

# Hydraulic redistribution of soil water in *Populus euphratica* Oliv. in a central Asian desert riparian forest

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## ABSTRACT

Hydraulic redistribution has been widely confirmed to occur in the arid and semi-arid ecosystems. However, no research has documented the existence of such a water use/sharing mechanism in the desert riparian forests of the lower reaches of the Tarim River. The current study continuously monitored the sap velocity of roots, micro-meteorological factors and volumetric soil water content at different soil depths and different distances from the trunk to verify whether *Populus euphratica* Oliv., the dominant species of the riparian forest, has a hydraulic redistribution mechanism and to document its influence factors and ecological effects. We also sampled the stable isotope  $\delta^{18}\text{O}$  in both soil and plant samples. On the basis of this data, the magnitude of hydraulic redistribution, its driving factors and ecological effects were estimated statistically. The results demonstrate that *P. euphratica* possesses clear hydraulic lift properties, and the effect of hydraulic lift was distinct at depths of 60–120 cm in the soil within a distance of 4 m from the trunk. This soil moisture spatial variation was attributed to the spatial distribution of the root system. Furthermore, hydraulic lift can improve soil moisture, providing approximately 10–20% of daily water used in the upper soil layers (0–120 cm). By increasing the availability of water in the upper soil water, hydraulic lift can facilitate the existence of some herb species in the *Populus* community. For the first time, we have estimated the extent of hydraulic redistribution in these ecosystems, and the data indicate that hydraulic lift is an important process in the desert riparian forests in the extremely arid regions of Central Asia. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS hydraulic lift; meteorological factors; root distribution; sap flow; volumetric water content in soil

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Water resources are the dominant limiting factor in extremely arid ecosystems (Liu *et al.*, 2004; Hao *et al.*, 2010). The three primary natural sources of water for plants in arid regions are surface flow, precipitation and groundwater (Flanagan and Ehleringer, 1991; Horton and Clark, 2001; Gries *et al.*, 2003; Chimner and Cooper, 2004). However, the supply from surface flow (e.g. runoff, rivers, streams and lakes) is usually very limited, both spatially and temporally. So, most vegetation in arid areas relies on precipitation and groundwater, or a combination of the two. However, stream flow in the lower reaches of the Tarim River completely dried up after 1970, although intermittent water diversion from the upper reservoirs has occurred nine times since 2000. This region has a dry desert climate, with an annual precipitation of 17.4–42.0 mm. Consequently, groundwater is the only water source for vegetation in the lower reaches of the river (Hao *et al.*, 2010).

As the water table lowered when the river dried up, the condition of the vegetation obviously degenerated in the lower reaches of Tarim River (Liu *et al.*, 2004; Liu *et al.*, 2005). Facing such a predicament, researchers have used artificial water conveyance since 2000 as a method to save the vegetation and protect the ecosystem. Under this unique hydrological process, researchers paid attention

on the relationship between groundwater and plants. On the basis of detailed field observational data, many studies analysed the response of groundwater (Chen *et al.*, 2004a; Chen *et al.*, 2010; Li *et al.*, 2010; Xie and Yuan, 2010), vegetation cover, species diversity, biomass, community composition and plant growth to the artificial water conveyance (Liu *et al.*, 2005; Zhang *et al.*, 2005; Chen *et al.*, 2008; Ye *et al.*, 2009; Li and Xu, 2010; Sun *et al.*, 2011).

Given the lack of stream flow, a simple water-depth management strategy may be necessary to protect the vegetation. So, many studies were carried out to reveal the appropriate ecological groundwater depth. These studies tried to establish a simple and effective way to reflect the complex plant–water relationship, using a variety of different perspectives and scales such as using biochemical parameters (Chen *et al.*, 2004b; Zhuang and Chen, 2006; Ruan *et al.*, 2009), photosynthesis characters (Chen *et al.*, 2006b; Zhou *et al.*, 2010), leaf water potential of individual plants (Fu *et al.*, 2006) or by studying community stability (Chen *et al.*, 2006a; Hao *et al.*, 2009; Hao *et al.*, 2010) and groundwater quality (Li *et al.*, 2010). Although considerable research has been carried out, water use strategies such as hydraulic lift have not been considered. During this study, we also found that even under lower water conditions (usually a groundwater depth lower than 8 m), the original desert riparian forest vegetation still survives (Hao *et al.*, 2009). One of the reasons is probably caused by water supply commensalism established between the shallow-rooted and

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deep-rooted plants, meaning that the latter provide water to the former via hydraulic lift.

Hydraulic lift is the process by which soil water is passively transferred by the water potential gradient from the lower wet soil layer to the upper dry layer through plant roots (Caldwell *et al.*, 1998; Burgess *et al.*, 2001). Recent studies have shown the same process can happen in reverse (Caldwell *et al.*, 1998; Burgess *et al.*, 2001). Therefore, the transfer process of soil water via roots is generally called root hydraulic redistribution. Hydraulic redistribution can improve soil water (Burgess *et al.*, 2001; Munoz *et al.*, 2008), delay the embolism of plant roots (Domec *et al.*, 2004; Domec *et al.*, 2006) and enhance the nutritional status of deeply rooted plants during arid periods (Querejeta *et al.*, 2007). Zou *et al.* (2005) discovered the soil water potential threshold that promotes hydraulic lift. Scholz *et al.* (2008) researched the relationship between hydraulic lift to features of root distribution and root hydraulic conductance. Also, researchers have studied the ecological effect of hydraulic redistribution and developed models related to it (Ryel *et al.*, 2002; Ludwig *et al.*, 2003; Oliveira *et al.*, 2005). Overall, hydraulic redistribution exists widely in arid and semi-arid areas (Hultine *et al.*, 2003; Hultine *et al.*, 2004; Leffler *et al.*, 2005), temperate forests (Domec *et al.*, 2004; Warren *et al.*, 2005; Brooks *et al.*, 2006) and tropical savanna forests (Ludwig *et al.*, 2003; Zou *et al.*, 2005), but no formal studies have looked at hydraulic redistribution in extremely arid areas of central Asia. Further studies are needed to reveal the factors influencing the occurrence of hydraulic redistribution in plant roots, such as the spatial distribution of roots, micro-meteorological conditions and transpiration rate. Experimental evidence of

hydraulic lift and its ecological effects will greatly extend our understanding of the appropriate depth of groundwater needed by plants in arid areas, which is an important criterion for ecological restoration and ecosystem management.

The objectives of this study are as follows: (i) to observe the temporal characteristics of hydraulic lift by using measured sap velocity data; (ii) to determine the relationship between meteorological factors, root distribution and the occurrence of hydraulic lift; (iii) to assess the fluctuation in soil moisture associated with hydraulic lift; and (iv) to identify the potential ecological effects induced by hydraulic lift. This study provides a representative case study for the analysis of hydraulic redistribution in extremely arid inland river regions.

## MATERIALS AND METHODS

### Study area

The experiments were conducted in the lower reaches of the Tarim River-YingSu transect in northwestern China (Figure 1) on 5–19 August 2009. The site is located at the northeastern edge of the Taklimakan Desert in the temperate continental zone. The climate is arid desert with an average annual temperature of 11.5 °C and mean average precipitation of 17.4–42.0 mm. The study area is relatively flat, and the groundwater depth is 6–8 m. At this site, soil texture is sand, sandy loam, clay loam and loamy clay at soil depths of 0–20, 20–80, 80–100 and 100–140 cm, respectively. The most common plants include *Populus euphratica*, *Tamarix ramosissima* Ledebour, *Tamarix hispida* Willd., *Lycium ruthenicum* Murray, *Alhagi sparsifolia* Shaparenko ex Keller and Shaparenko and *Salsola* sp.

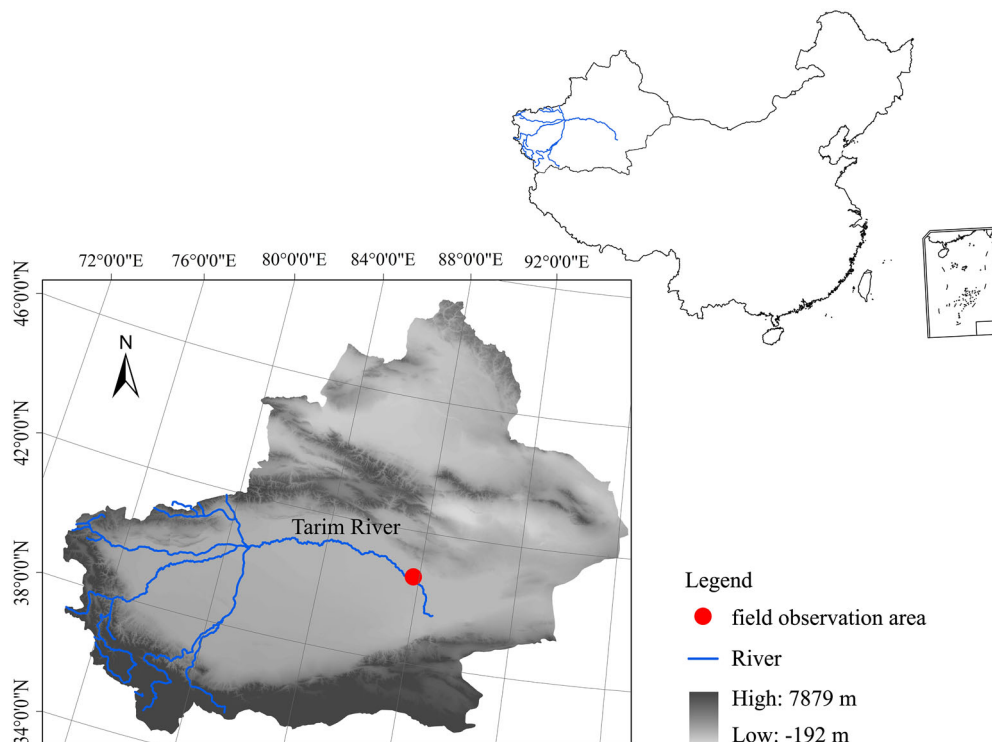


Figure 1. The location of the study area and the field observation site in the lower reaches of Tarim River.

During the experiments, it was sunny without precipitation. The average temperature was 29.9 °C, the average daily temperature difference was 13.4 °C and the average wind speed was 0.92 m s<sup>-1</sup> with a maximum speed of 6.12 m s<sup>-1</sup>.

#### Study species

We chose three healthy individuals of *P. euphratica*, a productive species of desert riparian forests, as the study species. The height, diameter at breast height and the crown diameter of the selected trees were 9–15 m, 32–48 cm and 390 × 510–370 × 580 cm, respectively. From the three original trees, we selected one as the sample to observe soil water change. To avoid interference from the nearby plants, we chose three relatively isolated *P. euphratica* individuals with few accompanying species near them (e.g. *A. sparsifolia* with height <20 cm) as the sample tree, and the distance from the nearest *P. euphratica* to the sample tree was about 12 m.

#### Monitoring sap velocity

We used the heat ratio method (ICT International Pty. Ltd, Armidale, NSW, Australia) to continuously monitor the sap flow in the roots of the trees (Burgess *et al.*, 1998; Burgess *et al.*, 2001).

The soil around the base of each tree was carefully excavated (as careful as possible to maintain the integrity of the root systems) to expose the proximal region of the large lateral roots (diameter >4 cm) and the tap root. In general, when the depth of the soil profiles reached 1 m, the target root was well exposed. Two probe sets were eudipleurally inserted into the tap root (root collar), and three probe sets were inserted into the three lateral roots (diameter >4 cm). That is, one tap root and three lateral roots were instrumented. After installation, the probes were protected with plastic boxes and then covered with approximately 20 cm of soil. In addition, the soil profile and roots were covered with a tarpaulin to prevent radiant heating from direct sunlight (Hultine *et al.*, 2003). Environmental variables, including wind speed, air temperature, leaf temperature, soil temperature at 10 cm soil depth and relative air humidity, were measured with an auto-meteorological station (ICT International Pty. Ltd). All of the sap flow and meteorological sensors were connected to a data logger (SL5 Data Logger and DataBus System, ICT International Pty. Ltd) with cable lines. The measurements were conducted every hour, from 5 to 19 August. We calculated the heat pulse velocity according to the equation (Burgess *et al.*, 1998):

$$V_h = k/x \cdot \ln(v_1/v_2) \cdot 3600$$

where  $k$  is the thermal diffusivity of green (fresh) wood,  $x$  is the distance (0.6 cm in this study) between the heater and each temperature probe, and  $v_1$  and  $v_2$  are the increases in temperature (relative to the initial temperatures) at equidistant points downstream and upstream, respectively. Thermal diffusivity ( $k$ ) was assigned a nominal value of  $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$  at the beginning of the sap velocity measurement, and this value was further resolved once the

sapwood properties were measured. All other corrections for probe misalignment and mechanical damage were made following Burgess *et al.* (2001). At the end of the study, we determined a precise baseline (zero flow) for the root sap flow by cutting all of the roots to stop the sap flow (Burgess *et al.*, 2001). The vapour pressure deficit (VPD) was also calculated on the basis of air temperature and relative air humidity using the following equation (Campbell and Norman, 1998):

$$VPD = a \cdot e^{(bT/T+c)} \cdot (1 - h_r)$$

where  $VPD$  is the vapour pressure deficit,  $T$  is the leaf surface temperature,  $h_r$  is the relative air humidity, and  $a$ ,  $b$  and  $c$  are the constants of 0.611 kPa, 17.502 and 240.97 °C, respectively.

#### Root system and vegetation observation

We excavated four soil profiles in the four cardinal directions from the trunk. Each profile was 5 m long, 1 m wide and 1.4 m deep, and in which, the root systems were sampled at 1 m intervals. The sampling process was as follows: the profile was vertically divided into seven 20 cm layers, and in each layer, a 20 × 20 × 20 cm soil column was excavated. We screened these soil columns meticulously, and the roots of *P. euphratica* were processed and analysed using the WinRHIZO system (Regent Instruments Inc., Canada) after they were cleaned.

#### Monitoring soil moisture

Using the *Populus* trunk as the centre, we buried a row of six 1.4-m-long aluminium tubes spaced 1 m apart in each of the four cardinal directions (total of 24 tubes). The neutron number in each tube was measured by the CNC100 neutron moisture metre (Beijing Nuclear Instrument Corporation, Beijing, China), which was then converted to the volumetric water content in the soil (Moroke *et al.*, 2011). During the measurements, each tube was divided into six 20 cm layers (0–20, 20–40, 40–60, 60–80, 80–100 and 100–120 cm). The sampling at each layer was repeated three times with a time interval of 4 h.

#### $\delta^{18}\text{O}$ isotope sampling

The study included the analysis of  $\delta^{18}\text{O}$  in plants, including *P. euphratica*, *A. sparsifolia*, *Glycyrrhiza inflata* Batalin and *Apocynum venetum* L., soil samples in different layers and groundwater samples during the monitoring period. The soil was divided into seven layers 40 cm deep, and the soil samples were collected in every layer with a soil drill. Fresh xylem samples were collected from *A. sparsifolia*, *G. inflata* and *A. venetum*, whereas the sample of *P. euphratica* was collected by directly gathering the sap flow. The groundwater samples were collected from groundwater monitoring wells. All these samples were collected in triplicate. Samples were tested by the Stable Isotope Mass Spectrometry Laboratory, Chinese Academy of Forestry. The  $\delta^{18}\text{O}$  data from the 0–40 cm sample were abandoned because the vacuum

extraction results were not satisfactory. The  $\delta^{18}\text{O}$  data were examined using IsoSource software (Phillips *et al.*, 2005).

RESULTS

Sap velocity

The sap velocity data of the lateral roots of *P. euphratica* directly confirmed that this tree obviously exhibits hydraulic redistribution. Figure 2 shows the daily sap velocity change patterns in both the tap root and lateral roots. Both patterns show similar features: the sap velocity is relatively stable between 00:00 and 08:00 h; then the sap velocity begins to increase dramatically until it reaches a plateau at 10:00 h. The sap velocity then maintains this value until 20:00 h, at which point the sap velocity starts to drop steeply to the early morning level by 22:00 h. However, there is a distinct difference between the sap velocity in the tap root and lateral roots. First, the sap velocity in the tap root is generally higher than in the lateral roots. For instance, the tap root velocity was  $13.87\text{ cm h}^{-1}$  between 10:00 and 20:00 h, whereas the latter is only  $6.0\text{ cm h}^{-1}$ . Second, the sap velocity of lateral roots appears to be negative from 21:00 to 08:00 h the next morning. During this period, the average sap velocity is  $-1.59\text{ cm h}^{-1}$  and the maximum velocity is  $-2.56\text{ cm h}^{-1}$ ; the negative sign indicates a reverse flow in the lateral roots.

Analysis of root distribution

The field data show that the roots of *P. euphratica* are mainly distributed at a depth of 60–120 cm within 2 m of the trunk. Figure 3 shows the vertical distribution of roots with no roots in the upper 20 cm of the soil. Unlike the upper soil layer, the roots percentages of roots distributed in the other soil layers by length was 4.27, 12.57, 28.45,

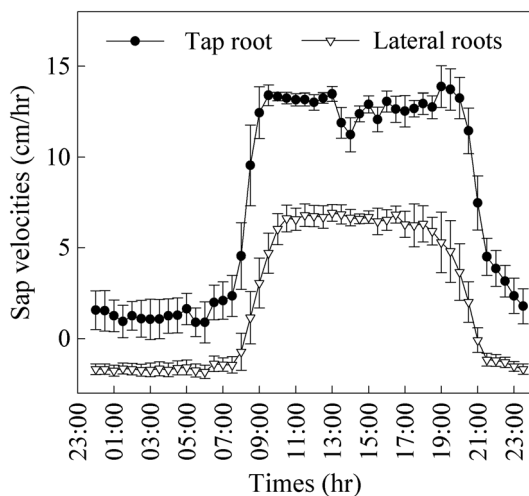


Figure 2. The daily sap velocity changes in both tap root and lateral roots, monitored between 5 and 19 August 2009. The data on the tap root were obtained by averaging 15 days of measurement values, whereas the data on lateral roots were averaged from the 15 days of measurements on three lateral roots.

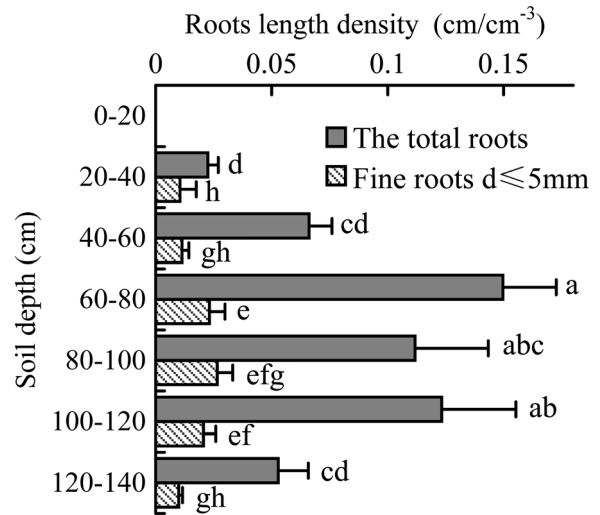


Figure 3. The vertical distribution of root length density of *Populus euphratica* Oliv. Data are averaged over 1 m (1, 2, 3, 4 and 5 m from the trunk centre) in N, E, S, and W directions around the trunk. Standard deviation ( $n=20$ ) is marked as the bars. SE means followed by different letters are significantly different by an LSD mean comparison test at  $P < 0.05$  (one-way ANOVA analysis).

21.33, 23.44 and 10% in soil depths of 20–40, 40–60, 60–80, 80–100, 100–120 and 120–140 cm, respectively. Roots were mainly distributed at depths of 60–120 cm, where 73.1% of the roots were found. The fine roots ( $d \leq 5\text{ mm}$ ) also had a similar vertical distribution, and 68.9% of the fine roots were found at depths of 60–120 cm. The analysis of the transverse distribution of root length and density (Figure 4) showed that most of the roots are scattered within 2 m of the trunk, in which the percentage of total roots (coarse + fine roots) and fine root density is 63.6 and 65.3%, respectively. At distances  $>2\text{ m}$ , the root density did not show pronounced fluctuations. The percent of the total and fine roots length density at 3, 4 and 5 m distance from the trunk were 12.5, 12.66 and 11.2% and 14.38, 13.97 and 6.37%, respectively.

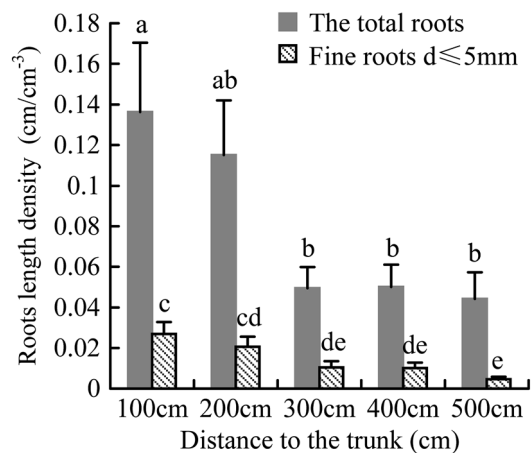


Figure 4. The transverse distribution of root length density of *Populus euphratica* Oliv. Data are averaged over different soil depths (0–20, 20–40, ..., 120–140 cm) in N, E, S, and W directions around the trunk. Bars indicate SE ( $n=24$ ). Means followed by different letters are significantly different by an LSD mean comparison test at  $P < 0.05$  (one-way ANOVA analysis).

*Soil water dynamics*

The volumetric soil water content, in all soil layers, obviously changes during the day, and the average daily soil water content dramatically decreases when the distance from the trunk is greater than 4 m. Figure 5 clearly shows a trend in which the water content gradually increases as depth increases in the soil, and it is more obvious at depths >60 cm. The highest water volume is found at depths of 100–120 cm in the soil, which is 77.8 times the amount of water in the 0–20 cm layer. Figure 5 also shows significant diurnal variation in the volumetric water content of different soil layers. The water content at night (from 21:00 to 09:00 h the next morning) is distinctly higher than during the day between 09:00 and 21:00 h, especially at depths of 40–60 cm. All of the other depths show the same pattern except at 0–20 cm: the water content, by volume, at the stopping point (09:00 h the next morning) of reverse sap velocity was significantly higher than that at the beginning point (21:00 h).

The average daily volumetric soil water content had a similar trend at different soil depths at distances of 1–6 m from the trunk. Within 4 m distance, the water content in all layers decreased slightly as the distance increased. The water content decreased dramatically beyond 4 m from the trunk and then stayed at relatively low levels (Figure 6).

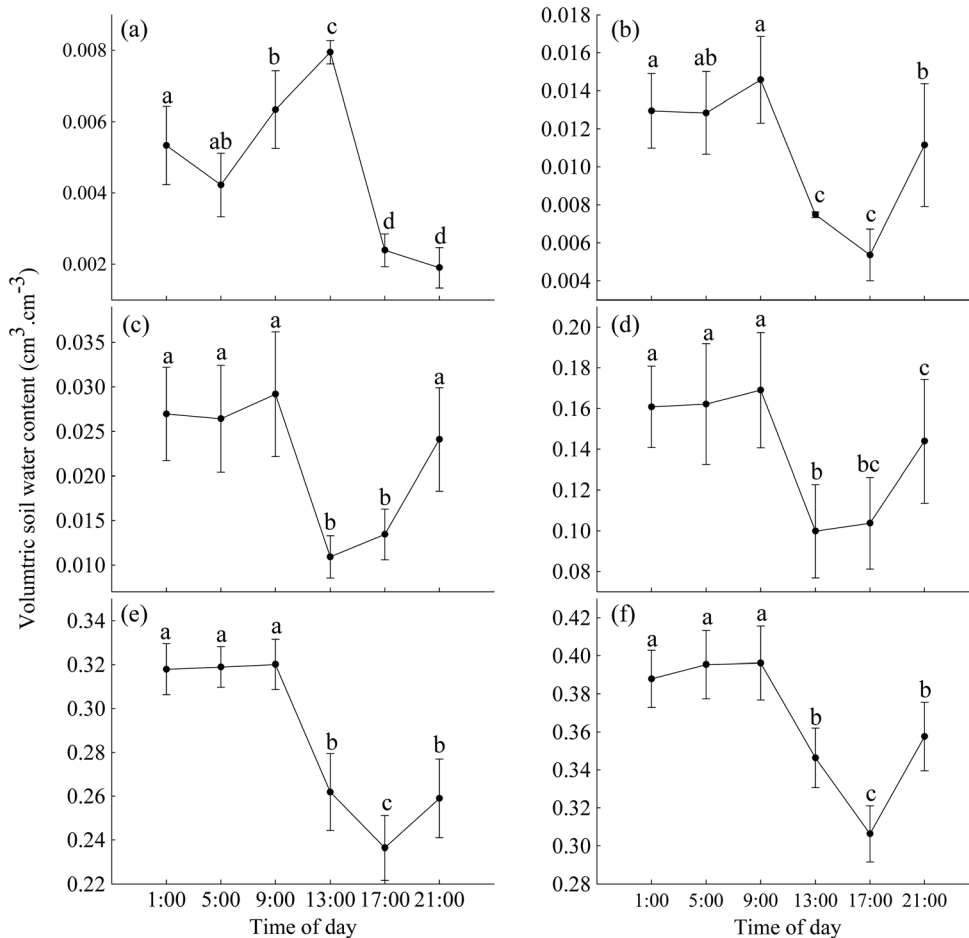


Figure 5. Variation of volumetric water content in (a) 0–20; (b) 20–40; (c) 40–60; (d) 60–80; (e) 80–100; and (f) 100–120 cm soil depths at different times. Points are mean in N, E, S, and W directions at 1 m distance from the trunk. Bars indicate SE ( $n=60$ ). Means followed by different letters are significantly different by an LSD mean comparison test at  $P < 0.01$  (one-way ANOVA analysis).

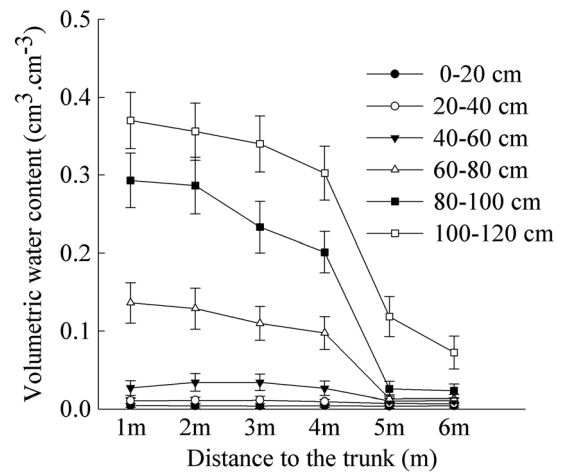


Figure 6. Variation of volumetric water content in different soil depths (0–20, 20–40, 40–60, . . . , 100–120 cm) at different distance to the trunk. Points are averaged from the monitored values of different times of each day and in N, E, S, and W directions during the 15 monitoring days; the bars indicate SE ( $n=360$ ).

After a night of hydraulic lift, the diurnal variation in water content in all soil layers possessed distinct spatial dependence (Table I). Table I reviews the diel variation of volumetric water content at the beginning and end of

Table I. The diel difference of volumetric soil water content in 0–120 cm soil depth (0–20, 20–40, . . . , 100–120 cm) at 1, 2, . . . , 6 m distance away from the trunk.

Soil depth (cm)	Average volumetric soil water content at different distance to the trunk					
	1 m	2 m	3 m	4 m	5 m	6 m
0–20	0.0036 ± 0.0007 <sup>a</sup>	0.0043 ± 0.0008 <sup>b</sup>	0.0048 ± 0.0009 <sup>c</sup>	0.0004 ± 0.0001 <sup>d</sup>	0.0005 ± 0.0001 <sup>de</sup>	0.0010 ± 0.0001 <sup>e</sup>
20–40	0.0045 ± 0.0008 <sup>ab</sup>	0.0048 ± 0.0009 <sup>a</sup>	0.0039 ± 0.0007 <sup>bc</sup>	0.0034 ± 0.0006 <sup>c</sup>	0.0035 ± 0.0007 <sup>c</sup>	0.0037 ± 0.0002 <sup>c</sup>
40–60	0.0088 ± 0.0009 <sup>a</sup>	0.0073 ± 0.0009 <sup>ab</sup>	0.0061 ± 0.0008 <sup>abc</sup>	0.0034 ± 0.0006 <sup>bcd</sup>	0.0029 ± 0.0005 <sup>d</sup>	0.0022 ± 0.0004 <sup>d</sup>
60–80	0.0153 ± 0.0010 <sup>a</sup>	0.0117 ± 0.0008 <sup>ab</sup>	0.0087 ± 0.0010 <sup>bc</sup>	0.0056 ± 0.0007 <sup>c</sup>	0.0034 ± 0.0006 <sup>d</sup>	0.0034 ± 0.0005 <sup>d</sup>
80–100	0.0189 ± 0.0011 <sup>a</sup>	0.0141 ± 0.0010 <sup>ab</sup>	0.0101 ± 0.0009 <sup>bc</sup>	0.0067 ± 0.0007 <sup>cd</sup>	0.0035 ± 0.0003 <sup>d</sup>	0.0032 ± 0.0002 <sup>d</sup>
100–120	0.0219 ± 0.0013 <sup>a</sup>	0.0161 ± 0.0012 <sup>ab</sup>	0.0113 ± 0.0014 <sup>bc</sup>	0.0088 ± 0.0018 <sup>c</sup>	0.0053 ± 0.0012 <sup>d</sup>	0.0041 ± 0.0013 <sup>d</sup>

Data in the table are mean in E, W, S, and N directions at different distance to the trunk (mean ± SE,  $n=60$ ). Means followed by different letters are significantly different by an LSD mean comparison test at  $P < 0.05$  (one-way ANOVA analysis). The volumetric soil water content was monitored in 09:00 h and 21:00 h during 5–19 August 2009.

reverse sap flow. The results show that the day and night water content variation at different distances from the trunk tends to increase with soil depth. In contrast, the diurnal variation of water content in any soil layers clearly decreases with an increasing distance from the trunk ( $P=0.05$ ) (e.g. the difference at  $\geq 4$  m from the trunk).

#### Relationship between meteorological factors and sap velocity

We monitored five meteorological factors: wind speed, air temperature, leaf temperature, relative humidity and VPD, which all showed significant daily changes. The air temperature, leaf temperature and VPD were higher during the day than at night, and the maximums were 4.3, 4.7 and 13.8 times the minimums, respectively. Change in humidity followed an opposite pattern: the maximum relative air humidity was 7.4 times the minimum. It was mostly windy during the experiments with an average wind speed of  $0.92 \text{ m s}^{-1}$  and a maximum of  $6.12 \text{ m s}^{-1}$ .

Statistical analysis was conducted on all of these factors (Table II).

Table III shows the correlation between sap velocity and the five meteorological factors. Relative humidity is negatively related to sap velocity, whereas all of the others are positively related to sap velocity. The VPD is the dominant factor in quantitative terms; all factors have a greater effect on the sap velocity in lateral roots in comparison with sap velocity at the tap root, with wind speed having the least influence on sap velocity.

#### $\delta^{18}\text{O}$ isotope characters

$\delta^{18}\text{O}$  values of soil samples decreased with the increasing of soil depth, especially at depths  $< 120$  cm. Isotopic enrichment is obvious at depths of 40–80 cm and reaches 0.189. Also, the variation of  $\delta^{18}\text{O}$  is small at depths  $> 120$  cm, and the  $\delta^{18}\text{O}$  values in deeper soil layers are close to that of groundwater. This indicates

Table II. Statistical analysis on all monitored meteorological factors (5–9 August 2009).

Statistical items	Wind speed ( $\text{m s}^{-1}$ )	Air relative humidity (%)	Air temperature ( $^{\circ}\text{C}$ )	Leaf temperature ( $^{\circ}\text{C}$ )	Vapour pressure deficit (kPa)
Average value	0.920	22.326	26.786	26.819	3.169
Standard deviation	0.050	0.434	0.338	0.365	0.081
Variance	1.287	97.345	59.101	68.862	3.410
Peak value	1.810	−0.333	−0.891	−0.910	−0.227
Skewness	1.388	0.569	0.004	0.130	0.811
Minimum value	0.000	7.020	9.670	9.334	0.571
Maximum value	6.122	52.010	41.740	43.830	7.904
Number of experiments	717	717	717	717	717

Table III. Correlation between the root sap velocity and the meteorological factors.

Sap velocity of roots	Wind speed ( $\text{m s}^{-1}$ )	Air temperature ( $^{\circ}\text{C}$ )	Leaf temperature ( $^{\circ}\text{C}$ )	Air relative humidity (%)	Vapour pressure deficit (kPa)
Tap root	0.393**	0.490**	0.498**	−0.378**	0.530**
Lateral roots	0.311**	0.605**	0.610**	−0.508**	0.627**

\*\*Correlation is significant at the 0.01 level (two-tailed); the average value of sap velocity at tap root is three times of that at the lateral roots of the same tree. The root sap velocity data were collected from 5 to 19 August.

that the moisture in deeper soil is steadily recharged by groundwater (Figure 7(a)).

The variation of  $\delta^{18}\text{O}$  values in the four species was also small. The smallest  $\delta^{18}\text{O}$  value was observed in *P. euphratica* (tree), whereas the largest appeared in *A. venetum* (herb). The  $\delta^{18}\text{O}$  values in the four species were close to the values of groundwater and deeper soil layers (>120 cm). This indicates that plants depend mainly on groundwater and deep soil moisture (Figure 7(b)).

We determined the plants water sources by analysing the different concentrations of  $\delta^{18}\text{O}$  in plants and different water sources. On the basis of the results (Table IV), *P. euphratica* mostly used groundwater and lower soil water (200–280 cm), which contributed 31 and 36.5% of water to the tree, respectively. *A. sparsifolia* mostly used the middle layer soil water and groundwater, which contributed 31 and 30.5% of the water to the herb, respectively. However, *A. venetum* used a considerable amount of the upper soil water (40–120 cm), and the contribution rate of upper soil water to the plant was

16–33%. *A. sparsifolia* and *G. inflata* both used upper soil water, and the contribution rate reached to 5–24% and 11–29%, respectively.

## DISCUSSION

### *Evidence of hydraulic lift in Populus euphratica*

Our results clearly show that *P. euphratica* living in desert riparian forests in extremely arid areas develops hydraulic lift. Existing research has shown a soil water gradient with an upper dry-low wet feature is necessary for hydraulic lift to occur (Burgess *et al.*, 2001), which was also shown to be true in *P. euphratica* (Figure 5). The soil water content increases significantly at depths >60 cm, and this satisfies one of the prerequisites for hydraulic lift. Conversely, the sap velocity data show that the lateral root sap flows in reverse at night, and this reverse flow lasts for about 10 h (Figure 2), which provides the most direct evidence for the occurrence of hydraulic lift in *P. euphratica*. It is assumed

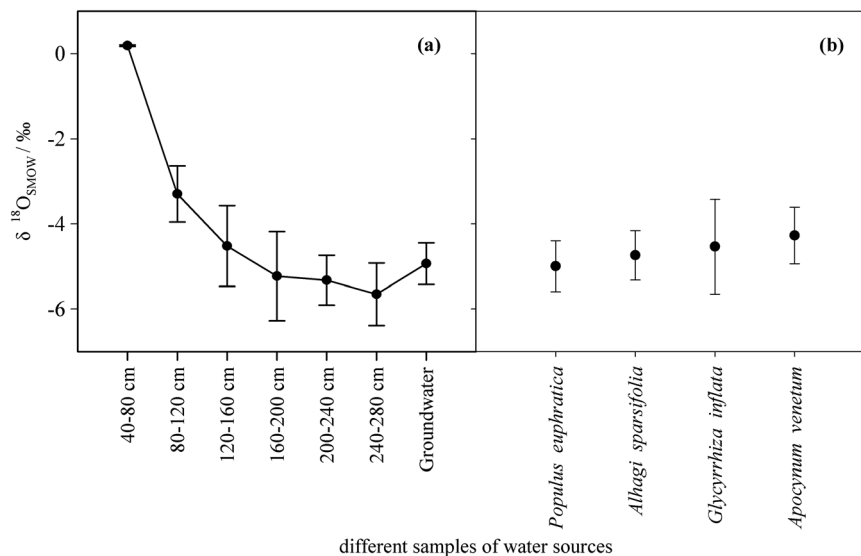


Figure 7.  $\delta^{18}\text{O}$  (H<sub>2</sub>O) isotope characters in different water sources (three repetitions): (a)  $\delta^{18}\text{O}$  (H<sub>2</sub>O, ‰) in soil samples and groundwater samples; (b)  $\delta^{18}\text{O}$  (H<sub>2</sub>O, ‰) in plants samples.

Table IV. Contribution proportion of four water sources, including the upper soil water, middle soil water, lower soil water and the shallow groundwater to the total water used by *Populus*.

Species	Contribution rate %	Upper soil (%)	Middle soil (%)	Lower soil (%)	Groundwater (%)
<i>Populus euphratica</i>	Mean	4.1	28.5	36.5	31
	Minimum	0	0	0	0
	Maximum	15	96	89	100
<i>Alhagi sparsifolia</i>	Mean	12.4	31	26.1	30.5
	Minimum	5	0	0	0
	Maximum	24	95	80	94
<i>Glycyrrhiza inflata</i>	Mean	18.2	29	24.4	28.5
	Minimum	11	0	0	0
	Maximum	29	89	75	88
<i>Apocynum venetum</i>	Mean	22.7	27.4	23	26.9
	Minimum	16	0	0	0
	Maximum	33	84	71	83

The water contributions were calculated by IsoSource mixing model (in 1% increment) based on the  $\delta^{18}\text{O}$  data.

that water content in the shallow-root soil must change if hydraulic lift is occurring (Caldwell *et al.*, 1998; Burgess, 2011). This is largely consistent with our data on soil water content (Figure 5), where the volume of water at the end of reverse sap velocity is significantly larger than at the beginning, which can be attributed to the occurrence of reverse sap velocity in the lateral roots of *P. euphratica*.

#### Factors determining hydraulic lift

Domec *et al.* (2004) and Ryel *et al.* (2002) demonstrated that water potential in the upper soil layer or root xylem is the key element influencing hydraulic lift; however, micro-meteorological conditions are also critical. We monitored four meteorological factors, wind speed, air temperature, leaf temperature and relative humidity, and also calculated the VPD. Our analysis indicates that the sap velocity at tap/lateral roots is closely related to the aforementioned factors, mostly the VPD. Therefore, the VPD may be the key meteorological factor in determining hydraulic lift in *P. euphratica*. We also found a significant correlation between sap velocity at the tap root and lateral roots during hydraulic lift (Figure 8). We can see that the absolute value of the latter gradually decreases as the former increases. This may indicate that in the night time, when water adsorption is fixed, the tap root transfers more water for transpiration (although sometimes the rate of transpiration at night is small) and the lateral roots release less water into the surrounding soil; this trend appears to be stronger under higher wind speeds when VPD and transpiration increase.

#### Assessment of the magnitude and ecological effects of hydraulic redistribution

With hydraulic lift, the diurnal variation of water content by volume in the soil demonstrated spatial and temporal variations (Table I), which is remarkably consistent with the spatial distribution of the roots of *P. euphratica*

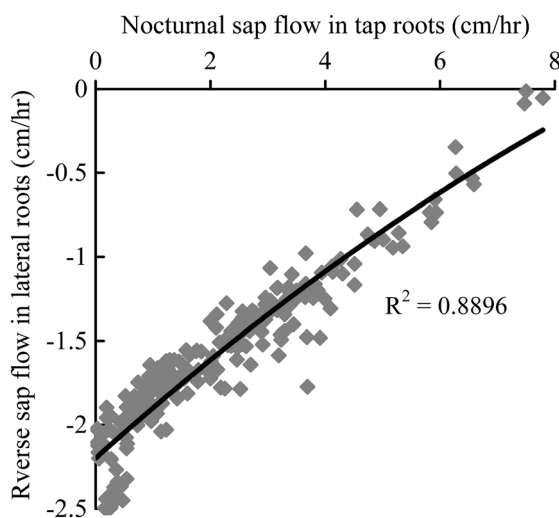


Figure 8. Reverse sap flow in lateral roots during the study period as a function of daily nocturnal sap flow measured at the base of the main stem or trunk.

(Figures 3 and 4). Once we measured the soil water changes under the influence of hydraulic redistribution, we can make a rough assessment on the magnitude of the redistributed water (Warren *et al.*, 2005; McMichael and Lascano, 2010; Warren *et al.*, 2011).

On the basis of the measured data (Figure 5), the difference of water content at the beginning and end of reverse sap flow can be considered to equal the amount of water increased by hydraulic lift, whereas the difference between the maximum (09:00 h) and minimum (17:00 h) water content (150.7 L/d, at a distance within 6 m from the trunk and 0–120 cm soil depth) can be considered to equal the amount of water lost through evapotranspiration from the entire root column in the soil. Consequently, the redistributed water is about 20% of the water loss by evapotranspiration. However, we should note that capillary adsorption occurring in the soil has not been considered in this estimation, so the actual value should be smaller. Conversely, if we assume that the amount of capillary adsorption equals the average nocturnal variation of water content (Figure 6) at a distance of 5–6 m from the trunk, then the increase in water by hydraulic lift is about 10% of the water lost by evapotranspiration. However, this assumption may not be accurate because the volumetric water content difference is not completely caused by capillary adsorption.

Simulation research showed that the amount of water moved by hydraulic redistribution was 50% greater than that moved by classic unsaturated flow within the entire rooting zone (Ryel *et al.*, 2002). Therefore, we believe that the ratio of redistributed water (by hydraulic lift) to water lost through evapotranspiration is between 10 and 20% in our study. In contrast to our study, in a seasonally dry ponderosa pine (*Pinus ponderosa*) forest, hydraulic redistribution of water accounted for at least 80% of the daily water recovery at depths of 15–65 cm (Warren *et al.*, 2011). So, we conjecture that the amount of hydraulic redistribution water may be closer to 20% of the daily water depletion in the *P. euphratica* forest of the lower reaches of Tarim River.

In other areas, research revealed that the total quantity of water moved by hydraulic redistribution was 54, 17 and 24.8% of water transpired from depths of 0–10, 40–50 and 110–120 cm, respectively, in an *Artemisia tridentate* community in Rush Valley in west central Utah, USA (Ryel *et al.*, 2002). The amount of hydraulic redistribution in cultivated crops, such as cotton, ranged from 11 to

Table V. Water contribution proportion of three sources for soil moisture in 80–120 cm layer.

Contribution rate %	40–80 cm soil moisture	120–160 cm soil moisture	Redistribution water
Mean (%)	29.3	37.2	33.4
Minimum (%)	0	23	0
Maximum (%)	34	76	69

The water contributions were calculated by IsoSource mixing model (in 1% increment) based on the  $\delta^{18}\text{O}$  data.



32% of the corresponding daily evapotranspiration (McMichael and Lascano, 2010). So, hydraulic lift may play a critical role as a positive adaptation strategy to arid conditions. From the perspective of individual plants, hydraulic lift improves the water adsorption efficiency in deep roots, increasing the carbon yield of the plant and increasing the availability of nutrients in shallow-rooted soil (Horton and Hart, 1998; Querejeta *et al.*, 2007).

The more important issue may be the idea that hydraulic redistribution can promote co-existence between deep-rooted and shallow-rooted plants on the scale of a plant community (Burgess, 2011; Prieto *et al.*, 2011). In the lower reaches of Tarim River, the herbs associated with *P. euphratica* are found to survive with groundwater depths of 4–6 m, which exceeds the ecological threshold (Chen *et al.*, 2004b), and they can even be found in locations with water depths of 6–8 m (Hao *et al.*, 2009). The likely mechanism behind this abnormal phenomenon is that the water requirement in shallow-rooted plants is met by water redistribution from the deep-rooted plants. To prove the hypothesis, this study determined the plants water sources by analysing  $\delta^{18}\text{O}$  between plants and different water sources. On the basis of the results (Table IV), *P. euphratica* mostly uses groundwater and lower soil water (200–280 cm), whereas *A. sparsifolia*, *G. inflata* and *A. venetum* all can use upper soil water (40–120 cm), and the contribution rate of the soil water used by these three plants water reached to 5–24, 11–29 and 16–33%, respectively. The results show that the hydraulic lift provided by *P. euphratica* is apparent at depths of 0–120 cm (Table I). So, the study analysed the water sources at depths of 80–120 cm in the soil using  $\delta^{18}\text{O}$  data. Three water sources exist at this depth: (i) water in the 40–80 cm soil layer; (ii) water in the 120–160 cm soil layer; and (iii) water lifted by roots of *P. euphratica*. As can be seen in Table V, water lifted by roots of *P. euphratica* can contribute approximately 33.4% of the water content in soil 80–120 cm deep. This demonstrates that hydraulic lift created by *Populus* can clearly improve soil moisture. In addition, if we integrated Tables IV and V, we can conclude that hydraulic redistribution water may meet 1.67–4.14, 3.67–9.68 and 5.34–11.02% of the water demand of *A. sparsifolia*, *G. inflata* and *A. venetum*, respectively. Research at Cornell University found that water from hydraulic redistribution can meet 0–61% water needs of shallow root plants, including shrubs and herbs (Dawson, 1993). Obviously, hydraulic redistribution can benefit community stability based on the results of this and other studies.

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