Liu *et al. Forest Ecosystems* (2021) 8:72
https://doi.org/10.1186/s40663-021-00353-5

Forest Ecosystems

RESEARCH **Open Access**

Partitioning tree water usage into storage and transpiration in a mixed forest

Ziqiang Liu[1], Qianqian Liu[1], Zijun Wei[1], Xinxiao Yu[2*], Guodong Jia[2] and Jiang Jiang[1]

Abstract

Background: Water migration and use are important processes in trees. However, it is possible to overestimate transpiration by equating the water absorbed through the plant roots to that diffused back to the atmosphere through stomatal transpiration. Therefore, it is necessary to quantify the water transpired and stored in plants.

Method: The $\delta^2H/\delta^{18}O$ technique and heat ratio method were used to explore the water usage of coniferous and broad-leaved tree species, including the proportions of water used for transpiration and water storage.

Results: *Platycladus orientalis* and *Quercus variabilis* had strong plasticity in their water usage from different sources. *Platycladus orientalis* primarily used groundwater (30.5%) and the 60–100-cm soil layer (21.6%) throughout the experimental period and was sensitive to precipitation, absorbing water from the 0–20-cm layer (26.6%) during the rainy season. *Quercus variabilis* absorbed water from all sources (15.7%–36.5%) except from the 40–60-cm soil layer during the dry season. In addition, it did not change its water source but increased its groundwater uptake during the rainy season. The annual mean water fluxes of *P. orientalis* and *Q. variabilis* were 374.69 and 469.50 mm·year^{-1}, with 93.49% and 93.91% of the water used for transpiration, respectively. However, nocturnal sap flow in *P. orientalis* and *Q. variabilis* was mainly used for water storage in the trunk rather than transpiration, which effectively alleviated drought stress and facilitated the transport of nutrients.

Conclusions: The water stored in both species comprised 6%–7% of the total water fluxes and, therefore, should be considered in water balance models.

Keywords: Water migration, Water uptake, Nocturnal sap flow, Transpiration

Introduction

Water is a key factor affecting the circulation of materials and plant growth in forest ecosystems (Nadezhdina et al. 2020). Plants absorb water from the soil through their roots and store it in their xylem, use it during photosynthesis, or lose it through evaporation through the stomata in their leaves (Weatherley 1982; Buckley et al. 2020; Barbeta et al. 2015; Huang et al. 2017; Molina et al. 2019). Stable hydrogen and oxygen isotope technology is a new technique for exploring the source of water in plants. This technology solves the challenge of quantifying plants' absorption ratio from each water source (Wang et al. 2017). Since there is no isotopic fractionation in hydrogen and oxygen isotopes during water uptake and transportation from xylem to leaves (Ehleringer et al. 1991), the hydrogen and oxygen isotopes in the xylem and water source can be compared based on the isotopic mass conservation law. Linear mixed models (Iso-Source) and Bayesian mixed models, including MixSIAR, MixSIR, and SIAR, have been used to quantify the ratio of water used by the plants from each water source (Phillips et al. 2005). Dawson and Ehleringer (1991) explored the use of stable hydrogen and oxygen isotope technology to distinguish between the water sources of plants and revealed that tree species that

---

* Correspondence: yuxinxiao1111@126.com
[2]Key Laboratory of Soil and Water Conservation and Desertification Combating of Ministry of Education, Beijing Forestry University, Beijing 100083, China
Full list of author information is available at the end of the article

grew by the riverside did not use river water but instead used soil water along the riverside. Since then, there have been several reports on the source of water utilized by plants in China and throughout the world (Moreno-Gutiérrez et al. 2012; Poca et al. 2019; Liu et al. 2020). Previous research has focused on comparing the differences in water sources among different plants or the variation in water usage by the same plant across different seasons (Nie et al. 2011; Yang et al. 2015; Poca et al. 2019). However, very few studies have focused on the water usage and symbiotic mechanism in coniferous and broad-leaved mixed forests under seasonal drought in rocky mountainous regions characterized by thin soils and high gravel content. Moreover, with incidences of seasonal drought becoming rampant and more intense in these regions owing to global climate change, the adaptations of species in these mixed forests to this heterogeneous change with changing water sources remain unclear.

Several studies have investigated the proportion of water absorbed from each source and quantified the diurnal transpiration (Palacio et al. 2014; Wu et al. 2016; Liu et al. 2020). Although previous studies have established that stomata are closed at night, and there is no sap flow during this period (Zeppel et al. 2014; Zhang et al. 2020), with the development and improvement in technologies, nocturnal sap flow has been confirmed in plants in different habitats (Hentschel et al. 2013; Siddiq and Cao 2018; Chen et al. 2020). Nocturnal sap flow has been rarely considered in traditional models owing to the small proportion of nocturnal sap flow compared to the overall sap flow. However, for some plant species, nocturnal sap flow comprises a large proportion of the overall sap flow (Alvarado-Barrientos et al. 2015; Di et al. 2019a, 2019b; Flo et al. 2019). For example, Barbeta et al. (2012) established that *Quercus ilex* (holly oak) growing in the Mediterranean climate with annual precipitation of 350 mm had a nocturnal sap flow of 40% of the overall flow. In addition, the nocturnal sap flow in *Q. oleoides* in the central USA increased from 8% during the rainy season to 20% during the dry season (Cavender-Bares et al. 2007). Based on these findings, nocturnal sap flow cannot be neglected. Nocturnal sap flow effectively improves the leaf and stem water potential before dawn and reduces embolisms in the xylem (Forster 2014). However, nocturnal sap flow is not equivalent to nocturnal transpiration (Binks et al. 2020). During the night, some sap is transpired through the stomata (30%–60%), and some is used to supplement the stem water (40%–70%) (Gribovszki et al. 2015). Huang et al. (2017) suggested that night transpiration can drive the supplementation of water.

Currently, there is no adequate technology for quantifying night transpiration and water supplementation owing to their simultaneous occurrence. However, based on the response relationship between transpiration and the vapor pressure deficit (VPD), transpiration and water supplementation can be distinguished (Resco de Dios et al. 2016; Siddiq et al. 2017; Di et al. 2019a, 2019b) since the main factor causing nocturnal transpiration is VPD. Therefore, when the VPD approaches zero, if sap flow still occurs, it supplements the stem water. However, if sap flow has a good fitting relationship with the large VPD, the sap flow is primarily used for transpiration.

Numerous studies have explored daytime transpiration and quantified the amount of water that transpired (Fu et al. 2016; Wu et al. 2019; McCormick et al. 2021). However, the amount of nocturnal water supplementation has largely been ignored. Consequently, substantial errors may occur when calculating the water balance in an ecosystem, impacting the development of management strategies. Therefore, if the amounts of each water fraction used for transpiration and nocturnal sap flow were accurately quantified, existing formulae or models for calculating water balance could be revised. Therefore, it is paramount to quantitatively distinguish the flux and proportion of water absorbed, transported and transpired in a mixed forest. In this study, we employed the isotope (δ^2H and δ^{18}O) technique and heat ratio method to i) determine the water absorption ratio from the different water sources and the symbiotic mechanism of the mixed forest; ii) quantify the amount of water that flows in the nocturnal sap and quantify the proportions of water transpired and stored in plants. Our results will provide a scientific reference for further research on the underlying mechanisms of water cycling in forest ecosystems.

Materials and methods

Site description

The study was conducted at the Forest Ecosystem Positioning Research Station in Beijing (40°03′ N, 116°05′ E). The station lies at an elevation of 240 m above sea level with a warm temperate semi-humid monsoon climate. The annual average precipitation and potential evapotranspiration were 630 and 1800 mm, respectively. June to September precipitation comprised 70% of the annual precipitation. The average annual temperature was 11.6 °C with 2662 h of sunshine. The primary forest vegetation includes

Platycladus orientalis and *Quercus variabilis* plantations established after the 1960s. *Broussonetia papyrifera*, *Vitex negundo*, *Lespedeza bicolor*, and other shrubs are underneath the canopy. The soil type is leached cinnamon with a thickness of 80–100 cm, the humus content is high, and the deep soil primarily consists of gravel.

Experimental design

Three plots measuring 20 m × 20 m each were established at the study area. Six *P. orientalis* and *Q. variabilis* with average height, diameter at breast height (DBH), and crown width were randomly selected from each plot (Table 1). In each plot, three ECH$_2$O soil moisture sensors (Decagon Devices, Pullman, WA, USA) were installed at three sampling points to measure the soil water content (SWC) at 0–20, 20–40, 40–60, 60–80, and 80–100 cm. The ECH$_2$O sensors were connected to a Em50/R data collection box (Decagon Devices, Pullman, WA, USA), which recorded data every 30 min and simultaneously stored it in a computer. The data for precipitation, radiation, atmospheric temperature, and relative humidity in the study area were collected from a forest weather station HOBO (U30-NRC; Onset, Bourne, MA USA) located 1 km away from the experimental plots.

Quantification of the water amounts used for physiological processes

Determination of the water source: branches, soil, and groundwater sampling

In each plot, three trees with good vigor and similar height/DBH were randomly selected, and their annual non-green branches (0.3–0.6 cm in diameter) were collected at the same height (5 and 6 m for *P. orientalis* and *Q. variabilis*, respectively) from the ground. The bark of the branches was removed to obtain the xylem. Three samples were collected per tree.

Three soil samples were collected from 0 to 20, 20–40, 40–60, 60–80, and 80–100 cm within a radius of 0.5 to 1 m from the sampled trees using an auger with a diameter of 3.5 cm and a length of 120 cm. The sampled branches and soil were immediately placed into a 50-mL sampling bottle, sealed with Parafilm®, and stored at − 4 °C until the isotopes were determined.

Simultaneously, three spring water samples (representing groundwater) were collected from the Miaolingshan Spring (40°03′ N, 116°05′ E) 310 m southwest of the plots.

Stable isotope analysis

The isotopic ratios in the samples were determined at the Ecohydrological Processes and Mechanisms Laboratory, Beijing Forestry University, China. The water in the soil and branches samples was extracted by low-temperature vacuum condensation, and $\delta^2H/\delta^{18}O$ was analyzed using a liquid water isotope analyzer (LGR DLI-100, USA). The ratio of ^2H and ^{18}O was recorded in parts per thousand of the "standard average ocean water" with a precision of determination of 0.3‰ and 0.1‰, respectively, and expressed as follows:

$$\delta X\ (‰) = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000 \tag{1}$$

The ratio of water absorption by trees

The isotopic ratios of water in the branches carry the isotopic information of all the water sources since water is absorbed through the roots. Owing to this, the Mix-SIAR model was used to quantify the water absorption ratio of trees (Phillips et al. 2005) using the following equations:

$$\delta X = c1\delta X1 + c2\delta X2 + c3\delta X3 + c4\delta X4 + c5\delta X5 \tag{2}$$

$$c1 + c2 + c3 + c4 + c5 = 1 \tag{3}$$

where, X is the $^2H/^{18}O$ value of tree branch water (‰); X_1, X_2, X_3, X_4, and X_5 are the $^2H/^{18}O$ values of soil water at 0–20, 20–40, 40–60, 60–100 cm, and groundwater levels, respectively; and c_1, c_2, c_3, c_4, and c_5 represent the absorption ratio of trees for soil water from 0 to 20, 20–40, 40–60, 60–100 cm, and groundwater levels, respectively.

Quantification of the amount of water for migration (*Q*)

Three *P. orientalis* and *Q. variabilis* tree species with an average tree height and DBH were selected at each observation point, which were the same points for the isotope sample collection in the plot. Three sap flow meters (SFM$_1$, HRM 30, ICT International PTY, Armidale, Australia) were installed at a height of roughly 1.35 m on the three selected

Table 1 Basic information about the tree species measured

Tree species	Number	Average height (m)	Diameter at breast height (cm)
Platycladus orientalis	37	7.16 ± 1.53	7.60 ± 2.83
Quercus variabilis	43	9.18 ± 1.15	11.59 ± 3.91

trees to monitor the sap flow rate. The SFM_1 flowmeter has three probes, which simultaneously measure two-way flows. Three cores were taken from each tree at roughly 1.35 m using a borer with 5 mm increments, and the radii of cross-sections and heartwood were measured with a ruler. Three cylindrical probes were inserted into the sapwood through the drilled holes. The device was wrapped and sealed with insulated and radiation-proof aluminum foil to prevent rainwater from entering and protect against direct solar radiation. The data acquisition interval of the SFM_1 flowmeter was set at 10 min, and the water that migrated through the tree was calculated using the following equations (Allen et al. 2011):

$$Q = V_s A_s = V_{ot} A_1 + V_{in} A_2 \tag{4}$$

$$V_s = \frac{V_h \rho_b (c_W + m_c c_s)}{\rho_s c_s} \tag{5}$$

$$V_h = \frac{k}{x} \ln\left(\frac{t_1}{t_2}\right) \times 3600 \tag{6}$$

Here, Q is the total migration (mL); V_s is the sap flow velocity ($cm \cdot s^{-1}$); A_s is the sapwood area (cm^2); V_{ot} and V_{in} are the sap flow velocities of the thermocouple inside and outside the temperature probe ($cm \cdot s^{-1}$), respectively; A_1 and A_2 are the areas of the outer ring and the inner ring, respectively (cm^2); V_h is the heat pulse rate ($cm \cdot s^{-1}$); k is the thermal diffusion coefficient of fresh wood; x is the distance between the thermal probe and the temperature probe; t_1 and t_2 are the variation in temperature in the upward and downward directions, respectively; ρ_b is the wood density ($g \cdot cm^{-3}$); c_w and c_s are the specific heat capacities of fresh wood ($1200\ J \cdot kg^{-1} \cdot {}^\circ C^{-1}$, 20 °C) and specific heat capacity of liquid flow ($4182\ J \cdot kg^{-1} \cdot {}^\circ C^{-1}$, 20 °C), respectively; m_c and ρ_s are the moisture content and density of fresh wood, respectively.

Quantification of the water used for migration

The water migrating through the trees can be divided into the water used in transpiration and storage.

Quantification of the used for water storage (Q_s)

The amount of water stored at night depends on the storage time as determined by the dislocation correlation method (Maherali and DeLucia 2001). The data series of sap flow velocity and the corresponding VPD/radiation were established according to the observation time sequence. The sap flow velocity and VPD/radiation based on dislocation were successively recorded every half hour, and a correlation analysis was conducted on the data after dislocation. The dislocation time corresponding to the maximum correlation coefficient was the storage time (The results of correlation analysis after dislocation are shown in the Supplemental Table S1). The migration flux during this time is the stored water. The VPD was calculated as

$$\mathrm{VPD} = 0.61078 \times e^{\frac{17.27 \times T_a}{T_a + 237.3}} \times (1 - \mathrm{RH}) \tag{7}$$

where T_a and RH are atmospheric temperature (°) and relative humidity (%), respectively.

Quantification of water used for transpiration (Q_{Tr})

Sap flow during the stomatal opening represents the rate of transpiration in a plant. Therefore, the water used for transpiration was quantified by determining the stomatal opening time via the VPD and radiation. The Q_{Tr} was determined by calculating the difference between the overall sap flow and water storage.

Data analysis

The statistical analyses were performed using SPSS 16.0 (SPSS, Inc., Chicago, IL, USA). Descriptive statistics were applied to calculate the means and standard deviations for each set of replicates. First, a one-way analysis of variance (ANOVA) was performed to test the effect of tree species on the migration flux, transpiration, and storage. A two-way ANOVA was then performed to analyze the differences in SWC, isotopic composition, season, and soil depth as independent factors. In addition, a three-way ANOVA was used to analyze the differences in water source using the soil depth, tree species, and season as independent factors.

Results

Variation in soil water content and meteorological conditions

The annual precipitation totals in 2015 and 2016 were 580.0 and 649.8 mm, respectively (Fig. 1), with the precipitation in June to September comprising 79.0% and 80.5% of the total annual precipitation in 2015 and 2016, respectively. June to September is the rainy season, while October to May comprises the dry seasons. During the dry season, the average SWC in the 0–20-, 20–40-, 40–60-, 60–80-, and 80–100-cm layers were 11.6%, 12.6%, 11.9%, 9.8%, and 9.2%, respectively. However, the SWC in the five soil layers increased at different degrees after it rained, followed by a decrease. The average SWC in the five layers during the rainy season was 16.5%, 17.0%, 17.6%, 14.0%, and 11.2%, respectively, 42.2%,

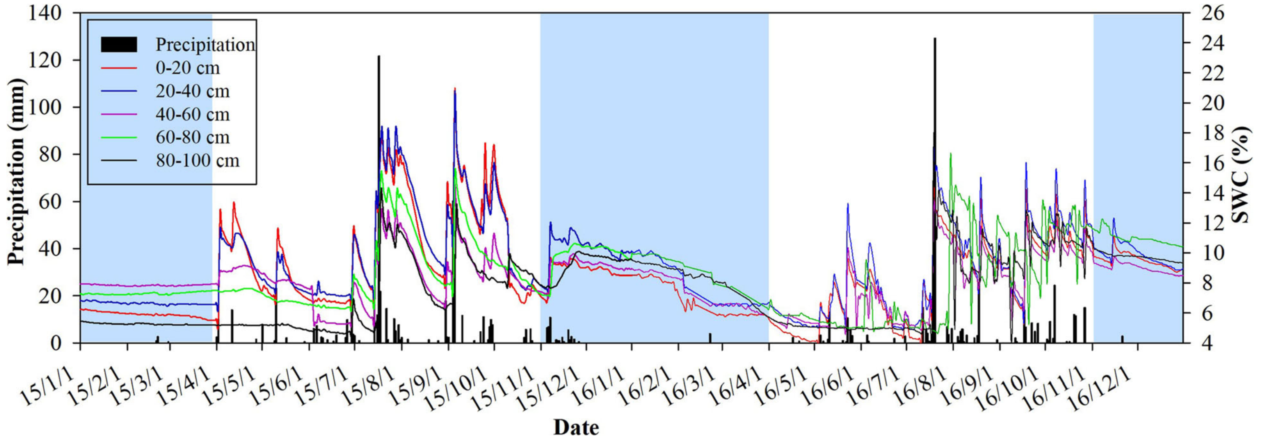

Fig. 1 Variation in precipitation and mean soil water content in the Forest Ecosystem Positioning Research Station, north China, during the study period. The blue shading corresponds to the dry season, while the white region corresponds to the rainy season

35.0%, 39.7%, 17.5%, and 13.9% higher than those in the dry season. After approximately 10 mm of precipitation, the SWC increased by 64.22% in the 0–20-cm layer, but no significant changes were observed in the other layers ($P > 0.05$). After > 50 mm precipitation, the SWC increased in all the five soil layers, with a lag time effect in the deeper layers.

The total solar radiation (TR) and VPD had a similar trend, with an initial increase and a subsequent decrease (Fig. 2). The peak VPD appeared 0–3 h later compared to TR. The TR was 0 and VPD > 0 Kpa from 19:00 to 06:00 at night. In January, mean and peak TR values were 87.1 and 174.6 $W \cdot m^{-2}$, respectively, while those of VPD values were 0.35 and 0.59 Kpa, respectively. The TR and VPD values gradually increased with seasonal variation from January to July and decreased from August to December. The mean and peak TR values reached 176.2 and 491.6 $W \cdot m^{-2}$ in July, which were 2.0- and 2.8-fold higher than the mean and peak values in January, respectively. In addition, the mean and peak values of VPD reached 2.57 and 6.84 Kpa in July, which was 7.3- and 11.6-fold higher than those in January, respectively. However, there were no significant differences in TR and VPD between January and December.

Water absorption by trees

The δ^2H and $\delta^{18}O$ in soil and branch water of *P. orientalis* and *Q. variabilis* significantly fluctuated across the different seasons (Figs. 3 and 4). The δ^2H and $\delta^{18}O$ in soil water were higher in the dry season than in the rainy season ($P < 0.05$), implying that the isotope fractionation effect in soil water in the dry season was more pronounced than in the rainy season. During the dry season, the δ^2H and $\delta^{18}O$ in the 0–20-cm layer were − 32% and − 2.13‰, which were 19.50%, 26.29%, 38.19%, and 53.59% higher than those in the 20–40-, 40–60-, 60–80-, and 80–100-cm layers, respectively ($P < 0.05$). However, the δ^2H and $\delta^{18}O$ in the 80–100-cm layer were significantly lower than those of the other layers ($P < 0.05$). Nevertheless, the δ^2H and $\delta^{18}O$ in each layer decreased gradually during the rainy season, with 96.93%, 46.84%, 38.76%, 25.92%, and 15.49% decreases, respectively across the five soil layers.

Branch water in *P. orientalis* ranged from − 105.63‰ to − 37.82‰ for δ^2H and − 14.09‰ to − 0.19‰ for $\delta^{18}O$, with more extreme values than those of *Q. variabilis* (− 99.89‰ to − 36.24‰ for δ^2H and − 13.58‰ to − 2.61‰ for $\delta^{18}O$). The mean values of δ^2H and $\delta^{18}O$ in the branch water in *P. orientalis* during the dry season were − 56.53‰ and − 4.99‰, which were 28.56% and 54.30% higher than those of *Q. variabilis*. Additionally, the δ^2H and $\delta^{18}O$ in the branch water in *P. orientalis* during the rainy season were 45.67% and 69.93% higher than those in the dry season, while in *Q. variabilis* they were 6.31% and 9.53% higher, respectively.

The water absorption by *P. orientalis* and *Q. variabilis* from the different water sources fluctuated with the season (Fig. 5). The two species absorbed water from the groundwater from the 60–100-cm layer, although *Q. variabilis* also absorbed water from the 0–20-cm (21.7%) and 20–40-cm (19.9%) layers during the dry season. In the rainy season, *P. orientalis* used groundwater (30.5%) and water from the 60–100-cm soil layer (21.6%) and 0–20-cm layer (26.6%). The absorption ratio of water from the 20–40-cm layer used by *Q. variabilis* during the rainy season was 47.4% lower than during the dry season, but the absorption ratio of groundwater increased by 68.2%.

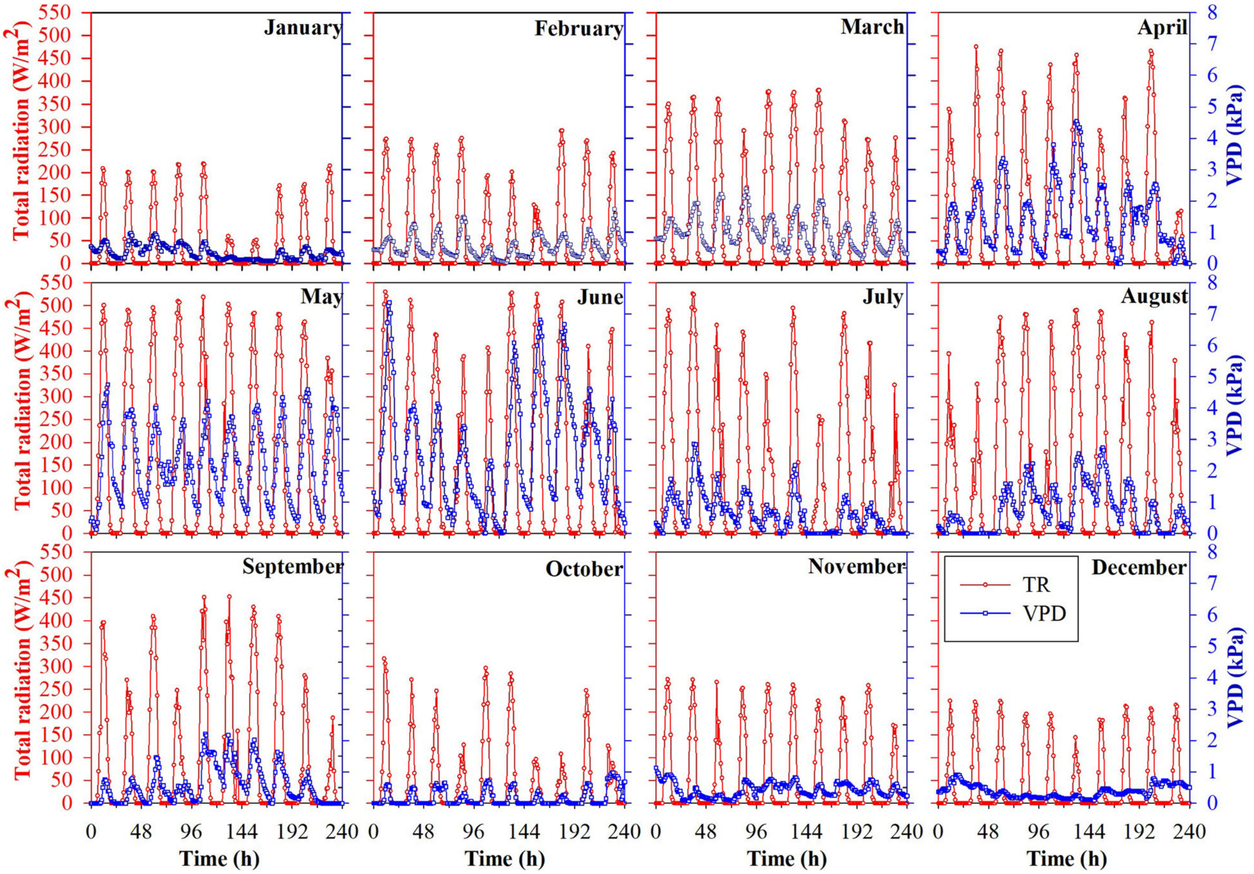

Fig. 2 Variation in total solar radiation (TR) and vapor pressure deficit (VPD) in the Forest Ecosystem Positioning Research Station, North China, during the study period. The figure shows the observation data of TR and VPD randomly selected for 10 consecutive days each month

P. orientalis used less water from the 20–40-cm and 40–60-cm soil layers, whereas *Q. variabilis* used less water from the 40–60-cm soil layer throughout the experimental period.

Water migration of *P. orientalis* and *Q. variabilis*

The sap flow rate (SFR) of *P. orientalis* during the dry season were bimodal over the observation period (Fig. 6). SFR gradually increased, reaching its maximum at 11:00 and 14:30, respectively, followed by a decrease. In contrast, the variation in SFR of *Q. variabilis* showed no peak during the dry season but had a single peak during the wet season. The mean SFR in *P. orientalis* ($0.0008\,\mathrm{cm\cdot s^{-1}}$) was four times higher than that of *Q. variabilis*, and the maximum SFR in *P. orientalis* ($0.0022\,\mathrm{cm\cdot s^{-1}}$) was 4.4 times higher than that of *Q. variabilis* during the dry season. Additionally, the mean SFR in *Q. variabilis* during the wet season was 6.5 times that in the dry season, while the mean SFR of *P. orientalis* during the wet season was not significantly different from that in the dry season ($P > 0.05$).

The proportions of water used in transpiration and water storage

The annual mean water fluxes in *P. orientalis* and *Q. variabilis* were 374.69 and $469.50\,\mathrm{mm\cdot year^{-1}}$, respectively (Fig. 7). The average sap flux in *P. orientalis* was 20.19% lower than that of *Q. variabilis*. The amounts of water used by *P. orientalis* for transpiration and storage were 350.3 and $24.41\,\mathrm{mm\cdot year^{-1}}$, respectively, accounting for 93.49% and 6.51% of the sap flow, respectively. Moreover, the amounts of water used by *Q. variabilis* for transpiration and storage were 440.85 and 28.65 $\mathrm{mm\cdot year^{-1}}$, respectively, accounting for 93.91% and 6.09% of the sap flow, respectively, which implies that the plants used most of the water for transpiration. However, there was no significant difference in water used by *P. orientalis* and *Q. variabilis* for transpiration and storage ($P > 0.05$).

Discussion

Water absorption by trees

P. orientalis and *Q. variabilis* showed different water usage in the same habitat, related to their root distribution and water conditions. More than 50% of the *P. orientalis*

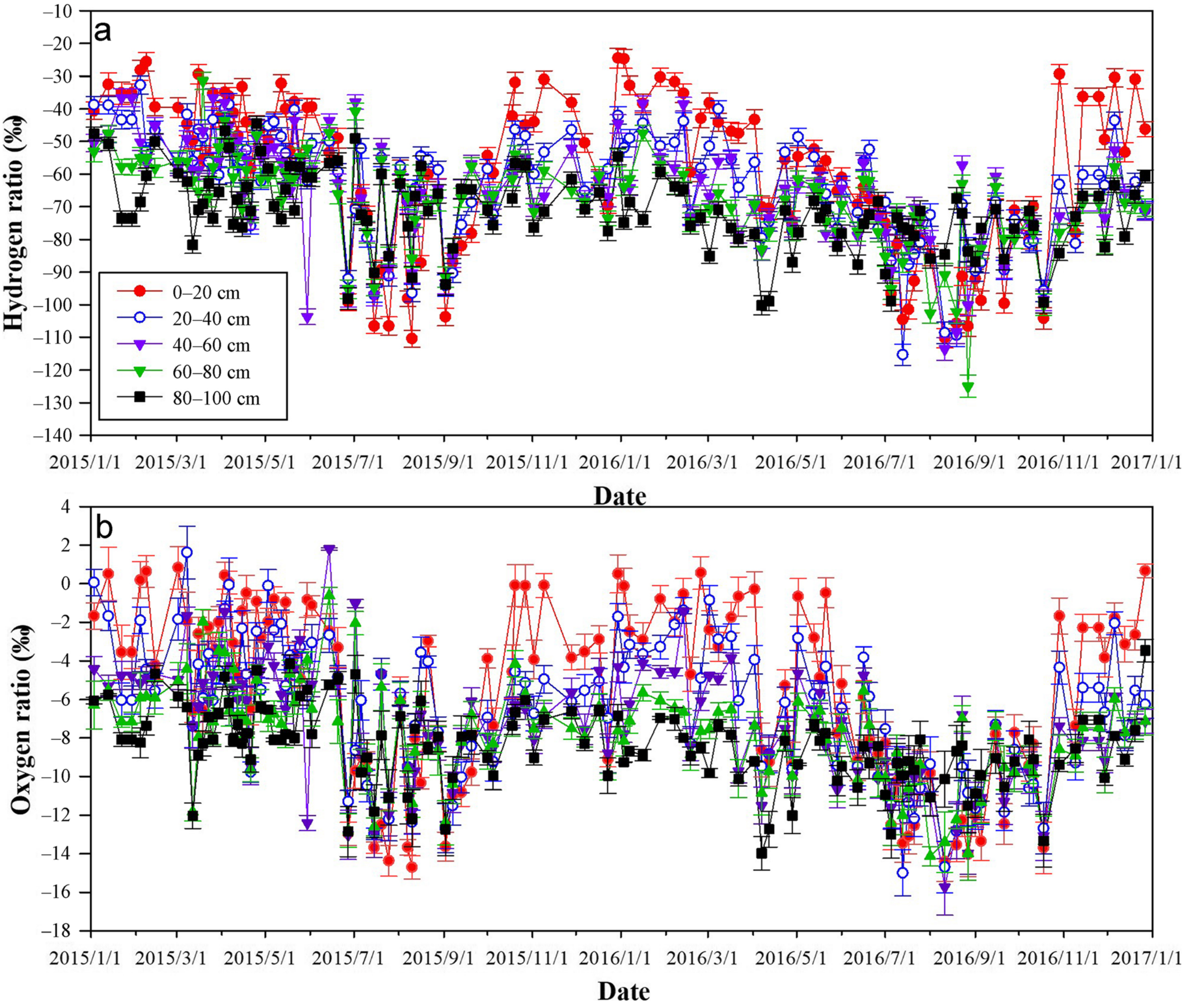

Fig. 3 Variation in mean (± SD) isotopic values of soil water in the Forest Ecosystem Positioning Research Station, North China during the study period

root biomass is distributed in the 0–20-cm layer (Liu et al. 2019), and its highly developed surface root system of *P. orientalis* is more sensitive to precipitation. Therefore, *P. orientalis* used water from the 0–20-cm layer following precipitation, consistent with findings of Jia et al. (2017), who established that *P. orientalis* primarily absorbed water from the surface soil during the rainy season to maintain normal physiological activities and then switched its water source to deep soil layers during the dry season. This phenomenon is known as a "dimorphic" structural feature of the root system (Evaristo et al. 2016; Cuneo et al. 2018; Poca et al. 2019). Previous studies have also established variation in water usage from different sources in *Q. pubescens*, *Populus*, *Robinia pseudoacacia*, and *Pinus tabulaeformis* (Gebauer and Ehleringer 2000; Liu et al. 2020; Ripullone et al. 2020).

In contrast to *P. orientalis*, 79.2% of the main root system of *Q. variabilis* is highly developed and uniformly distributed in different soil layers (Liu et al. 2019); hence, it can use multiple water sources. However, it uses a higher surface soil water ratio during the dry season, possibly owing to the short transport distance of surface soil water and the lower energy consumption. This suggests that *Q. variabilis* prefers surface soil water during the dry season, consistent with previous findings, which established that plants with uniform root distributions preferentially absorb water from surface soil layers (Fan et al. 2017; Cai et al. 2018; Cuneo et al. 2018). However, *Q. variabilis* absorbs water from the deep soil layers via its highly developed root system to maintain a high transpiration rate during

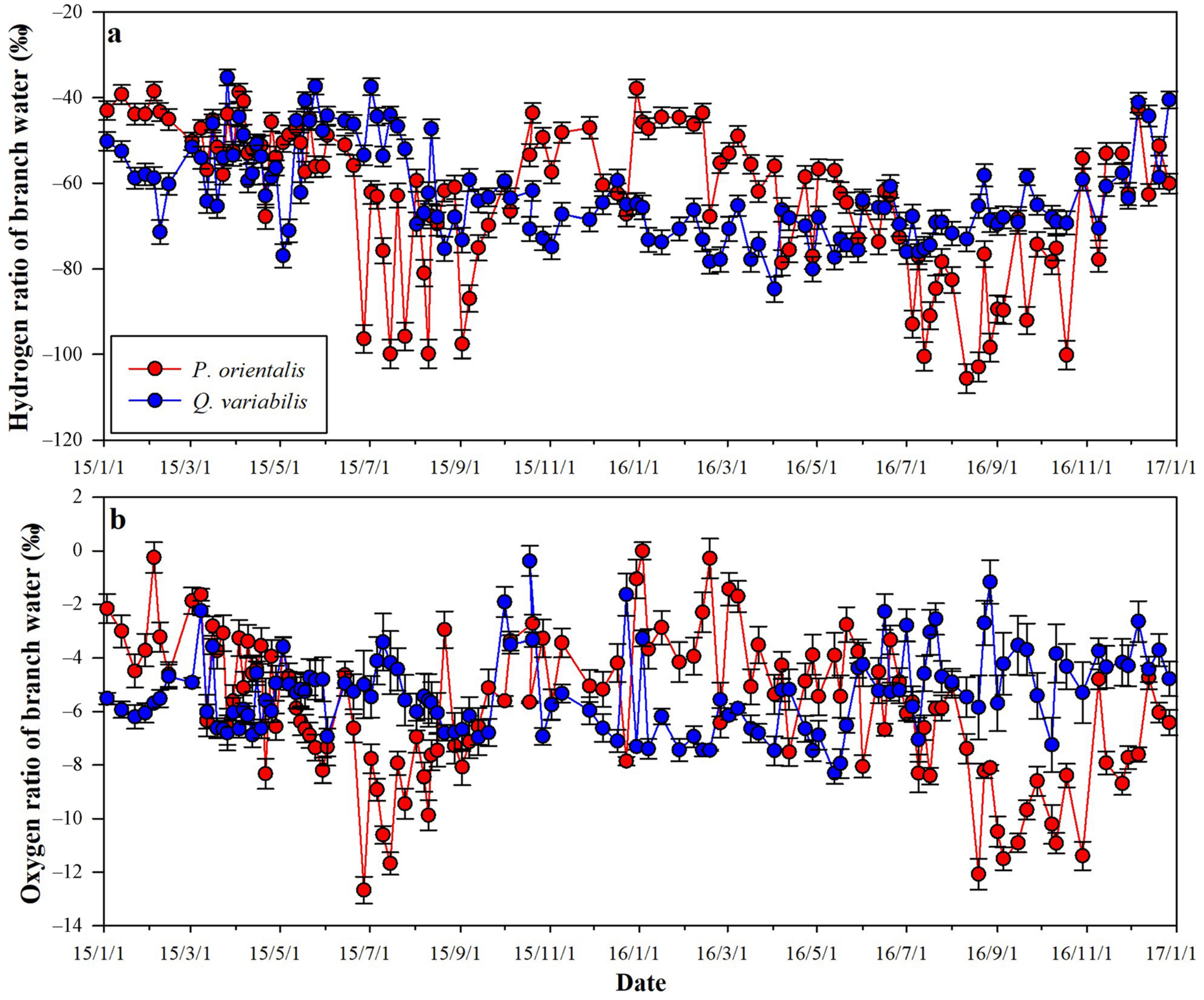

Fig. 4 Typical diurnal variation in mean (± SD) isotopic values in *Platycladus orientalis* and *Quercus variabilis* branch water in the Forest Ecosystem Positioning Research Station, North China during the study period

the rainy season. Wang et al. (2017) and Peddinti et al. (2020) have demonstrated that several plants can take up deep soil water and groundwater through their developed roots throughout the growing season, ensuring a stable water supply. The threshold value of the root system response to SWC is one of the key factors affecting water usage (Cuneo et al. 2018). In our study, the *P. orientalis* root system was more sensitive to precipitation than that of *Q. variabilis*. These water uptake patterns in *P. orientalis* and *Q. variabilis* from different water sources result from long-term adaptation to seasonal arid environments. Such strategies help reduce competition for water with other tree species and improve symbiotic ability among community species (Yang et al. 2015; Jia et al. 2017; Liu et al. 2019).

Water migration and use

We observed significant differences in water usage and distribution between the two tree species, which could be related to their characteristics. Molina et al. (2019) established that the aboveground biomass and defoliation cycle are the main factors affecting SFR. In our study, the SFR of *P. orientalis* was higher than that of *Q. variabilis* during the dormant period, probably because *Q. variabilis* is a broad-leaved deciduous species, which had already shed its leaves, while *P. orientalis* retained its leaves. In addition, the xylem vessel diameter and the crown width of *Q. variabilis* were greater than those of *P. orientalis*, which significantly improved the efficiency of water migration. In addition, *Q. variabilis* had more stomata per leaf area than *P. orientalis*, and the rate of

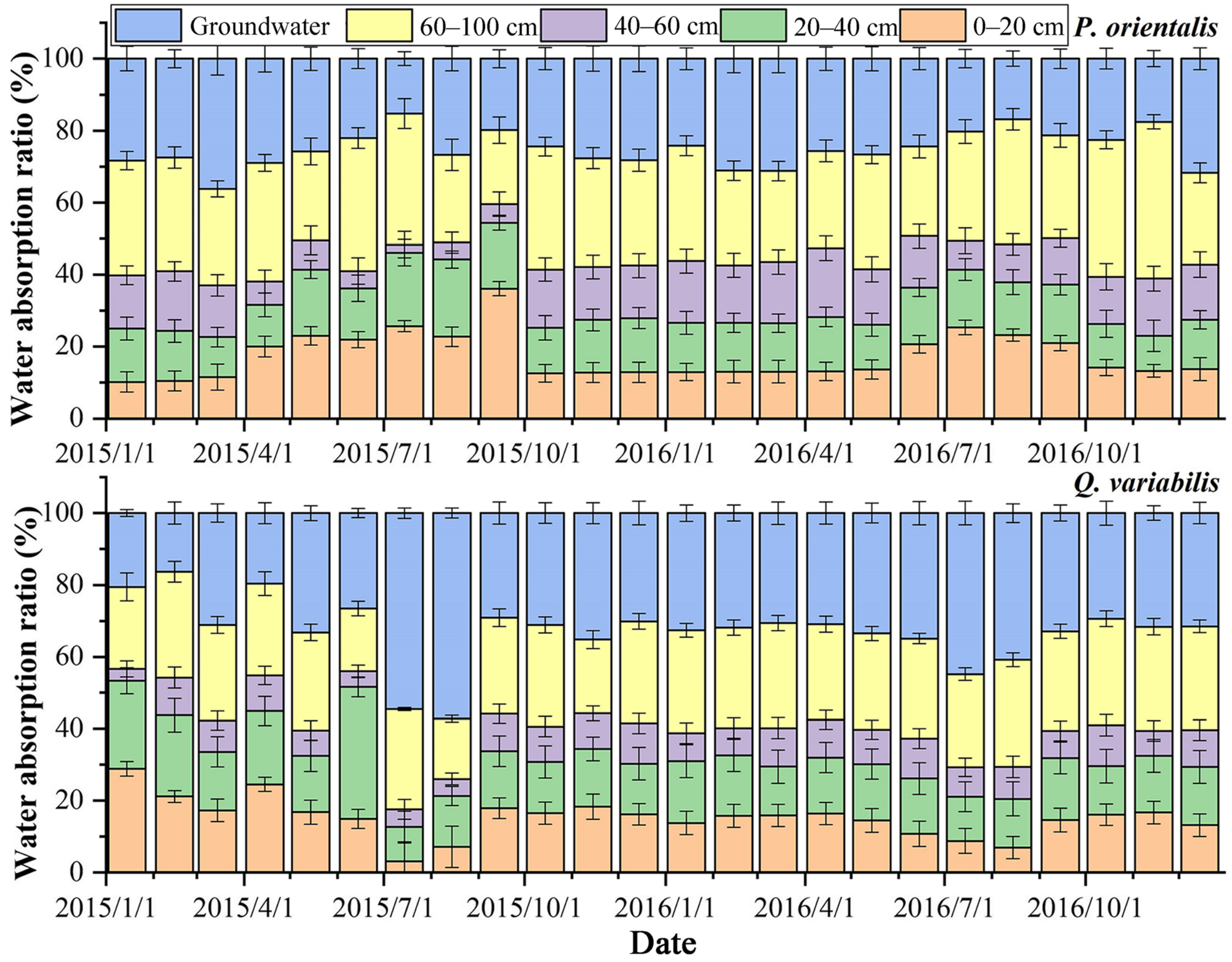

Fig. 5 Mean (± SD) absorption ratios of *Platycladus orientalis* and *Quercus variabilis* from different water sources in the Forest Ecosystem Positioning Research Station, North China during the study period

water diffusion was higher, resulting in a higher SFR. Nocturnal sap flow does not necessarily represent nocturnal transpiration since there is a time lag effect in sap flow and stomatal aperture at night (Phillips et al. 2003). A positive correlation between nocturnal sap flow and the VPD indicates water used for transpiration by the trees at night (Green et al. 1989; Hogg and Hurdle 1997; Fisher et al. 2007). Otherwise, this water will be stored in the trunk at night. However, in this study, the correlation between sap flow rate and VPD was weak, implying that the sap flow at night was used for water storage in the trunk but not for nocturnal transpiration. The presence of nocturnal fluid flow comprising 5%–6% of total sap flow has been confirmed in both *P. orientalis* and *Q. variabilis*, which is consistent with the findings in previous studies (Forster 2014; Siddiq and Cao 2018; Chen et al. 2020). The water storage capacity of trees depends on the trunk volume and the water pressure difference between the tree volume and root cap (Huang et al. 2017). This is consistent with the tree capacity, nocturnal water storage, and transpiration during the day in *Q. variabilis* being significantly higher than in *P. orientalis.* Nocturnal water storage alleviates drought stress and helps plants overcome intense evaporation in the dry season (Huang et al. 2017). Nocturnal sap flow also facilitates oxygen and nutrient transport. For example, in *Betula*, it provides sufficient oxygen to sapwood parenteral cells (Daley and Phillipa 2006).

In addition, the phenomenon of hydraulic redistribution in *P. orientalis* was previously established in our study area (Liu et al. 2019). Nocturnal sap flow reduces the water potential in plant leaves, negatively affecting the hydraulic redistribution (Yu et al. 2018; Howard et al. 2009). Moreover, the findings in our

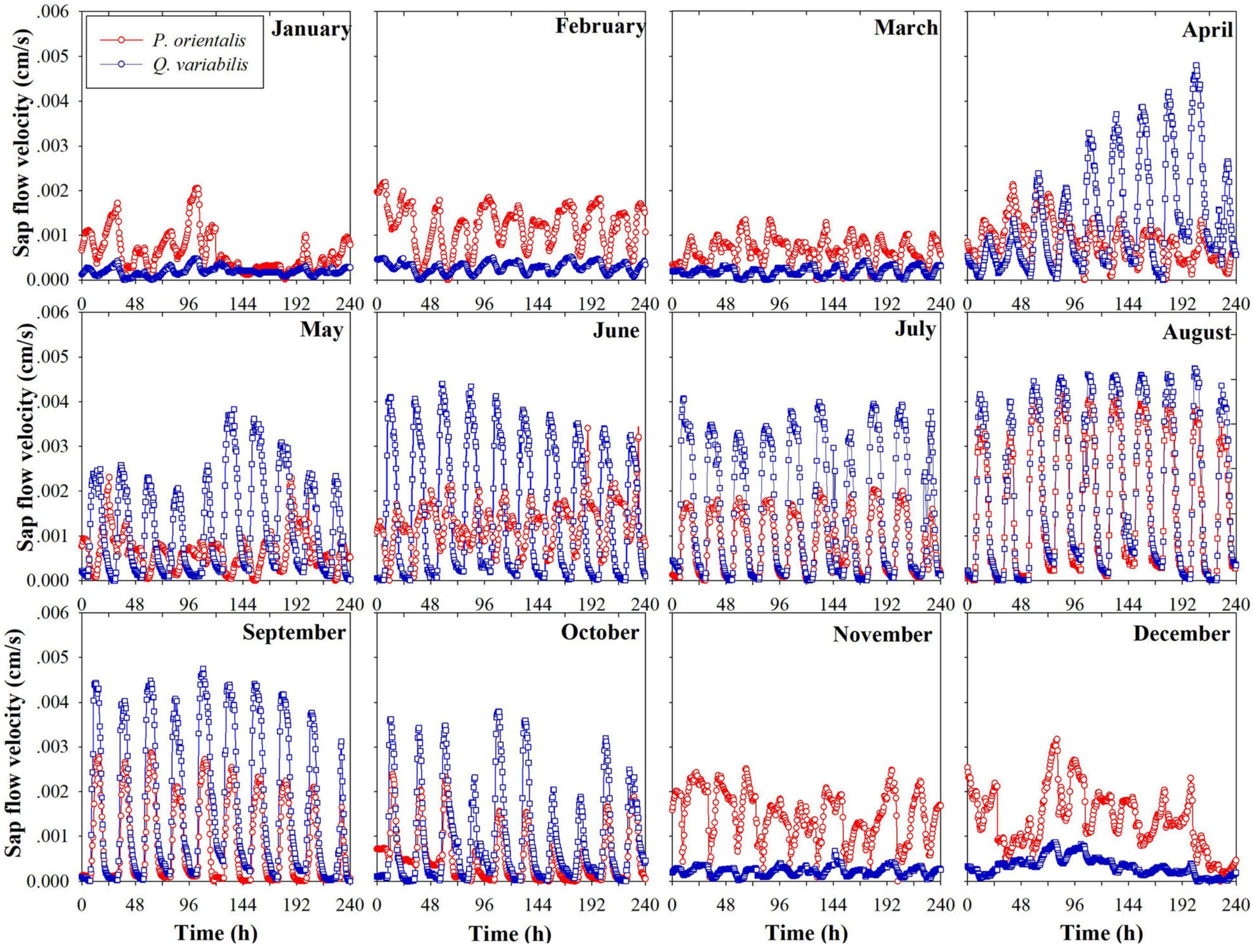

Fig. 6 Typical diurnal variation in sap flow rates in *Platycladus orientalis* and *Quercus variabilis* in the Forest Ecosystem Positioning Research Station, North China during the study period. The figure shows the observed sap flow rates randomly selected for 10 consecutive days in each month

study suggest that nocturnal sap flow and root hydraulic redistribution can occur simultaneously, consistent with previous findings, which demonstrated hydraulic redistribution contributes to the occurrence of nocturnal sap flow (Matimati et al. 2014; Fu et al. 2018; Hafner et al. 2020). The root hydraulic redistribution in *P. orientalis* effectively alleviates the spatial heterogeneity of soil water that meets its water requirement and neighboring trees (Matimati et al. 2014; Fan et al. 2017). *P. orientalis* water usage facilitates water sharing, which is conducive to the coexistence of different species. Although the sap flow and diurnal transpiration in *P. orientalis* were lower than those of *Q. variabilis*, the proportion of water stored was higher in *P. orientalis*, implying that *P. orientalis* balances the water deficit better than *Q. variabilis*. This also explains why *P. orientalis* is widely distributed as a pioneer tree species in North China. The amount of water stored in *P. orientalis* and *Q. variabilis* comprised 6%–7% of the total water quantity, which cannot be ignored.

Conclusions

We used an isotope technique and the heat ratio method to quantify the utilization ratio of water source and sap flow and determine the proportion of water used in transpiration and storage. The results indicated that *P. orientalis* and *Q. variabilis* uptake water from multiple sources simultaneously and showed strong plasticity to water sources. *P. orientalis* was sensitive to the variation in SWC and quickly absorbed surface soil water during the rainy season. *Q. variabilis* absorbed water from sources with higher and stable water content and did not change its sources, but did increase its uptake of groundwater during the rainy season. The sap flow in *P. orientalis* and *Q. variabilis* was mainly used for transpiration, and 6%–7% of the water was used for

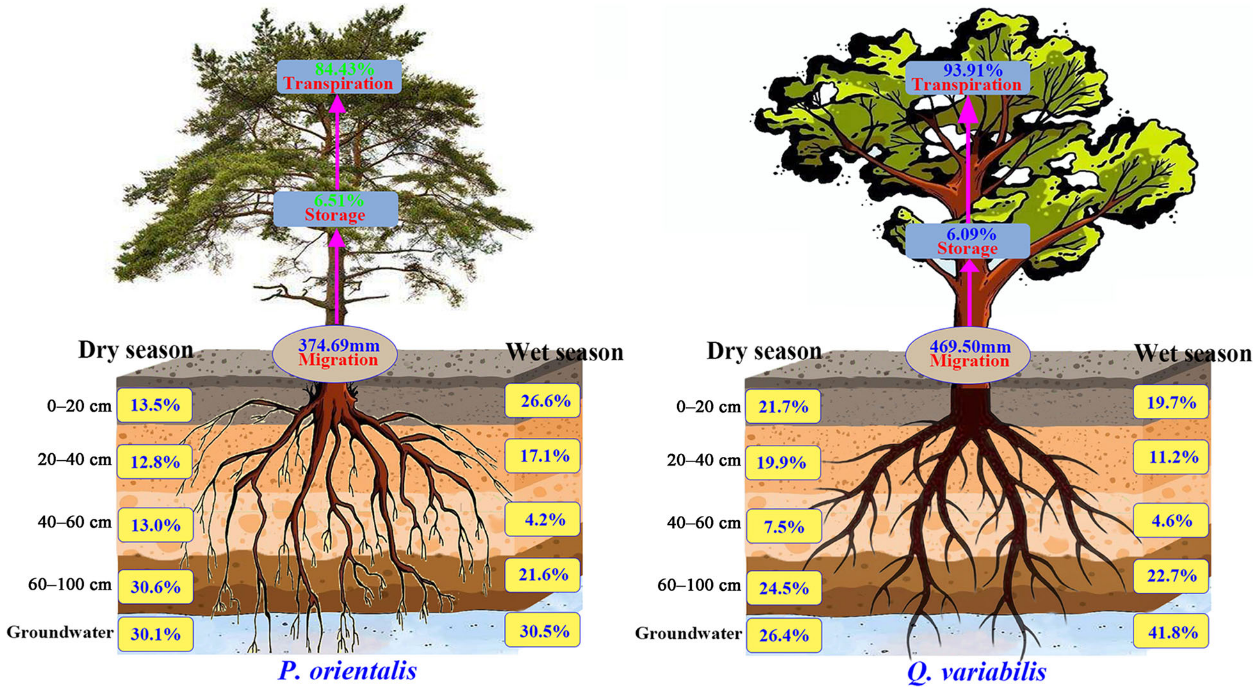

Fig. 7 Schematic representation of water uptake, migration, and use in *Platycladus orientalis* and *Quercus variabilis*. The blue font in the yellow box indicates the absorption ratio of trees from each water source during the dry and wet seasons. The numbers that are light blue indicate the migration flux in trees throughout the year, while the pink arrow indicates the water usage process in trees

storage in the trunk. However, a long-term survey of plant water movement partitioning is needed to provide more insights on the partitioning of tree water usage into storage and transpiration in such mixed forest systems.

Abbreviations

VPD: Vapor pressure deficit; DBH: Diameter at breast height; SWC: Soil water content; S: Water storage; Q_{Tr}: Quantification of the water used for transpiration; SFR: Sap flow rates; TR: Total solar radiation

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40663-021-00353-5.

Additional file 1.

Acknowledgments

We thank Huan Zhang and Weiwei Lu for their help with fieldwork.

Authors' contributions

LZ, JG, LQ, and YX conceived and designed the experiment. LZ and ZH participated in setting up the experiments and data collection. All the authors participated in compiling and analyzing the data and preparing the manuscript.

Funding

This research was funded by the National Natural Science Foundation of China (No. 42007182) and the self made experimental teaching instruments of Nanjing Forestry University in 2021 (nlzzyq202127).

Availability of data and materials

Available on request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not Applicable.

Competing interests

The authors declare no competing interests.

Author details

[1]Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037, China. [2]Key Laboratory of Soil and Water Conservation and Desertification Combating of Ministry of Education, Beijing Forestry University, Beijing 100083, China.

Received: 16 July 2021 Accepted: 20 October 2021

References

Allen RG, Pereira LS, Howell TA, Jensen ME (2011) Evapotranspiration information reporting: I. factors governing measurement accuracy. Agr Water Manage 98(6):899–920. https://doi.org/10.1016/j.agwat.2010.12.015

Alvarado-Barrientos MS, Holwerda F, Geissert DR, Muñoz-Villers LE, Gotsch SG, Asbjornsen H, Dawson TE (2015) Nighttime transpiration in a seasonally dry tropical montane cloud forest environment. Trees 29(1):259–274. https://doi.org/10.1007/s00468-014-1111-1

Barbeta A, Mejia-Chang M, Ogaya R, Voltas J, Dawson TE, Penuelas J (2015) The combined effects of a long-term experimental drought and an extreme drought on the use of plant-water sources in a Mediterranean forest. Glob Change Biol 21(3):1213–1225. https://doi.org/10.1111/gcb.12785

Barbeta A, Ogaya R, Peuelas J (2012) Comparative study of diurnal and nocturnal sap flow of *Quercus ilex* and *Phillyrea latifolia* in a Mediterranean holm oak forest in Prades (Catalonia, NE Spain). Trees 26(5):1651–1659. https://doi.org/10.1007/s00468-012-0741-4

Binks O, Coughlin I, Mencuccini M, Meir P (2020) Equivalence of foliar water uptake and stomatal conductance? Plant Cell Environ 43(2):524–528. https://doi.org/10.1111/pce.13663

Buckley TN, Turnbull TL, Pfautsch S, Gharun M, Adams MA (2020) Differences in water use between mature and post-fire regrowth stands of subalpine *Eucalyptus delegatensis* R. baker. Forest Ecol Manag 270:1–10. https://doi.org/10.1016/j.foreco.2012.01.008

Cai G, Vanderborght J, Langensiepen M, Schnepf A, Hüging H, Vereecken H (2018) Root growth, water uptake, and sap flow of winter wheat in response to different soil water conditions. Hydrol Earth Syst Sci 22(4):2449–2470. https://doi.org/10.5194/hess-22-2449-2018

Cavender-Bares J, Sack L, Savage J (2007) Atmospheric and soil drought reduce nocturnal conductance in live oaks. Tree Physiol 27(4):611–620. https://doi.org/10.1093/treephys/27.4.611

Chen Z, Zhang ZQ, Sun G, Chen L, Chen S (2020) Biophysical controls on nocturnal sap flow in plantation forests in a semi-arid region of northern China. Agric For Meteorol 284:107904. https://doi.org/10.1016/j.agrformet.2020.107904

Cuneo IF, Knipfer T, Mandal P, Brodersen CR, McElrone AJ (2018) Water uptake can occur through woody portions of roots and facilitates localized embolism repair in grapevine. New Phytol 218(2):506–516. https://doi.org/10.1111/nph.15032

Daley MJ, Phillipa NG (2006) Interspecific variation in nighttime transpiration and stomatal conductance in a mixed New England deciduous forest. Tree Physiol 26(4):411–419. https://doi.org/10.1093/treephys/26.4.411

Dawson TE, Ehleringer JR (1991) Streamside trees that do not use stream water. Nature 350(6316):335–337. https://doi.org/10.1038/350335a0

Di N, Wang Y, Clothier B, Liu Y, Jia LM, Xi BY, Shi HX (2019a) Modeling soil evaporation and the response of the crop coefficient to leaf area index in mature *Populus tomentosa* plantations growing under different soil water availabilities. Agric For Meteorol 264:125–137. https://doi.org/10.1016/j.agrformet.2018.10.004

Di N, Xi B, Clothier B, Wang Y, Li G, Jia LM (2019b) Diurnal and nocturnal transpiration behaviors and their responses to groundwater-table fluctuations and meteorological factors of *Populus tomentosa* in the North China plain. Forest Ecol Manag 448:445–456. https://doi.org/10.1016/j.foreco.2019.06.009

Ehleringer JR, Philips SL, Schuster WSF, Sandquist DR (1991) Differential utilization of summer rains by desert plants. Oecologia 88(3):430–434. https://doi.org/10.1007/BF00317589

Evaristo J, Mcdonnell JJ, Scholl MA, Bruijnzeel LA, Chun KP (2016) Insights into plant water uptake from xylem-water isotope measurements in two tropical catchments with contrasting moisture conditions. Hydrol Process 30(18): 3210–3227. https://doi.org/10.1002/hyp.10841

Fan Y, Miguez-Macho G, Jobbágy EG, Jackson RB, Otero-Casal C (2017) Hydrologic regulation of plant rooting depth. PNAS 114(40):10572–10577. https://doi.org/10.1073/pnas.1712381114

Fisher JB, Baldocchi DD, Misson L, Dawson TE, Goldstein AH (2007) What the towers don't see at night: nocturnal sap flow in trees and shrubs at two AmeriFlux sites in California. Tree Physiol 27(4):597–610. https://doi.org/10.1093/treephys/27.4.597

Flo V, Martinez-Vilalta J, Steppe K, Schuldt B, Poyatos R (2019) A synthesis of bias and uncertainty in sap flow methods. Agric For Meteorol 271:362–374. https://doi.org/10.1016/j.agrformet.2019.03.012

Forster MA (2014) How significant is nocturnal sap flow? Tree Physiol 34(7):757–765. https://doi.org/10.1093/treephys/tpu051

Fu C, Wang G, Bible K, Goulden ML, Saleska SR, Scott RL, Cardon ZG (2018) Hydraulic redistribution affects modeled carbon cycling via soil microbial activity and suppressed fire. Glob Change Biol 24(8):3472–3485. https://doi.org/10.1111/gcb.14164

Fu S, Sun L, Luo Y (2016) Combining sap flow measurements and modelling to assess water needs in an oasis farmland shelterbelt of *Populus simonii carr*, in Northwest China. Agr Water Manage 177(177):172–180. https://doi.org/10.1016/j.agwat.2016.07.015

Gebauer RLE, Ehleringer JR (2000) Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81(5): 1415–1424. https://doi.org/10.1890/0012-9658(2000)081[1415:WANUPF]2.0.CO;2

Green SR, McNaughton KG, Clothier BE (1989) Observations of night-time water use in kiwifruit vines and apple trees. Agric For Meteorol 48(3-4):251–261. https://doi.org/10.1016/0168-1923(89)90072-5

Gribovszki Z, Kalicz P, Szilágyi J, Kucsara M (2015) Riparian zone evapotranspiration estimation from diurnal groundwater level fluctuations. J Hydrol 349(1–2):6–17

Hafner BD, Hesse BD, Grams TEE (2020) Friendly neighbours: hydraulic redistribution accounts for one quarter of water used by neighbouring drought stressed tree saplings. Plant Cell Environ 7:13852

Hentschel R, Bittner S, Janott M, Biernath C, Holst J, Ferrio JP, Gessler A, Priesack E (2013) Simulation of stand transpiration based on a xylem water flow model for individual trees. Agric For Meteorol 182:31–42. https://doi.org/10.1016/j.agrformet.2013.08.002

Hogg EH, Hurdle PA (1997) Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. Tree Physiol 17(8-9):501–509. https://doi.org/10.1093/treephys/17.8-9.501

Howard AR, Iersel MWV, Richards JH, Donovan LA (2009) Night-time transpiration can decrease hydraulic redistribution. Plant Cell Environ 32(8):1060–1070. https://doi.org/10.1111/j.1365-3040.2009.01988.x

Huang C-W, Domec J-C, Ward EJ, Duman T, Manoli G, Parolari AJ, Katul GG (2017) The effect of plant water storage on water fluxes within the coupled soil-plant system. New Phytol 213(3):1093–1106. https://doi.org/10.1111/nph.14273

Jia G, Liu Z, Chen L, Yu X (2017) Distinguish water utilization strategies of trees growing on earth-rocky mountainous area with transpiration and water isotopes. Ecol Evol 7(24):10640–10651. https://doi.org/10.1002/ece3.3584

Liu ZQ, Jia GD, Yu XX (2020) Variation of water uptake in degradation agroforestry shelterbelts on the North China plain. Agric Ecosyst Environ 1(287):106697. https://doi.org/10.1016/j.agee.2019.106697

Liu ZQ, Yu XX, Jia GD (2019) Water uptake by coniferous and broad-leaved forest in a rocky mountainous area of northern China. Agric For Meteorol 265:381–389. https://doi.org/10.1016/j.agrformet.2018.11.036

Maherali H, DeLucia EH (2001) Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. Oecologia 129(4):481–491. https://doi.org/10.1007/s004420100758

Matimati I, Verboom GA, Cramer MD (2014) Do hydraulic redistribution and nocturnal transpiration facilitate nutrient acquisition in aspalathus linearis? Oecologia 175(4):1129–1142. https://doi.org/10.1007/s00442-014-2987-6

McCormick EL, Dralle DN, Hahm WJ, Tune AK, Schmidt LM, Chadwick KD, Rempe DM (2021) Widespread woody plant use of water stored in bedrock. Nature 597(7875):225–229. https://doi.org/10.1038/s41586-021-03761-3

Molina AJ, Aranda X, Llorens P, Galindo A, Biel C (2019) Sap flow of a wild cherry tree plantation growing under mediterranean conditions: assessing the role of environmental conditions on canopy conductance and the effect of branch pruning on water productivity. Agr Water Manage 218:222–233. https://doi.org/10.1016/j.agwat.2019.03.019

Moreno-Gutiérrez C, Dawson TE, Nicolás E, Querejeta JI (2012) Isotopes reveal contrasting water use strategies among coexisting plant species in a Mediterranean ecosystem. New Phytol 196(2):489–496. https://doi.org/10.1111/j.1469-8137.2012.04276.x

Nadezhdina N, David JS, Pinto CA, David TS (2020) Root sap flow as a tool to establish hydrological thresholds for plant growth and survival. Agr Water Manage 241:106388. https://doi.org/10.1016/j.agwat.2020.106388

Nie YP, Chen HS, Wang KL, Tan W, Deng PY, Yang J (2011) Seasonal water use patterns of woody species growing on the continuous dolostone out cropsand nearby thin soils in subtropical China. Plant Soil 341(1–2):399–412. https://doi.org/10.1007/s11104-010-0653-2

Palacio S, Azorín J, Montserrat-Martí G, Ferrio JP (2014) The crystallization water of gypsum rocks is a relevant water source for plants. Nat Commun 5(8):4660. https://doi.org/10.1038/ncomms5660

Peddinti SR, Kambhammettua BVNP, Lad RS, Šimůnek J, Gade RM, Adinarayana J (2020) A macroscopic soil-water transport model to simulate root water uptake in the presence of water and disease stress. J Hydrol 587:124940. https://doi.org/10.1016/j.jhydrol.2020.124940

Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models: alternative methods. Oecologia 144(4):520–527. https://doi.org/10.1007/s00442-004-1816-8

Phillips N, Ryan M, Bond B, McDowell N, Hinckley T, Čermák J (2003) Reliance on stored water increases with tree size in three species in the Pacific northwest. Tree Physiol 23(4):237–245. https://doi.org/10.1093/treephys/23.4.237

Poca M, Coomans O, Urcelay C, Zeballos SR, Bodé S, Boeckx P (2019) Isotope fractionation during root water uptake by *Acacia caven* is enhanced by arbuscular mycorrhizas. Plant Soil 441(1-2):485–497. https://doi.org/10.1007/s11104-019-04139-1

Resco de Dios V, Loik ME, Smith R, Aspinwall MJ, Tissue DT (2016) Genetic variation in circadian regulation of nocturnal stomatal conductance enhances carbon assimilation and growth. Plant Cell Environ 39(1):3–11. https://doi.org/10.1111/pce.12598

Ripullone F, Camarero JJ, Colangelo M, Voltas J (2020) Variation in the access to deep soil water pools explains tree-to-tree differences in drought-triggered dieback of mediterranean oaks. Tree Physiol 40(5):591–604. https://doi.org/10.1093/treephys/tpaa026

Siddiq Z, Cao KF (2018) Nocturnal transpiration in 18 broadleaf timber species under a tropical seasonal climate. Forest Ecol Manag 418:47–54. https://doi.org/10.1016/j.foreco.2017.12.043

Siddiq Z, Chen YJ, Zhang YJ, Zhang JL, Cao KF (2017) More sensitive response of crown conductance to VPD and larger water consumption in tropical evergreen than in deciduous broadleaf timber trees. Agric For Meteorol 247:399–407. https://doi.org/10.1016/j.agrformet.2017.08.028

Wang J, Fu B, Lu N, Zhang L (2017) Seasonal variation in water uptake patterns of three plant species based on stable isotopes in the semi-arid loess plateau. Sci Total Environ 609:27–37. https://doi.org/10.1016/j.scitotenv.2017.07.133

Weatherley PE (1982) Water uptake and flow in roots. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology II. Springer, Berlin, pp 79–109. https://doi.org/10.1007/978-3-642-68150-9_4

Wu XP, Liu S, Luan J, Wang Y, Cai C (2019) Responses of water use in Moso bamboo (*Phyllostachys heterocycla*) culms of different developmental stages to manipulative drought. For Ecosyst 6(1):31. https://doi.org/10.1186/s40663-019-0189-8

Wu Y, Du T, Li F, Li S, Ding R, Tong L (2016) Quantification of maize water uptake from different layers and root zones under alternate furrow irrigation using stable oxygen isotope. Agr Water Manage 168:35–44. https://doi.org/10.1016/j.agwat.2016.01.013

Yang B, Wen X, Sun X (2015) Seasonal variations in depth of water uptake for a subtropical coniferous plantation subjected to drought in an east Asian monsoon region. Agric For Meteorol 201:218–228. https://doi.org/10.1016/j.agrformet.2014.11.020

Yu T, Feng Q, Si J, Mitchell PJ, Forster MA, Zhang X (2018) Depressed hydraulic redistribution of roots more by stem refilling than by nocturnal transpiration for *Populus euphratica* Oliv. In situ measurement. Ecol Evol 8(5):2607–2616. https://doi.org/10.1002/ece3.3875

Zeppel MJB, Lewis JD, Phillips NG, Tissue DT (2014) Consequences of nocturnal water loss: a synthesis of regulating factors and implications for capacitance, embolism and use in models. Tree Physiol 34(10):1047–1055. https://doi.org/10.1093/treephys/tpu089

Zhang H, Levia DF, He B, Wu H, Liao A, Carlyle-Moses DE, Liu J, Wang N, Li J, Fu C (2020) Interspecific variation in tree- and stand-scale stemflow funneling ratios in a subtropical deciduous forest in eastern China. J Hydrol 590:125455. https://doi.org/10.1016/j.jhydrol.2020.125455