

## RESEARCH ARTICLE

# Responses of two desert riparian species to fluctuating groundwater depths in hyperarid areas of Northwest China

Engui Li<sup>1,2</sup>  | Yaqin Tong<sup>1,2</sup> | Yongmei Huang<sup>1,2</sup> | Xiaoyan Li<sup>1,2</sup> | Pei Wang<sup>1,2</sup> | Huiying Chen<sup>1,2</sup> | Chongyao Yang<sup>1,2</sup>

<sup>1</sup>State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Beijing, China

<sup>2</sup>School of Natural Resources, Faculty of Geographical Science, Beijing Normal University, Beijing, China

## Correspondence

Yongmei Huang, School of Natural Resources, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China.  
Email: ymhuang@bnu.edu.cn

## Funding information

National Natural Science Foundation of China, Grant/Award Numbers: Grant NSFC 91425301 and NSFC 912253003

## Abstract

In the hyperarid region of Northwest China, frequent variations in hydrological environments present challenges to the persistence of riparian plants. The main objective of this study was to determine whether two desert riparian species (*Populus euphratica* and *Tamarix ramosissima*) differed in their water uptake patterns and ecophysiological responses to fluctuating groundwater depths (GWDs). This study was conducted in typical desert riparian ecosystems in the downstream Heihe River basin, Northwestern China, where the GWD continuously increases during growing season. Stable oxygen composition ( $\delta^{18}\text{O}$ ) in xylem water, soil water, and groundwater, as well as leaf water potential and gas exchange were monitored. Results showed that *P. euphratica* used a higher ratio of soil water, whereas *T. ramosissima* relied more on groundwater and deep soil water. As the GWD increased during the growing season, both species modified their water use patterns, but they did so differently, *P. euphratica* extracted an increasing proportion of deep soil water and groundwater, whereas *T. ramosissima* took an increasing ratio of groundwater at critical growth stages. *P. euphratica* exhibited decreases in its daily maximum photosynthetic rate ( $A_{\max}$ ) and stomatal conductance ( $g_{\max}$ ) as the GWD increased, whereas those of *T. ramosissima* changed little. In summary, both species shift to use greater ratio of more reliable water sources with the increasing GWD, but the switching of water sources could not sufficiently compensate for the impact of drought stress on gas exchange for *P. euphratica*.

## KEYWORDS

desert riparian species, downstream Heihe River basin, gas exchange, groundwater depth, stable oxygen isotopes, water sources

## 1 | INTRODUCTION

Desert riparian zones are characterized by low precipitation and high evaporative demand and experience profound drought. Groundwater serves as an important resource for plant growth, survival, and distribution in these areas (Evaristo & McDonnell, 2017; Miller, Chen, Rubin, Ma, & Baldocchi, 2010; Stromberg, Tluczek, Hazelton, & Ajami, 2010). Desert riparian species are always exposed to great variability

in groundwater depth (GWD) because of seasonal discharge variations and episodic moisture inputs (Naiman & Décamps, 1997; Smith, Devitt, Sala, Cleverly, & Busch, 1998). These frequent variations in hydrological environments can profoundly impact the persistence of plants if that do not acclimate to this variability (Grossiord et al., 2017).

To survive groundwater fluctuations, desert riparian species developed ecological adaptations that include plastic water uptake

patterns and tight stomatal regulation, both of which are beneficial upon persistence to disturbance. For instance, many riparian species can alternate between extracting water from groundwater and soil water sources in response to changes in GWD (Andrews, Flanagan, Sharp, & Cai, 2012; Chen, Chen, Xu, & Li, 2016; Lamontagne, Cook, O'Grady, & Eamus, 2005; Rossatto, de Carvalho Ramos Silva, Villalobos-Vega, Sternberg, & Franco, 2012; Snyder, 2000; Sun, Long, & Ma, 2016). The ability to switch between water sources is related to the architecture of functional roots (Ehleringer & Dawson, 1992; Zencich, Froend, Turner, & Gailitis, 2002); a dimorphic root system can help plants avoid water deficit (Horton & Clark, 2001). Strong stomatal control is an important mechanism for limiting water loss. Down-regulation of stomatal conductance ( $g_s$ ) can minimize the water potential gradient in the xylem to prevent drought-induced xylem cavitation (Brodribb, Feild, & Jordan, 2007; McDowell et al., 2008; Sperry, 2000). Stomata closure can reduce transpirational water loss but at the expense of restricting  $\text{CO}_2$  diffusion into leaves during photosynthesis (Hetherington & Woodward, 2003; McDowell et al., 2008). Whether shift in water resources can actually compensate for drought, impacts on plant physiology has not been well studied. As was expected, more groundwater and deep soil water acquisition during the dry season contributed to the maintenance of relatively higher photosynthesis activity in many tree species (Drake, Froend, & Franks, 2011; Zunzunegui et al., 2017), however, other studies have reported that shifts in water sources did not alleviate the effects of drought stress on tree gas exchange (Grossiord et al., 2017; Sun, Meng, Zhang, & Wan, 2011). Understanding the differences in water uptake patterns, stomatal control and their link between species could provide insights into ecological adaptation strategies and could be used to predict the dynamics of desert riparian species in fluctuating environments.

*Tamarix ramosissima* is invasive in southwestern United States and many riparian gallery forests of *Populus* in southwestern United States have been replaced by *Tamarix*, as water has been withdrawn from riparian systems for agriculture (Busch & Smith, 1995; Sala, Smith, & Devitt, 1996; Smith et al., 1998). Many studies have demonstrated that the water relations between *Populus* and *T. ramosissima* differed (Glenn et al., 1998; Glenn & Nagler, 2005; Gries et al., 2003). For example, *Populus* is vulnerable to xylem cavitation and embolism (Tyree, Kolb, Rood, & Patino, 1994), whereas *T. ramosissima* is more drought tolerant than *Populus* in riparian ecosystems (Glenn & Nagler, 2005; Smith et al., 1998). Furthermore, *T. ramosissima* exhibits more plastic rooting ability for extracting water from dry soil than *Populus euphratica* does (Horton & Clark, 2001; Li, Yu, et al., 2013). In case of the downstream Heihe River basin (HRB), the second largest endorheic river in arid Northwest China, *P. euphratica* and *T. ramosissima* are two primary constructive species in desert riparian ecosystems. Due to the limited water supply from surface flows, desert riparian forests in this hyperarid area are considered groundwater dependent ecosystems (GDEs) (Eamus, Zolfaghar, Villalobos-Vega, Cleverly, & Huete, 2015; Fu, Chen, & Li, 2013; Liu, Guan, Zhao, Yang, & Li, 2017). The two species differ in their distributions in this region. *P. euphratica* usually forms pure stands that have strip distribution

characteristics restricted to the bank of the river, whereas pure *T. ramosissima* shrub exhibits a relatively broader distribution range from the beaches of the river to the margins of the Gobi Desert (Ding et al., 2017; Zhu, Yu, Wang, Zhang, & Yu, 2012). The two groups rarely appear in the form of large area of mixed stands. In the last half of the 20th century, increased water consumption for irrigation in the midstream HRB has severely lowered the groundwater table and thus has caused degeneration of the riparian forests in the downstream area (Fu, 2008; Fu et al., 2013; Qi & Luo, 2006; Zhu et al., 2016). Since 2000, an ecological water conveyance project (EWCP) has been implemented to restore the degraded ecosystems in the downstream HRB. There have been two or three water releases from the upstream each year, resulting in approximately  $10.39 \times 10^8 \text{ m}^3$  of river water that infiltrated into the groundwater of the downstream areas (Cai et al., 2015). The implementation of the EWCP dramatically altered the natural hydrology scenarios in the riparian areas of the downstream HRB. The GWD fluctuates periodically each year: a dramatic elevation occurs in May (Guo, Feng, & Li, 2009), followed by a gradually decrease until the end of the growing season (Figure 2b,d) (Wang, Zhang, Yu, Fu, & Ao, 2011). The effects of different GWDs on performance of *P. euphratica* and *T. ramosissima* have been widely studied in desert riparian area in Northwestern China (Chen et al., 2016; Chen, Chen, Xu, & Li, 2010; Gries et al., 2003; Li, Yu, et al., 2013; Si, Feng, Yu, & Zhao, 2015; Yu et al., 2013); however, most studies focused on the consequences of steady-state GWD gradients, rather than effects of fluctuation in GWD induced by manipulations of hydrology on riparian plants. Whether fluctuation in the GWD is beneficial or not to *P. euphratica* and *T. ramosissima* in riparian zones remain unknown.

To fill this knowledge gap, we adopted isotopic approaches to compare and to assess variations in water uptake patterns in *P. euphratica* and *T. ramosissima* as increased GWD. Leaf water potential and gas exchange measurements were conducted simultaneously to address the differences in ecophysiological responses of the two species with the increasing groundwater depth during the growing season. Given the known differences in water relations between the two species, we addressed the following hypothesis: (a) *P. euphratica* and *T. ramosissima* might use different water sources, and both species would respond to increased GWD by extracting higher ratio of groundwater as a result of soil water depletion; and (b) changes of the water source patterns as the GWD increased may result in different ecophysiological performance between the two species.

## 2 | MATERIAL AND METHODS

### 2.1 | Study site description

This study was conducted in an undisturbed perennial riparian zone in Sidaoqiao, which is located in the center of the Ejina Oasis in the downstream HRB. The climate of the area is extremely arid. The mean annual precipitation is less than 42 mm, and the mean annual evaporation is greater than 3,700 mm (Zhu et al., 2012); thus, the precipitation

provides nearly no water to plants. The monthly mean air temperature is 27.0°C in July and -11.7°C in January (Yu et al., 2013). We selected two primary sites where *P. euphratica* and *T. ramosissima* typically grew in the riparian areas. The *P. euphratica* woodlands site (PW site; 41.99 N, 101.13E) was located 1.0 km from the river bank in a riparian *P. euphratica* forest reserve in the Ejina Oasis, and the *T. ramosissima* scrubland site (TS site; 42.00 N, 101.14E) was approximately 0.8 km from the river bank. The TS site was located approximately 1.5 km northeast of the PW site (Figure 1); both sites belong to the Heihe Watershed Allied Telemetry Experimental Research (HiWATER) program (Li, Cheng, et al., 2013). At the PW site, the mean age of the *P. euphratica* was approximately 120 years; mean height, diameter at breast height (DBH) and canopy diameter were 13.20 ± 1.57 m, 0.46 ± 0.07 m, and 3.81 m × 3.27 m, respectively. The mean stand density was 71 ± 9 tree ha<sup>-1</sup>, and the canopy cover was 40%. The TS site consisted of a pure *T. ramosissima* scrubland with no other understory plants; the mean height, basal diameter and canopy diameter of the individual scrub were 1.90 ± 0.06 m, 0.02 ± 0.01 m, and 2.15 m × 2.00 m, respectively. In addition, the stand density was 133 ± 16 shrub ha<sup>-1</sup> at the TS site (Table 1). The soil physical properties differed between the two sites. The sand content was much higher at depths below 100 cm at the PW site than at the TS site, whereas the silt and clay contents were lower at the PW site than at the TS site. The soil organic matter (SOM) content within the top 100 cm at the TS site was significantly higher than that of the PW site (Table 2).

Automatic weather stations were present at both experimental sites. The Air temperature (Ta), net radiation (Rn) and precipitation (P) were recorded. Groundwater wells were installed at both study sites. Each well was 10 m in depth and equipped with a HOBO water level logger (Onset Computer Corporation, Bourne, MA), which records pressure head readings (absolute pressure) every 30 min. The GWD from the soil surface was calculated using HOBOWare 3.0.

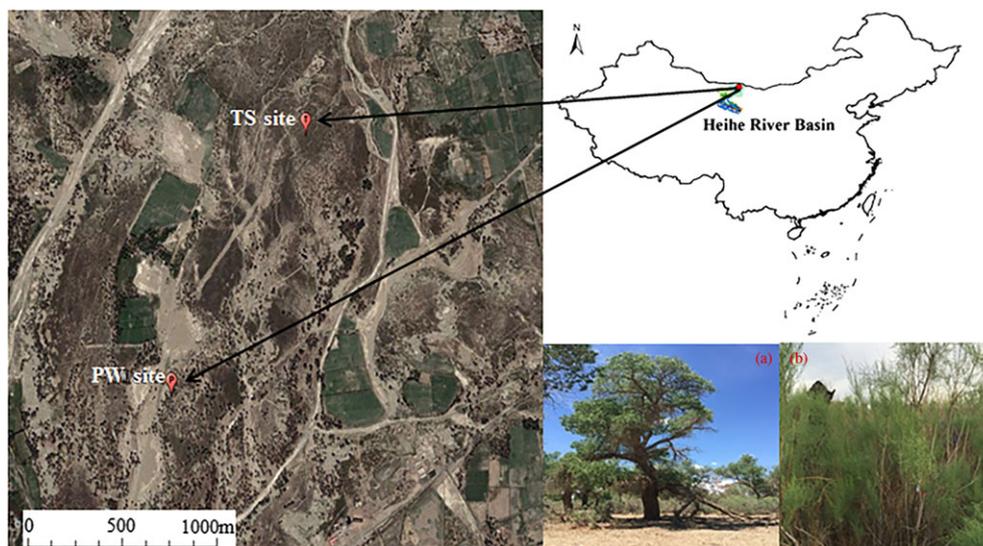
**TABLE 1** Community characteristics of the *Populus euphratica* woodland (PW site) and *Tamarix ramosissima* scrubland (TS site). Height, DBH (basal diameter for *T. ramosissima*), density, basal area and canopy diameter were determined on three sub-sampled quadrats at each site

	<i>P. euphratica</i> woodlands	<i>T. ramosissima</i> scrublands
Height (m)	13.20 ± 1.57	1.90 ± 0.06
DBH or basal diameter (m)	0.46 ± 0.07	0.02 ± 0.01
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	42.70 ± 5.4	—
Density (tree ha <sup>-1</sup> )	71 ± 9	133 ± 16
Canopy diameter (m × m)	3.81 × 3.27	2.15 × 2.00

## 2.2 | Plant xylem tissue, soil water, and groundwater sample collection

During the growing season (from June to September) of 2016, we performed five intensive field sampling investigations on 8 June, 6 July, 22 July, 11 August, and 19 September (DOYs 160, 188, 204, 224, and 260).

For stable isotopic analyses, plant, soil water, groundwater samples were collected on the same day as were the water potential and gas exchange measurements. On each sampling date, suberized twigs (diameter of 0.2–0.5 cm, length 4–5 cm) were taken from the sun-exposed branches of three to five healthy individuals of each species selected randomly within the plots between 08:00 a.m. and 09:00 a.m.. To prevent the isotopic fraction of xylem water, all green tissues (leaves and green bark) were removed and the lignified twig sections were immediately sealed in 15-ml screw-cap glass vials, which were then wrapped with Parafilm®. Concurrent with plant tissue sampling, soil samples were concomitantly collected for determination of isotope ratios and gravimetric water content. Using a 7.5 cm diameter hand bucket auger, three replicate soil cores were



**FIGURE 1** Location of the study sites in desert riparian ecosystems in downstream Heihe River, and photos for the two species (a) *Populus euphratica* at PW site; (b) *Tamarix ramosissima* at TS site

**TABLE 2** Particle size composition (% of total sample) and soil nutrient along the soil profiles at the two study sites. Particle size composition was classified according to the United States Department of Agriculture (USDA) classification system

Depth (m)	PW site					TS site				
	Sand (%)	Silt (%)	Clay (%)	TN (g/kg)	SOM (g/kg)	Sand (%)	Silt (%)	Clay (%)	TN (g/kg)	SOM (g/kg)
0–0.3	35.28	61.31	3.41	0.68	9.76	40.13	57.83	2.04	0.38	15.32
0.3–1.0	44.15	52.60	3.25	0.63	5.88	38.78	56.50	4.72	0.36	30.25
1.0–1.5	72.01	26.85	1.14	0.48	3.14	42.90	54.11	2.99	0.42	4.80
1.5+	93.20	6.72	0.08	0.57	11.62	72.98	26.03	0.99	0.71	4.97

Clay: <0.002 mm, silt: 0.002–0.05 mm, sand: 0.05–2 mm. TN: total nitrogen; SOM: soil organic matter; PW site: *Populus euphratica* woodlands site; TS site: *Tamarix ramosissima* scrubland site.

collected from each site at depth increments of 0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.5, 0.5–0.7, 0.7–1.0, 1.0–1.2, 1.2–1.5, 1.5–1.8, and 1.8–2.0 m. At the TS site, soil cores were only drilled to 180 cm in DOY 160 and DOY 188, during which times the GWD was close to 2.0 m. The collected soil samples were divided into two portions: one portion was sealed in 15-ml screw-cap glass vials for isotopic analysis, and the other portion was dried in an oven at 105°C for 24 h for determination of the gravimetric soil water content (SWC, %). All plant and soil samples were transported to the laboratory in a portable refrigerator. Groundwater samples from groundwater wells were collected into 50-ml plastic vials on each sampling date. All of the samples were subsequently stored in a refrigerator (–10°C) until water extraction and isotopic analysis.

### 2.3 | Stable isotope analysis and calculation

Water from plant xylem and soil samples was extracted with cryogenic vacuum distillation method (Sternberg, Deniro, & Savidge, 1986; West, Patrickson, & Ehleringer, 2006). The stable hydrogen ( $\delta^2\text{H}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotopic compositions of all samples were analysed by an isotopic ratio infrared spectroscopy (IRIS) system (LWIA, Model DLT-100; Los Gatos Research Inc., Mountain View, CA, USA). The  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  raw values were normalized to the Vienna Standard Mean Ocean Water (V-SMOW) scale based on three laboratory standards (LGR 3C, LGR 4C, and LGR 5C). The long-term analytical uncertainty was determined to be 1‰ for  $\delta^2\text{H}$  and 0.1‰ for  $\delta^{18}\text{O}$ . The stable isotopic ratios were calculated as:

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

where  $R$  represents the molar abundance ratios ( $^2\text{H}/\text{H}$  or  $^{18}\text{O}/^{16}\text{O}$ ), and the standard subscript refers to V-SMOW.

Residual organic contaminants produced during the extraction procedure can interfere with the analyses of xylem and soil samples, resulting in erroneous stable isotope data (West, Goldsmith, Brooks, & Dawson, 2010). To eliminate the effect of organic contaminants, all results were checked for spectral interference with Spectral Contamination Identifier (LWIA-SCI), post-processing software (Los Gatos Research Inc., Mountain View, CA, USA), and the  $\delta^{18}\text{O}$  values of the xylem samples were corrected by a standard curve (Schultz, Griffis, Lee, & Baker, 2011). Extraction and isotopic analysis of the

plant and water samples were performed at the State Key Laboratory of Earth Surface Process and Resource Ecology, Beijing Normal University.

### 2.4 | Shoot water potential and gas exchange measurements

On the same dates with collections of isotopic samples, we randomly selected five healthy individuals of each species for water potential and gas exchange measurements. Predawn water potential ( $\Psi_{\text{pd}}$ ) before dawn (04:00 a.m.–05:00 a.m.) and midday water potential ( $\Psi_{\text{md}}$ ; 12:00 p.m.–13:00 p.m.) were measured using a Scholander-type pressure chamber (Model 600D; PMS Instruments Co., Corvallis, OR, USA). For each measurement set, three distal twigs were collected from fully exposed, south-facing branches of each selected individual, and then measured immediately after being cut from plants.

The maximum net photosynthetic rate ( $A_{\text{max}}$ ;  $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ ) and maximum leaf stomatal conductance ( $g_{\text{max}}$ ;  $\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$ ) were measured with an LI-6400 portable photosynthetic system (Li-COR Inc., Lincoln, NE, USA). The measurements were carried out between 08:00 a.m. and 10:00 a.m. solar time when maximum photosynthetic rate values for the two species were expected according to our preliminary diurnal measurements (data not shown). For each species, five sun-exposed shoots were measured from each of the five individuals. Three measurement replications for each shoot at the intervals of 15 s were made. Gas exchange measurements were not conducted on 22 July (DOY 204) because of equipment failure.

### 2.5 | Quantification of water sources

Oxygen isotopic fractions are negligible during water uptake by the roots of xerophytic plants in arid environments (Costelloe et al., 2008; Ellsworth & Williams, 2007; Lin, Sternberg, Ehleringer, Hall, & Farquhar, 1993). Therefore, we used oxygen isotopes to evaluate plant water uptake patterns. The IsoSource mixing model (Phillips & Gregg, 2003) was used to estimate the feasible contributions of potential water sources to both species. The source increment was defined as 1‰ and mass balance tolerance was set to 0.1.

To simplify the number of endpoints of the IsoSource model, the water sources were reclassified. On the basis of the similarities in the  $\delta^{18}\text{O}$  values within each sampling layer, the data were combined into four layers: 0–30, 30–100, 100–200 cm, and groundwater. The

SWC-weighted-mean approach was used to calculate the  $\delta^{18}\text{O}$  value of each soil layer (Liu, Wang, Li, Liu, & Li, 2014; Snyder & Williams, 2003; Wu et al., 2016). Therefore, four potential water sources were identified for both species as follows:

- (1) Shallow soil water (0–0.3 m), in which the  $\delta^{18}\text{O}$  values and SWC varied significantly as time progressed and were strongly influenced by evaporation;
- (2) middle soil water (0.3–1.0 m), in which  $\delta^{18}\text{O}$  was lower than shallow soil water and varied moderately as time progressed; and in which SWC changed significantly as time progressed;
- (3) deep soil water (1.0–2.0 m), in which the  $\delta^{18}\text{O}$  values changed little throughout the soil profile and showed no significant monthly variations, and in which the SWC varied significantly both as time progressed and across depth variation; and
- (4) groundwater, in which the  $\delta^{18}\text{O}$  values were constant throughout the study period.

The mixing model is defined as:

$$\delta_p = f_1\delta_{ss} + f_2\delta_{ms} + f_3\delta_{ds} + f_4\delta_{gw}$$

$$1 = f_1 + f_2 + f_3 + f_4,$$

where  $\delta_p$  is the  $\delta^{18}\text{O}$  values of plant xylem water;  $\delta_{ss}$ ,  $\delta_{ms}$ ,  $\delta_{ds}$ , and  $\delta_{gw}$  refer to the  $\delta^{18}\text{O}$  signatures of the shallow soil water, middle soil water, deep soil water, and groundwater, respectively; and  $f_1$ ,  $f_2$ ,  $f_3$ , and  $f_4$  denote the contribution rates of each source.

## 2.6 | Data analysis

One-way analysis of variance followed by post hoc Tukey's test at  $\alpha = 0.05$  was used to assess temporal variations in the  $\delta^{18}\text{O}$  values of the water samples, SWC, and gas exchange measurement data.

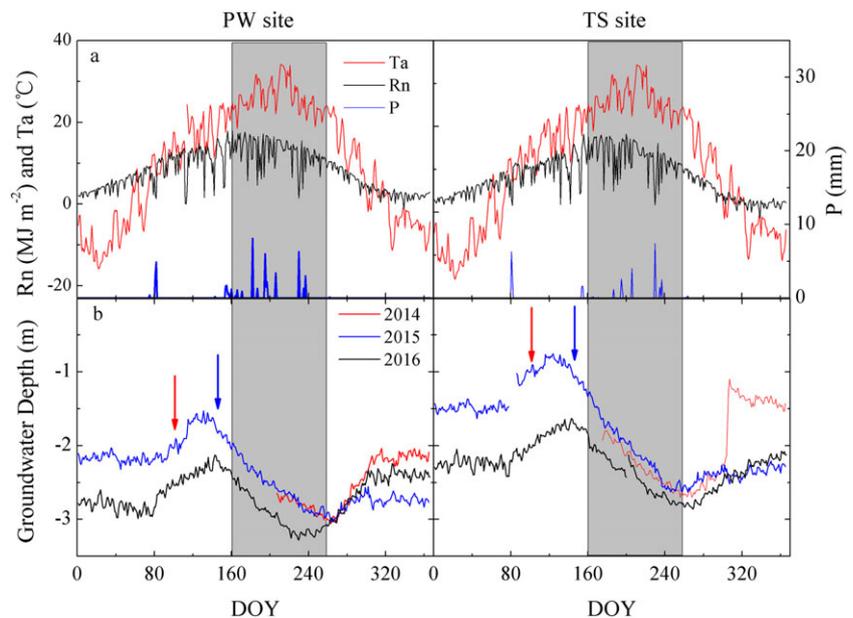
Independent-sample *t* tests were used to test the differences for both xylem  $\delta^{18}\text{O}$  and water potential ( $\psi_{pd}$ ,  $\psi_{md}$ ) between the two species. Pearson's correlations between  $g_{max}$  and  $\psi_{md}$ , and between xylem  $\delta^{18}\text{O}$  values and physiological variables ( $A_{max}$  and  $g_{max}$ ) were analysed using linear functions ( $p < 0.05$ ). All statistical analyses were performed using SPSS 20 (IBM Corp, Armonk, NY).

## 3 | RESULTS

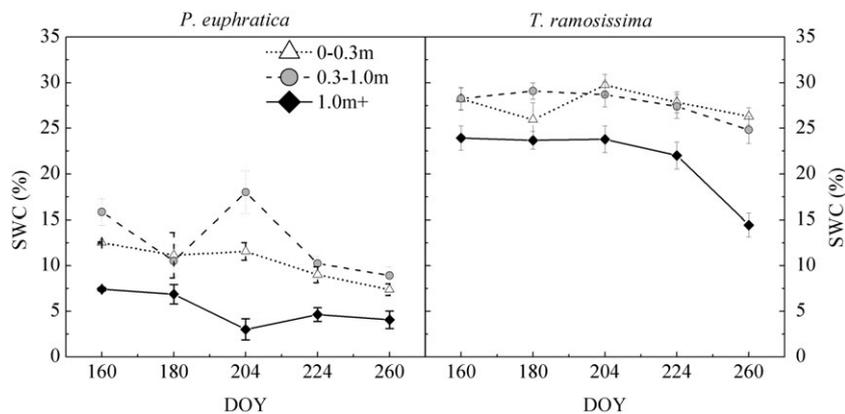
### 3.1 | Meteorological conditions and variations in the GWD and SWC

The daily  $T_a$ ,  $R_n$ , and  $P$  at the PW site and TS site were shown in Figure 2. The total precipitation in 2016 at the PW site and TS site was 49.8 and 33.2 mm, respectively; all precipitation events were less than 10 mm. Both sites experienced similar micro climatic conditions, which consisted of little precipitation, high temperatures, and intense solar radiation. The water conveyance from upstream started on April 11 (DOY 102) and ended on May 22, 2016 (DOY 143), and the water reached the river course in the lower reaches of HRB in mid-May. After water conveyance, the GWD at the PW site and TS site increased from 2.1 m to 3.3 m and from 1.7 m to 2.9 m during the study period (DOY 160–260), respectively (Figure 2b,d).

The SWC changed markedly as both time progresses and as depth increased at both sites (Figure 3 and Figure S1). At the PW site, the mean SWC decreased gradually from 12.52% to 7.37% in the top 0.3 m, and from 15.84% to 8.92% in the 0.3–1.0 m layer during the experimental period. The mean SWC below 1.0 m was greatly lower than that in shallow and middle layers, and decreased from 7.42% to 4.07% as time progressed. At the TS site, the SWC did not fluctuate as much as it did at the PW site, whereas that below 1.0 m decreased dramatically from 22.34% to 14.44% in the end of the growing season (DOY 224–260).



**FIGURE 2** Meteorological parameters at the two study sites in 2016: mean daily air temperature ( $T_a$ ), daily net radiation ( $R_n$ ), daily precipitation ( $P$ ), and daily mean groundwater depth (GWD) in 2014–2016; shaded area indicates the samplings period. Red arrows indicate the beginning date of ecological water conveyance project (EWCP) from upstream Heihe River, blue arrows indicate the end date of the EWCP



**FIGURE 3** Soil water content with standard error bars in soil water (shallow, middle, and deep layers: 0–0.3, 0.3–1.0, and 1.0+ m, respectively) at the *Populus euphratica* woodlands site (a) and *Tamarix ramosissima* scrubland site (b)

### 3.2 | Isotopic values in xylem water and potential water sources

The xylem water  $\delta^{18}\text{O}$  values significantly differed between *P. euphratica* and *T. ramosissima* during the measurement period; the values ranged from  $-4.34$  to  $-6.68\text{‰}$  and from  $-5.53$  to  $-6.70\text{‰}$ , respectively. Seasonal decline in xylem water  $\delta^{18}\text{O}$  values were observed for both species, PW:  $F(4, 15) = 20.16$ ,  $p < 0.001$  and TS:  $F(4, 15) = 10.06$ ,  $p < 0.05$  (Figure S2).

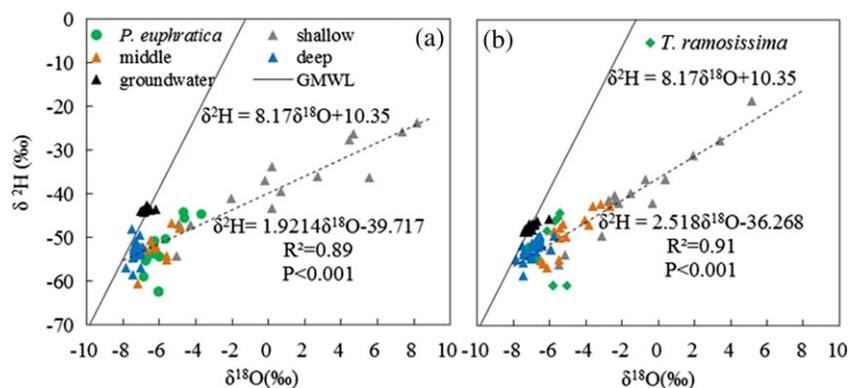
The soil water  $\delta^{18}\text{O}$  values at both sites presented similar variations with depth (Figure 3, and Figure S1). The soil water  $\delta^{18}\text{O}$  values in the top 0.3 m were clearly higher than those in the other layers and varied significantly as time progressed. The  $\delta^{18}\text{O}$  values in the 0.3–1.0 m layer decreased continuously with depth and exhibited moderate monthly variations. The soil water  $\delta^{18}\text{O}$  values in the layers below 1.0 m were uniform and exhibited no significant monthly variations. The values from our soil water samples at both sites lay on the right of the global meteoric water line (GMWL:  $\delta^2\text{H} = 8.17\delta^{18}\text{O} + 10.35$ ) with slopes of 1.9 and 2.5. The small slopes suggested that soil water was subjected to substantial evaporation. The groundwater  $\delta^{18}\text{O}$  values at both sites did not vary significantly throughout the experimental period (Figure 3c,d), the means were  $-6.63\text{‰}$  and  $-6.97\text{‰}$ , respectively. The xylem water  $\delta^{18}\text{O}$  values of *P. euphratica* were distributed along with the soil water and groundwater, whereas those of *T. ramosissima* were approximately distributed around the deep soil water and groundwater (Figure 4); indicating that the xylem water of *P. euphratica* was absorbed from different layers of soil water

and groundwater sources, whereas that of *T. ramosissima* was absorbed mainly from deep soil water and groundwater sources.

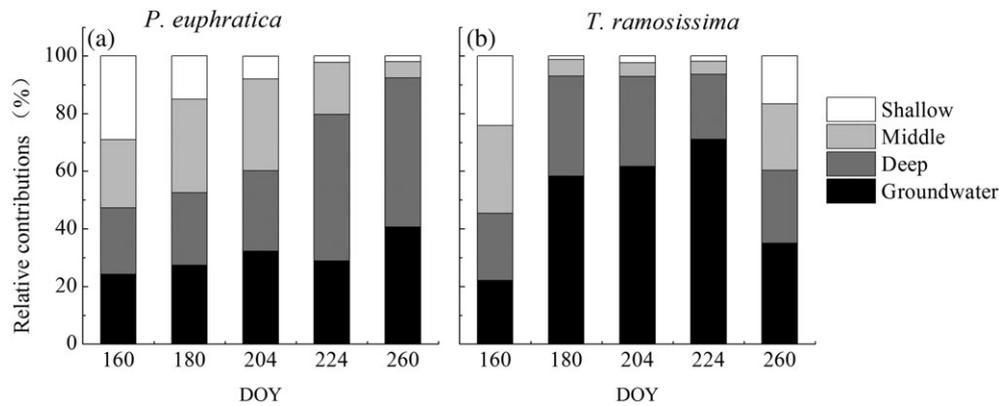
### 3.3 | Estimation of the feasible contributions of potential water sources

The water source contributions varied between the two species (Figure 5). *P. euphratica* extracted great proportion of various soil water sources during the experimental period. The contribution of soil water sources (including shallow, middle, and deep soil water) was approximately 59.3% to 75.8% (Figure 5a). *T. ramosissima* took up great ratio of deep soil water and groundwater at the peak of the growing season (DOY180–224).

For *P. euphratica*, when the GWD was approximately 2.1 m (DOY 160), the four water sources contributed equally: 29.0%, 23.7%, 23.1%, and 24.2% for the shallow soil water, middle soil water, deep soil water, and groundwater, respectively. As the GWD increased, the contributions of the shallow and middle soil water decreased gradually, whereas those of deep soil water and groundwater increased dramatically. When the GWD increased to 3.3 m (DOY 260), the deep soil water and groundwater became dominant; their contributive proportions were 51.7% and 40.7%, respectively. *T. ramosissima* exhibited definitive shifts in its water sources. At the beginning of the growing season, during which time the GWD was approximately 1.7 m (DOY 160), the four water sources contributed equally. *T. ramosissima* rapidly shifted to extract most of its water from



**FIGURE 4** The regression relationships between  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  in soil water, groundwater and xylem water at *Populus euphratica* woodlands site (a) and *Tamarix ramosissima* scrubland site (b) shown with global meteoric water line (with black line) and soil water line (with dashed line)



**FIGURE 5** Variations in fraction of water uptake from shallow, middle, deep soil layers, and groundwater sources for *Populus euphratica* trees at PW site (a) and *Tamarix ramosissima* scrubs at TS site (b). Column heights represent the mean values of relative contributions of the potential water sources. All results were derived from the IsoSource model

the groundwater and deep soil water as the GWD increased (DOY 188–224); the contributive proportions were approximately 58.3%–71.1% and 34.7%–22.5% from the groundwater and deep soil water, respectively. A subsequent decrease in groundwater proportions was observed when the GWD increased to 2.9 m at the end of the growing season (DOY 260) (Figure 5b).

### 3.4 | Variations in leaf water potential, $A_{\max}$ and $g_{\max}$

*P. euphratica* presented significantly higher seasonal-mean ( $\pm$ SE)  $\Psi_{pd}$  and  $\Psi_{md}$  than did *T. ramosissima*,  $-0.64 \pm 0.03$  vs.  $-2.02 \pm 0.08$  MPa,  $F(1, 48) = 11.10$ ,  $p < 0.001$ ;  $-2.50 \pm 0.12$  vs.  $-3.81 \pm 0.17$  MPa,  $F(1, 48) = 2.30$ ,  $p < 0.001$ . Both species exhibited a significant decrease in  $\Psi_{md}$  throughout the growing season, PW:  $F(4, 20) = 14.72$ ,  $p < 0.001$ ; TS:  $F(4, 20) = 9.40$ ,  $p < 0.001$ . The  $\Psi_{md}$  decreased from  $-2.12$  to  $-2.83$  MPa in *P. euphratica* and from  $-3.30$  to  $-4.36$  MPa in *T. ramosissima*, respectively. Neither *P. euphratica* nor *T. ramosissima* exhibited a significant decrease in  $\Psi_{pd}$  throughout the growing season (Figure 6a,b,e,f).

*P. euphratica* displayed slight increases in  $A_{\max}$  and  $g_{\max}$  at the beginning of the growing season, but then displayed reductions of  $\sim 46\%$  in  $A_{\max}$  and of  $\sim 43\%$  in  $g_{\max}$  when the GWD increased from 2.3 to 2.8 m (Figure 6c,d). *T. ramosissima* changed little in both  $A_{\max}$  and  $g_{\max}$  throughout the experimental period (Figure 6g,h).

### 3.5 | Relationships between xylem water isotope values and gas exchange rates

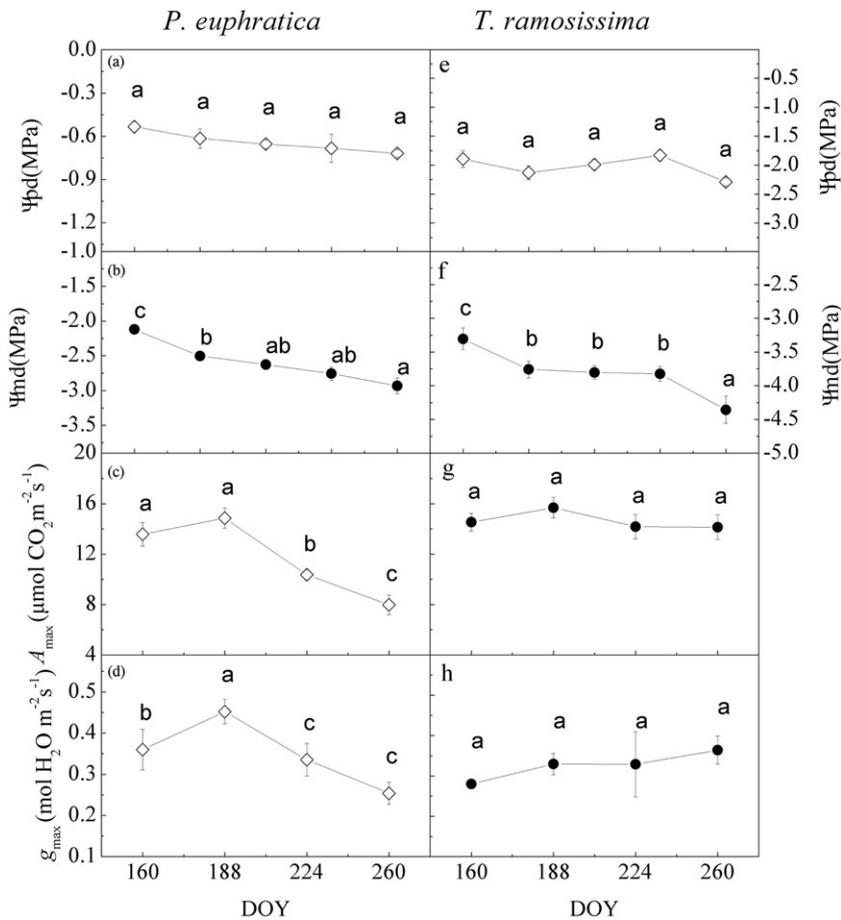
We found significant positive relationships between xylem water  $\delta^{18}\text{O}$  values and both  $g_{\max}$  ( $p = 0.044$ ) and  $A_{\max}$  ( $p = 0.020$ ) for *P. euphratica* (Figure 7a for  $g_{\max}$  and Figure 7c for  $A_{\max}$ ). These strong relationships suggest that as *P. euphratica* extracted greater ration of deep soil water and groundwater, gas exchanges decreased. No significant relationships between  $g_{\max}$ ,  $A_{\max}$ , and xylem water  $\delta^{18}\text{O}$  values were observed for *T. ramosissima* (Figure 7b,d).

## 4 | DISCUSSION

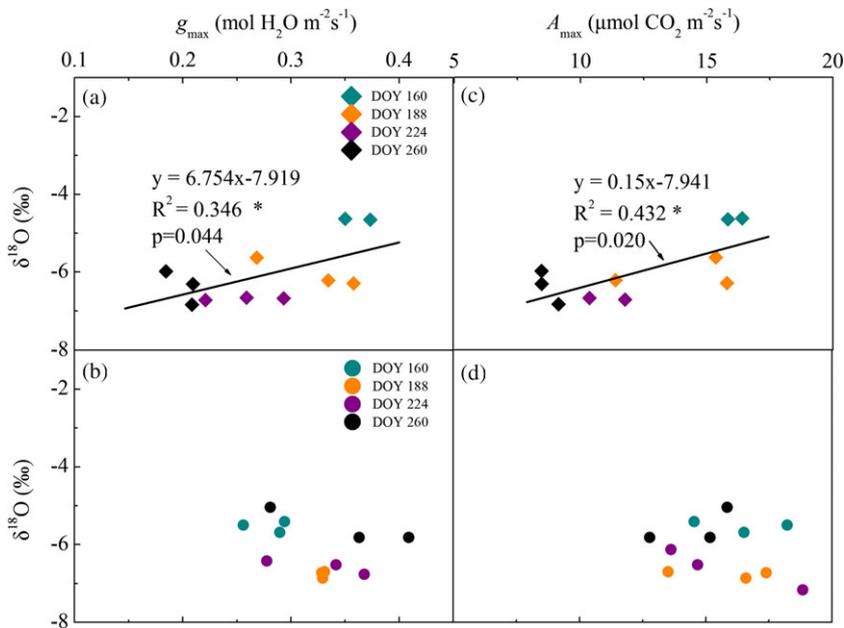
### 4.1 | Differences in water source patterns between species

*P. euphratica* and *T. ramosissima* exhibited distinct water uptake patterns in the riparian zone in downstream HRB, which support our first hypothesis. The isotopic data evidenced that groundwater and deep soil water (deeper than 100 cm+) were the main water sources for *T. ramosissima*, although it could also use all available water sources at the beginning and the end of the growing season. In contrast, *P. euphratica* relied more on various soil water (Figures 4 and 5). This result was also supported by the variations in SWC. In the TS site, shallow and middle soil water changed little during the experimental period (Figure 3), suggesting that *T. ramosissima* had limited use of shallow and middle soil water, but to utilize more reliable deep soil water and groundwater directly (Figure 5b). In the PW site, the SWC in each layer decreased gradually (Figure 3a). Moreover, the xylem water  $\delta^{18}\text{O}$  values approached those for shallow, middle, and deep soil water (Figure 4a), suggesting that *P. euphratica* consumed a high proportion of combination of various soil water, as supported by the IsoSource outputs in Figure 5a. Hence, we inferred that *P. euphratica* growing in the riparian area may be sensitive to the change of soil water. The dependence on soil water may partially explain why *P. euphratica* restricted to the river bank where the soil water was always well recharged. The soil water available for *P. euphratica* trees in the riparian zone should be a mixture of (a) water already resident in the unsaturated soil, (b) river water recharge from the upstream HRB, and (c) groundwater that may be accessible to the deep soil layer. We did not focus on the interaction between soil water, groundwater, and river in the present study, which needed further study.

In the present study, both species were found to modify their water uptake patterns in response to the increase in GWD, but they did so differently, with *P. euphratica* extracted an increasing proportion of deep soil water and groundwater and *T. ramosissima* took an increasing ratio of groundwater at critical growth stages (DOY



**FIGURE 6** Comparison of variations in  $\Psi_{pd}$  (a,e),  $\Psi_{md}$  (b,f), daily maximum leaf-areas based photosynthetic rate ( $A_{max}$ ; c,g), and stomatal conductance ( $g_{max}$ ; d,h) with  $\pm$ SE of *Populus euphratica* (diamonds) and *Tamarix ramosissima* (circles) during study period. Letters denote significant differences between sampling dates



**FIGURE 7** Relationships between xylem water  $\delta^{18}\text{O}$  and (a,b) maximum stomatal conductance ( $g_{max}$ ) and (c,d) maximum  $\text{CO}_2$  assimilation ( $A_{max}$ ) for *Populus euphratica* (diamonds) and *Tamarix ramosissima* (circles) across all sampling dates. The equation,  $R^2$  and  $p$  values are given. \* $p < 0.05$ . The relationships for *T. ramosissima* were not significant

180–224) (Figure 5). The  $\delta^{18}\text{O}$  values of deep soil water and groundwater were more depleted than that of shallow and middle soil water (Figure 4 and Figure S1). Hence, seasonal declines in xylem water  $\delta^{18}\text{O}$  values for *P. euphratica* and more depleted xylem water  $\delta^{18}\text{O}$  values in

*T. ramosissima* were observed in the peak of the growing season (Figure S2). Rooting distributions define the depth from which plants can absorb water (Ehleringer, Phillips, Schuster, & Sandquist, 1991). Yu et al. (2013) excavated the root systems of *P. euphratica* and

*T. ramosissima* at sites where the GWD was similar to the present study sites and reported that both species presented deep taproots below the groundwater table. Furthermore, *P. euphratica* presented clusters of dense fine roots (<2 mm in length) in layers at approximately 0.2 and 0.6 m-depths within the soil profile, whereas *T. ramosissima* presented an extended dense fine root layer at a depth of approximately 0.4–1.0 m. The dimorphic root systems make it possible for both species to switch their water sources among various soil depths. At the onset of the growing season, *P. euphratica* abstracted water from all potential water sources, however, as the soil dried in shallow and middle layers, the root hydraulic conductivity could be reduced (Martre, North, & Nobel, 2001; Vandeleur et al., 2009), and thus, the reduced water uptake efficiency of roots in this layers. Therefore, a greater proportion of water was taken from deeper water sources by deep roots. The changes in plant water sources were also closely related to root growth. *Tamarix ramosissima* was reported to presents greater root elongation rate at the onset of the growing season to reach the groundwater (Child et al., 2009; Gries et al., 2003; Horton & Clark, 2001; Li, Yu, et al., 2013). New roots are of high hydraulic conductivity, and thus especially efficient in water uptake. Therefore, *T. ramosissima* exhibited high absorption ratio of groundwater during the peak of the growing season. At the end of the growing season, when groundwater table reached its lowest level (Figure 2d), *T. ramosissima* use all available water sources not primarily deeper water sources (Figure 5b). This was mainly because the groundwater supply to deep soil layer was reduced, and resulted in dramatically decrease of the soil water content in deep layer (Figure 3b). The usage of groundwater and deep soil water was therefore hindered at this stage. Consequently, shallow and middle soil water became an important supplement for *T. ramosissima* in resistance to drought stress. The different water uptake patterns of the two desert riparian species reflect their adaptations to specific habitats, and the ability to switch to extracting deeper and more reliable water sources make it possible for the two species to survive in such a water-limited area.

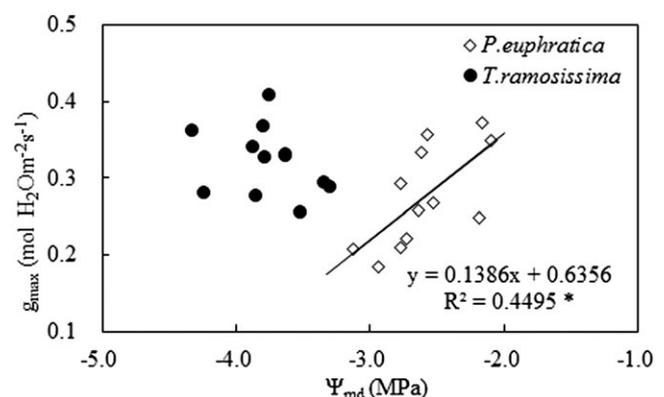
## 4.2 | Changes in ecophysiological characteristics of the two species and implications

Plants with access to reliable water sources in semiarid and arid areas would keep constant  $\Psi_{pd}$  values across arid season (Williams & Ehleringer, 2000). The SWC within the deep soil layers decreased greatly at both sites (Figure 3), and the shallow soil water was subjected to strong evapotranspiration consumption during the growing season. However, the  $\Psi_{pd}$  for both species did not changed significantly during the experimental period despite the occurrence of significant decreases in SWC. This is direct evidence that groundwater was a constant available water source for *P. euphratica* and *T. ramosissima* as the dry season progressed. *T. ramosissima*, in the present study, experienced much higher predawn leaf water potentials than that in the riparian area in free-flowing Hassayampa River, Arizona (below  $-3.5$  Mpa) (Horton, Kolb, & Hart, 2001). These results

could be explained by that *T. ramosissima* in the present study relied more on groundwater instead of unsaturated soil water (Figure 5).

The ability of plants to switch to extracting water from reliable reservoirs is a crucial acclimation strategy for xeric species, which exposed to fluctuated hydrological environments (Rossatto et al., 2012; Snyder & Williams, 2003; Voltas, Lucabaugh, Chambel, & Ferrio, 2015). In the present study, both species were found to modify their water uptake patterns to extract more reliable water sources in response to the increase in GWD. Without a doubt, deep soil water and groundwater resources may alleviate drought stress on plants and allow them to survive in hyperarid area (Domec et al., 2006; Zhang et al., 2017). However, ecophysiological data in this study support the assumption that shifts in water sources may not always compensate for drought stress on tree ecophysiology (Grossiord et al., 2017). In the present study,  $A_{max}$  significantly decreased from 14.85 to 7.97  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for *P. euphratica* during the peak of the growing season (Figure 6). This was similar to the result reported by Chen et al. (2010), which the maximum photosynthetic rates decreased from 14.64 to 10.28  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  when the GWD increased from 4.12 to 7.74 m (Chen et al., 2010). One explanation for the decreases in  $A_{max}$  for *P. euphratica* was that it not only use groundwater but also a great proportion of soil water from different depth (Figure 5a). However, the soil water content was very low in the PW site (Figure 3a), so it can not compensate for the water lost by transpiration. *T. ramosissima* depends more on water from deep soil water and groundwater than *P. euphratica* (Figure 5), thus, it can maintain stable gas exchange rate under the water condition in the present study (Figure 6g,h). This result was consistent with that of Horton et al. (2001), which reported that there was no relationship between stomatal conductance and water potential in dry season when gas exchange stable for *Tamarix*.

*P. euphratica* has also been reported to exert tight stomatal control to limit water loss and to avoid dehydration during dry season (Gries et al., 2003). Our result agreed with the water-saving strategy because the stomatal conductance was correlated with  $\Psi_{md}$  for *P. euphratica* (Figure 8). Stomatal regulations play important role in preventing drought induced xylem cavitation for plants (Choat, Sack, & Holbrook,



**FIGURE 8** Maximum stomatal conductance ( $g_{max}$ ) of *Populus euphratica* and *Tamarix ramosissima* versus midday water potential ( $\Psi_{md}$ ). \* $p < 0.05$ . Error bars are not shown

2007). However, this control also resulted in the restriction of CO<sub>2</sub> diffusion into the leaf during photosynthesis (Hetherington & Woodward, 2003), and consequently reduced carbon assimilation rate in the present study (Figure 6c). Compared with *P. euphratica*, there was no clear correlation between  $g_{\max}$  and water potential for *T. ramosissima* (Figure 8). We speculate that there may be other factors that limit the gas exchange for *T. ramosissima*. Overall, ecophysiological data evidenced that the changes of water sources to deep soil water and groundwater was associated with the reductions in gas exchange for *P. euphratica* (Figures 6c,d and 7a,c). Thus, although the acclimated water uptake patterns may be necessary for *P. euphratica* in response to the fluctuations in the GWD, it did not fully counteract the impact of drought stress on tree ecophysiology. The result was similar to that of previous studies. Otieno et al., (2006) found no growth was recorded during drought period for *Quercus suber*, even if this species extracted most of its water from deep soil layers and maintain stable predawn water potential.

We compared the different water use patterns and ecophysiological traits of the two species in response to fluctuations in GWD in the present study. A frequent future fluctuation of the GWD under the climate change and manipulations are to be expected. Ecological water conveyance project is of critical importance to maintain the sustainability of the desert riparian ecosystem. In terms of our experimental results, we suggest that both suitable GWD and sufficient soil water content should be considered to maintain optimal physiological performance for *P. euphratica* when determining the optimum ecological water requirement of the desert riparian area in downstream HRB.

## 5 | CONCLUSIONS

The GWD in the riparian zone of the downstream HRB fluctuated periodically, but continuously increased throughout growing season. Data allowed us to conclude that *P. euphratica* used a higher ratio of soil water, whereas groundwater and deep soil water were the main water sources for *T. ramosissima*. Both species modified their water use patterns in response to the increase in GWD, but they did so differently, with *P. euphratica* extracted an increasing proportion of deep soil water and groundwater and *T. ramosissima* took an increasing ratio of groundwater at critical growth stages. These findings can provide quantitative implications for further studies on determination of the optimum ecological water requirement in the desert riparian area in downstream HRB. Our study also provides a comparison of ecophysiological responses of the two desert riparian species in response to the increased GWD. *P. euphratica* displayed reductions in  $A_{\max}$  and  $g_{\max}$  with increasing GWD, whereas *T. ramosissima* changed little in both  $A_{\max}$  and  $g_{\max}$  throughout the experimental period. Specifically, there were linear positive relationships between the xylem water  $\delta^{18}\text{O}$  values and  $A_{\max}$  and  $g_{\max}$  for *P. euphratica*, suggesting that shifts in water sources may not fully compensate for drought stress on ecophysiology for *P. euphratica* in the hyperarid downstream HRB.

## ACKNOWLEDGEMENTS

We thank Prof. Qi from Northwest Institute of Eco-Environment and Resources, CAS for providing the data set of groundwater depth. We also thank all the scientists and engineers who participated in the HiWATER field campaigns. The meteorological data obtained from HiWATER can be downloaded at <http://heihedata.org/hiwater>.

## CONFLICT OF INTEREST

None declared.

## FUNDING

This study was financially supported by the National Natural Science Foundation of China (Grant NSFC 912253003).

## ORCID

Engui Li  <https://orcid.org/0000-0003-1983-7436>

## REFERENCES

- Andrews, S. F., Flanagan, L. B., Sharp, E. J., & Cai, T. (2012). Variation in water potential, hydraulic characteristics and water source use in montane Douglas-fir and lodgepole pine trees in southwestern Alberta and consequences for seasonal changes in photosynthetic capacity. *Tree Physiology*, *32*, 146–160. <https://doi.org/10.1093/treephys/tpr136>
- Brodribb, T. J., Feild, T. S., & Jordan, G. J. (2007). Leaf maximum photosynthetic rate and venation are linked by hydraulics. *Plant Physiology*, *144*, 1890–1898. <https://doi.org/10.1104/pp.107.101352>
- Busch, D. E., & Smith, S. D. (1995). Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern US. *Ecological Monographs*, *65*, 347–370. <https://doi.org/10.2307/2937064>
- Cai, Y., Huang, W. R., Teng, F., Wang, B. B., Ni, K., & Zheng, C. M. (2015). Spatial variations of river-groundwater interactions from upstream mountain to midstream oasis and downstream desert in Heihe River basin, China. *Hydrology Research*, *47*, 501–520.
- Chen, Y. P., Chen, Y. N., Xu, C. C., & Li, W. H. (2010). Photosynthesis and water use efficiency of *Populus euphratica* in response to changing groundwater depth and CO<sub>2</sub> concentration. *Environmental Earth Sciences*, *62*, 119–125. <https://doi.org/10.1007/s12665-010-0502-x>
- Chen, Y. P., Chen, Y. N., Xu, C. C., & Li, W. H. (2016). The effects of groundwater depth on water uptake of *Populus euphratica* and *Tamarix ramosissima* in the hyperarid region of Northwestern China. *Environmental Science and Pollution Research*, *23*, 17404–17412. <https://doi.org/10.1007/s11356-016-6914-8>
- Child, M. F., Milton, S. J., Dean, R. W. J., Lipsey, M. K., Puttick, J., Hempson, T. N., ... Wistebaar, T. (2009). Tree-grass coexistence in a flood-disturbed, semi-arid savanna system. *Landscape Ecology*, *25*, 315–326. <https://doi.org/10.1007/s10980-009-9409-x>
- Choat, B., Sack, L., & Holbrook, N. M. (2007). Diversity of hydraulic traits in nine Cordia species growing in tropical forests with contrasting precipitation. *New Phytologist*, *175*, 686–698. <https://doi.org/10.1111/j.1469-8137.2007.02137.x>
- Costelloe, J. F., Payne, E., Woodrow, I. E., Irvine, E. C., Western, A. W., & Leaney, F. W. (2008). Water sources accessed by arid zone riparian trees in highly saline environments, Australia. *Oecologia*, *156*, 43–52. <https://doi.org/10.1007/s00442-008-0975-4>
- Ding, J., Zhao, W., Daryanto, S., Wang, L., Fan, H., Feng, Q., & Wang, Y. (2017). The spatial distribution and temporal variation of desert riparian forests and their influencing factors in the downstream Heihe

- River basin, China. *Hydrology and Earth System Sciences*, 21, 2405–2419. <https://doi.org/10.5194/hess-21-2405-2017>
- Domec, J. C., Scholz, F. G., Bucci, S. J., Meinzer, F. C., Goldstein, G., & Villalobos-Vega, R. (2006). Diurnal and seasonal variation in root xylem embolism in neotropical savanna woody species: Impact on stomatal control of plant water status. *Plant, Cell & Environment*, 29, 26–35. <https://doi.org/10.1111/j.1365-3040.2005.01397.x>
- Drake, P. L., Froend, R. H., & Franks, P. J. (2011). Linking hydraulic conductivity and photosynthesis to water-source partitioning in trees versus seedlings. *Tree Physiology*, 31, 763–773. <https://doi.org/10.1093/treephys/tptr068>
- Eamus, D., Zolfaghar, S., Villalobos-Vega, R., Cleverly, J., & Huete, A. (2015). Groundwater-dependent ecosystems: Recent insights from satellite and field-based studies. *Hydrology and Earth System Sciences*, 19, 4229–4256. <https://doi.org/10.5194/hess-19-4229-2015>
- Ehleringer, J. R., & Dawson, T. E. (1992). Water-uptake by plants—Perspectives from stable isotope composition. *Plant, Cell & Environment*, 15, 1073–1082. <https://doi.org/10.1111/j.1365-3040.1992.tb01657.x>
- Ehleringer, J. R., Phillips, S. L., Schuster, W. S., & Sandquist, D. R. (1991). Differential utilization of summer rains by desert plants. *Oecologia*, 88, 430–434. <https://doi.org/10.1007/BF00317589>
- Ellsworth, P. Z., & Williams, D. G. (2007). Hydrogen isotope fractionation during water uptake by woody xerophytes. *Plant and Soil*, 291, 93–107. <https://doi.org/10.1007/s11104-006-9177-1>
- Evaristo, J., & McDonnell, J. J. (2017). Prevalence and magnitude of groundwater use by vegetation: a global stable isotope meta-analysis. *Scientific Reports*, 7, 1–12. <https://doi.org/10.1038/srep44110>
- Fu, A. H., Chen, Y. N., & Li, W. H. (2013). Water use strategies of the desert riparian forest plant community in the lower reaches of Heihe River Basin, China. *Science China Earth Sciences*, 57, 1293–1305. <https://doi.org/10.1007/s11430-013-4680-8>
- Fu, B. (2008). Analysis on the main causes resulting in vegetation degeneration in the Heihe River basin: Analysis on the main causes resulting in vegetation degeneration in the Heihe River basin. *Arid Zone Research*, 25, 219–224.
- Glenn, E., Tanner, R., Mendez, S., Kehret, T., Moore, D., Garcia, J., & Valdes, C. (1998). Growth rates, salt tolerance and water use characteristics of native and invasive riparian plants from the delta of the Colorado River, Mexico. *Journal of Arid Environments*, 40, 281–294. <https://doi.org/10.1006/jare.1998.0443>
- Glenn, E. P., & Nagler, P. L. (2005). Comparative ecophysiology of *Tamarix ramosissima* and native trees in western U.S. riparian zones. *Journal of Arid Environments*, 61, 419–446. <https://doi.org/10.1016/j.jaridenv.2004.09.025>
- Gries, D., Zeng, F., Foetzi, A., Arndt, S. K., Bruelheide, H., Thomas, F. M., ... Runge, M. (2003). Growth and water relations of *Tamarix ramosissima* and *Populus euphratica* on Taklamakan desert dunes in relation to depth to a permanent water table. *Plant, Cell & Environment*, 26, 725–736. <https://doi.org/10.1046/j.1365-3040.2003.01009.x>
- Grossiord, C., Sevanto, S., Dawson, T. E., Adams, H. D., Collins, A. D., Dickman, L. T., ... McDowell, N. G. (2017). Warming combined with more extreme precipitation regimes modifies the water sources used by trees. *New Phytologist*, 213, 584–596. <https://doi.org/10.1111/nph.14192>
- Guo, Q. L., Feng, Q., & Li, J. L. (2009). Environmental changes after ecological water conveyance in the lower reaches of Heihe River, Northwest China. *Environmental Geology*, 58, 1387–1396. <https://doi.org/10.1007/s00254-008-1641-1>
- Hetherington, A. M., & Woodward, F. I. (2003). The role of stomata in sensing and driving environmental change. *Nature*, 424, 901–908. <https://doi.org/10.1038/nature01843>
- Horton, J. L., & Clark, J. L. (2001). Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. *Forest Ecology and Management*, 140, 239–247. [https://doi.org/10.1016/S0378-1127\(00\)00314-5](https://doi.org/10.1016/S0378-1127(00)00314-5)
- Horton, J. L., Kolb, T. E., & Hart, S. C. (2001). Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant, Cell & Environment*, 24, 293–304. <https://doi.org/10.1046/j.1365-3040.2001.00681.x>
- Lamontagne, S., Cook, P. G., O'Grady, A., & Eamus, D. (2005). Groundwater use by vegetation in a tropical savanna riparian zone (Daly River, Australia). *Journal of Hydrology*, 310, 280–293. <https://doi.org/10.1016/j.jhydrol.2005.01.009>
- Li, J., Yu, B., Zhao, C., Nowak, R. S., Zhao, Z., Sheng, Y., & Li, J. (2013). Physiological and morphological responses of *Tamarix ramosissima* and *Populus euphratica* to altered groundwater availability. *Tree Physiology*, 33, 57–68. <https://doi.org/10.1093/treephys/tps120>
- Li, X., Cheng, G. D., Liu, S. M., Xiao, Q., Ma, M. G., Jin, R., ... Xu, Z. W. (2013). Heihe watershed allied telemetry experimental research (HiWATER): Scientific objectives and experimental design. *Bulletin of the American Meteorological Society*, 94, 1145–1160. <https://doi.org/10.1175/bams-d-12-00154.1>
- Lin, G. H., Sternberg, L. D. S. L., Ehleringer, J. R., Hall, A. E., & Farquhar, G. D. (1993). Hydrogen isotopic fractionation by plant roots during water uptake in coastal wetland plants. In A. E. Hall, & G. D. Farquhar (Eds.), *Stable isotopes and plant carbon-water relations* (pp. 497–510). San Diego: Academic Press.
- Liu, B., Guan, H. D., Zhao, W. Z., Yang, Y. T., & Li, S. B. (2017). Groundwater facilitated water-use efficiency along a gradient of groundwater depth in arid northwestern China. *Agricultural and Forest Meteorology*, 233, 235–241. <https://doi.org/10.1016/j.agrformet.2016.12.003>
- Liu, W. J., Wang, P. Y., Li, J. T., Liu, W. Y., & Li, H. M. (2014). Plasticity of source-water acquisition in epiphytic, transitional and terrestrial growth phases of *Ficus tinctoria*. *Ecophysiology*, 7, 1524–1533. <https://doi.org/10.1002/eco.1475>
- Martre, P., North, G. B., & Nobel, P. S. (2001). Hydraulic conductance and mercurysensitive water transport for roots of *Opuntia acanthocarpa* in relation to. *Plant Physiology*, 126, 352–362. <https://doi.org/10.1104/pp.126.1.352>
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- Miller, G. R., Chen, X., Rubin, Y., Ma, S., & Baldocchi, D. D. (2010). Groundwater uptake by woody vegetation in a semiarid oak savanna. *Water Resources Research*, 46, 2290–2296. <https://doi.org/10.1029/2009wr008902>
- Naiman, R. J., & Décamps, H. (1997). The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics*, 2, 621–658. <https://doi.org/10.1146/annurev.ecolsys.28.1.621>
- Phillips, D. L., & Gregg, J. W. (2003). Source partitioning using stable isotopes: Coping with too many sources. *Oecologia*, 136, 261–269. <https://doi.org/10.1007/s00442-003-1218-3>
- Qi, S. Z., & Luo, F. (2006). Land-use change and its environmental impact in the Heihe River basin, arid northwestern China. *Environmental Geology*, 50, 535–540. <https://doi.org/10.1007/s00254-006-0230-4>
- Rossatto, D. R., de Carvalho Ramos Silva, L., Villalobos-Vega, R., Sternberg, L. d. S. L., & Franco, A. C. (2012). Depth of water uptake in woody plants relates to groundwater level and vegetation structure along a topographic gradient in a neotropical Savanna. *Environmental and*

- Experimental Botany*, 77, 259–266. <https://doi.org/10.1016/j.envexpbot.2011.11.025>
- Sala, A., Smith, S. D., & Devitt, D. A. (1996). Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave Desert floodplain. *Ecological Applications*, 6, 888–898. <https://doi.org/10.2307/2269492>
- Schultz, N. M., Griffis, T. J., Lee, X., & Baker, J. M. (2011). Identification and correction of spectral contamination in 2H/1H and 18O/16O measured in leaf, stem, and soil water. *Rapid Communications in Mass Spectrometry*, 25, 3360–3368. <https://doi.org/10.1002/rcm.5236>
- Si, J., Feng, Q., Yu, T., & Zhao, C. (2015). Nighttime sap flow and its driving forces for *Populus euphratica* in a desert riparian forest, Northwest China. *Journal of Arid Land*, 7, 665–674. <https://doi.org/10.1007/s40333-015-0009-0>
- Smith, S. D., Devitt, D. A., Sala, A., Cleverly, J. R., & Busch, D. E. (1998). Water relations of riparian plants from warm desert regions. *Wetlands*, 18, 687–696. <https://doi.org/10.1007/BF03161683>
- Snyder, K. (2000). Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agricultural and Forest Meteorology*, 105, 227–240. [https://doi.org/10.1016/s0168-1923\(00\)00193-3](https://doi.org/10.1016/s0168-1923(00)00193-3)
- Snyder, K. A., & Williams, D. G. (2003). Defoliation alters water uptake by deep and shallow roots of *Prosopis velutina* (Velvet Mesquite). *Functional Ecology*, 17, 363–374. <https://doi.org/10.1046/j.1365-2435.2003.00739.x>
- Sperry, J. S. (2000). Hydraulic constraints on plant gas exchange. *Agricultural and Forest Meteorology*, 104, 13–23. [https://doi.org/10.1016/S0168-1923\(00\)00144-1](https://doi.org/10.1016/S0168-1923(00)00144-1)
- Sternberg, L. D. S. L., Deniro, M. J., & Savidge, R. A. (1986). Oxygen isotope exchange between metabolites and water during biochemical reactions leading to cellulose synthesis. *Plant Physiology*, 82, 423–427. <https://doi.org/10.1104/pp.82.2.423>
- Stromberg, J. C., Tluczek, M. G. F., Hazelton, A. F., & Ajami, H. (2010). A century of riparian forest expansion following extreme disturbance: Spatio-temporal change in *Populus/Salix/Tamarix* forests along the Upper San Pedro River, Arizona, USA. *Forest Ecology and Management*, 259, 1181–1189. <https://doi.org/10.1016/j.foreco.2010.01.005>
- Sun, S. J., Meng, P., Zhang, J. S., & Wan, X. C. (2011). Variation in soil water uptake and its effect on plant water status in *Juglans regia* L. during dry and wet seasons. *Tree Physiology*, 31, 1378–1389. <https://doi.org/10.1093/treephys/tpr116>
- Sun, Z. Y., Long, X., & Ma, R. (2016). Water uptake by saltcedar (*Tamarix ramosissima*) in a desert riparian forest: Responses to intra-annual water table fluctuation. *Hydrology Process*, 30, 1388–1402. <https://doi.org/10.1002/hyp.10688>
- Tyree, M. T., Kolb, K. J., Rood, S. B., & Patino, S. (1994). Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? *Tree Physiology*, 14, 455–466. <https://doi.org/10.1093/treephys/14.5.455>
- Vandeleur, R. K., Mayo, G., Shelden, M. C., Gilliam, M., Kaiser, B. N., & Tyerman, S. D. (2009). The role of plasma membrane intrinsic protein aquaporins in water transport through roots: Diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. *Plant Physiology*, 149, 445–460. <https://doi.org/10.1104/pp.108.128645>
- Voltas, J., Lucabaugh, D., Chambel, M. R., & Ferrio, J. P. (2015). Intraspecific variation in the use of water sources by the circum-Mediterranean conifer *Pinus halepensis*. *New Phytologist*, 208, 1031–1041. <https://doi.org/10.1111/nph.13569>
- Wang, P., Zhang, Y. C., Yu, J. J., Fu, G. B., & Ao, F. (2011). Vegetation dynamics induced by groundwater fluctuations in the lower Heihe River basin, Northwestern China. *Journal of Plant Ecology*, 4, 77–90. <https://doi.org/10.1093/jpe/rtr002>
- West, A. G., Goldsmith, G. R., Brooks, P. D., & Dawson, T. E. (2010). Discrepancies between isotope ratio infrared spectroscopy and isotope ratio mass spectrometry for the stable isotope analysis of plant and soil waters. *Rapid Communications in Mass Spectrometry*, 24, 1948–1954. <https://doi.org/10.1002/rcm.4597>
- West, A. G., Patrickson, S. J., & Ehleringer, J. R. (2006). Water extraction times for plant and soil materials used in stable isotope analysis. *Rapid Communications in Mass Spectrometry*, 20, 1317–1321. <https://doi.org/10.1002/rcm.2456>
- Williams, D. G., & Ehleringer, J. R. (2000). Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. *Ecological Monographs*, 70, 517–537.
- Wu, H. W., Li, X. Y., Jiang, Z. Y., Chen, H. Y., Zhang, C. C., & Xiao, X. (2016). Contrasting water use pattern of introduced and native plants in an alpine desert ecosystem, Northeast Qinghai-Tibet Plateau, China. *Science of the Total Environment*, 542, 182–191. <https://doi.org/10.1016/j.scitotenv.2015.10.121>
- Yu, T., Feng, Q., Si, J., Xi, H., Li, Z., & Chen, A. (2013). Hydraulic redistribution of soil water by roots of two desert riparian phreatophytes in northwest China's extremely arid region. *Plant and Soil*, 372, 297–308. <https://doi.org/10.1007/s11104-013-1727-8>
- Zencich, S. J., Freund, R. H., Turner, J. V., & Gailitis, V. (2002). Influence of groundwater depth on the seasonal sources of water accessed by *Banksia* tree species on a shallow, sandy coastal aquifer. *Oecologia*, 131, 8–19. <https://doi.org/10.1007/s00442-001-0855-7>
- Zhang, C. C., Li, X. Y., Wu, H. W., Wang, P., Wang, Y. P., Wu, X. C., ... Huang, Y. M. (2017). Differences in water-use strategies along an aridity gradient between two coexisting desert shrubs (*Reaumuria soongorica* and *Nitraria sphaerocarpa*): isotopic approaches with physiological evidence. *Plant and Soil*, 416, 1–19. <https://doi.org/10.1007/s11104-017-3183-3>
- Zhu, J. T., Yu, J. J., Wang, P., Zhang, Y. C., & Yu, Q. (2012). Interpreting the groundwater attributes influencing the distribution patterns of groundwater-dependent vegetation in northwestern China. *Ecohydrology*, 5, 628–636. <https://doi.org/10.1002/eco.249>
- Zhu, Y. H., Chen, Y. N., Ren, L. L., Lü, H., Zhao, W. Z., Yuan, F., & Xu, M. (2016). Ecosystem restoration and conservation in the arid inland river basins of Northwest China: Problems and strategies. *Ecological Engineering*, 94, 629–637. <https://doi.org/10.1016/j.ecoleng.2016.06.107>
- Zunzunegui, M., Boutaleb, S., Diaz Barradas, M. C., Esquivias, M. P., Valera, J., Jauregui, J., ... Ain-Lhout, F. (2017). Reliance on deep soil water in the tree species *Argania spinosa*. *Tree Physiology*, 00, 1–12. <https://doi.org/10.1093/treephys/tpx152>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Li E, Tong Y, Huang Y, et al. Responses of two desert riparian species to fluctuating groundwater depths in hyperarid areas of Northwest China. *Ecohydrology*. 2019;12:e2078. <https://doi.org/10.1002/eco.2078>