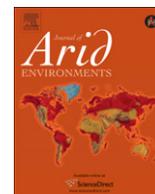


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Hydraulic lift in *Populus euphratica* Oliv. from the desert riparian vegetation of the Tarim River Basin

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ABSTRACT

In the Tarim River Basin, the desert riparian forest vegetation is under high-temperature and aridity stress. However, the vegetation can grow continuously because of deep rooting that can reach groundwater, which can thus redistribute water into the upper soil profile. This paper describes patterns of hydraulic lift by *Populus euphratica* Oliv. and discusses its ecological effects. Our results show that the tap root sap velocity of *P. euphratica* Oliv. is positive during the day and night. However, a reverse sap flow was observed in the lateral roots during the night. The soil water content of the subsoil was higher than that of the topsoil at depths of 0–120 cm. When the sap flow of the lateral roots was reversed at night, the soil water content clearly increased. In particular, at depths of 60–120 cm, the soil water content at 4:00 was 28–38% greater than that at 16:00. The vapor pressure deficit was a factor that predominantly affected the root sap velocity, and the smaller vapor pressure deficit often facilitated a reverse sap flow in the lateral roots. Our findings demonstrate the hydraulic lift characteristics and ecological effects that occur in the desert riparian forest in extremely arid regions of middle Asia

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1. Introduction

There are three primary natural sources of water for plants in arid regions: surface flow, precipitation, and groundwater (Chimner & Cooper, 2004; Flanagan & Ehleringer, 1991; Gries et al., 2003; Hipondoka et al., 2003; Horton & Clark, 2001; Lamontagne et al., 2005). However, the supply from surface flow (e.g., surface runoff, rivers, streams, lakes) is generally very limited, both spatially and temporally. Therefore, most arid vegetation relies on precipitation, groundwater, or a combination of the two. In the lower reaches of the Tarim River in China, the stream flow has completely dried up since 1970. The region has a dry, desert climate, with an annual precipitation of 17.4–42.0 mm, and predominantly dry and windy weather. Consequently, groundwater is the only water source for the vegetation in the lower reaches of the Tarim River (Li & Zhang, 2003).

In semi-arid and arid regions, such as the Tarim River Basin, not all plants have deep root systems. However, plants with shallow roots can also grow normally, just as those with deep roots can, and can absorb soil water from deep soils under long-term drought stress. This has been attributed to the adaptive strategies of drought-tolerant plants. One of these adaptive strategies is in the leaf structure (Yiotis et al., 2006). Another, more important, factor is the water sharing that

occurs between deep-rooted and shallow-rooted plants, whereby deep-rooted plants supply a certain amount of water to shallow-rooted plants through “hydraulic lift” (Dawson, 1993). The hydraulic lift of root systems has been widely documented in different floral regions, including the semi-arid (riparian) and arid areas of North America (Hultine et al., 2003a, 2003b, 2004; Leffler et al., 2005; Ryel et al., 2002, 2003, 2004), temperate zone forests (Brooks et al., 2002, 2006; Domec et al., 2004; Warren et al., 2005), croplands (Wan et al., 2000), savanna forests in America and Africa (Ludwig et al., 2003, 2004; Moreira et al., 2003; Scholz et al., 2002; Zou et al., 2005), forests of Mediterranean-type regions in Australia (Burgess et al., 2000a, 2000b, 2001), and Amazonian trees (Lee et al., 2005; Oliveira et al., 2005; Rocha et al., 2004). These studies have verified and evaluated the processes, mechanism, and ecological significance of hydraulic lift, based on a broad spatiotemporal scale and many species. However, because little research has focused on the desert riparian forests distributed in middle Asia, such as that in the Tarim River Basin, it is still unclear whether the hydraulic lift effect also exists in this vegetation. Consequently, we have only limited knowledge about the water-use strategies of these plants.

The Tarim River is located on the northern border of the Taklimakan Desert of Xinjiang, China. In the past 50 years, local intensive economic and social development has vastly increased the consumption of water from the Tarim River, which has caused the stream flow in the lower reaches (at 321 km) to cease completely. Consequently, the groundwater table has dropped significantly,

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which has led to a serious decline in the natural vegetation in the affected area. Large patches of herbaceous plants, such as *Phragmites communis* Trin., *Apocynum venetum* L., and *Alhagi sparsifolia* (B. Keller et Shap.), have died out. Large expanses of the *Populus euphratica* Olivier and *Tamarix* spp. plant communities have also degenerated. Wind erosion and land desertification processes have become very intense (Liu et al., 2007).

To preserve this endangered desert riverbank forest vegetation and restore the damaged ecosystem, the Ecological Water Conveyance Project (EWCP), which encompasses Bosten Lake to the Kongque River, was initiated in 2000 to recharge water into the lower reaches of the Tarim River. Implementation of the project has raised the groundwater table and promoted vegetation renewal (Chen et al., 2006). However, the limited water resources are very precious in arid regions. Therefore, understanding the water-use and-sharing mechanisms of plants in the region, and the maintenance of an appropriate groundwater depth, is necessary to circumvent succession towards vegetation types that are intolerant of additional moisture from groundwater, or succession towards swampy vegetation types (Oleg et al., 2001) in the lower reaches of the Tarim River. To ensure that the vegetation here can grow normally, a simple water-depth management plan is required to protect the vegetation. However, present research that focuses on the relationship between vegetation and groundwater depth does not consider the water-using strategies of plants, such as the hydraulic lift. Once there is experimental evidence of hydraulic lift and its ecological effects, our understanding of the appropriate groundwater depth will be extended and reformed. Therefore, groundwater depth can act as an important criterion of ecological water delivery.

The objective of this study was to explore the hydraulic lift effect of *P. euphratica* Oliv., the constructive species of a desert riparian forest, using the heat ratio method (HRM) to continuously monitor root sap flow, and a gravimetric method to analyze the corresponding soil water content. This research should provide a case study for the analysis of hydraulic redistribution in extremely arid inland-river regions.

2. Materials and methods

2.1. Study site

The field work was carried out at Yengsu in the lower reaches of the Tarim River, located in northwest China. This region is situated in the temperate continental zone and has a dry desert climate, with an annual precipitation of 17.4–42.0 mm, and predominantly dry and windy weather. The monitoring started in 17:00 of 9 Sep. and ended in 15:00 of 23 Sep., 2008. So the 15 consecutive diel (in the study areas, daytime from 8:00 to 21:00 that is just same with the sunrise and sunset time) monitoring data were collected. During the monitoring period, the sky was clear, with no precipitation events, but there were strong winds (average wind speed of 1.93 m/s, maximum wind speed of 5.30 m/s) at the end of the monitoring period. The study site has a flat terrain and a simple soil type, which is dominated by aeolian sandy soil. Several salt-adapted halophyte species, including *P. euphratica* Oliv., *Tamarix* spp., *Lycium ruthenicum*, *A. sparsifolia*, and *Salsola* sp., live along the riverbank in this area. Generally, the vegetation structure is very simple, with only a few plant species present.

2.2. Study species

We chose *P. euphratica* Oliv. as the study species because the tree is the constructive species of the riparian forest community, and because it has a huge and deep-rooted system; thus, the hydraulic redistribution and ecological significance of the tree would be more

obvious. Three *P. euphratica* Oliv. trees, 50 m apart, with a diameter at a breast height of about 35–50 cm and a tree height of about 10–15 m, were selected for monitoring. We excavated the coarse root systems around the base of the three individuals, down to 1.2 m, to investigate their rooting distribution. The observation showed that all of these trees have a dimorphic root system. We monitored the sap flow in all of the tap roots and in the four lateral roots of each of the three trees.

2.3. Sap flow measurement and environmental variables

We used the heat ratio methods (HRM, ICT International Pty Ltd, Armidale, NSW, Australia) to take continuous monitoring of the sap flow in the roots of the study trees. A single HRM30 sensor consists of a 3-needle design, integrated into a microprocessor controlled Smart Interface, with a 5 m long cable. The two temperature needles from one sensor comprise one upstream-downstream pair, and each needle contains two thermocouples for the determination of sap velocity at two depths within the sapwood. Standard needles are 35 mm long, and have two thermocouples located 7.5 mm and 22.5 mm from the tip of the needle. Both thermocouples, within a single temperature needle, utilize one common constantan wire.

The soil around the base of each tree was carefully excavated, as carefully 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. A single probe set was inserted into the tap root, and four probe sets were inserted into four lateral roots (diameter >4 cm). In all, one tap root and four lateral roots were instrumented on each tree. After installation, the probes were protected by plastic boxes, and were covered with approximately 20 cm of soil. In addition, the soil profile and roots were covered with a tarpaulin to prevent radiant heating by direct sunlight (Hultine et al., 2003b). Environmental variables, including the wind speed, leaf temperature, ground surface temperature, and relative air humidity, were measured with an auto-meteorological station (ICT International Pty Ltd). All the sap flow and meteorological sensors were connected to a data logger (SL5 Data Logger and DataBus System, ICT International Pty Ltd) by cable lines. The measurements were recorded every hour, during the period from September 10 to September 22. We calculated the heat pulse velocity by the equation (Burgess et al., 1998):

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

where k is the thermal diffusivity of green (fresh) wood, x is the distance (0.6 cm in the study) between the heater and either temperature probe, and v_1 and v_2 are the increases in temperature (from initial temperatures) at equidistant points downstream and upstream, respectively, x cm from the heater. Thermal diffusivity (k) is assigned a nominal value of $2.5 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$ at the beginning of sap flow measurement, and this value is further resolved once the sapwood properties have been measured. All other corrections for probe misalignment and wounding (mechanical damage) were made according to 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 in order to stop the sap flow (Burgess et al., 2001).

In addition to the auto monitoring meteorological variables described above, the vapor pressure deficit was also calculated by leaf surface temperature and relative air humidity, with the following equation (Campbell & Norman, 1998):

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

where VPD is the vapor pressure deficit, T is the leaf surface temperature, hr is the relative air humidity, and a , b , c are parameters 0.611 kPa, 17.502 and 240.97°C, respectively.

The soil water content was measured by a gravimetric method. Soil samples were collected by the dig soil profile (a depth of 120 cm) at a distance of 1 m to the trunk. The sampling depths along the soil profile were 0–20, 20–40, 40–60, 60–80, 80–100, and 100–120 cm. Soil was symmetrically collected into an aluminous box in every soil layer (three replications); the soil was sampled four times a day at 04:00, 10:00, 16:00, and 22:00. After the soil samples were collected, they were weighed with electronic balance (weighing accuracy is 0.01 g), and were taken back to the laboratory and weighed again after drying.

The HOBO groundwater level logger (Campbell Scientific, Logan, UT, USA) was installed in the groundwater monitoring well in the study site in 2008. The automatic monitoring began in August 2008, and the groundwater was monitored every 18 h because of the groundwater depth changing slowly.

The natural vegetation occurring around each well was examined in July of each year. Forty-four plant sampling sites were chosen in the lower reaches along the groundwater monitoring transects. We performed these investigations during 2006–2008.

3. Results

3.1. Change of groundwater depth

During the study period, we continuously monitored the groundwater depth in the study area with the HOBO groundwater

level logger. The results indicated that the average groundwater depth of the area is 6.26 m, and that the changing amplitude is 0.14 m. The groundwater depth showed a gradual deepening trend, due to the extreme drought and that no water was delivered to the river course in the lower reaches (Appendix 1 electronic version only).

3.2. Root sap flow

The sap flow velocity in the tap root of *P. euphratica* Oliv. had a distinctive diurnal variability (Fig. 1). The sap flow velocity increased rapidly after 9:00, reaching a peak value at about 14:00. After 19:00, the sap flow velocity decreased rapidly, and this low velocity was maintained throughout the night (21:00 to 8:00 of the next morning). The maximum value for the sap flow velocity was 25.65 cm/h, and the minimum velocity was only 0.21 cm/h. In contrast to the tap root, the sap flow velocity in the lateral roots showed various diurnal changes (Fig. 1). Reverse sap flow was detected in the lateral roots, which is considered to be the most important evidence for hydraulic lift. The diurnal changes in the sap flow velocity of the lateral roots had multiple peaks. In general, the reverse sap flow in the lateral roots began at 21:00 or 22:00, and ended at 9:00 or 10:00 the next day. The duration of the reverse flow was about 12 h. However, not every lateral root displayed a negative sap flow velocity. One of the lateral roots of the second and the third tree recorded no negative values, even during the

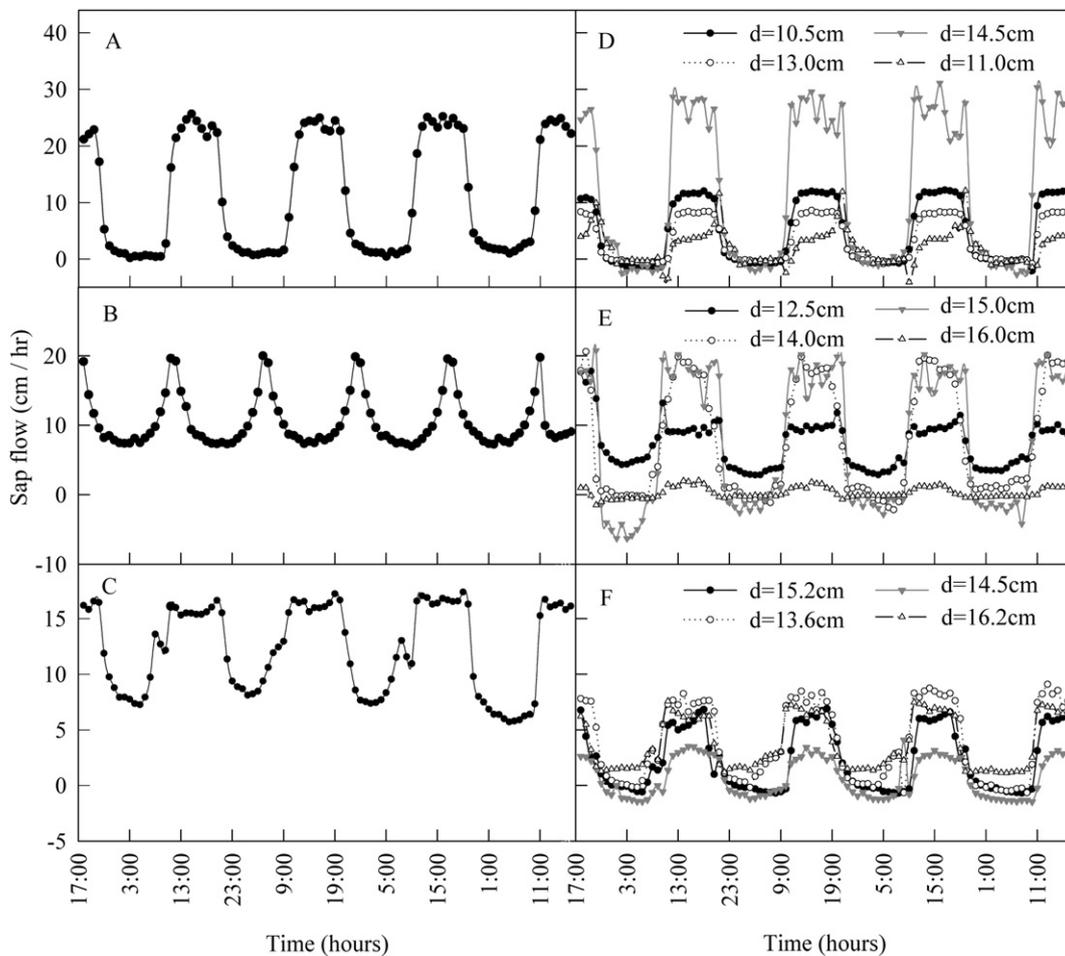


Fig. 1. Sap flow velocity (V_h) in the tap root and lateral root of *P. euphratica* Oliv. during September 10 to 22. A, B, C show the diurnal and nocturnal variations of tap root of three trees, respectively, over four days; D, E, F show the diurnal and nocturnal variations of lateral root of three trees, respectively, over four days. Points in D, E and F present the sap velocities of the lateral roots, which have different diameters.

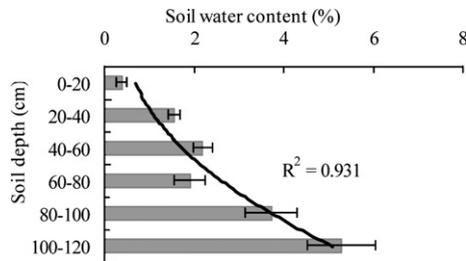


Fig. 2. The daily average soil water content in six soil depths from three soil profiles ($n = 144$). The soil water content is the weight percentage of soil water and drying soil. The soil water content was monitored during 12 days in every soil profile.

night. Thus, one lateral root had no reverse sap flow in both the second and third trees monitored. However, the fact that most of the lateral roots had reverse sap flow confirms the presence of hydraulic lift in *P. euphratica* Oliv.

3.3. Soil water content

The soil water content was also sampled and analyzed at depths of 0–20, 20–40, 40–60, 60–80, 80–100, and 100–120 cm in the same time period that the sap flow was monitored. Our results indicate that the soil water content gradually increased from the shallow soil to the deep soil in the soil profile. The soil water content clearly increased at soil depths of >20 cm, and the soil water content reached its maximum value at a depth of 100–120 cm. In general, the daily average soil water content in the soil profiles was 5.28% (Fig. 2).

The water content at different soil depths also showed varying diurnal trends (Fig. 3). Every day at 4:00, the soil had its maximal water content, and at a depth of 100–120 cm, the maximum value was 6.41%. Every day at 10:00, the soil also had high water content, but it was lower than at 4:00. The minimum water content occurred at 16:00 and 22:00, although the changing trends showed some differences. Fig. 3 illustrates the important fact that the soil water content at night was higher than it was during the day at soil depths >60 cm, and that the soil water content was maximal at 4:00.

3.4. Relationship between sap flow and meteorological factors

Meteorological factors have obviously diel patterns (Appendix 2 electronic version only). Surface temperature, leaf temperature and VPD had the same trends of change, and increased rapidly after 9:00, reaching a peak value at about 14:00 to 16:00. After 16:00, these values decreased rapidly and reached a minimum value at about 8:00. During forenoon and at noon, the surface temperature was higher than the leaf temperature, but the trend was reversed during afternoon. Contrary to the trend of changing temperature

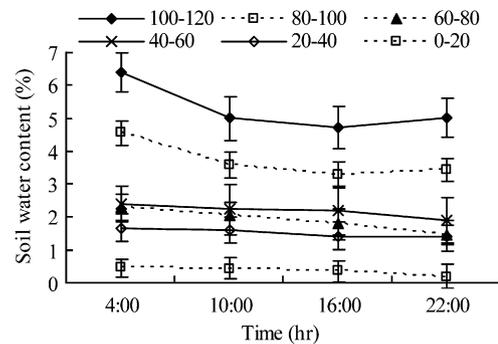


Fig. 3. The average soil water content at different times and soil depths from three soil profiles ($n = 36$). The soil water content is the weight percentage of soil water and drying soil. The soil water content was monitored for 12 days in every soil profile. The soil water content at different times depths was significantly different ($p = 0.01$). The soil water content at different times showed that it had a significant difference between 4:00 and 10:00, 16:00, 22:00 ($p = 0.05$), and there was no significant difference at 10:00, 16:00 and 22:00 ($p = 0.05$). The results were calculated by a two-way ANOVA analysis.

and VPD, the relative air humidity was higher during the night than during the day.

Correlation analysis (Table 1) of root sap velocity and meteorological factors indicated that (1) root sap velocity had an obvious correlation with all of the meteorological factors, except for the wind speed; (2) the relative air humidity showed a negative correlation, while other factors showed positive correlation in these meteorological factors, which correlated with root sap velocity; and (3) the vapor pressure deficit always had the maximum correlation coefficient with that of the lateral root sap velocity.

The stepwise regression was used to explain the complex relationship between the meteorological factors and the sap flow velocity of the lateral roots. The regression equation, in which V_s presents the sap flow velocity, and VPD represents the vapor pressure deficit, are as follows:

$$V_s = 2.95VPD - 2.058 (R = 0.747)$$

Because the regression analysis rejected other meteorological variables, the leaf surface pressure deficit becomes an important factor that can strongly affect the sap flow of the lateral roots.

4. Discussion

Our study is the first to demonstrate the nocturnal reverse sap flow in the lateral roots of *P. euphratica* Olivier in a desert riparian forest in middle Asia, extending knowledge about the occurrence of hydraulic lift in extremely arid regions. The conclusion that *P. euphratica* Olivier has the hydraulic lift effect is based on the following evidence. First, during the 12 days of continuous

Table 1
Correlation analysis between root sap velocity of the three *Populus euphratica* Oliv. and corresponding meteorological factors during the monitoring period.

		Wind speed	Air relative humidity	Leaf temperature	Surface temperature	Vapor pressure deficit
Tap root	Pearson correlation	0.462**	-0.614**	0.624**	0.655**	0.610**
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.000
	N	288	288	288	288	288
Lateral roots	Pearson correlation	0.112	-0.689**	0.719**	0.738**	0.757**
	Sig. (2-tailed)	0.057	0.000	0.000	0.000	0.000
	N	288	288	288	288	288

**Correlation is significant at the 0.01 level (2-tailed); lateral root sap velocity is the average value of four lateral roots of the same tree. The root sap velocity data collected from three trees in four days, respectively, from September 10 to 22.

monitoring, although the sap flow velocity of the tap root was positive, the sap flow velocity of the lateral roots presented negative values at night (the lateral roots had nocturnal reverse flow). This phenomenon indicates that the lateral roots release the water that is absorbed by the tap root from the deep soil into the shallow soil. The second piece of evidence for hydraulic lift comes from the soil water content data that was measured over the same period. Previous research (Baker & Van Bavel, 1988; Xu & Bland, 1993) showed that one of the preconditions for hydraulic lift is that the soil has a water potential gradient that is caused by a dry shallow soil and a wet deep soil. However, if the plants have hydraulic lift, the soil water content in the shallow soil should increase. Our monitoring showed that the water content of the shallow soil was lower than that of the deep soil, and that the soil water content gradually increased from the top to the bottom in the 0–120 cm soil profile. This changing trend in the soil water content establishes that a soil water potential gradient existed between the shallow and deep soil, and would thus allow for HL to occur between these layers. Furthermore, an analysis of the soil water content at different soil depths over time demonstrated that the soil water content reached a maximum value at 4:00. The soil water content was 28–38%, and was 8–22% higher at 4:00 than the soil water content at 16:00, at depths of 60–120 cm and 0–60 cm, respectively. The great increase in the soil water content during the night may be attributed to the hydraulic lift in the lateral root. However, the capillary rise can lead to the increase of soil moisture also during the night. In order to supply enough data to prove the ecological effects of hydraulic lift, we monitored the soil moisture in a soil depth of 0–120 cm at 1, 2, 3, 4, 5 and 6 m distances away from the trunk of the three same trees, by the CNC100 neutron moisture meter (Beijing Nuclear Instrument Corporation, Beijing, China). The monitoring time was 4:00 and 16:00, and the monitoring period was from July 5 to 20 in 2009. The results demonstrated that the soil moisture is higher during the night than in the day. The difference of soil moisture during the night and day has a decreasing trend, with an increase in distance to the trunk (Table 2). In general, the capillary rise of moisture was a certain value in small areas, such as the distance of 6 m away from the trunk. Therefore, hydraulic lift should be the reason that there was a decrease diel difference in soil moisture with an increase in distance to the trunk. In addition, the root length density also decreased with increasing of distance to the trunk (Yang et al., 2006).

The distribution of the tree root is the third evidence. Previous studies on the root distribution of *P. euphratica* Oliv. in similar arid environments (Yang et al., 2006) have shown that in a soil profile of 0–120 cm, almost all of the roots, including the fine roots (<2 mm), are concentrated at a soil depth of 60–120 cm. Therefore, based on the distribution of the roots, it is easy to understand why the soil water content increases at the 60–120 cm soil depth with the reverse flow in the lateral root during the night.

Why does hydraulic lift occur most often in plants during the night? If it is related to some nocturnal physiological process, how can we explain the hydraulic lift that occurs in the daytime (Xu & Bland, 1993)? To address this problem, we should analyze the relationship between lateral root sap velocity and meteorological factors. In the lower reaches of the Tarim River, the yearly average precipitation is less than 30 mm, whereas the evaporation is greater than 2700 mm, so the natural rainfall has almost no ecological effect on the natural vegetation. During the monitoring period, there were no rainfall events in the study area. Consequently, the vapor pressure deficit can have a critical effect on the sap velocity of root systems. Regression analysis of the root sap flow velocities and leaf surface pressure deficit showed that when the vapor pressure deficit is smaller, the sap flow velocity becomes negative. In this study, when the vapor pressure deficit was smaller than 1 Kpa, the lateral root sap velocity almost became negative. This result explains why hydraulic lift occurs most often during the night, because the vapor pressure deficit is generally smaller during the night than during the day. If the vapor pressure deficit becomes small enough during the day, the hydraulic lift effect may occur also at this time. We suggest that the leaf vapor pressure may be the most important factor that affects the occurrence of hydraulic lift. However, this hypothesis requires further revision and testing.

The water resource is the most important ecological factor limiting vegetation in arid regions. Previous studies have shown that hydraulic lift may also be one of the most important adaptive strategies in long-term evolution (Oliveira et al., 2005), in addition to deep rooting (Nepstad et al., 1994) and stomata control (Cunningham, 2004). At the scale of individual plants, hydraulic lift can increase the efficiency of deep root water absorption, increasing the carbon gains of plants, and improving the availability of nutrients in shallow soils (Dawson, 1998; Horton & Hart, 1998). Recent research (Brooks et al., 2006; Domec et al., 2004; Warren et al., 2005) has shown that hydraulic lift can extend the period of water availability, which is beneficial in maintaining the physical activity and hydraulic conductivity of plant tissues. Hydraulic lift can also postpone the period of root embolization caused by a decline in the soil water potential. At the vegetation community scale, hydraulic lift can affect the water use of plants. Within a single community, different plants absorb water from different sources, so that the water required by shallow-rooted plants can be supplied by deep-rooted plants through hydraulic lift. The mutual benefits of this water-use mechanism allow communities to maintain their species diversity and community stability (Dawson, 1993; Burgess et al., 2000; Scholz et al., 2002).

In the lower reaches of the Tarim River, the vegetation structure is simple, with only a few plant species (Song & Fan, 2000). Our study found that 19 species of higher plants inhabit the study area, two of which were trees, six were shrubs, and 11 were herbs (Appendix 3 electronic version only). The vertical structure of the *P. euphratica* Oliv. community can be classified as three strata—tree

Table 2

The diel difference of volume water content in 0–120 cm soil depth (0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, 80–100 cm) at 1 m, 2 m, 3 m, 4 m, 5 m and 6 m distance away from the trunk ($n = 15$). The volumetric water content was monitored in 4:00 and 16:00 during 5 July to 20 July in 2009.

Soil depth (cm)	Volumetric water content at different distance to the trunk ($\text{cm}^3 \text{cm}^{-3}$)					
	1 m	2 m	3 m	4 m	5 m	6 m
0–20	0.0021 ± 0.0006 ^a	0.0027 ± 0.0007 ^a	0.0024 ± 0.0006 ^{ab}	0.0030 ± 0.0005 ^{bc}	0.0023 ± 0.0006 ^b	0.0033 ± 0.0005 ^c
20–40	0.0066 ± 0.0018 ^a	0.0072 ± 0.0014 ^a	0.0070 ± 0.0009 ^a	0.0062 ± 0.0008 ^{ab}	0.0069 ± 0.0003 ^b	0.0064 ± 0.0005 ^b
40–60	0.0097 ± 0.0027 ^a	0.0144 ± 0.0031 ^a	0.0092 ± 0.0012 ^b	0.0094 ± 0.0012 ^b	0.0096 ± 0.0012 ^b	0.0102 ± 0.0011 ^b
60–80	0.0243 ± 0.0031 ^a	0.0313 ± 0.0094 ^b	0.0139 ± 0.0018 ^c	0.0139 ± 0.0022 ^{cd}	0.0127 ± 0.0015 ^{cd}	0.0122 ± 0.0012 ^d
80–100	0.0694 ± 0.0098 ^a	0.0955 ± 0.0230 ^b	0.0482 ± 0.0058 ^{ac}	0.0244 ± 0.0035 ^{cd}	0.0189 ± 0.0012 ^d	0.0195 ± 0.0013 ^d

Means followed by different letters are significantly different (the difference of volumetric water content at different distance) by an LSD mean comparison test at $p < 0.01$ (One-way ANOVA analysis).

stratum, shrub stratum and herbaceous stratum. The tree stratum is dominated by *P. euphratica* Oliv., while the shrub stratum is composed of single *Tamarix* spp., *L. ruthenicum* and *Halimodendron halodendron* or a combination of them and other shrubs; the herbaceous stratum is composed of *A. sparsifolia*, *A. venetum* and *P. communis*, etc. The typical *P. euphratica* Oliv. community found in areas with a groundwater depth of 2 m to 9 m. When the groundwater depth is more than 9 m, the communities are downgraded to the simple *Tamarix* spp. community.

To restore the previously degradation of natural riparian vegetation, the central and local governments undertook an ecological water conveyance project in the dried river course of the Tarim River Basin. The key problem in the water conveyance process is how to determine the appropriate groundwater level in which the natural vegetation can grow normally. To address the problem, researchers studied the physiological response of individual plants to different groundwater depths (Chen et al., 2004; Ruan et al., 2007). The results showed that when the groundwater depth deepens to 2.65 m, the *P. communis* is under severe water stress.

The appearance frequency of plants in different groundwater depth classes revealed that herbaceous plants appeared mostly in the sampling plots that had a 0–6 m groundwater table depth, and that the trees were distributed in a much wider range. Furthermore, other study (Hao et al., 2009) showed that the herbs always have wider ecological niche at groundwater depths of 4 m to 6 m than at other groundwater depths. For instance, *P. communis* can live and hold the higher ecological niche at a groundwater depth that exceeded their critical groundwater depth. The main reason that herbs, which have shallow roots, can appear at groundwater depths of 4–6 m might be the hydraulic lift effect of deeper root plants, such as *P. euphratica* Oliv. in this study. The distribution range of the horizontal root system of *P. euphratica* Oliv. can reach up to 5 m (Yang et al., 2006), and this hydraulic lift should have a significant impact on the water use of plants in the *P. euphratica* Oliv. community. A greater understanding of hydraulic lift should bring new perspectives to the study of appropriate groundwater depths and also extend our understanding of the mechanism of plant water use and the eco-hydrological processes in arid regions.

5. Conclusions

The root sap velocity of *P. euphratica* Oliv. shows obvious diurnal variations. The sap flow velocity increased in the morning, and reached their peak value at noon, followed by a decrease in the afternoon, and the maintenance of a lower velocity during the night. The sap flow velocity in the tap root was always positive. However, the sap flow in the lateral root showed a nocturnal reverse flow, which directly confirms the phenomenon of hydraulic lift in *P. euphratica* Oliv.

The soil water content showed a gradually increasing trend from the top to the bottom of the 0–120 cm soil profile, which meets the soil water potential requirement for hydraulic lift. After the hydraulic lift effect occurred, the soil water content increased significantly, especially at a soil depth of 60–120 cm. The increase in soil water content was 28–38% at a soil depth of 60–120 cm at 4:00, relative to that at 16:00. The changes in the soil water content correspond to the distribution of the root system, which is also concentrated at a soil depth of 60–120 cm.

The sap flow velocity of roots is significantly correlated with meteorological factors. The main meteorological factor that affects the sap flow velocity in the lateral roots is the vapor pressure deficit. After further analysis, we inferred that a smaller vapor pressure deficit might readily promote hydraulic lift.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2010.01.005.

References

- Baker, J.M., Van Bavel, C.H.M., 1988. Water transfer through cotton plants connecting soil regions of differing water potential. *Agronomy Journal* 80, 993–997.
- Brooks, J.R., Meinzer, F.C., Coulombe, R., Gregg, J., 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology* 22, 1107–1117.
- Brooks, J.R., Meinzer, F.C., Warren, J.M., Domec, J.C., Coulombe, R., 2006. Hydraulic redistribution in a Douglas-fir forest: lessons from system manipulations. *Plant, Cell and Environment* 29, 138–150.
- Burgess, S.S.O., Adams, M.A., Bleby, T.M., 2000a. Measurement of sap flow in root of woody plants: a commentary. *Tree Physiology* 20, 909–913.
- Burgess, S.S.O., Adams, M.A., Turner, N.C., White, D.A., Ong, C.K., 2001. Tree root: conduits for deep recharge of soil water. *Oecologia* 126, 158–165.
- Burgess, S.S.O., Adams, M.A., Turner, N.C., Ong, C.K., 1998. The re-distribution of soil water by tree root systems. *Oecologia* 115, 306–311.
- Burgess, S.S.O., Pate, J.S., Adams, M.A., Dawson, T.E., 2000b. Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Annals of Botany* 85, 215–224.
- Campbell, G.S., Norman, J.M., 1998. *An Introduction to Environmental Biophysics*. Springer-Verlag, New York, Berlin, Heidelberg, pp. 36–51.
- Chen, Y.N., Li, W.H., Chen, Y.P., Zhang, H.F., Zhuang, L., 2004. Physiological response of natural plants to the change of groundwater level in the lower reaches of Tarim River. *Xinjiang. Progress in Natural Science* 14 (11), 975–982.
- Chen, Y.N., Zilliacus, H., Li, W.H., Zhang, H.F., Chen, Y.P., 2006. Groundwater level affects plant species diversity along the lower reaches of the Tarim River, Western China. *Journal of Arid Environments* 66, 231–246.
- Chimner, R.A., Cooper, D.J., 2004. Using stable oxygen isotopes to quantify the water source used for transpiration by native shrubs in the San Luis Valley, Colorado, USA. *Plant and Soil* 260, 225–236.
- Cunningham, S.C., 2004. Stomatal sensitivity to vapour pressure deficit of temperate and tropical evergreen rainforest trees of Australia. *Tress Structure and Function* 18 (4), 399–407.
- Dawson, T.E., 1998. Water loss from tree root influences soil water and nutrient status and plant performances. In: Flores, H.E., Lynch, J.P., Eissenstat, D.M. (Eds.), *Radical Biology: Advances and Perspectives on the Function of Plant Root*. Current Topics in Plant Physiology, vol. 17. American Society of Plant Physiologists, Rockville, Maryland, USA, pp. 195–210.
- Dawson, T.E., 1993. Hydraulic lift and water use in plants: implications for performance, water balance and plant–plant interactions. *Oecologia* 95, 565–574.
- Domec, J.C., Warren, M., Meinzer, F.C., Brooks, J.R., Coulombe, R., 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* 141, 7–16.
- Flanagan, L.B., Ehleringer, J.R., 1991. Stable isotope composition of stem and leaf water: applications to the study of plant water use. *Functional Ecology* 5, 270–277.
- Gries, D., Zeng, F., Foetzki, A., Arndt, S.K., Bruehlheide, H., Thomas, F.M., Zhang, X., 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.
- Hao, X.M., Chen, Y.N., Li, W.H., 2009. Indicating appropriate groundwater tables for desert river-bank forest at the Tarim River, Xinjiang, China. *Environmental Monitoring and Assessment* 152, 167–177.
- Hipondoka, M.H.T., Araniba, J.N., Chirara, C., Lihavha, M., Macko, S.A., 2003. Vertical distribution of grass and tree root in arid eco-systems of Southern Africa: niche differentiation of competition. *Journal of Arid Environments* 54, 319–325.
- 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.
- Horton, J.L., Hart, S.C., 1998. Hydraulic lift: a potentially important ecosystem process. *Trends in Ecology and Evolution* 13, 232–235.
- Hultine, K.R., Cable, W.L., Burgess, S.S.O., Williams, D.G., 2003a. Hydraulic redistribution by deep root of a Chihuahuan desert phreatophyte. *Tree Physiology* 23, 353–360.

- Hultine, K.R., Scott, R.L., Cable, W.L., Goodrich, D.C., Williams, D.G., 2004. Hydraulic redistribution by a dominant, warm-desert phreatophyte: seasonal patterns and response to precipitation pulses. *Functional Ecology* 18, 530–538.
- Hultine, K.R., Williams, D.G., Burgess, S.S.O., Keefer, T.O., 2003b. Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia* 135, 167–175.
- 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.
- Lee, J.E., Oliveira, R.S., Dawson, T.E., Fung, I., 2005. Root functioning modifies seasonal climate. *Proceedings of the National Academy of Sciences of the United States of America* 102, 17576–17581.
- Leffler, A.J., Peek, M.S., Ryel, R.J., Ivans, C.Y., Caldwell, M.M., 2005. Hydraulic redistribution through the root systems of senesced plants. *Ecology* 86, 633–642.
- Li, X.M., Zhang, X.M., 2003. Water condition and restoration of natural vegetation in the southern margin of the Taklimakan Desert. *Acta Ecologica Sinica* 23 (7), 1449–1453.
- Liu, Y.B., Chen, Y.N., Deng, J.M., 2007. Saving the “Green Corridor” recharging groundwater to restore riparian forest along the lower Tarim River, China. *Ecological Restoration* 25 (2), 61–66.
- Ludwig, F., Dawson, T.E., Kroon, H., Berendse, F., Prins, H.H.T., 2003. Hydraulic lift in *Acacia tortilis* trees on an East African savanna. *Oecologia* 134, 293–300.
- Ludwig, F., Dawson, T.E., Prins, H.H.T., Berendse, F., de Kroon, H., 2004. Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters* 7, 623–631.
- Moreira, M.Z., Scholz, F.G., Bucci, S.J., Stenberg, L.S., Goldstein, G., Meinzer, F.C., Franco, A.C., 2003. Hydraulic lift in a neotropical savanna. *Functional Ecology* 17, 573–581.
- Nepstad, D.C., de Carvalho, C.R., Davidson, E.A., Jipp, P., Lefebvre, P.A., Negreiros, G.H., Silva, E.D., Stone, T.A., Trumbore, S.E., Vieira, S., 1994. The role of deep root in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372, 666–669.
- Oleg, A., Dalibor, H., Josip, K., Dragan, B., 2001. Modelling groundwater regime acceptable for the forest survival after the building of the hydro-electric power plant. *Ecological Modelling* 138, 277–288.
- Oliveira, R.S., Dawson, T.E., Burgess, S.S.O., Nepstad, D.C., 2005. Hydraulic redistribution in three Amazonian trees. *Oecologia* 145, 354–363.
- Rocha, H.R., Goulden, M.L., Miler, S.D., Menton, M.C., Pinto, L.D.V.O., Freitas, H.C., Figueira, A.M.S., 2004. Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. *Ecological Application* 14, 22–32.
- Ruan, X., Wang, Q., Chen, Y.N., Li, W.H., 2007. Physiological response of riparian plants to watering in hyper-arid areas of Tarim River, China. *Frontiers of Biology in China* 1, 54–61.
- Ryel, R.J., Caldwell, M.M., Yoder, C.K., Leffler, A.J., 2002. Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. *Oecologia* 130, 173–184.
- Ryel, R.J., Caldwell, M.M., Leffler, A.J., Yoder, C.K., 2003. Rapid soil moisture recharge to depth by roots in a stand of *Artemisia tridentata*. *Ecology* 84, 757–764.
- Ryel, R.J., Leffler, A.J., Peek, M.S., Ivans, C.Y., Caldwell, M.M., 2004. Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. *Oecologia* 130, 173–184.
- Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., 2002. Hydraulic redistribution of soil water by neotropical savanna trees. *Tree Physiology* 22, 603–612.
- Song, Y.D., Fan, Z.L., 2000. The water resource and ecology in Tarim River, China. Xinjiang People Press, Urumqi. Chinese with English summary.
- Wan, C.G., Xu, W.W., Sosebee, R.E., Machado, S., Archer, T., 2000. Hydraulic lift in drought-tolerant and susceptible maize hybrids. *Plant Soil* 219, 117–126.
- Warren, J.M., Meinzer, F.C., Brooks, J.R., Domec, J.C., 2005. Vertical stratification of soil water storage and release dynamics in Pacific Northwest coniferous forests. *Agricultural and Forest Meteorology* 130 (1–2), 39–58.
- Xu, X., Bland, W.L., 1993. Reverse water-flow in sorghum root. *Agronomy Journal* 85, 384–388.
- Yang, L., Zhang, Q.L., Chang, J.B., 2006. Spatial distribution characteristics of root of *Populus euphratica*. *Journal of Inner Mongolia Agricultural University* 27 (1), 15–17.
- Yiotis, C., Manetas, Y., Psaras, G.K., 2006. Leaf and green stem anatomy of the drought deciduous Mediterranean shrub *Calicotome villosa* (Poiret) Link. (Leguminosae). *Flora* 201, 102–107.
- Zou, C.B., Barnes, P.W., Archer, S., McMurtry, C.R., 2005. Soil moisture redistribution as a mechanism of facilitation in Savanna tree shrub clusters. *Oecologia* 145, 32–40.