



# Water utilization of typical plant communities in desert steppe, China

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**Abstract:** Water is a limiting factor in the restoration and construction of desert steppe. Exploring plant water sources is necessary to understand soil-plant interactions and species coexistence; however, water sources of major plant communities within the desert steppe of Ningxia Hui Autonomous Region, China remain poorly understood. In this study, we analyzed the water uptake of plants in four typical communities: *Agropyron mongolicum* Keng.; *Sophora alopecuroids* Linn.; *Stipa breviflora* Griseb., and *Achnatherum splendens* (Trin.) Nevski communities. Stable isotopes  $\delta D$  and  $\delta^{18}O$  in the xylem of plant and soil water at different soil depths were analyzed. An IsoSource model was used to determine the soil depths from which plants obtained water. Results showed that *A. mongolicum* community obtained water predominantly from 0–20 and 40–80 cm depth, *S. alopecuroids* community from 0–20 cm depth, *S. breviflora* community from 0–40 cm depth, and *A. splendens* community from 0–20 and 80–140 cm depths. *S. alopecuroides* had a wider range of soil depths for water extraction, i.e., utilizing different water sources depending on habitat, and the plasticity of its water uptake pattern determined its role in different communities. Water source of plants relayed heavily on the distribution of their roots. Competition for soil water exists between different plant life forms in the sierozem habitat (*A. mongolicum*, *S. alopecuroids*, and *S. breviflora* communities), and in the sandy soil habitat (*A. splendens* community). The use of soil water by *A. splendens* community is more spatially differentiated, and shrubs and herbs can coexist stably. Under the pattern of extended drought period in the future, sierozem habitat may be more favorable for the formation of a dominant monoculture community type of perennial fibrous plants. In aeolian sandy soil habitat, *A. splendens* had a strong competitive advantage, and the growth of shallow-rooted plants was easily suppressed.

**Keywords:** stable isotope; water source; IsoSource model; soil water; desert steppe

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## 1 Introduction

Desert steppe is a crucial part of northwestern China's ecological barrier, and is the driest grassland ecosystem type with harsh natural conditions, significant climate fluctuations, fragile ecosystems, and low resilience. Excessive anthropogenic exploitation, regional climate warming, and drying further encourage vegetation degradation and desertification (Kang et al., 2007; Zhou et al., 2021)

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within desert steppe ecosystem. After nearly 40 a of vegetation restoration, efforts across northwestern China including fencing, plantation construction, grassland reseeding, and the establishment of a straw checkerboard, has led to an increase in average grassland coverage from 30% to 56%, effectively mitigating desertification within this region (Li et al., 2006; Li et al., 2013; Liu et al., 2019). Previously, high-density and single-species vegetation restoration has resulted in vegetation density, biomass, and cover that were not compatible with the carrying capacity of water resources (Li et al., 2021). Grassland vegetation restoration still face sustainability issues such as simple community structure, low proportion of dominant species, and fragile ecosystem function (Wu et al., 2008; Li et al., 2014; Pan et al., 2021; Wang et al., 2021). The sierozem and other type of soils have degenerated into aeolian sandy soil and sand-covered sierozem, resulting in variations of water requirement of desert plants (Li et al., 2014; Huang and Zhang, 2016). To further understand the self-sustaining ecological functions of species composition, productivity, stability, and material energy cycle, restoration must focus on the relationship between vegetation and soil water resources (Ru et al., 2015; Song et al., 2018; Wang et al., 2021a). The balance between vegetation and soil within desert grasslands is fragile due to variable soil composition, depth influencing soil water availability, and water uptake patterns for plants (Song et al., 2015; Wu et al., 2016). Thus, exploring the pattern of water resource utilization by different species in desert steppe, and revealing the relationship between plant water use and soil water supply capacity may provide a theoretical basis for sustainable vegetation restoration.

Due to the key role of water in vegetation restoration and construction in desert steppe, fluctuations in precipitation may lead to substantial changes in community composition and ecosystem structure (Adler and Levine, 2007). Therefore, it is necessary to determine the water utilization sources of vegetation in desert steppe and their competitive relationship (Zeng and Ma, 2013; Huang and Zhang, 2015). An effective method for evaluating plant water use strategies includes the use of hydrogen stable isotope tracer techniques (Ehleringer and Dawson, 1992). By analyzing the composition of hydrogen (D and H) and oxygen ( $^{18}\text{O}$  and  $^{16}\text{O}$ ) isotopes in both soil water and xylem water of plants, it is possible to trace water utilization by plants at varying soil depths and further understand vegetative adaption to arid and semi-arid environments (Ehleringer and Dawson, 1992; Zhu et al., 2014).

Additionally, multiple species living in the same habitat may have distinct water use patterns (Eggemeyer et al., 2009; Wu et al., 2016). Based on the theory of niche complementarity (Loreau et al., 2001; Yang et al., 2010), the partitioning of water sources among coexisting species improves the use of available soil water and increases ecosystem resilience to drought (Yang et al., 2010). For example, in arid environments, perennial deep-rooted plants survive by absorbing deep soil water or groundwater, while most annual plants develop shallow roots and make use of short-term precipitation through surface soil (Ehleringer and Dawson, 1992). In the Loess Plateau, *Vitex negundo* Linn. displays a great degree of ecological plasticity as it is able to use water from deeper soils as water stress increases and may successfully coexist with species that use water from surface soil layer (Wang et al., 2017). Some plants show a resource-dependent water use strategy. On the Colorado Plateau, distinct plants compete for use of the same water source: perennial bunch grass with shallow roots, subshrubs with dimorphic roots, and a predominantly deep-rooted woody shrub. Each species depends on deep soil water under drought conditions and shallow soil water under humid conditions (Schwinning et al., 2005). In Inner Mongolia, *Leymus chinensis* (Trin.) Tzvel., *Agropyron cristatum* (Linn.) Gaertn., and *Stipa grandis* P. Smirn. utilize deep soil water when it was available, shifting to rainwater when subsoil water has been depleted (Yang et al., 2010). In desert steppe, three herbaceous plants obtain water mainly from shallow soil as precipitation increases (Hu et al., 2021). The aforementioned studies as well as other relevant literature have focused mainly on the mechanisms of species adaptation to drought, but have not fully established the water use sources of plants and their adaptability to different soil habitats at the community level.

Here, we aim to investigate the water utilization sources of four typical communities

(*Agropyron mongolicum* Keng., *Sophora alopecuroids* Linn., *Stipa breviflora* Griseb., and *Achnatherum splendens* (Trin.) Nevski) in desert steppe of the Haba Lake Nature Reserve in Yanchi County, Ningxia Hui Autonomous Region, China using stable hydrogen and oxygen isotopes. Due to differences in soil water availability and the distribution of plant roots, plants in desert steppe likely have separate ecological niches for obtaining soil water in a limited habitat (Dodd et al., 1998; Eggemeyer et al., 2009; Wu et al., 2016). Therefore, we hypothesize that water sources of the four communities are different, and that the coexisting plants have different water uptake patterns in response to the availability of soil water. The objectives of our study are to: (1) investigate the isotopic composition of soil water and its vertical gradient along soil profile; and (2) compare the water utilization sources of the four communities and their responses to soil water availability.

## 2 Materials and methods

### 2.1 Study area

The study area is located in the Haba Lake Nature Reserve, Yanchi County, Ningxia Hui Autonomous Region of northern China with an altitude of 1300–1622 m a.s.l. (37°36'17"–38°02'04"N; 106°53'23"–107°39'40"E). The area is temperate and semi-arid, with a typical continental monsoon climate. Precipitation is scarce and unevenly distributed during the year, with an average annual precipitation of 298 mm and an average annual evaporation of 2250 mm. The groundwater table is located between 3 and 8 m below the ground surface (Hu et al., 2021). Restricted by regional climate and soil, water availability in the soil layer above 100 cm is most conducive for plant growth, and soil water is the main source for plants (Wang et al., 2021b). The main soil types are sierozem, sand-covered sierozem, and aeolian sandy soil. The main vegetation types are shrubs, herbs, and sand-resistant plants (Song, et al., 2018; Wang, et al., 2021). Four plant communities are widely distributed across the area: *S. breviflora* community, as original zonal vegetation type of desert steppe, is mainly preserved in the sierozem habitat with no or slight desertification, and a hard soil texture; *S. alopecuroids* community and *A. mongolicum* community are mostly located on the slope in the sand-covered sierozem habitat; and *A. splendens* community is located in the low-lying beach, and exists in an aeolian sandy soil habitat.

### 2.2 Experimental design and sample collection

Due to the long-term drought in 2021, the annual precipitation was only 238 mm (Fig. S1). The amount of 56% precipitation events was less than 5 mm. Most precipitation occurs from August to October. There were two main precipitation events before sampling on 8 September: 28.4 mm on 3 September and 6.9 mm on 5 September (Fig. S1). The variation of precipitation  $\delta D$  values ranged from  $-124.9\text{‰}$  to  $21.0\text{‰}$  (Fig. S1). With the increase of precipitation (P), precipitation  $\delta D$  values tended to be depleted ( $\delta D = -4.672P - 2.914$ ,  $R^2 = 0.525$ ,  $P < 0.05$ ). With the decrease in daily mean temperature (T), precipitation  $\delta D$  values decreased ( $\delta D = 14.291T - 307.494$ ,  $R^2 = 0.473$ ,  $P < 0.05$ ).

In 2021, the average soil water content of different plant communities was stable, and there was no significant difference in soil water content of *A. mongolicum*, *S. breviflora*, and *A. splendens* communities from May to November ( $P > 0.05$ ). Soil water content of *S. alopecuroids* community in September had no significant difference with other months ( $P > 0.05$ ; Fig. S2). In addition, through field investigation, after the precipitation event on 3 September, the yellow plants due to drought gradually turned green, and all species grew vigorously in this period. At this time, the competition for available water was the fiercest. Thus, the experiment was conducted on 8 September (Su et al., 2013).

From late July to early September of 2021, ten event-based precipitation samples were collected in the experimental area. The rainwater collector was constructed with a 10-cm diameter funnel and a plastic bottle. We measured the hourly precipitation greater than 0.1 mm as the basis

for the start of precipitation, and considered precipitation to be finished when the hourly value was less than 0.1 mm (Li et al., 2021). Vantage Pro2 automatic weather station was used to record meteorological data such as temperature and precipitation, obtaining weather data every 0.5h. Water samples were collected immediately after precipitation and placed into an 8-mL glass bottle. Samples were immediately sealed with a polyethylene parafilm membrane, stored at  $-20^{\circ}\text{C}$  to prevent water evaporation loss. In each community, five plots of  $1\text{m}\times 1\text{m}$  were established as duplicates, with 20 plots in total (see Table S1 for main plant species in the communities). From May to November of 2021, the volumetric soil water was collected. Volumetric soil water was measured every 15 d using a time domain reflectometry probe. The depth of measuring was 0–140 cm, measured at 20-cm intervals. Plant and soil samples were collected on 8 September, 2021. Ten healthy plants of the same species were selected from each plot. The phloem tissue of plants was removed to avoid isotopic fractionation of xylem water (Dawson, 1996; Wu et al., 2016). Herbaceous plants were also collected from the root crown due to the close relation of their isotopic composition to the source water (Barnard et al., 2006; Wu et al., 2016). All plant samples (92 total) were placed into glass vials with screw caps, sealed with polyethylene parafilm, and kept frozen in a freezer ( $-20^{\circ}\text{C}$ ) for isotopic analysis. There were 140 soil samples in total. Root samples were also taken and sealed in a plastic bag, and brought back to the laboratory for further analysis.

### 2.3 Isotopic analyses

Water extractions from plant xylem and soils, as well as isotopic analyses of samples, were conducted at the Huake Jingxin Stable Isotope Laboratory of Tsinghua University, Shenzhen City, China. Water in plant xylem and soil samples were extracted using a cryogenic vacuum distillation system (Horton et al., 2003; Hu et al., 2021). The isotopic composition of all of the liquid samples, including precipitation, plant and soil water extracts, was analyzed by an Isotope Ratio Mass Spectrometer (IRMS) system (Mat253, Thermo Fisher Scientific, Inc., USA). The measurement precision by IRMS was consistently  $\pm 1\text{‰}$  for  $\delta\text{D}$  and  $\pm 0.2\text{‰}$  for  $\delta^{18}\text{O}$ . The calculation of isotopic ratios was expressed as follows:

$$\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\text{‰}, \quad (1)$$

where  $\delta X$  is the  $\delta\text{D}$  or  $\delta^{18}\text{O}$  (‰); and  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the molar abundance ( $\text{D}^1\text{H}$  and  $^{18}\text{O}/^{16}\text{O}$ ) of the sample and standard, respectively.

### 2.4 Data analyses

To determine the water sources of plants in different communities, we compared the  $\delta\text{D}$  and  $\delta^{18}\text{O}$  values of xylem water and soil water. The similarity in the  $\delta\text{D}$  and  $\delta^{18}\text{O}$  values between sources was used to infer the plant's primary water sources. Under the guidance of isotopic mass conservation theory, this study adopted the IsoSource model (Phillips and Gregg, 2003) to calculate the percent contribution of water sources with the source increment set at 1.0‰ and the mass balance tolerance set at 0.2‰. According to the distribution characteristics of  $\delta\text{D}$  and  $\delta^{18}\text{O}$  values, we combined adjacent soil water layers with similar isotope values into one source and divided the layers into four sources (Phillips, et al., 2005; Hu et al., 2021): (1) 0–20 cm: the highest variation degree, which is vulnerable to meteorological factors such as precipitation and evaporation; (2) 20–40 cm: smaller variation degree than surface layer, which is affected by the mixing of precipitation and original soil water; (3) 40–80 cm: small variation degree, which is affected by large precipitation events; and (4) 80–140 cm: small variation degree with relatively stable.

The equations for calculating the contribution ratio were expressed as Equations 2 and 3:

$$\delta X = a_1\delta S_1 + a_2\delta S_2 + a_3\delta S_3 + a_4\delta S_4, \quad (2)$$

$$a_1 + a_2 + a_3 + a_4 = 1, \quad (3)$$

where  $\delta X$  is the  $\delta D$  or  $\delta^{18}O$ ;  $S_1$ – $S_4$  is the water source at 20-cm intervals; and  $a_1$ – $a_4$  is the proportion of  $S_1$ – $S_4$  for total xylem water absorption.

Statistical analyses were performed in SPSS v.25.0. After testing for the normality of residuals and homogeneity of variances, one-way analysis of variance was used to detect the differences in isotopic composition of plant xylem water and soil water among four communities. The Kruskal-Wallis test was used on the data with uneven variance, and the significance level was set at 0.05. The figures were plotted with OriginPro v.2022.

### 3 Results

#### 3.1 Soil moisture and isotopic composition

Average soil water content of the four communities varied at the time of collection (Fig. S3). On 8 September, average soil water content of *S. alopecuroids* community was 6.57%, which is significantly lower than other communities ( $P < 0.05$ ). Soil water content of *S. alopecuroids* community decreased rapidly in 0–60 cm soil depth, and stabilized in 60–140 cm soil depth. Average soil water contents of *A. splendens*, *A. mongolicum*, and *S. breviflora* communities were 11.42%, 8.84%, and 8.18%, respectively. Changes in soil water contents in these three communities showed a trend of first decreasing from 0 to 60 cm soil depth and then shifting to an increase from 60 to 140 cm soil depth. Soil water content of *A. splendens* community was significantly higher than those of other communities (Fig. S3).

Isotopic compositions of soil water varied with soil depth and plant community types (Figs. 1 and 2). Soil water isotope values of all four communities showed a trend of increasing and then decreasing. *A. mongolicum* community increased from 0 to 80 cm soil depth, then decreased from 80 to 140 cm soil depth. *S. alopecuroids* community increased from 0 to 60 cm soil depth, then decreased from 60 to 140 cm soil depth. *S. breviflora* and *A. splendens* communities increased from 0 to 40 cm soil depth, then decreased from 40 to 140 cm soil depth. Soil moisture in 0–20 cm soil depth was affected by recent precipitation. The depleted isotope composition in this depth was significantly different ( $P < 0.05$ ) than that of 40–140 cm soil depth. There were significant differences ( $P < 0.05$ ) in the isotopic compositions of soil water in 40–140 cm soil depth among different communities. *S. breviflora* community had the highest  $\delta^{18}O$  values, followed by *S. alopecuroids*, *A. splendens*, and *A. mongolicum* communities (Fig. 2). *S. breviflora* community also had the highest  $\delta D$  values, followed by *S. alopecuroids*, *A. mongolicum*, and *A. splendens* communities (Fig. 1).

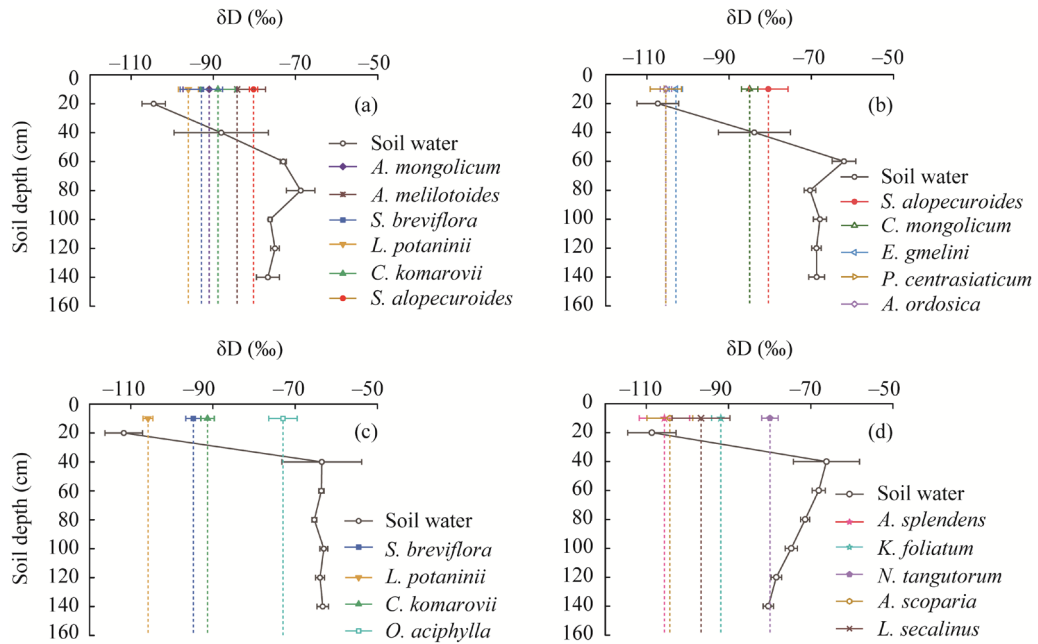
#### 3.2 Isotopic compositions in xylem water

In *A. mongolicum* community,  $\delta D$  values of perennial herbs and subshrubs were significantly different ( $P < 0.05$ ), though  $\delta^{18}O$  values showed no significant difference ( $P > 0.05$ ). In *S. alopecuroids* community, there was no significant difference ( $P > 0.05$ ) in isotopic compositions among annual herbs, perennial herbs, and subshrubs. In *S. breviflora* community, there was no significant difference ( $P > 0.05$ ) in isotopic compositions between subshrubs and perennial herbs. In *A. splendens* community, there was a significant difference in isotopic compositions between shrubs and perennial herbs (Table 1).

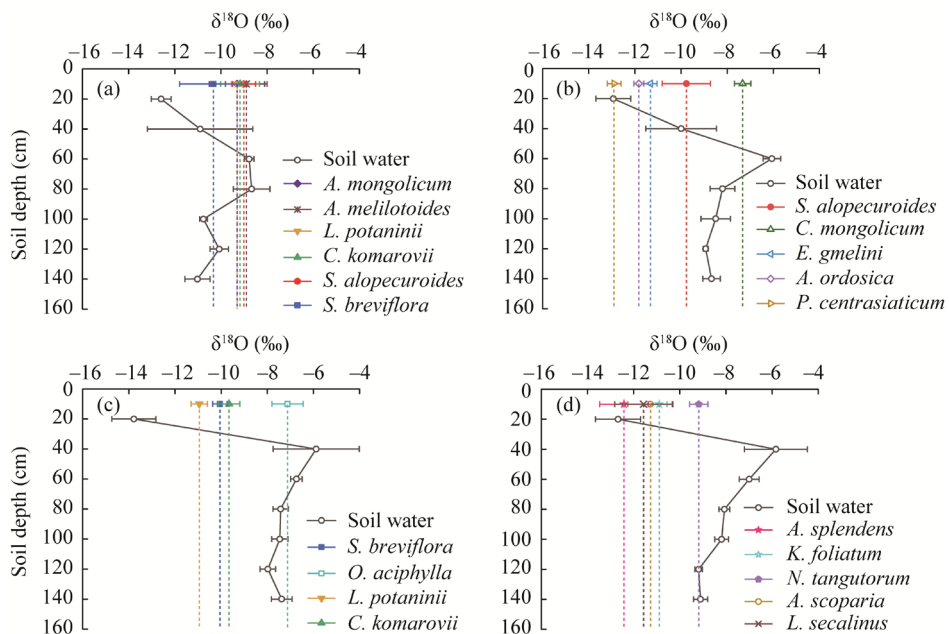
$\delta D$  and  $\delta^{18}O$  values of annual herbs showed no significant difference ( $P > 0.05$ ) across different communities.  $\delta D$  values and  $\delta^{18}O$  values of perennial herbs were significantly different in different communities ( $P < 0.05$ ). Isotope values of perennial herbs in *A. splendens* community were significantly lower than those in *A. mongolicum* community.  $\delta D$  values of subshrubs were not significantly different ( $P > 0.05$ ) in different communities, but  $\delta^{18}O$  values were significantly different ( $P < 0.05$ ) in those communities (Table 1). Negative isotope values of subshrubs in *S. alopecuroids* community exceeded those of other communities.

#### 3.3 Proportion of plant water uptake in different communities

$\delta D$  and  $\delta^{18}O$  values indicate that plants in *A. mongolicum* community derived most of their water



**Fig. 1**  $\delta D$  value of soil depth (0–140 cm) and xylem water (vertical dashed line) in different plant communities. Bars represent standard errors. (a), *A. mongolicum* community; (b), *S. alopecuroides* community; (c), *S. breviflora* community; (d), *A. splendens* community.



**Fig. 2**  $\delta^{18}O$  value of soil depth (0–140 cm) and xylem water (vertical dashed line) in different plant communities. Bars represent standard errors. (a), *A. mongolicum* community; (b), *S. alopecuroides* community; (c), *S. breviflora* community; (d), *A. splendens* community.

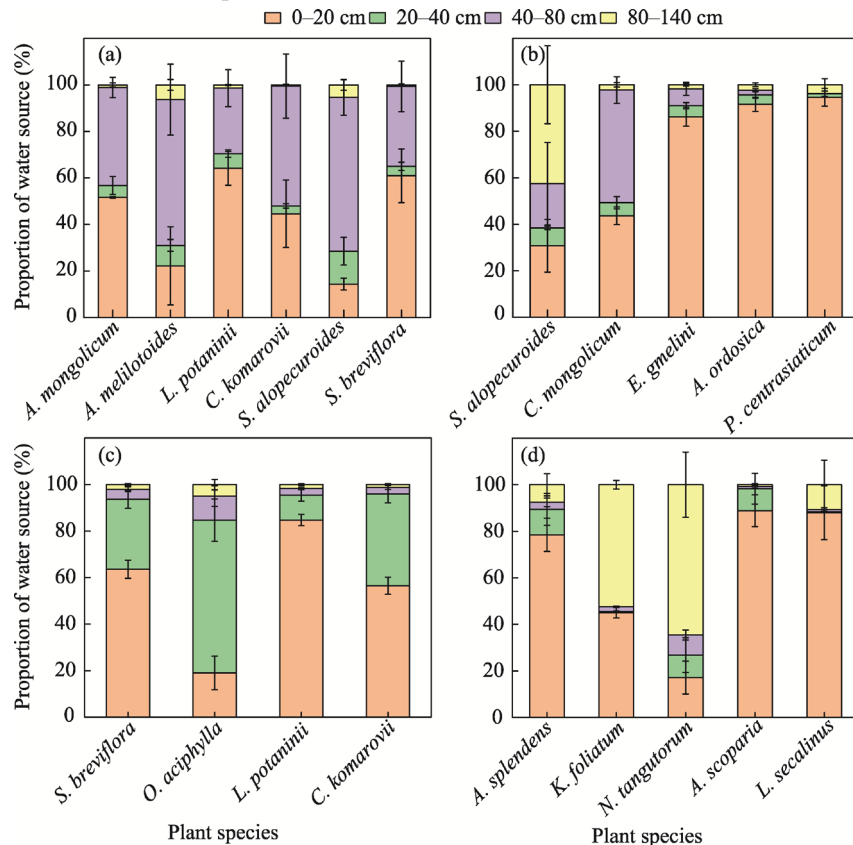
from 0 to 80 cm soil depth, while plants in *S. alopecuroides*, *S. breviflora*, and *A. splendens* communities derived most of their water from 0 to 40 cm soil depth (Figs. 1 and 2). According to IsoSource model (Fig. 3), plants in *A. mongolicum* community mainly absorbed water from 0 to 20 cm (43.88%) and from 40 to 80 cm (46.59%) soil depths. Plants in *S. alopecuroides* community mainly absorbed water from 0 to 20 cm (71.16%) soil depth. Plants in *S. breviflora* community

**Table 1** Comparison of  $\delta D$  and  $\delta^{18}O$  values of xylem water of different life forms in four plant communities

Community type	Life form	$\delta D$ (‰)	$\delta^{18}O$ (‰)
<i>A. mongolicum</i>	Herbaceous perennial	$-85.05 \pm 2.01^{Aa}$	$-8.74 \pm 0.41^{Aa}$
	Subshrub	$-96.08 \pm 2.43^{Ab}$	$-9.30 \pm 0.25^{Aa}$
<i>S. alopecuroides</i>	Annual	$-93.97 \pm 3.17^{Aa}$	$-9.32 \pm 0.69^{Aa}$
	Herbaceous perennial	$-91.54 \pm 4.84^{ABa}$	$-11.17 \pm 0.70^{BCa}$
	Subshrub	$-105.36 \pm 1.30^{Aa}$	$-11.82 \pm 0.48^{Ba}$
<i>S. breviflora</i>	Herbaceous perennial	$-93.03 \pm 1.29^{ABa}$	$-9.85 \pm 0.27^{ABa}$
	Subshrub	$-89.37 \pm 5.73^{Aa}$	$-9.04 \pm 0.73^{Aa}$
<i>A. splendens</i>	Annual	$-104.30 \pm 5.58^{Ab}$	$-11.27 \pm 0.98^{Aa}$
	Herbaceous perennial	$-110.50 \pm 4.20^{Bb}$	$-13.63 \pm 0.79^{Cb}$
	Shrub	$-84.40 \pm 2.60^a$	$-9.82 \pm 0.41^a$

Note: Different uppercase letters within the same life form indicate significant differences among different communities at  $P < 0.05$  level. Different lowercase letters within the same community indicate significant differences among different life form at  $P < 0.05$  level.

mainly absorbed water from 0 to 20 cm (55.93%) and from 20 to 40 cm (36.55%) soil depths. Plants in *A. splendens* community mainly absorbed water from 0 to 20 cm (62.92%) and from 80 to 140 cm (26.39%) soil depths. Annual herbs and perennial herbs predominantly extracted water from 0 to 20 cm (72.93% and 55.07%) and from 40 to 80 cm (18.87% and 26.09%) soil depths. Subshrub predominantly extracted water from 0 to 20 cm (64.84%) and from 20 to 40 cm (21.74%) soil depths. Shrub predominantly extracted water from 0 to 20 cm (31.07%) and from 80 to 140 cm (58.52%) soil depths.



**Fig. 3** Mean proportion of water source for each species in different plant communities. Bars represent standard errors. (a), *A. mongolicum* community; (b), *S. alopecuroides* community; (c), *S. breviflora* community; (d), *A. splendens* community.

## 4 Discussion

### 4.1 Isotopic compositions in soil water

In our study,  $\delta D$  and  $\delta^{18}O$  values of xylem water of plants closely resemble those of soil water, indicating a likely dependence by plants on soil water.  $\delta D$  values and  $\delta^{18}O$  values of soil water in four plant communities increased, then decreased slightly before stabilizing as soil depth increased, which is consistent with previous studies (Zhu et al., 2020; Gao et al., 2021). A possible explanation for these trends may be the fact that vertical gradient of soil water was simultaneously influenced by evaporation and infiltration; as soil vertical gradient water mixed with rainwater, significant fluctuations in isotopic compositions of shallow soil water occur (Penna et al., 2018; Sprenger et al., 2018). In our study, isotopic compositions of soil water in 0–20 cm soil depth was the lowest, and varied significantly from that of soil depths greater than 40 cm (Figs. 1 and 2). Shallow soil water is greatly affected by meteorological factors such as precipitation and evaporation. Soil water isotopic compositions in 0–20 cm soil depth resembled that of precipitation on 3 September ( $\delta D$ :  $-115.3\text{‰}$  ( $\pm 9.6\text{‰}$ );  $\delta^{18}O$ :  $-15.9\text{‰}$  ( $\pm 1.1\text{‰}$ )). Isotope values of soil water in 20–80 cm soil depth were higher than that of surface depth, which reflected that soil water in this depth resulted from a mixture of recent precipitation events (Liu et al., 2021). Rainwater moves through soil pores, and then mixes with the existed soil water, resulting in vertical change of isotopic compositions (Eggemeyer et al., 2009; Wang et al., 2017). In desert steppe, rainfall is generally difficult to replenish directly to 80–140 cm soil depth. Additionally, soil water at deeper depths largely comes from precipitation after growing season and large snow melting in spring. However, these events do not frequently occur in desert environments, annual isotopic values of deep soil water remain relatively stable (Liu et al., 2020).

There was no significant difference in soil water isotopes between 0 and 40 cm soil depth across different communities ( $P > 0.05$ ), there was a significant difference in soil water isotopes below 40 cm ( $P < 0.05$ ). The difference in soil water isotopes at shallow depths may be contributed to the direct effects of precipitation and evaporation. Evaporation has little effect below 40 cm, and infiltration and migration of water in deep soil continues to increase (Zhang et al., 2017). Soil physical properties differ among different soil depths, which may affect the extent to which precipitation, infiltration, and evaporation influence the depth of soil water and isotopic composition (Wu et al., 2016). In *S. alopecuroides* community, soil from 0 to 50 cm depth was sand-covered sierozem; from 50 to 80 cm depth was calcium accumulation; and from 80 to 140 cm depth was weathered bedrock residual soil (Fig. S4). Sand-covered sierozem had greater particle size and porosity than calcium accumulation soil. Thus, water is able to infiltrate the soil rapidly from 0 to 60 cm depth. Calcium accumulation soil possessed a hard texture and compact structure that hindered water infiltration, implying that soil water below 60 cm depth remained stable with a low percentage of water, as demonstrated by wetting front and isotopic front down to 60 cm depth (Figs. 1, 2 and S3). The highest isotope values occurred in 60 cm soil depth (Figs. 1 and 2). This is likely due to precipitation that occurred prior to sampling has a weak effect on this soil depth. Other influential factors may include the long-term unsaturated state of soil water, the continuous movement of soil water from liquid to gas, and continuous fractionation and enrichment (Zhu et al., 2014). Soil profile of *A. splendens* community was aeolian sandy soil with a high sand content. Its loose soil structure and large pores resulted in strong soil permeability. Compared with other communities, water seepage velocity was rapid, so the deep soil water possessed negative isotope values due to the replenishment of precipitation. Soil water isotope values of *S. breviflora* exceeded that of *A. mongolicum* community. Both soil types were sierozem, but the soil of *A. mongolicum* community was coarser. The difference in soil water isotope values may be due to the coarse texture of the shallow soil of *A. mongolicum* community, which was conducive to water infiltration. Soil texture of *S. breviflora* community was hard, rendering water infiltrations difficult. Instead, water accumulated on the surface soil depth, which does not significantly influence the water isotope composition of deep soil. Furthermore, soil water isotope values may be also related to the distribution of plant roots (Fig. S3). Plant root zones in *A.*



*mongolicum* community may aid the infiltration of precipitation into the deep soil depth through preferential flow (Wu, et al., 2016), resulting in negative isotope values in 80–140 cm soil depth. Additionally, hydraulic redistribution of soil profile water by roots may change the isotope value of soil water (Wu, et al., 2016). In summary, soil moisture from 0 to 20 cm depth was most affected by precipitation, while the response of soil moisture to precipitation lessened with increasing depth. Soil from 40 to 140 cm depth appeared to be more regulated by soil texture, and the vertical distribution of soil moisture varied among habitats. Soil moisture of *A. splendens* community was significantly higher than that of other communities, especially in deeper soil, indicating that precipitation effectively replenished the aeolian sandy soil habitat. Soil types of *S. alopecuroids*, *A. mongolicum*, and *S. breviflora* communities were all sierozem, but their desertification degree varied. Soil moisture in 0–40 cm depth was the highest in *S. alopecuroids* community, followed by *A. mongolicum* community, and then *S. breviflora* community.

#### 4.2 Water uptake patterns at different communities

All four communities displayed a high utilization degree of 0–20 cm soil water, which is likely due to the fact that a high proportion of roots was found in the upper 20 cm of soil (Fig. S3). Plant water sources were related with their respective proportion of fine roots (Ellsworth and Sternberg, 2015). Species that have shallow root systems might have denser root hairs and increased absorption areas in surface soil depth, which contributes to surface water usage (Schenk and Jackson, 2005; Wang et al., 2017). Soil moisture in 0–20 cm depth in desert steppe was significantly affected by precipitation (Wang et al., 2003). In this study, precipitation amount of 28.4 mm, occurred before sampling increased soil moisture of surface soil depth. Plants mainly used shallow soil water when possible, to mitigate energy consumption (Lv et al., 2017). Most plants in a semi-arid steppe can reach the depth of 20 cm in their life history (Wang et al., 2021). For areas with limited precipitation gradients, habitat differences become key factors affecting soil water availability (Moeslund et al., 2013; Wang et al., 2021). For example, Chen et al. (2019) found that niche breadth of the same species varied across different habitats. Certain species that were dominant in one habitat were the auxiliary species in another, mainly due to the fact that different habitat conditions lead the same species to develop into different niches. The variation in water uptake patterns could lead to ecological niches distinguished by complementary uses of resources, which facilitates species coexistence (Asbjornsen et al., 2008). Plants optimize their water intake strategy through self-regulation (Zhou et al., 2013). Among *A. mongolicum* communities, deep-rooted *S. alopecuroides* mainly absorbed water from 40 to 80 cm soil depth. As the dominant plant in a vegetation community, *S. alopecuroids* absorbed water from 80 to 140 cm soil depth, in addition to shallow water depth (Fig. 3). Generally, when available, plant roots will extract resources from shallow depth to minimize energy expenditure (Ogle and Reynolds, 2004; Wu et al., 2016). Because soil water content of *A. mongolicum* community was high, *S. alopecuroides* tended to use relatively shallow soil water. Soil water content of *S. alopecuroids* community was low, so *S. alopecuroids* not only absorbed available shallow soil water but also extracted deep soil water to cope with drought, making use of more stable deep soil water. Deeper soil water was less exposed to evaporation, and competition for it was less severe (Cristina et al., 2012). *S. alopecuroides* utilized different water sources based on environmental context, indicating that its root water-absorbing mode was plastic and able to adapt to soil water conditions. Plasticity of plant water use strategies determines plant role (dominant species or auxiliary species) in a given community, enabling stable coexistence of different species and adaptation to different habitats (Asbjornsen et al., 2008).

There was a significant difference in  $\delta D$  values of xylem water between perennial herbs and subshrubs in *A. mongolicum* community, but there was no significant difference in  $\delta^{18}O$  values (Table 1). Differences in  $\delta^{18}O$  values may be due to the isotope fractionation of xerophytes or that the difference between hydrogen atoms and their isotopes exceeded that of oxygen atoms (Zheng et al., 2015). In various ecosystems, different species divide soil water resources in space (Ehleringer and Dawson, 1992; Dodd et al., 1998; Yang et al., 2010). Soil type of *A. mongolicum*

was sand-covered sierozem, and water was concentrated on the surface and in the deep soil depth. Both perennial herbs and subshrubs mainly utilized moisture in 0–20 and 40–80 cm soil depths (Fig. 3). With similar water absorption horizons, *A. mongolicum* and *L. potaninii* likely compete for water availability (Zeng and Ma, 2013).

In *S. alopecuroids* community, there was no significant difference in isotope compositions among subshrubs, perennial herbs and annual herbs (Table 1), indicating that they competed water from the same soil depth. In addition to surface soil water, *S. alopecuroids* and *C. mongolicum* would utilize water from 80 to 140 cm and from 40 to 80 cm soil depths, respectively, to avoid resource competition (Fig. 3). The ability to maintain water utilization at optimal soil depth may explain the fact that *S. alopecuroids* became the dominant species. Subshrubs and herbs had the same water uptake patterns, and both tended to utilize surface soil water (Fig. 3), which is consistent with the findings of Zhu et al. (2020). Because subshrubs had a more developed root system than herbaceous plants, when faced with water deficits, subshrubs can take advantage of this morphological advantage by increasing water absorption capacity to resist drought (Jin et al., 2021). Subshrubs may have occupied a strong competitive position, which was not conducive to the formation and development of herbaceous depth, and hindered the restoration and construction of grassland plant diversity (Li et al., 2021).

In *S. breviflora* community, there was no significant difference in isotope compositions between subshrubs and perennial herbs, which compete for soil moisture in 0–40 cm soil depth (Table 1). *S. breviflora* community was mainly located in the non-desert sierozem habitat. Soil texture of this habitat was hard with a high clay content. After precipitation, soil was difficult to infiltrate, but stored more water in 0–40 cm soil depth (Fig. S3). These depths were subject to high evaporative losses, resulting in a transient water resource in the topmost soil depths (Dodd et al., 2002). Perennial drought-tolerant plants with fine branches, such as *S. breviflora*, have high root density in a small range of soil. These roots enable the plant to be highly competitive in accessing any small and transient pools of available soil water in the surface soil depth (Dodd et al., 2002). In addition, *S. breviflora* community thrived in high terrain, and plants in the high terrain use more shallow soil water than those in the low terrain (Nippert and Knapp, 2007; Zhu et al., 2014). In the study area, most precipitation was less than 10.0 mm. The amount of precipitation influenced soil moisture in 0–20 cm soil depth, rendering shallow soil suitable for the survival of dominant tufted grasses such as *S. breviflora* (Ohte et al., 2003). In this study, 60%–63% of water in *S. breviflora* came from 0–20 cm soil depth (Fig. 3). *S. breviflora* are considered nurse plants in arid ecosystems as they have positive effects on other species (Wang et al., 2018), though this positive effect depends on soil moisture condition. When soil water was scarce, *S. breviflora* negatively impacted the annual plant community, which eventually resulted in a decrease of grassland diversity (Miguel et al., 2016). Given the low level of precipitation, there were basically no annual plants in *S. breviflora* and *A. mongolicum* communities. The lack of plant diversity within these communities indicates that drought caused *S. breviflora* to become competitive, rather than facilitating the growth of other plants. Future prolonged drought intervals in semi-arid steppes (Chen and Wang, 2012) populated by sierozem habitats with poor water resources may result in the formation of communities dominated by perennial fibrous root plants.

In *A. splendens* community, there were significant differences in isotopic compositions among shrubs, perennial herbs, and annual herbs (Table 1), indicating that in *A. splendens* community, different plants absorb water from different soil depths. Shrubs make more use of deep soil water, with a utilization rate in 80–140 cm soil water greater than 50% (Fig. 3). *A. splendens* community was low-lying, and located in an aeolian sandy soil habitat, with coarse-textured topsoil that allowed precipitation to enter the subsoil and accumulate in deeper soil depths (Dodd et al., 2002). The deep-rooted shrubs allow them access to subsoil moisture resources that are unavailable to shallow-rooted companion species (e.g., grasses) (Dodd et al., 2002). Asbjornsen et al. (2008) found that water absorption depth of two annual crops was less than 20 cm during the growing season, and the depth range of water extraction during the growing season was relatively narrow, indicating that water absorption ecological plasticity was low. *Artemisia scoparia* Waldst. et Kit.,

an annual plant, is a typical R-strategy species, i.e., it produces a large number of small individual offspring, and has strong seed reproduction ability. Once the conditions are suitable, they will germinate in large quantities. The plant species has strong adaptive characterizes that allow it to successfully invade and settle in different habitats. *A. scoparia* grows rapidly in rain, and has a high diffusion ability (Chen et al., 2019). Plant species with an "opportunistic" water use strategy depend heavily on shallow soil water (<40 cm) even in a drought period (Cristina et al., 2012). These plants depend heavily on a fluctuating and shallow soil water pool that is subjected to rapid evaporation and uptake by competitors in semi-arid habitats (Cristina et al., 2012). Root absorption depth of *A. splendens* responded to these changes in soil water. The lateral roots used shallow soil water during wet season, while the axial root absorbed deep soil water during dry season (Wu et al., 2015). In this study, *A. splendens* mainly used surface soil moisture, which may be due to the soil moisture caused by precipitation before sampling. Additionally, water absorption depth of roots can be altered by root plasticity, implying that *A. splendens* out-competed associated plants with shallow roots. And continuous drought inhibits shallow-root plants. Even if precipitation causes germination during growing season, there may be insufficient water in the soil after a long period of drought to maintain annual plants growth.

## 5 Conclusions

The IsoSource model based on stable  $\delta D$  and  $\delta^{18}O$  was applied to determine water uptake patterns of four plant communities in desert steppe of northwestern China. The isotopic compositions of shallow soil water were more enriched. Soil characteristics and texture strongly affected the vertical distribution of soil water content and isotopic composition in deep soil depth by affecting water infiltration.

All four plant communities had high utilization degree of surface soil water. *S. alopecuroids* and *S. breviflora* communities obtained water predominantly from shallow soil depths, while *A. mongolicum* and *A. splendens* were capable of obtaining water from both shallow and deep soil depths. *S. alopecuroides* had a wider range of soil depths for water extraction, indicating greater ecological plasticity and favorable adaptation to drought environment. *S. breviflora*, *A. scoparia* and *L. secalinus* had narrower ranges, and utilized surface level water, relating to the distribution range of their root system. The difference of soil habitat leads to the difference of soil water availability, which in turn affects the water use patterns of plants and the spatial differentiation of plant communities. Competition for soil water exists between different plant life forms in the sierozem habitats (*A. mongolicum*, *S. alopecuroids*, and *S. breviflora* communities). Precipitation replenishes the aeolian sandy soil habitat (*A. splendens* community) more effectively, and the use of soil water by this community is more spatially differentiated. Thus, shrubs and herbs can coexist stably in *A. splendens* community. Our study provides a reference for determining the allocation and proportional contribution of water resources, and provides a basis for ecological management and vegetation restoration of desert steppe.

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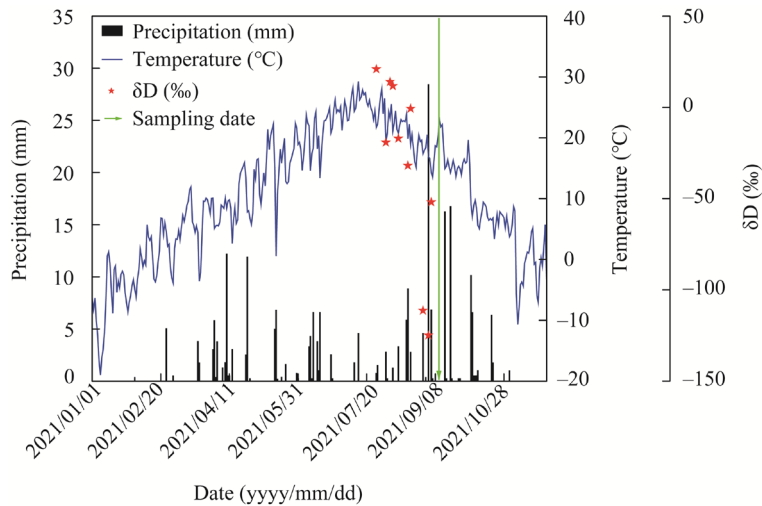
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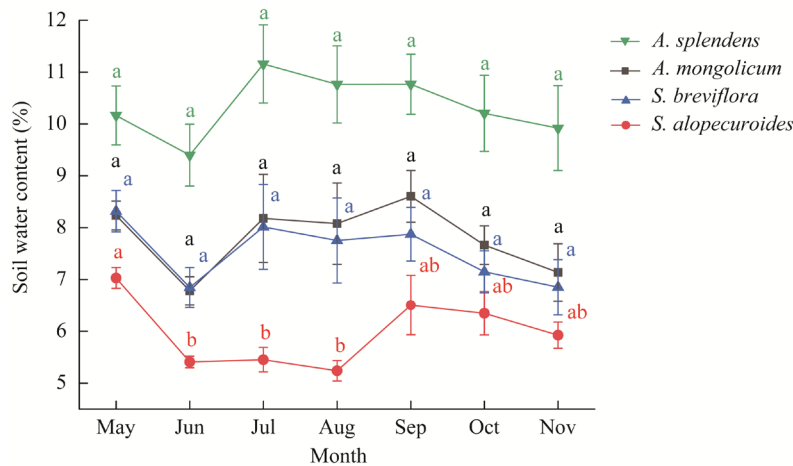
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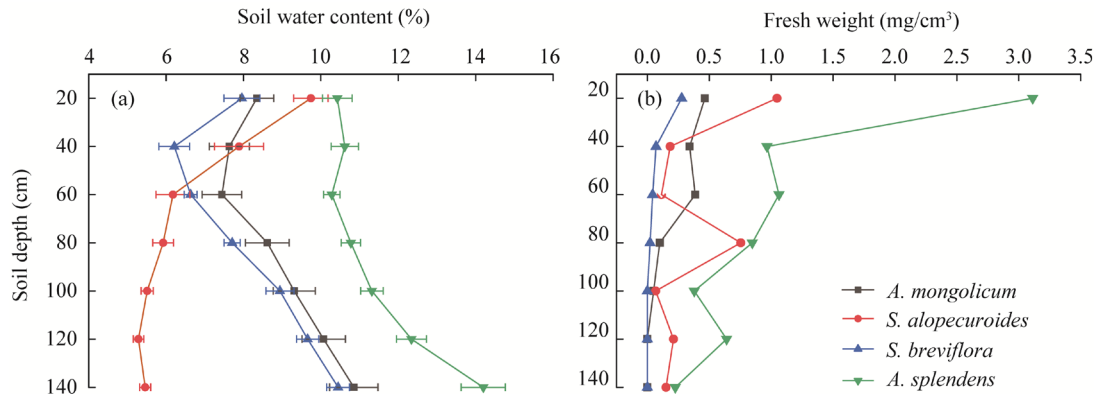
# Appendix



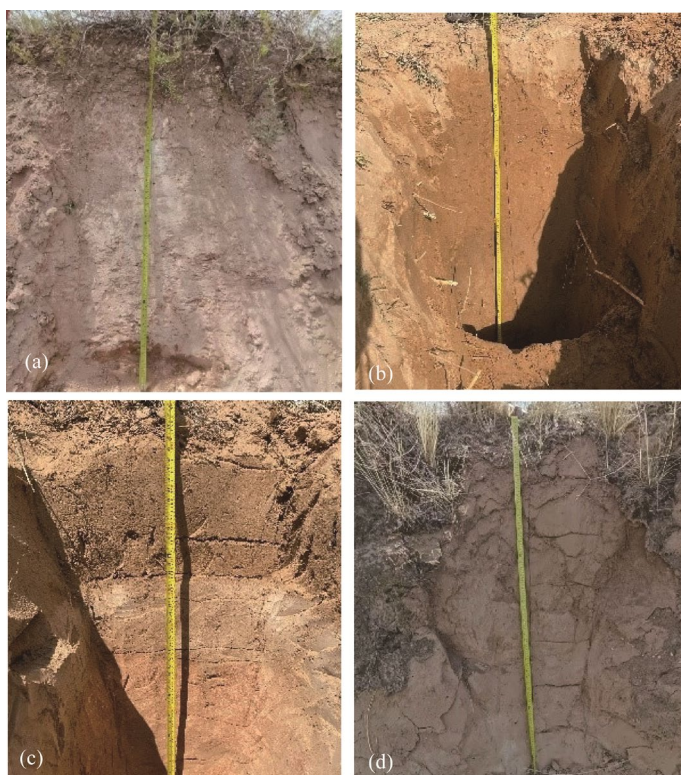
**Fig. S1** Daily precipitation, fluctuation of  $\delta D$  values for precipitation event, and average daily temperature in 2021. Arrow indicates sampling date.



**Fig. S2** Soil water content from May to November of 2021. Different lowercase letters indicate a significant levels of soil water content in different months within the same community type at  $P < 0.05$  level. Bars are standard errors.



**Fig. S3** (a), soil water content in different soil layer; (b), vertical distribution of root fresh weight in different plant communities. Bars are standard errors.



**Fig. S4** Photograph of soil profile of four communities. (a), *A. mongolicum*; (b), *S. alopecuroids*; (c), *S. breviflora*; (d), *A. splendens*.



**Table S1** Basic information of four typical communities and isotopic composition of xylem water

Community	Species	Abbreviation	Family	Life form	Abundance	Coverage (%)	Important value	$\delta D$ (‰)	$\delta O$ (‰)
Agropyron mongolicum Community	<i>Agropyron mongolicum</i>	<i>A. mongolicum</i>	Gramineae	Herbaceous perennial	15.00±1.76	3.73±0.53	0.27±0.08	-86.73±3.82 <sup>ab</sup>	-7.89±0.81 <sup>a</sup>
	<i>Astragalus melilotoides</i>	<i>A. melilotoides</i>	Leguminosae	Herbaceous perennial	3.36±0.69	0.95±0.21	0.09±0.01	-79.66±4.72 <sup>a</sup>	-8.04±0.71 <sup>a</sup>
	<i>Lespedeza potaninii</i>	<i>L. potaninii</i>	Leguminosae	Subshrub	4.54±0.79	1.33±0.25	0.06±0.01	-96.08±2.43 <sup>b</sup>	-9.30±0.25 <sup>a</sup>
	<i>Cynanchum komarovii</i>	<i>C. komarovii</i>	Asclepiadaceae	Herbaceous perennial	1.89±0.39	0.94±0.20	0.09±0.01	-88.87±4.20 <sup>ab</sup>	-9.17±0.84 <sup>a</sup>
	<i>Sophora alopecuroides</i>	<i>S. alopecuroides</i>	Leguminosae	Herbaceous perennial	5.50±0.69	1.40±0.17	0.12±0.01	-77.13±2.16 <sup>a</sup>	-8.26±0.55 <sup>a</sup>
Sophora alopecuroides Community	<i>Stipa breviflora</i>	<i>S. breviflora</i>	Gramineae	Herbaceous perennial	19.67±3.22	2.50±0.34	0.17±0.02	-92.89±5.16 <sup>b</sup>	-10.33±1.47 <sup>a</sup>
	<i>Sophora alopecuroides</i>	<i>S. alopecuroides</i>	Leguminosae	Herbaceous perennial	8.40±1.00	3.33±0.30	0.34±0.02	-80.44±4.76 <sup>a</sup>	-9.77±1.04 <sup>b</sup>
	<i>Corispermum mongolicum</i>	<i>C. mongolicum</i>	Chenopodiaceae	Annual	44.00±14.57	1.50±0.50	0.17±0.04	-84.99±2.02 <sup>a</sup>	-7.33±0.35 <sup>a</sup>
	<i>Echinops gmelini</i>	<i>E. gmelini</i>	Compositae	Annual	25.00±6.14	1.25±0.21	0.25±0.14	-102.94±1.60 <sup>b</sup>	-11.33±0.29 <sup>c</sup>
	<i>Artemisia ordosica</i>	<i>A. ordosica</i>	Compositae	Subshrub	-	-	-	-105.36±1.38 <sup>b</sup>	-11.83±0.22 <sup>cd</sup>
Stipa breviflora Community	<i>Pennisetum centrasiaticum</i>	<i>P. centrasiaticum</i>	Gramineae	Herbaceous perennial	9.33±1.10	-	0.04±0.004	-105.68±2.61 <sup>b</sup>	-12.99±0.37 <sup>d</sup>
	<i>Stipa breviflora</i>	<i>S. breviflora</i>	Gramineae	Herbaceous perennial	30.86±3.62	6.33±0.39	0.40±0.02	-94.74±1.84 <sup>b</sup>	-10.05±0.31 <sup>b</sup>
	<i>Oxytropis aciphylla</i>	<i>O. aciphylla</i>	Leguminosae	Subshrub	2.43±0.69	1.5±0.27	0.07±0.02	-72.94±3.46 <sup>a</sup>	-7.12±0.68 <sup>a</sup>
	<i>Lespedeza potaninii</i>	<i>L. potaninii</i>	Leguminosae	Subshrub	2.13±0.58	0.83±0.17	0.05±0.01	-105.78±1.20 <sup>c</sup>	-10.95±0.36 <sup>b</sup>
	<i>Cynanchum komarovii</i>	<i>C. komarovii</i>	Asclepiadaceae	Herbaceous perennial	1.60±0.13	0.96±0.13	0.12±0.01	-91.32±1.64 <sup>b</sup>	-9.66±0.47 <sup>b</sup>
Achnatherum splendens Community	<i>Achnatherum splendens</i>	<i>A. splendens</i>	Gramineae	Herbaceous perennial	2.93±0.46	17.20±1.36	0.48±0.02	-105.61±6.13 <sup>bc</sup>	-12.42±1.05 <sup>bc</sup>
	<i>Kalidium foliatum</i>	<i>K. foliatum</i>	Chenopodiaceae	Shrub	2.00±0.00	3.00±2.00	0.06±0.03	-91.88±2.25 <sup>ab</sup>	-10.89±0.34 <sup>ab</sup>
	<i>Nitraria tangutorum</i>	<i>N. tangutorum</i>	Zygophyllaceae	Shrub	28.10±12.72	3.15±0.85	0.15±0.02	-79.92±1.98 <sup>a</sup>	-9.18±0.40 <sup>a</sup>
	<i>Artemisia scoparia</i>	<i>A. scoparia</i>	Compositae	Annual	92.33±9.50	1.75±0.29	0.30±0.02	-104.28±5.58 <sup>bc</sup>	-11.27±0.98 <sup>ab</sup>
	<i>Leymus secalinus</i>	<i>L. secalinus</i>	Gramineae	Herbaceous perennial	44.40±21.02	1.00±0.00	0.19±0.05	-115.37±7.04 <sup>c</sup>	-14.85±1.25 <sup>c</sup>

Note: Different lowercase letters within the same community indicate significant differences among different plant species at  $P<0.05$  level. - means no value.