

Adaptation strategies of *Tamarix ramosissima* seedlings in the hinterland of Taklimakan Desert, China

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Abstract

Purpose

Salt cedar (*Tamarix ramosissima* Ledeb.) is an excellent species of shrub that is used for windbreaks and to fix sand in desert of northwest China. The successful settlement of *T. ramosissima* seedlings and their growth into mature individuals require their adaptation to various adverse conditions, which is the key to naturally regenerating the *Tamarix* population.

Methods

We measured the morphological characteristics of the *T. ramosissima* seedlings, such as rooting depth, root: shoot ratio, taproot diameter, specific root length (SRL), specific root area (SRA), and specific leaf area (SLA), physiological characteristics, such as stable isotope ratios of xylem water, soil water, and leaves, as well as the leaf water content (LWC).

Results

The distribution of primary and lateral roots of *T. ramosissima* seedlings with larger BSD was more apparent than that of the small ones. As the BSD increased, the taproot depth and diameter of the *T. ramosissima* seedlings increased, and the root: shoot ratio, SRL, SRA, and SLA decreased. For the *T. ramosissima* seedlings shallow soil water was an important component of the water source. The mean LWC of *T. ramosissima* seedlings with different BSDs was 68.80%. The leaf carbon stable ratios ($\delta^{13}\text{C}$) trend was not obvious.

Conclusion

These results showed that with better soil water conditions in their habitat, the *T. ramosissima* seedlings were less likely to develop deeper root systems downward, allocated more biomass to the aboveground, and their growth rate diminished as the BSD increased.

Introduction

The allocation of biomass to plant organs plays an important role in their acquisition of resources and competition to survive (Tilman 1988, Olff 1991). Optimal partitioning theory (OPT) suggests that plants should allocate biomass to the organ that acquires the most limiting resource (Mccarthy & Enquist 2007). When plants are stressed by water and nutrients, the biomass allocated to the roots increases to obtain more water and nutrients (Zhang et al. 2020). The leaves and roots are important organs for energy and material exchange between plants and the environment. Leaf functional traits and root morphological

characteristics can be used as indicators of resource utilization strategies, which can reflect the adaptation and competitive ability of different species or provenances, to survive during the long-term evolutionary process (Vendramini et al. 2002, Hodge et al. 2009). Previous studies have analyzed the plant root depth (Fan et al. 2016, Xu et al. 2016), root: shoot ratio (Liu et al. 2013), specific root length (SRL) (Vries et al. 2016), specific root area (SRA) (Wang et al. 2021), specific leaf area (SLA) (Garnier et al. 2001, Liu et al. 2017) and other morphological indicators that indicate that plants can change their morphology through regulation and adapt to changes in environmental conditions to increase their chances of survival.

The root system of plants covers the entire soil profile, and the active roots, which primarily absorb water, are usually confined to a certain soil profile. The multiple functions of stable isotope techniques, such as tracers, integrations, and indicators, as well as the characteristics of rapid detection and accurate results (Lin 2013) facilitate the study of plant water sources and water use efficiency (WUE). Thus, they provide a means to effectively study the water source of plants and understand the dynamics of plant water use, which has led to their wide use. Water is a key limiting factor for plants in arid desert areas and one of the most important factors that affect plant growth and development in arid zones (Dube & Pickup 2001, Xu & Yan 2006). Arid desert areas have little precipitation and strong evaporation of surface water (Jia et al. 2012, Weine 2013). When the status of soil surface water changes, plants switch their sources of water (Chimner & Cooper 2004, Wang et al. 2011).

Desert plant species have evolved physiological processes to maintain tissue water status to some extent to survive in hyper water-deficient environments (Xiao et al. 2008). Plants with a stable source of water are less subject to external disturbances and usually have more stable physiological conditions (Wu et al. 2016). The content of leaf water is an important indicator of stomatal capacity, transpiration, photosynthesis, and respiration (Bowman 1989). Drought stress can decrease the content of leaf water in plants, and a more arid environment results in a lower content of leaf water (Wu et al. 2016). Plant WUE is an important indicator of plant water consumption and resistance to drought stress (Ehleringer & Cooper 1988), and the carbon stable ratios ($\delta^{13}\text{C}$) of leaves can indicate their long-term WUE (Farquhar et al. 1989). Studies have shown that the WUE of plants increases when the availability of soil water decreases, and there is a positive correlation between WUE and the $\delta^{13}\text{C}$ of leaves (Santini et al. 2016, Yong et al. 2017, Zhang et al. 2017).

The Daryaboyi Oasis is located at the end of the Keriya River, which is the second largest river at the southern edge of the Tarim Basin; this oasis is subject to relatively little interference and thrives under natural conditions, with relatively "primitive" characteristics (Shi et al. 2021). Salt cedar (*Tamarix ramosissima* Ledeb.) (bush species) is one of the dominant species in the Daryaboyi oasis. The *Tamarix* spp. community plays an important role in the protection of oasis biodiversity and evolution and the prevention of desertification (Huang & Gao 2004, Ma et al. 2009). The seedling stage is the most vulnerable stage during plant settlement and the stage at which the plants are most likely to die (Xu et al. 2016). The successful settlement and growth of *T. ramosissima* seedlings into mature individuals need to adapt to various adverse conditions, which is the key to realizing the natural renewal of the *Tamarix*

population. River water is a critical parameter for the germination and growth of *T. ramosissima* seedlings in this study area. We analyzed the biomass allocation, morphology, physiological characteristics, and water use sources of *T. ramosissima* seedlings that had different basal stem diameters (BSD) during their early growth stages, which is important to help improve the understanding of water use and the mechanisms used by plants to adapt to arid zones. Therefore, we tested the following hypotheses: (1) *T. ramosissima* seedlings with different BSD respond differently in biomass allocation and morphological characteristics in an arid desert environment, and (2) *T. ramosissima* seedlings that have different BSD change their sources of water use and physiological characteristics to adapt to the arid environment.

Material And Methods

Study area

The study area is located at the Daryaboyi Oasis in the hinterland of Taklamakan Desert, Xinjiang, China (Fig. 1). It has a geographical location of 38°24'–38°34'N, 81°56'–81°90'E, an altitude of 1,100–1,300 m, and an area of approximately 324 km² (Li et al. 2021a, b). This area is part of a typical arid continental climate, with an average annual precipitation of less than 10 mm; the average relative humidity is 40.2%; the annual potential evaporation is 2,480 mm; the average annual temperature is 12.1°C, and there is a large difference in temperature between day and night (Yang et al. 2002, Zhang et al. 2019). The primary plant species in the oasis are *Populus euphratica* Olivier, *Tamarix* spp., *Alhagi sparsifolia* Shap, *Phragmites australis* (Cav.) Trin ex. Steud, and *Karelinia caspia* Less. The groundwater depth of the oasis tends to decrease from south to north, and the buried depth ranges from 1 m to 8 m; the winter and spring seasons have shallower water than the summer and autumn seasons (Shi et al. 2021). The annual runoff is relatively stable, with a large amount from September to February and a small amount from March to August (Imin et al. 2021). The soil is primarily sandy, and the contents of soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP) are 2.14 g·kg⁻¹, 0.08 g·kg⁻¹, and 0.50 g·kg⁻¹, respectively. The pH value of the soil is 9.22, and there are few soil nutrients.

Sample collection

This field test was conducted in the Daryaboyi Oasis in the hinterland of Taklamakan Desert, Xinjiang, China in mid-June 2021. There was surface runoff in the sampling area in early June 2021, and the groundwater depth was 2.40 m. Representative areas to distribute *T. ramosissima* seedlings were selected that were subject to less human interference and near the established groundwater observation wells in the oasis, and samples of their xylem, leaves, roots, and nearby soil were collected. We randomly selected nine sample plots (1 × 1 m) near the observation well, and the height, crown width, BSD, and density of *T. ramosissima* seedlings in the sample plots were measured, and the average values were 22.79 cm, 11.62 cm, 5.05 mm, and 34 seedlings/m², respectively.

Plant root sampling

The whole roots of 12 *T. ramosissima* seedlings with a BSD range of 0–11 mm were excavated in the sample plot, and their morphological information is shown in Table 1. Tools, such as shovels, tweezers, brushes, and thin wooden sticks, were used to carefully strip away the soil around the roots until they were fully exposed. We took great pains to maintain the integrity of the root system during the excavation. If there were broken roots, the roots were labeled. The position of their growth was recorded, and the roots were photographed for measuring SRA. The roots were separated from the aboveground parts and placed in numbered airtight bags.

Table 1
Morphological information of the whole roots excavated from *Tamarix ramosissima* seedlings (means ± SD)

Basal stem diameter (mm)	Plant height (cm)	Crown width (cm)	Rooting depth (cm)	Sample number
0–2	4.08 ± 0.80	3.73 ± 0.61	37.17 ± 23.13	3
2–5	11.40 ± 0.28	6.38 ± 3.65	62.5 ± 17.78	3
5–11	35.42 ± 5.30	37.9 ± 7.21	67.25 ± 18.89	6

Soil sampling

Soil samples were collected at intervals of 20 cm near the plants that had their whole root systems excavated. The soil was drilled until the soil water emerged, and there were three replicates per layer. The soil samples were divided into two parts. One soil sample was placed in an aluminum box and brought back to the laboratory to measure the gravimetric soil water content (SWC) by drying. The other was quickly placed in sample bottles, sealed with Parafilm, and placed in a heat insulation box with ice which was brought back to the laboratory for cryopreservation (storage below -20 °C) to analyze the stable isotope ratios of soil water. Three soil samples were simultaneously taken from the 0–20 cm layer in the sample plot and placed in sealed bags for numbering, which was used to determine the SOC, TN, TP, and pH value.

Plant xylem sampling

T. ramosissima seedlings that were growing well, free of insects and diseases, and had a representative BSD that ranged from 0 to 11 mm were randomly selected from the sample plots. They were divided into categories of 0–2 mm, 2–5 mm, and 5–11 mm based on the size of the BSD, which enabled their classification of B_{0–2}, B_{2–5}, and B_{5–11}, respectively. To avoid the influence of light and temperature on the test, each sampling was completed between 09:00 and 12:00 (Beijing time). First, the xylem was cut, and

the collected xylem samples were quickly placed in 8 mL glass bottles with a threaded mouth. The caps were tightened and sealed with Parafilm. The samples were placed in a heat insulation box with ice, and then brought back to the laboratory and stored below -20 °C.

Plant leaf sampling

The root system was cut to sample the aboveground part of the plant. The fresh weights of the aboveground tissues were immediately weighed along with the leaves of three seedlings from the 0–2 mm and 2–5 mm BSD seedlings, while the tissues of six 5–11 mm BSD seedlings were weighed, and a serial number was noted on an envelope, respectively, to determine the root: shoot ratio and content of leaf water, and leaves were photographed for measuring SLA.

Simultaneously with the xylem sampling, mixed leaf samples were collected from *T. ramosissima* seedlings with B_{0–2}, B_{2–5}, and B_{5–11} BSD classes in the sample plot. The leaves were rinsed with deionized water and then dried at 105 °C in an oven for 0.5 h. The samples were dried to a constant weight at 70 °C for 48 h. The leaves were then crushed with a grinder and screened through 100 mesh to determine the $\delta^{13}\text{C}$ of the leaves.

Sample measurement

The SOC was determined by the black dichromate oxidation method. The soil TN was measured by the semi-micro Kjeldahl digestion procedure. The soil TP was determined by spectrophotometry (Gao et al., 2021). The formula to calculate the gravimetric SWC is as follows:

$$\text{SWC} = \frac{(\text{FW}_{\text{soil}} - \text{DW}_{\text{soil}})}{\text{DW}_{\text{soil}}} \times 100\%$$

1

Where SWC is the gravimetric soil water content; FW_{soil} is the fresh weight of soil, and DW_{soil} is the dry weight of soil.

The calculation formula for the root: shoot ratio is as follows:

$$\text{Root: shoot ratio} = \frac{\text{DW}_{\text{belowground}}}{\text{DW}_{\text{aboveground}}}$$

2

Where the $\text{DW}_{\text{belowground}}$ is the dry weight of belowground, and $\text{DW}_{\text{aboveground}}$ is the dry weight of aboveground.

All the leaves and roots on the full-root excavation plant were placed on different white papers with references and photographed. Adobe Photoshop 2020 (Adobe, San Diego, CA, USA) was used for matting (Fig. 3). The software to calculate the leaf area was used to calculate the areas of leaves and total roots. The leaves and roots were then placed in a 60 °C oven for 48 h to determine the constant weight to calculate the SRL, SRA, and SLA. The formulae are as follows:

$$\text{SRL} = \frac{\text{RL}}{\text{RW}}$$

3

$$\text{SRA} = \frac{\text{RA}}{\text{RW}}$$

4

$$\text{SLA} = \frac{\text{LA}}{\text{LDW}}$$

5

Where SRL is the specific root length; RL is the total root length (cm), and RW is the total root mass (g). SRA is the specific root area; RA is the total root area (cm²); SLA is the specific leaf area; LA is the single leaf area (cm²), and LDW is the leaf dry weight (g).

The water in xylem and soil samples was extracted using a cryogenic vacuum distillation system (LI-2000; LICA United Technology Ltd., Beijing, China). The extracted water samples were filtered through a 0.22 µm filter and placed in 1.5 mL glass sample bottles. The hydrogen (δ²H) and oxygen (δ¹⁸O) stable isotope ratios of the samples were analyzed using an isotope ratio infrared spectroscopy analyzer (LWIA, DLT-100; Los Gatos Research, Inc., Mountain View, CA, USA) and expressed in standard delta notation (‰) with an analytical precision of 0.25‰ and 0.6‰ for δ¹⁸O and δ²H, respectively. The formulae for calculating the stable isotope ratios of hydrogen and oxygen are shown as follows:

$$\delta^2\text{H} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\text{‰}$$

6

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

7

where the δ²H and δ¹⁸O are the stable isotope ratios of hydrogen and oxygen of the corresponding samples. R_{sample} and R_{standard} are the ratios of heavy and light isotope abundance of elements in the samples and standard materials (e.g. ¹⁸O / ¹⁶O), respectively.

Since *T. ramosissima* is a halophyte (Iwanaga et al. 2014), and the hydrogen isotope could be fractionated (Lin & Sternberg 1993), $\delta^{18}\text{O}$ was used to determine the water source in this study. The water sources were determined by comparing the soil water $\delta^{18}\text{O}$ with the xylem water $\delta^{18}\text{O}$. Because the $\delta^{18}\text{O}$ of soil water in the different layers were not significantly different, the potential water sources and the contribution ratio of each potential water source were not further classified and calculated.

The leaf water content (LWC) was calculated as follows:

$$\text{LWC} = \left[\frac{\text{FW}_{\text{leaf}} - \text{DW}_{\text{leaf}}}{\text{FW}_{\text{leaf}}} \right] \times 100\%$$

8

Where LWC is the leaf water content; FW_{leaf} is the fresh weight of leaf, and DW_{leaf} is the dry weight of leaf.

The $\delta^{13}\text{C}$ of *T. ramosissima* leaves were determined using a Thermo Delta V Advantage (Delta-V; Thermo Fisher Scientific, Waltham, MA, USA). The formula for calculating the carbon stable isotope ratios is shown as follows:

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\text{‰}$$

9

where the $\delta^{13}\text{C}$ is the carbon stable isotope ratios of the corresponding samples. R_{sample} and R_{standard} are the ratios of heavy and light isotope abundance of elements in the samples and standard materials, respectively.

Statistical Analysis

A one-way analysis of variance (ANOVA) with SPSS 23.0 (IBM, Inc., Armonk, NY, USA) was used to compare the differences in the xylem water $\delta^{18}\text{O}$ ratios, root: shoot ratio, taproot diameter, SRL, SRA, SLA, and LWC of *T. ramosissima* seedlings of different diameter classes. Adobe Photoshop 2020 was used to mat the leaf and root images to calculate the SRA and SLA. The plots were drawn using Origin 2021 (OriginLab Corp., Northampton, MA, USA) software.

Results

Characteristics of gravimetric soil water content

The gravimetric SWC in the study area increased with the increase in soil depth (Fig. 2). The SWC varied from 5.80–25.84%, with an average of 15.12%, and it fluctuated in the 0–120 cm soil depth, with a varied range of 5.80–19.49%. Below the 120 cm soil depth, the SWC gradually increased.

Morphological characteristics of the *T. ramosissima* seedlings

The root morphological characteristics of the *T. ramosissima* seedlings varied with the size of BSD (Fig. 3). The taproots of *T. ramosissima* seedlings with a small BSD were obvious and had few lateral root branches (Fig. 3a, b). The taproots and lateral roots of *T. ramosissima* seedlings with large BSD were more apparent, and the lateral roots developed in the direction of greater water abundance (Fig. 3c). The values of BSD were 1.40 mm, 2.95 mm, and 10.63 mm; the taproot lengths were 35.4 cm, 54.1 cm, and 31.8 cm, respectively, and the root depths were 52 cm, 54.1 cm, and 108 cm, respectively. The depth of *T. ramosissima* seedling taproots with different values of BSD deepened as the BSD increased, and the root depth varied from 4.5 cm to 108.0 cm (Fig. 4).

With the increase in BSD, both the aboveground and belowground biomass of *T. ramosissima* seedlings increased, which resulted in a significant positive correlation (Fig. 5a). The root: shoot ratio of *T. ramosissima* seedlings decreased with the increase in BSD, and the average root: shoot ratio was 0.76 (Fig. 5b). With the increase in BSD classes, the taproot diameter of *T. ramosissima* seedlings increased from 1.25 to 7.97 mm, while the SRL, SRA, and SLA decreased (Fig. 6). The degrees of their ranges of variation were $3.40\text{--}84.42\text{ cm}\cdot\text{g}^{-1}$, $19.33\text{--}185.94\text{ cm}^2\cdot\text{g}^{-1}$, and $37.35\text{--}40.04\text{ cm}^2\cdot\text{g}^{-1}$, respectively. There were significant differences in the taproot diameter and SRL ($P_{\text{diameter}}=0.004$, $P_{\text{SRL}}=0.031$), but there were no significant differences in the SLA and SRA ($P_{\text{SLA}}=0.859$, $P_{\text{SRA}}=0.174$).

Stable isotopic composition of the soil water and xylem water of *T. ramosissima* seedlings

The soil $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in the study area are under the global meteoric water line (GMWL) and the local meteoric water line (LMWL), indicating that the soil water is affected by evaporative fractionation (Fig. 7a).

The $\delta^{18}\text{O}$ of soil water decreased first and then increased with the increase in soil depth (Fig. 7b), and its variation ranged from -6.93‰ to -4.74‰ . The $\delta^{18}\text{O}$ of soil water in the 0–20 cm depth were enriched, with a maximum value of -4.74‰ . When the soil depth was 100 cm, the soil water $\delta^{18}\text{O}$ was depleted, with a minimum value of -6.93‰ . There were no significant differences in the soil water $\delta^{18}\text{O}$ in different soil depths.

The $\delta^{18}\text{O}$ of the xylem water of *T. ramosissima* seedlings varied from -6.33‰ to -5.84‰ at different BSD (Fig. 7b). The $\delta^{18}\text{O}$ of B_{0-2} interacted with the soil water $\delta^{18}\text{O}$ in the 20–40 cm and 140–160 cm layers. The $\delta^{18}\text{O}$ of B_{2-5} interacted with the soil water $\delta^{18}\text{O}$ in the 40–60 cm and 120–140 cm layers. The $\delta^{18}\text{O}$ of B_{5-11} interacted with the soil water $\delta^{18}\text{O}$ in the 20–40 cm and 120–160 cm layers. There

were no significant differences in the xylem water $\delta^{18}\text{O}$ of *T. ramosissima* seedlings among the three diameter classes.

Characteristics of leaf water content and leaf $\delta^{13}\text{C}$ of the *T. ramosissima* seedlings

There were no significant differences in the LWC of *T. ramosissima* seedlings with different BSD classes (Fig. 8a). The variation of LWC ranged from 63.56–78.46%, with an average value of 68.80%, and its values were in the order of $B_{2-5} > B_{5-11} > B_{0-2}$.

The leaf $\delta^{13}\text{C}$ of *T. ramosissima* seedlings of the BSD classes ranged from -30.0‰ to -28.89‰ , with a small range of variation (Fig. 8b).

Discussion

In arid and semiarid areas, soil water is a key factor that restricts plant growth and reproduction, affects the development of individual plants, determines the types of plants, and limits the distribution of vegetation (Reynolds et al. 1999). In the Daryaboyi Oasis, the gravimetric SWC increased as the soil depth deepened, which was consistent with the results of soil water research in the Taklimakan Desert (Yan et al. 2008, Fu et al. 2011). Zeng et al. (2013) showed that the content of soil water in the southern fringe of the Taklimakan Desert ranged from 3–30%, which is close to the range of variation of SWC in this study area (5.80–25.84%). In our study area, surface water flows through, so the shallow soil has a high content of water (Fig. 2), which facilitated the survival and growth of seedlings with shallow roots.

In an arid desert environment, the common ecological mechanism of plant adaptation to drought is a highly developed root system, with a deeper root depth and a larger root: shoot ratio (Darrouzet-Nardi et al. 2006, Shan et al. 2008). Berntson (1996) found that the root morphological characteristics were closely related to the utilization of water and nutrient resources by the plant. In this study, the lateral root distribution of the *T. ramosissima* seedlings with larger BSD was more apparent (Fig. 3). The rooting depth of *T. ramosissima* seedlings with different BSD generally increased as the BSD increased (Fig. 4), indicating that the *T. ramosissima* seedlings developed roots and tended to absorb deeper stable soil water as the BSD increased. The vertical roots stopped growing when the SWC reached 30% (Zeng et al. 2013).

Studies show that the increase in root: shoot ratio enlarges the quantity of water and nutrients that is absorbed and enhances the ability of plants to resist drought and remain fertile; under irrigation conditions, the *T. ramosissima* seedlings were less likely to grow downward (Shan et al. 2008). Zeng et al. (2010) showed that the biomass of *T. ramosissima* seedlings was primarily distributed to the aboveground parts, and the mean root: shoot ratio was 0.75, which was very close to the trend of change

of the root: shoot ratio of *T. ramosissima* seedlings in this study (Fig. 5) and the average value (0.76). The small root: shoot ratio indicated that the soil water status in the study area was good, and more biomass was then allocated to the aboveground parts of the *T. ramosissima* seedlings (Fig. 5).

The taproot diameter of *T. ramosissima* seedlings increased as the BSD increased (Fig. 6a). SRL is the ratio of root length to biomass, which can represent the relationship between root gain and expenditure (Fitter 2002). The SRL values of *T. ramosissima* seedlings at different BSD classes were as follows: $B_{0-2} > B_{2-5} > B_{5-11}$ (Fig. 6b). It is generally believed that the plants that grow more quickly generally have a larger SRL than the plants that grow more slowly (Comas & Eissenstat 2004). The plant growth theory suggests that fast-growing plants generally have a larger SRA. In this study, with the increase in BSD, the SRA of *T. ramosissima* seedlings of different BSD decreased (Fig. 6c). Its range of variation was $19.33-185.94 \text{ cm}^2\cdot\text{g}^{-1}$, and the seedlings with the smallest BSD had the largest SRA. This trend indicated that seedlings with a small BSD applied a substantial amount of energy into developing root systems to acquire stable water sources. They developed more fine roots and a larger SRA. This is consistent with the conclusions of Gu et al. (2017) that plants with larger SRL and SRA had finer roots. Plants with a larger SRA are more efficient at absorbing higher amounts of water and nutrients (Rewald & Leuschner 2006), which showed that small seedlings need higher water and nutrients during rapid growth. The results of these previous studies can confirm that the changing trend of SRL and SRA in this study indicates that the root growth rate of the *T. ramosissima* seedlings decreases.

The SLA plays an important role in determining the productivity of plants, since the changes in leaf SLA reflect changes to the structure and nutritional content of leaves (Gong & Gao 2019). Studies have shown that plants with a low SLA live in relatively arid and barren environments (Patane` 2011), while those with a high SLA have a high rate of relative growth and productivity (Guerrero et al. 2014). Hu et al. (2021) studied the morphological changes of saxaul (*Haloxylon ammodendron*) in the Ebinur Lake wetland, Xinjiang, China, and showed that when the growing environment was dry and resources were scarce, *H. ammodendron* adapted to the environment by reducing its SLA. The SLA was higher when growing in a resource-rich environment, and therefore, *H. ammodendron* reduces the chance of losing water under drought stress by adjusting its leaf morphological characteristics to maintain relatively stable water content. In this study, the SLA of *T. ramosissima* seedlings varied from 37.35 to $40.04 \text{ cm}^2\cdot\text{g}^{-1}$ (Fig. 6d). We can conclude that as the *T. ramosissima* seedlings grew, the SLA barely changed; the SRA decreased significantly, and the seedlings put more biomass into the aboveground parts. In conclusion, with the increase in BSD of the *T. ramosissima* seedlings, the growth rate decreased, and the biomass was primarily allocated to the aboveground part. The morphological characteristics of this part did not exhibit any changes in response to the drought environment, indicating that the study area had good soil water conditions. This indicates that the conclusions were consistent with our hypothesis (1) that the *T. ramosissima* seedlings of different BSD respond differently in biomass allocation and morphological characteristics in an arid desert environment.

Since surface water had previously flowed through the sampling area, the groundwater was shallower. There were no significant differences in the $\delta^{18}\text{O}$ of soil water in the different soil depths. The xylem water stable isotope ratios of plants can reflect the stable isotope ratios of the soil water absorbed and utilized (Ehleringer 1992). Thus, there were no significant differences in the $\delta^{18}\text{O}$ of xylem water of the *T. ramosissima* seedlings in different diameter classes. In environments with severe water shortages, plants with deep-rooted habits can tolerate or avoid drought by absorbing deep soil water or groundwater (Zencich et al. 2002, Chimner & Cooper 2004, Dai et al. 2015). In this study, with the increase in BSD classes, the *T. ramosissima* seedlings increased the depth of soil water that they utilized (Fig. 7b). The $\delta^{18}\text{O}$ of B_{0-2} interacted with the $\delta^{18}\text{O}$ of the soil water in the 20–40 cm and 140–160 cm layers. The $\delta^{18}\text{O}$ of B_{2-5} interacted with the soil water $\delta^{18}\text{O}$ in the 40–60 cm and 120–140 cm layers. The $\delta^{18}\text{O}$ of B_{5-11} interacted with the soil water $\delta^{18}\text{O}$ in the 20–40 cm and 120–160 cm layers. Because the deepest rooting depth of *T. ramosissima* seedlings was 108 cm, the intersection of the xylem water $\delta^{18}\text{O}$ and soil water $\delta^{18}\text{O}$ below 120 cm was ignored. As the *T. ramosissima* seedlings grow, the range of water absorption and utilization increases. Alternatively, the shallow soil water is an important component of the water source.

Wang et al. (2021) showed that the average LWC of desert plants was 69.9%. The LWC of *T. ramosissima* seedlings in different BSD first increased and then decreased (Fig. 8a), with an average value of 68.8%. The leaf $\delta^{13}\text{C}$ is an indicator of WUE (Chen et al. 2011) that can reflect the ability of plants to effectively use water and affect their strategies of adapting to the environmental changes (Wan et al. 2022). A study by Imin et al. (2021) on the WUE of small *T. ramosissima* in the Daryaboyi Oasis showed that the average leaf $\delta^{13}\text{C}$ was -27.49‰ . In this study, the average leaf $\delta^{13}\text{C}$ of the *T. ramosissima* seedlings with different BSD was -29.52‰ (Fig. 8b). Gebrekirstos et al. (2011) showed that plants with a higher leaf $\delta^{13}\text{C}$ or WUE were more likely to survive and grow. A study by Li et al. (2012) on the morphological responses of *T. ramosissima* suggested that recent decreases in groundwater along the Tarim River could facilitate the growth of *T. ramosissima*. In this study, under the influence of surface water, as the BSD classes of *T. ramosissima* increased, the source of water deepened. However, the plants still primarily utilized shallow soil water, and the water physiology remained stable. This indicates that these conclusions are inconsistent with our hypothesis (2) that postulated that the *T. ramosissima* seedlings with different BSD would change their sources of water and physiological characteristics to adapt to the arid environment.

Conclusions

With the increase in BSD of *T. ramosissima* seedlings, the lateral roots developed in the direction of greater water abundance, while the root: shoot ratio, SRL, SRA, and SLA decreased, and the water utilization depth increased. The LWC and leaf $\delta^{13}\text{C}$ remained stable. Although the study area was in the hinterland of the Taklimakan Desert, which is nourished by surface water from the Keriya River, the groundwater was shallow. *T. ramosissima* seedlings put more biomass into the aboveground during their

growth process, which further showed that the surface water is highly significant to the survival and growth of *T. ramosissima* seedlings.

Declarations

Author contributions Flora Erkin: Methodology, Investigation, Field management, sample collection, Experimental analysis, and Writing - Original Draft; Yue Dai: Writing - Review & Editing, Field management, sample collection, and Funding acquisition; Anwar Abdureyim: Field management, sample collection, and Writing - Review & Editing; Wan-Yuan Huang: Sample collection, Experimental analysis; Mawlida Tayir: Sample collection, Experimental analysis.

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Data availability Not applicable.

Competing interests The authors declare no competing interest

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Figures

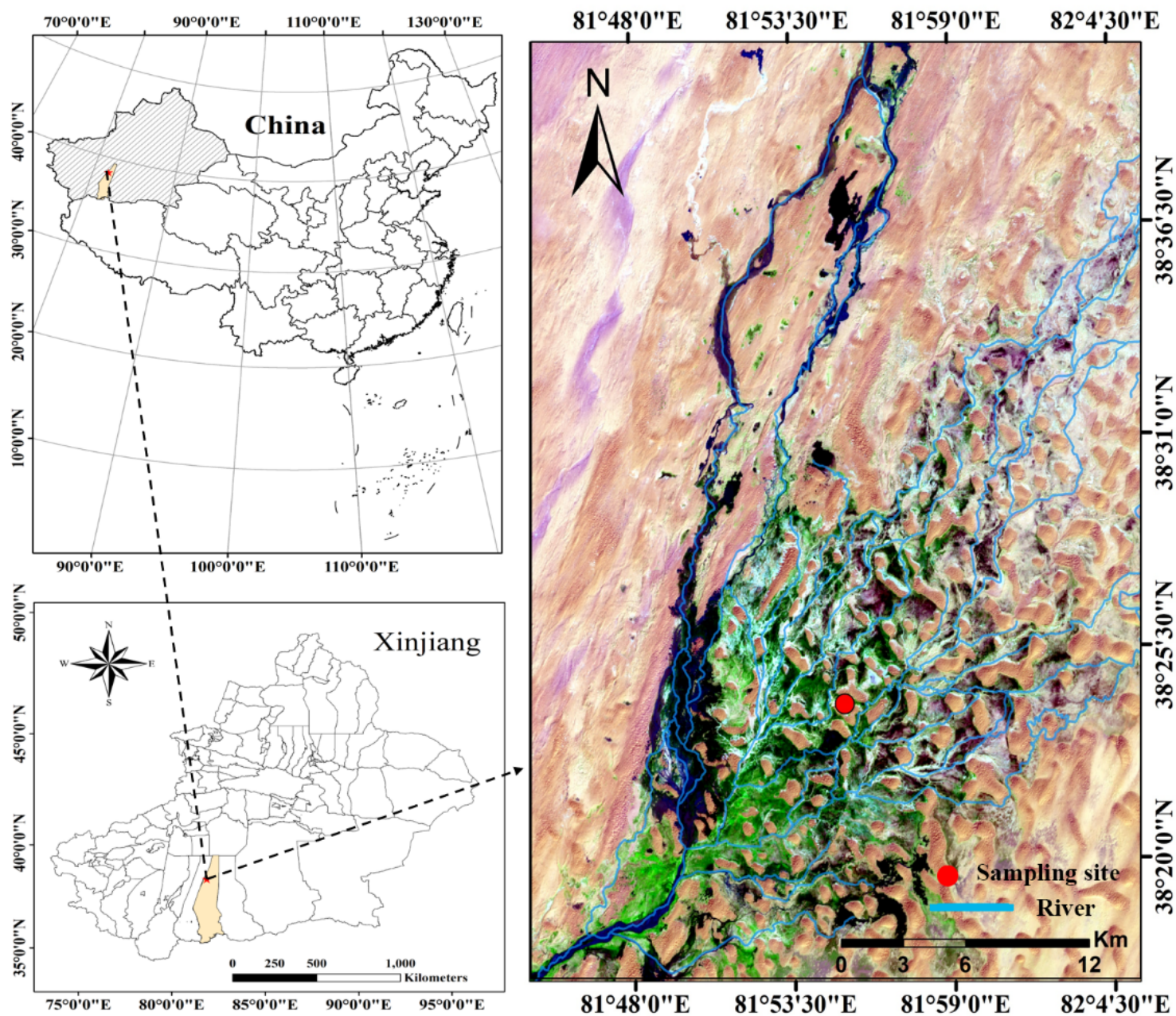


Figure 1

Location of the study sites

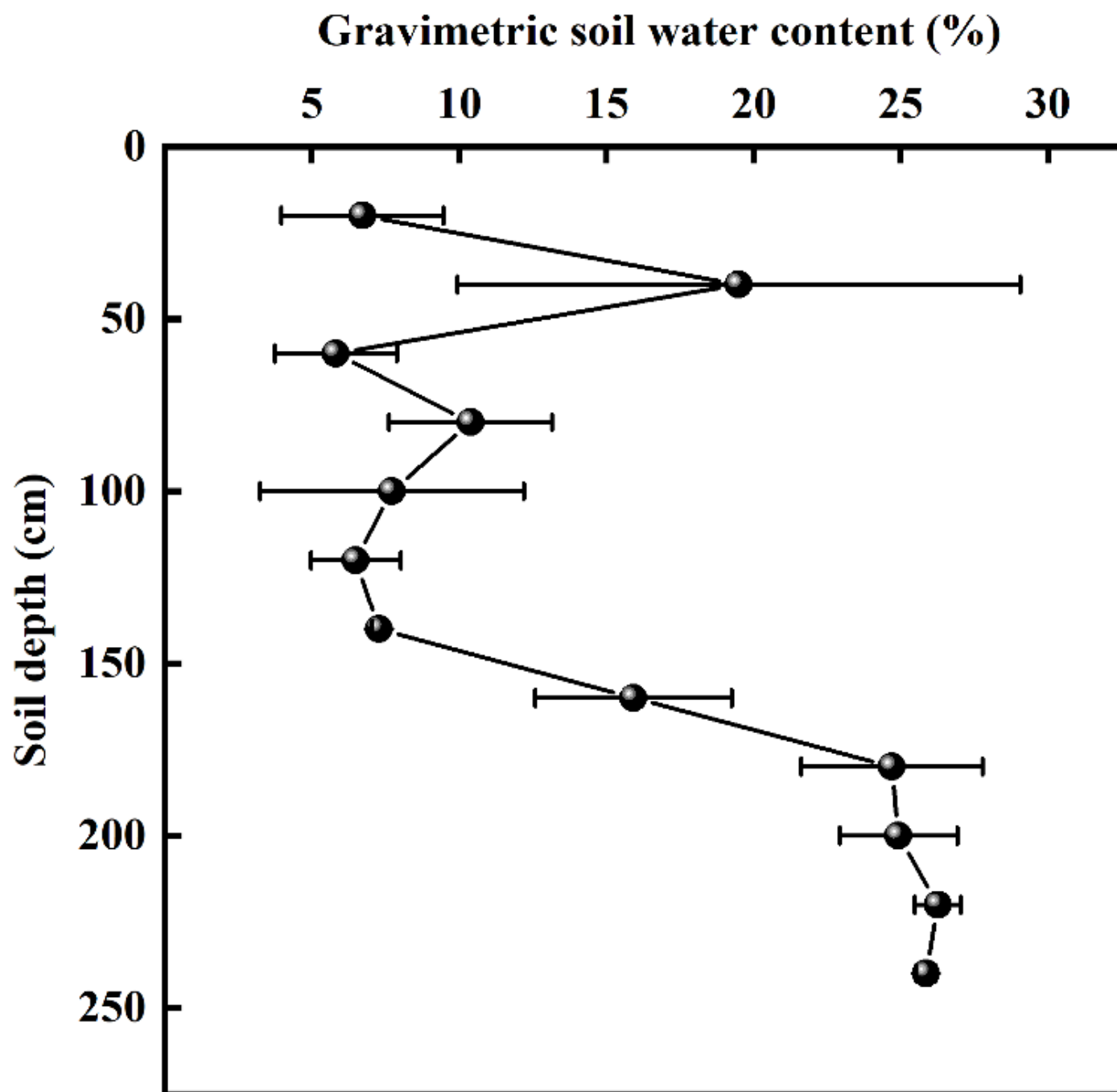


Figure 2

Variation of gravimetric soil water content at different depths at the Daryaboyi Oasis in the hinterland of Taklimakan Desert, China (means $\pm$ SD, n =3)

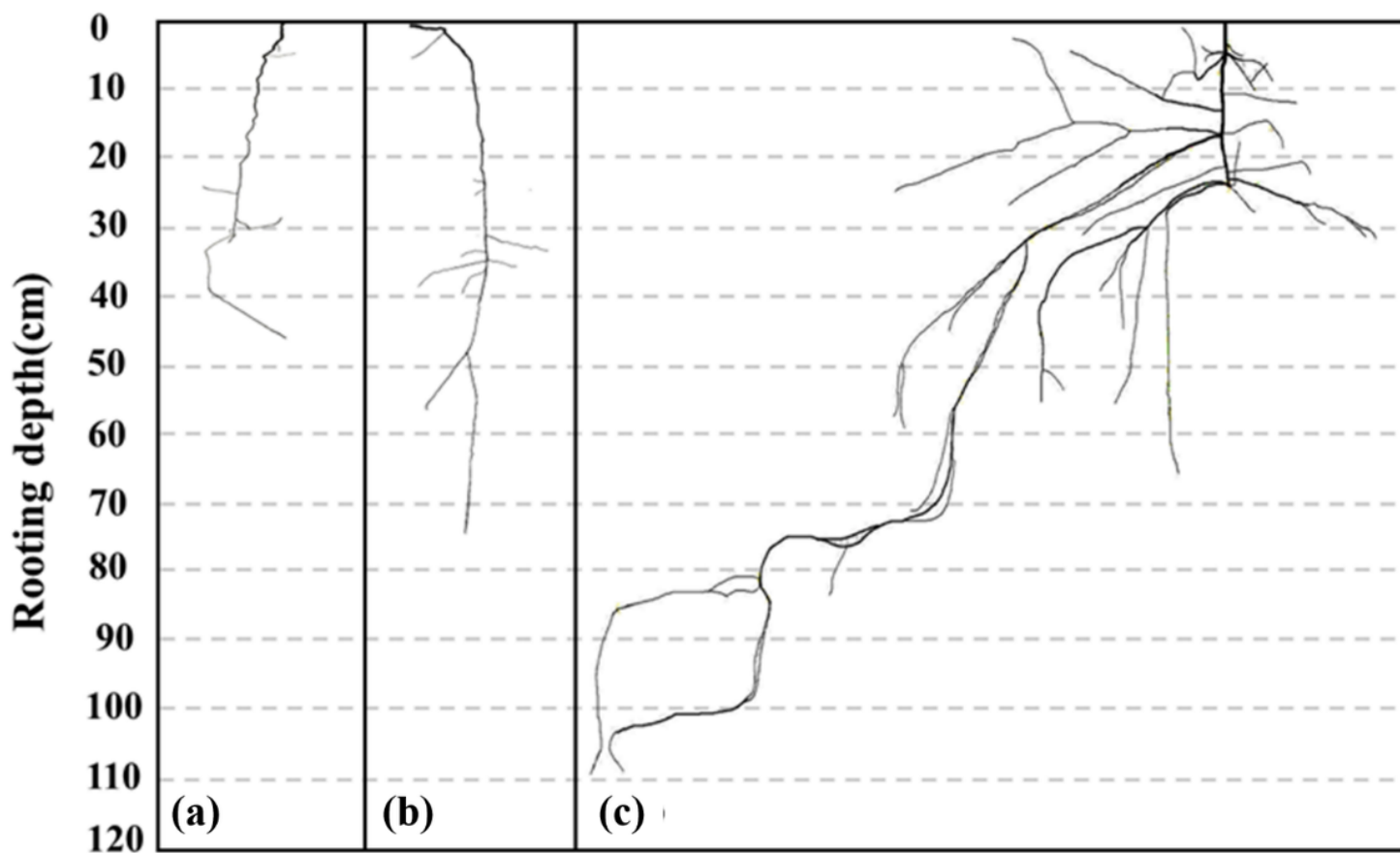


Figure 3

Root morphological characteristics of *Tamarix ramosissima* seedlings with different basal stem diameters. The basal stem diameters were as follows: (a) 1.40 mm; (b) 2.95 mm; (c) 10.63 mm

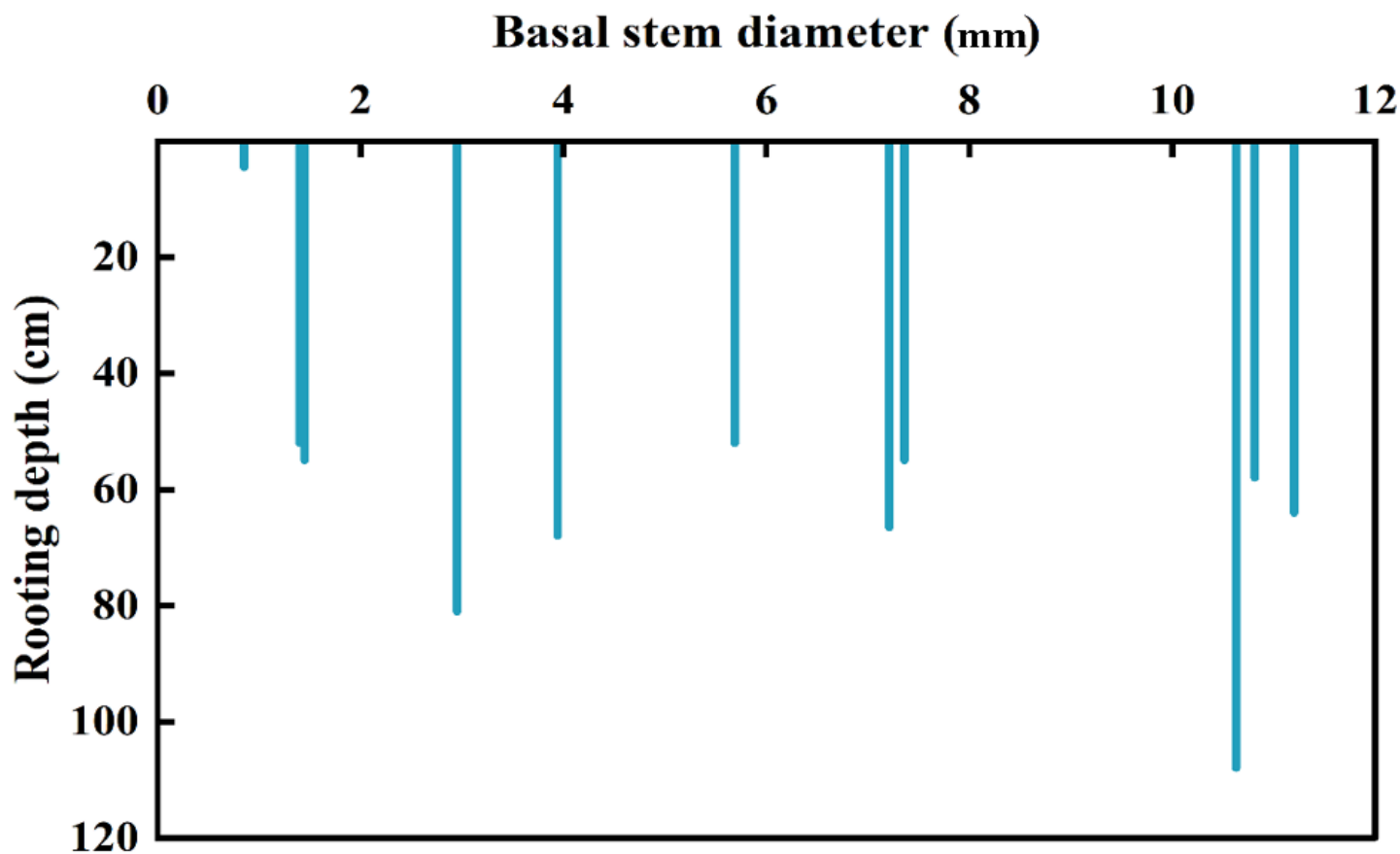


Figure 4

Taproot depths of *Tamarix ramosissima* seedlings with different basal stem diameters

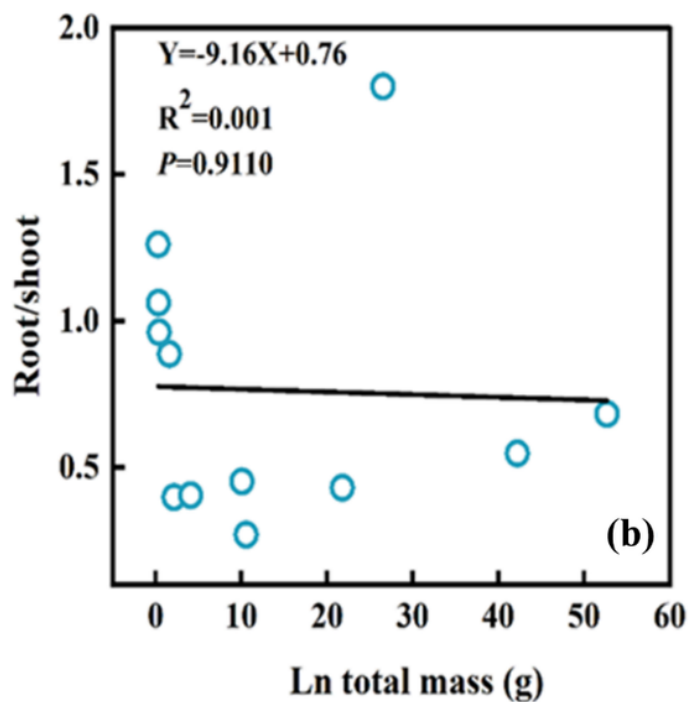
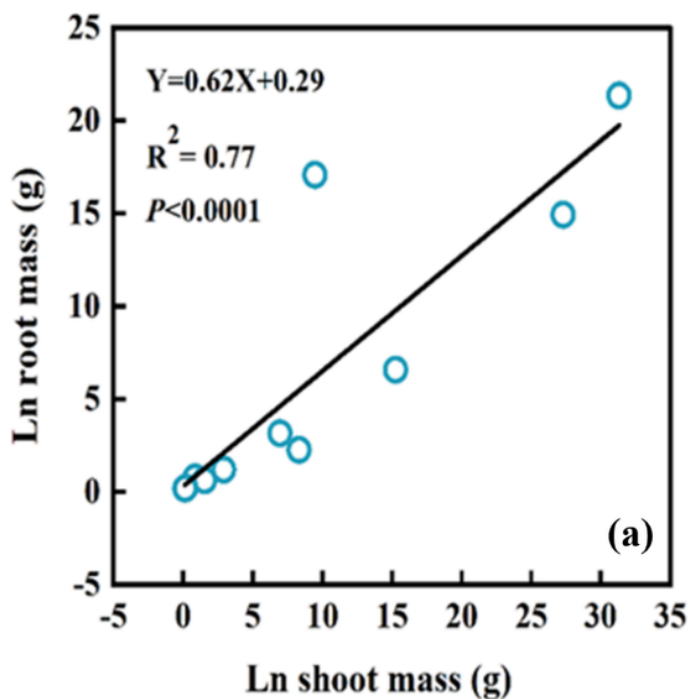


Figure 5

Aboveground and belowground biomass allocation of *Tamarix ramosissima* seedlings with different basal stem diameters

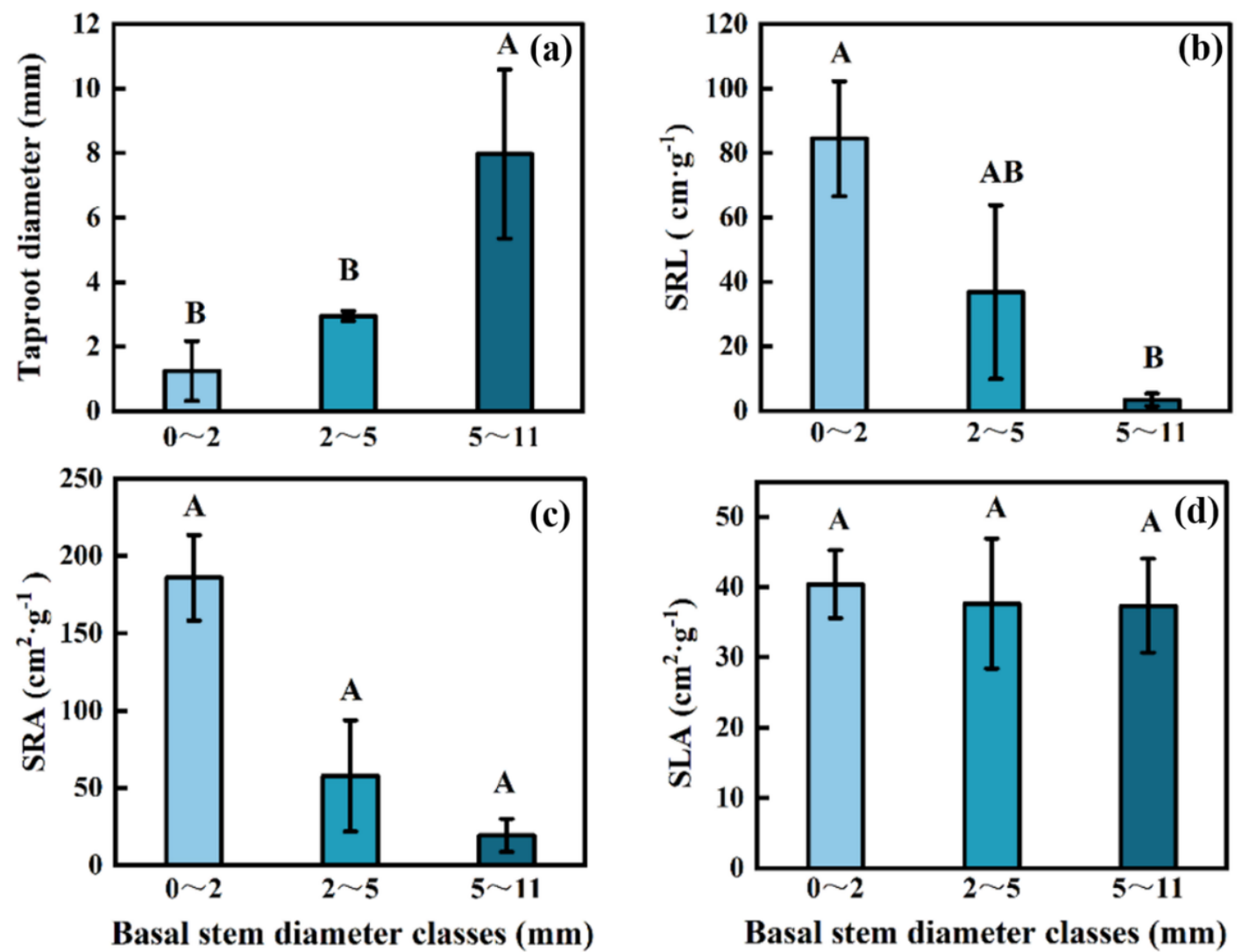


Figure 6

Taproot diameter (a), specific root length (b), specific root area (c), and specific leaf area (d) of *Tamarix ramosissima* seedlings with different basal stem diameters (means $\pm$ SD, $n = 3$)

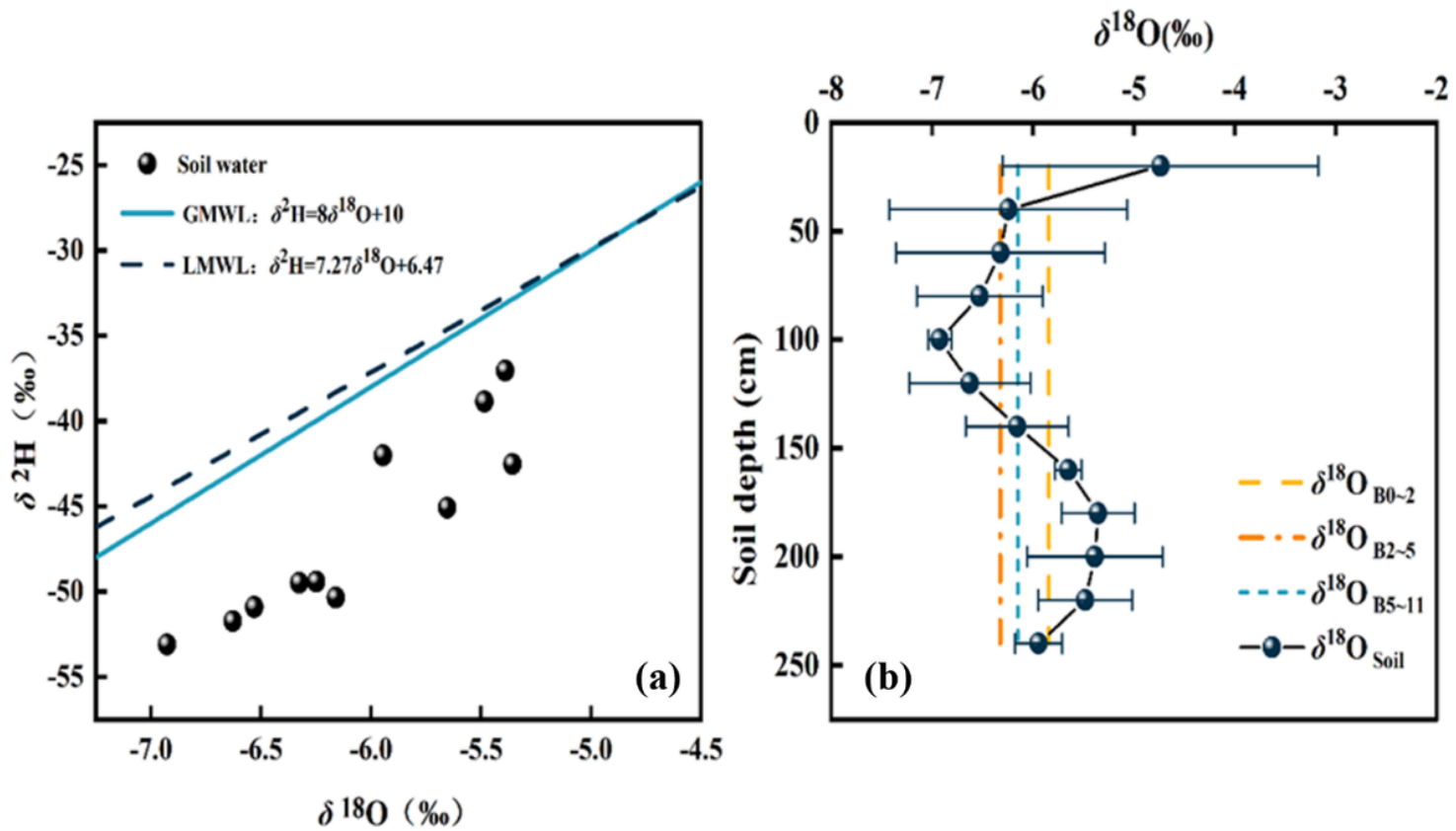


Figure 7

Stable hydrogen ($\delta^2\text{H}$) and oxygen ($\delta^{18}\text{O}$) isotopic compositions of soil water (a) and the $\delta^{18}\text{O}$ of soil water at different depths and xylem water of different BSD classes of *T. ramosissima* seedlings (b). In (a), the global meteoric water line (GMWL: $\delta^2\text{H} = 8\delta^{18}\text{O} + 10$, with the blue line) was from Craig (1961), and the local meteoric water line (LMWL: $\delta^2\text{H} = 7.27\delta^{18}\text{O} + 6.47$, with the black dashed line) was from Dong et al. (2020). The black dots are the $\delta^{18}\text{O}$ of soil water. In (b), the yellow, orange, and blue dashed lines are the $\delta^{18}\text{O}$ of B0–2, B2–5, and B5–11 respectively, the black dotted plot was the $\delta^{18}\text{O}$ of soil water. BSD, basal stem diameter.

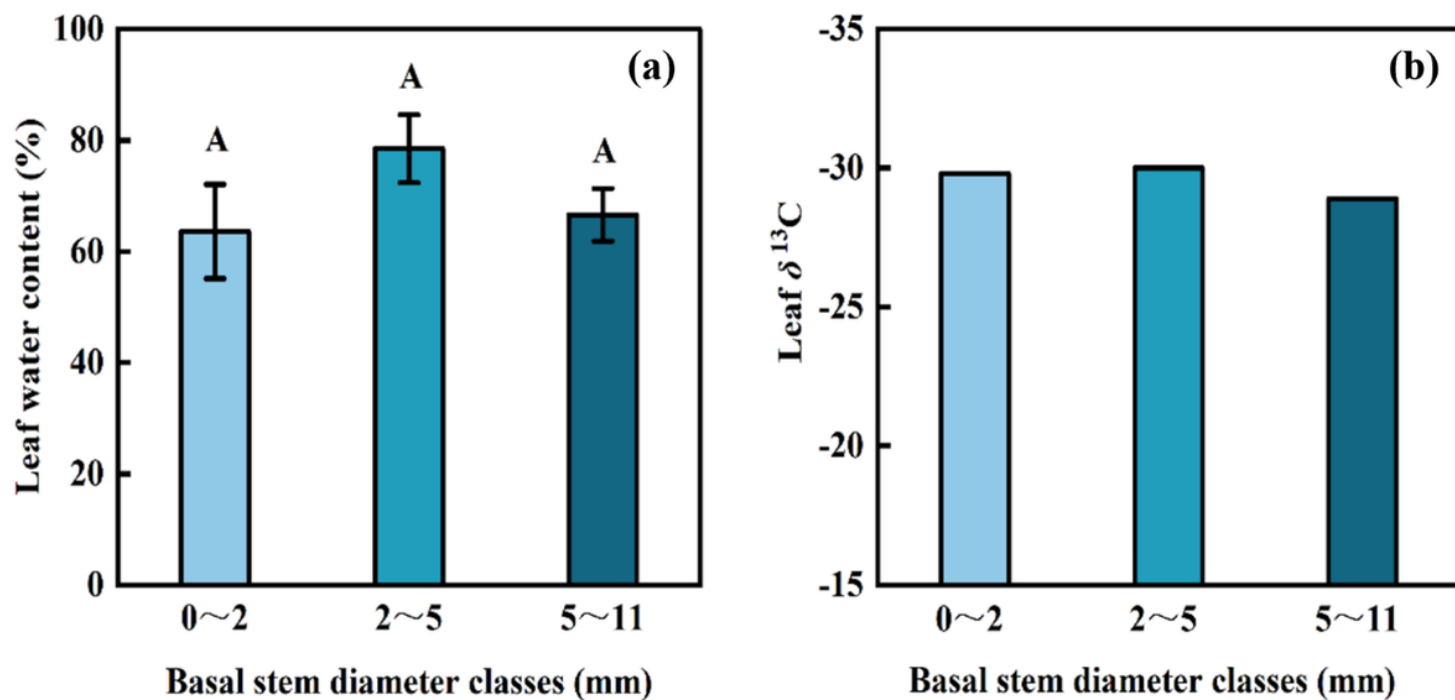


Figure 8

Leaf water content and leaf $\delta^{13}\text{C}$ of *Tamarix ramosissima* seedlings of different basal stem diameter classes