

Stable oxygen isotopes reveal distinct water use patterns of two *Haloxylon* species in the Gurbantonggut Desert

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Abstract

Aims *Haloxylon ammodendron* and *Haloxylon persicum* are the dominant species in the Gurbantonggut Desert, China, with the former grows at inter-dune lowland and the later grows at the sand dune. This study aims to investigate the dynamics of water usage of the two species and their responses to the soil water fluctuations resulting from summer precipitation.

Methods Oxygen isotope ratios ($\delta^{18}\text{O}$) were measured for xylem water, soil water in different soil layers (0–300 cm), precipitation water and groundwater. Four potential water sources were identified: shallow (0–40 cm), middle (40–100 cm) and deep soil water (100–300 cm), as well as groundwater. The water sources used by the two species were calculated using the IsoSource model.

Results When the upper soil water was abundant in early spring, *H. ammodendron* mainly used shallow soil water while *H. persicum* mainly used middle soil water;

when the upper soil water was depleted in summer, *H. ammodendron* mainly used groundwater while *H. persicum* mainly used deep soil water. Both species were conservative in using shallow soil water following the relatively large summer precipitations.

Conclusions The two *Haloxylon* species had distinct water use patterns during the growing season, which reflects their adaptations to their specific habitats in this water-limited desert environment. Large precipitations in dry summer hardly altered their water use patterns, which mean that these species are rather conservative in water use strategy.

Keywords Sister taxa · Stable oxygen isotopes · Soil water · Groundwater · Water sources · IsoSource model

Introduction

In desert environments, water is the principal factor limiting plant recruitment, carbon fixation, vegetation distribution and nutrient cycling (Noy-Meir 1973; Ehleringer and Cooper 1988; Stephenson 1990; Reynolds et al. 1999). Precipitation is the primary water source in desert ecosystems and annual precipitation patterns play a crucial role in shaping plant adaptations (Schwinning and Ehleringer 2001). Plant metabolic activity is largely tied to episodic precipitation events or ‘pulses’. The ability of plants to take up and utilize rainfall pulses during the growing season is determined in part by pulse timing, intensity and amount, and by hydrological properties of the soil that translate

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precipitation into soil water pulses available for uptake by plant roots (Hacke et al. 2000; Sperry and Hacke 2002; Fravolini et al. 2005). In addition, root morphology or architecture is another important determinant of the availability of soil water and is closely related with plant–water relations (Schulze et al. 1996; Nippert and Knapp 2007; Poot and Lambers 2008). Plants of deep-rooted habit are well adapted to avoid drought by accessing deeper water sources (Ehleringer et al. 1991; Chimner and Cooper 2004). The presence of and the ability to exploit a deep, dependable water source, such as groundwater, makes it possible for some plants to survive long periods without rain or to overcome seasonal water limitation (Zencich et al. 2002; Yang et al. 2011; Wu et al. 2013).

Topography affects the distribution of soil water and nutrients (Swanson et al. 1988). Sand dunes and interdunes have been shown to provide habitat heterogeneity and to profoundly influence the spatial and temporal distribution of soil water and nutrients across the landscape (Grigg et al. 2008; Li et al. 2010). Accordingly, vegetation on sand dunes and inter-dunes is largely influenced by temporal and spatial variation of soil water. It was reported that leaf water potential was less negative for sand dunes species than for inter-dunes species (Pavlik 1980; Rosenthal et al. 2005; Grigg et al. 2008), which may result from more available soil water to species on sand dunes than on inter-dunes (Rosenthal et al. 2005; Grigg et al. 2008) or the stronger stomatal regulation in the dune species (Pavlik 1980). The aforementioned investigations mainly used physiological measures to reveal plant and soil water relationships. However, potential water sources that plants might use in sand dunes and inter-dunes have been largely ignored, although these are vital in understanding the long-term adaptation mechanisms of desert plants to seasonal and spatial changes of soil water.

In the Gurbantonggut desert, the second largest desert in China, there is always a stable snow cover in winter, which acts as a natural reservoir to store water from winter precipitation for spring delivery to soils (Zhou et al. 2012). The accumulated snow melts quickly in early spring and therefore functions equivalently to a single heavy rainfall, recharging the soil profile and providing abundant moisture for the coming growing season (Zhou et al. 2009). In contrast, precipitation occurring in summer is easy to evaporate from the soil surface due to high evaporative demand, resulting in reduced infiltration and shallower and short-lived

moisture sources in soil (Xu and Li 2008). However, summer precipitation may play a variable, but critical role in the structure and function of community (Xu et al. 2007; Zou et al. 2010; Wu et al. 2013). Differential utilization of winter and summer precipitation by plants has an important effect on water balance and on plant composition of the local plant community (Xu et al. 2007; Wu et al. 2013; Fan et al. 2014). Within the background of global climate change, increased temperature and precipitation have been recorded in recent 50 years for this region (Li et al. 2013). In addition, in transition zones between deserts and oases, the groundwater table has fallen significantly as a result of the overexploitation of groundwater (Xu et al. 2007). Thus, studies are urgently needed to understand the water use patterns of the plants, especially the dominant species in this region, which will help us to evaluate the effect of global climate change and human activity on the local ecosystem.

Haloxylon ammodendron (C.A.Mey.) Bunge and *H. persicum* Bunge ex Boiss. et Buhse (Chenopodiaceae) are sister taxa in the *Haloxylon* genus, and are mainly distributed in Central Asia, the Middle East (Karakum and Kyzylkum Deserts), Iran and Afghanistan (Pyankov et al. 1999). The two species are the dominant species in the Gurbantonggut Desert. Both species are of great ecological and economic importance and are crucially important in stabilizing sand dunes. The two species share some similarities: both have tree life forms or grow as large shrubs depending on their age and environment (Pyankov et al. 1999); both have photosynthetic pathway of C_4 (Pyankov et al. 1999) but different water use efficiency (Tian et al. 2014); both species have deep root systems and therefore have the possibility to reach the groundwater (Xu and Li 2008; Zou et al. 2010) (Fig. A2). However, the two species distribute differently in their habitats. *H. ammodendron* mainly grows on inter-dune lowland and the flat slope of dunes while *H. persicum* mainly grows on the sand dune, and they rarely grow together. Compared with *H. ammodendron*, *H. persicum* is more tolerant to drought but less tolerant to salinity (Tobe et al. 2000; Song et al. 2005). Previous study on *H. ammodendron* in the Gurbantonggut Desert showed that roots of *H. ammodendron* could penetrate to 10 m below the surface in the sandy soil (Xu and Li 2008) and *H. ammodendron* appeared to be highly sensitive to large precipitation pulses in terms of the leaf water potential, transpiration, and water use efficiency (Zou

et al. 2010), indicating that groundwater and soil water may be two potential water sources for *H. ammodendron*. Compared with *H. ammodendron*, little is known about the potential water sources that *H. persicum* might use during the growing season. Hence, a field experiment was undertaken to investigate whether these two species growing on adjacent habitats have differences in water use patterns and whether they shift water sources to cope with the fluctuations in soil water resulting from summer precipitation.

Given the known differences in physical and hydraulic properties between the inter-dune and the dune habitats (Wang et al. 2004; Tang et al. 2009), the first hypothesis is that *H. ammodendron* growing at inter-dunes and *H. persicum* growing at dune crests have different water use patterns. Considering that summer drought is a characteristic feature in this desert and roots of *H. ammodendron* and *H. persicum* in the upper soil layer may be inactive due to the long-lasting period of low soil water content, the second hypothesis is that the two species have limited use of shallow soil water following the summer precipitation.

Materials and methods

Study site description

During the growing season (April–September 2013), a field experiment was conducted in the native habitats of *H. ammodendron* and *H. persicum* at the southern edge of the Gurbantonggut Desert, China (44°22'N, 87°55'E, 435 m asl). The site is in the vicinity of the Fukang Station of Desert Ecology, Chinese Academy of Sciences (44°17' N, 87°56'E, 475 m asl). This region has a continental arid temperate climate, with a hot dry summer and cold winter; the air temperature ranges from a minimum of −42.2 °C in winter to a maximum of 44.2 °C in summer (Zhou et al. 2012), and annual mean temperature is 6.6 °C; annual mean precipitation is 70–180 mm, of which 25 % is generally snowfall; and annual pan evaporation is about 2000 mm (Xu et al. 2007). Typically, this area has an average snow cover period of about 120 d from mid-November to mid-March of the following year. The depth of snow cover is about 20–30 cm. Due to input of snow-melt and rainfall, soil has the highest water content in spring, and this provides plenty of water for plants to germinate and grow (Zhou et al. 2009). The groundwater table is about 4 m deep. Dendritic and honeycomb dunes

characterize the landscape, and their heights are in the range of 5–12 m. Soil physical and hydraulic properties differ in inter-dune and dune crest habitats. Particle sizes of inter-dune soil were 26.34 % medium (0.500–0.250 mm), 39.08 % fine (0.250–0.125 mm), 30.16 % extremely fine (0.125–0.063 mm) and 4.42 % silt (<0.063 mm); and corresponding values for dune crest 55.28, 41.28, 3.26 and 0.18 % (Wang et al. 2004). Degree of porosity, bulk density and stable infiltration rate were 37.25 %, 1.44 g cm^{−3} and 1.64 mm min^{−1} for inter-dunes, respectively; and correspondingly 41.16 %, 1.62 g cm^{−3} and 5.97 mm min^{−1} for dune crests (Tang et al. 2009). There is no surface runoff during natural rainfalls both for dune crests and inter-dunes.

H. ammodendron and *H. persicum* are the dominant species in the Gurbantonggut Desert, with *H. ammodendron* mainly growing at inter-dunes, and *H. persicum* mainly at dune crests – the mean densities of adult plants were 700 and 120 plants ha^{−1} in their respective habitats. The sampling sites were chosen in their typical habitats for each species. In each sampling site, twenty-four mature individual shrubs of each species were selected – with about the middle age, approximately the averaged canopy size in the community and similar basal stem diameters. Average height, canopy radius and basal stem diameters were 2.16±0.15 m, 1.08±0.02 m and 10.7±1.3 cm (mean±standard error) for *H. ammodendron*, respectively; and correspondingly 2.70±0.12 and 1.13±0.04 m and 9.1±0.9 cm for *H. persicum*. All the 24 replicates per species grew on the same dune and in the same inter-dune. The sand dune site was 11 m higher than the inter-dune site, with the groundwater table at about 4 m for the inter-dune lowland and 15 m for dune crest.

Meteorological data, such as precipitation and air temperature were obtained by an automatic weather station (Campbell Scientific, Logan, Utah, USA) installed near the study site.

Sample collection

At each site, four individuals from the 24 samples were randomly chosen for analysis each month. Suberized twigs (diameter 0.1–0.3 cm, length 4–5 cm) from the plants were sampled in the middle of each month during April–September for extraction of xylem water. Twigs were sampled during 0800–0900 h for the duration of the experiment. One set of twigs was sampled from each of the four shrubs at each site, giving four measurements

per species for each sampling time. To prevent changes in the isotopic values through evaporation, all samples were immediately placed into screw-cap glass vials, then sealed with Parafilm and stored in a freezer before water extraction. The first samples were taken on day of year (DOY) 112 (April 22), and the last sampling was on DOY 258 (September 15).

The soil samples were collected using a hand auger for soil cores taken next to the sampled plants on the same days as the plants were sampled (also at monthly intervals). The total depth of soil sampling was 0–300 cm. Based on the similarities in the isotopic signature for the soil water, soil samples within 0–20 cm were obtained at 10-cm intervals, those within 20–100 cm at 20-cm intervals and those within 100–300 cm at 40-cm intervals. For each site, there were four replicates per soil layer. Then soil samples were divided into two parts: one was sealed in glass vials and frozen until used for isotopic analysis of soil water and the other was sealed in soil tins for subsequent measurement of gravimetric soil water content (SWC, %), obtained by oven drying method (Mathieu and Bariac 1996).

Precipitation samples included five snowfalls and 23 rainfalls from January to September. Rain samples were collected immediately after the end of rainfall, using a collector composed of a flask and a funnel. Snow samples were collected using a pail installed on the ground, and the collected snow was transferred to an airtight container to melt at room temperature. Once the rain and melted snow samples were ready, they were filtered with 0.22 μm pore-size filters, and then pipetted into screw-top vials sealed with Parafilm and refrigerated at 2 °C until isotope analysis. Groundwater samples were collected monthly from a nearby well and stored in the same way as rainwater before isotope analysis.

In order to investigate the responses of water use patterns of the two species to the summer rainfalls, we tracked two typical natural rainfalls in summer. Plant twigs were sampled on 1 day before the 15.1 mm of June rainfall (on DOY 171) and 1, 2 and 3 days after it, and then on 1, 2, 3, 6 and 9 days after the following 6.7 mm of rainfall (on DOY 175). Four soil sample replicates were collected near the sampled plants to obtain changes in SWC and isotopic values for soil water within the 0–100 cm layer, one soil sample next to each plant. Sampling intervals were 0–10, 10–20, 20–40, 40–60, 60–80 and 80–100 cm on the same day as the plants were sampled at each site. Soil samples were treated as previous described, to determine SWC and

oxygen isotopic composition of soil water. In addition, isotopic values of xylem were tracked every month after a relatively large rainfall to obtain changes of isotopic compositions in xylem water for both species. Plant twigs were sampled on 1, 2, 3 and 5 days after 6.7 mm of rainfall (on DOY 142); and on 1, 2, 3, 5 and 7 days after 4.2 mm of rainfall (on DOY 197), 3 mm (on DOY 216) and 7 mm (on DOY 243).

Analyses and calculation

Significant hydrogen isotopic fractionation has been observed during water uptake by certain halophytic or xerophytic plants (Lin and Sternberg 1993; Ellsworth and Williams 2007). However, oxygen isotopic fractionation is negligible during root water uptake (Lin and Sternberg 1993; Ellsworth and Williams 2007). Therefore, we used oxygen isotopes to determine plant water sources. Xylem water and soil water were extracted using a cryogenic vacuum distillation line (Ehleringer et al. 2000), and the extracted water samples were stored in sealed glass vials at 2 °C. Then the oxygen isotopic compositions of the samples were determined by an isotope ratio infrared spectroscopy (IRIS) analyzer—the Liquid Water Isotope Analyzer (LWIA, DLT-100, Los Gatos Research Inc., Mountain View, CA, USA). Analytical precision of individual measurement was $\pm 0.25\text{‰}$ for $\delta^{18}\text{O}$. The oxygen isotopic composition can be expressed as:

$$\delta^{18}\text{O} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\text{‰}$$

where R_{sample} and R_{standard} are the oxygen isotopic composition ($^{18}\text{O}/^{16}\text{O}$ molar ratio) of the sample and the standard water (Standard Mean Ocean Water, SMOW), respectively.

To eliminate the effect of methanol and ethanol contamination, the $\delta^{18}\text{O}$ values of the xylem water were corrected by a standard curve created by engineers from Los Gatos (Schultz et al. 2011). Procedures were described in Wu et al. (2013). A pre-experiment was carried out to test the accuracy of the corrections by comparing the data obtained by IRIS with those from the Isotope Ratio Mass Spectrometry (IRMS) (FinniganMAT253, Thermo finnigan, Bremen, Germany). We had randomly chosen seven individuals from the 24 samples for each species, taking one individual as one sample. Hence, there were total 14 samples. All samples were filtered by 0.22 μm pore-size filters. Each

sample was divided into two sub-samples and $\delta^{18}\text{O}$ values were measured by IRIS and IRMS, respectively. Analytical precision of xylem water measured by IRMS was $\pm 0.1\%$ for $\delta^{18}\text{O}$. We used standardized major axis (SMA) method in the SMATR program to test if the IRIS measurement (after correction) and IRMS measurement agree. SMATR (Standardized Major Axis Tests and Routines) is a free software for fitting bivariate lines to data and for making inferences about such lines (Warton et al. 2006). The result showed that the $\delta^{18}\text{O}$ values of xylem water obtained by IRIS after correction agreed well with IRMS measurement (Table A, Fig. A1). Hence, the oxygen isotopic compositions of the samples were only determined by IRIS.

Water sources classification

The isotopic values of xylem water were compared with those of potential water sources using the IsoSource model, and thus it was possible to obtain a feasible range of the different water sources used by both species at each sampling time (Phillips and Gregg 2003). Four potential water sources were used in our research (see below), and source increment was defined as 1 % and mass balance tolerance was defined as 0.1‰. We calculated the mean and possible range of water utilization in each month and after two selected large rainfalls for both species.

Based on the similarities in $\delta^{18}\text{O}$ values for soil water within each layer, monthly variation, and $\delta^{18}\text{O}$ values of xylem water for the two species, four potential water sources (0–40, 40–100 and 100–300 cm and groundwater) were identified for both inter-dune and dune crest as follows:

- (1) shallow soil water (0–40 cm) was the most isotopically unstable zone and $\delta^{18}\text{O}$ values varied significantly with month and depth;
- (2) middle soil water (40–100 cm) had lower $\delta^{18}\text{O}$ values and relatively mild monthly changes than shallow soil water;
- (3) deep soil water (100–300 cm) had relatively uniform $\delta^{18}\text{O}$ values within a soil profile and showed no significant monthly variations;
- (4) groundwater had relatively constant $\delta^{18}\text{O}$ values, ranged from -10.05 to -10.33% from April to September.

For the rainfall responses study of the two species, the $\delta^{18}\text{O}$ values of soil water in 0–100 cm

were traced after rainfall, while $\delta^{18}\text{O}$ values in 100–300 cm were taken as the nearest monitored values, obtained at monthly intervals.

Data analysis

One-way ANOVA was used to assess temporal patterns in $\delta^{18}\text{O}$ values of soil water by analyzing each site individually across the sampling periods at each soil depth ($p < 0.05$). Independent-sample *t*-tests were used to test the difference in $\delta^{18}\text{O}$ values of xylem water between *H. ammodendron* and *H. persicum* ($p < 0.05$). Pearson's correlations were used to test whether the $\delta^{18}\text{O}$ values of precipitation correlate with air temperature ($p < 0.01$). These statistical analyses were conducted using SPSS 16.0 (SPSS Inc., Chicago, IL, USA). Charting was processed using the software Origin 8.5 (OriginLab Corp., Northampton, MA, USA).

Results

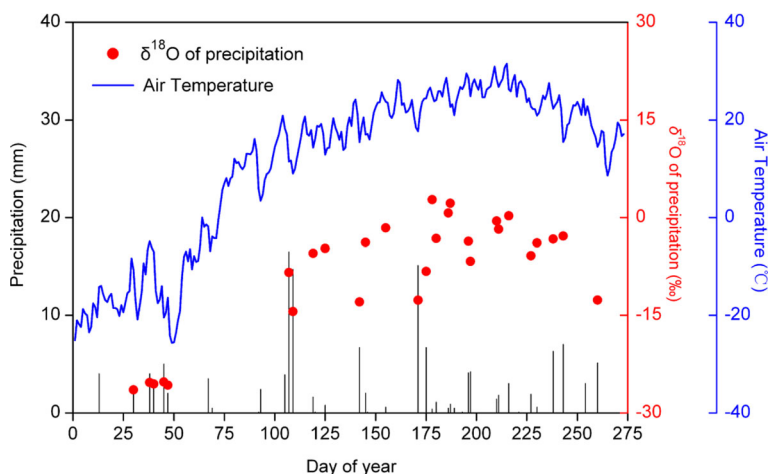
Precipitation distribution and isotopic composition of precipitation

In the study region, the total precipitation during January–September 2013 was 137.3 mm, and 80 % of the precipitations were less than 5 mm throughout the study period (Fig. 1). The largest precipitation was 16.5 mm on DOY 107. During the study period, the average daily air temperature ranged from -25.7 to 29.9 °C, and the average $\delta^{18}\text{O}$ values of precipitation ranged from -26.48 to 2.73% (Fig. 1). Temporal variations of $\delta^{18}\text{O}$ values of precipitation were positively correlated with the temporal variations of air temperature ($r = 0.917$, $p < 0.01$, $n = 28$).

SWC and isotopic composition of soil water

SWC changed with time and depth for both inter-dune and dune crest (Fig. 2a and c). In the top 40 cm of the soil profile, SWC was highest in April, with 7.15 % on inter-dune and 5.14 % on dune crest; and then dramatically dropped to 1.85 and 1.26 % in May, respectively. Thereafter, SWC changed little during June–September. In the depth of 40–100 cm, SWC had relatively mild monthly fluctuations for inter-dune compared with dune crest. It decreased from 3.16 % in April to 2.53 % in September on inter-dune; and correspondingly

Fig. 1 Precipitation and mean $\delta^{18}\text{O}$ values for precipitation and average daily air temperature during January–September 2013 in the Gurbantonggut Desert. The circles represent the means of $\delta^{18}\text{O}$ values, $n=4$, and the bar of standard errors was less than the size of the circle size and thus not shown



decreased from 5.01 to 0.92 % on dune crest. SWC below 100 cm increased greatly with depth at inter-dune but showed little variation at dune crest. During April–September, average monthly SWC increased from 3.83 ± 0.26 % at 100–140 cm to 15.48 ± 0.30 % at 260–300 cm on inter-dune, and correspondingly from 1.38 ± 0.31 to 1.25 ± 0.11 % on dune crest.

The $\delta^{18}\text{O}$ values of soil water for both inter-dune and dune crest had variations for months and depths (Fig. 2b and d). In the upper 40 cm layers, the $\delta^{18}\text{O}$ values of soil water were lowest in April, and then progressively increased and reached a maximum in September: from -11.01 to 3.92 ‰ on inter-dune, respectively, and from -11.84 to 2.01 ‰ on dune crest, respectively. The $\delta^{18}\text{O}$ values of soil water in 40–100 cm had relatively mild fluctuations with month. It increased from -6.70 ‰ in April to -4.92 ‰ in September on inter-dune, and correspondingly from -13.99 to -9.07 ‰ on dune crest. The $\delta^{18}\text{O}$ values of soil water in each layer below 100 cm showed no significant monthly variation ($F < 0.386$, $p > 0.851$, $n=4$ at inter-dune; $F < 1.314$, $p > 0.310$, $n=4$ at dune crest) (Fig. 2b and d). During April–September, the $\delta^{18}\text{O}$ values of soil water below 100 cm were relatively uniform along depth. Average monthly $\delta^{18}\text{O}$ values of soil water changed from -7.09 ± 0.10 ‰ at 100–140 cm to -9.83 ± 0.05 ‰ at 260–300 cm on inter-dune, and correspondingly from -12.26 ± 0.21 to -12.64 ± 0.11 ‰ on dune crest.

Isotopic composition of plant xylem water

Following a precipitation, the $\delta^{18}\text{O}$ values of xylem water for the two species firstly increased, and then they

gradually decreased (Fig. 3). The $\delta^{18}\text{O}$ values of xylem water for *H. ammodendron* and *H. persicum* were the lowest at the beginning of the growing season (Fig. 3), with -10.74 ± 0.26 and -13.24 ± 0.51 ‰ (both $n=4$), respectively. Thereafter, they became more enriched as the time progressed.

The $\delta^{18}\text{O}$ values of xylem water for *H. persicum* were significantly lower than for *H. ammodendron* ($p < 0.001$, $n=33$). During the growing season, the average $\delta^{18}\text{O}$ values of xylem water for *H. ammodendron* and *H. persicum* were -9.89 ± 0.04 and -12.02 ± 0.07 ‰, respectively. Average monthly $\delta^{18}\text{O}$ values of groundwater samples were -10.21 ± 0.05 ‰. Compared to *H. persicum*, the $\delta^{18}\text{O}$ values of xylem water for *H. ammodendron* were closer to those of groundwater.

Feasible contributions of potential water sources

H. ammodendron exhibited a shift in water use during the growing season (Fig. 4a). In April, the contributions of shallow soil water were in the range of 62–95 %, and the possible ranges of middle and deep soil water and groundwater were 0–8, 0–15 and 0–38 %, respectively. However, during May–September, the contribution of shallow soil water decreased dramatically while that of groundwater increased rapidly. Contributions of groundwater were in the range of 68–100 %.

H. persicum shifted its water sources seasonally (Fig. 4b). In April and May, the contributions of middle soil water occupied a large percentage of water usage, with possible ranges of 35–83 and 9–92 %, respectively. Contributions of deep soil water varied widely, with

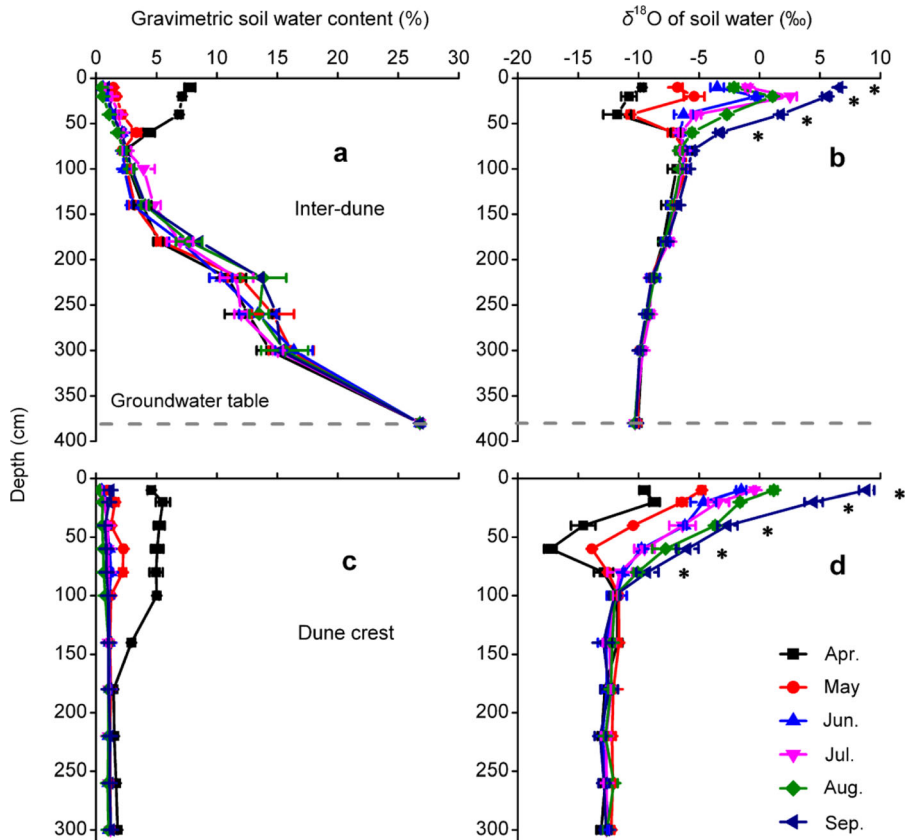


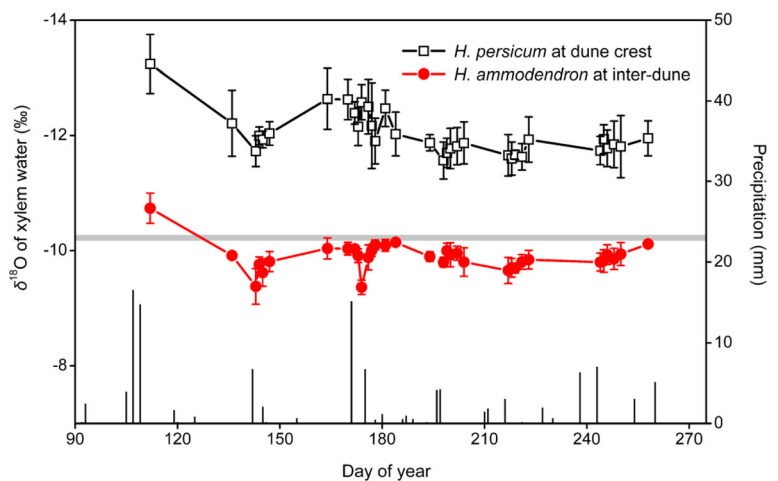
Fig. 2 Vertical profiles of gravimetric soil water content and $\delta^{18}\text{O}$ values of soil water measured at inter-dune (a, b) and dune crest (c, d) during the growing season (*beside a depth interval indicates

statistically significant difference at $p=0.05$). Error bars represent standard errors of mean SWC or $\delta^{18}\text{O}$ values ($n=4$)

possible ranges of 0–65 and 0–91 %, respectively. Meanwhile, contributions of groundwater were the same in April and May, with possible ranges of 0–21 %. During June–September, contributions of middle

soil water decreased dramatically while that of deep soil water became dominant, with possible range of 48–100 %. Meanwhile, contributions of groundwater were in the range of 0–36 %.

Fig. 3 Time series of mean $\delta^{18}\text{O}$ values of xylem water in *H. ammodendron* at inter-dune and *H. persicum* at dune crest and precipitation during 2013 growing season. Error bars represent standard errors of mean, $n=4$. The thick horizontal grey line represents the average monthly $\delta^{18}\text{O}$ values of groundwater (mean \pm SE, $n=6$)



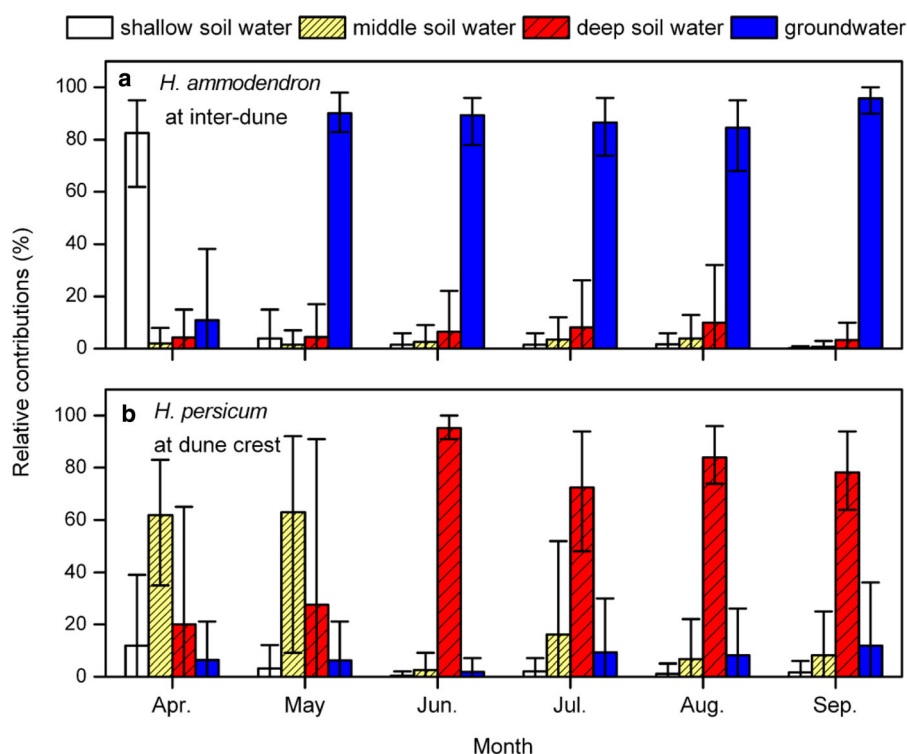


Fig. 4 Monthly changes in percentage contribution of potential water sources for *H. ammodendron* at inter-dune (a) and *H. persicum* at dune crest (b). Column heights represent the mean

value of relative contributions and bars represent the ranges of minimum / maximum, both were calculated using the IsoSource model (Phillips and Gregg 2003)

SWC and isotopic composition of soil water after rainfall

In the top 10 cm, SWC reached a maximum at 1 day (DOY 172) after 15.1 mm of rainfall (DOY 171) in both sites (Fig. 5a and b). The SWC of inter-dune had relatively stable values at 2 days (DOY 173) while that of dune crest rapidly decreased. However, SWC of both sites reached second peak values at 5 days (DOY 176) due to an additional 6.7 mm of rainfall at 4 days (DOY 175). Thereafter, they progressively decreased until the last day. Variation of SWC within 10–40 cm showed a time-lag effect. They reached a peak value at 2 days after 15.1 mm of rainfall for both sites. SWC of 40–100 cm was little influenced by these two rainfalls at both sites.

Compared to variations of SWC, $\delta^{18}\text{O}$ values of soil water showed opposite fluctuations in both sites (Fig. 5c and d). At the two sites, $\delta^{18}\text{O}$ values of soil water within 0–10 cm were significantly affected by rainfall. Their values reached the lowest at 1 day (DOY 172) after 15.1 mm of rainfall. Thereafter, $\delta^{18}\text{O}$ values of soil water of inter-dune remained stable at 2 days (DOY 173) while that of dune crest rapidly

increased – then $\delta^{18}\text{O}$ value of soil water at both sites progressively increased until the last day. The $\delta^{18}\text{O}$ values of soil water within 10–40 cm at both sites had relatively mild variations, and that of 40–100 cm were almost uninfluenced by these two rainfalls.

Feasible contributions of potential water sources after rainfall

After the 15.1 mm of rainfall on DOY 171, the *H. ammodendron* usage of shallow, middle and deep soil water gradually increased and reached a maximum at 3 days (DOY 174) from 0–6, 0–9 and 0–22 %, respectively, to 0–22, 0–30 and 0–60 %, respectively (Fig. 6a). Meanwhile, the usage of groundwater decreased from 78–96 to 40–82 %. Thereafter, the usage of shallow, middle and deep soil water constantly declined, while that of groundwater gradually increased despite an additional 6.7 mm of rainfall at 4 days (DOY 175).

For *H. persicum*, at 2 days (DOY 173) after the 15.1 mm of rainfall, the usage of shallow and middle soil water increased from nearly zero to 0–13 and 0–

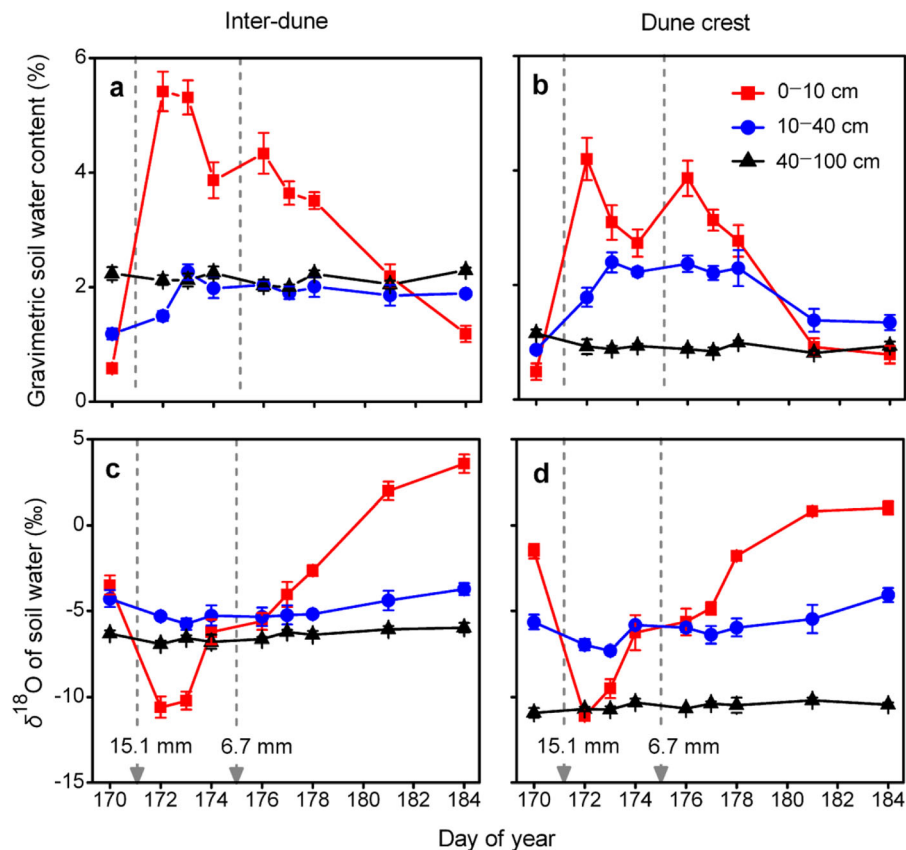


Fig. 5 Vertical profiles of gravimetric soil water content and $\delta^{18}\text{O}$ values of soil water before/after rainfall at soil layer of 0–100 cm at inter-dune (a, c) and dune crest (b, d). Arrows indicate the rainfall day. Error bars represent standard errors of mean SWC or $\delta^{18}\text{O}$ values, $n=4$

33 %, respectively (Fig. 6b). Meanwhile, the usage of deep soil water decreased from 91–100 to 67–90 %. Due to an additional 6.7 mm of rainfall at 4 days (DOY 175), the usage of shallow and middle soil water increased from 0–3 and 0–9 % at 3 days (DOY 174) to 0–11 and 0–41 % at 7 days (DOY 178), respectively. The usage of deep soil water decreased from 91–99 % at 3 days to 59–90 % at 7 days. Meanwhile, the usage of groundwater increased from 0–9 % at 3 days to 0–38 % at 7 days.

Discussion

Variations in isotopic compositions of the precipitation and groundwater

Variations in isotopic compositions of precipitation may result from differences in water vapor origins, atmospheric flow paths of vapor trajectories, temperature

and precipitation amounts (Dansgaard 1964; Yamanaka et al. 2007; Liu et al. 2014). In the northwest of China, including the study area, the $\delta^{18}\text{O}$ values of precipitation are closely linked with local air temperature (Liu et al. 2014). The $\delta^{18}\text{O}$ values of precipitation in our study also showed strong temperature dependence, with enriched values occurring in hot summer and depleted values occurring in cold winter.

Oxygen isotopic compositions of groundwater were in quasi-steady state (Figs. 2b and 3). Previous study showed that isotopic compositions of groundwater were a weighted average of annual precipitation inputs (Ehleringer and Dawson 1992). Mathieu and Bariac (1996) found that groundwater recharge process could be separated into two components: (1) slow infiltration through the soil matrix and the weathered basement; (2) fast and direct recharge through conducting fissured zones. In our case of the desert, groundwater was horizontally recharged from oasis, and the oasis was

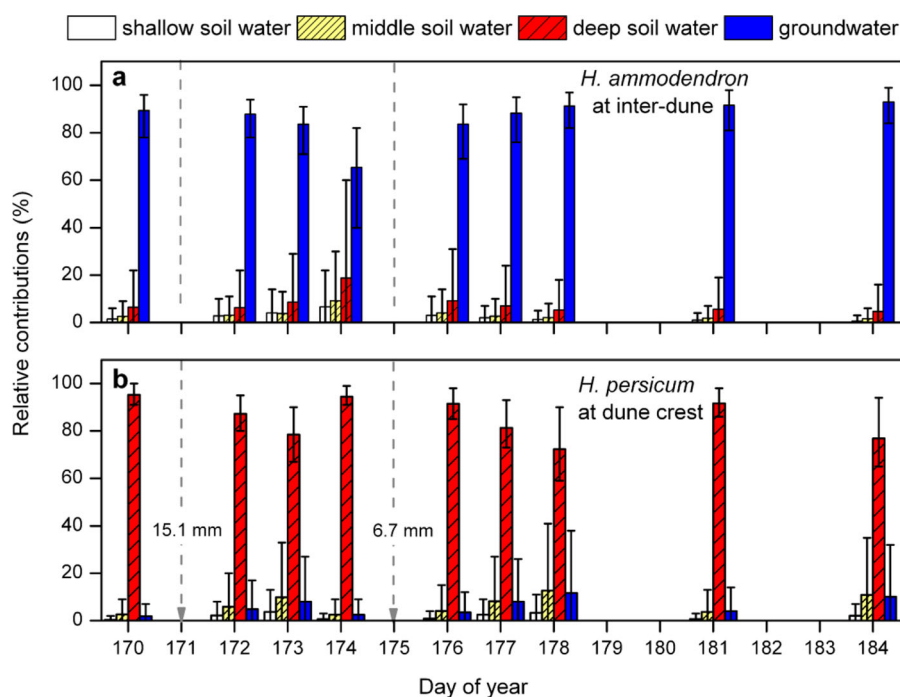


Fig. 6 Variation in water use patterns for *H. ammodendron* at inter-dune (a) and *H. persicum* at dune crest (b) before/after rainfall. Arrows indicate the rainfall day. Column heights represent

the mean value of relative contributions and bars represent the minimum/ maximum, both were calculated using the IsoSource model (Phillips and Gregg 2003)

irrigated by runoff from mountains. It seems that groundwater have no direct relations with local precipitations or precipitation of the current year.

Spatial patterns in soil water isotopic composition

In the study area, evaporation caused the enrichment of $\delta^{18}\text{O}$ values of soil water in the surface soil layer on inter-dune and dune crest (Fig. 2b and d). With the increasing depth of the soil layer, evaporation reduced, and isotope concentrations decreased approximately exponentially with depth to a relatively constant concentration (Fig. 2b and d), which were consisted with the research of Barnes and Allison (1983). The $\delta^{18}\text{O}$ values of soil water below 100 cm showed no significant monthly variation on both sites (Fig. 2b and d), indicating that evaporation had little impact on deep soil layer.

The upper soil layer had the lowest $\delta^{18}\text{O}$ values for both inter-dune and dune crest in April (Fig. 2b and d), which was recharged by snowmelt or rain with relatively depleted isotopic compositions. Snow samples had relatively depleted $\delta^{18}\text{O}$ values ($-25.69 \pm 0.22\%$) and

the snowmelt period generally ended in late March. Before we collected the soil samples of inter-dune and dune crest on DOY 112 (April 22), two large rainfalls occurred on DOY 107 (16.5 mm) and on DOY 109 (14.7 mm), with $\delta^{18}\text{O}$ values of -8.41 and -14.43% , respectively. At inter-dune site, the most depleted $\delta^{18}\text{O}$ values of soil water occurred at 20–40 cm depth (-11.77%), more positive than $\delta^{18}\text{O}$ values of the recent spring rain and snowmelt, implying that the upper soil water at inter-dune may be affected by evaporation, snowmelt and spring rain recharges accompanied by mixing with stationary soil water (Gazis and Feng 2004). At dune crest site, the most depleted $\delta^{18}\text{O}$ values of soil water occurred at 40–60 cm depth (-17.30%), more positive than $\delta^{18}\text{O}$ values of snowmelt but less negative than that of spring rain. This should have been the result of mixing between the snowmelt of the current year and the soil water that existed prior to the event (Gazis and Feng 2004). Our results agree with previous studies showing that snowmelt with low $\delta^{18}\text{O}$ values entered the upper soil horizon and labeled it with isotopically depleted water (Saxena 1984); and deep (>50 cm depth)

soil water could be replaced by snowmelt or substantial rainfall (Gazis and Feng 2004).

The average $\delta^{18}\text{O}$ values of soil water in dune crest were more depleted than that in inter-dune, especially in the deep soil layer (Fig. 2b and d). Soil physical properties differed at these two sites, which may affect the extent to which precipitation will infiltrate to a particular depth (Gazis and Feng 2004; Loik et al. 2004). Soils of dune crests had greater particle size, greater porosity and stable infiltration rate than that of inter-dunes (Wang et al. 2004; Tang et al. 2009). This permits rapid infiltration to deeper layers. Accordingly, precipitation infiltrated much deeper at dune crest than at inter-dune after snowmelt in April, as evidenced by the wetting front down to approximately 100 cm on dune crest but to approximately 40 cm only on inter-dune in April (Fig. 2a and c). Meanwhile, precipitation may suffer less evaporation at dune crest compared with that at inter-dune. In addition, soil at dune crest is easy to lose water and form a dry-soil layer at surface (Fig. 5a and b). As the thickness of the dry-soil layer increases, resistances for evaporation will increase (Barnes and Allison 1983). Hence, soil water in dune crest is less enriched by evaporation and isotopically depleted than that in inter-dune. Due to the isotopic composition of xylem water in the plant represents a mixture of water sources plant absorbed (Ehleringer and Dawson 1992; Ellsworth and Williams 2007), the influence of soil characteristics on isotopic composition of soil water may have significant effects on isotopic compositions of xylem water for *H. ammodendron* and *H. persicum*. This may explain the lower $\delta^{18}\text{O}$ values of xylem water for *H. persicum* than for *H. ammodendron* (Fig. 3).

Seasonal patterns in plant water utilization

H. ammodendron and *H. persicum* exhibited a shift in water use during the growing season. Due to the abundant upper soil water in April (Fig. 2a and c), *H. ammodendron* mainly absorbed shallow soil water while *H. persicum* relied on middle soil water (Fig. 4). The $\delta^{18}\text{O}$ values of soil water in middle soil layer (40–100 cm) on dune crest were more depleted than the upper 40 cm on inter-dune. Therefore, *H. persicum* had a significantly lower $\delta^{18}\text{O}$ signature in xylem water than *H. ammodendron* at the beginning of the growing season. With the long-lasting period of low water content in the shallow and middle soil layers from June to September (Fig. 2a and c), both species explored deep

soil water. *H. ammodendron* mainly used groundwater while *H. persicum* mainly used deep soil water (Fig. 4). Rooting depth and distribution define the depth to or volume from which plants can potentially extract water (Ehleringer et al. 1991; Xu and Li 2006). *H. ammodendron* and *H. persicum* both have roots distributed in the shallow and deep soil layers (Xu and Li 2008; Zou et al. 2010) (Fig. A2), which make it possible for them to shift water utilization among potential water sources. Previous study revealed that plants with roots distributed in the shallow and deep soil layers indeed exhibited a shift in water use from mainly shallow water during the wet season to predominantly deep water during the dry season (Rose et al. 2003; McCole and Stern 2007; Asbjornsen et al. 2008; Hasselquist et al. 2010). The ability to switch rapidly among different water sources could put a plant at an advantage if competition for water occurs within the ecosystem (Ehleringer and Dawson 1992).

H. ammodendron and *H. persicum*, sister taxa, growing on the adjacent inter-dune and dune crest habitats, had distinct water use patterns over the growing season (Fig. 4), which support our first hypothesis. According to Mazer et al. (2010), differences in the physiological performance of wild populations of closely related plant taxa may be the result of environmentally induced phenotypic plasticity or adaptive evolution (or a combination of the two). Different water usage of *H. ammodendron* and *H. persicum* may lead to niche partitioning. The separation of niches among species is expected to reduce the intensity of competition among them and it may thereby promote their coexistence (Fowler 1986).

H. ammodendron and *H. persicum* were conservative in using upper soil water following the relatively large summer precipitations. Rainfall firstly caused a fluctuation in SWC, and then $\delta^{18}\text{O}$ values of soil water and of xylem water changed (Figs. 3 and 5). After 15.1 mm of rainfall in June (on DOY 171), *H. ammodendron* and *H. persicum* decreased their reliance on deeper water sources and increased utilization of upper water sources (Fig. 6). However, *H. ammodendron* mainly took up groundwater and *H. persicum* mainly deep soil water. When an additional 6.7 mm of rainfall occurred at 4 days after the 15.1 mm of rainfall, *H. ammodendron* showed no apparent response. However, for *H. persicum*, the contribution of deep soil water declined to a minimum, from 91–99 to 59–90 % at 3 days after the second rainfall. There may be a threshold for the two species

to respond to the pulse of soil water caused by precipitation, with *H. persicum* possibly having a lower threshold than *H. ammodendron*. Studies have found that deep-rooted species may extract precipitation from upper layers when amounts were above some minimum threshold (Williams and Ehleringer 2000; West et al. 2007). According to Noy-Meir (1973), a number of rainfalls of 10–20 mm at intervals of a few weeks, which just maintain available soil water in the top 30 cm, will be highly advantageous for ephemerals. They will also enhance shrub growth, but survival of shrubs depends on the replenishment of the deep reserve at least once every 1–2 years by 40–100 mm falling in a short period. The 15.1 mm of rainfall in June indeed improved soil water content within 0–40 cm depth (Fig. 5a and b). However, this water may evaporate rapidly in dry summer and thus the two species would have little chance to rely on it. Meanwhile, the 15.1 mm of rainfall produced little recharge of soil water at 40–100 cm. Although the two species had roots distributed continuously throughout the whole soil profile (Xu and Li 2008; Zou et al. 2010) (Fig. A2), it seemed that the most active sites of water absorption were limited to deep soil water or groundwater for them, indicating that roots in the upper soil layer may be inactive due to the long-lasting period of low soil water content (Fig. 2a and c). Moreover, when timing and magnitude of rainfall are uncertain, full response to a simple signal may be premature and may decrease rather than increase plant growth (Noy-Meir 1973). Therefore, *H. ammodendron* and *H. persicum* were conservative in using shallow soil water following these two relatively large summer rainfalls. This confirmed our second hypothesis.

In the study area, temperature and precipitation (especially the extreme precipitation) show an increasing trend in recent 50 years (Li et al. 2013; Chen et al. 2014). Among the four seasons, the winter temperature change has been playing the most important role in the inter-annual change (Li et al. 2012). As *H. ammodendron* and *H. persicum* could use the upper soil water recharged by snowmelt at the beginning of the growing season, increased temperature and precipitation in winter may lead to an early onset of growing and acceleration of water absorption for the two species. If the extreme precipitation occurs in summer occasionally, the long-lasting period of low soil water content may inhibit roots activity in the upper soil layer, making this precipitation of limited use for these two species. If the precipitation occurs in summer heavily and frequently, the upper

roots of the two species are likely to be activated (Xu et al. 2007), therefore, precipitation may change water use patterns of the two species. However, further researches are needed to confirm the impact of climate change on water use patterns of the two *Haloxylon* species.

It was reported that *H. ammodendron* growing on heavy-textured soil mainly used upper soil water driven by precipitation and responded to rain pulses in terms of leaf water potential and transpiration (Xu and Li 2006; Xu et al. 2007). In heavy-textured soil, most feeder roots of *H. ammodendron* were distributed in the upper soil layer, and few feeder roots were distributed in the deeper soil (Xu and Li 2006; Xu et al. 2007), indicating that this species might be able to use deeper water sources at times of extreme drought (Xu and Li 2006; Xu et al. 2007). Compared with *H. ammodendron* growing on heavy-textured soil, *H. ammodendron* growing on sandy soil at inter-dune of the Gurbantonggut Desert developed much deeper and larger root systems (Xu and Li 2008; Zou et al. 2010). In our study, *H. ammodendron* growing on inter-dune had limited use of upper soil water after two relatively large summer rainfalls. The groundwater table was around 4 m deep in the study site and was easily accessible for roots of *H. ammodendron* due to its roots could penetrate 10 m below the surface in sandy soil (Xu and Li 2008). Besides, groundwater represents a reliable water source. In contrast, summer precipitation is variable and easy to evaporate from the soil surface due to high evaporative demand, resulting in reduced infiltration and shallower and short-lived soil moisture resources (Fig. 5a and b). It seems that shallow soil water recharged by precipitation represents a more unreliable water source. The presence of and ability to exploit a deep, reliable water source makes it possible for *H. ammodendron* to survive long periods without rain.

H. persicum growing on dune crest mainly used deep soil water and small amounts of groundwater. *H. persicum* develops deep and large root systems (Fig. A2), so that it was possible for this species to extensively absorb the limited water in the deep soil. The reasons for its limited use of groundwater were inferred as follows. Firstly, due to the average dune height was 11 m (around 15 m above the groundwater table), energy cost might be too high for *H. persicum* to move water up from the groundwater and maintain its normal growth. Secondly, in the study area, soil at inter-

dune is more saline than that at dune crest (Li et al. 2010). Salinity is probably an issue which affects seedling emergence and establishment of *H. ammodendron* and *H. persicum* (Tobe et al. 2000; Song et al. 2005). *H. ammodendron* shows greater adaptability to salinity than does *H. persicum* (Tobe et al. 2000), implying that *H. persicum* is less tolerant to salinity compared with *H. ammodendron* (Tobe et al. 2000; Song et al. 2005). The salinity degree of groundwater in the study area was high (6.1 g L^{-1} , water sample was collected and analyzed in 2009), indicating that groundwater might not be a good water source for *H. persicum* to absorb. Due to comparison studies on the salinity tolerance of the two species were carried out on seedlings (Tobe et al. 2000; Song et al. 2005), how adaptation of *H. persicum* to salinity at later stages remains unclear. Hence, the reason why *H. persicum* had limited use of groundwater needs more explorations.

Conclusions

In this study, we used stable oxygen isotopes to study the dynamics of water usage of two *Haloxylon* species and their responses to the soil water fluctuations resulted from summer precipitation. *H. ammodendron* growing on inter-dune and *H. persicum* growing on the adjacent dune crest had distinct water use patterns and were able to shift water utilization according to the upper soil water content: when the upper soil water content was abundant in early spring, *H. ammodendron* mainly used shallow soil water while *H. persicum* mainly used middle soil water; when the upper soil water content was depleted in summer, *H. ammodendron* mainly used groundwater while *H. persicum* mainly used deep soil water and small amounts of groundwater. Large precipitations in dry summer hardly altered their water use patterns, which mean that these species are rather conservative in water use strategy. The degree to which potential water sources were utilized by these species was largely dependent on specific sites and root distributions. The water use patterns of the two species reflect their adaptations to their specific habitats in this water-limited desert environment.

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