Water Utilization of Typical Plant Communities in Desert Steppe, China (Postprint)

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Abstract

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Full Text

Preamble

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 ecosystems. Exploring plant water sources is essential for understanding 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. This study analyzed water uptake patterns in four typical communities: *Agropyron mongolicum* Keng., *Sophora alopecuroids* Linn., *Stipa breviflora* Griseb., and *Achnatherum splendens* (Trin.) Nevski. Stable isotopes δD and δ^{18}O in plant xylem and soil water at different depths were analyzed, and an IsoSource model was used to determine the soil depths from which plants obtained water. Results showed that the *A. mongolicum* community obtained water predominantly from 0–20 cm and 40–80 cm depths, the *S. alopecuroids* community from 0–20 cm depth, the *S. breviflora* community from 0–40 cm depth, and the *A. splendens* community from 0–20 cm and 80–140 cm depths. *S. alopecuroides* exhibited a wider range of soil depths for water extraction, utilizing different water sources depending on habitat, and the plasticity of its water uptake pattern determined its role in different communities. Plant water sources depended heavily on root distribution patterns. Competition for soil water exists between different plant life forms in sierozem habitats (*A. mongolicum*, *S. alopecuroids*, and *S. breviflora* communities) and in sandy soil habitats (*A. splendens* community). The *A. splendens* community showed more spatially differentiated soil water use, enabling stable coexistence of shrubs and herbs. Under future scenarios of extended drought periods, sierozem habitats may favor the formation of dominant monoculture communities of perennial fibrous-rooted plants. In aeolian sandy soil habitats, *A. splendens* demonstrated strong competitive advantage, while 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 constitutes a crucial component of northwestern China's ecological barrier and represents the driest grassland ecosystem type, characterized by harsh natural conditions, significant climate fluctuations, fragile ecosystems, and low resilience. Excessive anthropogenic exploitation, regional climate warming, and drying further accelerate vegetation degradation and desertification within desert steppe ecosystems (Kang et al., 2007; Zhou et al., 2021). After nearly 40 years of vegetation restoration efforts across northwestern China—including fencing, plantation construction, grassland reseeding, and straw checkerboard establishment—average grassland coverage has increased from 30% to 56%, effectively mitigating desertification in the region (Li et al., 2006; Li et al., 2013; Liu et al., 2019). However, previous high-density, single-species restoration approaches have resulted in vegetation density, biomass, and cover that exceed the carrying capacity of water resources (Li et al., 2021). Grassland vegetation restoration continues to face sustainability challenges, including 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).

Sierozem and other soil types have degenerated into aeolian sandy soil and sand-covered sierozem, creating variations in water requirements for desert plants (Li et al., 2014; Huang and Zhang, 2016). To further understand the self-sustaining ecological functions related to species composition, productivity, stability, and material-energy cycling, restoration efforts 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 in desert grasslands is fragile due to variable soil composition and depth, which influence soil water availability and plant water uptake patterns (Song et al., 2015; Wu et al., 2016). Thus, exploring water resource utilization patterns by different species in desert steppe and revealing the relationship between plant water use and soil water supply capacity can provide a theoretical basis for sustainable vegetation restoration.

Given water's key role 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, determining water utilization sources of vegetation in desert steppe and their competitive relationships is essential (Zeng and Ma, 2013; Huang and Zhang, 2015). Hydrogen stable isotope tracer techniques offer an effective method for evaluating plant water use strategies (Ehleringer and Dawson, 1992). By analyzing hydrogen (D and H) and oxygen (^{18}O and ^{16}O) isotope composition in both soil water and plant xylem water, researchers can trace water utilization at varying soil depths and understand vegetative adaptation to arid and semi-arid environments (Ehleringer and Dawson, 1992; Zhu et al., 2014).

Multiple species coexisting in the same habitat may exhibit distinct water use patterns (Eggemeyer et al., 2009; Wu et al., 2016). Based on niche complementarity theory (Loreau et al., 2001; Yang et al., 2010), 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 utilize short-term precipitation through surface soil (Ehleringer and Dawson, 1992). On the Loess Plateau, *Vitex negundo* Linn. displays considerable ecological plasticity, using water from deeper soils as water stress increases and successfully coexisting with species that use surface soil water (Wang et al., 2017). Some plants exhibit resource-dependent water use strategies. On the Colorado Plateau, distinct plants—including perennial bunch grasses with shallow roots, subshrubs with dimorphic roots, and predominantly deep-rooted woody shrubs—compete for the same water source, with each depending 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 available, shifting to rainwater when subsoil water is depleted (Yang et al., 2010). In desert steppe, three herbaceous plants obtain water mainly from shallow soil as precipitation increases (Hu et al., 2021). While these studies have focused primarily on mechanisms of species adaptation to drought, they have not fully established plant water use sources and their adaptability to different soil habitats at the community level.

This study investigates 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 plant root distribution, plants in desert steppe likely occupy separate ecological niches for obtaining soil water in limited habitats (Dodd et al., 1998; Eggemeyer et al., 2009; Wu et al., 2016). Therefore, we hypothesize that the four communities have different water sources and that coexisting plants exhibit different water uptake patterns in response to soil water availability. Our study objectives are to: (1) investigate the isotopic composition of soil water and its vertical gradient along the soil profile; and (2) compare water utilization sources among the four communities and their responses to soil water availability.

2.1 Study Area

The study area is located in the Haba Lake Nature Reserve, Yanchi County, Ningxia Hui Autonomous Region, northern China, at an altitude of 1300–1622 m a.s.l. (37°36$‘17’‘–38°02’04’‘*N*; 106°53’23’‘–107°39’40”$E). The region has a temperate semi-arid climate with a typical continental monsoon pattern. Precipitation is scarce and unevenly distributed throughout the year, with average annual precipitation of 298 mm and average annual evaporation of 2250 mm. The groundwater table ranges from 3 to 8 m below the ground surface (Hu et al., 2021). Constrained by regional climate and soil conditions, water availability in the soil layer above 100 cm is most conducive for plant growth, and soil water represents the main water source for plants (Wang et al., 2021b).

The main soil types are sierozem, sand-covered sierozem, and aeolian sandy soil. The primary vegetation types include shrubs, herbs, and sand-resistant plants (Song et al., 2018; Wang et al., 2021). Four plant communities are widely distributed across the area: the *S. breviflora* community, as the original zonal vegetation type of desert steppe, is mainly preserved in sierozem habitats with no or slight desertification and hard soil texture; the *S. alopecuroids* and *A. mongolicum* communities are mostly located on slopes in sand-covered sierozem habitats; and the *A. splendens* community is located in low-lying beach areas within aeolian sandy soil habitats.

2.2 Experimental Design and Sample Collection

Due to prolonged drought in 2021, annual precipitation was only 238 mm (Fig. S1). Fifty-six percent of precipitation events were less than 5 mm, with most precipitation occurring from August to October. Two main precipitation events preceded sampling on September 8: 28.4 mm on September 3 and 6.9 mm on September 5 (Fig. S1). Precipitation δD values ranged from –124.9‰ to 21.0‰ (Fig. S1). With increasing precipitation (P), precipitation δD values tended to become more depleted ($\delta D = -4.672P - 2.914$, $R^2 = 0.525$, $P < 0.05$). With decreasing daily mean temperature (T), precipitation δD values decreased ($\delta D = 14.291T - 307.494$, $R^2 = 0.473$, $P < 0.05$).

In 2021, average soil water content across different plant communities remained stable, with no significant differences in soil water content for *A. mongolicum*, *S. breviflora*, and *A. splendens* communities from May to November ($P > 0.05$). Soil water content of the *S. alopecuroids* community in September showed no significant difference from other months ($P > 0.05$; Fig. S2). Field observations revealed that following the September 3 precipitation event, drought-yellowed plants gradually turned green and all species grew vigorously during this period, when competition for available water was most intense. Therefore, the experiment was conducted on September 8 (Su et al., 2013).

From late July to early September 2021, ten event-based precipitation samples were collected in the experimental area. The rainwater collector consisted of a 10-cm diameter funnel and plastic bottle. Hourly precipitation greater than 0.1 mm marked the start of a precipitation event, and events were considered finished when hourly values fell below 0.1 mm (Li et al., 2021). A Vantage Pro2 automatic weather station recorded meteorological data such as temperature and precipitation every 0.5 h. Water samples were collected immediately after precipitation in 8-mL glass bottles, sealed with polyethylene parafilm, and stored at −20°C to prevent evaporation loss.

In each community, five 1 m × 1 m plots were established as replicates, totaling 20 plots (see Table S1 for main plant species). From May to November 2021, volumetric soil water content was measured every 15 days using a time domain reflectometry probe at depths of 0–140 cm in 20-cm intervals. Plant and soil samples were collected on September 8, 2021. Ten healthy individuals of each species were selected per plot. Phloem tissue was removed to avoid isotopic fractionation of xylem water (Dawson, 1996; Wu et al., 2016). Herbaceous plants were collected from the root crown due to the close relationship between their isotopic composition and source water (Barnard et al., 2006; Wu et al., 2016). All plant samples (92 total) were placed in glass vials with screw caps, sealed with polyethylene parafilm, and frozen at −20°C for isotopic analysis. A total of 140 soil samples were collected. Root samples were also taken, sealed in plastic bags, and transported to the laboratory for further analysis.

2.3 Isotopic Analyses

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

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

where δX represents δD or δ^{18}O (‰), and Rsample and Rstandard are the molar abundance ratios (D/^{1}H and ^{18}O/^{16}O) of the sample and standard, respectively.

2.4 Data Analyses

To determine water sources of plants in different communities, we compared δD and δ^{18}O values of xylem water and soil water. Similarity in δD and δ^{18}O values between sources was used to infer primary water sources. Based on isotopic mass conservation theory, this study adopted the IsoSource model (Phillips and Gregg, 2003) to calculate the percent contribution of water sources, with source increment set at 1.0% and mass balance tolerance at 0.2%. According to δD and δ^{18}O distribution characteristics, adjacent soil water layers with similar isotope values were combined into single sources, dividing the profile into four sources (Phillips et al., 2005; Hu et al., 2021): (1) 0–20 cm: highest variation, vulnerable to meteorological factors such as precipitation and evaporation; (2) 20–40 cm: moderate variation, affected by mixing of precipitation and original soil water; (3) 40–80 cm: low variation, influenced by large precipitation events; and (4) 80–140 cm: low variation, relatively stable.

The contribution ratio equations were expressed as:

$$\delta X = a_1 S_1 + a_2 S_2 + a_3 S_3 + a_4 S_4$$

$$a_1 + a_2 + a_3 + a_4 = 1$$

where δX represents δD or δ^{18}O; S_1–S_4 represent water sources at 20-cm intervals; and a_1–a_4 represent the proportions of S_1–S_4 to total xylem water absorption.

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

3.1 Soil Moisture and Isotopic Composition

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

A. splendens community was significantly higher than other communities (Fig. S3).

Soil water isotopic composition varied with depth and community type (Figs. 1 and 2). All four communities showed a trend of increasing then decreasing isotope values. The *A. mongolicum* community increased from 0 to 80 cm, then decreased from 80 to 140 cm. The *S. alopecuroids* community increased from 0 to 60 cm, then decreased from 60 to 140 cm. The *S. breviflora* and *A. splendens* communities increased from 0 to 40 cm, then decreased from 40 to 140 cm. Soil moisture in the 0–20 cm depth was affected by recent precipitation, with depleted isotopic composition significantly different ($P < 0.05$) from that at 40–140 cm depth. Significant differences ($P < 0.05$) in soil water isotopic composition at 40–140 cm depth occurred among communities. The *S. breviflora* community had the highest $\delta^{18}O$ values, followed by *S. alopecuroids*, *A. splendens*, and *A. mongolicum* (Fig. 2 [Figure 2: see original paper]). The *S. breviflora* community also had the highest δD values, followed by *S. alopecuroids*, *A. mongolicum*, and *A. splendens* (Fig. 1 [Figure 1: see original paper]).

3.2 Isotopic Compositions in Xylem Water

In the *A. mongolicum* community, δD values of perennial herbs and subshrubs differed significantly ($P < 0.05$), though $\delta^{18}O$ values showed no significant difference ($P > 0.05$). In the *S. alopecuroids* community, no significant differences ($P > 0.05$) in isotopic composition occurred among annual herbs, perennial herbs, and subshrubs. In the *S. breviflora* community, no significant difference ($P > 0.05$) in isotopic composition existed between subshrubs and perennial herbs. In the *A. splendens* community, significant differences in isotopic composition occurred between shrubs and perennial herbs (Table 1).

δD and $\delta^{18}O$ values of annual herbs showed no significant difference ($P > 0.05$) across communities. However, δD and $\delta^{18}O$ values of perennial herbs differed significantly among communities ($P < 0.05$). Isotope values of perennial herbs in the *A. splendens* community were significantly lower than those in the *A. mongolicum* community. δD values of subshrubs showed no significant difference ($P > 0.05$) among communities, but $\delta^{18}O$ values differed significantly ($P < 0.05$) (Table 1). Negative isotope values of subshrubs in the *S. alopecuroids* community exceeded those of other communities.

3.3 Proportion of Plant Water Uptake in Different Communities

δD and $\delta^{18}O$ values indicated that plants in the *A. mongolicum* community derived most water from 0–80 cm soil depth, while plants in *S. alopecuroids*, *S. breviflora*, and *A. splendens* communities derived most water from 0–40 cm depth (Figs. 1 and 2). According to the IsoSource model (Fig. 3 [Figure 3: see original paper]), plants in the *A. mongolicum* community mainly absorbed water from 0–20 cm (43.88%) and 40–80 cm (46.59%) depths. Plants in the *S. alopecuroids* community primarily absorbed water from 0–20 cm (71.16%) depth. Plants in the *S. breviflora* community mainly absorbed water from 0–20 cm (55.93%) and 20–40 cm (36.55%) depths. Plants in the *A. splendens* community primarily absorbed water from 0–20 cm (62.92%) and 80–140 cm (26.39%) depths.

Annual herbs and perennial herbs predominantly extracted water from 0–20 cm (72.93% and 55.07%) and 40–80 cm (18.87% and 26.09%) depths. Subshrubs predominantly extracted water from 0–20 cm (64.84%) and 20–40 cm (21.74%) depths. Shrubs predominantly extracted water from 0–20 cm (31.07%) and 80–140 cm (58.52%) depths.

4.1 Isotopic Compositions in Soil Water

In this study, δD and δ^{18}O values of plant xylem water closely resembled those of soil water, indicating likely plant dependence on soil water. Soil water δD and δ^{18}O values in all four communities increased, then decreased slightly before stabilizing with increasing depth, consistent with previous studies (Zhu et al., 2020; Gao et al., 2021). These trends likely reflect simultaneous influence of evaporation and infiltration on the vertical soil water gradient; as soil water mixed with rainwater, significant fluctuations in isotopic composition occurred in shallow soil (Penna et al., 2018; Sprenger et al., 2018). Isotopic composition of soil water in the 0–20 cm depth was lowest and varied significantly from depths greater than 40 cm (Figs. 1 and 2). Shallow soil water is greatly affected by meteorological factors such as precipitation and evaporation. Isotopic composition of soil water at 0–20 cm depth resembled that of precipitation on September 3 (δD: −115.3‰ ($±$9.6‰); δ^{18}O: −15.9‰ ($±$1.1‰)). Isotope values of soil water at 20–80 cm depth were higher than surface values, reflecting mixing of recent precipitation with existing soil water (Liu et al., 2021). Rainwater moves through soil pores and mixes with existing soil water, resulting in vertical isotopic changes (Eggemeyer et al., 2009; Wang et al., 2017). In desert steppe, rainfall generally does not directly replenish depths below 80 cm. Deep soil water primarily originates from precipitation after the growing season and spring snowmelt, events that occur infrequently in desert environments, resulting in relatively stable annual isotopic values in deep soil water (Liu et al., 2020).

No significant difference in soil water isotopes occurred between 0 and 40 cm depths across communities ($P > 0.05$), but significant differences existed below 40 cm ($P < 0.05$). Differences in shallow soil water isotopes may result from direct effects of precipitation and evaporation. Evaporation has minimal effect below 40 cm, while infiltration and water migration continue increasing (Zhang et al., 2017). Soil physical properties differ among depths, affecting the extent to which precipitation, infiltration, and evaporation influence soil water depth and isotopic composition (Wu et al., 2016). In the *S. alopecuroides* community, soil from 0–50 cm depth was sand-covered sierozem; 50–80 cm was calcium accumulation layer; and 80–140 cm was weathered bedrock residual soil (Fig. S4). Sand-covered sierozem had larger particle size and porosity than calcium accumulation soil, enabling rapid infiltration to 60 cm depth. Calcium accumulation soil had hard texture and compact structure that hindered water infiltration, implying that soil water below 60 cm remained stable with low water content, as demonstrated by wetting and isotopic fronts extending to 60 cm depth (Figs. 1, 2 and S3). The highest isotope values occurred at 60 cm depth (Figs. 1 and 2), likely because precipitation before sampling had weak effects at this depth. Other factors may include the long-term unsaturated state of soil water, continuous liquid-to-gas movement, and continuous fractionation and enrichment (Zhu et al., 2014).

The soil profile of the *A. splendens* community consisted of aeolian sandy soil with high sand content. Its loose structure and large pores resulted in strong permeability. Compared with other communities, water seepage velocity was rapid, so deep soil water had negative isotope values due to precipitation replenishment. Soil water isotope values of the *S. breviflora* community exceeded those of the *A. mongolicum* community. Both soil types were sierozem, but the *A. mongolicum* community soil was coarser. The difference in isotope values may be due to the coarse texture of shallow soil in the *A. mongolicum* community, which facilitated water infiltration. The *S. breviflora* community had hard soil texture, making infiltration difficult and causing water accumulation in surface layers without significantly influencing deep soil isotopic composition. Soil water isotope values may also relate to root distribution patterns (Fig. S3). Plant root zones in the *A. mongolicum* community may facilitate precipitation infiltration to deep soil through preferential flow (Wu et al., 2016), resulting in negative isotope values at 80–140 cm depth. Additionally, hydraulic redistribution of soil profile water by roots may alter soil water isotope values (Wu et al., 2016).

In summary, soil moisture from 0–20 cm depth was most affected by precipitation, with the response lessening with increasing depth. Soil from 40–140 cm depth appeared more regulated by soil texture, with vertical moisture distribution varying among habitats. Soil moisture in the *A. splendens* community was significantly higher than in other communities, especially in deeper soil, indicating effective precipitation replenishment in aeolian sandy soil habitats. Soil types of *S. alopecuroids*, *A. mongolicum*, and *S. breviflora* communities were all sierozem, but their degree of desertification varied. Soil moisture in 0–40 cm depth was highest in the *S. alopecuroids* community, followed by the *A. mongolicum* community, and lowest in the *S. breviflora* community.

4.2 Water Uptake Patterns in Different Communities

All four communities showed high utilization of 0–20 cm soil water, likely because a high proportion of roots occurred in the upper 20 cm of soil (Fig. S3). Plant water sources were related to respective proportions of fine roots (Ellsworth and Sternberg, 2015). Species with shallow root systems might have denser root hairs and increased absorption areas in surface soil, contributing to surface water usage (Schenk and Jackson, 2005; Wang et al., 2017). Soil moisture in the 0–20 cm depth of desert steppe was significantly affected by precipitation (Wang et al., 2003). In this study, the 28.4 mm precipitation event before sampling increased surface soil moisture, and plants primarily used shallow soil water when possible to minimize energy consumption (Lv et al., 2017). Most plants in semi-arid steppes can reach 20 cm depth during their life history (Wang et al., 2021). In 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 habitats, with certain species dominant in one habitat but auxiliary in another, mainly because different habitat conditions cause the same species to develop different niches. Variation in water uptake patterns can lead to ecological niches distinguished by complementary resource use, facilitating species coexistence (Asbjornsen et al., 2008). Plants optimize their water intake strategy through self-regulation (Zhou et al., 2013).

In *A. mongolicum* communities, deep-rooted *S. alopecuroides* mainly absorbed water from 40–80 cm depth. As the dominant plant, *S. alopecuroids* absorbed water from 80–140 cm depth in addition to shallow depths (Fig. 3). Generally, when available, plant roots extract resources from shallow depths to minimize energy expenditure (Ogle and Reynolds, 2004; Wu et al., 2016). Because soil water content in the *A. mongolicum* community was high, *S. alopecuroides* tended to use relatively shallow soil water. In contrast, soil water content in the *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, utilizing more stable deep soil water. Deeper soil water was less exposed to evaporation and experienced less competition (Cristina et al., 2012). *S. alopecuroides* utilized different water sources based on environmental context, indicating plastic root water-absorbing modes adaptable to soil water conditions. Plasticity in plant water use strategies determines plant roles (dominant or auxiliary species) in given communities, enabling stable coexistence of different species and adaptation to different habitats (Asbjornsen et al., 2008).

Significant differences in δD values of xylem water occurred between perennial herbs and subshrubs in the *A. mongolicum* community, but δ^{18}O values showed no significant difference (Table 1). Differences in δ^{18}O values may result from isotopic fractionation in xerophytes or because differences between hydrogen atoms and their isotopes exceed those of oxygen atoms (Zheng et al., 2015). In various ecosystems, different species partition soil water resources spatially (Ehleringer and Dawson, 1992; Dodd et al., 1998; Yang et al., 2010). The soil type of *A. mongolicum* was sand-covered sierozem, with water concentrated on the surface and in deep soil layers. Both perennial herbs and subshrubs primarily utilized moisture in 0–20 cm and 40–80 cm depths (Fig. 3). With similar water absorption horizons, *A. mongolicum* and *L. potaninii* likely compete for water availability (Zeng and Ma, 2013).

In the *S. alopecuroids* community, no significant differences in isotopic composition occurred among subshrubs, perennial herbs, and annual herbs (Table 1), indicating competition for water from the same soil depths. In addition to surface soil water, *S. alopecuroids* and *C. mongolicum* utilized water from 80–140 cm and 40–80 cm depths, respectively, to avoid resource competition (Fig. 3). The ability to maintain water utilization at optimal soil depth may explain why *S. alopecuroids* became the dominant species. Subshrubs and herbs had similar water uptake patterns, both tending to utilize surface soil water (Fig. 3), consistent with findings of Zhu et al. (2020). Because subshrubs have more developed root systems than herbaceous plants, they can increase water absorption capacity to resist drought when facing water deficits (Jin et al., 2021). Subshrubs may occupy a strong competitive position, which is not conducive to herbaceous development and hinders restoration of grassland plant diversity (Li et al., 2021).

In the *S. breviflora* community, no significant difference in isotopic composition occurred between subshrubs and perennial herbs, which compete for soil moisture in the 0–40 cm depth (Table 1). The *S. breviflora* community was mainly located in non-desert sierozem habitats with hard texture and high clay content. After precipitation, infiltration was difficult, but more water was stored in the 0–40 cm depth (Fig. S3). These depths experienced high evaporative losses, creating transient water resources in surface layers (Dodd et al., 2002). Perennial drought-tolerant plants with fine branches, such as *S. breviflora*, have high root density in small soil ranges, enabling them to be highly competitive in accessing small, transient pools of available soil water in surface layers (Dodd et al., 2002). Additionally, the *S. breviflora* community thrived in high terrain, where plants use more shallow soil water than those in low terrain (Nippert and Knapp, 2007; Zhu et al., 2014). In the study area, most precipitation events were less than 10.0 mm, influencing soil moisture in the 0–20 cm depth and rendering shallow soil suitable for survival of dominant tufted grasses such as *S. breviflora* (Ohte et al., 2003). In this study, 60%–63% of water used by *S. breviflora* came from 0–20 cm depth (Fig. 3). *S. breviflora* is considered a nurse plant in arid ecosystems with positive effects on other species (Wang et al., 2018), though this effect depends on soil moisture conditions. When soil water was scarce, *S. breviflora* negatively impacted annual plant communities, eventually decreasing grassland diversity (Miguel et al., 2016). Given low precipitation levels, annual plants were basically absent from *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 growth of other plants. Future prolonged drought intervals in semi-arid steppes (Chen and Wang, 2012) with sierozem habitats and poor water resources may result in formation of communities dominated by perennial fibrous-rooted plants.

In the *A. splendens* community, significant differences in isotopic composition occurred among shrubs, perennial herbs, and annual herbs (Table 1), indicating that different plants absorbed water from different soil depths. Shrubs utilized more deep soil water, with utilization rates exceeding 50% in the 80–140 cm depth (Fig. 3). The *A. splendens* community was low-lying, located in an aeolian sandy soil habitat with coarse-textured topsoil that allowed precipitation to enter the subsoil and accumulate in deeper layers (Dodd et al., 2002). Deep-rooted shrubs accessed subsoil moisture resources unavailable to shallow-rooted companion species such as 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, with a relatively narrow extraction range, indicating low ecological plasticity. *Artemisia scoparia* Waldst. et Kit., an annual plant, is a typical R-strategy species that produces numerous small offspring and has strong seed reproduction ability. Once conditions are suitable, it germinates in large quantities. This species has strong adaptive characteristics that allow successful invasion and establishment in different habitats, growing rapidly after rain with high diffusion ability (Chen et al., 2019). Plant species with "opportunistic" water use strategies depend heavily on shallow soil water (<40 cm) even during drought periods (Cristina et al., 2012). These plants rely heavily on fluctuating, shallow soil water pools subject to rapid evaporation and competitor uptake in semi-arid habitats (Cristina et al., 2012). Root absorption depth of *A. splendens* responded to these soil water changes, with lateral roots using shallow soil water during wet seasons while axial roots absorbed deep soil water during dry seasons (Wu et al., 2015). In this study, *A. splendens* mainly used surface soil moisture, likely due to precipitation before sampling. Additionally, root water absorption depth can be altered by root plasticity, enabling *A. splendens* to outcompete associated shallow-rooted plants. Continuous drought inhibits shallow-rooted plants, and even if precipitation causes germination during the growing season, insufficient soil water after prolonged drought may prevent annual plant growth.

5 Conclusions

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

All four plant communities showed high utilization of surface soil water. *S. alopecuroids* and *S. breviflora* communities obtained water predominantly from shallow soil depths, while *A. mongolicum* and *A. splendens* could obtain 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 environments. *S. breviflora*, *A. scoparia*, and *L. secalinus* had narrower ranges, utilizing surface water related to their root system distribution. Differences in soil habitat lead to differences in soil water availability, which in turn affect plant water use patterns and spatial differentiation of plant communities. Competition for soil water exists between different plant life forms in sierozem habitats (*A. mongolicum*, *S. alopecuroids*, and *S. breviflora* communities). Precipitation replenishes the aeolian sandy soil habitat (*A. splendens* community) more effectively, and soil water use by this community is more spatially differentiated, enabling stable coexistence of shrubs and herbs. Our study provides a reference for determining the allocation and proportional contribution of water resources and offers a basis for ecological management and vegetation restoration of desert steppe.

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Appendix

Fig. S1 Daily precipitation, fluctuation of δD values for precipitation events, and average daily temperature in 2021. Arrow indicates sampling date.

Fig. S2 Soil water content from May to November 2021. Different lowercase letters indicate significant differences in soil water content among months within the same community type at $P < 0.05$ level. Bars represent standard errors.

Fig. S3 (a) Soil water content in different soil layers; (b) Vertical distribution of root fresh weight in different plant communities. Bars represent standard errors.

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

Note: Figure translations are in progress. See original paper for figures.

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