ANNALS OF
BOTANY
Founded 1887

Populus euphratica counteracts drought stress through the dew coupling and root hydraulic redistribution processes

Xue Fan[1,2,3], Xingming Hao[1,3,*], Sen Zhang[1,2,3], Zhuoyi Zhao[1,2,3], Jingjing Zhang[1,2,3] and Yuanhang Li[4]

[1]State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China, [2]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China, [3]Akesu National Station of Observation and Research for Oasis Agro-ecosystem, Akesu 843017, Xinjiang, China and [4]College of Life Sciences, Xinjiang Normal University, Urumqi 830054, China
[*]For correspondence. E-mail 2503096121@qq.com

• **Background** In arid and semi-arid areas, plants can directly absorb and use dew through their leaves, and some plants have the ability for hydraulic redistribution of their roots. Therefore, in arid areas, plants may redistribute dew to the soil, using the soil as a reservoir for short-term dry seasons, i.e. dew may participate in the hydraulic redistribution process of plants. This process plays an important role in plant survival and community stability.
• **Methods** To verify this hypothesis, we investigated the water use mechanism of *Populus euphratica* through a comprehensive observation of sap flow, water potential and soil water content using a heavy water tracer experiment under *in situ* field conditions.
• **Results and Discussion** Dewdrops contributed 28.3 % of soil moisture near the roots, and applying dew on leaves for several days significantly improved soil moisture status. Hydraulic redistribution in the roots mainly occurred from 2200 h at night to 800 h the following day and mainly occurred in the 20- to 80-cm soil layer. Water storage in the trunk is the intermediate link in the coupling process of foliar water uptake and hydraulic redistribution; water storage in the trunk is mainly replenished from May to July and consumed throughout the rest of the year. In conclusion, dew redistributes water into soil through the coupling process of foliar water uptake and hydraulic redistribution. *Populus euphratica* uses the trunk and soil for water storage to cope with water stress during short-term drought periods. Our findings provide a scientific basis for the restoration of different species in water-deficient areas, which is conducive to maintaining vegetation ecosystem stability in areas of desertification and improving the soil water balance.

Key words: *Populus euphratica*, foliar water uptake, hydraulic redistribution, dew.

INTRODUCTION

Burgess *et al.* first confirmed the downward transmission of water in roots in 1998 and defined the regulation of soil water by roots as 'hydraulic redistribution' (HR) (Burgess *et al.*, 1998). Ever since the concept was put forward, it has been widely considered in studies on plant water use (Alagele *et al.*, 2021; Gerjets *et al.*, 2021). Hydraulic redistribution can improve the drought resistance of temperate forests and is an important factor for forest growth and stability (Töchterle *et al.*, 2020; Hafner *et al.*, 2021). It helps plants absorb water in tropical rainforests and contributes to their growth and development (Eller *et al.*, 2016). In arid areas, plants make up for soil moisture deficiency through HR (Hill *et al.*, 2021). Studies have shown that the root water redistribution process has multiple manifestations, including HR of fog water (FHR), hydraulic lift, hydraulic descent, lateral redistribution and tissue dehydration (Richards and Caldwell, 1987; Burgess and Dawson, 2004). FHR refers to the process wherein fog water or dew absorbed by leaves is transported to the dry root–soil interface through the trunk and root xylem, and this process mostly occurs at night when precipitation and air humidity are high (Burgess and Dawson, 2004; Zhang *et al.*, 2019).

Some studies have shown that FHR can reverse the sap flow from the trunk and roots, and the water absorbed by leaves can be transported through the trunk to the soil near the root system, improving the plant's water status (Eller *et al.*, 2013; Cassana *et al.*, 2016). FHR is a significant factor affecting plant water storage; it can effectively alleviate water deficits, prolong water availability and the growing periods of plants with deeper roots, maintain the physiological activity of plant tissues and improve the soil water content of neighbouring plants, and plays a key role in promoting plant growth (Huang *et al.*, 2017; Gerjets *et al.*, 2021). However, it is difficult to simulate falling dew and collect samples from trees *in situ*, and most of these studies observed the response mechanism of seedlings to dew by transplanting them into flowerpots; besides, most trees growing in flowerpots are young and have limited growth conditions (limited root depth, low nutrient utilization rate, fixed irrigation sequence) (Gerjets *et al.*, 2021; Liu *et al.*, 2021). Further, at short distances, the moisture content of the moist and dry parts of the soil varies greatly, and soil conditions are extreme (Gerjets *et al.*, 2021). Therefore, the response of plants grown *in situ* to precipitation should be further studied. There are several ways to determine whether

FHR has occurred, such as sap flow observation (Burgess *et al.*, 2000), apoplastic tracer experiments and gravimetric analysis (Limm *et al.*, 2009; Eller *et al.*, 2013). However, as these methods cannot accurately quantify the contribution rate of FHR, many studies have combined stable isotope labelling experiments with these methods for quantitative research (Eller *et al.*, 2013; Zhang *et al.*, 2019). Therefore, studies on the effect of plant FHR under natural field conditions require comprehensive observations of plant sap flow, the water potential of the soil–plant–atmosphere continuum (SPAC) and soil moisture, and these observations should be combined with isotope tracer experiments.

A prerequisite for the FHR process is foliar water uptake (FWU). Studies have shown that in tropical and temperate forests, as well as in semi-arid and sub-humid regions, trees can absorb dew through their leaves (Eller *et al.*, 2013; Berry *et al.*, 2019; Liu *et al.*, 2021; Tianshi and Chau, 2022). In extreme arid areas, the leaves of *Populus euphratica* seedlings can also absorb condensed water directly to cope with short-term droughts and soil water stress (Zhang *et al.*, 2019). In addition, significant root HR was observed in *P. euphratica* growing under extreme drought conditions (Hao *et al.*, 2013). Therefore, this species is likely to absorb dew and redistribute water from the roots at the same time. However, there is still no direct evidence to support this hypothesis. This study was based on an *in situ* experiment and aimed to: (1) reveal whether *P. euphratica* can directly absorb dew and redistribute it under *in situ* conditions; this was studied by comprehensive observation and a controlled experiment; and (2) describe the dynamic relationships among root HR, dew absorption and trunk water storage processes. We expect our results to help us better understand the water-use mechanism of trees in arid areas and provide a scientific basis for the formulation of restoration measures in degraded riparian forest ecosystems.

MATERIALS AND METHODS

Experimental design

The experiments and observational studies were carried out at the Akesu National Station of Observation and Research for Oasis Agro-ecosystem, Chinese Academy of Sciences (80°51′E, 40°37′N). The station is located in the upper reaches of the Tarim River, where the climate is warm temperate continental arid and solar radiation is high (total annual solar radiation 6000 MJ m^2). The average annual temperature is 11.84 °C. Evaporation is intense and precipitation is scarce; the annual potential evaporation is 2300–3000 mm and annual average precipitation is 45.7 mm. There are various types of soil in the lower reaches of the Tarim River, including *Populus euphratica* forest soil, meadow soil, new soil, saline soil and Aeolian soil. The soil texture is mainly silty loam soil, and groundwater depth is mostly <8 m, but even <12 m in some sections. The natural vegetation in this area mainly includes *P. euphratica*, *Tamarix ramosissima*, *Halimodendron halodendron*, *Alhagi sparsifolia* and *Phragmites communis* (Zhu *et al.*, 2021). This vegetation forms the ecological corridor of the Tarim River basin, and plays an important role as a windbreak, in sand-fixation and in maintaining the balance of ecosystems in this arid area.

Based on the field investigation, we selected two *P. euphratica* trees with a spacing of 4–5 m as standard trees A and B [standard tree A: diameter at breast height (DBH) 40 cm, height 10.3 m; standard tree B: DBH 32.6 cm, height 8 m]. The observations and experiment were carried out as follows: (1) from 1 October 2020 continuous monitoring of *P. euphratica* sap flow was carried out; based on these results, the change characteristics of *P. euphratica* sap flow were analysed; (2) from 1 May 2021 to 31 December 2021 continuous monitoring of the volumetric water content of *P. euphratica* roots was carried out to compare the changes in soil volumetric water content near the roots in different soil layers; (3) from 7 July 7 2021 to 6 August 2021 the water potential of *P. euphratica* roots and leaves was determined, and a stable isotope tracer experiment simulating dew transport was carried out simultaneously. Soil and water samples were analysed from 17 July 2021 to 17 August 2021.

Isotope tracer experiment with dew

From 8 July 2021, two *P. euphratica* trees under sap flow observation were selected as the sample trees. In order to eliminate interference from rainfall and dew under natural conditions, steel shelters were established for each of the two sample trees. Transparent polyethylene film was spread above and around the steel structure canopy, and a spraying system was set up in the direction of *P. euphratica* canopy growth. At night, the canopy was completely closed with this film and during the day it was opened around the canopy in order to ventilate it to mimic the external environmental conditions of the canopy. Soil irrigation was stopped for 1 week prior to the dew treatment, and the soil was covered with tarpaulins and isolated from the outer environment to prevent water from entering it (Fig. 1A–C).

Tagged water ($\delta D = 795.8 \pm 4.7‰$) was prepared using heavy ($\delta D = 99.9$ %) and distilled water ($\delta D = -54‰$) at a volume ratio of 1:15 000. At 0500 h every day, the configured tracer water was transported to the top of the *P. euphratica* canopy through the spray system, and dew-marked water was automatically, continuously and unidirectionally sprayed onto the *P. euphratica* canopy. Before each traced water treatment, soil samples from the *P. euphratica* root soil layers of 0–20, 20–40, 40–60, 60–80 and 80–100 cm were collected with a soil drill at 2100 h on the previous day, and each layer was sampled three times. Immediately after sampling, the soil samples were sealed and stored at −20 °C in a self-sealing bag in a refrigerator to prevent isotopic fractionation caused by water evaporation.

Populus euphratica soil water was extracted into a small test tube with a low-temperature vacuum extraction device. The heating temperature of low-temperature vacuum extraction was set to 95 °C, and the soil sample was extracted for 100 min. After extraction, it was sealed and stored in a 2-mL glass bottle at a low temperature (4 °C), and the content of soil water was determined using a Los Gatos Research liquid water isotope instrument (LGR, DLT-100, USA). The δD value was determined using the following equations (Phillips, 2001):

$$\delta \text{ D } () = [(R_{sample}/R_{standard}) - 1] \times 1000$$

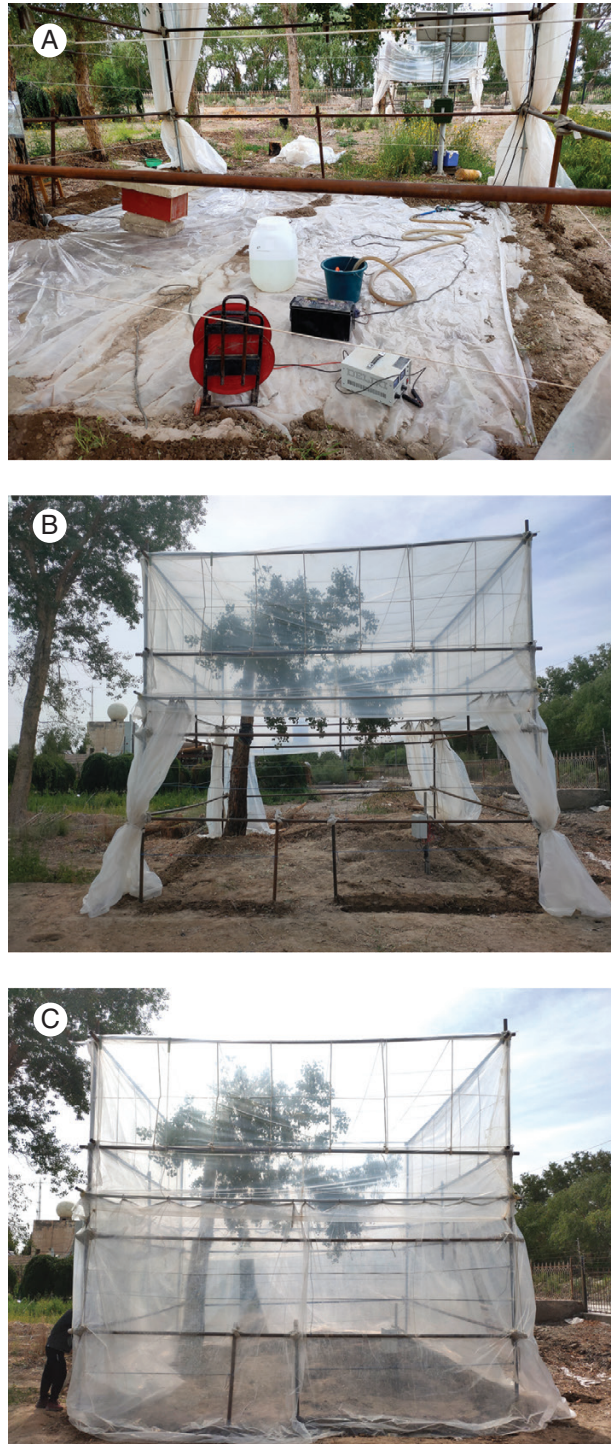$$\delta^{18}O () = [(R_{sample}/R_{standard}) - 1] \times 1000$$

FIG. 1. Layout of control experiment. (A) Internal arrangement of the two sample trees' canopies. (B) and (C) Arrangement with the canopies opened and closed.

where R_{sample} denotes the hydrogen and oxygen isotope values of corresponding samples, and $R_{standard}$ denotes the hydrogen and oxygen isotope values of International Standard Seawater samples. The ratios of heavy to light isotope abundances of elements in samples and international standard seawater D/H

are δD and $\delta^{18}O$. The measurement precision for $^{18}O/^{16}O$ was >0.1 ‰ and that for D/H was >0.3 ‰. The measurement error for δD was <1 ‰ and that for $\delta^{18}O$ was <0.2 ‰. The contribution rate of the dew to *P. euphratica* root soil was calculated according to the isotope mixing model (Phillips, 2001):

$$\delta_t = f_A \times \delta_A + (1 - f_A) \times \delta_B$$

where δt denotes the δD values of the soil water around *P. euphratica* roots, δA and δB denote the δD values of dew source A and irrigation water source B, respectively, and f_A is the utilization ratio of dew source A, which was calculated as follows (Zhang *et al.*, 2019):

$$f_A = \frac{\delta_t - \delta_B}{\delta_A - \delta_B} \qquad (4)$$

The absorption of canopy dew by *P. euphratica* was analysed by isotope tracing.

Measurement of volumetric water content

From 14 June 2021 to 14 October 2021 the volumetric water content of *P. euphratica* root soil was measured using the SM-300 soil moisture sensor (Delta-T, UK; measurement range 0–1 m³ m⁻³; measurement accuracy 0.025 m³ m⁻³). On 14 June 2021 the soil moisture sensor was calibrated indoors. Then, the root soil of two *P. euphratica* trees was divided into layers of 0–20, 20–40, 40–60, 60–80, 80–100, 100–150 and 150–200 cm, and soil moisture sensors were buried in each layer. The sensors were connected to two CR 1000 data acquisition boxes (Campbell Scientific, United States). The sensors were used to measure the soil volumetric water content quickly and in real time to explore the influence of soil volumetric water content difference on the water redistribution of *P. euphratica*.

Measurement of canopy and root water potential

From 8 July 2021 to 12 September 2021, three intact fine root samples were collected daily at 0030, 0830 and 1630 h in a 1-m profile of *P. euphratica* root soil, while three healthy leaves from the upper part of the canopy were collected on the sunny side of the sample trees and sealed in polyethylene bags immediately after collection was completed. The samples were brought back to the laboratory for determination within 3 min after collection was completed.

Root (ψ, MPa) and leaf (ψ, MPa) water potentials were measured with a 3115 portable pressure chamber water potential tester (SEC, USA). The measuring range of the water potential tester was 0–10 MPa and its accuracy was 0.01 MPa. The blades and roots were wrapped with wet gauze to prevent water loss and placed in the pressure chamber of the water potential tester. Then, the cover was tightened and pressurized with nitrogen at the speed of 0.02–0.05 MPa s⁻¹ until sap started flowing from the incision of the blade or root. After this, the pressure was immediately reduced by 0.15–0.20 MPa, and it was increased again until sap started flowing again from the incision; then, the water potential was read and recorded. The leaf and root water potentials of *P. euphratica* were continuously monitored, and the trunk water transport was analysed.

Measurement of sap flow

Trunk water storage is the main reason for the difference in sap flow rates between different parts of the trunk. Based on the assumption that the daily cumulative value of the crown and trunk base sap flow is equal every day, when the value obtained by subtracting the trunk base sap flow from the crown base sap flow was positive, water was being pumped from the trunk between the crown base and trunk base (Maherali and DeLucia, 2001).

Therefore, the change in the amount of water stored in the trunk can be determined by comparing the difference in the sap flow flux between the crown and trunk base. In the present study, sapwood (R_1) and heartwood radiuses (R_2) were determined by a growth cone. A set of sapwood trunk sap flow probes (TDP) using Granier thermal diffusion was installed at the crown and trunk base of each sample tree (Granier *et al.*, 1996). The probe was inserted, and clay was smeared over and around it to form a waterproof seal. A 1/4 spherical foam was installed and fixed on both sides of the probe to increase the adiabatic effect around it. Reflective foam aluminium film was used to wrap the trees, foam balls and TDP installation parts to form shading, sealed by tape, and prevent moisture from reaching the sensor along the tree trunk. The PC400 measurement program was started and connected to the data collector CR1000. From October 2020 to October 2021, the sap flow was measured every 1 min and the data were recorded every 15 min. The measured sample tree data were processed; the daily dt_M was calculated using the measured dt value every 15 min, and the dimensionless sap flow index K was introduced to calculate the sap flow rate V (cm s^{-1}). The equations used were as follows (Granier *et al.*, 1996):

$$K = (dt_M - dt)/dt$$

$$V = 0.0119 \times K^{1.231}$$

Sapwood area *SA* (cm^2) was calculated from sapwood (R_1) and heartwood radiuses (R_2) of the trees (Granier *et al.*, 1996):

$$SA = \pi(R_1{}^2 - R_2{}^2)$$

Sap flow flux F (g h^{-1}) was calculated as follows (Granier *et al.*, 1996):

$$F = SA \times V \times 3600$$

The change in sap flow flux of *P. euphratica* was analysed according to the sap flow flux of the trunk and crown bases.

Data analysis

The volume water content and sap flow data were sorted and analysed using Loggernet 4.6 and Excel software. In SPSS 26.0 software, ANOVA was used to analyse whether the difference in stable isotopes in the soil water of *P. euphratica* root before and after the dew treatment was significant (the significance level was 0.05, and an extremely significant difference was determined at 0.01). Origin 2019b software was used to draw charts.

RESULTS

Impact of dew on soil moisture

Results of the isotope tracing experiment showed that after dew labelled with stable isotope deuterium was sprayed on the canopy of *P. euphrati*ca, the value of δD in the 0–100 cm soil layer near the roots of *P. euphratica* A showed an increasing trend (Fig. 2A). Significant differences were observed between the soil water content near the roots of *P. euphratica* A 6 d after the labelled water treatment and near the roots of untreated *P. euphratica* A ($P < 0.05$). After 12 d of labelled water treatment, the δD value of soil water in *P. euphratica* A increased to a positive value of 99.62 ‰, which was significantly different compared with the soil water of *P. euphratica* treated with labelled water for 6 d ($P < 0.05$). After 24 d of the labelled water
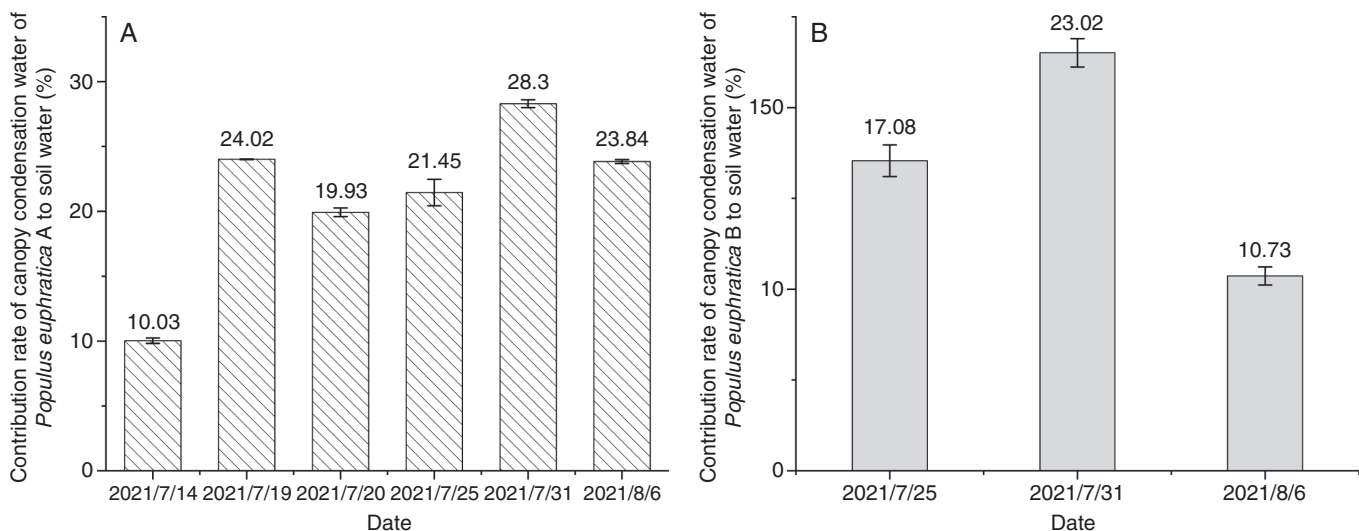

FIG. 2. Value of δD in soil water of *P. euphratica* under condensed water treatment ($n = 3$). Lower-case letters indicate significant differences between treatments at different times ($P < 0.05$).

treatment, the δD value of soil water of *P. euphratica* A reached the maximum value of 138.83 ‰. The δD value of soil water of *P. euphratica* A decreased slightly on 6 August, 6 d after the maximum value was reached, but it was still higher than that on 25 July and was not significantly different from that of soil water of *P. euphratica* A on 19 July. From 19 July, the canopy of *P. euphratica* B was also sprayed with a condensate labelled with stable isotope deuterium, and its soil water δD values also changed significantly (Fig. 2B). After the marked water treatment, the δD value of soil water in *P. euphratica* B increased continuously, reaching a maximum value of 105.73 ‰ on day 12 after the treatment, with a significant difference between the maximum value and the soil water control value ($P < 0.05$). The δD value of soil water in *P. euphratica* B decreased on the 18th day after the condensate treatment (6 August), but it was still higher and significantly different from the control value ($P < 0.05$). According to the analysis of the experimental setup, the only way to replenish heavy water in *P. euphratica* soil is through canopy absorption, transporting water to the trunk and root system, after which the root system releases heavy water to the soil through the water barrier made of polyethylene film, which can indicate water redistribution of canopy dew in *P. euphratica*.

On the sixth day after the dew treatment, the soil water δD value near *P. euphratica* A roots was increasing, and the contribution of dew to soil water near the root of *P. euphratica* A was 10.3 % (Fig. 3A). After 12 d of dew treatment, the contribution of dew to soil water in the vicinity of the root of *P. euphratica* A nearly doubled to 24.02 % compared with that 6 d before. After 24 d of dew treatment, the maximum contribution of dew to soil water reached 28.3 %. After 30 d of dew treatment (on 6 August), the experimental area started to cool down and the leaves started to turn yellow. At this time, the contribution of dew to soil water near the root of *P. euphratica* A decreased to 23.84 %. In general, the contribution of dew to soil water near the root of *P. euphratica* A fluctuated from 10.03 to 28.3 % during the 30 d of dew treatment, but it still showed an increasing trend as dew treatment progressed. For *P. euphratica*

B, the contribution of dew to the soil water increased rapidly to 17.08 % after 6 d of dew treatment (Fig. 3B). After 12 d of dew treatment, it increased to 23.03 %. However, after 18 d of dew treatment (in August) it decreased to 10.73 %. During the 18 d of dew treatment, the maximum value of dew contribution to soil water near the root of *P. euphratica* A occurred after 12 d, and the minimum value occurred after 18 d (August 6). The contribution rate fluctuated from 10.73 to 23.02 %. These findings indicated that continuous spraying of canopy dew significantly improved the soil water status of *P. euphratica*. Besides absorbing dew through leaves, the plants also transported dew through their leaves, trunk and root systems to the soil near the roots and stored it together with soil water, increasing the soil moisture content near the roots and using the soil as a reservoir of underground moisture.

Changes in soil volumetric water content

During July to August, the volumetric moisture content of the 20–40 cm soil layer around *P. euphratica* roots was the highest, at 34.86 %, and that of the 40–60 cm soil layer was the lowest, at 20.64 % (Fig. 4H). In general, the volumetric moisture content of the deeper soil layer (60–150 cm) was higher than that of the surface soil layer (0–20 cm) and the bottom of the observation surface (150–200 cm) (Fig. 4H). The volumetric water content of the 0–20 cm soil layer increased from 1000 to 1830 h during the day and reached a maximum value (24.85 %) at 1830 h. It then decreased from 1830 to 1000 h the next day and remained at a minimum value of 24.66 % from 0830 to 1000 h the next day (Fig. 4A). In contrast, the trend of soil volumetric water content in the 20–40 cm soil layer was the opposite of that in the 0–20 cm soil layer: it increased from 2200 to 0800 h and reached the maximum value of 34.89 % at 0700 and 0800 h (Fig. 4B). The trends of soil volumetric water content in the 40–60 and 60–80 cm soil layers were similar to that in the 20–40 cm soil layer (Fig. 4C, D). In general, the volumetric water content of the 40–60 cm soil layer was replenished from 2000 to 0530 h, while the rest of the day was dominated
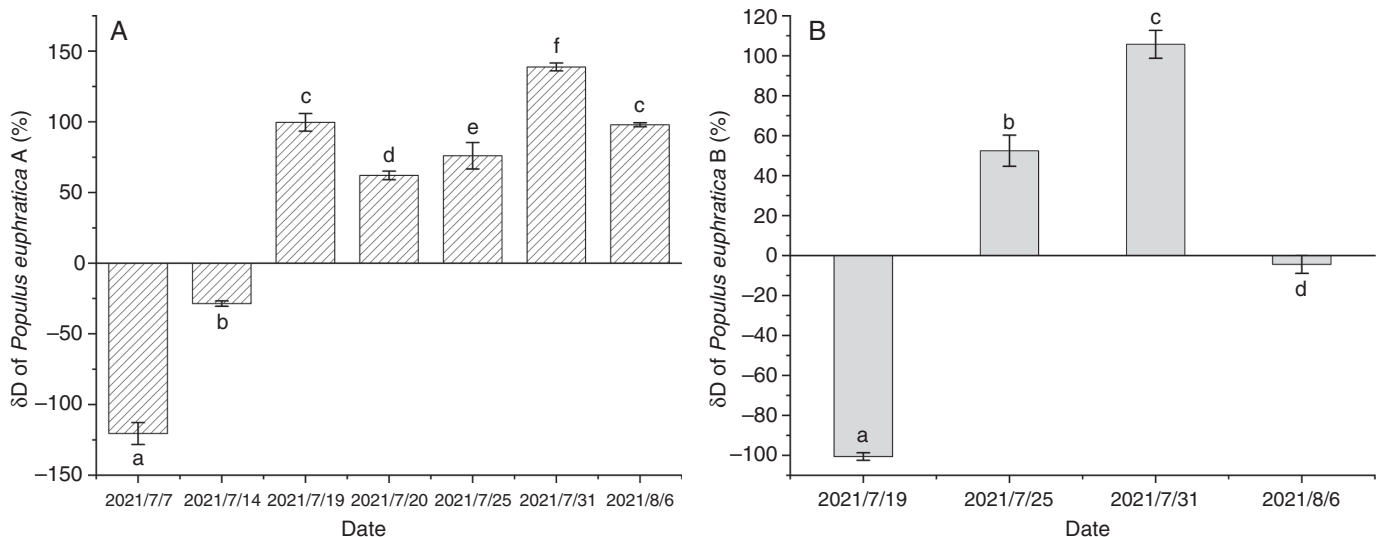

FIG. 3. Contribution of enriched D condensate to the soil water of *P. euphratica* ($n = 3$).
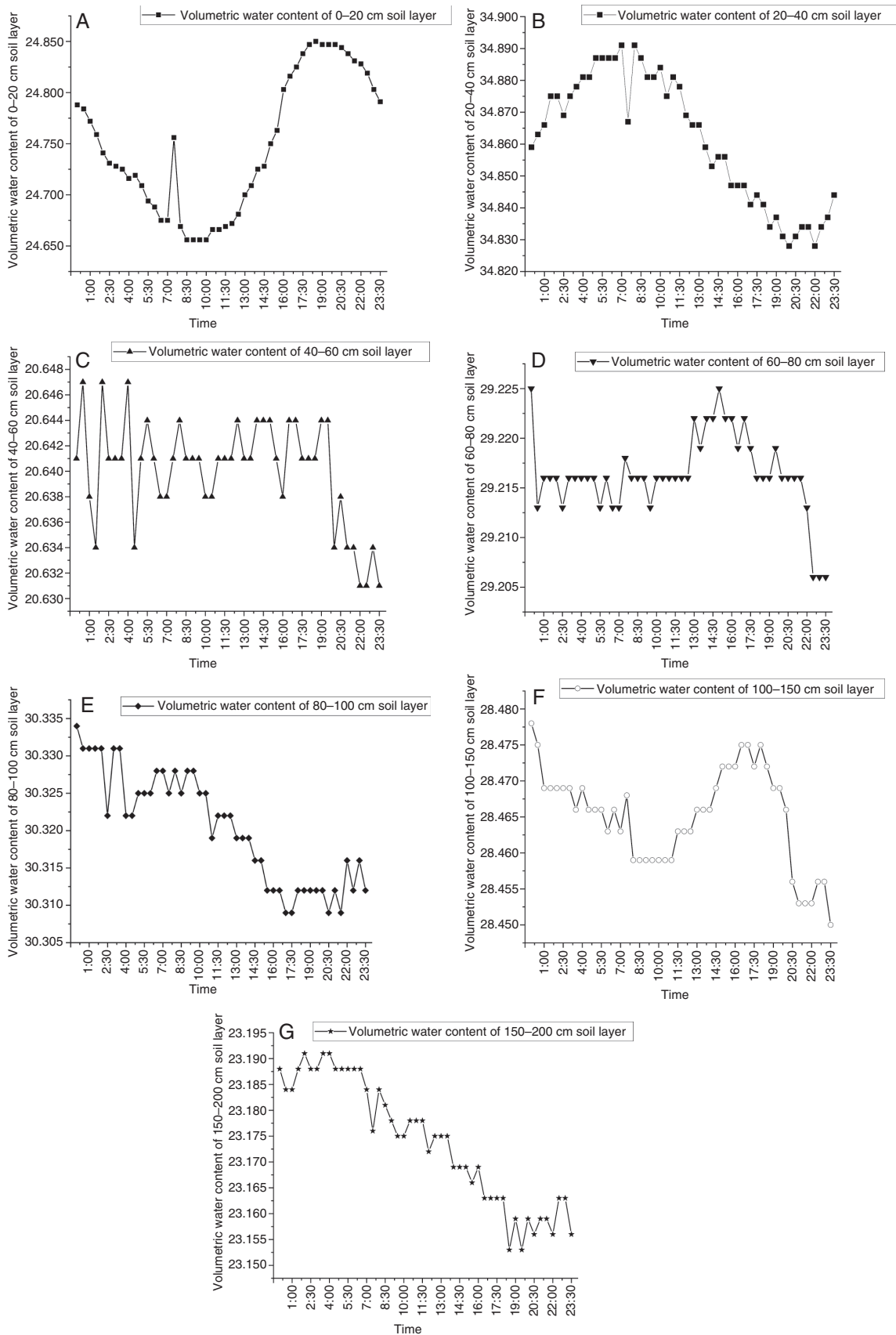
Fig. 4. Change in average daily soil volume water content from 7 July 2021 to 7 August 2021. (A–G) Trend of average daily water content in the 0–20, 20–40, 40–60, 60–80, 80–100, 100–150 and 150–200 cm soil layers, respectively. (H) Proportion of volumetric water content among different soil layers.

by water depletion. However, the volumetric water content of the 60–80 cm soil layer during this period was still higher than the average volumetric water content of the soil from 0830 to 2200 h during the day, indicating that the 60–80 cm soil layer was replenished with water during the night in the period from 2200 to 0830 h. In the 80–100 cm soil layer, the water content varied less during the night, and water replenishment occurred mainly during the daytime (Fig. 4E), as in the 100–150 cm soil layer (Fig. 4F). In the 150–200 cm soil layer, at the bottom of the soil observation surface, the soil volumetric water content generally showed a decreasing trend and was higher at night from 0000 to 0830 h than during the daytime, with an average value of 23.19 %. During the daytime, from 0830 to 0000 h, the soil volumetric water content was lower than during the night, with an average of 23.17 % (Fig. 4G). In general, the volumetric water content of *P. euphratica* roots increased at night from 0030 to 0830 h. During this time, the volumetric water content of the 20–80 and 150–200 cm soil layers increased. In contrast, the volumetric water content of the 0–20, 80–100 and 100–150 cm soil layers decreased at night, increased after 1000 h in the morning, and increased again at 1630 h in the afternoon.

Driver of sap flow

The water potential gradient across the SPAC system drives sap flow transport in plants (Kamakura *et al.*, 2021). In the present study, the water potential of *P. euphratica* A leaves fluctuated from −2.55 to −0.4 MPa, and its root water potential fluctuated from −2.6 to −0.4 MPa (Fig. 5A). The leaf water potential of *P. euphratica* B fluctuated from −3.88 to −0.37 MPa, and its root water potential fluctuated from −3.43 to −0.58 MPa (Fig. 5B). The maximum difference between *P. euphratica* A leaf and root water potential was 2.13 MPa, while in *P. euphratica* B it was 0.4 MPa. Both of these maximum differences occurred at 0030 h at night, when the leaf water potential was greater than the root water potential, and the water in *P. euphratica* had the driving force required for transport from leaves to roots. In the early morning at 0830 h the leaf water potential of *P. euphratica* A and B was still higher than the root water potential, but the difference between them was reduced at this time compared with that at 0030 h. This indicated that at 0830 h, with the increase in light and transpiration, the trunk flow reversal of *P. euphratica* was reduced. By 1630 h, the leaf water potential of the two sample trees was lower than the root water potential, and the water in *P. euphratica* was transported from the roots to the canopy leaves.

The relative change in the sap flow of *P. euphratica* has a certain seasonal pattern (Fig. 6). The monthly average value of trunk base sap flow reached the maximum value of 126.67 kg d^{-1} in May, and that of crown sap flow reached the maximum value of 79.27 kg d^{-1} in June. From May to July, the difference between crown and trunk base sap flow was negative, indicating that *P. euphratica* replenished a large amount of trunk storage water during this period, with a monthly average of 36.41 kg d^{-1}. From August to April, *P. euphratica* canopy leaves were sparse and its canopy sap flow decreased, with a monthly average of 33.18 kg d^{-1}. Except for a short period of trunk water replenishment in January, when *P. euphratica* warmed up, it continuously consumed trunk water to maintain normal life activities, with a monthly average of 14.88 kg d^{-1}.

DISCUSSION

Ecological effects of leaf surface absorption and trunk storage

In the present study, we combined trunk flow monitoring with stable isotope tracing to reveal the existence of FWU and trunk water storage in *P. euphratica* under *in situ* conditions in the field. Previous studies have shown that in arid and semi-arid areas with low soil water content, FWU is useful for many plants, such as *Platycladus orientalis* and *Pinus torreyana* (Liu *et al.*, 2021; Tianshi and Chau, 2022). The FWU of *P. euphratica* is ecologically important, as the rapid uptake of dew on the foliar surface helps maintain the water content in the leaves, promotes plant growth, increases plant survival,
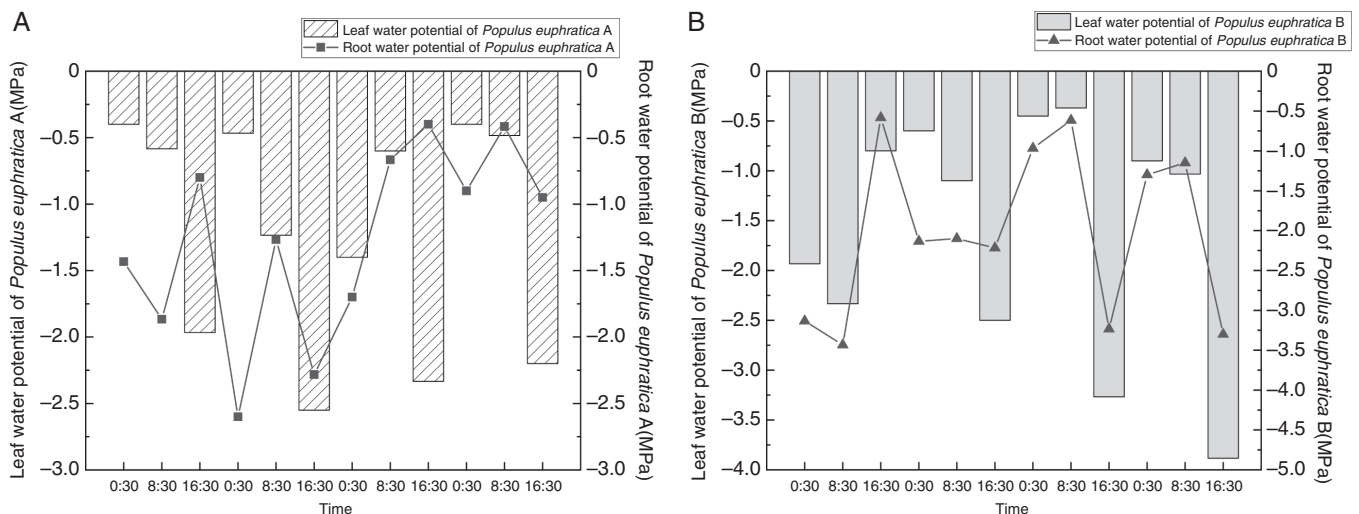

Fig. 5. Diurnal variation in leaf and root water potential of *P. euphratica* from 14 July 2021 to 17 July 2021.
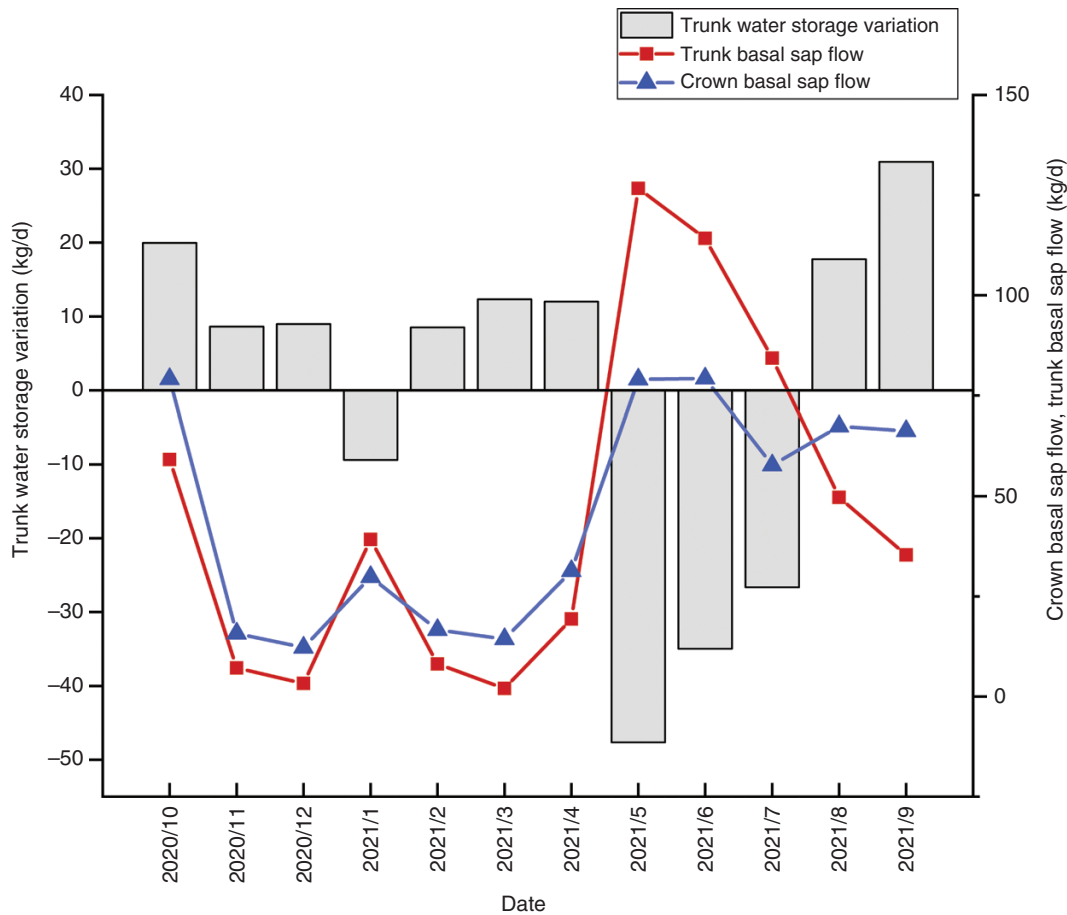
Fig. 6. Average monthly sap flow of *P. euphratica*.

and effectively mitigates the adverse effects of drought stress on plants (Liu *et al.*, 2021; Tianshi and Chau, 2022). The redistribution rate of water absorbed by plant leaves in arid regions is higher than the transport rate of water absorbed by the root system, so the water absorbed by leaves is important for plant growth (Gui *et al.*, 2021). In the California coast redwood ecosystem, 80 % of the dominant species in redwood forests can absorb water through the leaves, increasing the leaf water content by 2–11 %. Although the amount of water absorbed by leaves is relatively small compared with the total amount of water used by plants, the absorbed water can rehydrate plant leaves, increase water potential and contribute to plant development (Limm *et al.*, 2009). Water absorbed by the leaves is usually retained or transported to secondary branches and trunks (Limm *et al.*, 2009). It has been reported that, under precipitation, plants develop a water potential gradient from the leaf surface to the interior parts of the leaves, and passive water uptake occurs on the leaf surface. After water uptake on the leaf surface, reverse sap flow occurs within the tree, and water is transported from the canopy to the trunk; when rainfall continues, the trunk water potential becomes higher than the root water potential, causing the water stored in the trunk to flow towards the roots and soil (Schreel *et al.*, 2019). In the present study, we demonstrated that the water absorbed by the foliage of *P. euphratica* reverses the water transfer to the soil, and during

this process, when the condensate absorbed by the leaves enters the trunk, it is integrated with trunk water storage, and the water absorbed by the canopy directly promotes trunk growth (Steppe *et al.*, 2018). When root water uptake is insufficient, the change in trunk water storage is sufficient to meet the transpiration of the canopy (Čermák *et al.*, 2007). The results of the present study showed that, for 8 months of the year, the canopy sap flow of *P. euphratica* was much higher than the trunk sap flow, and the plants mainly consumed water from the trunk, which can lead to water shortage and stomatal closure if they only rely on the water absorbed by the root system (Williams *et al.*, 2021). In the remaining 4 months, under high temperature and strong light, *P. euphratica* stored the water in the trunk in addition to supplying canopy transpiration, with an average storage of 29.65 kg d^{-1}. Transpiration water consumption of *P. euphratica* A from May to July accounted for 66.73 % of the change in trunk water storage. When transpiration occurs, the first water consumed comes from the water stored in the main tree trunk, and during summer the water stored in the tree branches contributes little to transpiration (Williams *et al.*, 2021). Generally speaking, the more water is stored in the trunk of an individual tree, the more drought-resistant the tree is, as physiological activities can remain stable during seasonal changes, thus ensuring normal tree growth and development (Jiang *et al.*, 2021). Therefore, FWU and trunk water storage

are the most important water sources for the growth and development of *P. euphratica*.

Coupling process between leaf water absorption and hydraulic redistribution

In the process of leaf wetting, dew forms a water film on the leaf surface, which is then passively absorbed by the leaves through the FWU process. Subsequently, part of the water absorbed by the leaves enters the soil through the trunk and root system, resulting in reverse sap flow inside the trunk, which is the FHR process (Goldsmith, 2013). Many studies have shown that coupled FWU and FHR processes are common in dry-season plants in areas where canopy dew is frequent (Fu *et al.*, 2018; Steppe *et al.*, 2018; Zhang *et al.*, 2019; Gui *et al.*, 2021). Through this coupling process, trees in the subtropics can directly improve the water status of their trunks and soil near their roots and promote their trunk growth, which is important for the ecosystem of the site (Goldsmith, 2013; Steppe *et al.*, 2018). In tropical Brazil, this coupling process allows young trees exposed to fog to transport the water absorbed by their leaves to the soil near the roots during drought periods, which improves the water status of plant roots (Cassana *et al.*, 2016). In addition, the desert plant tamarisk also has the ability for FWU, and when humidity is high FHR occurs. As the sap flow rate is closely related to the humidity level, this coupling process plays an important role in improving plant physiological conditions (Li *et al.*, 2014). In the present study, stable isotope tracing of canopy condensate revealed that adult *P. euphratica* trees can absorb the condensate deposited on the leaf surface and transfer it to the soil around their roots under *in situ* conditions in the wild, indicating the occurrence of a coupling process of FWU and FHR. The contribution of dew to soil water near the roots was up to 28.3 % in *P. euphratica* A and up to 23.03 % in *P. euphratica* B. This was similar to the findings of the outdoor pot control experiment on *P. euphratica* seedlings, which showed that the contribution of dew to the soil water was up to 30.8 % (Zhang *et al.*, 2019). Sampling soil near the roots of *P. euphratica* under *in situ* conditions is more prone to errors, which may lead to underestimation or overestimation of the contribution of FHR. Therefore, there are differences in the contribution of labelled water to soil under *in situ* conditions and pot conditions. However, the experimental results of *in situ* experiments strongly prove that in desert riparian forests dew was involved in the FHR process of *P. euphratica*. Dew contributed water to the root soil of *P. euphratica* and was an important potential water source.

Driving mechanism of hydraulic redistribution in *P. euphratica*

Our study confirmed that *P. euphratica* has a water potential difference between 2200 and 0800 h at night, with a maximum difference of 2.13 MPa between the water potential of leaves and roots of *P. euphratica* A and a maximum difference of 0.4 MPa between the water potential of leaves and roots of *P. euphratica* B (Fig. 6). As long as a certain water potential gradient exists, the root system can redistribute water vertically or horizontally, which is driven by the water potential difference (Fu *et al.*, 2018). Therefore, *P. euphratica* is capable of

downward distribution of water, and may transfer water from the leaves or trunk to the roots, and from the top to the bottom of the *P. euphratica* and to the soil around their roots (Burgess and Bleby, 2006). Although the water potential of *P. euphratica* trunk and soil was not monitored in the present study, the results of monitoring the volumetric water content of the soil around the roots showed that the volumetric water content of surface (0–20 cm) and deep (80–150 cm) soil decreased continuously from 2200 at night to 0800 h the next day, while that of the middle soil (20–80 cm) increased continuously, and the deuterium value of the soil under dew-treated plants was significantly different from that of the soil under non-dew-treated plants. We suggest that the water potential difference drives the downward transfer of atmospheric condensate absorbed by the leaves, and the condensate is stored in the trunk, thus transforming it into trunk water storage. The trunk water storage is driven by the difference in water potential between the trunk and the soil, and the water is transferred to the dry root–soil interface through the trunk and the root system, which increases the soil water content around the plant roots, i.e. the water stored in the trunk is transferred down to the root–soil interface by the FHR process (Kobayashi and Tanaka, 2001; Burgess and Bleby, 2006). Damage to desert riparian forests in inland river basins in arid regions is mainly related to the rapid decline in groundwater and lack of soil moisture caused by river cut-offs (Chen *et al.*, 2009). Studies have shown that hydraulic lift occurs in woody plants in different regions, such as trees in desert areas as well as temperate and tropical forests, and that hydraulic lift can draw water from deep, moist soil layers and transfer it upwards to drier, shallow soil layers at night, which has important implications for plant–plant interactions (Richards and Caldwell, 1987; Neumann and Cardon, 2012). As a dominant species in the lower Tarim River, *P. euphratica* exhibits high hydraulic lift capacity, and its hydraulic lift process has been shown to provide water for the 0–120 cm soil layer around its roots (Hao *et al.*, 2013; Sun *et al.*, 2020). Therefore, the FHR and hydraulic lift processes of *P. euphratica* may occur simultaneously in the 20–80 cm soil layer around its roots to store water, and the plants can use the water stored in the soil during short-term drought. At the same time, it can increase the root soil biological activity in dry soil, accelerate the decomposition of soil organic matter, and promote the growth and development of *P. euphratica* and surrounding plants, which is important for the restoration of riparian forest ecosystems with *P. euphratica* as a dominant species in arid areas (Fu *et al.*, 2018).

Conclusions

The main conclusions of this study, which combined *in situ* integrated monitoring in the field with stable isotope tracing experiments, are as follows.

Populus euphratica has the ability to redistribute water from the canopy to the root soil through the leaves, trunk and root system, and a part of the trunk water can be transferred to the soil, resulting in additional depletion of trunk water storage. The contribution of dew to *P. euphratica* root soil water was found to be up to 28.3 %.

The water potential of *P. euphratica* leaves was higher than that of the root at night from 0000 h to 0830 h. Water stored in

the leaves and trunk has the drive to move from top to bottom inside the *P. euphratica*, and water redistribution mainly occurred at night in the 20–80 cm soil layer around *P. euphratica* roots.

Populus euphratica can provide water for transpiration through trunk water storage and root water uptake. The plants mostly replenished their trunk water storage from May to July, averaging 36.41 kg d^{-1}. During the rest of the year, they mainly consumed the water stored in the trunk, averaging 14.88 kg d^{-1}. At night and during periods of low biomass, the plants maintained a certain sap flow rate to replenish their trunk water storage and maintain water balance.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

ACKNOWLEDGEMENTS

We wish to thank the editor and anonymous reviewers, whose comments greatly improved the manuscript.

LITERATURE CITED

Alagele SM, **Jose S**, **Anderson SH**, **Udawatta RP. 2021**. Hydraulic lift: processes, methods, and practical implications for society. *Agroforestry Systems* **95**: 641–657. doi:10.1007/s10457-021-00614-w.

Berry ZC, **Emery NC**, **Gotsch SG**, **Goldsmith GR. 2019**. Foliar water uptake: processes, pathways, and integration into plant water budgets. *Plant, Cell and Environment* **42**: 410–423.

Burgess SSO, **Bleby TM. 2006**. Redistribution of soil water by lateral roots mediated by stem tissues. *Journal of Experimental Botany* **57**: 3283–3291.

Burgess SSO, **Dawson TE. 2004**. The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. *Plant, Cell and Environment* **27**: 1023–1034. doi:10.1111/j.1365-3040.2004.01207.x.

Burgess SSO, **Adams MA**, **Turner NC**, **Ong CK. 1998**. The redistribution of soil water by tree root systems. *Oecologia* **115**: 306–311. doi:10.1007/s004420050521.

Burgess SSO, **Pate JS**, **Adams MA**, **Dawson TE. 2000**. Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Annals of Botany* **85**: 215–224.

Cassana FF, **Eller CB**, **Oliveira RS**, **Dillenburg LR. 2016**. Effects of soil water availability on foliar water uptake of *Araucaria angustifolia*. *Plant and Soil* **399**: 147–157.

Čermák J, **Kučera J**, **Bauerle WL**, **Phillips N**, **Hinckley TM. 2007**. Tree water storage and its diurnal dynamics related to sap flow and changes in stem volume in old-growth Douglas-fir trees. *Tree Physiology* **27**: 181–198.

Chen YJ, **Chen YN**, **Liu JZ**, **Zhang EX. 2009**. Influence of intermittent water releases on groundwater chemistry at the lower reaches of the Tarim River, China. *Environmental Monitoring and Assessment* **158**: 251–264.

Eller CB, **Lima AL**, **Oliveira RS. 2013**. Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, *Drimys brasiliensis* (Winteraceae). *New Phytologist* **199**: 151–162. doi:10.1111/nph.12248.

Eller CB, **Lima AL**, **Oliveira RS. 2016**. Cloud forest trees with higher foliar water uptake capacity and anisohydric behavior are more vulnerable to drought and climate change. *New Phytologist* **211**: 489–501. doi:10.1111/nph.13952.

Fu C, **Wang G**, **Bible K**, *et al*. **2018**. Hydraulic redistribution affects modeled carbon cycling via soil microbial activity and suppressed fire. *Global Change Biology* **24**: 3472–3485. doi:10.1111/gcb.14164.

Gerjets R, **Richter F**, **Jansen M**, **Carminati A. 2021**. Hydraulic redistribution by hybrid poplars (*Populus nigra* x *Populus maximowiczii*) in a greenhouse soil column experiment. *Plant and Soil* **463**: 145–154. doi:10.1007/s11104-021-04894-0.

Goldsmith GR. 2013. Changing directions: the atmosphere-plant-soil continuum. *New Phytologist* **199**: 4–6. doi:10.1111/nph.12332.

Granier A, **Hue R**, **Barigah ST. 1996**. Transpiration of natural rain forest and its dependence on climatic factors. *Agricultural and Forest Meteorology* **78**: 19–29.

Gui Z, **Li L**, **Qin S**, **Zhang Y. 2021**. Foliar water uptake of four shrub species in a semi-arid desert. *Journal of Arid Environments* **195**: 104629. doi:10.1016/j.jaridenv.2021.104629.

Hafner BD, **Hesse BD**, **Grams TEE. 2021**. Friendly neighbours: hydraulic redistribution accounts for one quarter of water used by neighbouring drought stressed tree saplings. *Plant, Cell and Environment* **44**: 1243–1256.

Hao XM, **Chen YN**, **Guo B**, **Ma JX. 2013**. Hydraulic redistribution of soil water in *Populus euphratica* Oliv. in a central Asian desert riparian forest. *Ecohydrology* **6**: 974–983.

Hill AJ, **Dawson TE**, **Dody A**, **Rachmilevitch S. 2021**. Dew water-uptake pathways in Negev desert plants: a study using stable isotope tracers. *Oecologia* **196**: 353–361. doi:10.1007/s00442-021-04940-9.

Huang CW, **Domec JC**, **Ward EJ**, *et al*. **2017**. The effect of plant water storage on water fluxes within the coupled soil–plant system. *New Phytologist* **213**: 1093–1106.

Jiang P, **Meinzer FC**, **Fu X**, **Kou L**, **Dai X**, **Wang H. 2021**. Trade-offs between xylem water and carbohydrate storage among 24 coexisting subtropical understory shrub species spanning a spectrum of isohydry. *Tree Physiology* **41**: 403–415.

Kamakura M, **Tsuruta K**, **Azuma WA**, **Kosugi Y. 2021**. Hydraulic architecture and internal water storage of Japanese cypress using measurements of sap flow and water potential. *Ecohydrology* **14**: e2325.

Kobayashi Y, **Tanaka T. 2001**. Water flow and hydraulic characteristics of Japanese red pine and oak trees. *Hydrological Processes* **15**: 1731–1750. doi:10.1002/hyp.236.

Li S, **Xiao HL**, **Zhao L**, **Zhou MX**, **Wang F. 2014**. Foliar water uptake of *Tamarix ramosissima* from an atmosphere of high humidity. *Scientific World Journal* **2014**: 529308.

Limm EB, **Simonin KA**, **Bothman AG**, **Dawson TE. 2009**. Foliar water uptake: A common water acquisition strategy for plants of the redwood forest. *Oecologia* **161**: 449–459. doi:10.1007/s00442-009-1400-3.

Liu Z, **Zhang H**, **Yu X**, **Jia G**, **Jiang J. 2021**. Evidence of foliar water uptake in a conifer species. *Agricultural Water Management* **255**: 106993. doi:10.1016/j.agwat.2021.106993.

Maherali H, **DeLucia EH. 2001**. Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. *Oecologia* **129**: 481–491. doi:10.1007/s004420100758.

Neumann RB, **Cardon ZG. 2012**. The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytologist* **194**: 337–352. doi:10.1111/j.1469-8137.2012.04088.x.

Phillips DL. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* **127**: 166–170. doi:10.1007/s004420000571.

Richards JH, **Caldwell MM. 1987**. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* **73**: 486–489. doi:10.1007/bf00379405.

Schreel JDM, **Van de Wal BAE**, **Hervé-Fernandez P**, **Boeckx P**, **Steppe K. 2019**. Hydraulic redistribution of foliar absorbed water causes turgor-driven growth in mangrove seedlings. *Plant, Cell and Environment* **42**: 2437–2447.

Steppe K, **Vandegehuchte MW**, **Van De Wal BAE**, *et al*. **2018**. Direct uptake of canopy rainwater causes turgor-driven growth spurts in the mangrove

Avicennia marina. *Tree Physiology* **38**: 979–991. doi:10.1093/treephys/tpy024.

Sun L, **Yang L**, **Chen L**, **Yen H**, **Zhao F**, **Li S. 2020**. Evaluation of seasonal patterns of hydraulic redistribution in a humid subtropical area, East China. *Hydrological Processes* **34**: 1052–1062.

Tianshi E, **Chau PC. 2022**. Foliar water uptake in the needles of *Pinus torreyana*. *Plant Ecology* **223**: 465–477. doi:10.1007/s11258-022-01222-z.

Töchterle P, **Yang F**, **Rehschuh S**, *et al*. **2020**. Hydraulic water redistribution by silver fir (*Abies alba* Mill.) occurring under severe soil drought. *Forests* **11**: 162. doi:10.3390/f11020162.

Williams CB, **Reese Næsborg R**, **Ambrose AR**, **Baxter WL**, **Koch GW**, **Dawson TE. 2021**. The dynamics of stem water storage in the tops of Earth's largest trees – *Sequoiadendron giganteum*. *Tree Physiology* **41**: 2262–2278. doi:10.1093/treephys/tpab078.

Zhang Y, **Hao X**, **Sun H**, **Hua D**, **Qin J. 2019**. How *Populus euphratica* utilizes dew in an extremely arid region. *Plant and Soil* **443**: 493–508. doi:10.1007/s11104-019-04244-1.

Zhu C, **Abula A**, **Li W**, **Zhou H. 2021**. Ecosystem restoration of *Populus euphratica* forest under the ecological water conveyance in the lower reaches of Tarim River. *Arid Land Geography* **44**: 629–636.