



Water use patterns of co-occurring C₃ and C₄ shrubs in the Gurbantonggut desert in northwestern China

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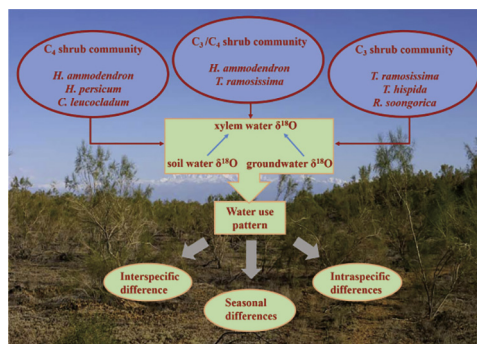
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HIGHLIGHTS

- Soil water content and isotopic value were affected by soil texture and groundwater table depth.
- Water sources of shrubs changed from shallow soil water to deeper sources across seasons.
- The studied shrubs coped with variations in soil water availability through root plasticity.
- Distinct shoot physiological traits relieve competition among shrubs with similar water sources.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 1 January 2018

Received in revised form 24 March 2018

Accepted 24 March 2018

Available online xxxx

Editor: Elena Paoletti

Keywords:

Stable oxygen isotope

Water sources

Water use pattern

C₃ and C₄ shrubs

ABSTRACT

In water-limited ecosystems, spatial and temporal partitioning of water sources is an important mechanism that facilitates plant survival and lessens the competition intensity of co-existing plants. Insights into species-specific root functional plasticity and differences in the water sources of co-existing plants under changing water conditions can aid in accurate prediction of the response of desert ecosystems to future climate change. We used stable isotopes of soil water, groundwater and xylem water to determine the seasonal and inter- and intraspecific differences variations in the water sources of six C₃ and C₄ shrubs in the Gurbantonggut desert. We also measured the stem water potentials to determine the water stress levels of each species under varying water conditions. The studied shrubs exhibited similar seasonal water uptake patterns, i.e., all shrubs extracted shallow soil water recharged by snowmelt water during early spring and reverted to deeper water sources during dry summer periods, indicating that all of the studied shrubs have dimorphic root systems that enable them to obtain water sources that differ in space and time. Species in the C₄ shrub community exhibited differences in seasonal water absorption and water status due to differences in topography and rooting depth, demonstrating divergent adaptations to water availability and water stress. *Haloxylon ammodendron* and *T. ramosissima* in the C₃/C₄ mixed community were similar in terms of seasonal water extraction but differed with respect to water potential, which indicated that plant water status is controlled by both root functioning and shoot eco-physiological traits. The two *Tamarix* species in the C₃ shrub community were similar in terms of water uptake and water status, which suggests functional convergence of the root system and physiological performance under same soil water conditions. In different communities, *Haloxylon ammodendron* differed in terms of summer water extraction, which suggests that this species exhibits plasticity with respect to rooting depth under different soil water conditions.

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Shrubs in the Gurbantonggut desert displayed varying adaptations across species and communities through divergent root functioning and shoot eco-physiological traits.

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1. Introduction

Water is essential for plant survival. This is particularly true in arid regions, where precipitation, as the main water input, is extremely low and highly variable. The soil water content is the most critical factor controlling plant growth and distribution in drought-prone desert ecosystems (Noymeir, 1973). Due to the scarcity and variability of precipitation, soil water availability in desert ecosystems is often highly variable, both temporally and spatially (Schwinning and Ehleringer, 2001). The variations of soil water in space and time are a key determining factor of plant distribution and community structure, including the balance of grasses and woody species in arid and semiarid ecosystems (Darrouzet-Nardi et al., 2006; Eggemeyer et al., 2009; Huxman et al., 2005). This may be further exaggerated under future climate change scenarios with a predicted increase in the frequency and intensity of drought and changes in regional precipitation patterns in several regions worldwide (Collins et al., 2013; Lewis et al., 2011; O'Brien et al., 2015; Timmermann et al., 1999). The implications of these changes in water-limited regions will be even more significant due to changes in rainfall patterns, as small changes in water availability can lead to large ecological consequences (Hoover et al., 2015). This trend will have a profound impact on the persistence and water use strategies of desert plants if they cannot acclimate to these novel conditions (Grossiord et al., 2017; Nicotra et al., 2010).

Dryland vegetation is composed of diverse plant functional types, which may respond quite differently to climate change (Wertin et al., 2015). Co-occurring species in desert ecosystems often adopt contrasting water use strategies, such as changes in rooting depth or the redistribution of fine roots within the soil profile, to cope with seasonal variations in soil water availability (Barbeta et al., 2015; Moreno-Gutierrez et al., 2012; Schwinning and Ehleringer, 2001). These general differences in root functioning have been proposed as mechanisms for desert plants to co-exist with different species in water-limited environments and to adapt to seasonal water scarcity. Thus, interspecific differences in plant root functioning are critical for plant water access and carbon-water balance (Grossiord et al., 2017). Additionally, shoot morph-physiological adjustment is another mechanism for desert plants to sustain growth during extended drought periods. Previous studies have reported that morph-physiological adjustment possibly occurs in both root and shoot systems to maintain the balance between water acquisition in the rooting zone and the water requirement of the shoot system (Li et al., 2005; Xu et al., 2007). Therefore, the way that plants acquire and utilize key resources, such as water, is an important component of their survival strategy.

The Gurbantonggut desert, one of the largest deserts in China, is a typical central Asian cold desert with stable snow cover during winter, rather infrequent and discrete summer rainfall (Fan et al., 2014; Zhou et al., 2012), and up to 40% vegetation cover (Zhang and Chen, 2002). During the wetter season of March to May, the soil has a relatively high water content due to snowmelt (Fan et al., 2014), but soil water is rapidly depleted as a result of the high evapotranspiration demand associated with increased temperature. The rather uneven summer precipitation pulses, together with the high evaporation, generate rapid and periodic fluctuations in soil moisture in the upper layers while the deeper soil moisture is relatively stable (Dai et al., 2014; Wu et al., 2014). The predicted variations in the seasonal precipitation pattern may cause periodic and chronic drought stress for desert vegetation.

Different functional types, e.g., photosynthetic pathways and rooting depths, of desert plants co-exist in the Gurbantonggut desert, and C_3 and C_4 shrubs are the dominant species in this desert ecosystem.

These shrubs might use water sources differently to co-exist in water-limited ecosystems and may respond differently to spatial and temporal changes in water conditions. Under future climate change, the threat faced by this wet winter and dry summer ecosystem may increase severely, as community structure and functioning will most likely be affected by the predicted increase in regional drought (Salmon et al., 2015). Understanding the water sources of coexisting shrubs with different functional traits and adaptation strategies will not only provide knowledge related to ecological niche differentiation, which can facilitate species coexistence (Chesson et al., 2004), but is also critical for accurate modeling, i.e., predicting species coexistence and the effect of climate change on ecosystem processes.

We studied the seasonal, inter- and intraspecific variations in the depth of water extraction by six different C_3 and C_4 shrubs under three soil water conditions to determine the spatial and temporal partitioning of the water source among functionally different coexisting shrubs. The studied desert shrubs are likely to adjust their water source according to the precipitation-induced temporal variation in soil water availability. Within a community, co-occurring species are predicted to explore different water sources through differentiation of rooting traits and to adapt to drought stress via distinct shoot eco-physiological traits. Given the differences in the soil water content and groundwater table depth, we hypothesized that shrubs in C_4 shrub community use shallow water and groundwater simultaneously during wetter season and shifted to groundwater during drier season while shrubs in the C_3 and C_3/C_4 mixed communities mainly rely on deeper soil water.

2. Materials and methods

2.1. Site and species description

This study was conducted at the Fukang Station of Desert Ecology, Chinese Academy of Sciences, which is located on the southern edge of the Gurbantonggut desert, Xinjiang, China (44°22'N, 87°55'E). The climate is characterized as a typical continental arid temperate climate with a hot dry summer from June to the end of August and a cold winter from December to March (Xu and Li, 2009; Xu et al., 2007). The annual precipitation ranges from 70 to 180 mm (1997–2016), the mean annual temperature is 6.6 °C (1997–2016), and annual potential evaporation is approximately 1000 mm (Fan et al., 2014; Xu et al., 2016). The vegetation is mainly composed of shrubs (*Haloxylon ammodendron* (C. A. Mey.) Bunge., *H. persicum* Bunge ex Boiss., *Tamarix ramosissima* Ledeb. Fl. Alt., and *Reaumuria soongorica* (Pall.) Maxim.). The area from the fringe of the alluvial plain is dominated by C_3 shrubs, whereas the sandy desert is occupied by C_4 shrubs. Perennial and ephemeral herbaceous species form the bottom layer of the shrub community (Dai et al., 2014; Fan et al., 2014; Xu and Li, 2006). At the fringe of the alluvial plain, the soil is fine textured (8.4% clay, 68.9% loam, and 22.7% sand), whereas the soil in the desert has a sandy texture (1.3% clay, 13.7% loam, and 85% sand) (Xu and Li, 2009) (Table S1).

The C_3 to C_4 vegetation gradient comprised three shrub communities (vegetation dominated by C_3 shrubs, C_3 and C_4 shrubs and C_4 shrubs, respectively) differed in soil water content and groundwater table depth. Three C_3 to C_4 shrub community gradients were used in this study for replication purposes. The three shrub communities are located 5–8 km apart from each other, with similar climate conditions and weather processes. The C_4 shrub community (referred to as the C_4 community hereafter), dominated by *H. ammodendron*, *H. persicum* and *Calligonum leucocladum* (Schrenk) Bge., is located at the edge of the

sandy desert with sandy-textured soil. The C₃ and C₄ mixed shrub community (referred to as the C₃/C₄ community hereafter) is dominated by *H. ammodendron* and *T. ramosissima*. The C₃ shrub community (referred to as the C₃ community hereafter) is dominated by *T. ramosissima*, *T. hispida* Willd. and *R. soongorica*; the characteristics of these shrubs are presented in Table S2. The C₃ and C₄ mixed shrub community and the C₃ shrub community are located at the fringe of the alluvial plain, which has fine-textured soil.

2.2. Collection of plant and soil samples

Soil samples were collected in April, June, August and October in 2015 and in April, July and September in 2016. During each field campaign, three soil cores were collected next to the three sampled shrubs using a handheld auger, and a total of nine soil profiles were sampled from each community. Based on prior knowledge of the soil water isotopic signature along the vertical soil profile, soil samples were collected at 10-cm intervals within the 0–20-cm depth, 20-cm intervals within the 20–100-cm depth and 40-cm intervals within the 100–300-cm depth. Each soil sample was divided into two parts: one part was sealed in a glass vial and was frozen at –20 °C until water extraction, and the other part was sealed in a tin box for gravimetric soil water content (referred to as GWC hereafter) determination using the oven-drying method.

Stems were sampled simultaneously with soil sample collection. Three plants per species were sampled at each site. To avoid transpiration-derived contamination, two- to three-year-old completely suberized twigs were used for stem water isotope composition sampling. Twigs, from which all green leaves were removed, were cut into 2–4-cm-long pieces, sealed in screw-top glass vials, and stored in a freezer (–20 °C) until water extraction.

2.3. Collection of precipitation and groundwater samples

Forty-nine event-based precipitation samples were collected from January to November in 2015 and 2016. During each rainfall event, a collector constructed from a flask and funnel was used for rain water collection. Rain water was sampled from the collector immediately after the rainfall stopped. Snow samples were collected using a pail installed on the ground and were sealed in a plastic bag and allowed to melt completely at room temperature. Groundwater samples were collected monthly from a nearby well. All samples were filtered and sealed in screw-top vials and stored in a freezer.

2.4. Oxygen isotope composition analysis and calculation of line-conditioned excess*

Soil and xylem water was extracted using a cryogenic vacuum distillation system. Soil and xylem samples were heated at 90–100 °C under a vacuum of 0.03 hPa for 2–3 h (Newberry et al., 2017; Orlowski et al., 2016). The evaporated water from these samples was subsequently captured in a liquid nitrogen cold trap (Ingraham and Shadel, 1992), which was accessible to isotope analysis. The extraction accuracy of cryogenic vacuum distillation system was >98%. The extracted water samples, together with the rainfall, snowfall and groundwater samples, were analyzed with a liquid water isotope analyzer (LWIA, DLT-100, Los Gatos Research Inc., Mountain View, CA, USA), with precision of 0.25‰ and 0.1‰ for δ¹⁸O and δ²H, respectively. The oxygen isotopic composition is expressed as:

$$\delta^{18}\text{O} = R_{\text{Sample}}/R_{\text{Standard}} - 1$$

where R_{Sample} and R_{Standard} represent the oxygen stable isotopic composition (¹⁸O/¹⁶O) of the sample and the standard water (Standard Mean Ocean Water, SMOW), respectively. To eliminate the effect of methanol and ethanol contamination, the δ¹⁸O values of xylem water were

corrected using a standard curve created by engineers from Los Gatos (Schultz et al., 2011). The specific procedures were described by Wu et al. (2014).

We calculated the line-conditioned excess* (lc-excess*) values, proposed by Landwehr and Coplen (2006a), of soil water and groundwater to determine the evaporation fractionation of soil water and groundwater isotopic compositions as follows:

$$\text{lc-excess}^* = [\delta^2\text{H} - a\delta^{18}\text{O} - b]/S$$

where a and b are the slope and y -intercept, respectively, of the LMWL, and S is the standard deviation measurement uncertainty for both δ¹⁸O and δ²H. The lc-excess is the deviation from LMWL, and a negative lc-excess value suggests that water has experienced evaporation fractionation during hydrological processes (Landwehr and Coplen, 2006a; Sprenger et al., 2016).

2.5. Stem water potential measurements

Stem water potential was measured monthly in 2015 (June to September) and in June, August and September in 2016 on three trees per species at each of the nine sampling sites using a pressure chamber (Model 3005, PMS Instrument Company, Albany, OR, USA.). Stem pre-dawn water potential was measured 30 min before sunrise, and midday water potential was measured at 1300 h.

2.6. Statistical analysis

Community differences in GWC and soil isotopic values were tested using a linear mixed model with community, year, and season as fixed effects. Inter- and intraspecific differences in the xylem water isotopic value and stem water potential were also analyzed using a linear mixed model, in which species, month, community, year, and season (or month) were set as fixed effects. Seasonal differences in xylem water isotopic values and stem water potentials of each species were analyzed using one-way analysis of variance (ANOVA) and univariate analysis based on a general linear model (GLM) with Tukey's honestly significant difference (HSD) post-hoc tests. Normality and homoscedasticity tests were checked for all data prior to analyses, and transformations (logarithm or square-root) were applied when necessary. Pearson's correlation coefficient was used in the correlation analysis. Data analyses were performed using SPSS 19.0 (SPSS Inc., Chicago, IL, USA). Linear and non-linear regression analysis and graphing were conducted using Origin 8.5 (Origin Lab Corp., Northampton, MA, USA).

2.7. Quantification and classification of plant water sources

The proportional contribution of sources to a mixture can be estimated using a stable isotope mixing model, such as the IsoSource model (Phillips and Gregg, 2003) and the SISUS model (Erhardt et al., 2014). The IsoSource mixing model was developed relatively earlier and is widely used in stable isotope-based water source studies (Benstead et al., 2006; Phillips et al., 2005). To compare the results from the current study with previously reported ones, we used the IsoSource mixing model to estimate the contribution of water from different soil depths for each shrub. Because there are more than two potential water sources, the mixing model can yield distribution of the proportions of feasible sources based solely on isotopic mass balance constraints. The mean relative contribution values were used for comparison in the Results and Discussion sections. Based on the similarities in the soil water δ¹⁸O value of each soil layer and its vertical and seasonal variations, soil layers were grouped into three sections. Therefore, four potential water sources, including groundwater, were considered for each community. However, due to differences in the distribution of soil water isotope values across the soil vertical depth among the

three communities, the three soil profile sections in each community differed slightly in terms of the combined soil depth. For example, the 0–60-cm soil layer was defined as the shallow soil layer for the three studied communities (Table S3). The middle soil layer was defined as 60–140 cm for the C₃ and C₃/C₄ communities, whereas it was defined as 60–140 cm and 60–180 cm for the sand dune and inter dune, respectively, in the C₄ community (Table S3). The deep soil layer was defined as 140–300 cm for the C₃ community, 140–220 cm for the C₃/C₄ community (soil layers below 220 cm were grouped with groundwater due to a strong similarity in the isotopic value and higher groundwater table at the site), and 180–300 cm and 140–300 cm for the sand dune and inter dune, respectively, in the C₄ community (Table S3).

3. Results

3.1. Precipitation and its $\delta^{18}\text{O}$ value

The two study years were similar in terms of the amount of rainfall (approximately 170 mm) but differed substantially in monthly precipitation distribution (Fig. 1). Due to less precipitation, spring (March–May) was drier in 2015 (30.4 mm) than in 2016 (64.2 mm). In summer (June–August) 2015, it was relatively wetter in early June and early August; however, the study area experienced a severe drought from late June to early August (the total amount of precipitation for the consecutive 50 days was 9.7 mm). Mid-summer of 2016 was wetter than that of 2015 because of the occurrence of two large rainfall events (13.9 and 12.6 mm) during July. Subsequently, a severe drought occurred with approximately 63 consecutive days with very low precipitation. The two study years were similar in terms of the amount of autumn (September–November) precipitation (52.5 mm in 2015 and 41.2 mm in 2016) (Fig. 1).

The oxygen isotope composition of precipitation ($\delta^{18}\text{O}_p$) showed more negative values during spring and autumn, compared with more positive values during summer (Fig. 1). Strong positive correlations were detected between $\delta^{18}\text{O}_p$ and ambient air temperature in 2015 and 2016 ($R^2 = 0.794$, $P < 0.001$ and $R^2 = 0.58$, $P < 0.001$ for 2015 and 2016, respectively). A significant correlation between $\delta^{18}\text{O}_p$ and the rainfall amount was detected in 2015 ($R^2 = 0.167$, $P < 0.05$) (Fig. S4).

3.2. Gravimetric soil water content, source water $\delta^{18}\text{O}$ value and Ic-excess^*

For the three studied shrub communities, GWC exhibited substantial soil depth and seasonal variations (Fig. 2). The GWC of deeper layers (180–300 cm) was higher than that of the upper layers (above 100 cm) in both study years. In each community, GWC in shallow layers (0–60 cm) showed strong seasonal differences, with higher GWC in spring than in summer and autumn (Fig. 2 and Table S5). In deeper layers, GWC had no significant seasonal variations (Fig. 2). The mean values of GWC in the C₃/C₄ community (2015: $8.47 \pm 0.59\%$; 2016: $7.59 \pm 0.72\%$) were higher than those in both the C₃ (2015: $7.59 \pm 0.72\%$; 2016: $6.05 \pm 0.28\%$) and C₄ community (2015: $4.12 \pm 0.3\%$; 2016: $4.17 \pm 0.37\%$).

The soil water oxygen isotope composition ($\delta^{18}\text{O}_s$) differed with depth above 100–140 cm (Fig. 3 and Table S6), soil water was more enriched in ^{18}O in upper layers compared to deeper layers (Fig. 3), and was relatively constant with soil depth beneath 100–140 cm. Seasonal variations in $\delta^{18}\text{O}_s$ were most pronounced in upper layers (0–60 cm), whereas few seasonal fluctuations were detected in middle to deeper layers (Fig. 3). Seasonal differences in $\delta^{18}\text{O}_s$ values in surface soil layers (0–60 cm) were only detected in the C₄ community in 2015 and 2016 and in the C₃ community in 2016 (Table S7). The C₄ community was more enriched in heavy isotopes (inter dune: 2015: $-4.05 \pm 0.55\%$, 2016: $-5.97 \pm 1.00\%$) compared with the C₃/C₄ (2015: $-8.35 \pm 0.22\%$, 2016: $-8.94 \pm 0.79\%$) and C₃ (2015: $-8.65 \pm 0.32\%$, 2016: $-8.57 \pm 0.96\%$) communities. There were no significant differences in the mean values of $\delta^{18}\text{O}_s$ between the C₃/C₄ and C₃ communities. GWC was negatively exponentially correlated with $\delta^{18}\text{O}_s$ in the three communities when data were pooled across all soil depths (C₄: $R^2 = 0.57$, $P < 0.01$, C₃/C₄ and C₃: $R^2 = 0.56$, $P < 0.01$) (Fig. S2), indicating that soil water in the drier layers was enriched in ^{18}O .

Soil water Ic-excess^* exhibited considerably negative values in our study, ranging from -5.90 to -83.24 , and changed with soil depth and season (Fig. 4), i.e., more negative values were observed in the upper layers (0–60 cm) than in the deeper layers and in drier seasons than in wetter seasons. Soil water Ic-excess^* in the C₄ community was significantly more negative than in the two other communities in both years ($P < 0.01$).

In each community, there were no apparent seasonal variations in the oxygen isotope composition of groundwater ($\delta^{18}\text{O}_g$). However,

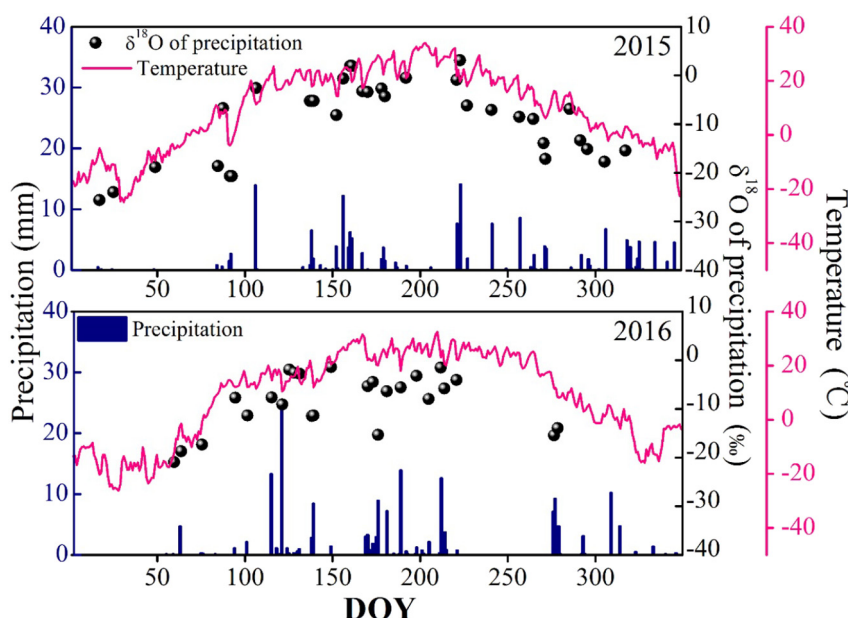


Fig. 1. Daily precipitation (mm), oxygen isotope composition (‰) of precipitation and daily temperature (°C) of 2015 and 2016 in Gurbantonggut desert.

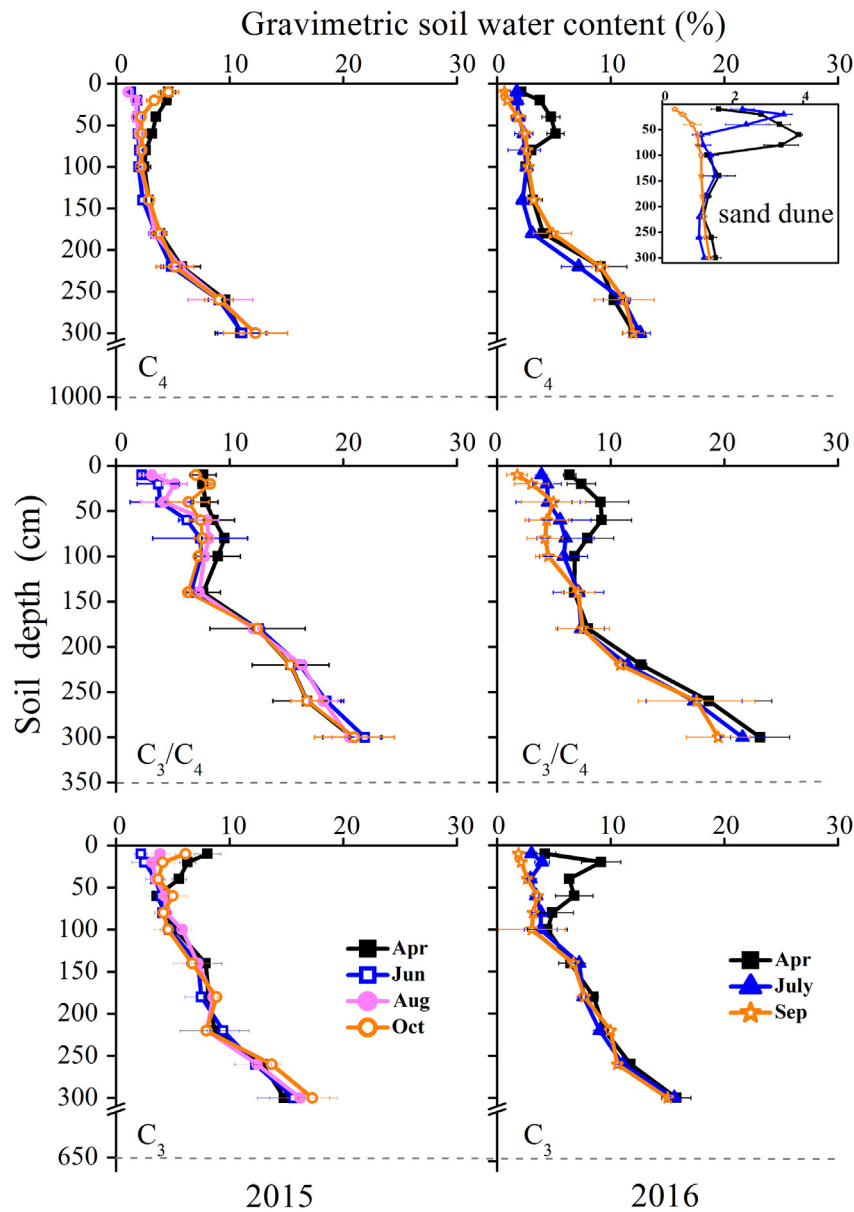


Fig. 2. Gravimetric soil water content (%) along the soil vertical depth in the C_4 shrub community (C_4), C_3/C_4 shrub mixed community (C_3/C_4) and the C_3 shrub community (C_3) during the growing season in 2015 and 2016. Dashed lines represent depth of groundwater table. Data are presented as mean \pm 1 standard error ($n = 6$).

community differences in $\delta^{18}O_g$ were detected, i.e., the $\delta^{18}O_g$ value in the C_4 community ($-12.09 \pm 0.06\text{‰}$) was significantly lower than that in the C_3/C_4 ($-10.29 \pm 0.03\text{‰}$) and C_3 ($-10.25 \pm 0.05\text{‰}$) communities (Fig. 3). Groundwater lc-excess^* was less negative, ranging from -10.5044 to -0.38154 , than the soil water lc-excess^* value (Fig. 4), indicating that groundwater experienced less evaporation fractionation in our study area.

3.3. Xylem water $\delta^{18}O$ value

Interspecific differences in the oxygen isotope composition of xylem water ($\delta^{18}O_x$) were detected in the C_3 and C_4 shrub communities but not in the C_3/C_4 mixed shrub community (Table 1 and Fig. 5). In the C_4 shrub community, the $\delta^{18}O_x$ value of *C. leucocladium* was significantly more positive than that of the two *Haloxylon* species in July and September 2016 ($P < 0.01$) (Fig. 5). The $\delta^{18}O_x$ value of *H. persicum* was significantly more negative than that of *H. ammodendron* in April and July 2016 ($P < 0.01$) (Fig. 5). In the C_3/C_4 shrub community, the interspecific difference in the $\delta^{18}O_x$ value between *T. ramosissima* and

H. ammodendron was only significant in August 2015 ($P < 0.05$) (Table 1 and Fig. 5). In the C_3 shrub community, the $\delta^{18}O_x$ value of *R. soongorica* was significantly more positive than that of the two *Tamarix* species in June 2015 and September 2016 and significantly more positive than that of *T. ramosissima* in October 2015 (Fig. 5). The $\delta^{18}O_x$ value of *T. ramosissima* was significantly more negative than that of *T. hispida* and *R. soongorica* in July 2016 (Fig. 5).

Significant seasonal variations in $\delta^{18}O_x$ were observed for most of the studied shrubs except *H. ammodendron* in the C_4 shrub community in 2015 and the C_3/C_4 community in both years (Table 2). However, we did not observe significant community differences in $\delta^{18}O_x$ for *H. ammodendron* and *T. ramosissima*.

3.4. The relationship between δD and $\delta^{18}O$ of source water

The local meteoric water line (LMWL) for the two study years (2015: $\delta D = 7.22 \times \delta^{18}O + 0.33$; 2016: $\delta D = 7.54 \times \delta^{18}O + 7.98$) had lower slopes than the global meteoric line (GMWL), indicating that enrichment of ^{18}O in precipitation was caused by evaporation (Fig. 6).

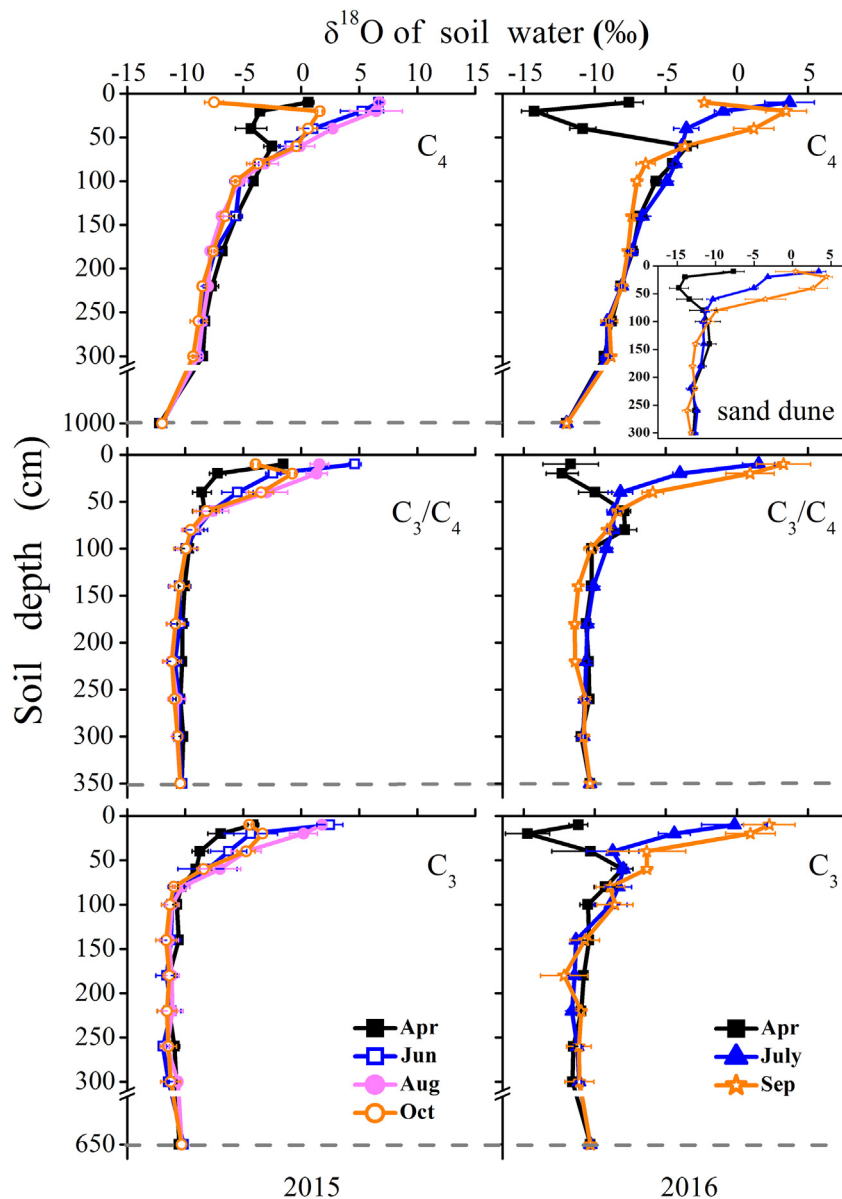


Fig. 3. Oxygen isotope composition (‰) of soil water along the soil vertical depth and groundwater in the C_4 shrub community (C_4), C_3/C_4 shrub mixed community (C_3/C_4) and the C_3 shrub community (C_3) during the growing season in 2015 and 2016. Dashed lines represent depth of groundwater table. Data are presented as mean \pm 1 standard error ($n = 6$).

However, the slope and intercept of the LMWL in 2016 were close to those of the GMWL, indicating that precipitation in 2016 underwent relatively less evaporative enrichment (Fig. 6) (Wu et al., 2016). The $\delta^{18}O_s$ values of the three communities were positioned on the lower right of the GMWL and LMWL, which implies that soil water in the studied area experienced strong evaporative enrichment (Fig. 6). The $\delta^{18}O_g$ values, lying on the GMWL, were less affected by evaporative enrichment (Fig. 6).

3.5. Plant water use

There were substantial seasonal and inter-annual variations in the water use of the studied shrubs (Fig. 7). In spring, the contributions of shallow soil water to plant water uptake differed between the two study years. The spring in 2016 was much wetter than that in 2015, which caused the shrubs to take up a relatively high proportion ($>40\%$) of shallow soil water during that period (Fig. 7). In the C_4 community, the contribution of shallow soil water to the water use of *H. ammodendron* in April 2015 (0–6.1%) was lower than that during the wet spring (0–49.1%). In the C_3/C_4 shrub community, the

contribution of shallow soil water to the water use of *H. ammodendron* and *T. ramosissima* increased from 0 to 24% and 0–23.6% in April 2015 to 0–41.2% and 0–44.7% in April 2016, respectively. With respect to *T. ramosissima* in the C_3 shrub community, the contribution increased from 0 to 31.2% in April 2015 to 0–64.2% in April 2016. Shallow-rooted shrubs, i.e., *C. leucocladium* and *R. soongorica*, obtained approximately 60% of their water from the 0–60-cm soil layer and 40% from the 60–80-cm soil layer in spring 2016 (Fig. 7). The proportion of deeper water sources (including middle and deep soil water as well as groundwater) extracted by plants increased with a decrease in the GWC of shallow soil (Fig. S3), indicating that shrubs reverted to deeper water sources due to the reduction in GWC in shallow soil layers during summer and autumn. In the C_4 shrub community, the contribution of groundwater to *H. ammodendron* gradually increased to 70–85% from June to October 2015 and to 60–90% from July to September 2016. Middle and deep soil water accounted for 59% and 88% of water used by *H. persicum* in July and September, respectively, in 2016. Shallow soil water was still intensely extracted by *C. leucocladium* in July (the contribution was approximately 80%); however, as drought progressed, this value decreased to 30% in September, and the contribution of middle

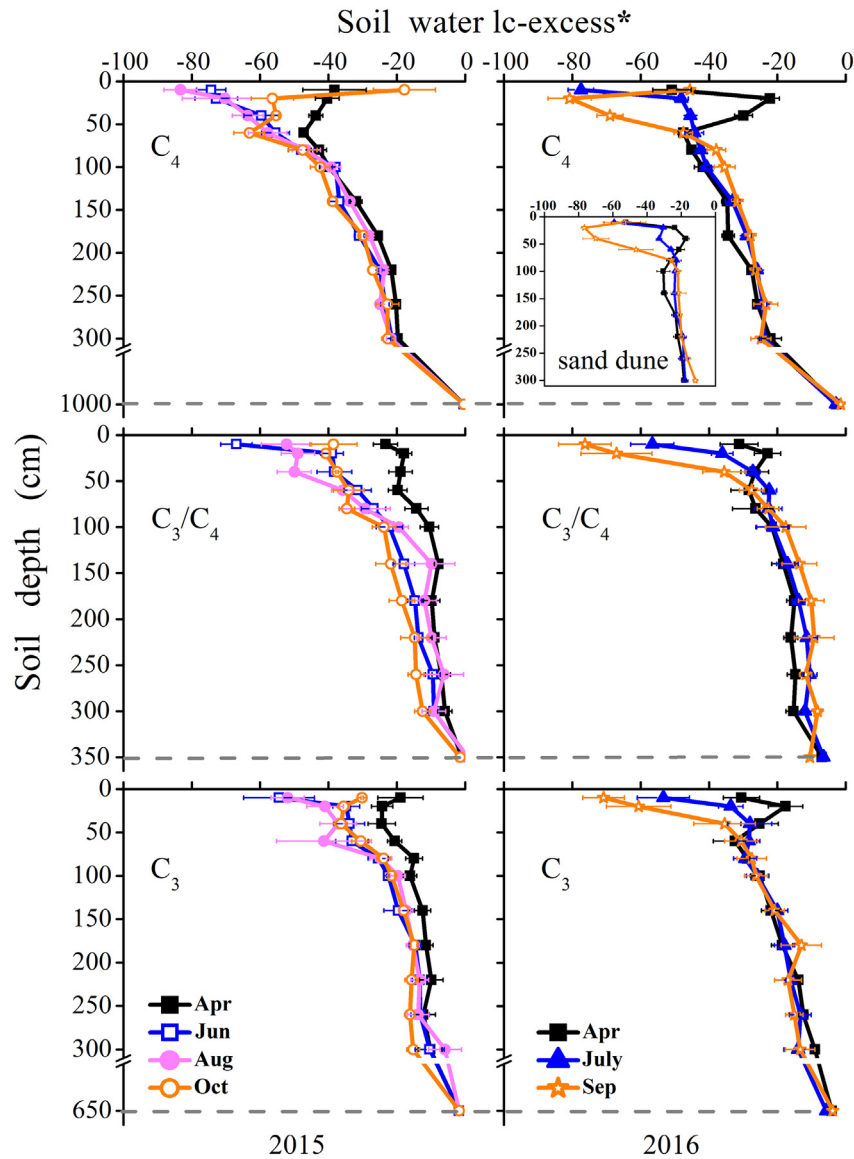


Fig. 4. Line-conditioned-excess (lc-excess*) values of soil water along the soil vertical depth and lc-excess* values of groundwater in the C_4 shrub community (C_4), C_3/C_4 shrub mixed community (C_3/C_4) and the C_3 shrub community (C_3) during the growing season in 2015 and 2016. Dashed lines represent depth of groundwater table. Data are presented as mean \pm 1 standard error ($n = 6$).

soil water increased to 70% (Fig. 7). With respect to *H. ammodendron* and *T. ramosissima* in the C_3/C_4 community and the two *Tamarix* species in the C_3 community, the contribution of the middle to deep soil water ranged from 45% to 90% during the growing season (except in July 2016); the contribution of groundwater was relatively small (0–30%) for these deep-rooted shrubs in both the C_3/C_4 and C_3 shrub communities throughout the growing season (except in July 2016). Strong seasonal and interannual variations in plant water source were observed for *R. soongorica* in the C_3 shrub community (Fig. 7c). Shallow soil water was the major water source in June and August 2015; however, the contribution of the 60–80-cm soil water layer increased dramatically in October 2015. In 2016, the 60–80-cm soil layer was the major water source in April and July, whereas shallow soil water was the major source in September (Fig. 7c).

3.6. Plant water potential

For most of the studied shrubs, predawn water potential (Ψ_{pd}) and midday (Ψ_{md}) water potential showed a decreasing trend with intensification of drought stress during the growing season (Fig. 8). In each

studied shrub community, there were significant interspecific differences in Ψ_{pd} and Ψ_{md} in 2015 and 2016 ($P < 0.01$) (Fig. 8 and Table 3). Patterns of monthly variations in Ψ_{md} were similar for all studied species, i.e., higher in June and lower from July to September (Fig. 8). In the C_4 shrub community, Ψ_{pd} and Ψ_{md} of the three studied C_4 species varied significantly among the sampling months in both years except for the Ψ_{md} of *C. leucocladium*, which was similar between June and August in 2016 (Tables S8, S6 and Fig. 8). The Ψ_{md} of *H. ammodendron* and *T. ramosissima* in the C_3/C_4 shrub community differed significantly among sampling months in both study years ($P < 0.01$), whereas there were no significant seasonal or inter-annual variations in Ψ_{pd} . Seasonal variations in both Ψ_{pd} and Ψ_{md} of the two *Tamarix* species in the C_3 community were significant only in 2015. The Ψ_{pd} and Ψ_{md} of *R. soongorica* varied significantly in both study years (Tables S8, S6 and Fig. 8).

In the C_4 shrub community, *H. ammodendron* had more negative Ψ_{pd} and Ψ_{md} values than in the C_3/C_4 community (except for June) ($P < 0.01$) (Table 4). Community differences in the Ψ_{pd} of *T. ramosissima* were only significant in September 2015 ($P < 0.05$). The Ψ_{md} of *T. ramosissima* in C_3/C_4 community significantly higher in June ($P <$

Table 1

Summary on the results of linear mixed model on interspecific and seasonal differences of xylem water oxygen isotope composition of shrubs in the C_4 , C_3/C_4 and C_3 shrub communities in 2015 and 2016. P values less than 0.1 are bolded.

Fixed effects	2015				2016			
	numDF	denDF	F	P value	numDF	denDF	F	P value
C_4								
Species					2	45	96.38	<0.01
Month					2	45	43.69	<0.01
Species \times month					4	45	23.30	<0.01
C_3/C_4								
Species	1	40	1.21	0.27	1	30	0.48	0.49
Month	3	40	7.31	<0.01	2	30	7.84	<0.01
Species \times month	3	40	1.45	0.24	2	30	0.31	0.73
C_3								
Species	2	45	13.13	<0.01	2	45	5.53	<0.01
Month	2	45	2.61	<0.1	2	45	1.13	0.33
Species \times month	4	45	1.27	0.29	4	45	5.16	<0.01

Table 2

Results of the one-way ANOVA on seasonal variations in xylem water oxygen isotope composition of the studied shrubs in the three communities (C_4 , C_3/C_4 , C_3) in 2015 and 2016. P values less than 0.1 are bolded.

Community	C_4			C_3/C_4			C_3		
	Df	F	P value	DF	F	P value	DF	F	P value
2015									
<i>H. ammodendron</i>	3	1.46	0.25	3	2.27	0.11	3	14.39	<0.01
<i>T. ramosissima</i>				3	6.72	<0.01	2	0.22	0.80
<i>T. hispida</i>							2	9.76	<0.01
<i>R. soongorica</i>									
2016									
<i>H. ammodendron</i>	2	2.88	<0.1	2	1.61	0.23			
<i>H. persicum</i>	2	14.61	<0.01						
<i>C. leucocladum</i>	2	48.80	<0.01						
<i>T. ramosissima</i>				2	18.65	<0.01	2	38.44	<0.01
<i>T. hispida</i>							2	42.88	<0.01
<i>R. soongorica</i>							2	0.88	0.43

4. Discussion

4.1. Seasonal and spatial dynamics in soil water content and soil water isotopic composition

As shown by the negative exponential correlation between GWC and $\delta^{18}O_s$ (Fig. S2), drier sites had more enriched soil water isotopic

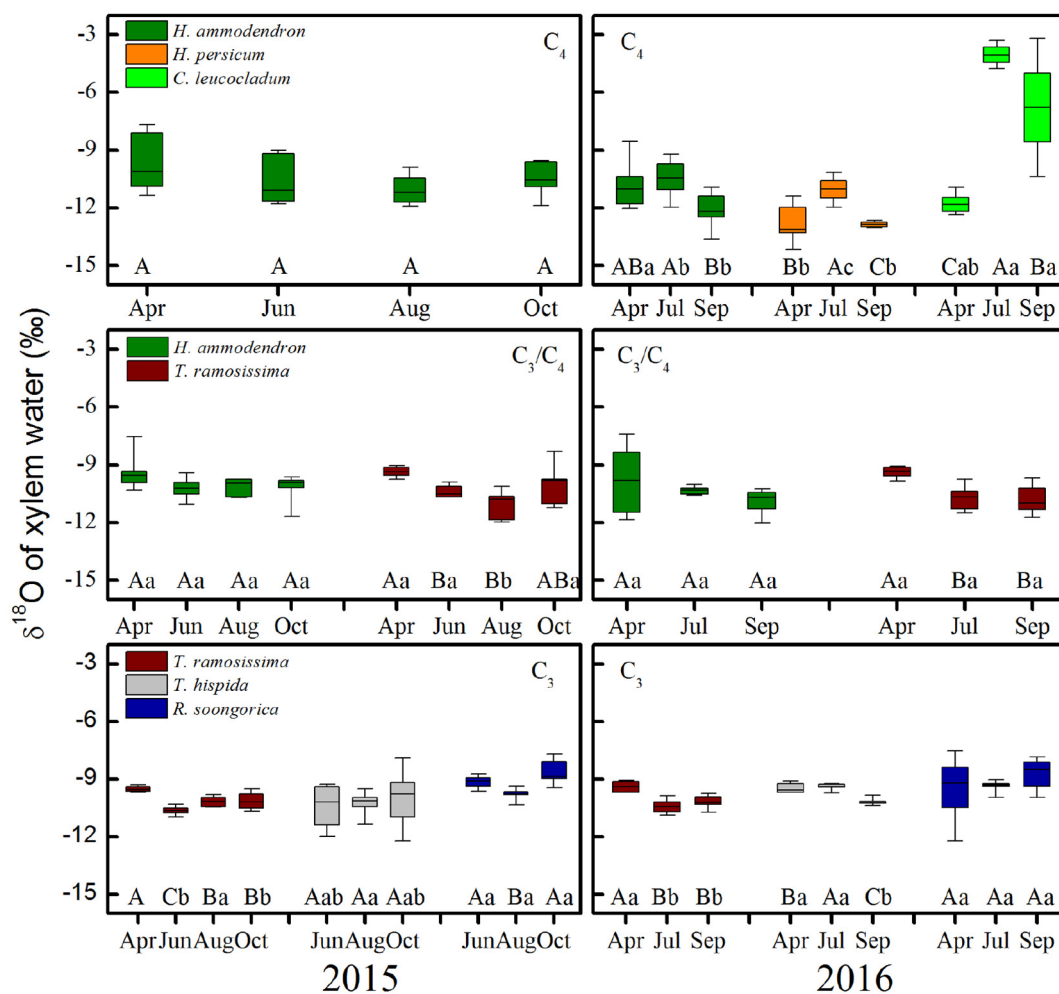


Fig. 5. Seasonal variations of oxygen isotope composition of xylem water for shrubs in the C_4 , C_3/C_4 and C_3 shrub communities in 2015 and 2016. The different uppercases represent seasonal differences in xylem water $\delta^{18}O$ for a given species. The different lowercases represent interspecific differences in xylem water $\delta^{18}O$ within a sampling month. Data are presented as mean \pm 1 standard error ($n = 6$).

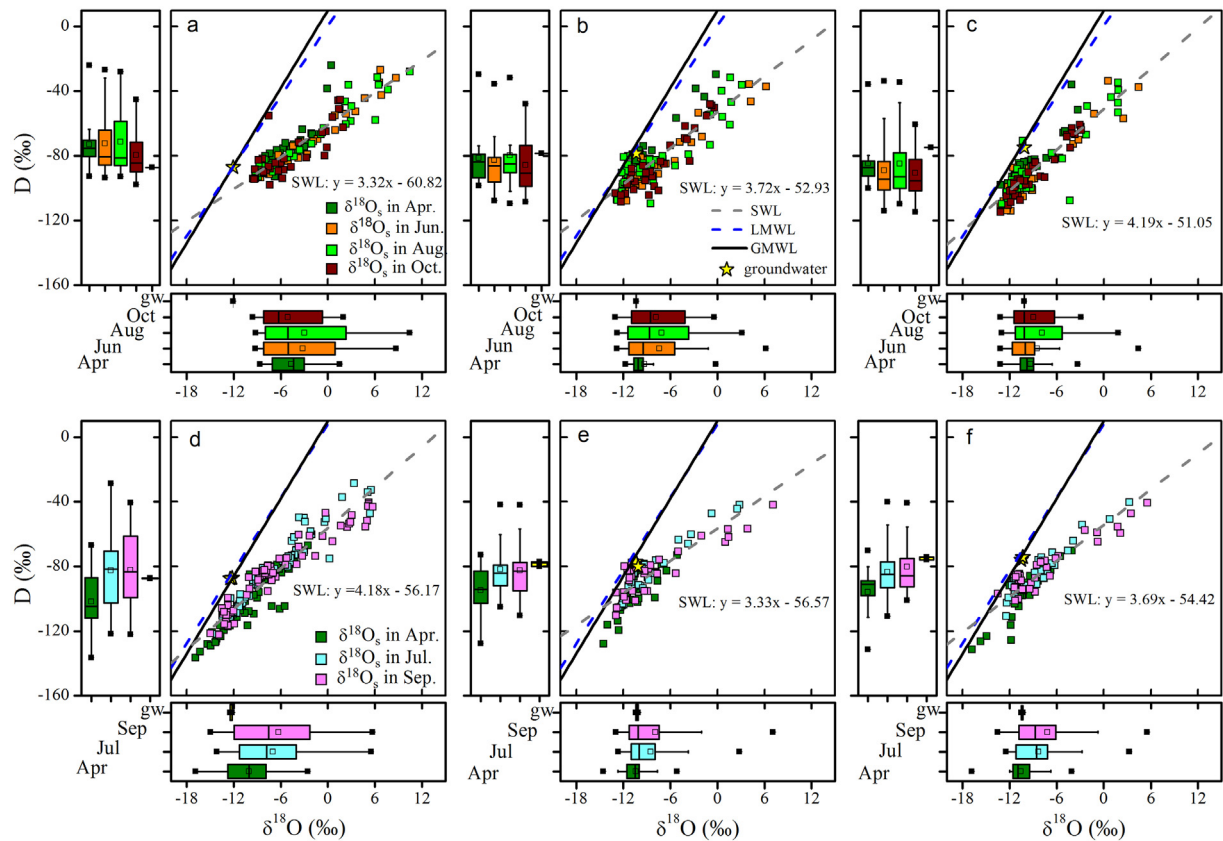


Fig. 6. Relationship between hydrogen (δD) and oxygen ($\delta^{18}O$) isotope composition of soil water and groundwater in 2015 (a,b,c) and 2016 (d,e,f) in the C_4 community (a and d), C_3/C_4 community (b and e) and C_3 community (c and f). Global meteoric line (GMWL with black-colored line), local meteoric water line (LMWL with dashed blue line) and soil water line (SWL with dashed gray line) are also presented. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

values in our study sites. Among the three communities, the C_3/C_4 community had the highest GWC and more negative $\delta^{18}O_s$ values, whereas the C_4 community had the lowest GWC and more positive $\delta^{18}O_s$ values. Community differences in GWC and $\delta^{18}O_s$ may have resulted from the differences in soil texture and the groundwater table depth rather than the amount of rainfall (the three shrub communities are not located far from each other). Unlike coarse-textured soil in the C_4 community, water in the two fine-textured soil communities (the C_3 and C_3/C_4 communities) is more tightly bound to fine clay particles (Zou et al., 2009). Fine-textured soils are associated with relatively lower water conductance and slower water loss to transpiration and drainage (McDowell et al., 2008), and a greater water retention capacity may contribute to the more negative soil water isotopic values in the C_3 and C_3/C_4 communities than in the C_4 community. In this study, a higher GWC was associated with a higher groundwater table, which implied that groundwater most likely recharged soil water via capillary rise in this desert region due to the scarcity of precipitation.

Seasonal fluctuations in GWC and $\delta^{18}O_s$ were detected in the upper layers, which may be attributed to infiltration of precipitation input with a distinct isotopic signature (Evaristo et al., 2016; Sprenger et al., 2017) and the strong evaporation fractionation (Fig. 4) in the study area. During early spring, soil water was recharged by snowmelt with a more depleted isotopic composition (Fig. 1) (Fan et al., 2014), which resulted in a higher water content and more depleted soil water isotopic compositions in the upper layers. During drier seasons, less precipitation coupled with higher temperatures (Fig. 1) and strong evaporative demand was probably the main factor that caused the reduction in GWC and the enrichment of ^{18}O in soil water in the surface layers of the soil profiles (Figs. 2 and 3) (Dai et al., 2014; Wang et al., 2017). More negative $lc\text{-}excess^*$ values in the upper layers (Fig. 4) and a greater deviation of summer soil water isotopic values from the LMWL (Fig. 6)

indicated that soil water in the study area underwent severe evaporation fractionation during summer (Landwehr and Coplen, 2006b; Sprenger et al., 2016). The soil water $lc\text{-}excess^*$ values further indicated that soil water evaporation fractionation was not limited to the upper layers, it extended to soil depths of 3 m in this arid climate, which is in line with the results of previous studies (Allison and Hughes, 1983; Singleton et al., 2004; Sprenger et al., 2016; Sprenger et al., 2017). However, seasonal fluctuations of $\delta^{18}O_s$ were not significant in the C_3/C_4 community in 2015 and 2016 and were only significant in 2016 in the C_3 community (Table S4). These results suggest that seasonal variations in $\delta^{18}O_s$ were not only controlled by water input and evaporation but were also influenced by soil texture.

4.2. Variations in water use patterns

All of the studied shrubs were similar in terms of their seasonal water use pattern, i.e., they preferentially took up a significantly higher proportion (>40%) of shallow soil water during the wet spring (in 2016) when water was plentiful in the upper soil layers and explored deeper water sources during the summer drought when the GWC of the upper soil layers decreased. This finding is consistent with the results of previous studies conducted on desert shrubs at the southern edge of the Gurbantonggut desert (Dai et al., 2014; Wu et al., 2014), suggesting that the studied shrubs have dimorphic root systems that enable them to access water sources that vary in space and time (Barbeta et al., 2015). However, in our study, inter-annual differences in spring precipitation resulted in differences between the two study years in terms of the contributions of shallow soil water (0–60 cm) during spring (Fig. 1). The study area received twice the amount of rainfall in April 2016 compared to that in April 2015 (43.1 vs. 18.2 mm), which subsequently caused a higher GWC in the shallow layer and resulted

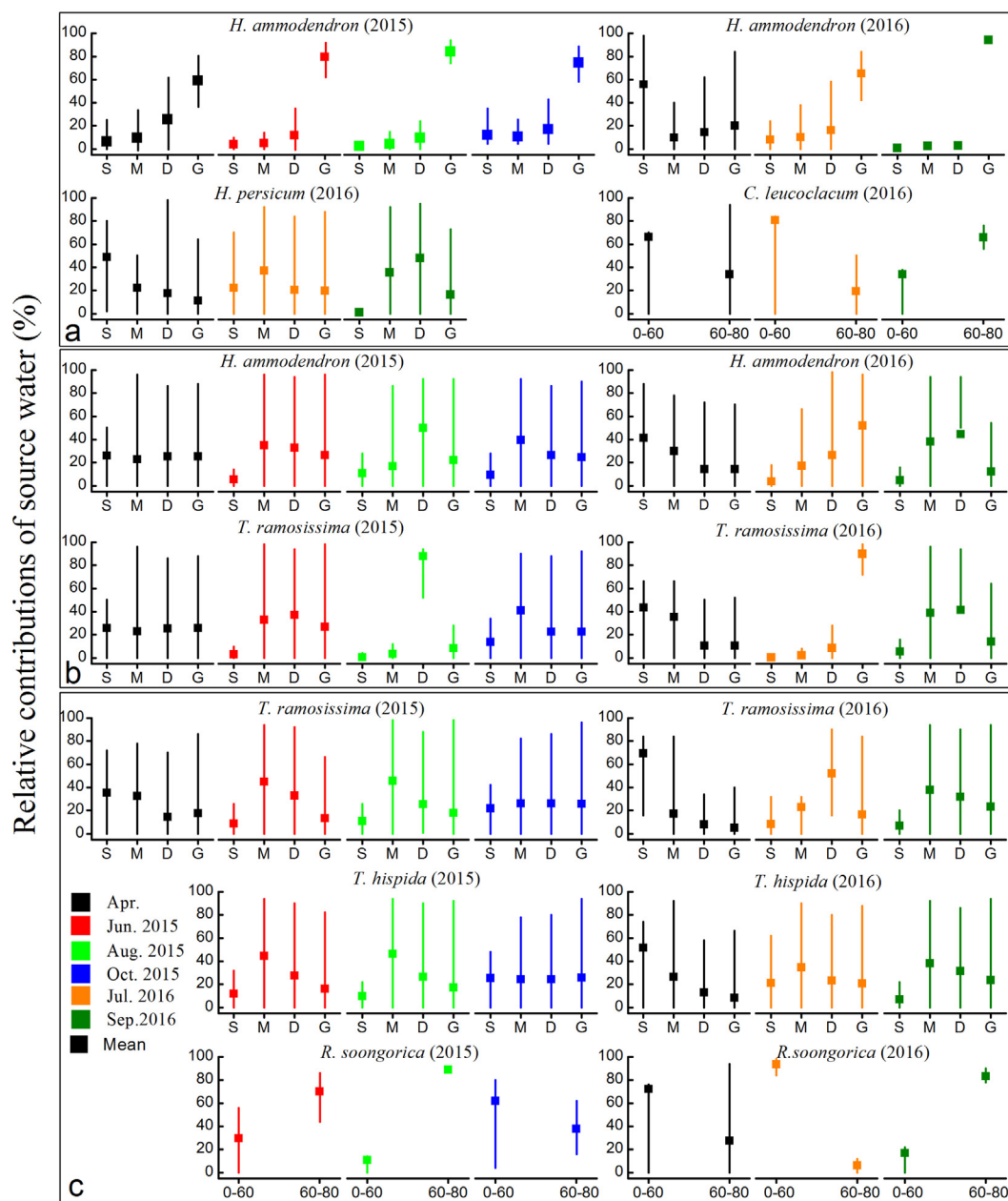


Fig. 7. Contributions of different water sources to the studied shrubs in the C_4 community (a), C_3/C_4 community (b) and C_3 community (c) in 2015 and 2016. Letters on X axis represent water sources of plants (S for shallow soil layer, M for middle soil layers, D for deep soil layers, G for groundwater). Squares represent the mean values and vertical bars represent the range from minimum values to maximum values of source water relative contribution. Contributions of different water sources were estimated using the IsoSource mixing model based on the oxygen isotopic signature of xylem water and potential water sources.

in a greater contribution of shallow soil water to spring water uptake in April 2016. We also observed a slight increase in water uptake from shallow soil layers in October 2015 when a slight increase in GWC occurred after several moderate rainfall events during late August to September (Figs. 1 and 2). These findings suggest that the studied shrubs relied on the rapid production and turnover of fine roots in the upper soil layers for adaptation to seasonal variation in soil water availability (Asbjornsen et al., 2008; Retzlaff et al., 2001). As the season progressed, increased soil temperature, together with decreased GWC, may have resulted in the dehydration or even death of fine roots distributed in upper soil layers (Barbata et al., 2015; Donovan and Ehleringer, 1994; Xu and Li, 2006). This situation, in turn, may have stimulated the production of fine roots in deeper soil layers where water was plentiful (Barbata et al., 2015; Dawson and Pate, 1996). Therefore, we assume that the capacity of plants to re-distribute their fine roots within the

soil profile is likely evidence of phenotypic plasticity in plant-water relationships (root functional distribution) (Barbata et al., 2015).

The studied shrubs explored deeper water sources during the dry period, but there were community and interspecific differences in the extraction of deeper water sources. In the C_4 community, the three C_4 shrubs exhibited three distinct water extraction patterns due to heterogeneity in topography and rooting depth. Unlike *H. ammodendron*, *H. persicum* growing on the sand dune relied on deep soil water instead of groundwater during drought periods. The rooting depth of *H. persicum* was far above the groundwater table, as the average height of the dune was 11 m (Dai et al., 2014) and the groundwater depth was 10 m; thus, the huge energy cost may have prevented root extension to groundwater sources (Dai et al., 2014; Xie et al., 2015). On the other hand, the groundwater salinity was higher than that of soil water in the dune (Li et al., 2010), and *H. persicum* is less tolerant of salinity

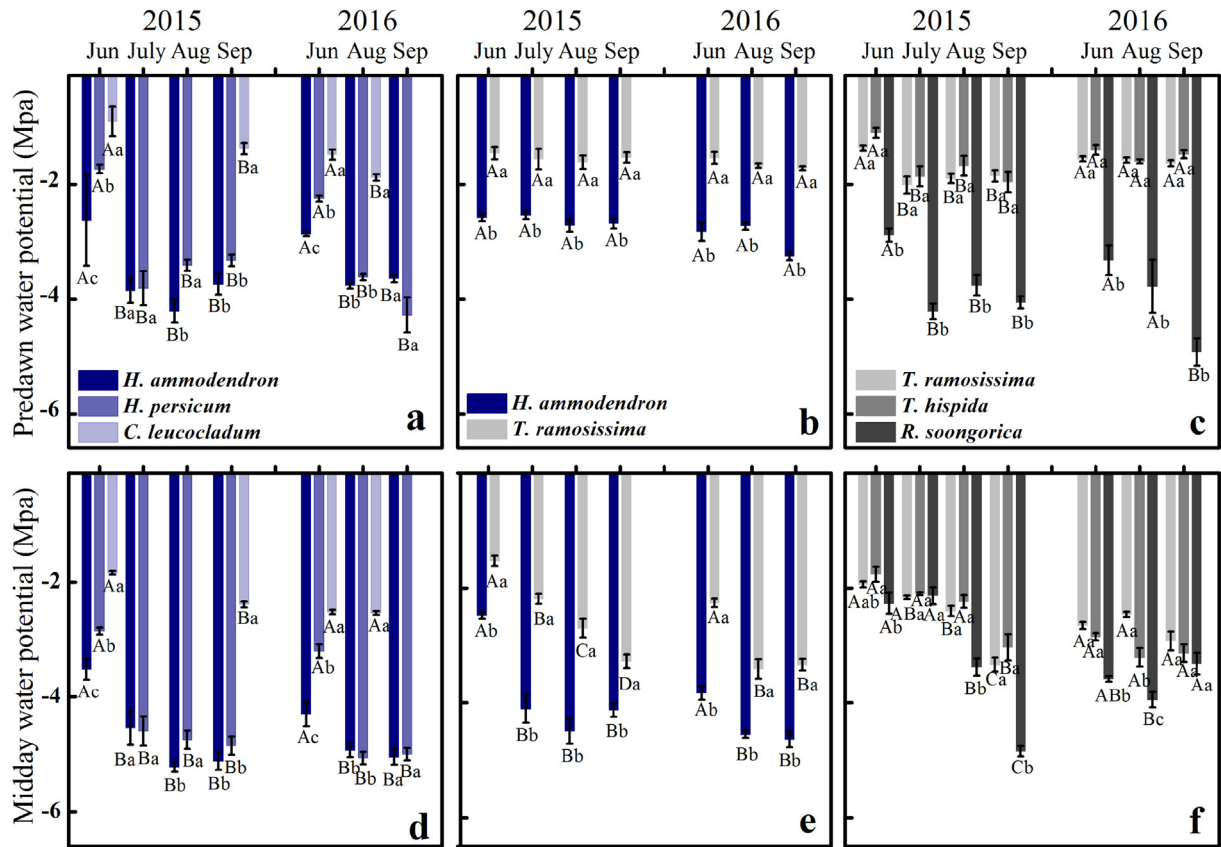


Fig. 8. Stem water potential of the studied shrubs in the C_4 (a, d), C_3/C_4 (b, e), C_3 (c, f) communities in 2015 and 2016. The different uppercases represent seasonal differences in stem water potential for a given species. The different lowercases represent interspecific differences in stem water potential within a sampling month. Data are presented as mean \pm 1 standard error ($n = 6$).

(Tobe et al., 2000; Xie et al., 2015), consequently, *H. persicum* may have avoided groundwater. The tap root of the shallow-rooted shrub *C. leucocladum* reached only 0.8 m while the lateral roots extended horizontally to 3–4 m; therefore, this species relied mainly on the shallower soil water layers recharged by precipitation, which caused its sensitive response to surface soil water fluctuations, such as defoliation during drought and re-emergence of leaves after heavy autumn rainfall. Similarly, in the C_3 community, the relatively shallow rooting depth of *R. soongorica* (average rooting depth of 0.8 m) (Xu and Li, 2006) resulted in the use of shallower water sources throughout the growing season compared to the two *Tamarix* species. These results indicate that spatial differentiation in the root system facilitated the coexistence of shrubs as well as reduced competition for limited sources within the community.

Although the shrubs discussed above differed in terms of water extraction, we found no interspecific differences in water extraction of the two deep-rooted shrubs, *H. ammodendron* and *T. ramosissima*, in the C_3/C_4 community and the two *Tamarix* species in the C_3 community (Figs. 5 and 7). Previous studies on root distribution reported similar rooting depths of *H. ammodendron* and *T. ramosissima* but classified *T. ramosissima* as a phreatophyte that relies heavily on groundwater, compared with *H. ammodendron*, which is a non-phreatophyte that takes up water from shallower soil layers (Xu and Li, 2009; Xu et al., 2007). In our study, *H. ammodendron* and *T. ramosissima* in the C_3/C_4 community both relied mainly on middle to deep soil water for most of the growing season (Fig. 7). The inconsistency between this study and the results of previous studies suggests that plant water uptake

Table 3

Summary on the results of the linear mixed model for interspecific and seasonal differences in predawn and midday water potential of the studied shrubs in the C_4 , C_3/C_4 , C_3 communities in 2015 and 2016. *P* values less than 0.05 are bolded.

2015	Predawn water potential				Midday water potential				2016	Predawn water potential				Midday water potential			
	numDF	denDF	F	<i>P</i> value	numDF	denDF	F	<i>P</i> value		numDF	denDF	F	<i>P</i> value	numDF	denDF	F	<i>P</i> value
C_4																	
Species	2	50	93.75	<0.01	2	50	100.33	<0.01	2	40	79.56	<0.01	2	40	145.58	<0.01	
Month	3	50	49.01	<0.01	3	50	49.42	<0.01	2	40	60.37	<0.01	2	40	49.77	<0.01	
Species \times month	4	50	5.03	<0.01	4	50	6.14	<0.01	3	40	11.06	<0.01	3	40	19.46	<0.01	
C_3/C_4																	
Species	1	40	198.8	<0.01	1	40	168.07	<0.01	1	30	288.13	<0.01	1	30	180.753	<0.01	
Month	3	40	0.75	0.53	3	40	53.64	<0.01	2	30	6.57	<0.01	2	30	39.237	<0.01	
Species \times month	3	40	0.24	0.86	3	40	6.76	<0.01	2	30	3.37	<0.05	2	30	1.538	0.23	
C_3																	
Species	2	60	304.92	<0.01	2	60	50.94	<0.01	2	45	245.31	<0.01	2	45	33.81	<0.01	
Month	3	60	29.06	<0.01	3	60	113.22	<0.01	2	45	9.86	<0.01	2	45	1.16	0.32	
Species \times month	6	60	1.78	0.12	6	60	10.66	<0.01	4	45	8.31	<0.01	4	45	3.53	<0.05	

Table 4
Summary on the results of the linear mixed model for intraspecific and seasonal differences of water potential in *Haloxylon ammodendron* and *Tamarix ramosissima* between the two different habitats in 2015 and 2016. *P* values less than 0.05 are bolded.

2015	Predawn water potential				Midday water potential				2016	Predawn water potential				Midday water potential			
	numDF	denDF	F	P value	numDF	denDF	F	P value		numDF	denDF	F	P value	numDF	denDF	F	P value
<i>H. ammodendron</i>																	
Community	1	40	100.55	<0.01	1	40	28.29	<0.01	1	30	45.99	<0.01	1	30	7.43	<0.05	
Month	3	40	14.03	<0.01	3	40	40.64	<0.01	2	30	23.87	<0.01	2	30	17.74	<0.01	
Community × month	3	40	10.89	<0.01	3	40	1.13	0.34	2	30	16.27	<0.01	2	30	0.53	0.95	
<i>T. ramosissima</i>																	
Community	1	40	8.51	<0.01	1	40	0.01	0.91	1	30	12.52	<0.01	1	30	7.19	<0.05	
Month	3	40	4.30	<0.05	3	40	81.39	<0.01	2	30	1.90	0.16	2	30	8.65	<0.01	
Community × month	3	40	2.00	0.13	3	40	4.32	<0.05	2	30	0.24	0.78	2	30	15.90	<0.01	

was determined by root activity rather than root presence (Dawson and Ehleringer, 1991; Prechsl et al., 2015). Furthermore, the relationship between root physical presence and functional activity is suggested to be species specific and to vary with time (Volkman et al., 2016). Thus, it is suggested that fine root production of the studied shrubs most likely exhibited substantial ecological plasticity in response to seasonal variations in soil water conditions. The detected habitat differences in the water absorption of *H. ammodendron* indicated that the rooting depth of this shrub varied spatially and temporally in response to changing soil water conditions.

Except for the aforementioned water use patterns, other competitive abilities of plants have also been reported such as deep-rooted plants can redistribute water through soil profile (hydraulic lift) (Dawson, 1993; Dawson et al., 1993). However, we did not observe apparent effects of hydraulic lifting processes, such as increased soil water content in the upper layers during drier season, or more depleted soil water isotopic values in upper layers which are identical to the deeper layers' or the groundwater' isotopic values. Higher soil temperature in the upper layers during hot summer season might dehydrate or kill the fine roots near the soil surface, which might inhibit roots of the shrubs to redistribute water. However this assumption is in need of further investigation.

4.3. Plant leaf water status under different water conditions

The studied shrubs exhibited similar trends in monthly variations in stem water potential (higher in June, lower from July to September); however, they experienced contrasting water stress due to the different soil water conditions and water extraction patterns (rooting patterns) (Table 3 and Fig. 8). The deep-rooted shrubs at the C₃/C₄ and C₃ community maintained relatively higher water potentials than the shrubs at C₄ community (Fig. 8 and Table 4). In addition, the higher and relatively constant Ψ_{pd} values of *H. ammodendron* in the C₃/C₄ community from June to September in 2015 indicated that plants growing at wetter sites had favorable soil water conditions and relatively stable water sources during the drier period of the growing season. Similar results were reported for semiarid shrubs in a Mediterranean-type ecosystem (Jacobsen et al., 2008), where desert shrubs with higher water potentials might access fairly stable deeper water sources.

In the C₃/C₄ community, although *H. ammodendron* and *T. ramosissima* utilized the same water sources throughout the growing season, the strong significant differences ($P < 0.01$) in water potentials throughout the season suggested that they experienced completely different water stress during summer. The similar water source and different water statuses of these shrubs suggested similar root functioning under the same water condition but very different hydraulic functioning in terms of the carbon-water balance. This is in line with the results of a previous study, which showed that co-occurring species use resources in different ways and adopt very different strategies to cope with water stress (Fowler, 1988). Stubbs and Wilson (2004) proposed that functional spacing of coexisting species should be considered as

evidence of competitive processes (Stubbs and Wilson, 2004). The non-significant difference in the water potential of the two *Tamarix* species with a similar water uptake pattern in the C₃ community suggested convergence of the root system and physiological performance in the two sister taxa under the same soil water condition.

The two shallow-rooted shrubs (*C. leucocladum* and *R. soongorica*) displayed a remarkably distinct water status compared with the deep-rooted shrubs growing in the same habitat and exhibited contrasting drought adaptation strategies. *R. soongorica* had the most negative water potential values among all shrubs and sustained its growth under severe water stress; thus, this species exhibited typical drought tolerant behavior. By contrast, *C. leucocladum* had better water status than the two deep-rooted *Haloxylon* species when shallow soil water was sufficient but underwent complete defoliation during extreme drought, as opposed to a further deterioration of water status, such as observed in *R. soongorica* or other shallow-rooted plants (Nardini et al., 2016). Defoliation seemed to be the drought avoidance strategy adopted by the shallow-rooted *C. leucocladum* in response to the drying out of the upper soil layer (Xu and Li, 2006). This phenomenon revealed not only the contrasting water extraction patterns but also the distinct hydraulic limit in coping with water scarcity. Therefore, desert shrubs might perform eco-physiological adjustments of both root and shoot systems to maintain the balance between water absorption and water consumption (Li et al., 2005; Xu and Li, 2006).

5. Conclusions

Differences in the soil water content of the three communities were influenced by soil texture and the depth of the groundwater table, which indirectly affected plant water sources. The studied plants have the ability to adjust their root functioning to cope with temporal and spatial variations in soil water availability, which is one of the key strategies of desert shrubs to adapt to periodic water scarcity. Differential water uptake among shrubs with distinct rooting depths is an important mechanism that enables desert shrubs to partition ecological niches and co-exist in water-limited ecosystems. In addition to root traits, distinct shoot eco-physiological performance was observed among shrubs with similar seasonal water uptake patterns under the same soil water condition, which might be beneficial to shrubs in terms of reduced competition for limited water sources. Various strategies were adopted by the studied shrubs to cope with drought stress, and these contrasting water use strategies should facilitate plant species co-existence and niche segregation (Moreno-Gutierrez et al., 2012). Understanding the water use patterns and drought adaptation strategies of desert plants is helpful in predicting changes in vegetation composition and the structure of desert ecosystems in response to future climate change.

Acknowledgements

This work was financially supported by National Natural Science Foundation of China (41671207, 31570470), Main Service Project of

Characteristic Institute of Chinese Academy of Sciences (TSS-2015-014-FW-5-1), State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences (G2014-02-01), the 9th Thousand Talents Program of China (2013). We thank all the staff at the Fukang National Station of Desert Ecology for their help in field and laboratory experiments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.03.307>.

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