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Water storage of plants cannot be ignored during the process of water movement

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Abstract

Water migration and use are important processes in trees. However, it is possible to overestimate transpiration by equating the water absorbed by plant roots with that diffused back to the atmosphere via the stomata. The $\delta^2\text{H}/\delta^{18}\text{O}$ technique and heat ratio method were used to explore the patterns of water use of coniferous and broad-leaved tree species to determine the proportions of water used for transpiration and water storage. Our results indicate that both species showed strong plasticity in their use of water sources. The species *Platycladus orientalis* (Oriental arbor-vitae) and *Quercus variabilis* (Chinese cork oak) primarily absorbed water from groundwater and the 60–100 cm soil layer, and *Q. variabilis* also absorbed water from the 0–20 cm and 20–40 cm soil layers during the dry season. Only *P. orientalis* was sensitive to precipitation and used water from the 0–20 cm layers. *Q. variabilis* did not change its water source but increased its uptake of groundwater during the rainy season. We observed reverse flow and hydraulic redistribution in *P. orientalis*, which alleviated the spatial heterogeneity of soil water and provided water for neighboring trees. Nocturnal sap flow in *P. orientalis* and *Q. variabilis* facilitated the storage of water in the trunk. The water used for storage in both species comprised 6–7% of the total quantity and therefore, should be considered in water balance models.

Key Words: Water migration; Water uptake; Nocturnal sap flow; Transpiration

1. Introduction

Water is a key factor that affects the circulation of materials and plant growth in forest ecosystems (Nadezhdina *et al.* 2020). Soil water is absorbed by plants through the roots and stored in the xylem or used for photosynthesis; it also evaporates and reaches the atmosphere through

leaf stomata (Weatherley et al. 1982; Buckley *et al.* 2012; Adrià *et al.* 2015; Huang *et al.* 2017; Molina *et al.* 2019). Stable hydrogen and oxygen isotope technology provides a new technical manner to explore the source of water for plants and solves the difficulty of quantifying the ratio of absorption of plants to each layer of water source (Wang et al. 2017). Because there is no isotopic fractionation of hydrogen and oxygen isotopes in water during the process of water uptake by plant roots and transportation from xylem to leaves (Ehleringer et al. 1991), the hydrogen and oxygen isotopic values of xylem and source water can be compared based on the isotopic mass conservation law. Mixed models (Iso-source or MixSIAR) were used to quantify the ratio of utilization by the plants of each layer of water source (Philips et al. 2005). Dawson and Ehleringer (1991) was the first research group to use stable hydrogen and oxygen isotope technology to explore the water sources of plants. They found that the tree species that grew on the riverside did not use the river water but used the soil water on the riverside. Since then, there have been reports about the water sources of plants in China and throughout the world (Nie et al. 2011; Moreno et al. 2012; Yang et al. 2015; Kirchen et al. 2017; María et al. 2019; Liu et al. 2020)

Several studies have investigated the ratio of absorption of plants for various water sources, as well as that of diurnal transpiration (Palacio *et al.* 2014; Wu *et al.* 2016; Liu *et al.* 2020). Although previous studies state that the stomata are closed at night, and there is no sap flow during this period (Zeppel 2014; Zhang *et al.* 2020), with the development and improvement of new technologies, the phenomenon of nocturnal sap flow has been confirmed in plants in different habitats (Hentschel *et al.* 2013; Siddiq *et al.* 2018; Chen *et al.* 2020). Owing to the small proportion of nocturnal sap flow to the overall sap flow, traditional models have rarely considered nocturnal sap flow. However, for some species, ecosystems and regions, nocturnal sap flow comprises a large proportion of overall sap (Susana *et al.* 2015; Di *et al.* 2019; Flo *et al.* 2019). For example, Barbeta *et al.* (2012) found that in *Quercus ilex* (holly oak) in a Mediterranean climate with limited precipitation, the nocturnal sap flow can reach 40% of the overall flow. Cavender *et al.* (2007) reported that the nocturnal sap flow of *Q. oleoides* in the central USA increased from 8% during the rainy season to 20% during the dry season. Against the background of such findings, nocturnal sap flow cannot be neglected. Nocturnal sap flow can effectively improve the leaf and stem water potential before dawn and reduce the formation of embolisms in

the xylem (Forster 2014). However, it should be highlighted that nocturnal sap flow is not equivalent to nocturnal transpiration (Binks *et al.* 2020). During the night, one part of the sap is transpired through the stomata, and the other part is used to supplement the stem water. Water supplementation comprises 40–70% of the nocturnal sap flow, whereas transpiration accounts for 30–60% of the nocturnal sap flow (Zoltán *et al.* 2015). Cheng *et al.* (2017) suggested that night transpiration can drive the supplementation of water. Currently, there is no adequate technology to observe the quantification of transpiration and supplementation of water, since these two processes occur simultaneously or successively. However, based on the relationship of response between transpiration and the vapor pressure deficit (VPD), transpiration and water supplementation can be distinguished (Resco *et al.* 2016; Siddiq *et al.* 2017; Di *et al.* 2019), based on the fact that the main factor that causes nocturnal transpiration is the water VPD. In this sense, when the water VPD approaches zero, if sap flow still occurs, it is used to supplement the stem water. If it 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 transported. However, the amount of nocturnal water supplementation has largely been ignored. As a consequence, when calculating the water balance of an ecosystem, substantial errors may incur, impacting the development of management strategies. If the amounts of each water fraction used for transpiration and nocturnal sap flow were accurately quantified, the existing formulae or models could be revised. In addition, frequent extreme precipitation events increase the spatiotemporal heterogeneity of soil water under the background of global climate change. However, it is not clear how tree species adapt to this heterogeneity by changing water sources. Therefore, it is urgent to quantitatively distinguish the adaptation process of the sources of water to soil water change in a mixed forest. In this study, we used the isotope ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) technique and heat ratio method to: i) explore how the water sources of tree species adapt to water variation; ii) quantify the amount of water that flows in the nocturnal sap and determine the proportions of transpiration and plant water storage. Our results provide a scientific reference to further investigate the underlying mechanisms of water cycling in forest ecosystems.

2. Materials and methods

2.1 Site description

This study was conducted in the Forest Ecosystem Positioning Research Station in Beijing (40°03'N, 116°05'E), with an average elevation of 240 m. The area is located in a semi-humid and semiarid continental monsoon climate zone in the warm temperate zone of north China. The annual average precipitation is 630 mm with an annual potential evapotranspiration of 1,800 mm. The precipitation is concentrated during the period from June to September, comprising 70% of the annual precipitation. The average annual temperature is 11.6°C with 2,662 hours of sunshine on average. The forest vegetation is primarily composed of *Platycladus orientalis* and *Quercus variabilis* plantations that were established after the 1960s. Underneath the canopy, *Broussonetia papyrifera*, *Vitex negundo*, *Lespedeza bicolor* Turcz, and other species of shrubs are present. The soil type is leached cinnamon soil with a thickness of 80–100 cm. The humus content in the surface soil is high, and the deep soil primarily consists of gravel.

2.2 Experimental design

We established three 20 × 20 m plots in the study area. Six *P. orientalis* and *Q. variabilis* plants were randomly selected from each plot, with average height, diameter at breast height (DBH), and crown width (Table 1). In each plot, an ECH₂O soil moisture sensor (Decagon Devices, Pullman, WA, USA) was installed at three sampling points to measure the soil water content (SWC) of 0–20, 20–40, 40–60, 60–80, and 80–100 cm. The ECH₂O sensors were connected to the Em50/R data collection box (Decagon Devices) that recorded every 30 min. We collected the data using a computer simultaneously as the samples were collected.

Table 1 Basic information about the tree species measured

Tree species	Number	Average height (m)	DBH(diameter at breast height cm)
<i>Platycladus orientalis</i>	37	7.16 ± 1.53	7.60 ± 2.83
<i>Quercus variabilis</i>	43	9.18 ± 1.15	11.59 ± 3.91

2.3 Quantification of the water amounts used for physiological processes

2.3.1 Determination of the water source

(1) Sampling of branches, soil, groundwater, and roots

In each sample plot, three trees with good growth and similar height/DBH were randomly

selected, and annual non-green branches (0.3–0.6 cm in diameter) were collected at the same height from ground. The green part of the branches was removed with scissors, and the xylem was retained. Three samples were collected from each tree.

Soil samples that were 0–20, 20–40, 40–60, 60–80, and 80–100 cm deep were collected from 0.5 to 1 m near the sampled trees using an auger with a diameter of 3.5 cm and a length of 120 cm. All the branches and soil samples that were collected 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 (116°05'E, 40°03'N) 310 m southwest of the plots.

(2) Stable isotope analysis

The isotopic ratios of the samples were determined in the Laboratory of Ecohydrological Processes and Mechanisms, Beijing Forestry University, Beijing, China. The water in soil and branches was extracted by low temperature vacuum condensation before analysis, and $\delta^2\text{H}/\delta^{18}\text{O}$ 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". The precision of determination was 0.3 and 0.1‰, respectively, and expressed as follows:

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

(3) Ratio of water absorption by trees

The isotopic ratios of water in the branches carry the isotopic information of all the water sources as water is absorbed by the tree roots. Owing to this fact, the MixSIAR model can be used to quantify the water absorption ratio of trees (Phillips & Gregg 2003) using the following equations:

$$\delta X = c_1\delta X_1 + c_2\delta X_2 + c_3\delta X_3 + c_4\delta X_4 + c_5\delta X_5 + c_6\delta X_6 + c_7\delta X_7 \quad (\text{Eq. 2})$$

$$c_1 + c_2 + c_3 + c_4 + c_5 + c_6 + c_7 = 1, \quad (\text{Eq. 3})$$

where δX is the $\delta^2\text{H}/\delta^{18}\text{O}$ value of tree branch water (‰); $X_1, X_2, X_3, X_4, X_5, X_6$, and X_7 are the $\delta^2\text{H}/\delta^{18}\text{O}$ values of each potential water source, respectively; and $c_1, c_2, c_3, c_4, c_5, c_6$, and c_7 represent the absorption ratio of trees to each potential water source.

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

The sap flow meters (SFM₁, HRM 30, ICT International PTY, Armidale, Australia), namely flow meters that utilized the heat ratio method (HRM) were installed at the DBH, taproots and used with the fine roots of selected plants to monitor sap flow rate. The SFM₁ flowmeter contains three probes, which can simultaneously measure two-way flows. In addition, the SFM₁ is more accurate at monitoring the sap flow rate. Three specimens each of *P. orientalis* and *Q. variabilis* that met the 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 cores were taken from each tree at the breast height (1.3 m) from different sections of the stem using a borer that had 5 mm increments, and the radii of cross-sections and heartwood were measured with a ruler. Three cylindrical probes were inserted into the sapwood of the tree hole at the breast height, taproots, and fine roots of each selected plant. The device was wrapped and sealed with insulated and radiation proof aluminum foil to prevent rainwater from entering and avoid direct solar radiation. The SFM₁ flowmeter set the data acquisition interval at 10 min, and the water that migrates through the tree can be calculated using the following equations:

$$Q = V_s A_s = V_{ot} A_1 + V_{in} A_2 \quad (\text{Eq. 4})$$

$$V_s = \frac{V_h \rho_b (c_w + m_c c_s)}{\rho_s c_s} \quad (\text{Eq. 5})$$

$$V_h = \frac{k}{x} \ln\left(\frac{t_1}{t_2}\right) \times 3600, \quad (\text{Eq. 6})$$

where Q is the total migration (mL); V_s is the sap flow velocity (cm/s); A_s is the sapwood area (cm²); V_{ot} and V_{in} are the sap flow velocity of the thermocouple inside and outside the temperature probe (cm/s), respectively; A_1 and A_2 are the areas of the outer ring and the inner ring, respectively (cm²); V_h is the heat pulse rate (cm/s); k is the thermal diffusion coefficient of fresh wood; t_1 and t_2 are the temperature variations in the upward and downward directions, respectively (ire ρ_b is the wood density (g/cm³); c_w and c_s are the specific heat capacity of fresh wood (1,200 J·kg⁻¹·°C⁻¹, 200 and of sap (water, 4,182 J·kg⁻¹·°C⁻¹, 202, and m_c and ρ_s are the moisture content and density of fresh wood, respectively).

2.3.3 Quantification of the water used for migration

The water migrated by trees can be divided into transpiration and water storage.

(1) Quantification of the water used for water storage (S)

Nocturnal sap flow does not necessarily represent nocturnal transpiration because it is also a very important supplement to diurnal water loss (Phillips et al. 2003). When there is a positive correlation between nocturnal sap flow and the VPD, it is considered that the trees transpire at night (Green et al 1989; Hogg and Hurdle 1997; Fisher et al 2007). Otherwise, the tree will store water at night. The storage time of water stored by trees was determined by fitting the correlation of the VPD and radiation with sap flow velocity after translation motion. The nocturnal sap flow was translated with time and fitted with the VPD. The translation time with the highest correlation was the water storage time of plants. The migration flux during this time was the water storage capacity. Formulae 4-6 describe the process of calculating the liquid flow rate. The VPD was calculated as follows:

$$VPD=0.61078 \times e^{\frac{17.27 \times Ta}{Ta+237.3}} \times (1 - RH) \quad (\text{Eq. 7})$$

where Ta and RH are atmospheric temperature ($^{\circ}$) and relative humidity (%), respectively.

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

Sap flow during the stomatal opening represented plant transpiration. Therefore, the water used for transpiration was quantified by determining the stomatal opening time via the VPD and radiation.

2.4 Data analysis

All 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, water quantity, and storage. A two-way ANOVA was then used 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. All data met the requirements of normal distribution and homogeneity of variance.

3. Results

3.1 Variations in soil water content and meteorology

The precipitation and SWC clearly varied in different seasons. The total precipitation values in 2015 and 2016 were 580.0 and 649.8 mm, respectively. The precipitation from June to September was 458.2 and 523.4 mm, comprising 79.0 and 80.5% of the total annual precipitation in 2015 and 2016, respectively. This is known as the rainy season, and the other months (October to May) are considered dry seasons. The average SWC in the 0–20, 20–40, 40–60, 60–80, and 80–100 cm layers during the dry season were 11.6, 12.6, 11.9, 9.8, and 9.2%, respectively. The SWC levels of the five layers during the rainy season were 16.5, 17.0, 17.6, 14.0, and 11.2%, respectively, which were 42.2, 35.0, 39.7, 17.5, and 13.9% higher than those in the dry season. The SWC in five soil layers increased at different degrees after it rained, followed by a decrease. After approximately 10 mm of precipitation, the SWC increased by 64.22% in the 0–20 cm layer, but no significant changes were observed for the other layers ($P > 0.05$). After amounts of precipitation that were > 50 mm, the SWC increased in all five soil layers, with a lag time effect in the deeper layers.

Figure 1 Variations of precipitation and mean soil water content in the Forest Ecosystem Positioning Research Station, north China, during the study period.

The total solar radiation (TR) and VPD varied in a similar manner, with an initial increase and a subsequent decrease; there was one single peak throughout the day (Fig. 2). The peak of VPD appeared 0–3 hours later than that of the TR. The TR was 0 W/m² from 19:00 to 06:00 at night, and the VPD values were generally > 0 Kpa owing to the vapor pressure from 19:00 to 06:00 at night. In January, the mean and peak values of TR were 87.1 and 174.6 W/m², respectively, and the mean and peak values of VPD were 0.35 and 0.59 Kpa, respectively. The TR and VPD values gradually increased with the seasonal variation from January to July. The mean

and peak values of TR reached 176.2 and 491.6 W/m² in July, which were 2.0- and 2.8-fold higher than the mean and peak values in January, respectively. The mean and peak values of TR decreased from August to December (96.7 and 216.6 W/m², respectively). The mean and peak values of VPD reached 2.57 and 6.84 Kpa in July, which were 7.3- and 11.6-fold higher than those in January, respectively. The mean and peak values of TR decreased from August to December (0.40 and 0.84 Kpa, respectively).

Figure 2 Variations in total solar radiation (TR) and 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. VPD, vapor pressure deficit.

3.2 Water absorption by trees

The $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of soil and branch water in *P. orientalis* and *Q. variabilis* fluctuated significantly with different seasons (Figs. 3 and 4). The $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of soil water were higher in the dry season than in the rainy season ($P < 0.05$), indicating that the isotope fractionation effect of soil water in the dry season was more pronounced than that during the rainy season. During the dry season, the levels of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ 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 ($P < 0.05$), while the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of the 80–100 cm layer were significantly lower than those of the other layers ($P < 0.05$). The $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of each layer decreased gradually during the rainy season, namely by 96.93, 46.84, 38.76, 25.92, and 15.49%, respectively, for the

Figure 3 Variations in mean ($\pm$ SD) isotopic values of soil water in the Forest Ecosystem Positioning Research Station, North China, during the study period.

The ranges of variation of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of branch water in *P. orientalis* (-105.63‰ to -37.82‰ for $\delta^2\text{H}$ and -14.09‰ to -0.19‰ for $\delta^{18}\text{O}$) were larger than those of *Q. variabilis* (-99.89‰ to -36.24‰ for $\delta^2\text{H}$ and -13.58‰ to -2.61‰ for $\delta^{18}\text{O}$). The mean values of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in the branch water of *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* (-72.68‰ and -7.70‰ , respectively). The levels of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in the branch water of *P. orientalis* during the rainy season were 45.67% and 69.93% larger than those in the dry season, while the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ levels in branch water of *Q. variabilis* increased by 6.31% and 9.53%, respectively, during the dry season.

Figure 4 Typical diurnal variations in mean ($\pm$ SD) isotopic values of soil and branch water in the Forest Ecosystem Positioning Research Station, north China, during the study period.

The water use ratios of *P. orientalis* and *Q. variabilis* to different water sources fluctuated with the seasons. *P. orientalis* and *Q. variabilis* primarily absorbed water from the groundwater and 60–100 cm layer during the dry season, and *Q. variabilis* also took up water from the 0–20 cm (21.7%) and 20–40 cm (19.9%) soil layers. *P. orientalis* not only used groundwater (30.5%) and water from the 60–100 cm soil layer (21.6%) during the rainy season but also water from the 0–20 cm layer (26.6%). The ratio of absorption of water from the 20–40 cm layer used by *Q. variabilis* during the rainy season was 47.4% lower than that during the dry season, but the ratio of absorption of groundwater uptake by *Q. variabilis* increased by 68.2%. After the rainy season, *P. orientalis* transferred its water sources to groundwater (41.2%) and the 60–100 cm soil layer (24.9%). Throughout the experimental period, *P. orientalis* used less water from the 20–40 cm and the 40–60 cm soil layers, whereas *Q. variabilis* used less water from the 40–60 cm soil layer.

Figure 5 Mean ($\pm$ SD) absorption ratios of *Platycladus orientalis* and *Quercus variabilis* for different water sources in the Forest Ecosystem Positioning Research Station, north China, during the study period.

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

The sap flow rates (SFR) of *P. orientalis* and *Q. variabilis* exhibited a "single peak" or "double peak," depending on the season (Fig. 6). The variation of SFR of *P. orientalis* during the dry season showed a "double peak" during the observation period. It gradually increased before 11:00, reached its maximum value at 11:00 and 14:30, respectively, and then decreased. In contrast, the variation of the SFR of *Q. variabilis* showed no peak during the dry season but had a single peak during the wet season. The mean SFR of *P. orientalis* (0.0008 cm/s) during the dry season was four times higher than that of *Q. variabilis* (0.0002 cm/s), and the maximum SFR of *P. orientalis* (0.0022 cm/s) was 4.4 times higher than that of *Q. variabilis* (0.0002 cm/s). The mean SFR of *P. orientalis* and *Q. variabilis* gradually increased during the rainy season with average values of 0.0008 cm/s and 0.0013 cm/s, respectively. The mean SFR of *Q. variabilis* during the wet season was 6.5 times than that in 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 mean SFR of *Q. variabilis* (0.0049 cm/s) was 62.5% higher than that of *P. orientalis* (0.0034 cm/s).

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

Since there was no reverse water migration in *Q. variabilis*, the relevant data of sap flow in *Q. variabilis* are not shown here. The “two-way” SFR of taproots, lateral roots, and tree stems of *P. orientalis* clearly fluctuated throughout the seasons. With the exception of August, the sap flow in the taproot and the lateral root of *P. orientalis* increased first and then decreased. Typically, the peak value was reached between 12:00 and 14:00, but the peak values depended on the season. The peak values of SFR in taproots and lateral roots were the highest in September, namely 93.6 and 60.6 cm³/h, respectively. The water in both the taproots and lateral roots migrated in reverse in August, with mean SFR values of 2.73 and −23.6 cm³/h, respectively. The sap flow of the stem of *P. orientalis* migrated upward during the entire experimental period. The SFR of tree stems increased first and then decreased from February to November. The peak value was 127.2 cm³/h in September. However, the SFR of the tree stem remained at 6.7 cm³/h in January and December and did not fluctuate.

Figure 7 Typical diurnal variation of “two way” water migration of *Platycladus orientalis* and *Quercus variabilis* in the tree.

3.4 Determination of the proportions of water used for transpiration and water storage

The annual mean upward water fluxes of *P. orientalis* and *Q. variabilis* were 374.69 and 469.50 mm/a, respectively (Fig. 8). The average sap flux of *P. orientalis* was 20.19% lower than that of *Q. variabilis*. The annual mean upward water flux of *Q. variabilis* was 24.9% higher than that of *P. orientalis*. The reverse water migration flux of *P. orientalis* was -8.7 mm/a, comprising 2.3% of the forward water flux. The amounts of water used by *P. orientalis* for transpiration and storage were 350.3 and 24.41 mm/a, respectively, comprising 93.49 and 6.51%, respectively, of the sap flux. The amounts of water used by *Q. variabilis* for transpiration and storage were 440.85 and 28.65 mm/a, respectively, comprising 93.91 and 6.09% of the total sap flow, respectively. This indicates that the plants used most of the water for transpiration. The water in *P. orientalis* flowed in reverse at a rate of 8.67 mm/a, comprising 2.26%, while *Q. variabilis* had no reverse flow.

Figure 8 Water flux of *Platycladus orientalis* and *Quercus variabilis* in the Forest Ecosystem Positioning Research Station, north China, during the study period.

Figure 9 Schematic representation of water uptake, migration, and use for *Platycladus orientalis* and *Quercus variabilis*. The blue font in the yellow box indicates the absorption ratio of trees to each water source during the dry and wet seasons. The numbers that are light blue indicate the migration flux of trees during the year, while the solid pink line arrow indicates the water use process of trees.

4. Discussion

4.1 Water absorption by trees

The species *P. orientalis* and *Q. variabilis* showed different patterns of water use in the same habitat, which may be related to the root distribution and water conditions. For *P. orientalis*, more than 50% of the root biomass is distributed in the soil layer of 0–20 cm (Liu et al. 2019), and the

highly developed surface root system of *P. orientalis* is more sensitive to precipitation. Therefore, this species used water from the surface soil layers after precipitation events. Jia et al. (2017) also found that *P. orientalis* primarily absorbed water from the surface soil during the rainy season to maintain normal physiological activities and switched its water source to deep soil layers during the dry season. This is known as a “dimorphic” structural feature of the root system (Evaristo et al. 2016; Cuneo et al. 2018; María et al. 2019). Previous studies also found that *Q. pubescens* L., *Populus*, *Robinia pseudoacacia* L., and *Pinus tabulaeformis* also varied in the use of their water sources (Ehleringer 2000; Liu et al. 2020; Francesco et al. 2020). In contrast to *P. orientalis*, the root system of *Q. variabilis* is uniformly distributed in different soil layers with a highly developed main root system. This species uses multiple water sources, but it uses a higher ratio of surface soil water during the dry season, probably because of the short transport distance of surface soil water and the lower energy consumption involved in its utilization. This suggests that *Q. variabilis* prefers surface soil water during the dry season, which is consistent with previous findings stating that plants with uniform root distribution preferentially absorb water from shallow soil layers (Fan et al. 2017; Cai et al. 2018; Cuneo et al. 2018). *Q. variabilis* absorbs water from the deep soil layers via its highly developed root system to maintain a high rate of transpiration during the rainy season. Wang et al. (2017) and Srinivasa et al. (2020) have demonstrated that several plants can take up deep soil water and groundwater through their developed roots throughout the growing season, thus, ensuring a stable water supply. In addition, the threshold value of the root system response to SWC is also one of the key factors that affect water use (Cuneo et al. 2018). In our study, the root system of *P. orientalis* was more sensitive to precipitation than that of *Q. variabilis*. The patterns of water uptake of *P. orientalis* and *Q. variabilis* to different water sources may be the result of long-term adaptation to seasonal arid environments, and such strategies not only help to reduce water competition with other tree species but can also improve the symbiotic ability of community species.

4.2 Water migration and use

We observed clear differences in the use of water and distribution of water proportion between the two tree species, which could be related to the characteristics of tree species themselves. Molina et al. (2019) also found that the aboveground biomass and defoliation cycle

were the main factors that affected the sap flow rate. In our study, the sap flow rate of *P. orientalis* was higher than that of *Q. variabilis* during the dormant period, probably because broad-leaved deciduous species, such as *Q. variabilis*, have already shed their leaves, while *P. orientalis* retained its leaves. The sap flow rate by *Q. variabilis* was significantly higher than that of *P. orientalis* during the growing season. This may be owing to the diameter of xylem vessel and the crown width of *Q. variabilis*, which were larger than those in *P. orientalis*, thus, significantly improving the efficiency of migration of water. In addition, *Q. variabilis* contains more stomata per leaf area than *P. orientalis*, and the speed of water diffusion is higher, resulting in a larger sap flow rate. In this study, the presence of nocturnal fluid flow was confirmed in both *P. orientalis* and *Q. variabilis*, comprising 5–6% of the total sap flow, which is consistent with the results of previous studies (Forster et al. 2014; Siddiq et al. 2018; Chen et al. 2020). However, the correlation between the rate of sap flow and VPD was poor, indicating that this part of the sap flow at night was used for water storage in the trunk but not for nocturnal transpiration. The water storage capacity of trees depends on the volume of trunk and the water pressure difference between the tree volume and root cap (Cheng et al. 2017). This can also be explained by the fact that tree capacity and transpiration during the day were significantly higher for *Q. variabilis* than for *P. orientalis*, and the nocturnal water storage of *Q. variabilis* was significantly higher than that of *P. orientalis*. Nocturnal water storage was found to help reduce potential differences in water, alleviate drought stress, and help plants to overcome intense evaporation in the drought season in a previous study (Huang et al. 2017). Nocturnal sap flow also facilitates the transport of oxygen and nutrients. For example, *Betula* provides sufficient oxygen to sapwood parenchyma cells during nocturnal transpiration (Daley and Phillips 2006).

In addition, the taproots had a positive sap flow, while the lateral roots had a reverse sap flow in *P. orientalis*, indicating that the root hydraulic system had redistributed in *P. orientalis*. Yu et al. (2018) and Howard et al. (2009) suggested that nocturnal sap flow could reduce the water potential of plant leaves, which could have a negative effect on hydraulic redistribution. Our study confirmed that nocturnal sap flow and root hydraulic redistribution can occur simultaneously, which is consistent with previous findings (Matimati et al. 2014; Fu et al. 2018; Hafner et al. 2020). The root hydraulic redistribution of *P. orientalis* not only effectively alleviates the spatial

heterogeneity of soil water but also provides water for itself and *Q. variabilis* (Matimati et al. 2014; Fan et al. 2017). This pattern of water use by *P. orientalis* facilitates water sharing and is therefore conducive for the coexistence of different species. Nevertheless, there was no reverse sap flow in *Q. variabilis*, which leads us to conclude that *P. orientalis* is more adaptable to soil water than *Q. variabilis*. Although the levels of sap flow and diurnal transpiration of *P. orientalis* were lower than those of *Q. variabilis*, the proportion of water stored by *P. orientalis* was higher than that of *Q. variabilis*, indicating that *P. orientalis* can better balance the water deficit in body than *Q. variabilis*. This also confirms that *P. orientalis* is widely distributed as a pioneer tree species. The amount of water used for photosynthesis and storage in *P. orientalis* and *Q. variabilis* comprised 6–7% of the total water quantity, and therefore, should not be ignored.

Conclusions

We used an isotope technique and the heat ratio method to quantify the water source and determine the water amounts used for transpiration and storage. Our results indicate that *P. orientalis* and *Q. variabilis* primarily absorbed water from groundwater and the 60–100 cm layer, and *Q. variabilis* also absorbed water from the 0–20 cm and 20–40 cm soil layers during the dry season. *P. orientalis* was sensitive to precipitation and also used groundwater and water from the 60–100 cm soil layer during the rainy season. *Q. variabilis* did not change its water source but increased its uptake of groundwater. We observed 2.26% reverse flow and hydraulic redistribution in *P. orientalis*. The average sap flux values of *P. orientalis* and *Q. variabilis* were 374.69 and 469.50 mm, respectively. Nocturnal sap flow in both species was used to store water in the trunk. In both species, the amount of water used for storage comprised 6–7% of the total water and therefore, should not be neglected in water balance models.

List of Abbreviations

Number	Abbreviations	Meaning
1	VPD	Vapor pressure deficit
2	DBH	Diameter at breast height
3	SWC	Soil water content
4	S	Water storage
5	Q _{Tr}	Quantification of the water used for transpiration
6	SFR	Sap flow rates
7	TR	Total solar radiation

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Author contributions

LZ, JG, LQ and YX planned and designed the research. LZ performed experiments and conducted fieldwork with the help of ZH. LZ analyzed the data and wrote the manuscript under the guidance of JG and YX. JJ led the compilation of data compilation and significantly contributed to the analysis of data and its interpretation and rewrote the final version of manuscript.

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Competing interests

The authors declare that they have no competing interests.

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