Hydraulic redistribution of soil water by roots of two desert riparian phreatophytes in northwest China’s extremely arid region

Tengfei Yu · Qi Feng · Jianhua Si · Haiyang Xi · Zongxing Li · Aifang Chen

Received: 6 November 2012 / Accepted: 11 April 2013 © Springer Science+Business Media Dordrecht 2013

Abstract

Aims As deep water uptake is limited by the low densities of fine roots at the subsoil layer at high evaporative demand, hydraulic redistribution (HR) is another possible mechanism that could account for the lack of water stress experienced by desert riparian phreatophytes during dry periods. The objectives of this study were to search for evidence that the roots of two desert riparian phreatophytes, Populus euphratica Oliv. and Tamarix ramosissima Ledeb., carry out HR and to investigate the pattern of this phenomenon in the broader scheme of plant water uptake by roots.

Methods To demonstrate HR, we present data on patterns of sap flow in the stems or branches and lateral roots of those two phreatophyte species and soil volumetric moisture content where these species grow.

Results During the dry season, we observed reverse or acropetal flow in the lateral roots of P. euphratica, a pattern consistent with hydraulic lift. With the onset of heavy rains, this pattern reversed, indicating water movement from moist topsoil to dry subsoil, i.e. hydraulic descent. After lateral irrigation by creek, water moved downward to dry subsoil and outward to opposite sides, suggesting lateral hydraulic redistribution via roots at night and during the day, which may be mediated by stem tissues and, by inference, the radial sectoring in the xylem. Although no direct evidence indicated reverse sap flow of lateral roots and associated HR in T. ramosissima, several factors indicate that HR is occurring: (1) diel fluctuations of volumetric moisture content in the upper soil layer and (2) the identification of primary water sources as groundwater and vadose zone water through stable isotope studies. As a result, we inferred that HR occurs in T. ramosissima via adventitious roots with diameters of 2–5 mm and length of 60–100 cm in the upper soil layer, rather than via lateral roots; further investigation is needed to substantiate this.

Conclusions We confirm and extend previous knowledge on HR patterns of P. euphratica and add a new species, T. ramosissima, to the wide list of existing species involved in HR. However, these two desert riparian phreatophytes exhibit remarkable differences
in their patterns and pathways of HR that are possibly associated with root architecture.

**Keywords** Desert riparian phreatophytes · Hydraulic redistribution · Root sap flow · Soil volumetric moisture content

**Introduction**

Water deficit is a limiting factor for survival and growth of desert plants (Noy-Meir 1973). Interestingly, several studies showed that desert species could maintain stable eco-physiological activity as well as typical vegetation of mesic climates (Gries et al. 2003; Nagler et al. 2003; Sala et al. 1996). It seems that desert species can develop adaptive strategies to tolerate seasonal or even chronic drought (Cleverly et al. 2006; Xu and Li 2006). Deep water uptake has been suggested as a potential mechanism to explain the drought tolerance of phreatophytes, plants with long tap roots and access to groundwater sources. During prolonged dry seasons, the roots of phreatophytes not only obtain required water from groundwater (Anderson 1982; Gries et al. 2003; Sala et al. 1996), but also forage for mineral nutrients in the upper soil layers when the surface soil dries out (Zeng et al. 2006; Prieto et al. 2012b). However, since most of the fine roots (<2 mm diameter) of desert species are near the soil surface (upper 30 cm) (Jackson et al. 1996, 1997), we might expect that, under conditions of drying upper soil and high evaporative demand, total water uptake is limited by the low densities of fine roots at the subsoil layer.

An alternative explanation for the drought tolerance of desert species is the hydraulic redistribution (HR) of soil water that moves passively through the roots in an upward (hydraulic lift, HL), downward (hydraulic descent, HD), or lateral direction (Burgess et al. 1998; Hultine et al. 2003; Nadezhdina et al. 2010; Warren et al. 2007). HR occurs whenever the gradient in soil water potential between soil layers is stronger than the overall gradient between the soil and atmosphere; this occurs most often at night, when evaporative demand is low (Burgess et al. 1998). The effects of HR may actually contradict expected plant and ecosystem responses to drought because, at least in the short-term, plants may ameliorate their own levels of water stress by essentially extending root survival and growth (Bauerle et al. 2008), which will ultimately affect the rates of water transfer to the atmosphere. Therefore, documenting HR is important for water balance, performance in drought conditions, and plant–plant interactions (Armas et al. 2010; Dawson 1993; Prieto et al. 2012a; Scott et al. 2008).

HR has been well documented in arid and semiarid ecosystems in the southwestern United States, western Australia, and Africa (Caldwell and Richards 1989; Hultine et al. 2003; Richards and Caldwell 1987; Yoder and Nowak 1999). Little research has been done on the HR of desert riparian species in arid regions of central Asia (Hao et al. 2010). This is especially true for facultative phreatophytes such as saltcedar (Tamarix spp.) (Gries et al. 2003), probably due to the assumption that saltcedar can derive its water supply directly from deeper groundwater and is able to tolerate drought (Anderson 1982). Busch et al. (1992), however, reported that facultative T. ramosissima is also capable of extracting water from unsaturated soil layers, giving it a significant competitive advantage over the native obligate phreatophytes, Populus spp. and Salix spp. that derive water solely from the water table.

The study site, a typical desert riparian forest in northwestern China, is dominated by riparian phreatophytes consisting of Populus euphratica Oliv. trees and Tamarix ramosissima Ledeb. shrubs. Xi et al. (2011) observed nocturnal increases in the water content of upper layer within those stands during the dry period, and Zhou et al. (2004) reported that the vertical distribution of soil water content was associated with root density, but no reasonable explanation was given for this. Thus, we speculated that those phreatophytes may exhibit HR. The objectives of this study were to search for evidence that the roots of these two phreatophytes carry out HR and to investigate the pattern of this phenomenon in the broader scheme of plant water uptake by roots, based on measurement of sap flow in the stems or branches and roots and soil moisture content where these two phreatophyte species grow.

**Materials and methods**

**Study site and species**

The study was carried out between April and October 2012 at the Alxa Desert Eco-hydrology Experimental Research Station (Alxa Station), Chinese Academy of
Sciences (42°01′N, 100°21′E, 883.5 m asl.), about 800 m west of the Heihe River in western Inner Mongolia (Ejin Banner, Alxa League) (Si et al. 2007). The observation site is located approximately 200 m northwest of Alxa Station. The climate of the area is extremely arid with an average annual precipitation of 37.4 mm, more than 75 % of which falls from June to August. The pan evaporation of 3390.3 mm is about 90 times greater than the precipitation. Mean temperatures in July of 27.0 °C and in January of −11.7 °C, have been recorded at the Ejin weather station from 1959 to 2011. Apart from precipitation, the river water of the Heihe River and the resultant groundwater provide the main water sources to sustain local residents and ecosystems.

Soils at the site are sandy loam and silt loam above 82 cm and below 124 cm, respectively, with a distinct sand layer between them (Table 1), and the soil parent material is fluvial sediment with gray-brown desert soil and a sulfate salt crust at the soil surface. The soil water retention curve was calculated by RETC version 6.02 (University of California Riverside, Riverside, CA, USA), as indicated in Table 1. The riparian forest consists of remnant populations of broad-leaved *P. euphratica* and extensive thickets of *T. ramosissima* that often occur in monocultures or mixtures (Si et al. 2007). The former species is found at a higher density (148 stems ha⁻¹) than the latter (42 stem ha⁻¹) and contributes most (approximately 75 %) to the total basal area of the two species (approximately 88 % of 106.00 m² ha⁻¹ total tree basal area) because the average diameter of *P. euphratica* is much larger than that of *T. ramosissima*. The understorey is dominated by grasses, predominantly *Sophora alopecuroides* L., *Karelinia caspica* (Pall.) Less., and *Achnatherum splendens* (Trin.) Nevski. We selected two individuals each of *P. euphratica* and *T. ramosissima* to measure the sap flow; the two groups were separated by about 200 m. A fence (30×30 m) was erected around each of the two study groups to exclude animals.

### Sap flow measurements

We used sap flow sensors with the heat ratio method (HRM, ICT Inc., Armidale, Australia) to make continuous measurements of sap flow in the stems (for *P. euphratica*) or branches (for *T. ramosissima*) and roots of our selected species. The HRM, described in detail in Burgess et al. (2001), basically measures the increase in temperature following a heat pulse at two symmetrical points. We inserted one heater and a pair of copper-constantan thermocouples radially into the xylem tissue of stems (North, 130 cm height) or branches (North, 30 cm height) and the major lateral roots (East, 30 cm to 40 cm depth and 50 cm apart from stem base) of all specimens. Each thermocouple had two junctions to measure sap velocity in the xylem tissue located at 7.5 mm (In) and 22.5 mm (Out) from the tip of the needle. A metal guide (with three holes carefully drilled on a parallel line, spaced 6 mm apart) was used to help drill holes and minimize probe misalignment during insertion. Because of the greater temperature difference between the tree and sensor, the reflective bubble-foil shielding was used to insulate the sensor. All probes were connected to an AM416 multiplexer (Campbell Scientific Inc., Logan, Utah, USA) powered by 12 V car batteries. The heater was set up to send a pulse every 30 min and temperature ratios were recorded continuously with a data logger (CR10x, Campbell Scientific Inc. Logan, UT, USA) connected to the multiplexer by four shielded conductor cables.

The heat pulse velocity \( V_h \) was calculated following Burgess et al. (2001) as:

\[
V_h = \frac{k}{x} \ln \left( \frac{v_1}{v_2} \right) \times 3600
\]

### Table 1 Parameters of soil bulk density (\( \rho_b \)) and porosity, and fitting parameters for soil water retention curves, in which \( \alpha \) and \( n \) are Van Genuchten (1980) model parameters, \( K_s \) is saturated soil hydraulic conductivity

<table>
<thead>
<tr>
<th>Depth cm</th>
<th>( \rho_b ) g cm⁻³</th>
<th>Sand %</th>
<th>Silt %</th>
<th>Clay %</th>
<th>( \alpha ) cm⁻¹</th>
<th>( n )</th>
<th>( K_s ) cm h⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–7</td>
<td>1.05</td>
<td>46.74</td>
<td>47.71</td>
<td>5.56</td>
<td>0.0069</td>
<td>1.5767</td>
<td>6.88</td>
</tr>
<tr>
<td>7–20</td>
<td>1.43</td>
<td>49.17</td>
<td>43.86</td>
<td>6.97</td>
<td>0.0147</td>
<td>1.4728</td>
<td>1.52</td>
</tr>
<tr>
<td>20–47</td>
<td>1.41</td>
<td>42.13</td>
<td>51.54</td>
<td>6.33</td>
<td>0.0100</td>
<td>1.5291</td>
<td>1.57</td>
</tr>
<tr>
<td>47–82</td>
<td>1.28</td>
<td>28.45</td>
<td>63.86</td>
<td>7.69</td>
<td>0.0049</td>
<td>1.6972</td>
<td>2.75</td>
</tr>
<tr>
<td>82–124</td>
<td>1.47</td>
<td>99.00</td>
<td>0.86</td>
<td>0.14</td>
<td>0.0311</td>
<td>4.4586</td>
<td>59.80</td>
</tr>
<tr>
<td>124–160</td>
<td>1.54</td>
<td>25.37</td>
<td>70.80</td>
<td>3.83</td>
<td>0.0086</td>
<td>1.5643</td>
<td>1.42</td>
</tr>
</tbody>
</table>
where $k$ is the thermal diffusivity of the fresh wood, $x$ is the distance between the heater and the thermocouples (fixed value of 0.6 cm), and $v_1$ and $v_2$ are the differences between the initial temperature at the two thermocouples (downstream and upstream of the flow in relation to the heater, respectively) and the temperature measured after a heat pulse. Initially we used a fixed value for $k$ of $2.5 \cdot 10^{-3}$ cm$^2$ s$^{-1}$, but we corrected this after we determined the thermal properties of wood. All corrections for wound and misalignment of the probes were made according to Burgess et al. (2001). The parameters of selected samples and xylem are shown in Table 2. The sap flow velocity ($V_s$, cm h$^{-1}$) was calculated following Burgess et al. (2001).

We used the HRM technique because of its suitability for quantifying low sap velocities and its ability to detect reverse sap flows (negative flows) (Burgess et al. 2001). This allows water flows to be monitored in the stems and roots for a wide range of species, sizes, and environmental conditions, including drought. We present sap flow velocities instead of volumetric flow rates because for the latter, quantities could not simply scale with the size of each individual root monitored. Not all roots could be monitored using volumetric flow rates and, further, summing all lateral roots is difficult where roots with intermediate orientations are present. We chose to analyze the HR of the two phreatophyte species using dry season data from May to September.

Soil water status and investigation of root systems

The soil volumetric moisture content ($\theta$) was measured using multisensor, frequency domain capacitance probes (EnviroSCAN, Sentek, Adelaide, AU) in $T$. ramosissima stands. The probes contained five annular capacitance sensors and were installed into a c. 6 cm diameter PVC access tube, with sensors spaced at depths of 10 cm, 30 cm, 50 cm, 80 cm, and 140 cm. Each capacitance sensor was frequency-normalized by calibration against air and water in the laboratory to ensure the precision of measurement. The field-based calibration equations of different soil textures where sensors installed were applied to attain reliable soil volumetric water content in accordance with the Sentek calibration manual (Sentek Pty Ltd, Adelaide, AU). Soil temperature ($T_s$) corresponding to $\theta$ of five depths was quantified using soil temperature sensors (Campbell 109SS, Campbell Inc.). Both variables were taken at 10 min intervals and recorded continuously with a data logger (CR1000, Campbell Inc.). The 30 min and daily averages were computed to analyze the diurnal and daily variations in $\theta$ and $T_s$.

Soil moisture content was measured gravimetrically and then multiplied by soil bulk density ($\rho_b$, g cm$^{-3}$) to obtain $\theta$. Soil, c. 2 m west of the selected trees, was sampled monthly using an auger from 0 cm to 160 cm depth at 20 cm intervals (three sets of samples were obtained). Intensive observations were made before (20 May) and after (25 May) lateral irrigation of the site by creek water, c. 3 m east of the nearest specimens. We used a soil pit to take soil block samples at different depths from the two selected trees on 22 July. Soil samples were taken at 20 cm intervals from 0 cm to 160 cm (3 samples per layer). Immediately after sampling, we brought the samples to the laboratory and washed the soil from the roots. Roots in each layer were divided into two size classes based on root diameter: fine roots ($\leq$2 mm) and coarse roots (>2 mm). The length of the fine roots was determined using root analysis system (WinRHIZO Pro 2008a, Regent Instruments Inc. Quebec City, Quebec, Canada). Ultimately, we calculated fine root length density ($RLD$,

<table>
<thead>
<tr>
<th>Species</th>
<th>Sections</th>
<th>$DBH$ cm</th>
<th>$A_s$ cm$^2$</th>
<th>$m_w$ %</th>
<th>$\rho_b$ g cm$^{-3}$</th>
<th>$k$ $10^{-3}$cm$^2$s$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. euphratica</em></td>
<td>Stem</td>
<td>47.9±6.08</td>
<td>310.13±57.97</td>
<td>20.42±5.00</td>
<td>0.41±0.01</td>
<td>2.98±0.21</td>
</tr>
<tr>
<td></td>
<td>Lateral roots</td>
<td>6.90±1.27</td>
<td>152.04±55.15</td>
<td>33.33±0.00</td>
<td>0.44±0.04</td>
<td>2.58±0.04</td>
</tr>
<tr>
<td><em>T. ramosissima</em></td>
<td>Branch</td>
<td>2.75±0.35</td>
<td>23.95±6.10</td>
<td>30.27±0.01</td>
<td>0.73±0.02</td>
<td>2.91±0.02</td>
</tr>
<tr>
<td></td>
<td>Lateral roots</td>
<td>4.30±0.28</td>
<td>60.69±11.18</td>
<td>37.62±1.61</td>
<td>0.51±0.02</td>
<td>2.55±0.01</td>
</tr>
</tbody>
</table>

$DBH$ is diameter at breast height, $A_s$ is sapwood area, $m_w$ is water content of sapwood, $\rho_b$ is the basic density of wood (dry weight/green volume) and $k$ is thermal diffusivity of green (fresh) wood. The values are presented as mean ± S.D. ($n=4$)
cm cm$^{-3}$) from the total length ($L$, cm) of the roots divided by the volume ($V$, cm$^3$) of soil core.

Leaf and soil water potential and groundwater table

The leaf and soil samples were collected at predawn, midday, and midnight over a two-day period (30–31 August) to monitor the diurnal variation of leaf and soil water potential ($\psi_l$ and $\psi_s$, respectively). Nine leaf samples were collected at each sampling: three each from the upper, middle, and lower crown of the tree. Likewise, nine soil samples were taken: three each at depths of 5 cm, 10 cm, and 20 cm. The samples were immediately taken to the laboratory and the $\psi_l$ and $\psi_s$ were determined using a dew-point water potential meter (WP4C, Decagon devices, USA). The groundwater table (m) was measured at 5-day intervals via underground wells adjacent to the selected trees.

Statistical analyses

Descriptive statistics were used to calculate average and standard deviation (S.D.). For gravimetric $\theta$ and RLD data, the Kolmogorov–Smirnov test was used to check normality. If the data failed, the data were transformed by logarithmic prior to analysis. The homogeneity of variances was checked using Levene’s test. One-way repeated measures ANOVA with a Mauchly’s test of sphericity and Tukey post hoc test ($P<0.05$) were used to examine variations in gravimetric $\theta$ and RLD with depth and soil and leaf water potentials with time. The same test was used to examine differences in means for $\theta$ before and after irrigation. Relationships among variables were examined by correlation analysis. All statistical analysis and charting was processed using Origin8.0 software (OriginLab Corp., Northampton, MA, USA).

Results

Root system and soil and leaf water conditions

The soil pit samples and RLD calculations revealed a significantly dense fine root layer at approximately 60 cm ($F=77.62$, $P<0.01$) for P. euphratica and 40–60 cm ($F=17.14$, $P<0.05$) for T. ramosissima in the soil profile (Fig. 1a). Soil cores also revealed that some larger diameter roots were established below the groundwater table. The $\theta$ obtained from soil pits showed a distinctly higher value at 40–60 cm ($F=14.77$, $P<0.05$ for P. euphratica; $F=6.27$, $P<0.05$ for T. ramosissima, respectively), but it was not significantly different from that at soil layer depths of 140 cm to 160 cm (Fig. 1b), and in particular there was a significant negative correlation to RLD for T. ramosissima ($R^2=0.67$, $P=0.05$). Continuous measurement of water potential over 2 days showed that $\psi_l$ at midday was significantly lower than at predawn and midnight ($F=4.47$, $P<0.05$) for P. euphratica; this is especially true ($F=17.49$, $P<0.01$) for T. ramosissima and $\psi_s$ ($F=28.74$, $P<0.01$) (Fig. 2). We observed plentiful adventitious roots with diameters of

Fig. 1 Vertical variation of a fine root length density (RLD, cm cm$^{-3}$; mean + S.D. $n=3$) and b volumetric moisture content ($\theta$, cm$^3$ cm$^{-3}$; mean + S.D. $n=9$) of soil for root zone of P. euphratica (gray bars) and T. ramosissima (black bars) in depths. The $\theta$ was measured at 25 May, 31 July and 6 September, 2012.
2–5 mm and lengths of 60–100 cm in the upper soil layer and a clumped pattern of shallow-rooted herbaceous plants, such as Karelinia caspica (Pall.) Less., Scorzonera Mongolia Maxim., and Phragmites communis Trin., at depths of 20–60 cm, around the crown of T. ramosissima, but only existing sporadically in the clearing area.

Patterns of sap flow

Before the rainfall (20–24 July), the stems of P. euphratica exhibited a positive, higher rates of sap flow during both day and night. Concurrently, sap flow rates in lateral roots were negative, with lower rates at night, i.e. moving away from the stem base towards the root tips, and positive rates during periods of high transpiration demand in the daytime (Fig. 3a). Long-term measurement on the stems and lateral roots of P. euphratica was similarly informative (data not shown). This pattern of sap flow strongly suggests hydraulic lift, in which water absorbed in deep, moist soil was released in the upper, dry soil profiles at night and stored there until it was resorbed by roots the next day. After the rainfall (24 July, 12.4 mm), the sap flow of the stems exhibited a sharp reduction or even negative flow. Although sap flow rate in the lateral roots was still negative, the magnitude of sap flow velocity was 1.77 and 2.57 times greater on the nights after the rainfall (25–28 July) than on the nights before the rainfall (20–24 July). The negative sap flow of the stems suggests possible foliar uptake (FU) in which water absorbed by leaves moved downward. However, the pattern of sap flow in T. ramosissima was markedly different from that of P. euphratica (Fig. 3b). The sap flow velocity in lateral roots of T. ramosissima was positive during both day and night. Long-term measurement on the lateral roots of T. ramosissima was similarly informative (data not shown). However, the sap flow velocity in the branches of T. ramosissima decreased remarkably and even became negative during rainfall. It seems that downward water transport occurrence, which make less water available for transpiration, allowed water absorbed by adventitious roots to be transported to the subsoil layer, but not through the lateral roots.

Lateral irrigation of the dry soil surface from a nearby creek (c. 3 m) may have introduced large differences in soil water content and, by inference, soil water potential between locations; these were higher
than the differences between soil and crown water potentials observed at night. As shown in Fig. 4, water can move passively from wet to dry soil locations very quickly through roots: sap flow responded almost immediately to irrigation in the lateral roots and stems of a _P. euphratica_ tree during the dry summer period. Before irrigation, sap flow dynamics were similar in both lateral roots and the stems (Fig. 4a). However, heterogeneous soil moisture, introduced by lateral irrigation in the root zone, caused abrupt differences in lateral roots and stems sap flow dynamics. The downward flow in the outer root xylem (LR-out) increased immediately at night and the upward flow decreased, even reversing direction, during the day. Upward flow in the inner root xylem (LR-in) decreased continuously both at day and night, and finally became negative. Upward flow in the outer stem xylem (T-out) decreased both day and night, similar to LR-in and the inner stem xylem (T-in), except that the midday reduction seemed to disappear after lateral irrigation. Far from the creek, the sap flow of _T. ramosissima_ was not affected by lateral irrigation (data not shown).

The difference in soil water potential caused more water to transfer downward at night and less water to transfer upward in the daytime (Table 3). During the irrigation periods (21–22 May), upward sap flow velocity of stems were reduced on average by 32.25% at night and 5.82% in the day compared to the days before irrigation (17–20 May). However, downward water transfers in roots increased by an average of 14.28% at night, while upward water transfer decreased by 68.75% during the day. After irrigation (23–26 May), sap flow fluxes of stems gradually recovered and were roughly equal to the average before irrigation by the fourth day (Fig. 5a). The θ of soil at opposite of lateral roots measured was significantly increased after irrigation (_F=9.40, _P<0.01_) at the 40–60 cm depth (Fig. 5b).

### Patterns of soil water content

Generally, soils tend to dry from the surface downward due to greater root densities in the upper profile and direct evaporation from surface during drying season. However, continuously recorded (May to September 2012) diurnal variations in θ of soil for the _T. ramosissima_ stand showed that the θ at 30 cm and 50 cm was greater than that at 10 cm and 80 cm during the dry season (Fig. 5). The θ in the shallow (10 cm) and deep (140 cm) layers was likely controlled by rainfall and groundwater, but neither of these factors has as much effect on soil moisture at depths of 30 cm and 50 cm. Pronounced diel fluctuations with daily on average decrease of 0.0031 cm³ cm⁻³ and increase of 0.0017 cm³ cm⁻³ in θ occurred at the 30 cm depth before rainfall (20–24 July) when the upper portions of the soil profile were relatively dry (Fig. 6). After rainfall (25 July), there were remarkable increases at 10 cm and 140 cm, but decreases at 30 cm and 50 cm with little changed at 80 cm (Fig. 6). The relationship between θ and the corresponding soil temperature (_T_s_) at 30 cm suggests no obvious correlation during a
typical dry season (13 May to 18 August), but before and after this period the correlation was significant ($R^2 = 0.97$ and 0.99, $P=0.01$, respectively) (Fig. 7a). Of particular interest, the $\theta$ of soil at 30 cm was positively correlated to $V_h$ of branch overall forward 3 h (Fig. 7b, $R^2=0.63$, $P=0.01$).

### Discussion

**Hydraulic redistribution of *P. euphratica***

On nights during the dry season (May to September), we observed reverse or acropetal flow in the lateral roots of *P. euphratica* (Fig. 3a), a pattern consistent with HL (Burgess et al. 1998; Hao et al. 2010; Bleby et al. 2010). In addition, our study first observed possible FU (Burgess and Dawson 2004) (Fig. 3a) and HD (Burgess et al. 1998 Smith et al. 1999) (Fig. 4a), as well as horizontal hydraulic redistribution (HHR) that characterise the movement of water through roots in soil in horizontal directions (Brooks et al. 2002) (Fig. 4b) after heavy rainfall and lateral irrigation by creek water, respectively. These phenomena (HL, HD, FU, and HHR) are the multiple facets of HR (Nadezhdina et al. 2010). The maximal negative sap velocity of lateral roots (i.e. HL) was on the order of 0.5–2 cm h$^{-1}$, which is similar in magnitude to rates of reverse flow reported by Hao et al. (2010) for this species. Thus, we confirm that *P. euphratica* can redistribute water by its roots, and extend the occurrence of HL to HR in extremely arid regions.

Interestingly, after lateral irrigation by creek water, the sap flow velocity was significantly reduced in the stems, but increased in the outer roots xylem of *P. euphratica*. A possible hypothesis to explain the reduced transpiration of the stems might also be stem-mediated HR, which redistributes water from the wet

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**Table 3** Sap flow velocity ($F_s$, cm h$^{-1}$) of stem and lateral roots for *P. euphratica* before (17–20 May), during (21–22 May), and after irrigation event (23–26 May)

<table>
<thead>
<tr>
<th></th>
<th>Before</th>
<th>Irrigation</th>
<th>After</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day</td>
<td>Night</td>
<td>Day</td>
</tr>
<tr>
<td>Stem</td>
<td>36.45±3.41a</td>
<td>34.33±2.69b</td>
<td>35.91±2.99a</td>
</tr>
<tr>
<td>Lateral roots</td>
<td>21.55±3.25a</td>
<td>14.60±3.11b</td>
<td>18.18±4.19c</td>
</tr>
<tr>
<td></td>
<td>0.96±0.49a</td>
<td>0.30±0.26b</td>
<td>1.17±0.66c</td>
</tr>
<tr>
<td></td>
<td>−0.91±0.31a</td>
<td>−1.04±0.22b</td>
<td>−0.88±0.25a</td>
</tr>
</tbody>
</table>

The values are presented as mean ± S.D. (day: $n=52$ for irrigation and $n=102$ for before and after; night: $n=44$ for irrigation and $n=90$ for before and after, respectively). Different letters indicate significant differences ($P=0.05$) among before, during and after irrigation was applied.

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**Fig. 5** Continuously recorded (April to October 2012) average diurnal variation in soil volumetric moisture content ($\theta$, cm$^3$ cm$^{-3}$) of *T. ramosissima* stand at Ejin, Northwest China in response to precipitation (mm) and groundwater depth (GD, m)

**Fig. 6** Diel fluctuations of volumetric moisture content ($\theta$, cm$^3$ cm$^{-3}$) in root zone of *T. ramosissima* within different soil layers (left axis: 10 cm; right axis: 30 cm, 50 cm, 80 cm and 140 cm) with a precipitation event (black arrow, 12.4 mm)
to the dry part of the roots and makes less water available for transpiration. This phenomenon has been confirmed for eucalyptus species (Burgess and Bleby 2006) and for Douglas fir (Nadezhdina et al. 2009). Our work not only directly confirms the lateral redistribution of water through its roots for *P. euphratica*, but also that the stem was involved in this process (Fig. 5a). Also, a bidirectional flow pattern within the lateral roots was detected, where the outer root xylem showed reverse flow behavior, while the water in the inner root xylem flowed upwards (Fig. 4a). We hypothesized that the stem base in connection with the inner root xylem, which suggesting the possible radial sectoring of root xylem (Burgess and Bleby 2006; Nadezhdina et al. 2009). The water absorbing from the wet side adjacent to river was transported to the stem, when the pit resistance is overcome the circumferential movement of sap flow around the heartwood becomes available to the downstream flow, however the outer xylem sap flow was upward due to the transpiration pull during the days. Thus, the pattern of water moving of root xylem simultaneously in two opposite directions became possible.

Although, the sap flow of the lateral roots farthest from the creek was not measured, we hypothesized that water flows into the dryer lateral roots on this side on the basis of the significantly increased θ observed at 40 cm to 60 cm depths on opposing sides of *P. euphratica* following lateral irrigation (Fig. 4b). This may indicate that HHR, rather than soil water transport independent of roots, causes water to move laterally to opposite soil through lateral roots at night and during the day; the saturated soil water diffusion in sandy/silt loam between 7 cm and 82 cm depths (about 1–2 cm h⁻¹, Table 1) was far less than root sap flow velocity (Fig. 4a). Even if the saturated hydraulic conductivity was high for the sandy layer of 82 cm to 124 cm, the remarkable increase of θ observed at 40 cm to 60 cm depths was not the result of lateral flow of water, since the θ at the sand/silt interface of 120 cm should be increased, rather than decreased (Fig. 4b).

The experiment with lateral irrigation indicates that HHR occurs in *P. euphratica*. The situation created by the artificial diversion might frequently occur in riparian forests in which only a part of the root system has access to water. This could have significant ecological consequences. The HHR observed in *P. euphratica* allowed the tree to better deal with seasonal drought by restoring the water moisture at deeper and broader soil zones. Through HHR, water is not only supplied to the aboveground tree parts, but also to the whole root system as well, allowing the tree to take advantage of nutrient uptake from a larger area around the tree (Prieto et al. 2012b). Because the *T. ramosissima* trees were farther from the creek, the HHR of this species cannot be discussed as part of the present study. Further work is needed to determine the prevalence of HHR in woody plants of desert ecosystems, i.e. does it reflect certain root architectures, growth forms, soil types or climatic factors? Such knowledge could provide further insights into flow paths and source-sink relationships within a plant (Bleby et al. 2010).

Hydraulic redistribution of *T. ramosissima*

*T. ramosissima* (saltcedar) is an invasive facultative, rather than obligate phreatophyte (Gries et al. 2003). Like native riparian trees, *Tamarix* can transpire large

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![Fig. 7](image-url)
quantities of water (Cleverly et al. 1997; Nagler et al. 2005; Sala et al. 1996). However, unlike many co-occurring native phreatophytes, constant physiological function has been reported for Tamarix, even during the dry season (Cleverly et al. 1997; Devitt et al. 1997; Gries et al. 2003). The use of multiple water sources included groundwater and vadose-zone soil water by Tamarix is a possible explanation for its drought tolerance (Busch et al. 1992; Nippert et al. 2010; Sala et al. 1996; Xu and Li 2006).

More difficult to explain is the $\psi_1$ (minimum: $-1.76$ MPa, Fig. 2), which is well above reported (Pockman and Sperry 2000) cavitations threshold and safety margin values for this species (50% cavitations at $-4.5$ MPa and fully cavitations at $-7.0$ MPa), and the $\theta$ of soil (more than 0.3 cm$^3$ cm$^{-3}$), which is higher at depths of 30 cm and 50 cm than at 10 cm, 80 cm, and even 140 cm during the typical dry season (Fig. 5). At the lower Heihe River, the yearly average precipitation is less than 40 mm, whereas the evaporation is greater than 3,000 mm, thus the natural rainfall has almost no effect on the higher $\theta$ of soil. During dry periods, groundwater is the main source of water for desert riparian phreatophytes within the study site. However, the capillary fringe cannot extend to 80 cm above the groundwater table based on an estimation of the capillary fringe using 0.73 divided by soil particle radius with a mean of 0.01 cm (using 0.2 mm for sand grain size) (Zhou et al. 2004). A possibly explanation for the higher $\psi_1$ and $\theta$ of soil at intermediate depths is HR, especially HL of soil water by the roots of T. ramosissima.

Our sap flow measurements did not provide direct evidence to support HL of T. ramosissima (Fig. 3b). Despite this, we believe that HL may occur in this species on the basis of other evidence. Firstly, pronounced diel fluctuations in $\theta$ occurred at depths of 30 cm during midsummer (20–24 July) when the upper portions of the soil profile were relatively dry (Fig. 6), and there was no significant correlation with the corresponding soil temperature ($T_s$) at 30 cm during a typical dry season (13 June 13 to 29 August) (Fig. 7a), but the relationship between $\theta$ and sap flow velocity ($V_s$) (Fig. 7b) was significant, that may associated with root systems distribution in this layer (Fig. 1). These indicate that the diel fluctuations observed for $\theta$ were caused by HL rather than soil temperature diel fluctuations (Warren et al. 2007). Secondly, a comparison of $\delta^{18}$O values of soil water, groundwater, and plant water of T. ramosissima (Zhao et al. 2008) indicates that the primary water source is from groundwater and vadose-zone water from at 30 cm to 50 cm depth. Busch et al. (1992) also report that T. ramosissima was capable of extracting water from unsaturated soil layers. From these data, we can conclude that the higher value of $\theta$ at 30 cm and 50 cm cannot be explained by capillary rise from the shallow groundwater depth; one probable scenario is that the root systems of the trees were absorbing groundwater, transporting it, and then releasing it into the soil at 30 cm to 50 cm, strongly suggesting HL (Caldwell and Richards 1989; Dawson 1993; Warren et al. 2007).

HD is another pattern of HR in the roots of T. ramosissima. In this case, rainfall is absorbed by adventitious roots, not branches (Fig. 3b) or lateral roots within shallow soil and transferred downward by tap roots to the relatively drier, subsoil layer. The decrease in sap flow velocity in lateral roots after rain (Fig. 5a) suggests that water consumption of the plant may compensate partly by water uptake of adventitious roots from the upper soil. More support for HD comes from the diel fluctuations of $\theta$ in T. ramosissima root zone (Fig. 6); there is a remarkable increase in $\theta$ at 10 cm and 140 cm after rain, but it decreases at 30 cm and 50 cm, and shows little change at 80 cm. This indicates that rainfall is transported by taproots to the subsoil layer rather than through infiltration. HD may result in the short-term storage of water in deep soil to support root growth and may reduces losses by soil evaporation from the soil (Burgess et al. 1998; Smith et al. 1999).

In conclusion, our study confirms previous knowledge on HR patterns for P. euphratica and adds a new species, T. ramosissima, to the wide list of existing species involved in HR. However, two desert phreatophytes exhibit remarkable differences in patterns and pathways of HR that may be associated with different root architecture. The sap flow in the lateral roots of P. euphratica demonstrates both vertical and horizontal HR (HL, HD, and HHR) and possible FU. Although there is no direct support of root sap flow for T. ramosissima, other evidence suggests T. ramosissima also does HR: (1) diel fluctuations of soil water content in drier upper soil layer and (2) the use of groundwater and vadose zone water as primary water sources. We hypothesize that the pathway of HR for T. ramosissima occurs via adventitious roots in the shallow soil layer rather than lateral root measured. The
sap flow of adventitious roots was not measured due to technical difficulties in this study and this needs further substantiation.

Acknowledgments Financial support is gratefully acknowledged to Key Project of the Chinese Academy of Sciences (No. KZZD-EW-04-05), General Program of National Natural Science Fund of China (No. 91025024; 91025002) and Chinese Academy of Sciences Visiting Professorship for Senior International Scientists. The authors also thank two anonymous reviewers for their very constructive and valuable reviews and comments, which helped to improve this paper.

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