

Soil water potential determines the presence of hydraulic lift of *Populus euphratica* Olivier across growing seasons in an arid desert region

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Abstract

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Hydraulic lift (HL) of deep-rooted plants is a water adaptation phenomenon to extreme drought conditions which would subsequently improve the survival of shallow-rooted plants in an arid desert area. There is an ongoing debate on whether the difference in water potential between plant roots and soils determine the presence of HL, thus considerable research efforts are needed to improve our understanding. In this study, we used the Ryel model and comparative analysis to determine the changes in soil water potential (SWP), the soil layer of obtaining water from plant roots (SLOW), the amount water released from plant roots into soils, and the total amount of release water of HL (H_T) of five stratified soil layers at different depths (i.e. 0–10, 10–40, 40–70, 70–100 and 100–150 cm) across plant growing season (i.e. June, August and October). The results showed that SLOW always appeared in the lowest SWP soil layer, and that lowest SWP differed among soil layers. The lowest SWP soil layer and SLOW shifted from shallow to deep soil layers across the growing seasons. Additionally, H_T decreased across the growing seasons. Fine root biomass decreased in shallow whereas increased in deep soil layers across growing seasons. Our results proved the water potential difference among soil layers determined the presence of HL in an arid desert region. The changes in water potential difference among soil layers might shift the lowest SWP soil layer from shallow to deep soil layers, and as a consequent decrease H_T across plant growing seasons.

Keywords: deep-rooted plants; extreme drought environment; fine roots distribution; soil layers

Hydraulic lift (HL) is the process of water movement from moist layer to dry layers of the soil profile through deep-rooted plant roots at night when transpiration is reduced (RICHARDS, CALDWELL 1987; CALDWELL et al. 1998). Since HL changes the spatial pattern of soil water via water movement

upward or laterally among different soil layers, it is considered as an important physiological mechanism in biodiversity and ecosystem stability in the arid desert regions (RICHARDS, CALDWELL 1987; PRIETO 2010; PRIYADARSHINI et al. 2015). It is generally well understood that water always transmits

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from the high to the low water potential positions (KRAMER, BOYER 1995). In the process of HL, water is being lifted from the moist soil layers to the drier layers via plant roots (RICHARDS, CALDWELL 1987; PRIETO et al. 2012, 2016), suggesting that the differences in water potential might exist among soil layers and plant roots (HORTON, HART 1998; PRIETO et al. 2012). Based on the modeling and theoretical research, many studies speculated that water potentials differed among soil layers, and between plant roots and its adjacent soil layers might determine the presence of HL (KRAMER, BOYER 1995; CALDWELL et al. 1998; SCHOLZ et al. 2008). However, due to the environmental and experimental restrictions, many empirical studies did not observed the differences in water potential between soils and plant roots during the presence of HL (SCHOLZ 2002; HAO 2009; PRIETO et al. 2012). Thus, there is an ongoing debate on whether the difference in water potential between plant roots and soils determine the presence of HL.

Soil water potential (SWP) threshold of HL refers to the marginal level at which of plant roots releasing water into its adjacent soils. For a given soil layer, owing to plant roots releasing water into their adjacent soils at the moment of the present of HL (HORTON, HART 1998; PRIETO et al. 2012), SWP might be lower than an SWP threshold. It is increasingly being reported that the magnitude of SWP threshold of HL depends on the relative relationship between the roots water potential (RWP) and SWP (KRAMER, BOYER 1995; CALDWELL et al. 1998; SCHOLZ et al. 2008). Due to the water transportation from plant roots to stem and leaves, previous studies indicated that RWP decreases from deep roots to shallow roots in the plant (ZIMMERMANN 1984; KRAMER, BOYER 1995). Oppositely, because SWP could be influenced by the variations in fine roots distribution, and the relationship between roots and soils (SHEIN, PACHEPSKY 1995; TIERNEY et al. 2003), it has no monotonically decreasing trends with soil depth and RWP (EISSENSTAT, YANAI 1997; JIANG et al. 2006; HAO et al. 2013). Thus, it is possible that the relative relationship between RWP and SWP, as a consequent influence SWP threshold may vary among soil layers within the process of HL. However, whether and how the SWP threshold changes among soil layers is yet to be understood.

Previous studies indicated that SWP varies across plant growing season induced by the changes in plants requirements in water and minerals (JOSLIN, HENDERSON 1987; ISHIKAWA, BLEDSOE 2000). In an arid desert region, SWP increases along growing season in shallow soil layers, whereas decreases in deep soil layers (YANG, LÜ 2011; HAO et al. 2013).

These subsequently results in the shift of the lowest SWP soil layers from shallow to deep soil layers across plant growing season (JOSLIN, HENDERSON 1987; ISHIKAWA, BLEDSOE 2000). In addition, based on previous evidences and water physiological theories, water always releases from the plant roots into the lowest SWP soil layer via HL process (ZIMMERMANN 1984; CALDWELL et al. 1998). In these cases, in line with the lowest SWP soil layer, the soil layer of obtaining water from plant roots (SLOW) in HL process might shift from shallow into deep soil layers across plant growing season. However, whether SLOW changes among soil layers across plant growing season, is currently unclear.

The total amount of water released from plant roots into soils in HL (H_T) is the most important index to evaluate the effect of HL on local ecosystem (HAO 2009; PRIETO et al. 2012; YANG et al. 2014). In order to underscore the importance of HL in the arid desert ecosystems, numerous previous studies have used models or sap flow to estimate H_T throughout or at a specific stage of the plant growing season (CALDWELL et al. 1998; HAO 2009; PRIETO et al. 2012; YU et al. 2013; YANG et al. 2014). However, whether and how H_T change along plant growing season are generally designed without concern for these studies (CALDWELL et al. 1998; PRIETO et al. 2012; YU et al. 2013; YANG et al. 2014). It is reported that H_T has a positive relationship with water potential difference between the moist and drier layers of the soil profile (CALDWELL et al. 1998; PRIETO et al. 2012; YANG et al. 2014). In the arid desert region, due to the reduction in transpiration and water utilization of plants, the water potential difference amongst soil layers decrease across plant growing seasons (YANG, LÜ 2011; HAO et al. 2013; YU et al. 2013). Thus, it may be possible that H_T decreases across plant growing season.

Populus euphratica Olivier, a deciduous plant with high drought and salinity tolerances, is a constructive species for the desert forest in the arid desert region (HAO et al. 2010; YU et al. 2013; YANG et al. 2014). In our and others' previous studies, the results indicate that *P. euphratica* owning HL, and which lift water from deeper to shallow soil layers at night (HAO et al. 2010; YANG, LÜ 2011; YU et al. 2013; YANG et al. 2014). However, the underlying mechanisms for explaining the occurrence and change of HL across the growing seasons are yet to be understood. Therefore, in this study, we aim to explore the relationship between soil water potential and the presence of HL across the growing season in an arid desert region. Specifically, we addressed the following three major questions:

(i) Whether the relative relationship between RWP

and SWP cause the difference in SWP threshold among soil layers during the presence of HL?

(ii) Whether variation in SWP shift the lowest SWP soil layer and SLOW from shallow into deep soil layers across plant growing seasons?

(iii) Whether the reduction in water potential difference amongst soil layers cause any decrease in H_T across plant growing seasons?

This study will contribute greatly to improve the knowledge about the physiological and ecological adaptability of the plant to the extreme conditions in the arid environment.

MATERIAL AND METHODS

Study site. The study was conducted in the Ebinur Lake Wetland Nature Reserve (ELWNR) in the western margin of the Gurbantonggut desert in the Xinjiang Uygur Autonomous Region of western China (44°30'–45°09'N, 82°36'–83°50'E). The annual precipitation ranges from 30 to 160 mm whereas the evaporation ranges from 1,200 to 3,800 mm, and the sunlight hours reach approximately 2,800 h·yr⁻¹. Temperature ranges from –33 to 44°C with average temperatures ranges from 6 to 8°C. Due to the extremely dry conditions and the sparse rainfall, the climate of the region is typical arid temperate. The site has a moderate slope and sandy soil (YANG et al. 2014). Groundwater is the main water resource of the local ecosystem, and groundwater level ranges from 1.8 to 2.0 m. Sand dunes are observed at 3 km north of the site (YANG et al. 2017).

Experimental design and measurements. In this study, one typical desert forest area (5 × 5 km, i.e., 25 km²) of *P. euphratica* was established as the experimental area. This forest contained 48 individuals of *P. euphratica* with the vegetal coverage is 4%. Based on the terrain of the experimental site, we randomly selected three 10 × 10 m areas as experimental plots. Each plot just has one mature individual of *P. euphratica*, and the biometric conditions such as plant DBH, height and crown area did not differ among these three individuals. In addition, three individuals of *P. euphratica* were selected at the distance of least 6 m from each other in order to prevent the water disturbance and mutual water transportation. It is reported that the root length of *P. euphratica* was shorter than 12 m in the horizontal direction in ELWNR (HAO 2009; YANG, LÜ 2011; YU et al. 2013). Thus, three 5 × 5 m plots located at least 12 m far from each experimental plot, without *P. euphratica* and their roots, were randomly selected as the control plots. There is no difference in

groundwater table between experimental and control plots.

To distinguish the difference in water transportation among soil layers, one soil profile was randomly drilled in each experimental and control plots, hence six soil profiles in total. The soil profile was divided into five soil layers, i.e. 0–10, 10–40, 40–70, 70–100, and 100–150 cm. The deepest soil layer was 150 cm as the groundwater level is at approximately 160 cm in the experimental site. Two respective probes were placed at each soil layer for measuring soil moisture – SMET10 (Huier, China) and SWP – HR-33T (Decagon, USA) on 16th April 2010. The soil profiles were then covered with the initial drilled soil. Plant growing season was divided into three stages (i.e. June, August and October, represented early, middle and late stage of growing season, respectively). Within each stage of plant growing season, the measurement was conducted continuously for six days with 30 min interval for each measurement. Additionally, one soil sample per 10 cm² at each soil layer and hence in total 30 samples in experimental and control plots were collected to measure fine root biomass (diameter ≤ 2 mm), root distribution and soil water transport properties in June, August and October, respectively. This provides the vertical distribution changes in fine root biomass, soil water transportation properties and root distribution across plant growing season. Soil water transportation properties include the unsaturated soil hydraulic conductivity, residual and saturated volumetric water contents, relative water saturation, soil saturated hydraulic conductivity and the half soil water potential where soil hydraulic conductance is reduced by 50%.

HL simulation. HL presence was a precondition of the changes in H_T , SWP thresholds and SLOW among soil layers across plant growing season. In our previous study, HL was verified to present in *P. euphratica* by using isotope tracing and comparison analysis in soil water content between experimental and control plots (YANG, LÜ 2011; YANG et al. 2014).

There are no direct methods to measure and calculate the amount of water released from plant roots into soils in HL at present (RICHARDS, CALDWELL 1987; CALDWELL et al. 1998; PRIETO et al. 2012). Modeling simulation is considered as the most effective way to estimate and calculate the change in the amount of water released from plant roots into soils in HL process (BURGESS et al. 1998; RYEL et al. 2002; HAO et al. 2010; PRIETO et al. 2012). Ryel model is a one-dimensional model in simulating vertical changes of soil water content among different soil layers (Eqs 1–9) (RYEL et al. 2002). It is also normally used to compute the amount of water released from

plant roots to soils in HL process (RYEL et al. 2002; PRIETO et al. 2012). Within this model, the changes in water content at a given soil layer were assumed to be due to vertical unsaturated flow, redistribution via roots and transpiration. Water redistributed by roots was modeled as a function of the distribution of active roots, radial conductivity of water between the root-soil interface and transpiration activity. In this model, the soil column was assumed to be consisting of layers having a uniform thickness with uniform water moving between layers:

$$\frac{dW_i}{dt} = \frac{dF_i}{dz} + H_i - E_i \quad (1)$$

where:

W_i – water storage (cm) in layer i ,

t – time (h),

F_i – net unsaturated flow of water into layer i ($\text{cm}\cdot\text{h}^{-1}$),

z – vertical thickness,

H_i – net water redistributed by roots into layer i ($\text{cm}\cdot\text{h}^{-1}$),

E_i – transpiration water loss from layer i ($\text{cm}\cdot\text{h}^{-1}$).

$$\frac{dF_i}{dz} = K(\theta_i) \left(\frac{d\Psi_i}{dz} + 1 \right) \quad (2)$$

where:

$K(\theta_i)$ – unsaturated soil hydraulic conductivity ($\text{cm}\cdot\text{h}^{-1}$) for volumetric water content θ ($\text{cm}^3\cdot\text{cm}^{-3}$) in layer i ,

Ψ_i – soil water potential.

$$K(\theta_i) = K_s S_i^{0.5} \left[1 - (1 - S_i^{1/m})^m \right]^2 \quad (3)$$

where:

K_s – soil saturated hydraulic conductivity,

S_i – relative saturation.

$$S_i = \frac{\theta_i - \theta_r}{\theta_s - \theta_r} \quad (4)$$

where:

θ_r – residual volumetric water content ($\text{cm}^3\cdot\text{cm}^{-3}$),

θ_s – saturated volumetric water content ($\text{cm}^3\cdot\text{cm}^{-3}$).

$$\theta_i = \frac{\theta_s - \theta_r}{\left[1 + |\alpha \Psi_i|^n \right]^m} \quad (5)$$

where:

α, n – parameters of the soil water characteristic curve based on soil characteristics,

$m = 1 - 1/n$.

$$H_i = C_{RT} \sum_j (\Psi_j - \Psi_i) \max(c_i, c_j) \frac{R_i R_j}{1 - R_x} D_{tran} \quad (6)$$

where:

C_{RT} – maximum radial soil-root conductance of the entire active root system for water ($\text{cm}\cdot\text{MPa}^{-1}\cdot\text{h}^{-1}$),

c_i – factor reducing soil-root conductance based on Ψ_i ,
 R_i – fraction of active roots in layer i (all R_i must be < 0.5),

D_{tran} – factor reducing water movement among layers by roots while the plant is transpiring, it was assumed to be 1.0 during the night when transpiration was minimal and 0.0 during the day,

$R_x = R_i$ when $\theta_i > \theta_j$ or $R_x = R_j$ when $\theta_j > \theta_i$.

$$R_x = \begin{cases} R_i, & \text{when } \dots \theta_i > \theta_j \\ R_j, & \text{when } \dots \theta_j > \theta_i \end{cases} \quad (7)$$

$$c_i = \frac{1}{1 + \left(\frac{\Psi_i}{\Psi_{50}} \right)^b} \quad (8)$$

where:

Ψ_{50} – half soil water potential (MPa) where conductance is reduced by 50%,

b – empirical constant.

$$E_i = E_{RT, \max} c_i R_i \quad (9)$$

where:

$E_{RT, \max}$ – maximum whole canopy transpiration rate ($\text{cm}\cdot\text{h}^{-1}$).

Based on the suggested methods in RYEL et al. (2002) and YANG and LÜ (2011), the simulated parameters of HL were calculated by the root distribution, the soil water transportation properties, SWP, soil moisture content and $E_{RT, \max}$. In this study, soil water transportation properties were determined using standard methods (LEFFLER et al. 2005), SWP and soil moisture content were measured respectively using SMET10 and HR-33T, $E_{RT, \max}$ was measured at the same experimental period of SWP and soil moisture content by using 255 Series Evaporation Stations – EP255 (Novalynx, Inc., USA). Additionally, in order to decrease the influence of data fluctuation on simulation, data from the last three days was selected from six continuous days to simulate the HL process in Ryel model in each stage of growing season.

Data analyses. In the present study, the total amount of release water of HL per day (H_T ; $\text{cm}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) was calculated using all day H_i (H_i ; i is the soil layer number; $\text{cm}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ amount of water released from roots into soil per hour; is the simulated result of Ryel modelling) of all soil layers in each stage of growing season. A scatter plot was performed between H_i and its corresponding SWP in order to show the differences in SWP thresholds of HL among soil layers. SWP value referred to SWP thresholds of i^{th} soil layer when $H_i = 0$, whereas $H_i > 0$ indicated plant roots releasing water into the i^{th} soil layer. Differences in the lowest SWP

and fine root biomass among soil layers, as well as among stages of growing season were tested by using one-way ANOVA. The difference in volumetric water content between experimental and control plots amongst five soil layers was tested by using the independent samples *t*-test.

HL simulation was analysed by using MATLAB (Version 7.10, 2010). Data management and statistical tests were conducted using SPSS (Version 19.0, 2011). The parameters of the soil water characteristic curve were calculated using RETC (Version 6.02, 2009). All statistical analysis was considered to be significant at $P < 0.05$.

RESULTS

Based on the scatter diagram of SWP against H_i , SWP thresholds differed among soil layers. The SWP threshold in 0–10, 10–40, 40–70 and 70 to 100 cm soil layers was -2.13 , -1.75 , -1.73 and -1.87 MPa, respectively (Fig 1).

Across the growing season, H_T decreased to 0.111 ± 0.005 in June, 0.012 ± 0.004 in August, and 0.008 ± 0.001 cm·m⁻²·d⁻¹ in October, respectively (Table 1). Based on the results of HL modelling and one-way ANOVAs, SLOW always appeared in the lowest SWP soil layer (Figs 2 and 3). The low-

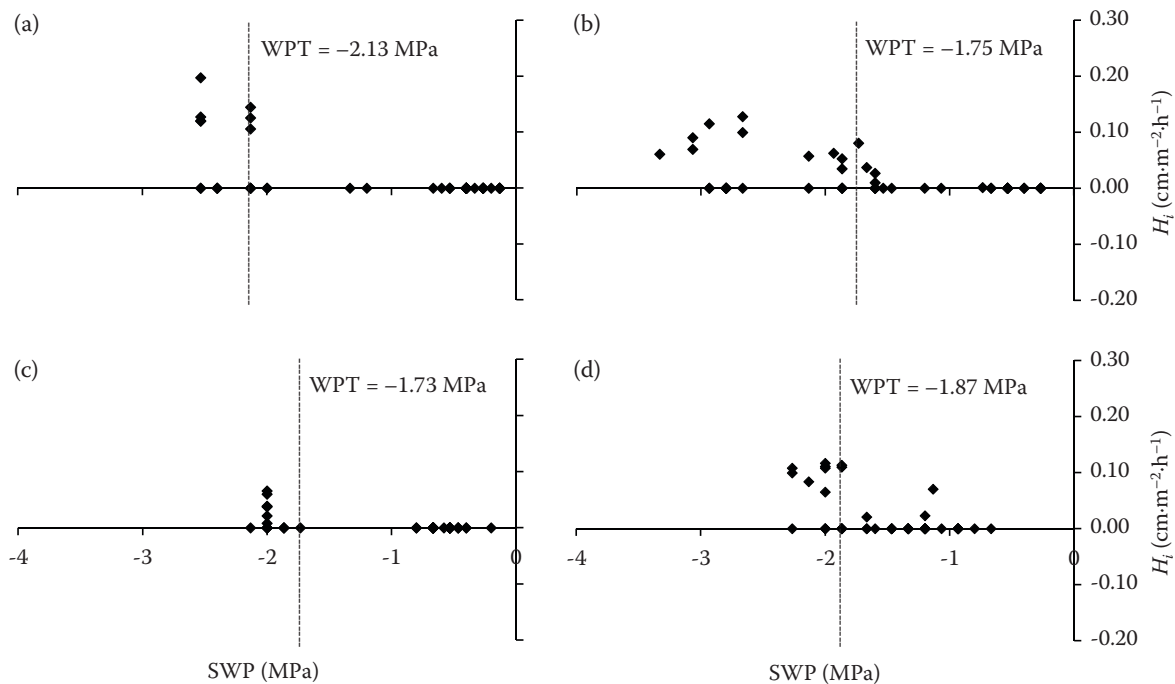


Fig. 1. Relationship between soil water potential (SWP) and the amount of release water of hydraulic lift per hour in i^{th} layer (H_i) among four soil layers. Soil layers include 0–10 (a), 10–40 (b), 40–70 (c), 70–100 cm (d) depth layers. $H_i > 0$ indicates the *Populus euphratica* Olivier roots release water into the soil. The dashed line in the figure is the SWP threshold (WPT) in the i^{th} layer, which represents the marginal SWP point of plant roots releasing water into its adjacent soils. 100–150 cm soil layer no present here as it is the water resource

Table 1. Variation in the total amount of water released of hydraulic lift – HL (H_T ; cm·m⁻²·d⁻¹) during plant growing season

Soil layer depth (cm)	Total amount of released water of HL in i^{th} layer at night		
	June	August	October
0–10	0.047 ± 0.001	–	–
10–40	0.004 ± 0.001	0.012 ± 0.001	–
40–70	–	0.003 ± 0.002	–
70–100	0.002 ± 0.000	–	0.008 ± 0.001
Total	0.053 ± 0.001	0.012 ± 0.004	0.008 ± 0.001

H_T was stimulated by Ryel model and equals the sum of the amount of release water from the five soil layers. Growing season includes early, middle and late stages, which refer to June, August and October, respectively. Soil layers include 0–10, 10–40, 40–70, 70–100 and 100–150 cm depth. Values in table are the mean stimulation results of two days in a given layer. “–” indicates the i^{th} soil layer no obtain water from *Populus euphratica* Olivier roots into at night. 100–150 cm soil layer no present here as it is the water resource

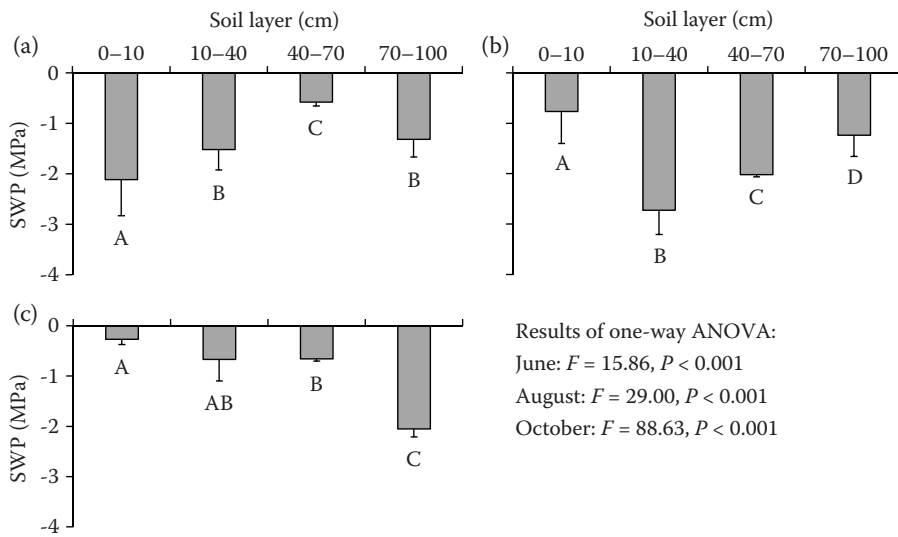


Fig. 2. Variation in soil water potential (SWP) among soil layers across the plant growing season. Growing seasons include early, middle and late stages, which refers to June (a), August (b), October (c), respectively. Soil layers include 0–10, 10–40, 40–70 and 70–100 cm depth layers. Different capital letters in each column indicate significant differences among soil layers ($P < 0.05$), whereas the same letters show no difference ($P > 0.05$). There is no 100–150 cm soil layer as it is the water resource

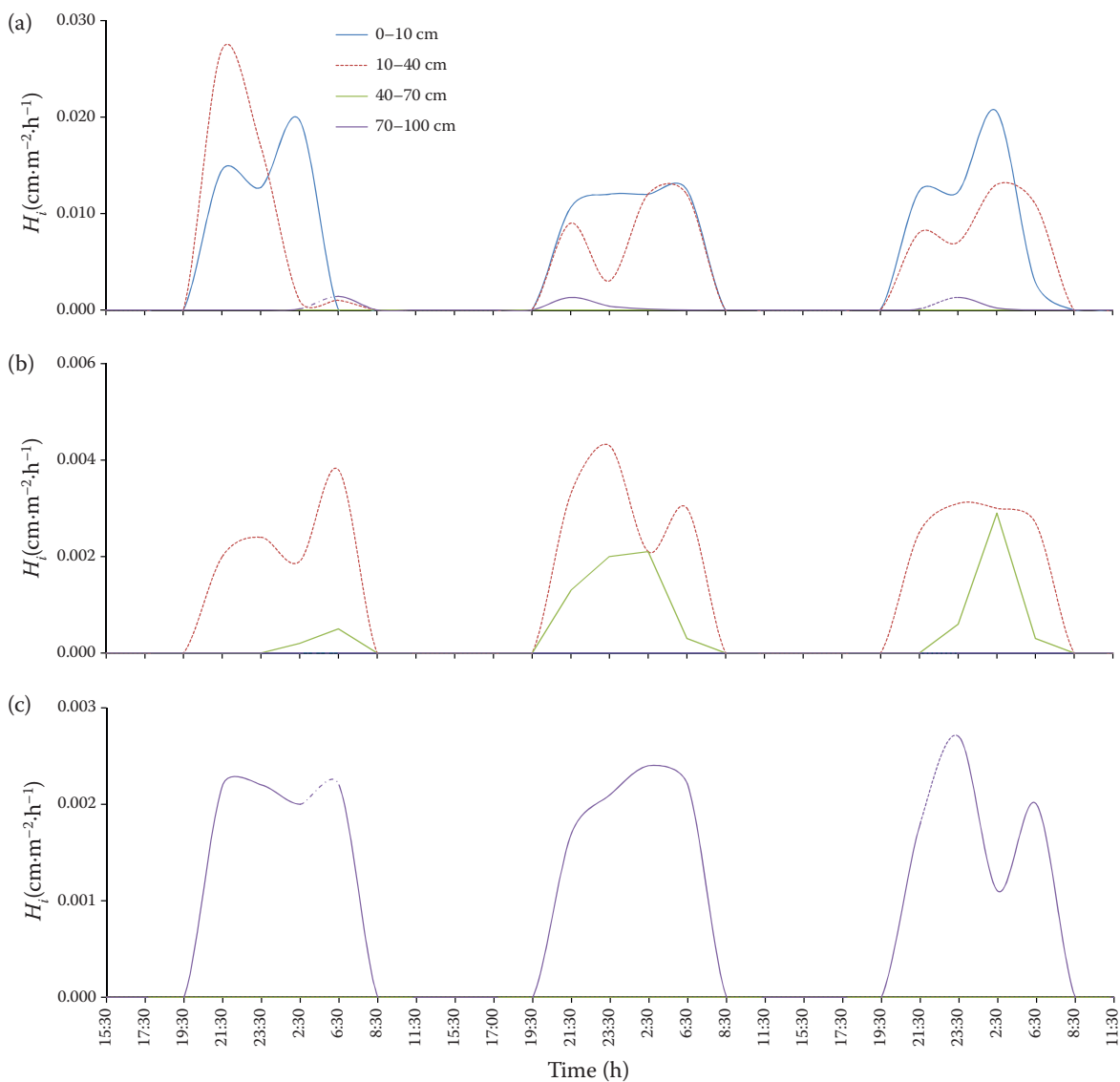


Fig. 3. Variation in the amount of release water of hydraulic lift per hour in i^{th} layer (H_i) among soil layers across plant growing season. H_i is computed by Ryel model simulation. $H_i > 0$ indicates that *Populus euphratica* Olivier roots release water into the soil. Growing seasons include early, middle and late stages, which refer to June (a), August (b), October (c), respectively. Soil layers include 0–10, 10–40, 40–70 and 70–100 cm depth layers. Data for 100–150 cm soil layer is not present here as it is the water resource

Table 2. Difference in soil volumetric water contents (%) between experimental and control plots across plant growing season

Soil layer depth (cm)	Growing season														
	June				August				October						
	experimental	control	F	t	P	experimental	control	F	t	P	experimental	control	F	t	P
0-10	0.157 ± 0.007	0.014 ± 0.003	16.90	19.06	0.000	0.086 ± 0.001	0.042 ± 0.002	13.73	17.24	0.000	0.028 ± 0.002	0.030 ± 0.003	1.27	-0.98	0.15
10-40	0.223 ± 0.003	0.160 ± 0.004	2.00	11.95	0.000	0.296 ± 0.001	0.189 ± 0.001	1.620	220.74	0.000	0.140 ± 0.006	0.182 ± 0.000	3.78	-7.10	0.000
40-70	0.357 ± 0.001	0.282 ± 0.001	7.19	536.32	0.000	0.202 ± 0.000	0.128 ± 0.001	9.50	127.94	0.000	0.175 ± 0.000	0.247 ± 0.006	7.69	-11.24	0.000
70-100	0.180 ± 0.000	0.172 ± 0.002	3.77	3.88	0.000	0.230 ± 0.000	0.213 ± 0.000	2.47	70.75	0.000	0.170 ± 0.000	0.216 ± 0.000	3.34	-346.31	0.000
100-150	0.297 ± 0.001	0.154 ± 0.001	3.34	1,074.72	0.000	0.176 ± 0.000	0.120 ± 0.000	497.78	451.80	0.000	0.194 ± 0.000	0.200 ± 0.000	1.26	-26.68	0.000

Soils are divided into 0-10, 10-40, 40-70, 70-100 and 100-150 cm depth layers based on the distributions of *Populus euphratica* Olivier roots and groundwater level. Plant growing season includes early, middle and late stages, which refers to June, August and October, respectively. Experimental plot refers to the place with growing *P. euphratica*, whereas the control plot no grows *P. euphratica*. The values in the table show the mean ± standard error of three continuous recording days (recording interval was 30 min) in consistent with Ryel modeling period

est SWP soil layer was 0-10, 10-40 and 70-100 cm in June, August and October, respectively (Fig. 2). SLOW appeared in 0-10, 10-40 and 40-70 cm in June, 10-40 and 40-70 cm in August, and 70 to 100 cm in October, respectively (Fig. 3). Comprehensively, SLOW and the lowest SWP soil layer shifted from shallow to deep soil layers across the growing season (Figs 2 and 3).

Soil volumetric water contents were significantly higher in the experimental than those in control plots in all soil layers in June and August ($P < 0.01$), whereas all layers in experimental were significantly lower than those in control plots in October ($P < 0.01$) (Table 2). In experimental plots, fine root biomass in 0-10 and 10-40 cm soil layers decreased during growing period, whereas no changes were observed in 70-100 and 100-150 cm soil layers. Besides, fine root biomass in 40-70 cm soil layer increased in early and middle stage, and decreased in the middle and late stages of the growing season (Fig. 4). The maximum of fine root biomass in 40-70 cm soil layer existed in August (Fig. 4).

DISCUSSION

The relationship between RWP and SWP led to the differences in SWP thresholds among soil layers

In this study our results demonstrated SWP thresholds differed among soil layers in the arid desert region, suggesting the presence of HL was the result of the comprehensive effects of plant roots adaptation and drought stress. SWP threshold referred to the marginal level at which of plant roots releasing water into its adjacent soils in HL. It was believed that the magnitude of SWP threshold was mainly determined by the relative potential differences between RWP and SWP (CALDWELL et al. 1998; HORTON, HART 1998; BROOKS et al. 2006; SCHOLZ et al. 2008). Due to the difference in response of varieties on soil depth between RWP and SWP, SWP threshold of HL would change among soil layers. Specifically, within the process of water transportation from soil to stem and leaves, RWP decreased with increasing of vertical distance of water transportation (ZIMMERMANN 1984). This phenomenon caused high water potential for deep roots, while the low water potential for shallow roots (KRAMER, BOYER 1995; HORTON, HART 1998; YANG, LÜ 2011; YU et al. 2013). In contrary, SWP has no obvious corresponding relationship with soil depth induced by the influence of fine root

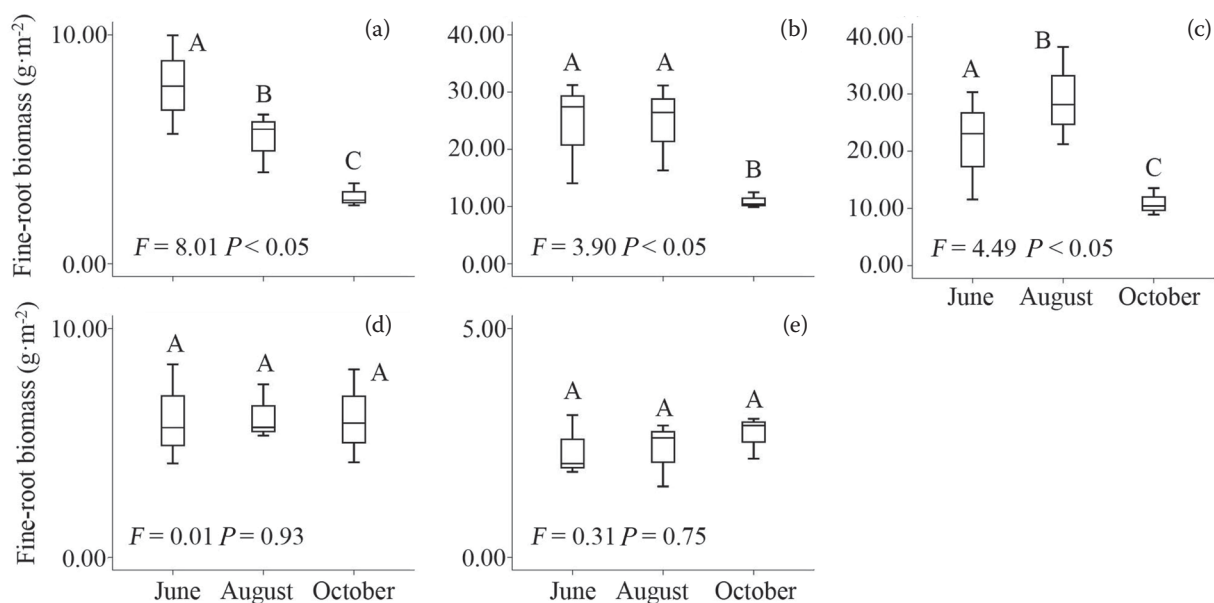


Fig. 4. Variation in fine root biomass among soil layers in the experimental plots across plant growing season. Plant growing seasons include early, middle and late stages, which refers to June, August and October, respectively. Soil layers include 0–10 (a), 10–40 (b), 40–70 (c), 70–100 (d), 100–150 cm (e) depth layers. Different capital letters in each subplot indicate significant differences among stages of growing season ($P < 0.05$), whereas the same letters show no difference ($P > 0.05$). F - and P -values are the results of one-way ANOVA for the variability of fine root biomass induced by growing season. Values are shown as mean \pm standard error

distribution (McELRONE et al. 2007; ESPELETA et al. 2014). The variations in groundwater level, soil water, salt and nutrient contents caused the unequal distribution of fine roots among soil layers, and changed the demand-supply relation in water between plant roots and soils (BURGESS et al. 1998; BAUERLE et al. 2008; HAO 2009). Thus, SWP has no inconsistent reduction with an increase of soil depths (ISHIKAWA, BLEDSOE 2000; ESPELETA et al. 2014; PRIETO et al. 2014; PRIETO, RYEL 2014). The relative potential differences between RWP and their adjacent SWP might differ among soil layers, and subsequently resulting in SWP thresholds differed among soil layers.

Fluctuations in fine roots distribution, water and mineral requirements drive the variations in SLOW and H_T across the growing season

In the present study, our results showed that 0–10, 10–40 and 70–100 cm soil layers were the soil layers with the lowest water potential in June, August and October, respectively), which consequently gained water from *P. euphratica* roots. This result confirmed the previous speculation that soil layer with the lowest water potential was the SLOW of HL (CALDWELL et al. 1998; PRIETO et al. 2012; YU et al. 2013; YANG et al. 2014). This

is because the presence of HL in a given soil layer was determined by the water potential difference between plants roots and their adjacent soils (CALDWELL et al. 1998; PRIETO et al. 2012). Due to the absence of transpiration, the water potential in the root system was basically a constant, roughly equalling to the water potential of deep soils during the presence of HL at night (PHILLIPS et al. 2002; WILLIAMS, ARAUJO 2002). On the contrary, SWP differed among soil layers at night in the arid desert regions due to the influence of the uneven distribution of water resource and roots (SHEIN, PACHEPSKY 1995; TIERNEY et al. 2003). In this case, the water potential difference between the plant roots and its adjacent soils may be different among the soil layers. Traditional physiological theories demonstrated that water transportation across plant stem, between roots and soils, and among soil layers were determined by water potential gradient (ZIMMERMANN 1984; RICHARDS, CALDWELL 1987; KRAMER, BOYER 1995). Water always transported from the high to the low potential places (ZIMMERMANN 1984; KRAMER, BOYER 1995). Thus, plant roots preferentially lifted water via stem to release water into soil layer with the lowest water potential in HL (CALDWELL et al. 1998; ARMAS et al. 2010; PRIETO et al. 2014).

In this study, our results showed that H_T decreased, as well as the lowest SWP soil layer shifted

from shallow to deeper soil layers across the growing season. These suggested that a trade-off between water release amounts of HL and the energy consumption of aquaporin might appear in the presence of HL (ORIAN, SOLBRIG 1977). Transpiration was considered as the main energy source for water absorption from soils to plant roots, as well as for water transportation across plant as no energy required (ZIMMERMANN 1984; KRAMER, BOYER 1995). However, in some particular cases, it was reported that energy-consuming aquaporin's might play an important role in water transportation between roots and their adjacent soils (PRIETO et al. 2012; JOHNSON et al. 2014). Specifically, plants spent their energy on active transport of water when they suffered from the extreme environment, e.g. the storage water in plants was insufficient to meet their metabolic activities, or plants urgently needed to lift water from groundwater into shallow soils via plant stems to absorb minerals (MCELDRONE et al. 2007; PRIETO et al. 2012; JOHNSON et al. 2014). Within the HL process, it may be not enough water potential difference to lift water from deep soil layers or groundwater to shallow soil layers due to transpiration shutoff at night (PRIETO et al. 2012). The fluctuations in fine roots distribution, plant requirements in water and minerals might determine the changes in HL across plant growing season (SCHOLZ et al. 2008; PRIETO et al. 2012; ESPELETA et al. 2014). It was reported minerals and water mainly stored in shallow and deep soil layers in the arid desert region, respectively (KRAMER, BOYER 1995; HORTON, HART 1998; YANG, LÜ 2011; YU et al. 2013). In the early stage of plant growing season (i.e. June), due to plant owning higher demand in minerals, *P. euphratica* develop numerous fine roots in shallow soil layers to absorb minerals (SHEIN, PACHEPSKY 1995; TIERNEY et al. 2003; CHENG et al. 2009). This might increase the water potential difference between fine roots and their adjacent soils, and subsequently, result in the lowest SWP soil layer appearing in shallow layers. Therefore, *P. euphratica* might spend more energy to lift much amount of water from deep into shallow soil layers. August was the middle stage of growing season in the arid desert region, the requirements in minerals in this period was lower than that in an early stage, whereas the water requirement was opposite (SARDANS, PEÑUELAS 2014). Thus, *P. euphratica* might spend little energy to lift water in minerals absorption, whereas in turn shift fine roots distribution from shallow to deep layers to obtain water. In this case, the lowest SWP soil layer and SLOW would appear

in the middle soil layers, as well as H_T was lower in August than that in June. In October, the requirements in water and minerals were usually less than those in middle and early stages (YANG et al. 2014), in order to absorb little minerals and water and to save energy consumption, plant fine roots would transfer to the deeper soil layers. The lowest SWP and SLOW appeared in 70–100 cm soil layer, and decreased H_T to the minimum.

In this study, fine root biomass of 0–10 and 10 to 40 cm soil layers decreased across plant growing season, whereas no changes were observed for 70 to 100 and 100–150 cm soil layers in the experimental plots. This also can prove the above underlying hypothesis about the trade-off between HL and energy consumption, indicating that the requirements in water and minerals changed the distribution pattern of fine root biomass. Besides, the change in soil volumetric water content between experimental and control plots can also indicate the changes in the SLOW and H_T were determined by the fluctuations in water and mineral requirements. In early and middle stages of plant growing season, SLOW appeared in shallow soil layers in order to meet the minerals and water requirements. This would improve soil volumetric water content in experimental plots, and in turn, led to the higher soil volumetric water content in all soil layers of experimental than these of control plots. In October, SLOW appeared in deep soil layers are due to the reduction in requirements of water and minerals. The shallow soil layers no longer obtained water from roots, whereas the small amount of survival fine roots continued to absorb water in experimental plots (YANG et al. 2014). In addition, owing to the higher plant abundance in experimental than that in control plots, the utilized soil water of plants was lower in shallow soil layers of control than that of experimental plots. Hence, soil volumetric water contents in shallow layers in experimental was lower than that in control plots, whereas deep soil layers were opposite. In this study, although fine root biomass and soil volumetric water content were used to indirectly prove a trade-off between water release amounts of HL and the energy consumption might appear in the presence of HL. However, the direct index of plant requirements in water and minerals such as transpiration consumption and mineral accumulations did not measure in this process and as consequence influence the expansion of our results. In order to deeply understand the mechanism of HL, additional studies and reasonable experiments are needed to conduct this underlying trade-off in future works.

CONCLUSIONS

This study demonstrates that SWP thresholds of HL differed among soil layers in the arid desert region, suggesting the presence of HL was the result of the comprehensive effects of plant roots adaptation and drought stress. The SLOW of *P. euphratica* HL shifted from shallow to deep soil layers across growing season. H_T decreased across the growing season. These mechanisms indicate that the presence of *P. euphratica* HL was determined by the difference in water potential among soil layers. The fluctuations in fine roots distribution, the plant requirements in water and minerals might cause the variance of HL across plant growing season. In addition, SLOW always appeared in the lowest SWP soil layer, and hence following a common perception in water physiology that water always transports from the high to the low potential positions. This study would be helpful to understand the ecological adaptability of the plant to extreme drought environment in the arid desert region.

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