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Ephemeral connectivity between trees and groundwater in a temperate forest in China

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ABSTRACT

The interspecific and temporal dynamics of tree water use are poorly understood. We investigated in high-temporal resolution patterns of water use of two tree species, *Platycladus orientalis* and *Quercus variabilis,* in a temperate mountainous monsoon forest in northern China. We leverage a unique sampling design where we systematically traced tree water source of ten individuals continuously throughout a three-year period (2015–2017) using stable isotopes of hydrogen and oxygen, coupled with root distribution assessment and measurements of transpiration rates. We observed species-specific patterns in tree water use. *Q. variabilis* withdrew water evenly from different soil layers without detectable seasonal changes in pattern in water use throughout the different years. By contrast, *P. orientalis* increases shallow source water uptake during the rainy season in all three years. Isotopic composition of both species plotted along an evaporation line below the local meteoric water line (LMWL). However, during sporadic periods in the rainy and transition season, *P. orientalis* plotted on the LMWL and showed similar isotopic to spring water. This suggests an *ephemeral* ecohydrological connectivity between tree water source and spring water during short periods within the wet and transition season. The observed distinct patterns in tree water use between the two species may be associated with root distribution characteristics. Besides root morphological traits, our data also suggest that the influence of overall stem volume (Vob) on water source contribution depends on the rainfall and species. Our results support the seasonality of ecohydrological separation observed in previous studies. Additionally, our data show that that ecohydrological separation may be species dependent in a temperate mountainous monsoon forest.

1. Introduction

Water availability is one of the key resources that determines plant species distribution across terrestrial ecosystems (Silvertown et al., 2015). On the other hand, plant transpiration represents about 60% of all evaporation flux on land (Good et al., 2015; Li et al., 2019; Schlesinger and Jasechko, 2014; Wei et al., 2017). Thus, plants play a key role in influencing climate conditions (Sheil, 2014), and regulating ecosystems hydrological cycle (Brantley et al., 2017). Changes in temperature and precipitation patterns are expected to increase drought frequency and forest mortality (Bose et al., 2021). Thus, a comprehensive understanding of plant water sources is crucial to improved projections of forest distribution (Good et al., 2017), tree mortality (Choat et al., 2018) and ecohydrological feedback between the biosphere and the atmosphere (Berg et al., 2016) under projected climate change scenarios.

Stable isotopes of hydrogen and oxygen (δ^2H and $\delta^{18}O$, respectively) have been used to trace vegetation water source and shed light on ecohydrological processes (Brooks et al., 2010; Tetzlaff et al., 2021; von Freyberg et al., 2020). This approach compares the isotopic signature of the plant xylem water with the potential water sources to infer the mixture of water sources contributing to xylem (Corbin et al., 2005; Edwin et al., 2014; Rothfuss and Javaux, 2017). Tree water use investigations have provided insights into intra-specific water source partitioning (Carrière et al., 2020c; del Castillo et al., 2016; Martín-Gómez et al., 2017), and seasonal tree water use (Barbeta et al., 2015; Deng et al., 2021; Sohel et al., 2021). These previous studies showed that

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depth of water source contribution is sensitive to seasonal climate fluctuations. Indeed, tree species shows seasonal shifts in the depth of root water uptake in response to soil water availability (Carrière et al., 2020b; Fan et al., 2017) and precipitation seasonality (Jia et al., 2017; Retzlaff et al., 2001), and in short-time scales shifts are triggered by changes in tree water status in response to environmental conditions (Nehemy et al., 2021).

Tree water use investigations in semiarid and arid regions have shown clear shifts in water source from shallow during the rainy season to deeper layers during the dry season (Dai et al., 2015; Nie et al., 2011). The plasticity of plant water uptake patterns in response to seasonal fluctuations in soil water availability has significant implications to maintaining vital plant functions (Chitra-Tarak et al., 2021; Klein, 2014; Voltas et al., 2015), such as transpiration and growth (Bréda et al., 2006; Schenk and Jackson, 2002). However, this information is incomplete in many ecosystems. Therefore, high-resolution and long-term observations of xylem and soil water isotopic composition covering the annual dry-wet cycle can provide understanding of tree water use and future insights into tree response to water availability under predicted changes in patterns of precipitation inputs (Konapala et al., 2020).

Besides tree water use plasticity and response to changes in patterns of moisture availability, the use of higher-frequency sampling of xylem and soil water throughout different seasons is especially important to understand tree water use and the connectivity with various sources of transpiration. Tree water source investigations have shown evidence of ecohydrological separation between trees and the more mobile water that recharge groundwater and later contribute to streams (Brooks et al., 2010; Evaristo et al., 2015; Goldsmith et al., 2012). These studies suggest that mixing process involving precipitation and soil matrix is incomplete and trees rely on soil water that is tightly bound to the soil matrix (Brooks et al., 2010). This pool of water stored in soil pores that supply transpiration appears to be functionally disconnected from water that contributes to streamflow. However, more recent investigations (Hervé-Fernández et al., 2016; Zhao et al., 2018) showed evidence of ecohydrological connectivity between trees and stream during the wet season. These studies showed that xylem water offset from more mobile water and observe in previous tree water use investigations could be explained by mechanisms that is seasonally dependent. Hervé-Fernández et al. (2016) and Zhao et al. (2018) studies proposed that the connectivity between trees and streams is subjected to seasonality. But evidence of this ecohydrological connectivity is limited to forests with high precipitation inputs during the wet season (*e.g.* 1413 mm in a rainy temperate forest (Hervé-Fernández et al., 2016) and 703 mm in subtropical monsoon forest (Zhao et al., 2018) or throughout the year (Geris et al., 2015). Further investigation of connectivity between trees and groundwater in more arid environments with increasing sampling frequency throughout wet-dry cycles would be useful to test mechanisms proposed in wetter climates.

Ecohydrological study in the critical zone is of utmost concern, especially for future forest management in areas that face critical water resources challenge (Carrière et al., 2020a; Creed et al., 2019; McDonnell et al., 2018). The assessment of intra-specific differences in access the diverse water sources may be relevant for understanding the impact of warming on contemporary populations and for tailoring mitigation strategies to climate change. Climate change is expected to increase the occurrence of extreme precipitation events (Myhre et al., 2019) and alter water balance dynamics (Reshmidevi et al., 2018), exposing mountainous forests in drought-prone areas to greater challenges of water accessibility. However, the understanding is incomplete regarding tree water use in temperate mountain forests where precipitation inputs concentrated during a short-period in the wet season. Insights in plant water use strategy in this area has important implications to comprehend adaptive mechanism underlying forest survival and which species may thrive under possible climate scenarios.

Here, we present a high-temporal resolution investigation on patterns of source water partitioning, and the ecohydrological connectivity between trees water source and groundwater in a temperate mountainous forest. We leverage a unique experimental setting where we continuously traced the water source of two species of contrasting growing forms throughout a three-year period (2015–2017) in an environment where potential evapotranspiration (PET) doubles precipitation inputs. We coupled stable isotopes of hydrogen and oxygen with individual morphological information of root and stem volume to specifically ask:

1. What is the source of transpiration in this temperate monsoon environment through the different seasons?
2. How does patterns of source water use vary among species and individuals with different morphological characteristics?
3. Do we observe an ecohydrological separation between trees and nearby spring during the wet season?

These findings have wide relevance for understanding the mechanism of tree water use, drought impact in species survival, and species coexistence in temperate mountain areas.

2. Materials and methods

2.1. Study site

The experimental site has an area of 16 km^2, and is located within the Jiufeng National Forest Park (116°05′39″-116°05′31″E, 40°03′27″-40°03′56″N, 150 m a.s.l.), Beijing, China, which covers an area of 16 km^2 (Fig. S1). The area is strongly influenced by the continental monsoon climate. The mean annual temperature is 11.6 °C (2000–2017). The annual potential evapotranspiration reaches 1100 mm. Meanwhile, the annual average precipitation is 660 mm (30 years average, 1988–2017), 70% of which occurs from June to September. Considering the diversity of species composition, we selected mixed-stands of *Platycladus orientalis*, an evergreen coniferous species and *Quercus variabilis*, a deciduous broad-leaved species as our research subject. The stands are a result of an afforestation campaign in 1970 s' to restore the native forest. The study area falls in the range of the karst hydrosystem in the West Mountain area in Beijing (Liu et al., 2019). The study site does not lie on the geological fault zone, anticline or syncline. Soils in our study site are characterized as a thin mountain cinnamon (Ustalf) which are calcareous soils formed mainly from weathering of gneissic granitite, limestone, and shale (Zheng et al., 2020). The depth of soil layer above the fractured granite bedrock ranges from 40 cm to 120 cm with an average depth of 60 cm. The humus is relative rich at the surface (10 cm). The upper layers (0–40 cm) contain a high amount of clay and a low amount of gravel. The deep layers (below 40 cm) feature the loam texture with a high amount of gravel (Liu et al., 2019).

2.2. Microclimatic and soil moisture measurements

Meteorological variables, including temperature, relative humidity, solar radiation, and precipitation were monitored by HOBO weather station (U30-NRC, Onset, USA), located 1 km away from the experimental plots. Soil water content was observed with ECH2O moisture sensors (Decagon, USA) at 20 cm-intervals from 0 to 100 cm. The soil water content data were recorded by the EM50 data collector (Decagon, USA). The data was recorded every 30 min.

2.3. Morphological traits

We sampled tree root system in August of 2015, 2016 and 2017 to obtain the vertical profile of root biomass. Soil samples were extracted using hand augers (inner diameter, d = 90 mm) at the depth of 0–20, 20–40, 40–60, 60–80 and > 80 cm. It was difficult to obtain soil samples beneath 80 cm due to the rocky nature of the underground layers. Therefore, the sampling depths varied below 80 cm until we reached bedrock. The deepest soil sampling was obtained from 120 cm deep. We selected three individual trees from each species, and sampled soil in

three different directions 50 cm away from each trunk. The samples from each corresponding individual were mixed and sealed in a bag and taken to the lab for further root biomass measurements. We first sieved the samples using a 5 mm sieves to separate the larger roots (d > 5 mm). Then, we used nylon mesh sieves to separate fine roots (≤2 mm) and coarse roots (d > 2 mm) (Akburak and Makineci, 2021; Finér et al., 2011). We used tweezers to collect the sieved roots. Root of different diameter classes were then oven dried at 70 °C for 48 h to get the root biomass (g). To understand the root biomass distribution along the examined soil profiles, we calculated the root biomass ratio (%) as the percentage of the weight of individual root diameter categories to the total root biomass of the soil profile.

We also measured DBH (diameter at breast height) and height to calculate stem volume over bark (Vob) for each sampling tree (Climent et al., 2008; Reinhardt et al., 2006).

2.4. Isotope sampling and analysis

To examine tree water sources in different seasons, we grouped the months into three main periods: the dry season, from November to April; the rainy season, from June to September; and two transition periods in May and October. We collected precipitation, spring, xylem and soil samples for water isotopic analysis during the three main seasons throughout 2015–2017. We collected simultaneously soil and xylem samples during each sampling campaign. This was done to determine the isotopic composition of the two species throughout the three-year period (original sample size: $n_{precip} = 142$, $n_{spring} = 51$, $n_{soil} = 1420$, $n_{xylem} = 5130$, n stands for sample size).

We collected three suberized branches per tree, immediately removed the bark and, stored in 50 ml vials sealed with Parafilm M® to avoid evaporative fractionation. We collected soil samples using soil augers within a 50 cm radius away from the truck of the individual tree. The soil sampling depths followed the same depth distribution as the root biomass excavation with maximum depth reaching the soil–bedrock interface (approximately 1 m depth). We changed the auger head after each drilling to avoid isotopic contamination from previous layers. We discarded approximately 3 cm of the 0–20 cm soil sample to eliminate the possible evaporative enrichment effect of the uppermost layer. Because that part of the dry season overlaps with winter, soil sampling was not possible during periods when the soil was frozen. Therefore, soil sampling during the dry season was less frequent and only occurred when soil thawed. During the rainy season and the transition period, the sampling campaigns were carried after rainfall events. Soil samples of each layer were stored in 50 ml vials and sealed with Parafilm M®. Xylem and soil samples were stored in a portable fridge and transported to the laboratory. In the laboratory, the samples were stored at −4℃ until isotopic analysis.

We collected precipitation near the meteorological station. We used ball-in-funnel type collectors (Prechsl et al., 2014) to minimize evaporative fractionation. Precipitation samples were collected after each rainfall event. We also collected grab samples of a nearby natural spring (~600 m distance from trees). The spring water seeps out of the ground and water flows throughout all seasons. We transferred water precipitation and spring samples to polyethylene vials, sealed with Parafilm M®, and transported back to the lab. Samples were refrigerated until analysis. Sampling campaigns were carried between morning and midday for all sampling materials.

Isotopic offset between xylem and soil/precipitation water source has been reported (Barbeta et al., 2020; Barbeta et al., 2019). Recent study cautioned that isotopic information of xylem water extracted through the cryogenic method might affect xylem water, and thus yield an isotopic offset (Chen et al., 2020). However, it has also been shown that cryogenic vacuum extraction can reveal reliable isotope results (Kühnhammer et al., 2021; Newberry et al., 2017). Moreover, the integration of oxygen isotope signals in the Bayesian inference framework can improve the source water attribution (Evaristo et al., 2017). Therefore, the xylem and soil water was extracted using cryogenic vacuum distillation (Koeniger et al., 2011). The isotopic compositions of all water samples were measured with a Liquid Water Isotope Analyzer (DLT-100, LGR Inc., USA) at the laboratory. Both δ^2H and $\delta^{18}O$ values can be measured simultaneously with this instrument. Isotope ratios are expressed as:

$$\delta^2 H \text{ or } \delta^{18} O = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \cdot 1000 \quad (1)$$

where R_{sample} and $R_{standard}$ indicate the isotope ratio of the samples were calculated relative to Vienna Standard Mean Ocean Water (VSMOW). The measurement accuracies of δ^2H and $\delta^{18}O$ were ± 0.83‰ and ± 0.36‰, respectively. Plants are abundant in organic matter which can lead to spectral contamination if such compounds are co-extracted during cryogenic vacuum distillation (Martín-Gómez et al., 2015). Among the diverse range of organic compounds methanol is shown to lead to larger discrepancies on isotopic measurements using laser spectrometry (Leen et al., 2012; Schultz et al., 2011). Spectrally contaminated samples were identified using the software provided by LGR (LWIA-Spectral Contamination Identifier v1.0, LWIA-SCI), and then post-corrected following method developed by (Schultz et al., 2011) and (Leen et al., 2012) and shown to be applicable to tree water isotopic measurements (Barbeta et al., 2019; Martín-Gómez et al., 2015). Specific contamination curve was individually fitted for the specific analyzer (see Supplementary Information).

2.5. Transpiration

Sap flow was monitored as a proxy of the transpiration of ten individual trees. Ten individuals of different DBH sizes were selected from each species (Table S1). Thermal dissipation probes (TDP, Dynamax Inc., Houston, TX, USA) were inserted following protocols (Chen et al., 2011). The 30 min-average was recorded in CR1000 data-logger (Campbell Scientific Inc., Logan, UT, USA). The sap flux density (J_s, $g \cdot cm^{-2} \cdot s^{-1}$) was calculated as follows:

$$J_s = 0.0119 \times \left(\frac{D_{TM} - D_T}{D_T}\right)^{1.231} \quad (4)$$

where D_{TM} and D_T are the maximum temperature difference and the temperature difference at time T between the two probes.

Transpiration (E_c, mm d^{-1}) was then calculated as follows:

$$E_c = (3600 \times \sum_{i=0}^{24} J_s \times A_s)/A_c \quad (5)$$

where A_s is the sapwood area (cm^2) and A_c is the canopy area (m^2) of the tree. 3600 is the coefficient for conversion from seconds to hour. A_s was determined through tree cores. Two cores were drilled along the north–south and the east–west of one sample trees. Cores were not taken from the sampled trees for TDP observation to avoid the possible influence from the wound. With the measurements of tree cores, A_s calculated as follows:

$$A_s = \pi(R_D - R_H)^2 \quad (6)$$

where R_D is the de-barked diameter, i.e. DBH minus bark thickness, R_H means the diameter of the heartwood which was derived by subtracting sapwood depth from R_D. The sapwood depth was determined by the color discrimination between sapwood and heartwood of the increment cores. Empirical relationships between DBH and A_s were established as $A_s = 0.852DBH^{2.0979}$($R^2 = 0.99$, $p < 0.01$)and $A_s = 0.785DBH^{2.0782}$($R^2 = 0.99$, $p < 0.01$)for *P. orientalis* and *Q. variabilis*, respectively. The A_s of un-cored trees were derived from these empirical relationships.

2.6. Tree water source partitioning and statistical analysis

We used the MixSIAR Bayesian mixing model (Stock et al., 2018) to

determine the contribution of potential water sources. The sampling dates were tested independently for their respective water source. Therefore, for each date, the xylem water was entered as the mixture information. The isotopic signatures of each potential water source were entered in the model as follows: soil water isotope data from (1) 3–40 cm, (2) 40–80 cm and (3) > 80 cm on the day of xylem sampling campaign. The 3–40 cm layer represents the upper layers where roots are abundant and is more affected by evaporation. Layers below 80 cm represents the deep layers at the soil bedrock interface, where the soil starts to be replaced by rocks and larger fractures might exist. In between these, the 40–80 cm represents the middle soil layer.

Line-conditioned excess (offset from the local meteoric water line (LMWL; $\delta^2H = 6.37\delta^{18}O - 6.61$)) can reflect the evaporative loss of different water source comparing to local precipitation. Henceforth, lc-excess was used to assess the offset of different water pools from the LWML. The line-conditioned excess was calculated following Landwehr and Coplen (2006):

$$lc-excess = \delta^2H - -a^*\delta^{18}O - -b$$

where a and b are the slope and intercept of the LMWL, respectively. Negative lc-excess values indicate isotopic enrichment due to evaporation.

In analogy to lc-excess, we also used sw-excess as suggested by Barbeta et al. (2019) to investigate the offset between xylem soil in relation to the soil. The soil water line excess is then defined as:

$$sw-excess = \delta^2H - a_s * \delta^{18}O - b_s$$

where a_s and b_s are the slope and intercept of the soil water line, respectively. Negative sw-excess indicated the xylem data plot below the soil water line of the corresponding soil water isotopes sampled on the same day. Since we used cryogenic vacuum distillation to extract soil water, sw-excess represents the distance of xylem water to bulk soil water, which is composed mainly of tightly bound and more mobile water.

One-way ANOVA was employed to test significant differences of samples that qualified the homogeneity of variance tests. Due to the sample size disparities of different seasons, the Kruskal-Wallis (K-W) test was used to detect significant differences of values among different seasons. We conducted partial correlation analysis to determine the importance of tree morphological traits on tree water source partitioning. The environmental variables served as the covariate variables in the partial correlation analysis, including soil volumetric water content (VWC, %), vapor pressure deficit (VPD, kPa), and solar radiation (R, MJ. m^{-2}). Statistical analyses were conducted using R software (version: 3.6.2).

3. Results

3.1. Environmental conditions

Solar radiation in 2017 (84.19 ± 2.43 S.E., S.E. stands for standard error W m^{-2}) was significantly lower than in 2015 (130.97 ± 4.07 S.E. W m^{-2}) and 2016 (75.83 ± 5.07 S.E. W m^{-2}) ($p < 0.05$, One-way ANOVA). There was no significant difference among the three years ($p > 0.05$, One-way ANOVA). Precipitation was 580 mm, 649 mm and 309.3 mm in 2015, 2016 and 2017, respectively. Soil water content demonstrated strong seasonality. This was consistent with the rainfall inputs in different seasons. Soil moisture increased close to saturation during the rainy season. This was especially the case for the surface layers. Moreover, the differences in soil moisture of different layers were small during the rainy season (Fig. 1).

3.2. Isotopic compositions of the soil water

We observed large variability in the isotopic composition of soil and precipitation throughout the different seasons (Fig. 2 & Fig. S2). Precipitation δ^2H and $\delta^{18}O$ followed a progressive depletion as the rainy season began, and became more enriched by the end of this period (Fig. 2a). The soil water was isotopically distinct from precipitation

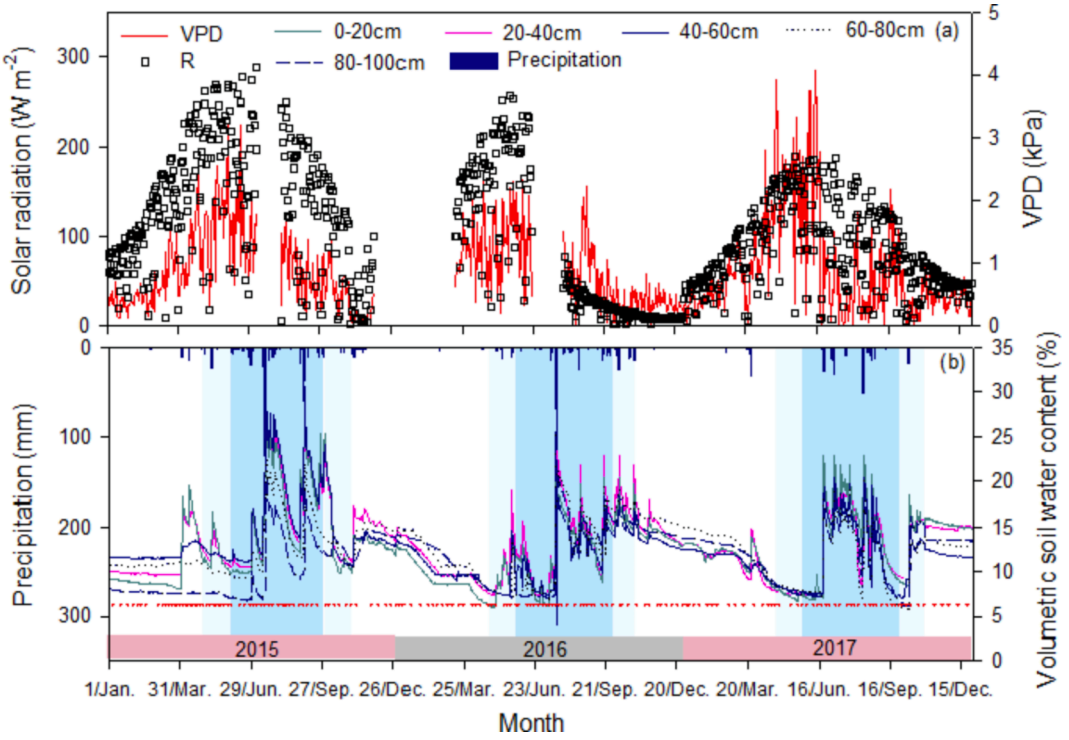

Fig. 1. Variation of the environmental factors during the observation campaign. Miss data were caused by power shortage. The blue rectangles indicate the rainy season (Jun. to Sep.) and the light blue rectangles indicate the transition period between the dry season to the rainy season (May and Oct.). VPD and R stand for vapor pressure deficit and radiation, respectively. The span of a year is marked with different colors along the × axis. Red circles indicate sample dates.

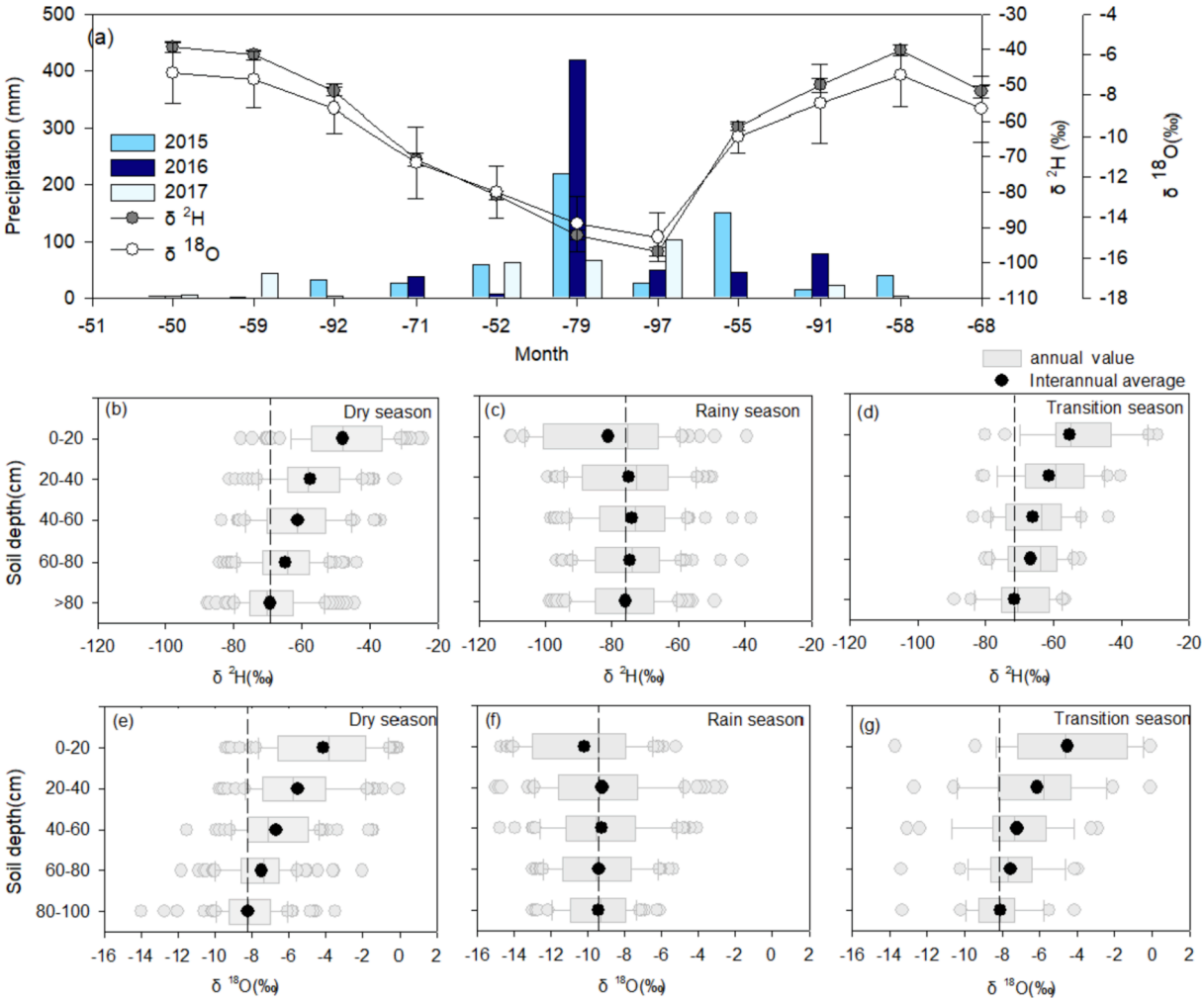

Fig. 2. Isotopic changes of soil water with the concurrent rainfall of different months (a) and comparison of soil water δ^2H (b-d) and $\delta^{18}O$ (e-g) among different layers during different seasons. The dash lines in b-g serve to facilitate comparison of the isotopic value among different soil layers.

during the study period ($p < 0.05$, One-way ANOVA). However, soil water isotopic composition still reflected the temporal trend of precipitation isotopic signature (Fig. 2b-g). Soil water isotopic composition was significantly more depleted in ^2H and ^{18}O in the rainy season than in the dry and transition season ($p < 0.05$ for both δ^2H and $\delta^{18}O$, respectively, K-W test). Therefore, the soil water δ^2H and $\delta^{18}O$ profile across the observation depth in the rainy season was different from that in the dry and transition season (Fig. 2c v.s. 2b & d, Fig. 2f v.s. 2e &2g). During the dry and transition season, the surface (3– 40 cm) soil water was more enriched in ^2H and ^{18}O than the deep layers, indicating evaporative fractionation at the surface. During this season, bulk soil water isotopic composition followed a consistent pattern of increasing depletion with depth. The latter was the opposite from what was observed in the soil water profile during the rainy season. In all seasons, the surface (0–20 cm) soil water was significantly different from the deeper layers, with few exceptions. The one-way ANOVA analysis detected significant differences among soil layers (Table 1), indicating isotopic heterogeneity along with the soil profile.

Table 1
Comparison of isotopic composition (δ^2H and $\delta^{18}O$) among different layers.

Soil depth (cm)	Dry season (n = 590)		Rain season (n = 630)		Transition period (n = 200)	
	δ^2H (‰)	$\delta^{18}O$ (‰)	δ^2H (‰)	$\delta^{18}O$ (‰)	δ^2H (‰)	$\delta^{18}O$ (‰)
3–20	−47.93 (1.94)^a	−4.10 (0.61)^a	−81.11 (4.71)^a	−10.16 (1.56)^a	−54.06 (2.35)^a	−4.53 (0.52)^a
20–40	−57.37 (1.78)^b	−5.49 (0.52)^b	−74.88 (3.76)^b	−9.21 (1.52)^b	−60.73 (2.67)^b	−6.14 (0.67)^b
40–60	−60.91 (1.86)^{bc}	−6.66 (0.46)^c	−74.01 (3.77)^c	−9.22 (0.95)^c	−66.00 (4.32)^c	−7.20 (0.28)^c
60–80	−64.41 (1.64)^c	−7.47 (0.55)^d	−74.56 (3.35)^a	−9.38 (0.99)^a	−66.09 (2.11)^d	−7.54 (0.36)^d
>80	−68.99 (1.88)^d	−8.19 (0.54)^e	−75.99 (3.16)^a	−9.39 (0.84)^a	−69.95 (1.65)^e	−8.09 (0.46)^e

Values are given as mean (S.E.).
Significant differences among layers are indicated by low case letters. Significance level are set at $p = 0.05$.
Surface layers: 3–40 cm, middle layers:40–80 cm, deep layers:>80 cm.

3.3. Discrimination of water sources and tree water uptake patterns

We observed distinct xylem water isotopic composition across the different species (Fig. 3). The isotopic signature of *P. orientalis* spread along soil water isotopic composition distribution on dual isotope space. This species also showed different xylem isotopic composition between the different seasons ($p < 0.05$ for xylem δ^2H; K-W test). *P. orientalis* xylem water isotopic composition plotted closer or overlapped with the spring water isotopic composition and the LWML during the transition and rainy season (Fig. 3a–c). The xylem water of this species was significantly more depleted in ^2H and ^{18}O during the rainy in relation to other seasons ($p < 0.01$; K-W test). By contrast, *Q. variabilis* maintained a

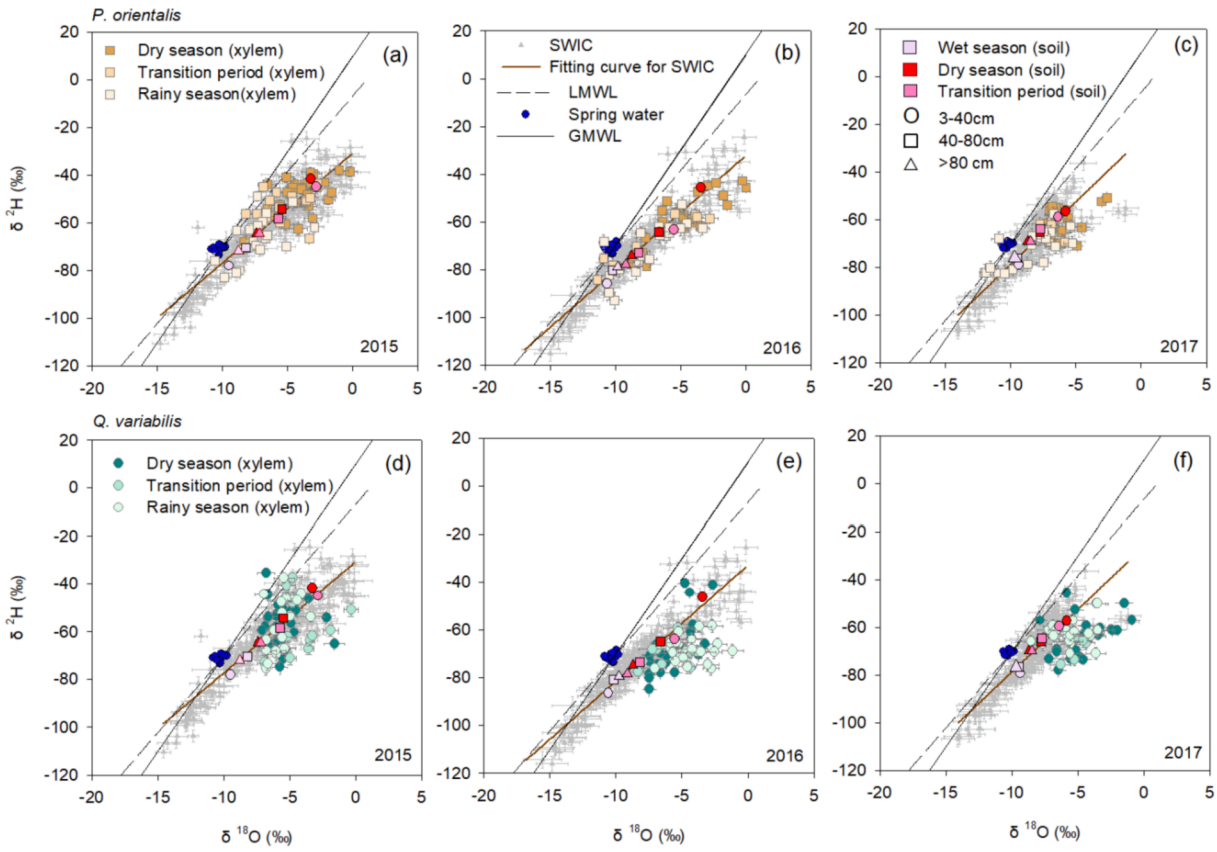

Fig. 3. Dual-isotope representation of xylem water isotopic composition of *P. orientalis* (a-c) and *Q. variabilis* (d-f) in comparison with soil water isotopic composition (SWIC) and spring water. The short-dashed lines indicate the local meteoric water line (LMWL) and the solid black line represents the global meteoric water line (GMWL). Soil water isotopic composition was fitted in brown lines.

relatively stable xylem isotopic composition, without significant differences across different seasons ($p > 0.05$; K-W test). Visual observation of the xylem water samples in the dual-isotope space indicated that some xylem samples from *Q. variabilis* also fell outside of the observed distribution of soil water isotopic composition (Fig. 3d–f) and showed to be slightly more fractionated isotopic composition than soil water.

Fig. 4 and S5 shows the mixing model analysis for *P. orientalis* and *Q. variabilis* during the three seasons. *P. orientalis* demonstrated a significant variation in water uptake patterns from different layers depending on seasonality (Fig. 4a & S5a), while *Q. variabilis* maintained a relative equal partitioning of water uptake among the different layers irrespective of seasonality (Fig. 4b & S5b). Dual isotope observations indicate that *P. orientalis* isotopic composition was more similar to shallow soil layers (Fig. S2 & S3) during the rainy and transition season. The soil water of the layer at 3–40 cm accounted for 41.49% and 27.86% of the xylem water of this species in the rainy season and transition period, respectively (Fig. 4a). *P. orientalis* relied on soil water below 40 cm reducing shallow soil water uptake during the dry season. The shift of water source from dry season to rainy season was observed as surface water contribution significantly increased from 26.01% to 41.49%. By contrast, water uptake by *Q. variabilis* from the surface and deep layers remained around 30–33% in all three seasons, respectively.

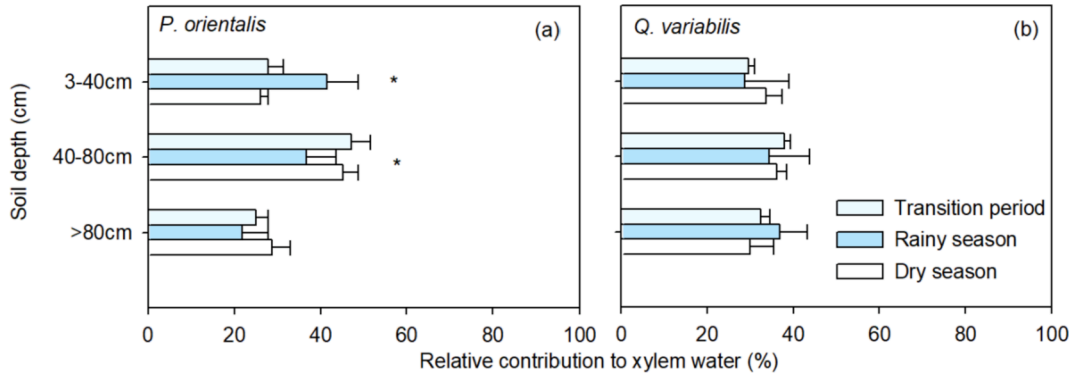

Fig. 4. Mean relative contribution of soil water to xylem water of *P. orientalis* (a) and *Q. variabilis* (b) in different seasons. Significant differences ($p < 0.05$) of the same soil layer among different seasons were indicated with the asterisk.

3.4. Ecohydrological separation and connectivity between trees and groundwater

We evaluated the isotopic offset between xylem and soil water using the sw-excess per sampling campaign (Fig. 5). Overall, the sw-excess of *Q. variabilis* (sw-excess = -7.96 ± 7.28; mean ± SD) was lower than *P. orientalis* (−1.60 ± 6.30) (Fig. 5a). The deviation of *Q. variabilis* from sw-excess of 0‰ occurred independent of rainy seasons or soil moisture conditions. Larger differences from a zero sw-excess for both species were observed during the dry season between 2016 and 2017. *P. orientalis* showed positive sw-excess during some occasions throughout the transition and rainy season. This indicates that bulk soil water was more depleted in heavy isotopes than xylem water.

The isotopic composition of spring water showed small deviation from that of the precipitation and spring lc-excess was close to 0 ‰ (i.e. plot close or on the LMWL, Fig. 5). Soil water and xylem lc-excess from *P. orientalis* and *Q. variabilis* were negative during the dry season indicating an offset from the LWML. However, *P. orientalis* showed lc-excess values close to 0 ‰ during sampling periods within the transition and rainy season of 2015, 2016 and the rainy season of 2017. On days where *P. orientalis* lc-excess was close to zero, we observed no significant difference between the xylem water of *P. orientalis* and that of the spring water. This was observed during 21 May-2 June 2015 ($p > 0.05$, K-W test), 6 Jun. 2015 ($p > 0.05$, K-W test), 11 Oct in 2016 ($p > 0.05$, K-W test), 4–8 Nov. in 2016 ($p > 0.05$, K-W test) and 20–28 Aug. in 2017 ($p > 0.05$, K-W test). The same was not observed for *Q. variabilis* which showed a constant negative lc-excess throughout the transition and wet seasons. *Q. variabilis* lc-excess was more negative than *P. orientalis* and soil water excess throughout the three years.

3.5. Tree morphological traits and source water partitioning

Q. variabilis and *P. orientalis* exhibited contrasting root biomass distributions along with the soil profile (Fig. 6). *P. orientalis* showed well-developed shallow lateral roots and deep-penetrating taproots. This is species also showed small variability in root biomass of different diameter classes within soil layers. *P. orientalis* showed an overall decline in root biomass with increasing soil depth (Fig. 6a). Specifically, the fine roots biomass was significantly higher at 0–20 cm depth than in deeper layers ($p < 0.05$, One-way ANOVA). By contrast, *Q. variabilis* demonstrated a relatively even distribution of root biomass along with the soil profile, except for the large roots (d > 5 mm) at the depth of 20–40 cm. Also, large roots (d > 5 mm) of this species were present in all layers and in larger proportions than roots of same diameter for *P. orientalis*. *Q. variabilis* fine roots were mainly found above 60 cm and in lower proportions than fine roots of *P. orientalis* (Fig. 6). Table 2 shows a constant positive correlation between root biomass and source of water uptake across different soil layers. However, the relationship between Vob and different soil layers depended on the species and seasonality.

4. Discussion

We know that transpiration is a dominant flux on land surface (Schlesinger and Jasechko, 2014; Wei et al., 2017), and that there are evidence of the connectivity between transpiration and streamflow during the wet season in more humid environments (Hervé-Fernández et al., 2016; Zhao et al., 2018; Geris et al., 2015). However, our knowledge is incomplete regarding the connectivity between source of

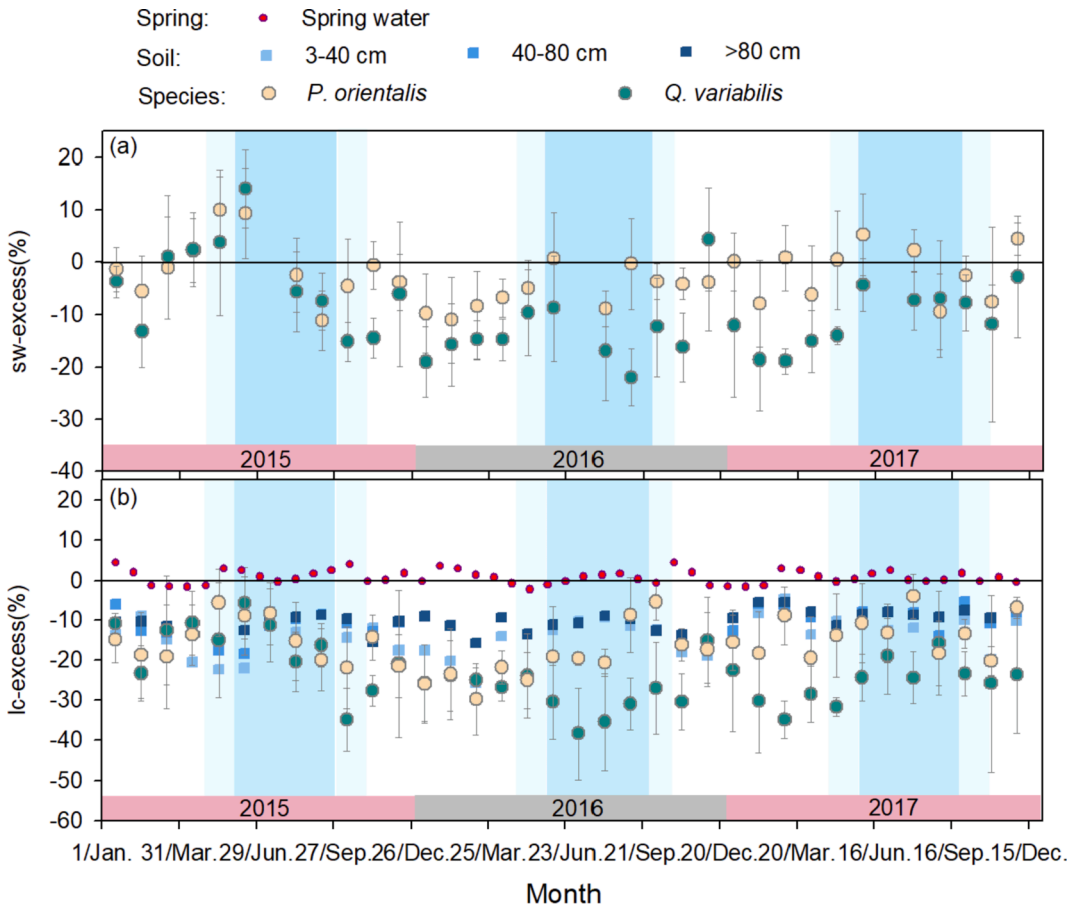

Fig. 5. Assessment of ecohydrological separation. sw-excess (a) is shown for xylem water of *P. orientalis* and *Q. variabilis* (mean ± SE). lc-excess (b) is also shown for the two species, and soil layers of 3–40 cm, 40–80 cm and below 80 cm (means, standard error not shown for the sake of visual clarity). The monthly average values are used to represent xylem water for both species.

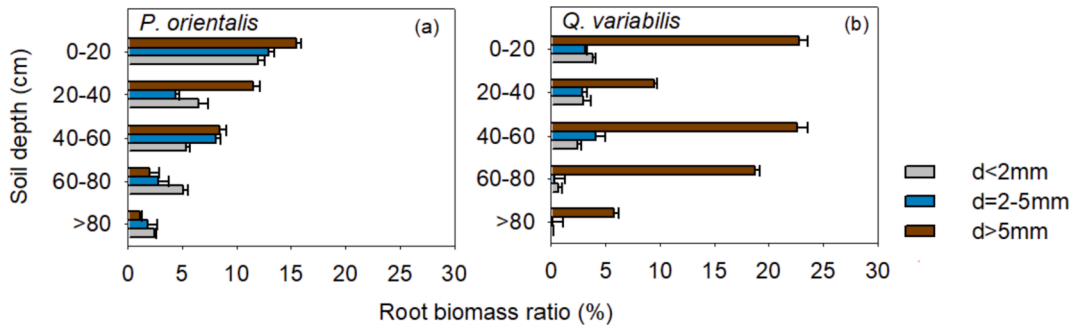

Fig. 6. Root biomass ratio (in %) distribution along the soil profile depth for (a) *Platycladus orientalis* and (b) *Quercus variabilis*.

Table 2
Partial correlations (Pearson coefficients) between the relative water source contribution from different soil layers and plant morphological characteristics with environmental factors being controlled covariates.

		Dry season			Rainy season			Transition period		
		Surface layers	Middle layers	Deep layers	Surface layers	Middle layers	Deep layers	Surface layers	Middle layers	Deep layers
P. orientalis	Vob	−0.291	**0.477**	**0.526**	**0.301**	**0.336**	**0.402**	0.290	0.223	**0.301**
	Root biomass	**0.371**	**0.582**	**0.618**	**0.518**	**0.526**	**0.558**	**0.355**	**0.465**	**0.693**
Q. variabilis	Vob	−0.241	0.259	0.392	**0.312**	**0.397**	**0.427**	0.212	**0.312**	**0.325**
	Root biomass	**0.368**	**0.418**	**0.498**	**0.418**	**0.446**	**0.458**	**0.325**	**0.338**	**0.353**

Abbreviations: Vob: stem volume.
Surface soil refers to soil layers of 3–40 cm, middle layer: 40–80 cm and deep soil refers to layers below 80 cm.
Significant coefficients of $p < 0.05$ are shown in bold.

transpiration and nearby spring in drier environments, specially across trees with distinct growing forms, an evergreen and a deciduous species. Our high-temporal resolution tree water source investigation in a temperate forest in China showed a distinct tree water use pattern between the two-coexisting species, and seasonal connectivity between trees and nearby spring (original sample size: $n_{precip} = 142$, $n_{spring} = 51$, $n_{soil} = 1420$, $n_{xylem} = 5130$, n stands for sample size). To our knowledge, we are the first to investigate ecohydrological separation in high-temporal resolution in a temperate mountainous forest and systematically trace tree water source throughout a three-year period.

4.1. Root morphology and water source partitioning

Our high-temporal resolution tree water source investigation showed a distinct tree water use pattern between coexisting *P. orientalis* and *Q. variabilis* tree species. We observed differences in the proportional contributions of water across soil layers throughout the different seasons between the two species. While *Q. variabilis* showed a more constant source water partitioning and equal contribution from different layers independent of the season, *P. orientalis* showed changes in source water partition with changes in seasonality. Our data suggest an increase in shallow soil water uptake during the rainy season by *P. orientalis*. Previous studies observed distinct patterns in water use by coexisting plants (Dai et al., 2015; del Castillo et al., 2016; Wang et al., 2020) and suggested that different strategies in source water uptake is a primary mechanism for plant coexistence (Schenk, 2008; Silvertown et al., 2015). Thus, observed patterns in tree water use brings ecological understanding about hydrological niche segregation and coexistence of individual species (De Deurwaerder et al., 2018).

Rooting depth and biomass are essential for trees to acquire water and nutrient and may help to explain distinct tree water use patterns among the different species. We showed that *P. orientalis* had more developed fine root system in the surface layers than the co-occurring species *Q. variabilis*. Fine roots are important for soil water uptake, and this may have resulted in the observed larger water uptake from the upper soil profile with increase water availability in the rainy season from *P. orientalis*. The maximized fine roots in shallow layers characterizes species with fast resource acquisition strategy, which are more opportunistic regarding water use (Moreno-Gutiérrez et al., 2012). By contrast, we observed a more developed deep root system in *Q. variabilis* with larger biomass of coarser roots than *P. orientalis*. The root biomass of *Q. variabilis* was also relatively evenly distributed across the soil profile. The higher proportion of coarse root biomass and well distributed across the soil profile characterized species with a more conservative root water acquisition strategy (Fort et al., 2017; Moreno-Gutiérrez et al., 2012). Thus, such root system may have enabled a steady access to water without any significant shifts in water uptake patterns across different seasons which may explain our observations. Additionally, *Q. variabilis* could have developed roots into the fractured bedrock and accessed rock moisture during the dry season. This is has been observed for other *Quercus* species (Hahm et al., 2020; Rempe and Dietrich, 2018). The more stable source water apportionment may have been also a result of a combination of hydraulic traits that allowed *Q. variabilis* to maintain stable water status, which may not have been the case for *P. orientalis*. The support of a stable water source observed in *Q. variabilis* is also indicated by a steadier transpiration rates when compared to *P. orientalis* throughout seasons (Fig. S4). We hypothesize that such changes in water uptake patterns observed through high-temporal sampling resolution may have been a result of changes in water status in *P. orientalis* and resulted in observed shifts with changes in soil wetness conditions. This has been previously observed in controlled conditions and proposed as the mechanism to explain source water apportionment (Nehemy et al., 2021).

4.2. Seasonal ecohydrological separation

Early work by Brooks et al. (2010) proposed the ecohydrological separation hypothesis by showing that trees use soil water that is more tightly bound and is isotopically distinct from the more mobile water that infiltrates the soil and travels through preferential flow paths and later contributes to streams. While a more mechanistic understanding is yet necessary to explain observed ecohydrological separation (Sprenger & Allen, 2020), this has been a useful hypothesis to understand patterns of tree water use across different study sites and seasons. Previous tree water use investigation by Hervé-Fernández et al. (2016) in a rainy temperate forest in Chile, and by Zhao et al. (2018) in a hillslope in a subtropical monsoon climate in China, supported the ecohydrological separation hypothesis during the dry season. However, they indicated a hydrological connectivity between trees and streams during the wet season. According to them this could be explained by larger antecedent precipitation amounts before sampling period. The previous studies were conducted in climates with relatively large precipitation inputs during the wet season, and until now, we lacked seasonal understanding between trees and underground streams in more arid climates.

Overall, xylem water from *Q. variabilis* was consistently distinct from spring water and showed a negative lc-excess. While this was also mostly the case for *P. orientallis*, there were specific sampling periods where this species xylem isotopic was not distinct from spring water and showed a lc-excess close to zero. Although we did not find any direct connection between these events and precipitation amounts, the overlap between xylem water and LMWL occurred during the transition and wet season. Thus, our data suggests an '*ephemeral*' ecohydrological connectivity between *P. orientallis*'s source water and spring sources at our sites (Fig. 5).

P. orientallis with higher proportion of fine roots at the shallow layers may have enable this species to acquire recent precipitation inputs and subsurface flow moving through the subsurface towards the spring during the rainy season. By comparison, the fine roots of *Q. variabilis* at surface layer accounts for small portion of total biomass, and across the whole soil profile it only accounts for 10%, which decrease the ability of this species to absorb water from surface layers. Although we were unable to obtain the root distribution within the fractured bedrock, it is possible that *Q. variabilis* developed deeper root system into the rock fractures. Therefore, the hydrogeological and morphological conditions may lay the foundation for the observed difference in ecohydrological separation between species.

5. Methodological limitations

The xylem water isotopic composition of *P. orientalis* overlapped with available soil water sources across all three years of observation. However, dual isotope assessment of *Q. variabilis* and sw-excess indicates that xylem water was more depleted in ^{2}H than bulk soil water sources. Previous work has shown that xylem water isotopic composition can be more depleted than soil water signatures, and this offset has been observed in particular for $\delta^{2}H$ (Barbeta et al., 2019; Tetzlaff et al., 2021). However, the mechanisms that explain this offset are still unknown. Several studies have discussed possible mechanisms that could affect xylem water isotopic signatures and result in an offset between xylem and soil water sources. This includes the role of mycorrhiza fungi during root water uptake (Poca et al., 2019), the mixing of internal water sources (Zhao et al., 2016; Nehemy et al., 2022), the influence of plant water status (Barbeta et al., 2020), possible fractionation caused by cryogenic extraction of xylem water (Chen et al., 2020), the extraction of bulk xylem water rather than sap water (Barbeta et al., 2022), or results influenced by more depleted-rock moisture (Hahm et al., 2020; Rempe and Dietrich, 2018; Oshun et al., 2016). Regardless of the relative magnitude of this offset between xylem and soil water, the steady assessment of water sources by *Q. variabilis* is still supported by the analysis during the three-year observed period. In contrast, *P. orientalis* xylem water was not observed to be more depleted in ^{2}H than soil water, as xylem plotted along soil water distribution on dual isotope space (Fig. 3). Thus, possible mechanisms that result in more negative $\delta^{2}H$ values may affect only, or more strongly, *Q. variabilis*.

Tree water source investigations rely on the adequate sampling of all available sources to root water uptake. We may have failed to characterize all sources for *Q. variabilis* since this species showed some xylem water isotopic composition that plotted outside of soil water distribution. Because we sampled until we met the soil bedrock interface, we hypothesize that *Q. variabilis* could have deeper roots that access water into the bedrock not sampled in our study site. The latter could more likely explain the offset between xylem and soil water for this species, which was also more evident during the dry and transition season. The use of rock moisture, as discussed above, has been previously reported in the literature as an important water source to sustain transpiration of other oak species (Hahm et al., 2020; Rempe and Dietrich, 2018) and forests in general during drier periods (McCormick et al., 2021). The water extracted from rocks is usually more depleted in ^{2}H and ^{18}O than soil water in previous studies (Hahm et al., 2020; Rempe and Dietrich, 2018; Oshun et al., 2016), and it could be a potential explanation to our observed offset between *Q. variabilis* and soil. The use of rock moisture by *Q. variabilis* may also support the steady water source across different seasons, as this deeper resource may be more reliable than water storage within the thin soil layer. Further research is needed to confirm this assumption by sampling rock moisture at the research site. To reduce uncertainties regarding xylem water isotopic composition and to disentangle possible causes of the offset between xylem and soil water one might consider using continuous *in situ* methods to measure xylem water and bypass uncertainties related to extraction approaches (Marshall et al., 2020; Volkmann et al., 2016), or record sample water content when using cryogenic extraction systems to understand potential effects of this method (Chen et al., 2020), since *in situ* monitoring is not suitable in remote areas. Accessing tree water isotopic heterogeneity by sampling phloem water (Nehemy et al., 2022), or sampling sap water directly instead of bulk xylem water (Barbeta et al., 2022) might also help to understand potential offsets in xylem isotopic values. Additionally, tree hydraulic monitoring might improve source water interpretations by not relying on stable isotopes alone (Nehemy et al., 2021; Dubbert et al., 2019).

6. Conclusion

Our observations highlight distinct tree water use patterns across species growing in a temperate forest environment in China during a long-term observation period. From an ecological perspective, our results show that co-occurring species in this karst environment explore different water sources. We also show that combining morphological traits with tracers can improve understanding of patterns in tree water use. The shallow rooted *P. orientalis* increases shallow soil water uptake during the rainy season, while the more deep-rooted *Q. variabilis* draws water evenly from different soil layers independent of seasonality. These findings were consistent throughout the three-year observation period and provided an understanding of how the studied ecosystem functions throughout the different seasons. By understanding how the current ecosystem functions, we can better evaluate how future climate warming may impact patterns in tree water use and potential shifts in species composition.

Our data suggested an *ephemeral* ecohydrological connectivity between *P. orientalis* and groundwater during the wet and transition period, but an ecohydrological separation for *Q. variabilis* irrespective of the precipitation seasonality. These observations were consistent across the three monitored years and seems to be a characteristic of the investigated ecosystem. The ephemeral occurrence of ecohydrological connectivity underlines the necessity to cover multiple seasons to improve understanding of the connectivity between transpiration and groundwater and its impact on water availability. Investigating tree

water sources continuously throughout different years provides important means to understanding tree water source partitioning and our ability to conceptualize how forests explore subsurface water storage.

CRediT authorship contribution statement

Guodong Jia: Conceptualization, Methodology, Data curation, Writing – original draft. **Magali F. Nehemy:** Writing – review & editing, Investigation. **Lixin Chen:** Data curation, Writing – original draft, Visualization, Investigation. **Xinxiao Yu:** Supervision, Funding acquisition. **Ziqiang Liu:** Methodology, Data curation.

Declaration of Competing 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2022.127887.

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