C freezer before water extraction.

Plant stems were collected during the morning period and stored in 12 mL vials. The vials were sealed with parafilm and stored in the cooler on ice. These plant stem samples were stored in a -20°C freezer before water extraction.

Leaves were also sampled and dried at 65°C for 48 h using an oven. The oven-dried leaves were powdered and stored in plastic vials to measure the carbon stable isotope composition.

Measurements of soil pH, EC and exchangeable ion content

The air-dried soils were suspended in deionized water (soil:water = 1:5). The pH and EC were determined with a pH meter (PHS-3C, LeiCi Co. Ltd., Shanghai, China) and a conductivity meter (DDS-307, LeiCi Co. Ltd., Shanghai, China), respectively.

HCO_3^- and CO_3^{2-} were determined using titration with hydrochloric acid, Cl^- was determined with $AgNO_3$ titration, SO_4^{2-} was indirectly determined with titration with EDTA, and Ca^{2+} and Mg^{2+} were determined by EDTA complexing titration. The Na^+ and K^+ contents

were measured with flame spectrometry using a flame photometer (FP640, Shanghai Precision Science Instrument Co., Ltd., China). Finally, the SAR was calculated with equation (1) (Qadir et al., 2007).

$$SAR = [Na^{+}] / ([Ca^{2+}+Mg^{2+}]/2)^{1/2} \quad (1)$$

where the concentrations of Na^{+}, Ca^{2+} and Mg^{2+} are expressed in $mmol \cdot L^{-1}$.

Water extraction and isotope analysis

The water in the soils and stems was extracted cryogenically in the Stable Isotope Laboratory at the Chinese Academy of Forestry. The hydrogen and oxygen isotope compositions were then determined with a liquid water isotope analyzer (LWIA, DLT-100, Los Gatos Research Inc., Mountain View, CA, USA). The repeated measurements with laboratory working standards had a precision of <1.5‰ and <0.2‰ for δD and δ^{18}O, respectively. The hydrogen and oxygen isotope ratios are reported in parts per thousand relative to standard mean ocean water (SMOW) as δD or δ^{18}O (‰) = ($R_{sample}/R_{standard}$-1).

Stable hydrogen and oxygen isotope compositions of plant xylem water are often used to quantify the contributions of different water sources (Dawson et al., 2002). However, care should be taken when using deuterium to determine the water sources of halophytes and xerophytes because of the potential occurrence of hydrogen isotope fractionation during water uptake (Ellsworth and Williams, 2007). Thus, we only use xylem δ^{18}O data to estimate the plant water sources in this study.

Plant stable carbon ($^{13}C/^{12}C$) isotope ratios were measured using an isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany). The carbon isotope ratios are reported in parts per thousand relative to the Pee Dee Belemnite (PDB) standard. $\delta^{13}C$ (‰) is expressed as $R_{sample}/R_{standard}$-1.

Statistical analysis

Differences in the isotopic parameters among sites and species were tested with one-way analysis of variance (ANOVA) using SPSS version 16.0. Mixed-effect analysis of variance was conducted to test the main effects of salinity type and soil depth and their interactions on the two studied soil parameters. The relationships among soil water hydrogen and oxygen isotope composition and SWC, EC, pH, and Na^+ and Cl^- content in the 0-100 cm soils were assessed using Pearson correlation analysis. Figures were drawn with Origin (version 8.5). Average values are reported as the arithmetic mean ± 1 standard error.

Results

Sodium adsorption ratio, pH, EC, and ion content

At the NSS site, the SAR showed a decreasing trend from the shallow to deeper soil layers (Fig. 1a), but the differences among the soil layers were not significant (Table 2). No systematic pattern of variation was detected in terms of the SAR at the ASS site (Fig. 1a, Table 2), but there were significant site differences in the SAR, with lower SAR values at the NSS site than those at the ASS site (Table 2). There were no significant differences in pH

among depths at either study site. However, the pH values at the NSS site were lower than those at the ASS site (Fig. 1b, Table 2). The EC values also showed a decreasing trend from the shallower to deeper soil depths at both sites. The ASS site had higher EC values than those at the NSS site (Fig. 1c, Table 2).

The HCO_3^- content was close to zero at both sites (Fig. 2a), and there were no significant differences in the HCO_3^- content between the two sites or among the soil layers at each site (Fig. 2b, Table 2). The Cl^- content decreased from the upper to the deeper soil layers at both study sites, and the Cl^- content was greater at the ASS site than at the NSS site (Fig. 2c, Table 2). In contrast, the SO_4^{2-} content showed no variation with soil depth, but the soil at the NSS site had a relatively lower SO_4^{2-} content than that at the ASS site (Fig. 2d, Table 2). There were significant differences between study sites and among soil depths in terms of the concentrations of Mg^{2+}, Na^+ and K^+, while there were no differences in Ca^{2+} content between the two study sites or among the different soil depths at each site (Fig. 2f). The Na^+ and Mg^{2+} contents at the ASS site were greater than those at the NSS site (Fig. 2eg, Table 2). In contrast, the soil at the ASS site had a lower K^+ content compared to that at the NSS site (Fig. 2h, Table 2).

Soil water content and soil water isotope composition

The SWC differed among the soil layers at both sites, increasing from approximately 12% in the 0-5 cm soil layer to over 25% in the 80-100 cm soil layer. However, no significant study site differences in SWC were detected (Fig. 3a, Table 2).

At both sites, the soil water isotopic composition of hydrogen (δ^2H) and oxygen (δ^{18}O) showed a clear decreasing trend along the soil profile (Fig. 3b & c, Table 2). Compared to that at the NSS site, the soil water at the ASS site was higher in ^{2}H and ^{18}O by 9.0‰ and 3.3‰, respectively.

Inferred depth of plant water uptake and xylem water isotope composition

Overlapping δ^{18}O values for plant water and soil water were observed at the NSS site but not at the ASS site (Fig. 4). At the NSS site, *K. caspia* and *P. australis* extracted water from the 60-80 cm soil layer, while *A. sparsifolia* utilized water from relatively shallow soil depths (40-60 cm). The depth of water uptake for *S. microphylla* reached 100 cm (Fig. 4a). At the ASS site, the δ^{18}O values for all plant species were more negative than those of the soil water in the soil layers from 0 to 100 cm, which suggests that all plants mainly utilized the soil water at depths greater than 100 cm (Fig. 4b).

The mean xylem δ^{18}O values differed among the plant species and between the two study sites (Fig. 5). At the NSS site, *A. sparsifolia* had significantly higher δ^{18}O values than *K. caspia*, *S. microphylla* and *P. australis*. At the ASS site, *A. sparsifolia* had the highest δ^{18}O value, and *T. hohenackeri* had the lowest δ^{18}O value. The xylem water of *K. caspia*, *S. microphylla* and *A. sparsifolia* at the NSS site was higher in ^{18}O by 2.10‰, 1.88‰ and 3.43‰, respectively, compared to that at the ASS site.

Water potentials

Water potentials displayed significant intraspecific and interspecific variation (Fig. 6). The predawn water potential of *K. caspia* was higher than that of *S. microphylla* and *A. sparsifolia* at both sites, while the midday water potential of *A. sparsifolia* was lower than that of *K. caspia* and *S. microphylla* at the two sites. The water potentials of *K. caspia*, *S. microphylla* and *A. sparsifolia* were higher at the NSS site than at the ASS site, except for the predawn water potential of *K. caspia*, suggesting that the water status of common plants at the NSS site was better than that at the ASS site.

Foliar carbon isotope composition

Significant interspecific differences in leaf carbon isotope composition ($\delta^{13}C$) were detected at the two saline-sodic sites (Fig. 7). At the ASS site, *S. microphylla* had the highest $\delta^{13}C$ value, while *K. caspia* had the lowest $\delta^{13}C$ value. At the NSS site, the plants significantly differed in their $\delta^{13}C$ values in the order of *S. microphylla* > *P. australis* > *K. caspia* > *A. sparsifolia*. Common species also displayed site differences in terms of their $\delta^{13}C$ values (Fig. 7). The foliar carbon isotope compositions of *K. caspia* and *S. microphylla* were 4.25‰ and 0.80‰ greater in ^{13}C at the NSS site than at the ASS site, respectively. However, *A. sparsifolia* was 1.48‰ more depleted in foliar ^{13}C content at the NSS site than at the ASS site.

Discussion

Xylem $\delta^{18}O$: environmental and genetic differences

$\delta^{18}O$ values for plant water and soil water overlapped at some depth range though the isotopic gradients for soils at the NSS site were severely depleted with soil depth, which inferred that all plants in the NSS site mainly utilized water from relatively shallow soil depths (0-100 cm). For the ASS site, although xylem $\delta^{18}O$ values did not overlap with ^{18}O signature of soil water from 0 to 100 cm, xylem water ^{18}O signatures are likely overlap with soil water values below 1 m according to the trend of the soil water ^{18}O signatures. Therefore, we can inferred that plants in the ASS site rely more on deep soil water (below 1 m) but less on shallow soil water compared to the NSS site. Our findings show that despite slight site differences in plant xylem $\delta^{18}O$, three species commonly found in our study area *(K. caspia*, *A. sparsifolia*, and *S. microphylla*) mainly utilize deeper soil water at the ASS site (higher salinity and alkalinity) than at the NSS site. This supports our hypothesis that plants can adjust their root systems to decrease the uptake of water from shallow soil and utilize deeper soil water under higher salinity and alkalinity. This is similar to studies conducted in the Everglades ecotone and coastal ecosystems, woody plants undergo spatial partitioning and temporal shifts in water uptake patterns to avoid the uptake of salt (Ewe and Sternberg, 2002; Ewe et al., 1999; Ewe et al., 2007). In the present study, soil Na^+, Cl^- and EC declined with depth (Fig. 1-2), we can see that soil salinity decreased with soil depth. The accumulation of salt in the soil can change the soil texture, subsequently decreasing the soil porosity and consequently reducing soil aeration and water conductance. In addition, high soil salinity and alkalinity cause the creation of a low water potential zone in the soil, making it increasingly

difficult for plants to acquire both water and nutrients (Mahajan and Tuteja, 2005; Yang et al., 2007). Therefore, plants switch to obtain water from deeper soil layers when suffering environmental stress from both salinity and alkalinization. Furthermore, in arid ecosystems, *A. sparsifolia* utilizes deeper soil water in saline soil compared to sandy soil (Cui et al., 2017). Plants under drought stress can also alter their root systems to maintain function and growth. For example, *Reaumuria songarica* and *Nitraria tangutorum* can shift to exploit deeper soil water when they experience drought stress in the upper soil layers (Wu et al., 2014). In addition, some species in semiarid environments can use water from hydraulic lift caused by other species to tolerate salinity (Armas et al., 2010). The capacity of plants to shift to the use of deeper water supplies varies among species due to differences in rooting functions and their degree of ecological plasticity (Asbjornsen et al., 2008). A previous study showed that *A. sparsifolia*, a phreatophyte species, has evolved deep roots and is exclusively dependent on groundwater in desert environments (Thomas et al., 2008). In this study, *A. sparsifolia* indeed showed higher plasticity in its water use pattern to cope with soil salinity and alkalinity than *K. caspia* and *S. microphylla* (Fig. 4).

The xylem ^{18}O signature differed among the studied plants in the ASS site, which imply potential interspecific differences in water sources. Variation in water uptake depths can lead to niche differentiation and complementary use of resources and, in turn, promote species coexistence and ecosystem function (Asbjornsen et al., 2008). It worthy to note that the differences in xylem ^{18}O signature among the shrubs were not as large as variation in soil water ^{18}O signature, which may reduce the confidence of our inference. However, the fluctuation of deep soil water ^{18}O signature is small because of low soil evaporation.

Therefore, although the variation in plant xylem water signatures is actually quite small, the water sources may differ among the studied plants. The shrubs (*N. sibirica* and *T. hohenackeri*) mainly utilized deep soil water at the ASS site. It has been reported that *N. sibirica* depends on soil water in the upper soil layers during spring and shifts to deep soil water in summer due to the existence of dual root systems: shallow lateral roots and deeply penetrating tap roots (Zhou et al., 2015). This result is similar to our observation, *N. sibirica* mainly used deep soil water in summer. *Tamarix* is a facultative phreatophyte whose roots are mainly distributed in deep soil layers and relies on groundwater (Tiemuerbieke et al., 2018; Xu and Li, 2006). In contrast, the herbaceous perennials (*K. caspia* and *P. australis*) and semishrubs (*A. sparsifolia* and *S. microphylla*) mainly extracted shallow soil water at the NSS site. The major soil layer from which *K. caspia* extracts water is the 50-100 cm layer in desert riparian forests (Chen et al., 2014), which is similar to our results from the NSS site. Interestingly, but strangely, we found that *K. foliatum* mainly used deeper water (below 100 cm). However, this result was in disagreement with its root distribution pattern (taproots penetrate to 70-80 cm deep) (Gao et al., 2010). We speculate that *K. foliatum* may utilize dew water, although this was not verified in our study. Indeed, there is some evidence that Mediterranean plants can take up dew water from the upper 0-2 cm soil layer (Filella and Peñuelas, 2003), and dewfall accounts for approximately 50% of the water uptake of some desert plants (Hill et al., 2015).

Leaf $\delta^{13}C$ and WUE in different saline environments

The leaf carbon isotope composition ($\delta^{13}C$) depends on environmental conditions and species-specific traits. In the present study, the two saline-sodic sites were not very far apart in distance and thus had similar climatic conditions. In addition, the SWC did not significantly differ at the two studied sites. Therefore, the foliar carbon isotope composition was mostly affected by the soil salinity and alkalinity (Table 2, S1).

Leaf $\delta^{13}C$ provides information on WUE integrated over extended periods (Farquhar et al., 1989) and has been extensively used in the study of plant carbon-water relationships (Filella and Peñuelas, 2003). In addition, the global mean $\delta^{13}C$ values for C_4 plants and C_3 plants are -14‰ and -28‰, respectively (O'Leary, 1988). In our study, the average $\delta^{13}C$ value of the C_3 species was -26.19‰, while that of the C_4 species was -13.53‰, which suggests that plants in the Shihezi area have a high WUE.

Intraspecific differences in $\delta^{13}C$ values between the two saline soils were also detected, with *A. sparsifolia* being more positive in $\delta^{13}C$ at the ASS site than at the NSS site. Furthermore, the soils at the ASS site had higher salinity than the soils at the NSS site (Fig. 1). This observation was in accordance with previous findings of higher $\delta^{13}C$ values following exposure to saline and alkaline growing conditions in the leaves of cotton (Brugnoli and Lauteri, 1991), barley (Jiang et al., 2006), *Bienertia sinuspersici* (Leisner et al., 2010), durum wheat (Glenn et al., 2012; Yousfi et al., 2012), *Populus cathayana* (Xu et al., 2013) and *Populus tomentosa* (Lu et al., 2018). The reason for the increase in $\delta^{13}C$ is a consequence of a stomatal limitation to photosynthesis under salinity stress (Farquhar et al., 1982; Yousfi et al., 2012). However, stomatal limitation did not account for the increase in $\delta^{13}C$ in *A. sparsifolia*

in this study. A decrease in stomatal conductance caused a concomitant reduction in the intercellular CO_2 concentration (C_i) under environmental stress, which eventually led to an increase in the foliar $\delta^{13}C$ value. When the CO_2 assimilation rate (A) is indirectly reduced by a reduction in stomatal conductance, C_i should decrease, while $\delta^{13}C$ should increase. In contrast, A is reduced by factors directly affecting leaf metabolism, causing C_i to increase and $\delta^{13}C$ to decrease (Farquhar et al., 1982). The latter may explain the lower value of $\delta^{13}C$ in *A. sparsifolia* at the NSS site.

In contrast, the $\delta^{13}C$ of *S. microphylla* was more negative at the ASS site than at the NSS site (Fig. 6). Similar results have been reported in *Atriplex confertifolia* (Sandquist and Ehleringer, 1995), *Aegiceras corniculatum* (Wei et al., 2008) and sugarcane (Meinzer et al., 1994). In this study, two studied sites were selected which had similar climatic conditions, but differed in soil properties, such as salinity and alkalinity. Salinity increases bundle sheath leakiness (ϕ) in C_4 plants, which causes a decrease in plant $\delta^{13}C$. In addition, Meinzer et al. (1994) discovered that C_4 monocots and dicots differ qualitatively with regard to the stomatal and biochemical regulation of gas exchange in response to salt stress, and Wei et al. (2008) showed that the $\delta^{13}C$ value of *A. corniculatum* is negatively correlated with salinity. There were contrasting responses of $\delta^{13}C$ to salinity between *S. microphylla* and *K. caspia*. Because it is a C_4 dicot, the foliar ^{13}C of *S. microphylla* was depleted at the ASS site, which may be attributed to increases in both ϕ and stomatal conductance (the g_s of *S. microphylla* at the ASS site was higher than that at the NSS site). The g_s of *K. caspia* at the ASS site was higher than that at the NSS site, so the variation of $\delta^{13}C$ values may result from leaf biochemical regulation rather than stomatal limitation. Some species showed increased WUE under higher

salinity, while others showed decreased WUE. This mismatch in trade-offs could be due to pervasive genetic constraints, perhaps acting in concert with processes of community assembly (Kimball et al., 2013). Plants differ in the stomatal and biochemical regulation of gas exchange in response to salt and alkali stress, which caused differences of $\delta^{13}C$ values in common species between the two studied sites. For our study, the inconsistent effects of salinity on foliar $\delta^{13}C$ may have resulted from species differences in salt and alkali tolerance.

Conclusions

The studied desert plants in different saline environments adopt various water use strategies to cope with salt stress. The three common species (*K. caspia*, *S. microphylla* and *A. sparsifolia*) were found to utilize shallow soil water at the NSS site but deeper soil water at the ASS site, showing that plants have the ability to adjust their root functioning to cope with soil salinity and alkalinity. Given that desert plants have contrasting water use patterns at the two saline-sodic sites, it is vital to take salinity types into consideration when addressing salinity problems via phytoremediation. Alkaline saline environments may require the presence of phreatophytes (*Tamarix*) or alkali-resistant halophytes (*Kochia sieversiana*) to improve soil alkalinity; such plants are able to avoid superficial salt stress and utilize deep soil water. However, salt-excluding halophytes, such as *Alhagi* (which shows higher ion selectivity by excluding Na^+ but accumulating Ca^{2+} in its leaves) (Arndt et al., 2004), are necessary to rehabilitate saline environments.

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Table 1

Information on the two saline sites, including soil type, location, elevation, and plant species and life form.

Table 2

Results of two-way ANOVA on the effects of salinity type, soil depth and their interaction on soil physiochemical variables. *P* values < 0.05 are bolded. The degrees of freedom for salinity type, soil depth, and their interaction are 1, 6, and 6, respectively.

Figure 1

Variation in the sodium adsorption ratio (SAR), pH and electrical conductance (EC) with soil depth at the two saline sites. Error bars represent standard errors of the mean (n=5).

Figure 2

Variation in ion content with soil depth at the two saline sites. Error bars represent standard error of the mean (S.E.) (n=5).

Figure 3

Variation in soil water content, δD and δ^{18}O with soil depth at the two saline sites. Error bars represent S.E. (n=5).

Figure 4

δ^{18}O values of the soil water and plant xylem at the NSS site (a) and ASS site (b). Data are presented as mean values ± 1 S.E.

Figure 5

Stem δ^{18}O values of the dominant plants at the NSS site and ASS site. Data are presented as mean values ± 1 S.E. Different letters above the bars indicate significant differences between the two species within a site. * indicates significant intraspecific differences between the sites.

Figure 6

Predawn water potentials (Ψ_{pd}) and midday water potentials (Ψ_{md}) of three common plants in the two saline soils. Data are presented as mean values ± 1 S.E. Different letters above the

bars indicate significant differences between the two species within a site. * indicates significant intraspecific differences between the sites.

Figure 7

Leaf $\delta^{13}C$ values of dominant plants at the ASS and NSS sites. Data are presented as mean values ± 1 S.E. Different letters above the bars indicate significant differences between the two species within a site. * indicates significant intraspecific differences between the sites.

Supporting information

Table S1 Pearson correlation coefficients between soil physiochemical parameters, including soil water hydrogen composition (δD), soil water oxygen composition ($\delta^{18}O$), soil water content (SWC), pH, electrical conductance, and Na^+ and Cl^- content, at the two saline study sites. The coefficients representing significant correlations are bolded. *, ** and *** represent correlations that are statistically significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

Table S2 Leaf gas exchange parameters of the dominant species at the two saline sites at approximately 12:00. Note: A = leaf net CO_2 assimilation (μmol CO_2 $m^{-2}s^{-1}$), g_s = stomatal conductance (mol H_2O $m^{-2}s^{-1}$), E = transpiration rate (mmol H_2O $m^{-2}s^{-1}$). Values are means ± 1 S.E.

Table 1

Information on the two saline sites, including soil type, location, elevation, plant species, families and life form.

Soil type	Location	Elevation (m)	Species	Families	Life form
Alkaline saline-sodic	85º25'49.1"E 44º39'29.7"N	346	*Nitraria sibirica*	Zygophyllaceae	C_3, Shrub
			Tamarix hohenackeri	Tamaricaceae	C_3, Shrub
			Karelinia caspia	Compositae	C_3, Perennial herb
			Suaeda microphylla	Chenopodiaceae	C_4, Semi-shrub
			Alhagi sparsifolia	Leguminosae	C_3, Semi-shrub
			Kalidium foliatum	Chenopodiaceae	C_3, Semi-shrub
Neutral saline-sodic	85º22'42.8"E 44º43'03.9"N	334	*Karelinia caspia*	Compositae	C_3, Perennial herb
			Suaeda microphylla	Chenopodiaceae	C_4, Semi-shrub
			Phragmites australis	Gramineae	C_3, Perennial herb
			Alhagi sparsifolia	Leguminosae	C_3, Semi-shrub

Table 2

Results of two-way ANOVA on the effects of salinity type, soil depth and their interaction on soil physiochemical variables. *P* values < 0.05 are bolded.

	Salinity type		Soil depth		Salinity type × Soil depth	
	F	*P*	*F*	*P*	*F*	*P*
SAR	58.66	**<0.001**	2.30	0.168	0.89	0.508
Soil pH	29.92	**0.002**	0.30	0.917	1.09	0.382
EC	16.74	**0.006**	14.98	**0.002**	0.87	0.525
SWC	0.07	0.805	45.71	**<0.001**	0.47	0.831
Soil water δ^2H	33.12	**0.001**	32.21	**<0.001**	2.33	**0.047**
Soil water δ^{18}O	59.91	**<0.001**	76.79	**<0.001**	1.67	0.149
Na^+ content	55.03	**<0.001**	15.52	**0.002**	0.91	0.493
K^+ content	6.67	**0.037**	36.10	**<0.001**	0.69	0.657
Ca^{2+} content	2.65	0.155	1.59	0.294	0.83	0.553
Mg^{2+} content	37.23	**0.001**	46.12	**<0.001**	0.29	0.939
Cl^- content	21.19	**0.004**	17.34	**0.001**	0.58	0.747
SO_4^{2-} content	7.36	**0.033**	3.82	0.064	0.20	0.977
HCO_3^- content	0.14	0.717	1.63	0.283	0.44	0.847

The degree of freedom of salinity type, soil depth, and their interaction is 1, 6, and 6, respectively. Note: SAR- Sodium adsorption ratio; EC- Electrical conductivity (dS m^{-1}); SWC- Soil water content (%); Soil water δ^2H and δ^{18}O (‰); All ion content (g Kg^{-1}).