

Article

Mutual Water Supply Existed Between the Root Systems of *Tamarix ramosissima* Ledeb. and *Alhagi sparsifolia* Shap. Under Extreme Drought Stress

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Abstract: To explain one of the reasons why two adjacent deep-rooted desert plants can coexist over long periods, mutual water supply between species was investigated. The study focused on δD and $\delta^{18}O$ stable isotopic characteristics of root water and soil water near the roots of *Tamarix ramosissima* Ledeb. and *Alhagi sparsifolia* Shap. in the Tarim River Basin in China during the growing season. The direct comparison method and the Mix SIAR model were employed to analyze the water sources of the plants and the contribution rates of each water source. A similarity proportional index was used to assess the hydraulic connections between plant species. The water sources of *T. ramosissima* and *A. sparsifolia* were soil water found at depths of 40 to 90 cm and 220 to 300 cm (a total contribution rate of 58.85%) and 130 to 190 and 240 to 300 cm (a total contribution rate of 81.35%) with groundwater depths of 2.5 to 3.0 m, respectively. When the groundwater depth increased to 4 m, the water sources for both *T. ramosissima* and *A. sparsifolia* were soil water at depths of 20 to 100 (a contribution rate of 70.60%) and 20 to 120 cm (a contribution rate of 49.60%), respectively. Both *A. sparsifolia* and *T. ramosissima* could lift water from deep soil or groundwater for their own growth needs and supply some water to each other, which suggests that desert plants were allowed to achieve mutual benefits and coexistence through hydraulic connections. These results enrich the theoretical understanding of desert plant coexistence and provide a scientific basis for desert vegetation restoration.

Keywords: hydraulic connection; species coexistence mechanism; *Tamarix ramosissima*; *Alhagi sparsifolia*; desert plant community



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1. Introduction

Studying interspecific hydraulic relationships in desert shrub communities in arid areas is a prominent topic in eco-hydrology. Under stress, certain species are more competitive than others, and this imbalance in competition leads to the elimination of less competitive species. Consequently, studying species interactions under drought stress has been a focal point for many researchers [1–3]. Previous studies have focused on species-rich communities, exploring mutual adaptation or competitive exclusion between species [4–7]. In contrast, sparsely vegetated communities in desert areas under drought stress have rarely been addressed. Much research on community species interactions has focused on pairwise competition, multispecies competition, and their roles in biodiversity maintenance [8]. Interspecific interactions, such as species interactions, have often been discussed

purely theoretically without specific indicators to explore how species interact. Ecologists must choose specific indicators to characterize interspecific relationships in multispecies systems and quantify the extent to which such relationships rely on mechanisms that involve more than two species. Additionally, Rich et al. [9] observed metabolic mutualism among microbial species. Therefore, it remains unclear whether resource mutualism exists among the shrub species in this study, such as the use of water resources and mutual support between plants. Current ecological theories cannot fully explain whether species in the natural communities of desert riparian forests share mutually supportive relationships with water resources.

To better understand interspecies water use, it is necessary to investigate the characteristics of plant–soil water transport and flux. Some studies have found that plants such as *Populus euphratica* Oliv. exhibit hydraulic lift, which brings deep soil water into shallow layers to support the growth of shallow-rooted vegetation. This adaptation suggests that desert riparian plants have evolved to develop various drought resistance and avoidance mechanisms despite extremely low soil moisture and nutrient content in arid regions. These include the sharing and using of groundwater and soil water [10]. Previous studies have shown that 71% of plant populations in desert riparian forests are clustered [11]. However, whether hydraulic connections exist among plant species that utilize this pattern remains uncertain. By gaining a deeper understanding of the effective utilization of water from the soil, groundwater, and roots of other plants by desert plants, the hydraulic relationships among plants can be better understood [12,13].

Tamarix ramosissima Ledeb. and *Alhagi sparsifolia* Shap. are dominant species with deep root systems in the desert riparian forest community of the Tarim River Basin [14]. *T. ramosissima* is a shrub or small tree with a height of 1 to 6 m and strong characteristics of adapting to the arid desert environment. It is not only an excellent windbreak and sand-fixing plant but also a water and soil conservation tree species and a greening afforestation tree species for saline-alkali land; and it is a good fuel and weaving building material [15]. *A. sparsifolia* is a semi-shrub 25 to 40 cm in height. It has many branches, a clump-like growth habit, a high grass layer, and good windbreaks and sand-fixation effects. The root system is well-developed and can be used for sand burial. It grows in sandy areas, on riverbanks, and at the edges of farmlands in desert regions. It is drought-resistant, saline-alkali-resistant, and waterlogging-resistant and has strong adaptability [16]. Previous studies have conducted extensive research on the water sources of *T. ramosissima* in different habitats, the physiological and ecological responses of *T. ramosissima* to water and salt stress, the water-use strategy of *T. ramosissima* [15,17–19], and the physiological and ecological responses of *A. sparsifolia* to drought stress and changes in the distribution pattern of *A. sparsifolia* [20–22]. Under the condition of better moisture, *T. ramosissima* mainly uses shallow soil water, precipitation, and surface water to survive. In arid or extremely arid environments, *T. ramosissima* mainly uses deep soil water and groundwater [15,17–22]. However, when *T. ramosissima* and *A. sparsifolia* are adjacent, it remains unclear whether there is mutual water assistance between *T. ramosissima* and *A. sparsifolia* when subjected to drought or extreme drought stress.

Desert riparian forests in the lower reaches of the Tarim River Basin are an important barrier preventing the Taklimakan Desert and Kuruk Desert from merging. Consequently, the protection and restoration of these forests is a long-term issue that needs attention. In the past 25 years, the local government has implemented conservation and restoration projects for riparian desert forests along the Tarim River Basin to mitigate the severe and ongoing degradation of natural vegetation since 2001 [23,24]. These projects have promoted the natural restoration of vegetation. Still, vegetation recovery has been limited to 3 km areas on both sides of the riverbank in the lower reaches of the Tarim River. To expand

the scope of plant restoration, it is essential to improve water use efficiency through new restoration measures that do not rely solely on existing ecological engineering methods. Therefore, it is crucial to understand the water-use patterns of plants in a community, explore whether mutualistic relationships exist among species, and reveal the mechanisms of mutual benefits between species. These insights provide a scientific basis for developing new technologies and measures to restore vegetation in riparian desert forests.

This study focused on typical *T. ramosissima* and *A. sparsifolia* shrub communities in the Tarim River desert riparian forest in Xinjiang, China. The water-use relationships between *T. ramosissima* and *A. sparsifolia* were examined, and the mechanism of interspecific hydraulic connectivity was revealed.

2. Plant Community and Methods

2.1. Study Area

The desert riparian forest in the lower reaches of the Tarim River Basin (Figure 1 [ArcGIS 10.6 software, URL: <https://www.esri.com> (accessed on 15 December 2023)], located in the southern Xinjiang Uygur Autonomous Region of China, has a temperate continental climate characterized by low precipitation and high evaporation. The average annual precipitation ranges from 17.4 to 42.8 mm, with evaporation capacity between 1800 and 2900 mm. The average annual temperature is 10.7 °C, with sunshine hours ranging from 2550 to 3500 h. Glacial and snowmelt water from the surrounding mountains serves as the primary water source for the Tarim River. Desert riparian forests depend mainly on water flowing through oases from mountainous regions, making water resources for these ecosystems scarce. Over the past half-century, desert riparian forests have been severely degraded by drought stress [11]. Despite long-term extreme drought conditions, these desert riparian forests still retain large areas of shrub communities dominated by *T. ramosissima* and supplemented by other shrubs and herbaceous plants such as *A. sparsifolia*, *Halimodendron halodendron* (Pall.) Voss, *Lycium ruthenicum* Murr., *Glycyrrhiza inflata* Batalin., *Karelinia caspia* (Pall.) Less, and *Apocynum venetum* L. Vegetation growth is mainly sustained by groundwater and soil moisture [11], which helps maintain the stability of desert ecosystems in the Tarim River Basin.

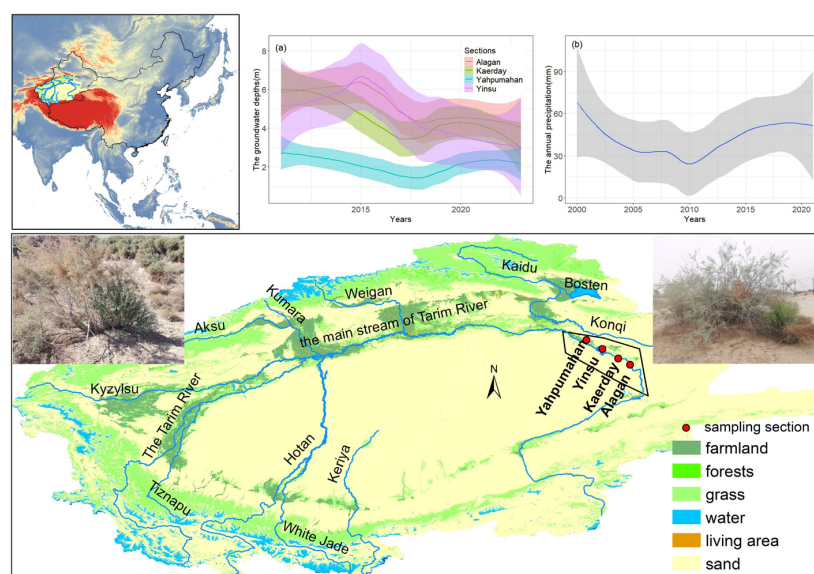


Figure 1. Location of sampling sections (red solid spheres) in the lower reaches of the Tarim River. (a) Annual mean groundwater depths in four sampling sections from 2001 to 2023; (b) Annual precipitation in the study area from 2001 to 2021. The source of the map is the Ministry of Natural Resources of China, and the map examination number is GS(2019)1697.

A field investigation of the soil profile (within 3 m underground) concluded that the soil in the study area was mainly wind-blown sandy soil. The vertical structure of the soil profile, from the surface to the deep layer, was sand, sandy loam, loam, and silty loam, reflecting the action of pedogenesis and wind accumulation in the Tarim River Basin [25].

2.2. Species Selection

Desert riparian vegetation in the Tarim River Basin shares similarities with desert riparian ecosystems worldwide [26]. It is primarily composed of trees, shrubs, and herbaceous plants such as *P. euphratica*, *Haloxylon ammodendron* (C.A. Mey.) Bunge, *L. ruthenicum*, *H. halodendron*, *A. venetum*, *Glycyrrhiza uralensis* Fisch., *K. caspia*, *Hexinia polydichotoma* (Ostenf.) H.L. Yang, *A. sparsifolia*, among others [11]. Under long-term extreme drought stress, herbaceous plants gradually degrade and disappear, decreasing species diversity [27]. The succession order of plant communities was as follows: arbor, shrub, and grass community stage; arbor and shrub community stage; and arbor or shrub community stage [11]. This succession indicates that the shrub community is more tolerant of extreme drought stress. According to land-use data derived from the Global Land Cover Characterization of the International Geosphere-Biosphere Program (<https://earthexplorer.usgs.gov/> (accessed on 5 January 2024)) for 2020, only 4% of the Tarim River Basin is forested; however, forests are crucial for the maintenance of ecosystem service functions. The dominant constructive species in riparian desert forests are *P. euphratica*, *T. ramosissima*, and *A. sparsifolia*, which coexist in these communities. In summary, we selected adjacent *T. ramosissima* and *A. sparsifolia* as study subjects in the lower reaches of the Tarim River. We selected medium-sized *T. ramosissima* trees (approximately 1 m in height, with a crown width of approximately 1.5 m × 1.5 m) and nearby *A. sparsifolia* plants for sample collection.

2.3. Data

2.3.1. Samples and Data Collection

(1) Groundwater depths

Since 2001, 30 groundwater monitoring wells have been drilled in the lower reaches of the Tarim River Basin at well depths of approximately 15 m. The groundwater depth has been measured continuously for 20 years. We chose four sections, Yahpumahan, Yinsu, Kaerday, and Alagan, with varying groundwater depths as the experimental areas (Figure 1). In August 2022 and 2023, a water-level instrument was employed to measure groundwater depth using existing groundwater depth monitoring wells.

(2) Plant root distribution investigation and root sample collection

During August 2022–2023, we investigated the root distribution and collected root samples of *T. ramosissima* and *A. sparsifolia* from the desert riparian forest of the Tarim River Basin. Most plant roots do not undergo stable isotope fractionation when soil absorbs water. In contrast, leaves can exchange isotopes with external water vapor through their stomata during transpiration, enriching heavy isotopes in the leaf water [28]. Therefore, only plant root water was selected for sample collection; leaf water samples were excluded. The main stem was taken as the center for the selected plants, and a radius of 0.5 to 1 m was marked. The soil profile of the root system was excavated, the root distribution was investigated, and root samples were collected. During the excavation process, an excavator was first used to remove excess soil on one side of the two plants. Soil was excavated at a horizontal distance of more than 20 cm from the plants and piled approximately 3 m away from them. To obtain a vertical section approximately 3 m deep and 1.5 m wide, the roots of this section were carefully excavated by facing the plants and using an iron shovel. A small iron shovel and brush were used to carefully remove the roots and obtain a relatively complete root system section to prevent damage and loss of fine roots in the area close to the plants. The

number of coarse and fine roots of *T. ramosissima* and *A. sparsifolia* within 3 m underground were recorded. Fine roots are usually defined as roots with diameters of less than 5 mm [29]. Photographs of the overall distribution of the root systems were obtained before collecting the root samples. For *T. ramosissima* and *A. sparsifolia*, the root depth was 2 m, and the radius was 1 m. Root samples were collected in layers of 0.1 m within a depth of 1.0 m and in layers of 0.2 m between depths of 1.0 to 2.0 m. Root samples were taken from three well-growing *T. ramosissima* trees (crown width less than 3 m × 3 m) and *A. sparsifolia* plants at depths less than 3 m underground. The samples were immediately placed in sealed bottles and analyzed. Three replicates were taken from the roots of each species to ensure that 0.75 to 1 mL of water had been extracted. The soil profile was backfilled after collection. Samples were collected on a typical sunny day.

(3) Soil samples

Soil samples near the root system were collected immediately to prevent soil evaporation. The samples were collected in different layers: 20–40, 40–80, 80–120, 120–160, 160–200, 200–220, 220–240, 240–260, 260–280, and 280–300 cm underground. Because of the high variation in isotopic values and soil water content in the topsoil (0–20 cm), which is easily influenced by precipitation and evaporation, we selected only soil layers below a depth of 20 cm for sample collection. Each layer of soil samples was divided into two parts: one part was placed in a 10 mL glass bottle, with three samples taken for each layer, and immediately sealed with a Parafilm membrane in a portable refrigerator for isotopic analysis of soil water. The other part was placed in an aluminum box, and the fresh weight was measured onsite. The samples were then returned to the laboratory and dried at 105 °C to determine the moisture content of the different soil layers. The samples were collected at noon.

2.3.2. Hydrogen and Oxygen Stable Isotope

The Los Gatos Research (LGR) liquid water isotope analyzer was used to determine the ratio of stable hydrogen and oxygen isotopes (D and ¹⁸O) in the sample, with a testing accuracy of ± 2‰. Each sample was analyzed six times, and the results of the first two analyses were discarded. The average of the final four analyses was used as the final result. The D and ¹⁸O contents were expressed as δD and δ¹⁸O, respectively. The measurement results were expressed as a thousand differences relative to the Vienna Standard Mean Ocean Water (V-SMOW) standard. The formula used was as follows:

$$\delta = \left(R_{\text{sample}} / R_{\text{standard}} - 1 \right) \times 1000\text{‰}$$

where R_{sample} is the ratio of heavy isotopes to light isotopes in water samples, also known as the isotope ratio; δ¹⁸O refers to ¹⁸O/¹⁶O; δD refers to ²H/¹H; R_{standard} refers to isotope ratios in V-SMOW. When the δ value is greater than 0, it indicates that the heavy isotope values in the sample are enriched compared to the standard value. When the δ value is less than 0, the heavy isotope value is depleted compared to the standard value.

2.3.3. Determination of Soil Moisture Content

The soil moisture content was determined using drying and weighing methods. The soil sample was placed in an aluminum box in an oven at a temperature of 105 °C for 24 h until it reached a constant weight. Subsequently, the masses of the dried soil samples were measured. The soil moisture content was calculated using the following equation:

$$\text{Soil moisture content} = (\text{mass of aluminum box and soil sample before drying} - \text{mass of aluminum box and soil sample after drying}) / (\text{mass of aluminum box and soil sample after drying} - \text{mass of empty aluminum box after drying}) \times 100$$

2.4. Data Analysis Methods

Excel 2010 software was used for data processing. Origin 2018 was used to create maps and analyze the statistical values of δD and $\delta^{18}O$ isotope ratios of root water and soil water in different soil layers of *T. ramosissima* and *A. sparsifolia*. Statistical values, such as the mean, standard deviation, deviation, and confidence interval, were calculated to study the compositional characteristics of the species isotopes.

2.4.1. Soil Water Excess Method

Desert plants in arid areas are more likely to use soil water than precipitation. The soil water excess method proposed by Barbeta et al. [30] was used to evaluate whether there was an isotopic shift between plant root water and its potential water source.

$$\text{Soil water excess} = \delta D - a_s \delta^{18}O - b_s$$

where a_s and b_s are the slope and intercept of the soil water line, respectively, at the same sampling point during the same period. δD and $\delta^{18}O$ are the corresponding hydrogen and oxygen isotope values of the root water samples, respectively. Soil water excess indicates the δD offset between the root water samples and the soil water line. A soil water excess greater than 0 indicates that the root water sample is more enriched in δD than the soil water, suggesting strong evaporation of root water. A soil water excess less than 0 indicates that the root water sample is more depleted in δD than the soil water, indicating weaker evaporation of root water.

2.4.2. Plant Water Source Tracing Method

To accurately determine the water sources of different plants, two methods were used to comprehensively analyze the water sources of plants and the contribution rates of each water source: the direct comparison method (DCM) and the mixed Stable Isotope Analysis in R 4.4.2 (MixSIAR) model. The direct comparison method can only qualitatively describe plant water sources but cannot quantitatively calculate the contribution rates of each water source. By comparing the isotope values of plant root water and soil water collected during the same period, the area where the two intersected or were close was considered the main water-absorbing layer of the plant. The mixed SIAR model calculates the contribution rate of each potential water source to plants. This model is run in the open-source software R 4.4.2, with input data including source data (δD and $\delta^{18}O$ values of potential water sources for each plant) and mixture data (δD and $\delta^{18}O$ values of plant roots). The specific methods are referenced in ref. [31].

2.5. Research Methods for Hydraulic Connections

The Similarity Proportional Index (PS index) and water niche differences between plants reflected the hydraulic connections between vegetation types. A high similarity ratio index between plants indicates significant competition between two plants for the same water source, which affects their coexistence and vice versa. After performing a similarity ratio analysis of the water sources of *T. ramosissima* and *A. sparsifolia*, the hydraulic connections between them were analyzed using conventional statistical methods.

The PS index indicates ecological niche overlap among organisms [16] was used to calculate the water-use efficiency of the plants [32]. The larger the PS index, the more likely the two plants will share the same main water source and compete for the same one. The smaller the PS index, the smaller the proportion of water utilized by both plants from the

same water source, indicating less competition for that water source. The formula used was as follows:

$$PS = 1 - 0.5 \sum_{i=1}^n |P_{1i} - P_{2i}|$$

where P_{1i} and P_{2i} represent the utilization ratios of the i th water source by the two compared plants.

3. Results

3.1. δD , $\delta^{18}O$ Characteristics and D-Excess of *T. ramosissima* and *A. sparsifolia*

The δD values in *T. ramosissima* roots moisture ranged from -73.17‰ to -50.57‰ , with an average of -66.13‰ . The minimum $\delta^{18}O$ value of the root moisture was -7.90‰ , and the maximum was 0.13‰ , with an average of -3.84‰ . For *A. sparsifolia*, the δD values of root moisture ranged from -79.88‰ to -66.93‰ , with an average of -73.02‰ . The minimum $\delta^{18}O$ value of the root moisture was -8.99‰ , and the maximum was -7.26‰ , with an average of -8.48‰ (Table 1). The slopes of the soil and root water hydrogen–oxygen lines were lower than those of the global and regional atmospheric precipitation lines, indicating evapotranspiration in soil and plant roots under arid conditions (Figure 2).

Table 1. δD , $\delta^{18}O$ Characteristics of *Tamarix ramosissima* Ledeb.'s and *Alhagi sparsifolia* Shap.'s roots and soil moisture near roots.

Samples	Groundwater Levels (m)	Isotope Values	Numbers	Minimum Values (‰)	Maximum Values (‰)	Average Values (‰)	Standard Deviation (‰)	Variations
<i>T. ramosissima</i> roots	<4	δD	26	-73.17	-50.57	-66.13	5.15	26.53
		$\delta^{18}O$	26	-7.90	0.13	-3.84	3.53	12.44
Soil moisture near <i>T. ramosissima</i> roots	2.5–3.0	δD	65	-67.15	-33.81	-59.11	6.97	48.64
		$\delta^{18}O$	65	-8.12	4.74	-1.62	3.19	10.0
<i>T. ramosissima</i> roots	4	δD	52	-79.71	-39.54	-59.19	8.36	69.81
		$\delta^{18}O$	52	-8.97	0.39	-2.64	3.79	14.38
<i>A. sparsifolia</i> roots	<4	δD	20	-79.88	-66.93	-73.02	3.33	11.06
		$\delta^{18}O$	20	-8.99	-7.26	-8.48	0.43	0.19
Soil moisture near <i>A. sparsifolia</i> roots	2.5–3.0	δD	41	-76.75	-31.08	-56.94	10.49	110.06
		$\delta^{18}O$	41	-8.28	4.48	-2.12	3.51	12.34
<i>A. sparsifolia</i> roots	4	δD	40	-79.71	-45.37	-60.11	7.19	51.67
		$\delta^{18}O$	40	-8.97	0.31	-3.54	3.93	15.42

Variations in soil moisture content led to changes in isotopic values of soil water near the roots. When groundwater depth was 4 m, δD values of soil water near *T. ramosissima* roots ranged from -79.71‰ to -39.54‰ , with an average of -59.19‰ . The $\delta^{18}O$ values of soil water near *T. ramosissima* roots ranged from -8.97‰ to 0.39‰ , with an average of -2.64‰ . When the groundwater depth ranged from 2.5 to 3 m, the ranges of δD and $\delta^{18}O$ values of soil water near *T. ramosissima* roots were wider than those under poor soil water conditions, with a range of -67.15‰ to -33.81‰ and -8.12‰ to 4.74‰ , with averages of -59.11‰ and -1.62‰ , respectively (Table 1).

Regarding the isotope characteristics of soil moisture near *A. sparsifolia* roots, when the groundwater depth was 4 m, the δD values of soil moisture ranged from -79.71‰ to -45.37‰ , with an average of -60.11‰ . The $\delta^{18}O$ values of soil water near *A. sparsifolia* roots ranged from -8.97‰ to 0.31‰ , with an average of -3.54‰ . When the groundwa-

ter depth ranged from 2.5 to 3 m, the ranges of δD and $\delta^{18}O$ values of soil water near *A. sparsifolia* roots were larger than those under poor soil water conditions, with a range of -76.75‰ to -31.08‰ and -8.28‰ to 4.48‰ , with averages of -56.94‰ and -2.12‰ , respectively (Table 1). These results indicate that as the soil moisture content increased, the soil water-heavy isotopes became more enriched, and soil water evaporation increased.

Analysis of soil water excess values between *T. ramosissima* and *A. sparsifolia* root water and their potential water resources revealed that the soil water excess values for both *T. ramosissima* and *A. sparsifolia* were less than 0, indicating weaker evaporation of root water.

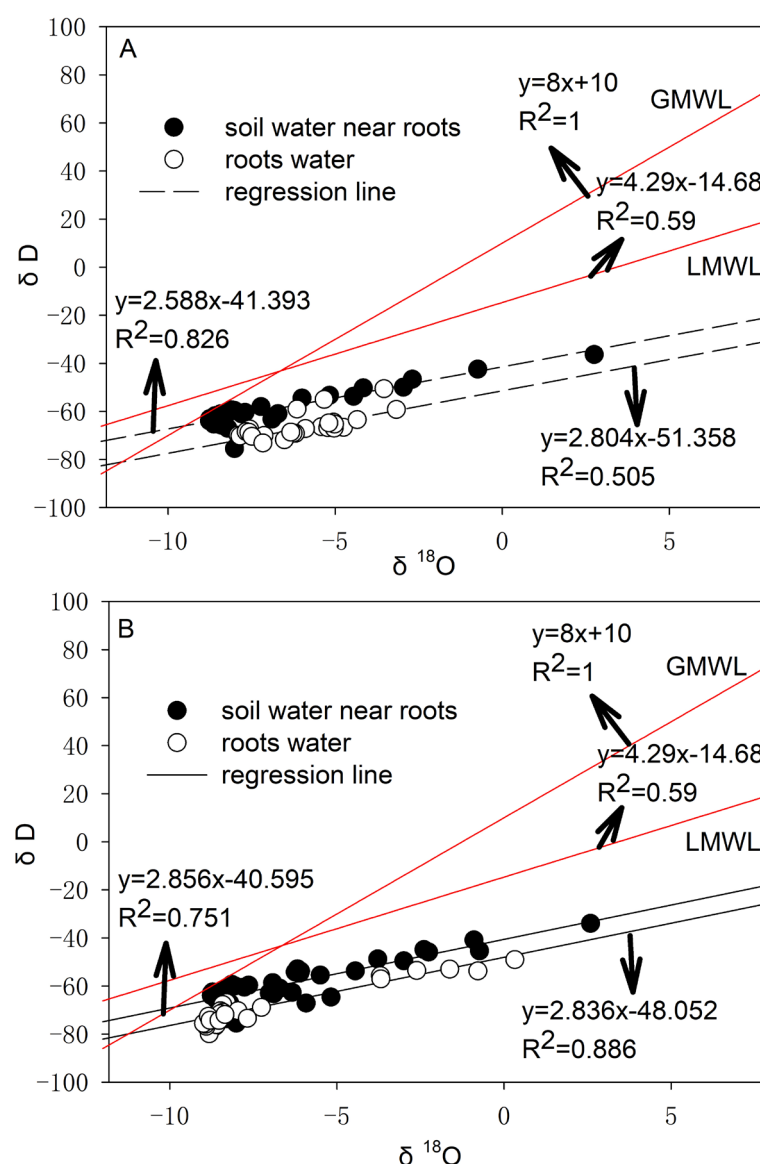


Figure 2. Dual-isotope plots of δD - $\delta^{18}O$ for soil water near roots and root water of (A) *Tamarix ramosissima* and (B) *Alhagi sparsifolia*. GMWL represents the global meteoric water line ($y = 8x + 10$). LMWL represents the local meteoric water line ($y = 4.29x - 14.68$).

3.2. Water Sources of *T. ramosissima* and *A. sparsifolia*

The results of the direct comparison method showed that when the groundwater depths were between 2.5 and 3 m, the *T. ramosissima* root system 40 to 90 cm deep was mainly supplied by soil water. When the groundwater depth was 4 m, the *T. ramosissima* root system 60 to 100 cm deep was primarily supplied with soil water. For *A. sparsifolia*, when the groundwater depth was between 2.5 and 3 m, the *A. sparsifolia* root system 130 to

190 cm deep was mainly supplied by soil water. However, at a groundwater depth of 4 m, soil moisture was not a water source for *A. sparsifolia* (Figure 3).

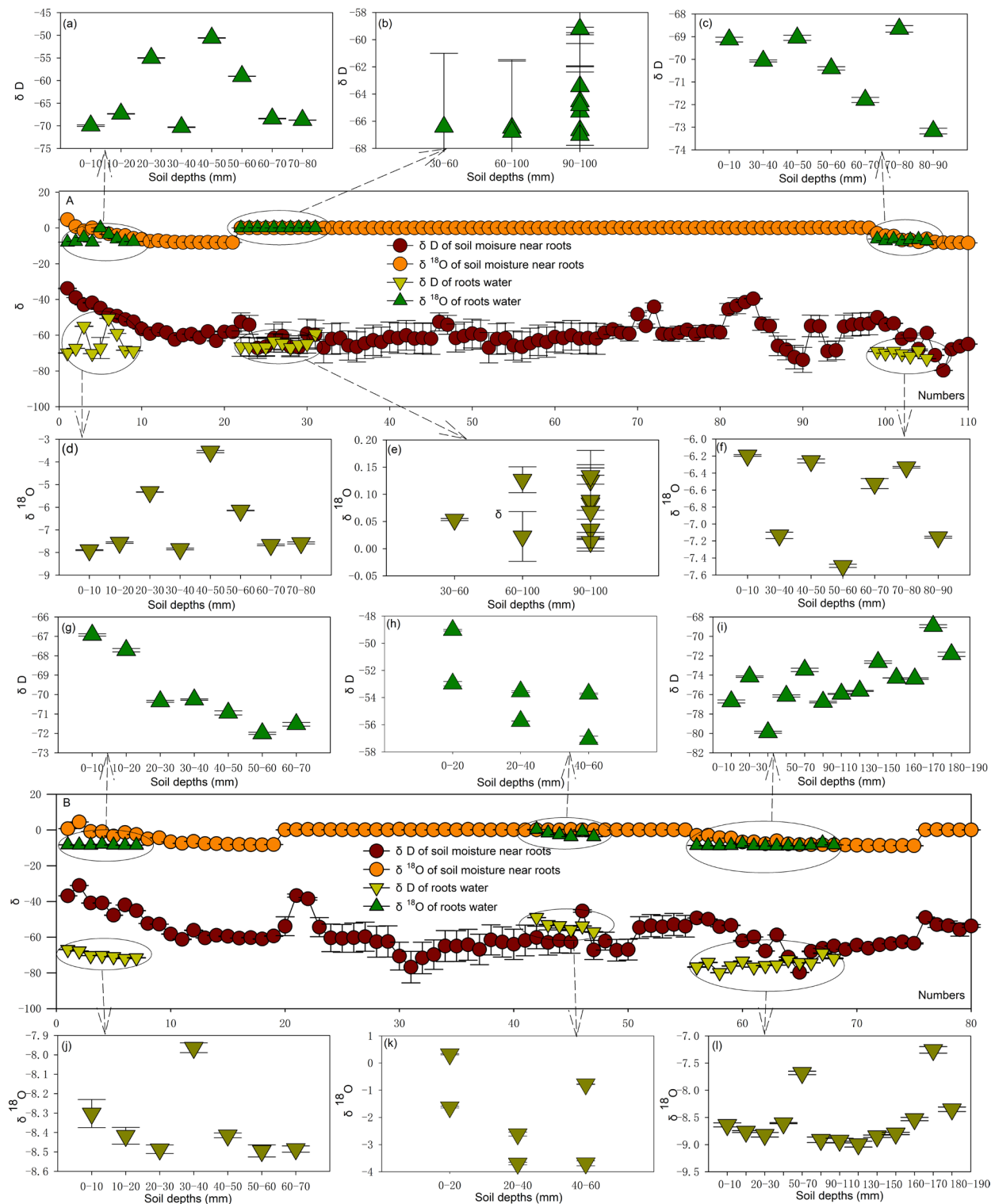


Figure 3. δ and $\delta^{18}\text{O}$ values of root water and soil moisture near the roots of *Tamarix ramosissima* Ledeb. (A) and *Alhagi sparsifolia* Shap. (B). δD (a,c) and $\delta^{18}\text{O}$ (d,f) of *T. ramosissima* root water (GD: 2.5–3.0 m); δD (b) and $\delta^{18}\text{O}$ (e) of *T. ramosissima* root water (GD: 4.0 m); δD (g,h) and $\delta^{18}\text{O}$ (j,k) of *A. sparsifolia* root water (GD: 4.0 m); δD (i) and $\delta^{18}\text{O}$ (l) of *A. sparsifolia* root water (GD: 2.5–3.0 m).

In addition, it was found that there was an intersection point between the δD and $\delta^{18}O$ values of *T. ramosissima* and *A. sparsifolia*, indicating a hydraulic connection between *T. ramosissima* and *A. sparsifolia* at 1 m underground (Figure 4).

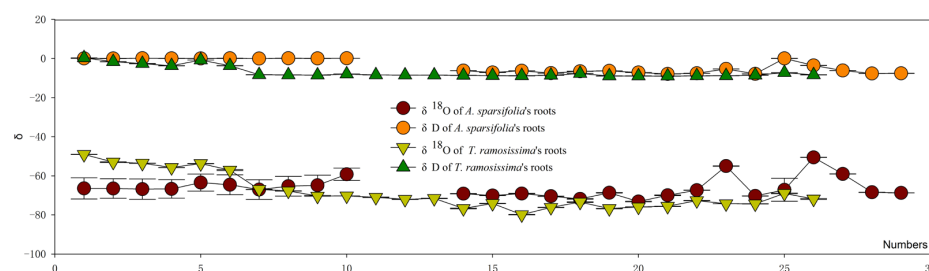


Figure 4. δD and $\delta^{18}O$ values of *Tamarix ramosissima* Ledeb.'s and *Alhagi sparsifolia* Shap.'s root water.

Using the MixSIAR model, it was found that when the groundwater depth was between 2.5 and 3 m in the *T. ramosissima* and *A. sparsifolia* communities, soil moisture near the roots of both plants at depths of 220 to 300 cm was the primary water source for *T. ramosissima*, with an average contribution rate of 51.90%. At a groundwater depth of 4 m, water required for *T. ramosissima* growth was mainly provided by shallow root water of *A. sparsifolia* (20 to 40 cm from the surface), with a contribution rate of 53.15% (Figure 5). *A. sparsifolia* releases shallow root water into the soil to supply water to *T. ramosissima* under drought conditions. For *A. sparsifolia*, when the groundwater depth was between 2.5 and 3 m, it primarily relied on deeper soil moisture at depths of 240 to 300 cm, with a contribution rate of 74.55%. When the groundwater depth was 4 m, the water needed for *A. sparsifolia* growth was provided by shallow soil moisture at 20 to 40 and 80 to 120 cm, with a total contribution rate of 49.60%. The former is water-absorbed and lifted from deep soil or groundwater by *A. sparsifolia* itself, and the latter is water-released by *T. ramosissima* 100 cm underground.

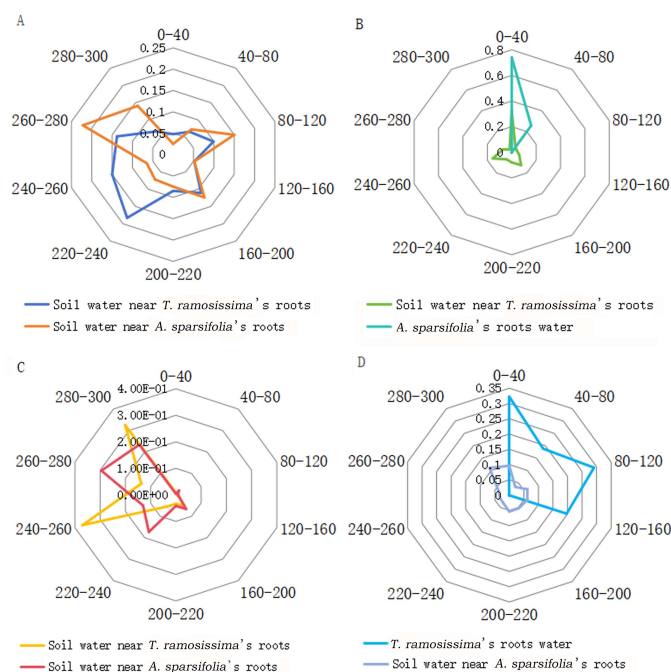


Figure 5. Contribution rate of each water source to *Tamarix ramosissima* Ledeb. and *Alhagi sparsifolia* Shap. root water absorption at different groundwater depths. (A) *T. ramosissima* at groundwater depth of 2.5–3.0 m; (B) *T. ramosissima* at groundwater depth of 4.0 m; (C) *A. sparsifolia* at groundwater depth of 2.5–3.0 m; (D) *A. sparsifolia* at groundwater depth of 4.0 m.

Combining the two methods, the study found that the main water-absorbing layer for *T. ramosissima* was soil water at depths of 40 to 90 and 220 to 300 cm, with a total contribution rate of 58.85% when the groundwater depth was between 2.5 and 3.0 m. When the groundwater depth was 4.0 m, the main water-absorbing layer of the plant was soil water at 20 to 40 and 60 to 100 cm depths, with a total contribution rate of 70.60%. The main water-absorbing layer for *A. sparsifolia* was soil water at depths of 130 to 190 and 240 to 300 cm, with a total contribution rate of 81.35% when the groundwater depth was between 2.5 and 3.0 m. At a groundwater depth of 4.0 m, the main water-absorbing layer for *A. sparsifolia* was soil water at 20 to 40 and 80 to 120 cm, with a total contribution rate of 49.60%.

3.3. Hydraulic Connection Between *T. ramosissima* and *A. sparsifolia*

By calculating the PS index, it was found that the PS index for soil moisture near the roots of *T. ramosissima* and *A. sparsifolia* was 0.652 and 0.815, respectively, when the groundwater depth was between 2.5 and 3 m. This indicates that the soil moisture near the roots of both plants shared the same water source: groundwater. The PS indices for root water and soil moisture near the roots of *T. ramosissima* and *A. sparsifolia* were 0.567 and 0.668 at a groundwater depth of 4 m, respectively. This indicated that as groundwater depth increased and soil water content decreased, the proportion of water drawn from the same water source and competition for the same water source for *T. ramosissima* and *A. sparsifolia* decreased. A clear hydraulic connection between both plants was found at the 4.0 m groundwater depth. Moreover, the similarity in water resources for *T. ramosissima* and *A. sparsifolia* was greater, indicating that they competed for soil water but also cooperated.

4. Discussion

4.1. Water Sources of Symbiotic and Nonsymbiotic *T. ramosissima* and *A. sparsifolia*

Desert riparian plants adopt different water-use strategies under varying climatic and hydrological conditions within arid inland river basins [33]. Under humid conditions, *T. ramosissima* primarily absorbs shallow soil water; however, under drought and extreme drought conditions, it mainly absorbs deep soil water (200–300 cm) and groundwater [14,33]. For example, in desert riparian plants, shallow soil water with a utilization rate of $30.7 \pm 12.6\%$ is the primary water resource under long-term ecological water conveyance. Under extreme arid stress in the Taklamakan Desert, the growth of *T. ramosissima* primarily depends on deep soil water and groundwater, with mean utilization rates of $34.5 \pm 5.1\%$ and $32.2 \pm 1.9\%$, respectively [15,17,34]. In the case of *A. sparsifolia*, it can absorb soil water from depths of 50 to 200 cm in extremely arid regions [32].

Interspecific associations in coexisting *T. ramosissima* and *A. sparsifolia* communities reflect the interactions between plants and dynamic changes in the community [35]. In the early stages of community succession, competition between species is weak, and interspecific associations are scattered, which benefits species coexistence [18]. Research on the competitive and interactive relationships between species in the later stages of community succession is limited. Hao et al. [10] found that *P. euphratica* can “hydraulic lift” to support the growth of herbs. At the same time, Wang et al. [32] showed that water competition between *T. ramosissima* and *A. sparsifolia* was weak. This study found that *T. ramosissima* utilizes soil water and groundwater while also effectively using water released by surrounding plants to meet its own water requirements (Figure 5). At a groundwater depth of 4 m, *T. ramosissima* provided water to *A. sparsifolia* from the underground soil at a depth of 100 cm (Figure 5). For *A. sparsifolia*, Zhou et al. [36] found that shallow soil water is primarily used in arid regions. Under different drought stress gradients, *A. sparsifolia* employs various drought adaptation strategies [37]. Our findings indicate that *A. sparsifolia*

mainly uses water from deeper soil layers when the groundwater depth is 2.5 to 3.0 m but relies only on groundwater and a small amount of water released by *T. ramosissima* when the groundwater depth is 4.0 m (Figure 5).

In summary, *T. ramosissima* and *A. sparsifolia*, which are deep-rooted plants, may interact with water through their hydraulic lift mechanisms under extreme drought stress. On a plant-specific scale, hydraulic lifting can enhance the water absorption efficiency of deep roots, increase the availability of nutrients in shallow soils, maintain the physiological activity and hydraulic conductivity of plant tissues, and delay the time when the soil water potential falls to the critical level, which could otherwise lead to root embolism [38,39]. The conclusions of this study are consistent with those of previous studies [14,15,17,32–34]. However, under extreme drought stress, they act as water sources for each other.

4.2. Driving Mechanism of Water Sources of Symbiotic *T. ramosissima* and *A. sparsifolia*

T. ramosissima utilizes different soil moisture layers across various habitats and water conditions because of differences in soil moisture among habitats [40]. Previous studies have found that the main water source of *T. ramosissima* is deep soil water (80–150 cm) in hillside habitats, shallow soil water (0–30 cm) in floodplain habitats [14], and deep soil water (1.6–4.0 m) and groundwater (<9 m) in extremely arid desert zones [25–27,30]. In this study, the water absorption characteristics of *T. ramosissima* and *A. sparsifolia* primarily involved deep soil water and groundwater in an arid climate with little precipitation, which was consistent with previous studies [15,17,34,40]. The different water-use conditions of desert plants are related to water availability; when there is a lack of surface water and shallow soil water supply, desert plants tend to use deep soil water and groundwater [14,15,17,34,40]. There were two peaks in the soil moisture content: in the shallow soil layer (40–100 cm) and near the groundwater level (240–300 cm) (Supplementary Figure S1). It is easy to understand that the soil water content near the groundwater level is high; however, the high soil water content in the shallow layer in areas with extremely low precipitation may be related to the “hydraulic lift” function of desert plants [10]. Therefore, under extreme drought conditions, they can instead use soil water at these two depths; however, their use of shallow soil water may be temporary, and the specific amount and time of absorption need to be further studied.

Additionally, we found that at a groundwater depth of 2.5–3 m, soil water content had a significant positive effect on the $\delta^{18}\text{O}$ of *T. ramosissima* root water (Figure 6C). This indicates that higher soil water content enhances the transpiration of *T. ramosissima* root water through its leaves. Soil water content had a significant negative effect on both δD and $\delta^{18}\text{O}$ of *A. sparsifolia* root water at a groundwater depth of 2.5–3.0 m, suggesting that transpiration of *A. sparsifolia* root water was weak with a slight increase in soil water content. When the groundwater depth was 4 m, there was a significantly positive correlation between soil water content and both δD and $\delta^{18}\text{O}$ of *A. sparsifolia* root water, indicating that *A. sparsifolia* root water transpired strongly with a slight increase in soil water content (Figure 6F).

Differences in the main water sources of *T. ramosissima* and *A. sparsifolia* in different habitats are closely related to their root distribution [41–43]. The growth of *T. ramosissima* roots is closely associated with groundwater depth, soil water content, and salt content [44]. Song et al. [45] found that drought conditions tend to reduce the number of root branches in *T. ramosissima*. The mean groundwater depth in the study area was approximately 3 m. Both plants had fewer branches within 3 m of the soil surface (Figure 7), which was consistent with the findings of Song et al. [45] and Su et al. [44].

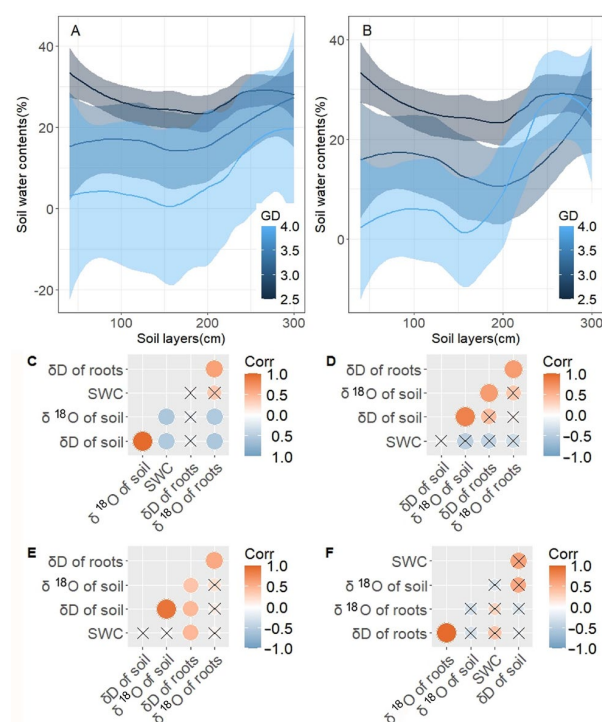


Figure 6. Soil water content (SWC) at different groundwater depths (GD) (A) *Tamarix ramosissima* Ledeb. and (B) *Alhagi sparsifolia* Shap. and the correlation between SWC and δD , ^{18}O of soil and root water (C) *T. ramosissima* at groundwater depth of 2.5–3.0 m; (D) *A. sparsifolia* at groundwater depth of 2.5–3.0 m; (E) *T. ramosissima* at groundwater depth of 4.0 m; (F) *A. sparsifolia* at groundwater depth of 4.0 m. The “x” symbol represents a significant correlation.



Figure 7. Images of root distribution of *Tamarix ramosissima* Ledeb. and *Alhagi sparsifolia* Shap. obtained through field investigation.

Under drought conditions, *T. ramosissima* and *A. sparsifolia* relied on groundwater for long-term survival. Groundwater rises through soil pores to replenish the soil water. Influenced by groundwater and rising pore water, fine roots are mainly distributed at depths of 100 and 250 cm underground [44], representing the main water absorption depths for the plants. These depths also had high soil moisture content (Figure 6), indicating that water was supplied at these two soil depths. The soil water at a depth of 250 cm was primarily influenced by groundwater, while the soil at a depth of 100 cm may have been supplied by other vegetation through “hydraulic lift”.

4.3. Research Limitations and Future Perspectives

The limitations of this study are mainly reflected in two aspects: the small sample size and the single research method used. Only four plants were selected from each section, with 16 plants in the four sections; 244 sets of plant, soil hydrogen and oxygen isotope values were obtained. In the future, increasing the number of samples may be more conducive to improving the accuracy of this study. In addition, only the hydrogen and oxygen isotopes of plant and soil water were measured to judge the source of plant water without combining other methods to comprehensively analyze the source of plant water and the connection between plants. Various methods should be used to comprehensively verify water mutual assistance relationships among desert plants. Various coexisting desert plants can also be selected to systematically reveal whether this kind of water mutual assistance relationship is generally present between different desert plants.

5. Conclusions

This study has enhanced our understanding of mutual water supply among desert plant species under extreme drought stress. The δD and $\delta^{18}O$ values of root water and rhizosphere soil water of *T. ramosissima* and *A. sparsifolia* under different groundwater depths were analyzed. The results showed that there were significant differences in the water sources of plants. When the groundwater depth was 2.5 to 3.0 m, the water sources of *T. ramosissima* and *A. sparsifolia* were the soil water at a depth of 40 to 300 cm. However, when the groundwater depth was 4.0 m, the water sources were the soil water at a depth of 20 to 120 cm. This indicates that as the groundwater depth increases and the drought conditions intensify, desert plants tend to utilize shallow groundwater. In desert areas, where the precipitation is extremely low, plant growth mainly depends on groundwater. When groundwater depth increases, shallow soil can provide the water required for plant growth. Based on the hydraulic lifting function of desert deep-rooted plants, it can be inferred that *T. ramosissima* and *A. sparsifolia* also possess the functions of hydraulic lifting and mutual water supply. This approach enables plants to cooperate and achieve mutualism.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f16030482/s1>, Figure S1: Soil water content in different soil layers underground under the different groundwater depths. (a): the groundwater depth of 4 m; (b): the groundwater depth of 2.5–3.0 m.

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