Stable oxygen-hydrogen isotopes reveal water use strategies of Tamarix taklamakanensis in the Taklimakan Desert, China Postprint

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Abstract

Tamarix taklamakanensis, a dominant species in the Taklimakan Desert of China, plays a crucial role in stabilizing sand dunes and maintaining regional ecosystem stability. This study aimed to determine the water use strategies of T. taklamakanensis in the Taklimakan Desert under a falling groundwater depth. Four typical T. taklamakanensis nabkha habitats (sandy desert of Tazhong site, saline desert-alluvial plain of Qiemo site, desert-oasis ecotone of Qira site and desert-oasis ecotone of Aral site) were selected with different climate, soil, groundwater and plant cover conditions. Stable isotope values of hydrogen and oxygen were measured for plant xylem water, soil water (soil depths within 0-500 cm), snowmelt water and groundwater in the different habitats. Four potential water sources for T. taklamakanensis, defined as shallow, middle and deep soil water, as well as groundwater, were investigated using a Bayesian isotope mixing model. It was found that groundwater in the Taklimakan Desert was not completely recharged by precipitation, but through the river runoff from snowmelt water in the nearby mountain ranges. The surface soil water content was quickly depleted by strong evaporation, groundwater depth was relatively shallow and the height of T. taklamakanensis nabkha was relatively low, thus T. taklamakanensis primarily utilized the middle (23%$±1±5±2±4±2±1±$2%, respectively) and may also use groundwater because the height of T. taklamakanensis nabkha was relatively high in these habitats and the soil water content was relatively low, which is associated with the reduced groundwater depth due to excessive water resource exploitation and utilization by surrounding cities. Consequently, T. taklamakanensis showed distinct water use strategies among the different habitats and primarily depended on the relatively stable water sources (deep soil water and groundwater), reflecting its adaptations to the different habitats in the arid desert environment. These findings improve our

understanding on determining the water sources and water use strategies of T. taklamakanensis in the Taklimakan Desert.

Full Text

Preamble

Stable Oxygen-Hydrogen Isotopes Reveal Water Use Strategies of *Tamarix taklamakanensis* in the Taklimakan Desert, China

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Abstract

Tamarix taklamakanensis, a dominant species in the Taklimakan Desert of China, plays a crucial role in stabilizing sand dunes and maintaining regional ecosystem stability. This study aimed to determine the water use strategies of *T. taklamakanensis* under declining groundwater depths. Four typical *T. taklamakanensis* nabkha habitats were selected: the sandy desert of Tazhong, the saline desert-alluvial plain of Qiemo, and the desert-oasis ecotones of Qira and Aral. These sites represent different climate, soil, groundwater, and plant cover conditions. Stable isotope values of hydrogen and oxygen were measured for plant xylem water, soil water (0–500 cm depth), snowmelt water, and groundwater. Four potential water sources—shallow, middle, and deep soil water, as well as groundwater—were investigated using a Bayesian isotope mixing model. Groundwater in the Taklimakan Desert was not completely recharged by precipitation, but rather through river runoff from snowmelt water in nearby mountain ranges. In the sandy desert habitat, where surface soil water content was quickly depleted by strong evaporation, groundwater depth was relatively shallow, and nabkha height was relatively low, *T. taklamakanensis* primarily utilized middle (23%$±1±5±2±4±2±1±$2%, respectively) and may also have used groundwater, as nabkha height was relatively high and soil water content was relatively low—conditions associated with reduced groundwater depth due to excessive water resource exploitation by surrounding cities. Consequently, *T. taklamakanensis* exhibited distinct water use strategies among habitats, primarily depending on relatively stable water sources (deep soil water and groundwater), reflecting its adaptations to different habitats in this arid desert environment. These findings improve our understanding of water sources and use strategies of *T. taklamakanensis* in the Taklimakan Desert.

Keywords: *Tamarix taklamakanensis*; water use strategies; stable isotopes; Bayesian isotope mixing model; deep soil water; groundwater; Taklimakan Desert

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Introduction

Water is an indispensable factor for plant growth, vegetation distribution, and community composition [?, ?, ?]. In desert ecosystems, water is extraordinarily valuable and has a decisive impact on plant survival and distribution. Precipitation and groundwater are the primary water sources, with groundwater playing a vital role in shaping plant adaptations because precipitation is very limited and unpredictable [?]. For decades, it was commonly accepted that soil moisture represented the remains of the last precipitation event in desert environments [?]. However, previous studies have indicated that in shifting sand dunes, rainfall of less than 13.40 mm cannot be utilized by plants as it may be completely evaporated before infiltrating into deep soil layers [?, ?]. Furthermore, soil water content (SWC) in desert ecosystems is extremely variable in both space and time [?]. Therefore, desert plants generally experience chronic or periodic water-deficit conditions. Perennial plants must adjust their water use strategies to survive and meet their growth and metabolic requirements, and their roots must acquire sufficient groundwater or residual soil water to tolerate prolonged drought [?]. Desert plants also face high vulnerability to climate change in these extreme habitats, and climate change combined with groundwater over-exploitation could severely damage desert species and affect these fragile ecosystems [?, ?]. Consequently, obtaining a comprehensive understanding of plant water use strategies in desert environments is critical.

The Taklimakan Desert is the largest shifting sand desert in China, with sand dunes formed by aeolian processes. The desert has been severely affected by human activities and is highly susceptible to changes in water availability. As the dominant species, *Tamarix taklamakanensis* plays a crucial role in stabilizing sand dunes and maintaining the function and structure of the desert ecosystem [?]. In the Taklimakan Desert, long-term accumulation of alternating sand and litter layers around *T. taklamakanensis* [?, ?] results in the formation of a specific biogeographic unit called the *T. taklamakanensis* nabkha, with heights ranging from 3 to 15 m and lengths from 5 to 50 m (long axis) [?]. These nabkhas are mainly distributed in the lower reaches of the Tarim River and the hinterland of the Taklimakan Desert [?]. However, degeneration and extinction of *T. taklamakanensis* nabkhas have occurred due to human activities and climate change, directly affecting the stability of the local desert ecosystem [?]. Currently, little is known about the water use strategies of *T. taklamakanensis* at nabkha locations. A clear understanding of the water sources used by this species will help assess the effects of human activities and climate change on the local ecosystem.

Stable isotope analysis is a powerful tool extensively utilized to identify plant water sources [?, ?, ?, ?, ?]. Different water sources have diverse isotope signatures due to physical and climatic factors [?, ?, ?], and stable isotope fractionation is generally not observed during water uptake by root systems [?]. Thus, the isotope composition of plant xylem water reflects the stable isotope information of potential water sources [?, ?]. Plant water sources can be identified by comparing isotope ratios of xylem water to concentrations of all potential sources [?, ?, ?]. In China, water sources and use strategies of *Tamarix ramosissima*, *Tamarix laxa*, and *Tamarix chinensis* have been explored in the Gurbantunggut Desert, Badain Jaran Desert, Heihe River Basin, and Dunhuang Oasis [?, ?, ?, ?], with findings indicating that these plants rely on water from different soil depths [?, ?, ?]. However, previous studies on *T. ramosissima* have focused mainly on desert riparian belts and the upper and lower reaches of the Tarim River Basin [?, ?], observing that *T. ramosissima* primarily used groundwater and deep soil water below 200 cm [?, ?]. Nevertheless, understanding of potential water sources and use strategies of *T. taklamakanensis* remains severely limited due to environmental factors (e.g., precipitation, groundwater depth, micro-topography) and human activities across different habitats. This represents a critical research gap, particularly regarding water use strategies within *T. taklamakanensis* nabkhas, despite the importance of these habitats for understanding adaptive mechanisms of desert plants to spatial changes in soil water.

Our study aimed to determine water sources and use strategies of *T. taklamakanensis* in four habitats (sandy desert of Tazhong, saline desert-alluvial plain of Qiemo, and desert-oasis ecotones of Qira and Aral) in the center and fringe of the Taklimakan Desert using stable isotope analysis. Given known differences in micro-climate, soil, and groundwater depth [?, ?], our first hypothesis was that *T. taklamakanensis* employs different water use strategies across habitats. Considering that aridity is typical in the Taklimakan Desert and plant roots in surface soil layers may be inactive due to prolonged low SWC, our second hypothesis was that this species mainly utilizes middle and deep soil water and/or groundwater, especially in habitats with extremely arid conditions.

2.1 Study Sites

The Taklimakan Desert is located in Northwest China, covering an area of 33.76\$×10^{4}\$ km^2 (37°-41°N, 77°-90°E), with approximately 85% composed of shifting sand [?]. It is a significant sand-dust source area with dust events occurring up to 100 days annually [?]. Mean annual precipitation ranges from 24.00 to 65.30 mm, while mean annual evaporation reaches up to 3000.00 mm —about 30-140 times greater than precipitation. Summer precipitation quickly evaporates from surface soil layers under high evaporation, decreasing surface soil water. Tributaries and transitional rivers formed by summer snowmelt from mountains permit oasis formation along the desert fringe [?]. With no rainy season, annual plants typically do not grow in this region; predominant species are shrubs including *T. taklamakanensis*, *Populus euphratica*, *Karelinia caspia*, and *Alhagi sparsifolia*.

The formation and development of *T. taklamakanensis* nabkhas are primarily affected by wind and hydraulic erosion. Four sampling sites representing typical nabkha habitats were selected across the Taklimakan Desert (Fig. 1 [Figure 1: see original paper]; Table 1 ; [**?**]). Site A, located in the central Taklimakan Desert near the Taklimakan Desert Research Station of the Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, had approximately 20% plant cover with scattered shifting sand on the nabkha surface. Site B, near Qiemo County in the southeastern fringe along the desert highway (transition zone between alluvial plain and desert), had 50% plant cover with saline soil and salt crust formation due to strong summer evaporation. Site C, in the southern fringe about 10 km from Qira County, is a desert-oasis ecotone with 30%-35% plant cover and shifting sand with light salinization. Site D, near Aral city in the northern fringe, is also a desert-oasis ecotone with 40%-45% plant cover, moderately salinized soil, and a thin salt crust (Table 1). Soil texture was mainly aeolian sand at all four sites.

At each site, four mature individual *T. taklamakanensis* nabkhas were selected, with adjacent nabkhas (about 500 m apart) considered representative of middle-sized nabkhas. Across all sites, average nabkha height, length, and width were 3.13 (\$±0.53), 7.37(±0.66), *and*5.72(±\$0.46) m, respectively (Table 1).

2.2 Sample Collection and Analysis

Field sampling was conducted in July 2017 with no precipitation events during the period. Sampling generally occurred at mid-day. At each site, four soil cores were collected from four *T. taklamakanensis* nabkhas using a handheld auger, totaling 16 soil cores per site. Based on prior knowledge of soil water isotope profiles [**?**], soil samples were collected at 20-cm intervals within the 0-500 cm depth. Each sample was separated into two subsamples: one packaged immediately in an airtight bottle and refrigerated at -20°C for isotope analysis, and another sealed in soil tins for SWC analysis by oven-drying. Soil particle size fractions were measured using a laser particle sizer (Mastersizer 2000, Malvern Instruments Ltd., Worcestershire, UK). Following US classification standards, soil particles were categorized as clay (<0.002 mm), silt (0.002-0.050 mm), very fine sand (0.050-0.100 mm), and fine sand (0.100-0.250 mm).

Plant samples were collected on the same days as soil samples. Six twigs of *T. taklamakanensis* were sampled from each nabkha. To avoid isotope fractionation, completely suberized twigs (diameter: 0.3-0.5 cm; length: 4.0-5.0 cm) were sampled for xylem water extraction. Immediately after sampling, all leaves and green bark were removed from stems, and plant samples were promptly placed in screw-cap glass bottles, sealed with parafilm, and stored at -20°C until isotope analysis.

Groundwater samples were obtained from nearby wells approximately 10-20 km from each site. To assess potential snowmelt water contributions to groundwater isotope signatures, snowmelt water was collected from bedrock canyons in the Tianshan and Kunlun Mountains. Snowmelt water represents perennial precipitation in the Taklimakan Desert. Both groundwater and snowmelt water samples were rapidly placed in glass vials, sealed with parafilm, and stored at 4°C for later isotope analysis.

2.3 Stable Isotope Analysis

Deuterium (^{2}H) and oxygen (^{18}O) isotope values of soil water and groundwater were used to describe potential water sources and compared with δ^2H and δ^{18}O values of plant xylem water. Soil water and plant xylem water were extracted using a cryogenic vacuum distillation apparatus (Picarro L2120-I, USA) [**?**]. All water samples were filtered using 0.22- m pore size filters, pipetted into small screw-cap glass vials, sealed with parafilm, and refrigerated at 2°C.

A liquid water isotope analyzer (DLT-100, Los Gatos Research Inc., Mountain View, USA) was utilized for stable isotope measurements, with analytical precision of $±$0.25‰ and $±$1.00‰ for δ^{18}O and δ^2H, respectively. Stable isotope values are expressed as:

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

where R_{sample} and R_{standard} are the stable isotope values (molar ratios of ^{2}H:H and ^{18}O:^{16}O) of the sample and standard water (standard mean ocean water), respectively [**?**].

Due to low water content, stable isotope values of plant xylem water and soil water may be erroneous because of organic contamination from methanol and ethanol. Therefore, isotope values were corrected using a standard curve [**?**].

2.4 Classification of Water Sources

A Bayesian isotope mixing model was used to identify plant water sources across habitats. This model incorporates both δ^{18}O and δ^2H, generally producing more robust results by utilizing a Bayesian framework to determine the proportional contribution of each source to a mixture. The model was implemented in the software package SIAR (Stable Isotope Analysis in R) [**?**] to determine potential water sources contributing to plant xylem water.

Based on similarities in δ^{18}O and δ^2H values of soil water, SWC within each depth, and plant xylem water values, four potential sources were classified when running the Bayesian model. δ^{18}O and δ^2H values for each soil depth were determined using the SWC-weighted mean approach [**?**], with soil water categorized as: (1) shallow soil water (0–200 cm), the most unstable layer with significantly varying δ^{18}O and δ^2H values; (2) middle soil water (200–400 cm), with lower

δ^{18}O and δ^{2}H values and relatively weak changes; (3) deep soil water (400–500 cm), with relatively consistent isotope composition and SWC showing no significant differences among depths; and (4) groundwater, with relatively constant δ^{18}O and δ^{2}H values.

2.5 Data Analysis

Meteorological data were obtained from the Meteorological Information Center of Xinjiang and China Meteorological Data Network (http://data.cma.cn/data/weatherBk.html). All statistical analyses were performed using SAS 9.2 (North Carolina, USA). Tukey' s test (t-test) evaluated differences in isotope compositions of soil water, groundwater, and plant xylem water at each site ($P<0.05$). Linear regression models established relationships between δ^{18}O and δ^{2}H. Figures were plotted using Origin 2017 (OriginLab Corp., Northampton, USA).

3.1 Climate Characteristics of Sampling Sites

Monthly mean temperature was typically lowest in January and highest in July at all sites (Fig. 2 [Figure 2: see original paper]). Precipitation occurred mainly between May and August, accounting for approximately 80%-90% of annual totals at Tazhong, Qiemo, and Qira, and about 90% from May to October at Aral. Mean annual evaporation was highest at Tazhong, followed by Qira, while Qiemo and Aral had relatively low evaporation. At Tazhong, plant cover was very low due to limited precipitation and intensive evaporation [**?**]. At Qira and Aral, precipitation was relatively high and evaporation relatively low, resulting in higher plant cover (Table 1). At Qiemo, precipitation was very low but plant cover was relatively high, with species such as *Phragmites australis* and *Halostachys caspica* observed, possibly related to summer flood alluvium.

3.2 SWC and Stable Isotope Values of Soil Water

In extremely dry desert ecosystems, SWC is very low and water movement is affected by climate factors, soil properties, and groundwater [**?**]. Previous studies indicate that rainfall of approximately 15.00 mm may be completely evaporated within about 20 days after the event under arid conditions, preventing infiltrated water from being enclosed by sand layers and stored long-term [**?**, **?**]. At our study sites, monthly precipitation was less than 12.00 mm (Fig. 2), and single precipitation events seldom exceeded 10.00 mm, indicating that SWC was not fully derived from precipitation [**?**]. We therefore suggest that precipitation has minimal influence on SWC at these sites. Soil in *T. taklamakanensis* nabkhas was mainly composed of silt and sand (Fig. 3 [Figure 3: see original paper]), a texture that may facilitate rapid infiltration of large rainfall amounts to replenish deep soil water. Consequently, SWC was affected by soil texture and groundwater (Figs. 3 and 4a; [**?**, **?**]).

SWC increased with soil depth at all sites (Fig. 4a [Figure 4: see original paper]). At Tazhong, SWC within 0–400 cm was extremely low, attributed primarily to sparse precipitation and strong evaporation (Fig. 2). At Qiemo, SWC within 0-400 cm was significantly lower than in 400-500 cm ($P<0.05$). High plant cover (50%) and surface salt crust resulted in significantly higher SWC at Qiemo than at other sites ($P<0.05$). Additionally, clay content in 0-400 cm at Qiemo was significantly higher than at other sites ($P<0.05$), contributing to relatively good water retention (Figs. 3 and 4a). At Qira, the upper soil layer (0-200 cm) was affected by strong evaporation, resulting in low SWC, while values in 200-400 cm showed no significant differences from those in 400-500 cm ($P>0.05$). At Aral, SWC showed no significant variations within 0-500 cm ($P>0.05$) and differed significantly from other sites.

Previous studies demonstrate enrichment of heavy isotopes in shallow soil water relative to deep soil water and groundwater due to surface evaporation [?, ?]. Soil water was not extracted from 0-80 cm at Tazhong or 0-20 cm at Aral due to extremely low SWC. At all four sites, evaporation likely caused δ^2H and δ^{18}O enrichment in shallow soil water (0-200 cm depth; Figs. 4b and c). With increasing depth, evaporation influence decreased. Isotope values in 200-400 cm showed relatively weak variations, and values below 400 cm showed no significant variations at each site (Figs. 4b and c). Accordingly, isotope values gradually decreased to relatively constant values with depth, indicating minimal evaporation impact on deep soil layers.

In the Taklimakan Desert, very low mean annual precipitation resulted in minimal influence on shallow soil water and stable isotope ratios [?, ?]. At Tazhong and Qiemo, δ^2H and δ^{18}O in 0-200 cm were more enriched than in 200-500 cm ($P<0.05$). Isotope values at Tazhong and Qiemo were more depleted (especially in deep layers) than at Qira and Aral (Figs. 4b and c). Isotope values decreased with depth, and deep soil water values were similar to groundwater at Tazhong and Qiemo (Figs. 4 and 5), demonstrating groundwater recharge of soil water. At Qira and Aral, groundwater depth may have declined due to excessive water resource exploitation in populated areas [?, ?]. δ^2H and δ^{18}O values within 0-500 cm showed significant variations ($P<0.05$). Specifically, δ^{18}O values were more enriched in 0-200 cm than in 200-400 cm, progressively decreasing to relative minima in 400-500 cm (Fig. 4c). Additionally, δ^2H:δ^{18}O ratios of soil water deviated to the right of groundwater ratios (Figs. 5c and d). Therefore, no evidence indicated soil water recharge by groundwater above 500 cm at Qira and Aral, suggesting that stable isotope variations were affected by evaporation and groundwater depth.

3.3 Stable Isotope Ratios of Groundwater and Potential Recharge Sources

The global meteoric water line (GMWL: $\delta^2H=8\delta^{18}O+10$; [?]), local meteoric water line (LMWL: $\delta^2H=7.27\delta^{18}O+6.47$, $R^2=0.94$; [?]), and δ^2H:δ^{18}O ratios of soil water, snowmelt water, groundwater, and plant xylem water are plotted in Figure 5 [Figure 5: see original paper].

δ^2H:δ^{18}O ratios of snowmelt water matched well with the LMWL, indicating that local snowmelt water contributed a proportion of precipitation (Fig. 5). Groundwater ratios deviated to the right of GMWL and LMWL at Qiemo (Fig. 5b). Groundwater δ^2H:δ^{18}O ratios were lower than snowmelt water ratios (Fig. 5b), but δ^{18}O values were similar to snowmelt water (Table 2). At Tazhong, Qira, and Aral, groundwater ratios were close to GMWL and LMWL, but δ^2H and δ^{18}O values were higher than snowmelt water (Figs. 5a, c, and d; Table 2), suggesting groundwater recharge by snowmelt water runoff.

[**?**] showed that groundwater isotope composition represents a weighted average of long-term rainfall inputs. [**?**] indicated that groundwater recharge processes could be divided into: (1) slow infiltration through soil matrix and weathered basement, and (2) fast direct recharge through conducting fissured zones. This theory was not completely suitable for the Taklimakan Desert because mean annual precipitation is very low (Fig. 2) and rainfall often evaporates completely before infiltrating soil. Infrequent precipitation thus has negligible effect on plant growth, and direct groundwater recharge by precipitation is probably uncommon. However, groundwater can be recharged by river runoff from mountain precipitation in this region [**?**].

3.4 Stable Isotope Ratios of Plant Xylem Water and Potential Sources

δ^2H:δ^{18}O ratios of soil water and plant xylem water deviated to the right of GMWL and LMWL at all sites (Fig. 5), indicating effects of strong evaporation due to extremely dry climate conditions. δ^{18}O values of plant xylem water were more depleted at Tazhong and Qiemo than at Qira and Aral, while δ^2H values were more depleted at Qiemo than at other sites. At Tazhong, Qiemo, and Qira, δ^2H values of plant xylem water were similar to groundwater, though δ^{18}O values were more enriched than groundwater at all sites. At Aral, both δ^2H and δ^{18}O values of plant xylem water were more enriched than groundwater (Table 2). [**?**] indicated that SWC in surface soil layers is reduced to low levels and may become inaccessible to plants under extremely dry conditions. In our study, δ^2H and δ^{18}O values of plant xylem water were significantly more depleted than soil water within shallow depths, and SWC was very low in 0–200 cm at all sites (Fig. 4). This low SWC was scarcely accessible to *T. taklamakanensis*, and enriched isotope values of shallow soil water were rarely observed in plant xylem water.

Field sampling was conducted during summer (July), when precipitation was judged non-significant for plant growth due to extreme rarity [**?**], and typically no water was stored in surface soil layers (Fig. 2; [**?**]). Potential plant xylem water sources were identified using a Bayesian isotope mixing model, with results shown in Figure 6 [Figure 6: see original paper]. Probability density graphs for each end-member were superimposed on relative contribution plots. [**?**] showed that plants may differentially utilize water from different soil depths, and use of potential water sources may be an adaptive selection to improve survival under extremely dry conditions [**?**]. Therefore, plant xylem water likely represents a mixture of different sources.

T. taklamakanensis showed shifts in water use strategy among habitats. At Tazhong, δ^2H:δ^{18}O ratios of plant xylem water were similar to soil water at 180–240 cm and below 420 cm, and to groundwater (Fig. 5a). Contributions of shallow, middle, and deep soil water and groundwater to xylem water were 10% ($±2±1±5±$2%), respectively (Fig. 6). This indicated that *T. taklamakanensis* in sandy desert habitat used multi-layer soil water and groundwater. Due to extremely rare precipitation and strong evaporation (Fig. 2), plant cover was very low, SWC in shallow and middle layers was extremely low (<1%; Fig. 4), preventing utilization of shallow soil water. Groundwater depth was relatively shallow (5.0–6.0 m) at Tazhong (Table 1), and could recharge deep soil water through capillary action [**?**]. We also found that *T. taklamakanensis* had a developed absorption root system below 200 cm, extending even below 500 cm (Fig. 7 [Figure 7: see original paper]). We therefore inferred that middle and deep soil water and groundwater were the primary xylem water sources.

At Qiemo, *T. taklamakanensis* nabkhas were distributed in the transition zone between alluvial plain and desert. δ^2H:δ^{18}O ratios of plant xylem water were similar to groundwater and soil water below 360 cm (Fig. 5b). Deep soil water contributed 55% ($±4±1±1±$2%), respectively (Fig. 6). This suggested that plant xylem water was mainly derived from deep soil water, followed by groundwater. At Qiemo, thick salt crusts formed on the surface due to flood alluvium and summer evaporation, and shallow groundwater depth (4.5–5.5 m) resulted in relatively high SWC and plant cover (50%). These findings confirmed that *T. taklamakanensis* mainly used deep soil water and groundwater in this saline desert-alluvial plain habitat.

At Qira, δ^2H:δ^{18}O ratios of plant xylem water were most similar to soil water below 480 cm (Fig. 5c). Deep soil water contributed 35% ($±1±1±1±$1%), respectively (Fig. 6). At Aral, δ^2H:δ^{18}O ratios of plant xylem water were more enriched than groundwater, most similar to soil water below 400 cm (Fig. 5d). Deep soil water contributed 38% ($±2±2±1±$1%), respectively (Fig. 6). Previous studies indicated groundwater depths of 11.0–16.0 m at Qira and 8.0–10.0 m at Aral [**?**, **?**]. [**?**] showed that *T. taklamakanensis* could not survive when groundwater depth exceeded 15.7 m. Nabkhas were relatively high at Qira and Aral (Table 1), suggesting that deep soil water was the primary water source in desert-oasis ecotone habitats, with groundwater also being essential.

Since groundwater depth was relatively deep at Qira and Aral, we inferred that soil water could not be completely recharged by groundwater. This may be partially explained by increasing water resource demands in these populated areas, causing declining groundwater depth. Nabkhas were higher at Qira than at Aral, and groundwater depth was deeper at Qira, partly explaining why *T. taklamakanensis* could absorb soil water below 480 cm at Qira but only below 400 cm at Aral. These findings confirmed that *T. taklamakanensis* can tolerate arid environments and supported our hypothesis that it utilizes middle and deep soil water and/or groundwater, demonstrating that surface soil layer roots may be inactive due to low SWC—an adaptive choice under dry, water-deficient desert conditions.

3.5 Implications of *T. taklamakanensis* Nabkhas

Groundwater and deep soil water were dominant water sources for plant survival in the Taklimakan Desert, where groundwater depth ranged from 3.0 to 15.0 m [?]. Most *T. taklamakanensis* nabkhas were distributed in fringe regions, with heights of 3.00-15.00 m and lengths of 5.00-50.00 m (long axis) [?]. In our study sites, average nabkha height and length were about 3.00 and 7.00 m, respectively. *T. taklamakanensis* can grow on high sand dunes, primarily utilizing deep soil water and groundwater for survival and growth. However, as nabkha height increases (above 15.00 m) and groundwater depth drops below root extent, nabkhas may degenerate and plants may die, intensifying desertification [?]. Groundwater depth did not limit survival and growth in this study. Therefore, *T. taklamakanensis* nabkhas may reflect changes in groundwater depth and act as indicators of environmental change in desert environments.

[?] showed that *T. taklamakanensis* may obtain groundwater through deep roots and acquire water from unsaturated soil areas [?]. [?] indicated that *T. taklamakanensis* establishes through seed germination in lowland zones and clonal growth on dune crests and slopes [?]. During field sampling, we found clonal establishment with taproots extending horizontally for a certain distance before gradually extending downward (Fig. 7). Several *T. taklamakanensis* plants within a certain distance shared the same taproot system within the same nabkha (Fig. 7). These results confirmed the capability of *T. taklamakanensis* to grow on high sand dunes.

4 Conclusions

This study used stable isotope analysis to investigate water use strategies of *T. taklamakanensis* growing on nabkhas in different habitats. In the Taklimakan Desert, groundwater was recharged by river runoff from snowmelt water in nearby mountain ranges. *T. taklamakanensis* exhibited different water use strategies across habitats, changing patterns according to climate characteristics, nabkha size, groundwater depth, plant cover, and soil texture. In sandy desert habitat with depleted surface SWC, *T. taklamakanensis* primarily utilized middle and deep soil water and groundwater. In saline desert-alluvial plain habitat where SWC increased with depth, it mainly used deep soil water followed by groundwater. In desert-oasis ecotones, it primarily utilized deep soil water and may also have used groundwater. Thus, potential water sources were largely dependent on groundwater depth and specific habitats. The water use strategies of *T. taklamakanensis* mirrored its adaptation to different habitats in the desert ecosystem.

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